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A NEW ABELISAURID (DINOSAURIA, THEROPODA) FROM THE LAMETA FORMATION (CRETACEOUS, MAASTRICHTIAN) OF INDIA

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Abstract — Many isolated dinosaur bones and teeth have been recovered from Cretaceous rocks in India, but associated remains are exceedingly rare. We report on the discovery of associated cranial and postcranial remains of a new abelisaurid theropod from latest Cretaceous rocks in western India. The new taxon is characterized by exceptionally elongated supratemporal fenestrae and a unique median nasofrontal protuberance. Postcranial elements include vertebrae and portions of the pelvic girdle and hind limbs. The ilium, in particular, is robustly constructed. Much of the large-bodied theropod material collected from latest Cretaceous rocks in central and western India may pertain to this abelisaurid. The new Indian species is more closely allied to *Majungatholus* from Madagascar and *Carnotaurus* from South America than to related forms on Africa. Paleobiogeographic interpretation of this phylogenetic pattern, however, must be tempered by the lack of terrestrial faunas of similar age on several of these landmasses: pre-Maastrichtian Cretaceous vertebrates are virtually unknown on Madagascar and India, and post-Cenomanian vertebrates are very poorly sampled on Africa.

INTRODUCTION

Fossil vertebrates of Late Cretaceous age on southern continents are of particular interest because of the dynamic paleogeography of the period. During the Cretaceous, Gondwana broke apart into separate landmasses, isolating once-contiguous terrestrial faunas. The timing, sequence, and degree of isolation among these landmasses, however, remain controversial (Smith et al., 1994; Hay et al., 1999; Maisey, 2000; Cracraft, 2001). This uncertainty is compounded by the

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FIG. 1 — Map of India showing principal Late Cretaceous (Maastrichtian) dinosaur localities in the Lameta Formation.

relative scarcity of diagnostic Cretaceous Gondwanan vertebrate fossils, whose relationships could offer evidence of prior geographic connections. Among southern landmasses, Cretaceous vertebrates are best documented on South America. This is largely a result of intensive investigations of strata in Argentina over the last 30 years (summarized in Bonaparte, 1978, 1996). More recently, well preserved Cretaceous skeletal material has been discovered in Africa (Jacobs, et al., 1993; Sereno et al., 1994, 1996, 1998, 1999, 2001; Smith et al., 2001) and Madagascar (Forster et al., 1996, 1998; Krause et al., 1997, 1999; Sampson et al., 1998, 2001; Forster, 1999; Carrano et al., 2002), which has allowed faunal comparisons between these three landmasses.

Despite Indo-Pakistan's excellent Permian (Ray and Bandyopadhyay, 2003) and Triassic (Bandyopadhyay and Sengupta, 1999) records, its Cretaceous vertebrates are poorly known and consist almost entirely of isolated bones and teeth (e.g., Rana, 1990; Sahni and Bajpai, 1991; Prasad and Rage, 1991, 1995; Prasad and de Broin, 2002; Rana and Wilson, in press). Although numerous and spanning much of Vertebrata (Khosla and Sahni, 2003), few of these remains are adequate for detailed comparisons with genera from neighboring landmasses. Dinosaurs are known from numerous, isolated bones that form the basis for more than fifteen species (Loyal et al., 1996), only one of which is known from a reasonably complete skeleton whose association is documented (*Isisaurus colberti* Jain and Bandyopadhyay, 1997; Wilson and Upchurch, 2003).

We report here on a new abelisaurid theropod that preserves portions of the skull and postcranial skeleton. The associated bones of this dinosaur were discovered in the early 1980's in latest Cretaceous (Maastrichtian) beds near Rahioli in the western Indian state of Gujarat (Fig. 1). The new material begins to resolve longstanding questions of association among the many isolated theropod bones discovered in similar-age rocks in central India (Matley, 1923; Huene and Matley, 1933), and is complete enough to be placed in a phylogenetic and paleobiogeographic context.

HISTORY OF THEROPOD DISCOVERIES IN INDIA

Early discoveries at Bara Simla.— Indian dinosaurs were first reported from the so-called "Central Provinces," a collection of districts that included "Jubbulpore" (= Jabalpur) and Chanda districts, which are now part of Maharashtra and Madhya Pradesh states (Fig. 1). The first named Indian dinosaur, the sauropod "*Titanosaurus indicus*" (Lydekker, 1877), was based on two caudal vertebrae originally described in the posthumous memoirs of Hugh Falconer (1868). These vertebrae had been collected some 40 years earlier in Upper Cretaceous rocks above the "Main Lameta limestone" at Bara Simla Hill near Jabalpur. This hill would continue to yield isolated bones and teeth over the next half century, including a tooth described as "*Orthogoniosaurus matleyi*" (Das-Gupta 1930), the first Indian dinosaur named as a theropod.

Between 1917 and 1919, Charles Matley made the first intensive excavations at Jabalpur, collecting many bones from the western slope of Bara Simla (Fig. 1). At first, Matley (1921) thought his collection of bones from the "Carnosaur bed" belonged to a single individual of a new theropod, although apparently only the ilia and sacrum were found in close approximation. The "Carnosaur bed" was situated below the "Main Lameta limestone" (Matley, 1921: pl. 17). Shortly thereafter, Matley (1923) reinterpreted several of the bones (ilia, sacrum, tibia, and scutes) as pertaining to a new stegosaur, which he named *Lametasaurus indicus*. Despite several reports of stegosaur bones from India (Huene and Matley, 1933; *Brachypodosaurus gravis*, Chakravarti, 1934; *Dravidosaurus blanfordi*, Yadagiri and Ayyasami, 1979), none share derived characters with that clade. As shown below, Matley's ilia and sacrum, now unfortunately lost, do pertain to a theropod, as first suggested by Chakravarti (1935). The scutes recovered from the "Carnosaur bed" may or may not be associated, given that osteoderms of various sizes and forms have been reported in both theropods ("*Nuthetes*", Owen, 1854; *Ceratosaurus*, Madsen and Welles, 2000) and titanosaurian sauropods (*Saltasaurus*, Powell, 1980; *Ampelosaurus*, Le Loeuff, 1995; Malagasy titanosaur, Dodson et al., 1998; *Magyarosaurus*, Csiki, 1999), as well as in thyreophorans and crocodylomorphs.

In a seminal review, Huene and Matley (1933) named nine new theropod genera and species, based on Matley's collection from Bara Simla and a smaller collection from of similar age localities in "Phisdura" (= Pisdura), some 150 km to the south (Fig. 1). Six pertain to medium-to-large-sized theropods (*Indosuchus raptorius*, *Indosaurus matleyi*, *Ornithomimoides mobilis*, *O. barasimlensis*, *Dryptosauroides grandis*, *Coeluroides largus*) and three to smaller-bodied species (*Laevisuchus indicus*, *Jubbulpuria tenius*, *Compsosuchus solus*). Many of these taxa, however, are based on bones of dubious association or immature individuals, and some of the holotypic material is now damaged or lost. Re-evaluation of this collection will help clarify their taxonomic basis (Novas and Bandyopadhyay, 1999; Sereno and Wilson, in preparation).

In 1922 at Bara Simla, Barnum Brown discovered well preserved theropod jaw bones and three caudal vertebrae that may to pertain to a single individual, although no field notes regarding their original disposition are known. These jaw bones later were referred to *Indosuchus* and, following Walker (1964), identified as tyrannosaurid (Chatterjee, 1978). More recently, they have been correctly reinterpreted as pertaining to an abelisaurid theropod (Bonaparte et al., 1990; Molnar, 1990; Chatterjee and Rudra, 1996).

Recently, Chatterjee and Rudra (1996) reported the discovery at Bara Simla of additional cranial bones pertaining to a theropod (lacrimal, jugal, angular; ISI R163), although these bones have yet to be described. They were used with Brown's jaw bones from the same locality (though not necessarily the same horizon) to make a composite skull reconstruction of *Indosuchus raptorius* (Chatterjee and Rudra, 1996: fig. 14).

Recent discoveries in Gujarat.— During the 1980's, paleontologists of the Geological Survey of India uncovered important dinosaurian nesting grounds and bone sites in the Lameta Formation in western India near the village of Rahioli (Fig. 1). Dinosaurian eggs and egg clutches were found in limestone horizons (Mohabey, 1984, 2001; Srivastava et al., 1986) thought to be correlative with the "Main Lameta limestone" at Bara Simla, some 700 kilometers distant (Khosla and Sahni, 1995). Sauropod and theropod teeth (Mathur and Srivastava, 1987) and bones (Mathur and Pant, 1986; Mohabey, 1987, 1989) were discovered in calcareous sandstone and conglomeratic levels underlying the egg-bearing limestone at Rahioli. Mathur and Srivastava (1987: pl. 1-2) attributed six distinctive theropod teeth to two taxa: *Majungasaurus crenatissimus* and *Megalosaurus* sp. Tooth form, however, can vary dramatically along and between the tooth rows in some ceratosaurs (e.g., *Masiakasaurus*; Carrano et al., 2002), so it is possible that these teeth pertain to a single taxon. Chatterjee and Rudra (1996:517) mentioned "a nearly complete skeleton of *Indosuchus* from [the] Raiholi [sic] site" of Gujarat. Their brief description noted several salient features, such as the lack of pleurocoels in presacral vertebrae, the short forelimb length relative to hind limb, the footed pubis, and stout hind limb elements. An accompanying skeletal reconstruction, however, appears to contradict aspects of the description (Chatterjee and Rudra, 1996: fig. 13). The long bones in the reconstruction, for example, are not particularly stout, as are most of the abelisaurid long bones from Jabalpur (Matley, 1923: pl. 11; Huene and Matley, 1933: pl. 18).

The new specimen we describe here was discovered by one of us (SS) during the 1982-4 excavation of a series of connected quarries near the village of Rahioli, an area that is now protected as a National Park (Sahni, 2001).

Summary.— The apparent diversity of Cretaceous theropods from India (11 named species) is based in large part on fragmentary material. Only two specimens are known from remains found in close proximity, based on first-hand information. These include the ilia and sacrum of *Lametasaurus indicus* (Matley, 1923) and the paired premaxillae, maxilla, and dentary collected by Brown and later attributed to *Indosuchus raptorius* (Chatterjee, 1978). The partial skeleton mentioned by Chatterjee and Rudra (1996) may pertain to a third such specimen, but its association has not yet been documented. Below we describe an Indian abelisaurid known from associated cranial and postcranial bones that will begin to resolve such associations among other Indian theropod taxa.

INSTITUTIONAL ABBREVIATIONS

GSI — Geological Survey of India, Kolkata (Calcutta).
ISI — Indian Statistical Institute, Kolkata (Calcutta).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen 1842
THEROPODA Marsh 1881
CERATOSAURIA Marsh 1884b
ABELISAURIDAE Bonaparte and Novas 1985

Rajasaurus narmadensis, new genus and species
Figs. 2-15

Holotype.— GSI Type No. 21141/1-33, a partial skeleton consisting of a braincase, cervical centrum, partial dorsal vertebrae, sacrum, partial caudal vertebrae, partial scapula, partial ilia, left proximal pubis, right femur, left distal femur, right distal tibia, right proximal fibula, right and left

TABLE 1 — Field numbers for elements of the holotypic specimen of *Rajasaurus narmadensis* (GSI Type No. 21141).

Element	Field number	Pit number	Year collected	GSI Type No.
Braincase	4	4	1984	21141-1
Mid-cervical	45	7	1984	21141-2
Anterior dorsal	258	3A	1983	21141-3
Anterior dorsal	110	3	1983	21141-4
Anterior dorsal	112	3	1983	21141-5
Mid-dorsal	72	3	1983	21141-6
Posterior dorsal	109	3	1983	21141-7
Posterior dorsal	103	3	1983	21141-8
Posterior dorsal	83	3	1983	21141-9
Posterior dorsal	64	3	1983	21141-10
Dorsal	118	3	1983	21141-11
Dorsal	253	3A	1983	21141-12
Dorsal	78	3	1983	21141-13
Sacral 1	87	3	1983	21141-14
Sacrals 2-5	77	3	1983	21141-15
Sacral 6	89	3	1983	21141-16
Anterior caudal	117	3	1983	21141-17
Anterior caudal	96	3	1983	21141-18
Anterior caudal	102	3	1983	21141-19
Mid-caudal	111	3	1983	21141-20
Mid-caudal	9	7	1984	21141-21
Mid-caudal	179	4	1983	21141-22
Left scapula	139	4	1983	21141-23
Right ilium	86	3	1983	21141-24
Left ilium	94	3	1983	21141-25
Left pubis	187	5	1983	21141-26
Right femur	101	3	1983	21141-27
Left distal femur	170	4	1983	21141-28
Right distal tibia	38	2	1983	21141-29
Right proximal fibula	6	7	1984	21141-30
Right metatarsal II	107	3	1983	21141-31
Left metatarsal II	7	7	1984	21141-32
Left metatarsal IV	151	4	1983	21141-33

metatarsal II, and right metatarsal IV (Table 1; Fig. 2). Casts of several of these elements are housed in the University of Michigan Museum of Paleontology (UMMP 9085).

Type locality.— Temple Hill, near Rahioli (23° 3' 26.2" N, 73° 20' 30.8" E). The bones of the holotypic specimen were preserved across approximately seven meters of the quarry; the braincase was located 3.75 m from the sacrum. We regard the holotype as representing a single individual because of the match in relative size of elements (Table 2), the presence of several paired bones, and the proximity of the sacrum, ilia, and posterior dorsal and anterior caudal vertebrae (Fig. 2). The specimen was preserved within a scatter of sauropod bones that represent several individuals. Of these, long bones predominate, some of which are broken. Thus, some sorting and transport occurred during bone accumulation, although there is no clear evidence of directionality imposed by current flow. There are probably additional bones beyond the edges of the current map, which shows only those portions excavated from 1982 through 1984.

Referred specimens.— The ilia and sacrum described as *Lametasaurus* by Matley (1923) from Bara Simla (now lost) match the holotype of *Rajasaurus* in its heavy construction and strongly

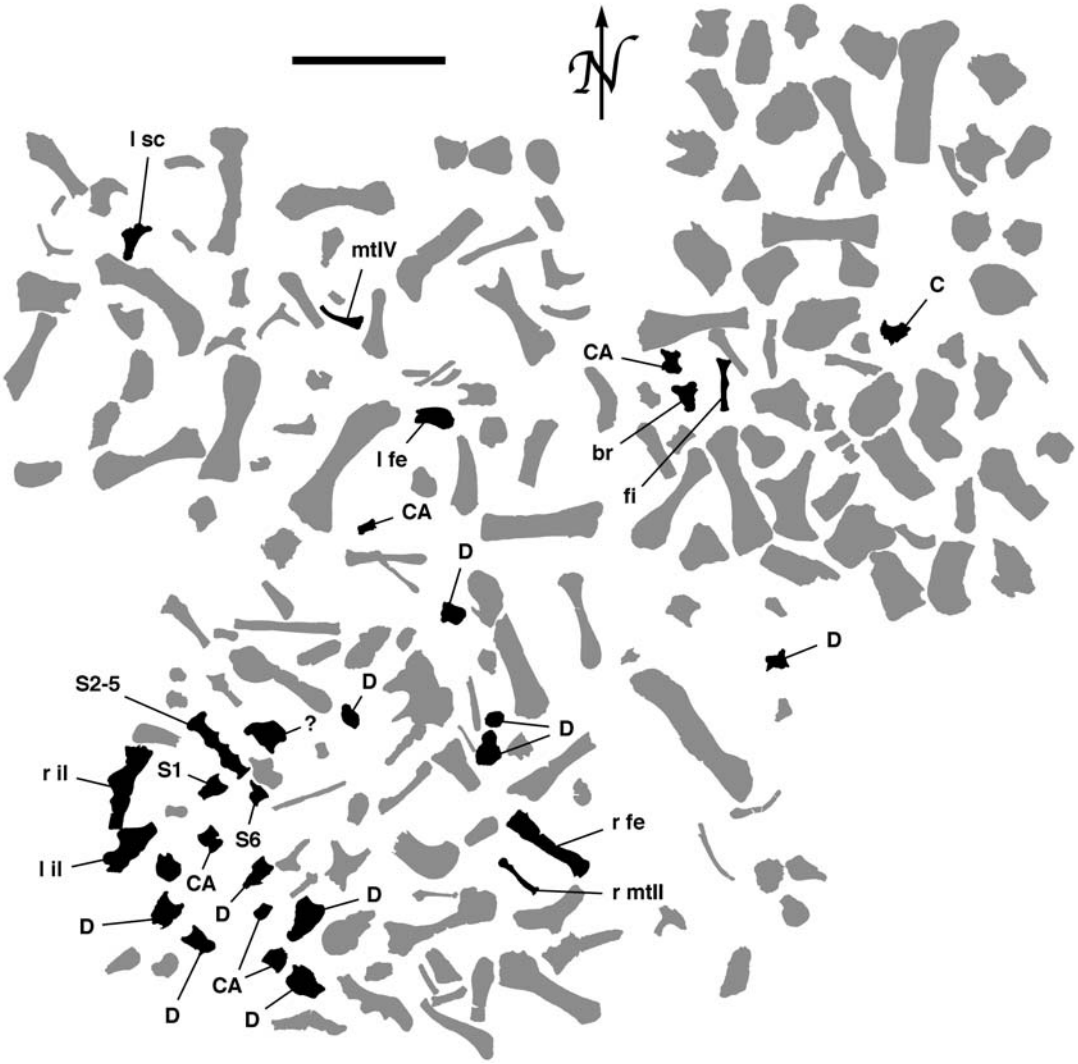

FIG. 2 — Quarry map of Temple Hill locality near Rahioli in Gujarat State (after original quarry maps drafted in 1982-84 by S. Srivastava.) Bones in black pertain to the holotypic specimen of *Rajasaurus narmadensis* (GSI Type No. 21141); shaded bones pertain to titanosaurian sauropods. Abbreviations: *br*, braincase; *C*, cervical vertebra; *CA*, caudal vertebra; *D*, dorsal vertebra; *fe*, femur; *fi*, fibula; *il*, ilium; *l*, left; *mt*, metatarsal; *r*, right; *S*, sacral vertebra; *sc*, scapula. Roman numerals indicate digit number; Arabic numerals indicate vertebral number. Scale bar equals 1 m.

divergent preacetabular process, but other key morphological details of the ilia cannot be compared. These specimens may pertain to *Rajasaurus narmadensis*, which appears to represent a heavy-bodied, stout-limbed abelisaurid. Both the Bara Simla and Rahioli localities, however, have also yielded a second, slender-limbed abelisaurid (Huene and Matley, 1933: pl. 16; Chatterjee and Rudra, 1996). Furthermore, none of the theropod braincase material found at Bara Simla (Huene and Matley, 1933: pls. 9, 10) closely matches that of the holotype of *Rajasaurus*, which has anteroposteriorly elongate supratemporal fossae and a nasofrontal horn (see Description below). We reserve formal reference of material to *Rajasaurus narmadensis* until a taxonomic review of the collection of bones from Bara Simla is completed (Sereno and Wilson, in preparation).

TABLE 2 — Comparison of skeletal dimensions among the neotheropods *Rajasaurus*, *Carnotaurus* (Bonaparte et al., 1990), *Majungatholus* (M. Carrano, personal communication), *Lametasaurus* (Matley, 1923), and *Sinraptor* (Currie and Zhao, 1994). All measurements are in millimeters; "e" indicates an estimated measure. Abbreviations: *fm*, foramen magnum; *isped*, ischial peduncle; *pped*, pubic peduncle.

Dimension	*Rajasaurus*	*Carnotaurus*	*Majungatholus*	*Lametasaurus*	*Sinraptor*
Occiput, top of *fm* to top of nuchal wedge	105	190	—	—	98
Dorsal centrum 4, length	87	108	—	—	85
Ilium, length from *pped* to *isped*	360	390	—	370	386
Sacrals 1-5, length	566	528	—	610	490e
Femur, distal breadth	150	198	127	—	207
Tibia, distal breadth	193	—	134	223	200
Fibula, proximal antero-posterior length	100	—	106	—	125
Metatarsal II, length	276	—	199	—	376

Formation, age, and distribution.— The skeleton was preserved in "infratrappean" sediments of the Lameta Formation exposed in Gujarat State near the village of Rahioli (Dwivedi et al., 1982; Mathur & Pant, 1986; Mohabey, 1987). The bones were preserved in a conglomeratic layer that lies below a dinosaur tooth-bearing calcareous sandstone (Mathur and Pant, 1986; Srivastava et al., 1986; Mathur and Srivastava, 1987). Both of these layers, in turn, underlie an egg-bearing limestone unit equivalent to the "Main Lameta limestone" at Bara Simla (Khosla and Sahni, 1995), which has been regarded as latest Cretaceous (Maastrichtian) in age on the basis of microvertebrates and associated microfossils (Sahni and Bajpai, 1991) and its stratigraphic position below the Deccan Trap flood basalts. The basalts, radiometrically dated as 65.5 million years before present, fall within the 29R paleomagnetic chron (Courtillot et al., 1986, 1996). During the latest Cretaceous, *Rajasaurus narmadensis* may have been distributed across the region now occupied by the Narmada River Valley from Rahioli to Bara Simla (Fig. 1).

Diagnosis.— *Rajasaurus narmadensis* is characterized by the following autapomorphies: median nasofrontal prominence, with the frontals forming only the posterior rim of the prominence; supratemporal fenestrae anteroposteriorly elongate, with length approximately 150% transverse breadth of frontal; and robust ilium with transversed ridge separating brevis fossa from acetabulum.

Etymology.— *Raja*, prince or princely (Sanskrit); *sauros*, lizard (Greek). The specific epithet refers to its distribution across the Narmada Valley.

DESCRIPTION

Skull

Braincase.— The coossified braincase is well preserved but lacks the distal ends of the paroccipital processes and parietal alae, the basal tubera and basipterygoid processes, and the ventral margin of the orbitosphenoids (Figs. 3-4). The laterosphenoid head and lateral margin of the

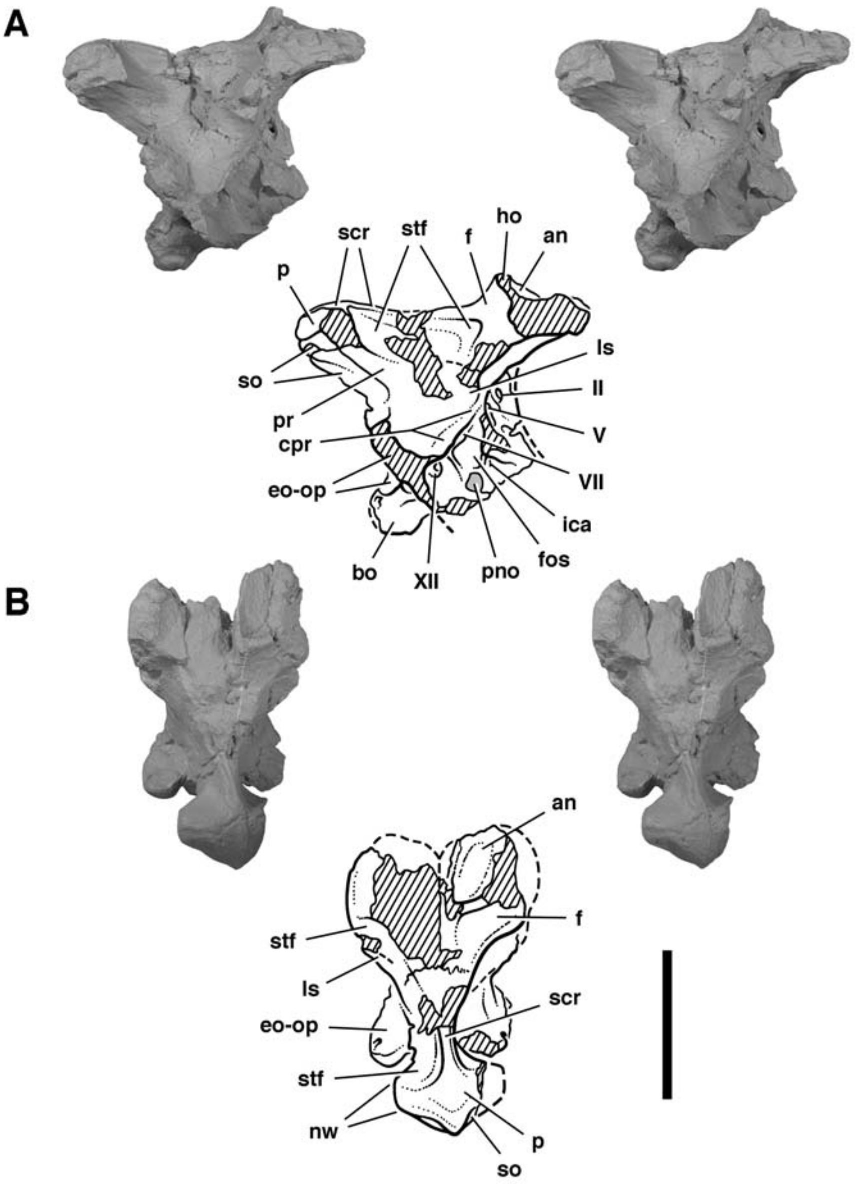

FIG. 3 — Stereopairs and line drawings of the braincase (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/1) in A, right lateral, and B, dorsal views. Cross-hatching indicates broken bone and tone indicates matrix. Abbreviations: *an*, articular surface for nasal; *bo*, basioccipital; *cpr*, crista prootica; *eo-op*, exoccipital-opisthotic; *f*, frontal; *fos*, fossa; *ho*, horn; *ica*, internal carotid artery; *ls*, laterosphenoid; *nw*, nuchal wedge; *p*, parietal; *pno*, pneumatic opening; *pr*; prootic; *scr*, sagittal crest; *so*, supraoccipital; *stf*, supratemporal fenestra. Roman numerals denote openings for cranial nerves. Scale bar equals 10 cm.

parietal and frontal are preserved on the left side but broken off on the right side. On the other hand, the frontal contribution to the nasofrontal horn is preserved on the right side but broken away on the left. The supratemporal fenestrae are extremely elongate (Fig. 3), in contrast to the subquadrate fenestrae in other abelisaurids such as *Carnotaurus* (Bonaparte et al., 1990) and

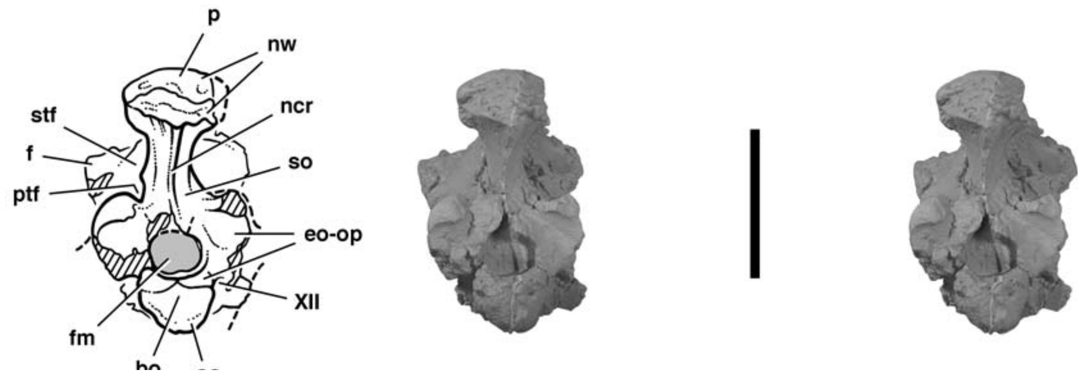

FIG. 4 — Stereopairs and line drawing of the braincase (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/1) in posterior view. Cross-hatching indicates broken bone and tone indicates matrix. Abbreviations: *bo*, basioccipital; *eo-op*, exoccipital-opisthotic; *f*, frontal; *fm*, foramen magnum; *ncr*, nuchal crest; *nw*, nuchal wedge; *oc*, occipital condyle; *p*, parietal; *ptf*, posttemporal foramen; *so*, supraoccipital; *stf*, supratemporal fenestra. Roman numeral denotes opening for cranial nerve. Scale bar equals 10 cm.

Majungatholus (Sampson et al., 1998). *Indosaurus* (Huene and Matley, 1933: pl. 10, fig. 1) likewise has abbreviate supratemporal fenestrae, but the condition in *Indosuchus* cannot be determined because the parietals have been truncated obliquely (Huene and Matley, 1933: 42, pl. 9 fig. 2B). In the basal forms *Ceratosaurus* (Madsen and Welles, 2002) and *Herrerasaurus* (Sereno and Novas, 1992), the supratemporal fossa extends far anteriorly, but the fenestra itself is not elongate.

In the following, description the bones of the skull roof (parietal, frontal) are followed by the median (supraoccipital, basioccipital, basisphenoid) and then paired (exoccipital-opisthotic, prootic, laterosphenoid, orbitosphenoid) bones of the braincase. Principal measurements are given in Table 3.

The **parietal** is a fused median bone. Its contacts with the frontal, exoccipital-opisthotic, prootic, and laterosphenoid are coossified. Traces of an interdigitating suture with the frontal are preserved anteriorly, and the suture with the supraoccipital is visible posteriorly and may not have been completely coossified (Fig. 3B). In this posterior region, the lateral margin of the parietal is sheared off, showing a cross-sectional thickness of nearly two centimeters. More anteriorly on the right side, a missing piece also reveals that the roof of the parietal is thickened. In dorsal view, the parietal forms the medial border of the supratemporal fossae. The rims of these fossae form rounded edges that converge posteriorly to form a low sagittal crest, which turns laterally along the apex of the nuchal wedge. In dorsal view, a thickened triangular flange of the parietal extends over the nuchal process of the supraoccipital, completely capping the latter as in other abelisaurids. In lateral view, the apex of the nuchal process is moderately elevated above the anterior portion of the parietal (Fig. 3A). A parietal crest is present in *Indosuchus* but apparently not *Indosaurus*, in which the preserved portion of the parietal is transversely thickened between the supratemporal fenestrae (Huene and Matley, 1933: pl. 10, fig. 1a)

The **frontal**, like the parietal, is thickened throughout its length. It attains its maximum thickness of about four centimeters above the posterior portion of the orbit. The frontal of *Indosaurus* is similarly thickened, but that of *Indosuchus* is much thinner by comparison (Huene and Matley, 1933: pl. 9, fig. 2B; pl. 10, fig. 1B). The frontal contacts the parietal posteriorly, the nasal anteriorly, the postorbital laterally, and the orbitosphenoid and laterosphenoid ventrally. The surface of the frontal is smooth, in contrast to the sculptured texture of *Indosuchus* (GSI K27/685, 690). The frontal is transversely broad and expands laterally into a robust articular surface for the postorbital, which it shares with the laterosphenoid. A trough-shaped, grooved articular surface is

TABLE 3 — Principal dimensions of the bones of *Rajasaurus narmadensis* (GSI Type No. 21141) in mm.

Braincase	
Maximum transverse width across frontals	122
Frontal horn height	24
Foramen magnum, transverse width	35
Foramen magnum, dorsoventral height	27
Supratemporal fossa, anteroposterior length	95
Occiput, width across posttemporal openings	104
Foramen magnum (dorsal margin) to summit of nuchal process	105
Nuchal process, transverse width	86
Occipital condyle, transverse width	48
Occipital condyle, dorsoventral height	38
Cervical centrum	
Centrum length	85
Centrum, anterior height	86
Centrum, anterior width	91
Left parapophysis, dorsoventral height	42
Left parapophysis, anteroposterior length	43
Dorsal vertebra	
Preserved height	193
Centrum length	87
Centrum, anterior height	99
Centrum, anterior width	83
Parapophysis, dorsoventral height	41
Parapophysis, anteroposterior length	23
Caudal vertebra	
Centrum length	99
Centrum, anterior height	87
Centrum, anterior width	72
Ilium (left)	
Preserved length	360
Ischial peduncle, maximum length	90
Ischial peduncle, length of articular peg	45
Iliac peduncle, maximum length of base	134
Brevis shelf, width of base	91
Femur (left)	
Preserved length	230
Distal breadth	150
Tibia (right)	
Preserved length	340
Minimum shaft breadth	100
Distal breadth	193
Fibula (right)	
Preserved length	287
Proximal breadth (maximum), transverse	40
Proximal length, anteroposterior	100
Midshaft length (minimum), anteroposterior	30

TABLE 3 (continued).

Metatarsal II (right)	
Total length	276
Proximal breadth, transverse	50
Proximal length, anteroposterior	60
Distal breadth, transverse	60
Distal length, anteroposterior	70

present anteriorly for the nasal, as preserved on the right side (Fig. 3). The posterior margin of the nasal articulation is positioned near the posterior margin of the orbit, as in other abelisaurids. In *Indosuchus*, in contrast, the nasal articulation is positioned near the anterior margin of the orbit and the exit for the olfactory nerve (Huene and Matley, 1933: pl. 9, fig. 2). The posterior border of the nasal trough is bounded by a raised, rounded lip, the anterior surface of which is also grooved for contact with the nasal. On the lateral side of the articular trough, the lip is broken away. On the medial side, the lip decreases in width and height, although it would have formed a narrow, anteriorly tapering wedge between the extremities of the nasals in the midline. The grooved articular trough appears to have been a platform to hold the thickened ends of the nasals. Together, the frontals and nasals would have formed a low median horn, as in some individuals of *Majungatholus* (Sampson et al., 1998). In *Rajasaurus narmadensis,* however, the horn would have been composed primarily of the nasals rather than the frontals. No such frontal excrescence is preserved in *Indosuchus* or *Indosaurus*.

Ventrally, the orbital roof is gently arched anteroposteriorly but nearly flat transversely (Fig. 3A). There is no development of an orbital fossa on the frontal. Near the midline on the right side is present a trough for the olfactory tract that would have been floored by the orbitosphenoid. Posteriorly, the frontal forms the anterior margin of the supratemporal fossa. The rim of the fossa is prominent but not developed as an overhanging shelf. The anterior wall of the fossa is very steeply inclined, exposed more in posterior than dorsal view of the braincase (Figs. 3B, 4). This is quite unusual, as the frontal portion of the fossa is usually shallow and broadly exposed in dorsal view.

The **supraoccipital** contacts the parietal dorsally and laterally and the exoccipital-opisthotic ventrally. In posterior view, the supraoccipital is a very tall bone, as in other abelisaurids (Fig. 4). It appears to reach the foramen magnum ventrally, but its sutures in this area are not clear. Above the foramen magnum, the supraoccipital becomes wedge-shaped, expanding in transverse width and anteroposterior depth toward its dorsal end. The median nuchal crest for attachment of the nuchal ligament is very prominent as in other abelisaurids. In lateral view, the supraoccipital is strongly arched posteriorly, so that the nuchal wedge extends beyond the level of the occipital condyle (Fig. 3A).

The **basioccipital** forms the majority of the occipital condyle and the ventral margin of the foramen magnum. It contacts the exoccipital-opisthotic dorsally and the basisphenoid anteriorly. Although the surface of the condyle is somewhat eroded, its relatively small size resembles that of other abelisaurids such as *Carnotaurus* and *Majungatholus* (Fig. 4). The basioccipital projects posteroventrally with the plane of the skull roof held horizontal, as seen in lateral view (Fig. 3A). This contrasts with the elongate, more horizontally-projecting occipital condyle of *Indosaurus*. Cranial nerve XII opens as a pair of foramina in a common oval fossa, as best preserved on the right side. In ventral view, the keeled ventral neck between the condyle and tubera has a greater length than in *Majungatholus*. The basioccipital forms the posterior aspect of the basal tubera, which are broader transversely than is the occipital condyle. Most of the tubera and the floor of the basisphenoid fossa are broken away.

The **basisphenoid** contacts the basioccipital, exoccipital-opisthotic, and prootic, although its sutures are completely coossified except in the region of the basal tubera. Its contribution to the borders of the cranial nerve foramina, therefore, cannot be determined (Fig. 3A). The cross-section through the basal tubera shows that much of this portion of the basisphenoid is hollow.

This space presumably opened ventrally as the basisphenoid fossa, the external opening of which is relatively small in *Majungatholus* (Sampson et el., 1998). In lateral view, two large fossae on the lateral side of the braincase are formed at least in part by the basisphenoid, as best preserved on the right side (Fig. 3A). The more posterior is the better exposed of the two in lateral view. It opens anterolaterally and may communicate with the pneumatic cavity above the basal tubera. The more anterior of the two fossae opens posterolaterally and is partially covered in lateral view by a prominent prootic-basisphenoid flange. The foramen for the carotid artery is located posterior to the apex of this smaller fossa. The diameter of the foramen is small, approximately that of cranial nerve VII. Cranial nerve VII is located in the dorsal portion of the fossa. The foramen for the carotid artery is located in the anterior portion of the fossa. More anteriorly, the parasphenoid rostrum is broken away.

The **exoccipital-opisthotic** contacts the parietal, supraoccipital, prootic, basioccipital, and basisphenoid, although most of these sutures have closed and are not visible. The base of the paroccipital process is preserved on each side. Near its contact with the supraoccipital, the dorsal margin of the exoccipital-opisthotic is notched and would have formed the ventral margin of the posttemporal foramen as in *Majungatholus* (Fig. 4). Lateral to this notch, the margin is swollen. In posterior view, the lateral edge of the foramen magnum is sharp and everted, lateral to which is a broad fossa. The exoccipital-opisthotic forms the lateral wall of the foramen magnum and extends posteroventrally as a pedicel that contributed to the dorsolateral corner of the occipital condyle. Anteriorly on the floor of the braincase, the pedicels are separated by the basioccipital. The pedicels converge toward one another so that their anterior corners are in contact in the midline. Lateral to the occipital condyle, the exoccipital-opisthotic forms the lateral margin of the basal tubera, as in other neotheropods.

In lateral view, the otic region is deeply inset and roofed by a prominent flange (crista prootica) that extends anteriorly onto the prootic (Fig. 3A). The otic fossa is divided by the crista interfenestralis into two large foramina, as fully exposed on the right side. The posteroventral opening is the fenestra ovalis; the anterodorsal opening is the jugular foramen.

The **prootic** is divided into dorsal and ventral portions by the prominent crista prootica, which is developed as a ventrally projecting flange rather than just a prominent ridge, as in many other theropods. The crista prootica is similarly developed as a prominent flange in *Majungatholus*, and this may characterize the braincase in abelisaurids (Fig. 3A). Immediately ventromedial to the crista prootica is a small oval fossa preserved on both sides. The ventral lip bounding the fossa is sharp and trough-shaped in mid-section for passage of cranial nerve VII. The foramen is located in the fossa between the crista prootica and the ventral lip. Ventral to this small fossa is a much larger subtriangular fossa, here identified as the lateral fossa, which is broadly exposed in lateral view. This large fossa is bounded posteriorly and separated from the otic fossa by a vertical crest (Fig. 3A). The trigeminal foramen for cranial nerve V and the optic foramen for cranial nerve II are located near each other and are similar in size. The trigeminal foramen is an oval slit best preserved on the left side. The trigeminal foramen opens anteriorly rather than laterally. It cannot be determined if there was a separate opening for the ophthalmic branch (V_1) as in some other theropods. The pituitary fossa, located ventral to the trigeminal and optic foramina, has irregular openings in its roof. These may well represent postmortem breakage.

The **laterosphenoid** is situated dorsal to the trigeminal and optic foramina and contacts the frontal, postorbital, prootic, and orbitosphenoid. Its suture with the frontal is visible ventrally inside the orbit. All of its other sutures are closed. It arches laterally from the side wall of the braincase to a small head, which would have been covered by the postorbital. The head of the laterosphenoid is preserved only on the left side, where it abuts the frontal.

The posterior portion of the **orbitosphenoid** is preserved on the right side. It extends anteriorly from the laterosphenoid, enclosing the forebrain and the olfactory tract. The anterior half of the bone on the right side is broken away, exposing a depression on the frontal for the olfactory tract. In lateral view, the oval optic foramen is broadly exposed and best preserved on the right side. As with the laterosphenoid, the ventral contacts of the orbitosphenoid are obscured by fusion, so its contribution to the foramina for the other cranial nerves cannot be determined.

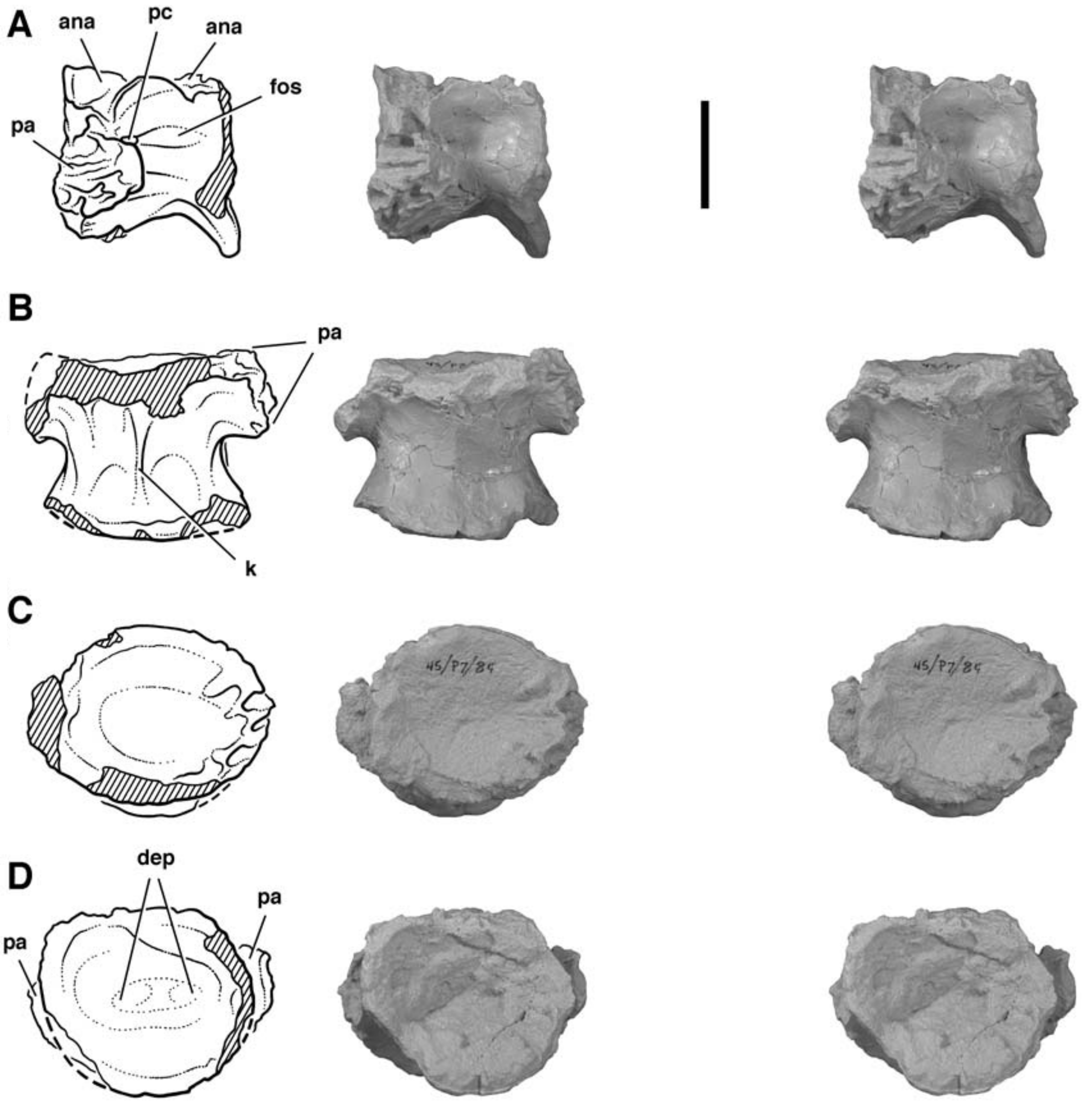

FIG. 5 — Stereopairs and line drawings of a mid-cervical centrum (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/2) in A, left lateral; B, ventral; C, anterior; and D, posterior views. Cross-hatching indicates broken bone. Abbreviations: *ana*, articulation for neural arch; *dep*, depression; *fos*, fossa; *k*, keel; *pa*, parapophysis; *pc*, pleurocoel. Scale bar equals 5 cm.

Axial Skeleton

Cervical centrum.— A single mid-cervical centrum is preserved near the braincase in Pit 7 (Figs. 2, 5). The spool-shaped centrum is proportionately shorter than those of *Ceratosaurus* (Gilmore, 1920), *Majungatholus* (Sampson et el., 1998), and *Carnotaurus* (Bonaparte et al., 1990). As in the cervical vertebrae of these other large-bodied ceratosaurs, the posterior face of the centrum is deeply concave (Fig. 5D). In contrast to these ceratosaurs, the anterior centrum face is gently concave rather than convex (Fig. 5C). Both anterior and posterior faces of the centrum are broader than tall, as in *Majungatholus* and *Carnotaurus*.

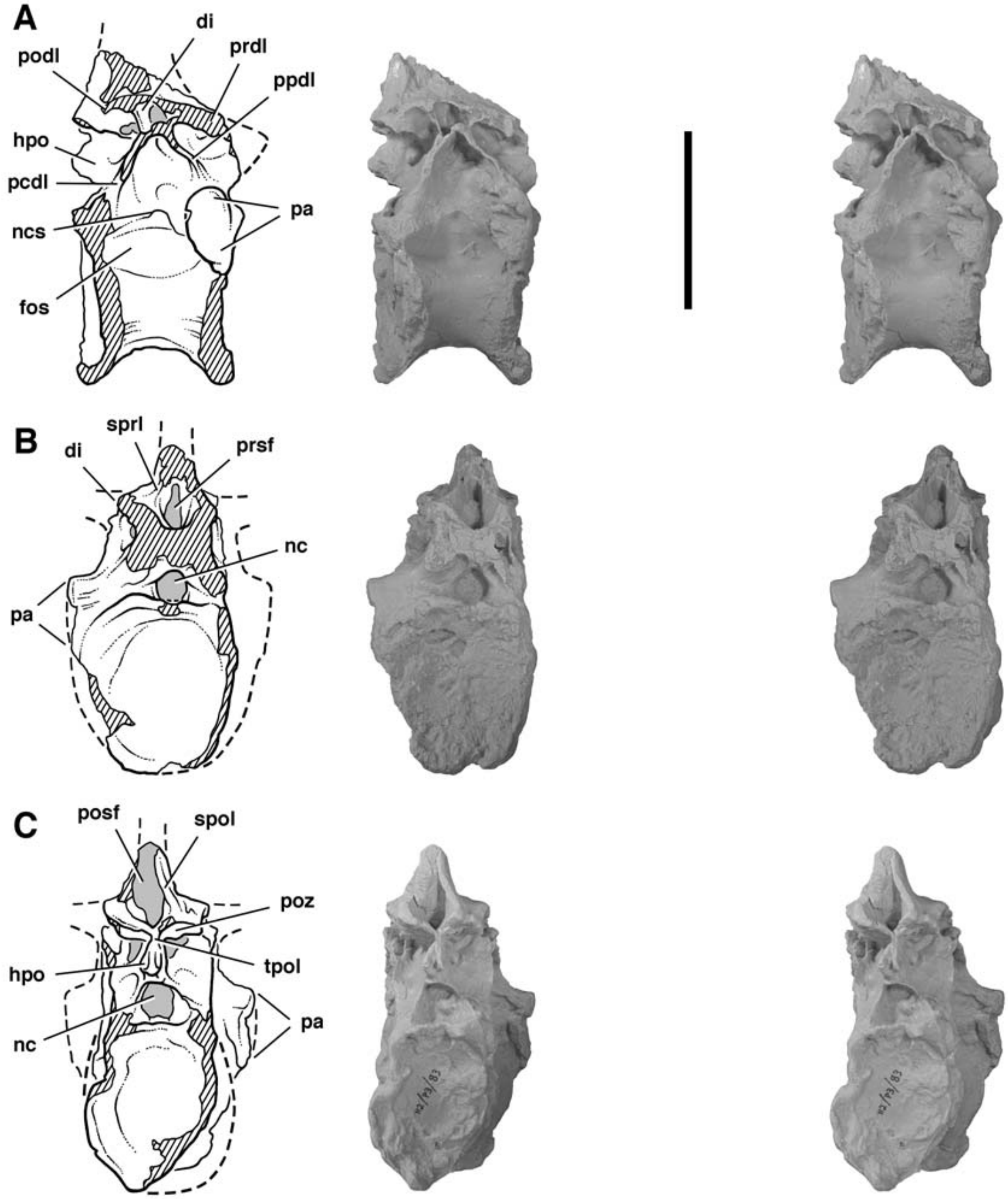

FIG. 6 — Stereopairs and line drawings of an anterior dorsal vertebra (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/5) in A, right lateral; B, anterior; and C, posterior views. Cross-hatching indicates broken bone and tone indicates matrix. Abbreviations: *di*, diapophysis; *fos*, fossa; *hpo*, hyposphene; *nc*, neural canal; *ncs*, neurocentral suture; *pa*, parapophysis; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *posf*, postspinal fossa; *poz*, postzygapophysis; *ppdl*, paradiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *prsf*, prespinal fossa; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *tpol*, intrapostzygapophyseal lamina. Scale bar equals 10 cm.

In lateral view, the anterior face of the centrum is elevated relative to the posterior face, and the cervical series presumably followed a sigmoid curve (Fig. 5A). The parapophysis, located at mid-height along the anterior rim of the centrum, is very large and laterally prominent (Fig. 5B). An oval fossa is located posterodorsal to the parapophysis and contains two small pneumatic openings. In other large-bodied ceratosaurs, such as *Ceratosaurus*, *Majungatholus*, and *Carnotaurus*, a pair of pneumatic openings are also present in cervical vertebrae, although they are not positioned as far anteriorly as in *Rajasaurus narmadensis*. A very low median keel is present on the anterior half of the centrum, as seen in ventral view (Fig. 5B).

Dorsal vertebrae.— Several partial dorsal vertebrae are preserved in a small cluster near the sacrum and ilium in Pit 3 (Fig. 2). One of these preserves the centrum and most of the neural arch; the prezygapophyses and distal ends of the transverse processes and neural spine are broken away (Fig. 6). Most likely it constitutes the fourth dorsal vertebra, based on the form and position of the parapophysis in the articulated presacral column of *Carnotaurus* (Bonaparte et al., 1990: fig. 15).

The centrum is spool-shaped, with its articular faces deeper than broad, opposite the condition in the cervical vertebra described above (Fig. 6B, C). The centrum is gently amphicoelous. However, these proportions must be confirmed in more perfect exemplars. A subtriangular fossa extends from the dorsal margin of the centrum onto the neural arch (Fig. 6A). The dorsal margins of the fossa are inset, and it is deepest at the fused neurocentral suture. There are no pneumatic openings within the fossa. In *Carnotaurus*, in contrast, the fossa has a lenticular shape and opens into the centrum via a single pneumatopore (Bonaparte et al., 1990: fig. 15).

The neural arch is highly pneumatized. There are a number of small pneumatic diverticulae and several laminae that separate larger pneumatic fossae between the parapophysis, diapophysis, and zygapophyses. In lateral view, the paradiapophyseal and posterior centrodiapophyseal laminae extend ventrally from the diapophysis to enclose the fossa described above (Fig. 6A). Another pair of nearly horizontal laminae extend from the transverse process to the zygapophyses (pre- and postzygodiapophyseal laminae). The fossae between these four diapophyseal laminae have several diverticulae that invade the base of the neural arch and prezygapophyses. The large, elliptical parapophysis is located on the anterior base of the neural arch, just anterior of the lateral fossa (Fig. 6A). In anterior and posterior views, paired laminae (spinoprezygapophyseal, spinopostzygapophyseal) enclose a narrow median fossa as they extend dorsally from the zygapophyses to the neural spine (Fig. 6B, C). The postzygapophyses are longer anteroposteriorly than broad transversely and have a nearly horizontal orientation. Short, vertical intrapostzygapophyseal laminae join each postzygapophysis to the well developed hyposphene (Fig. 6C).

Sacrum.— The ventral half of the sacrum is preserved (Fig. 7). Six sacral centra are present, with the anteriormost (S1) and posteriormost (S6) sacral centra free from the coossified middle four centra (S2-5). The centra are somewhat elongate, and their width tapers from both ends towards the middle of the sacrum (Table 3; Fig. 7B). The parapophyseal component of the sacral ribs is preserved on all but the first sacral centrum. In lateral view, the sacrum shows little ventral arching, although there is some ventral offset of the anterior and posterior articular faces of sacral 1 and 5, respectively (Fig. 7A). No sacral attachment scars are visible on the medial aspect of the ilium. Like *Rajasaurus*, the sacrum of *Lametasaurus* includes at least five vertebrae that appear to lack arching and taper slightly at midlength (Matley, 1923: pl. 8). However, no derived similarities could be identified between these two elements.

Caudal vertebrae.— Several caudal vertebrae were found near the sacrum (Fig. 2). None are complete, but a few are well preserved. In one large caudal centrum that was located near the base of the tail, the anterior face is offset dorsal to the posterior face (Fig. 8A). The amphicoelous centrum is strongly transversely compressed compared to the spool-shaped presacral centra, and the ventral keel is prominent (Fig. 8B, C). A portion of the neural arch is fused to the centrum. There are no obvious chevron facets, although the ventral margins of the centrum are weathered.

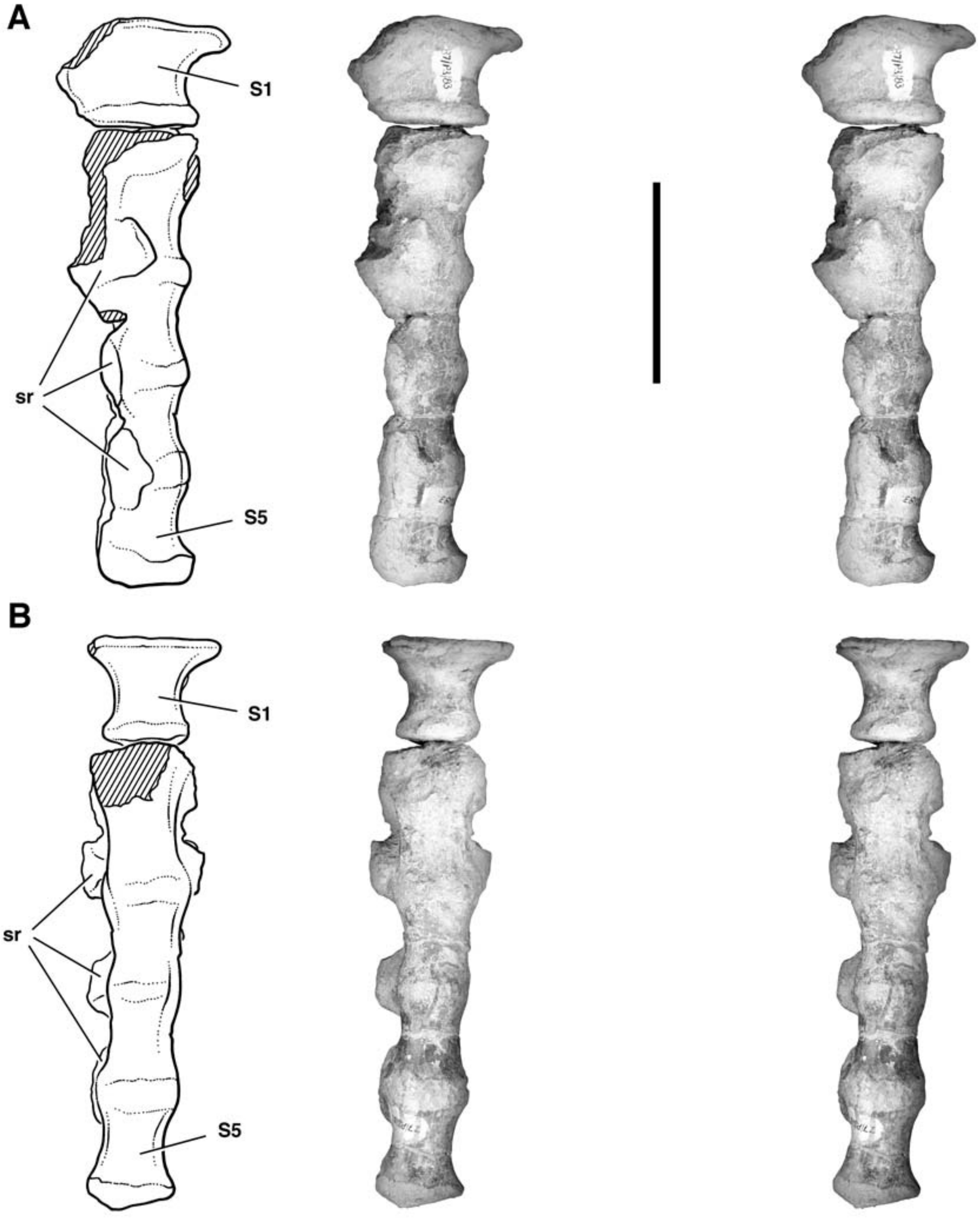

FIG. 7 — Stereopairs and line drawings of the sacrum of *Rajasaurus narmadensis* (GSI Type No. 21141/14-15) in A, left lateral, and B, ventral views. Cross-hatching indicates broken bone. Abbreviations: *S1* and *S5*, first and fifth sacral vertebrae; *sr*, sacral rib. Scale bar equals 20 cm.

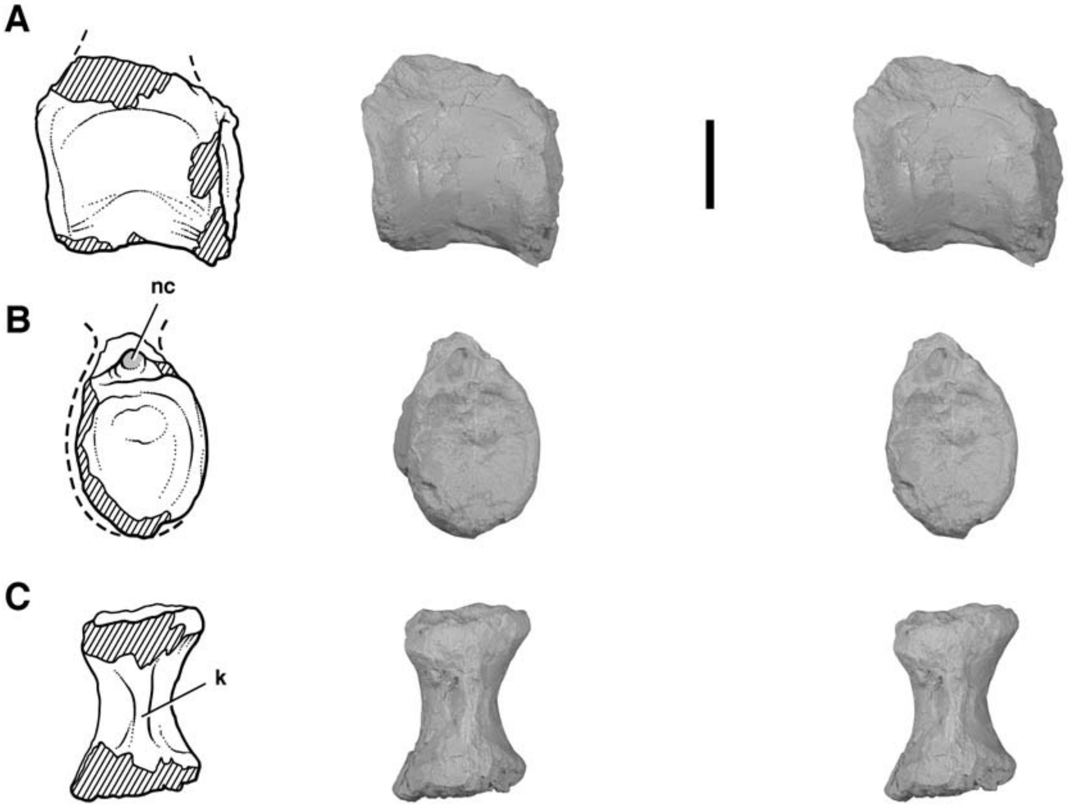

FIG. 8 — Stereopairs and line drawings of an anterior caudal vertebra (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/19) in A, left lateral; B, anterior; and C, ventral views. Cross-hatching indicates broken bone and tone indicates matrix. Abbreviations: *k*, keel; *nc*, neural canal. Scale bar equals 5 cm.

Appendicular Skeleton

Ilium.— The distal ends of the pre- and postacetabular processes of both ilia are broken, but other portions of this robustly built bone are preserved (Fig. 9). The broad and very short pubic peduncle is truncated distally at approximately 50° from the horizontal as seen in lateral view (Fig. 9A). There is virtually no free anterodorsal margin to the peduncle, as in the ceratosaurs *Ceratosaurus* and *Majungatholus*. An arcuate trough separates the anterodorsal edge of the peduncle from the preacetabular process. In ventral view, the articular end of the pubic peduncle is subtriangular (Fig. 9B). The broken base of a cone-shaped articular peg for an opposing socket on the pubis is located on the ventral half of the distal articular surface, similar to that in *Ceratosaurus* and *Majungatholus* (Sampson et al., 1998: fig. 2F). The narrow, vertically oriented ischial peduncle projects well below the pubic peduncle. The tip of the ischial peduncle is also developed as a cone-shaped articular peg for an opposing socket on the ischium, as in *Ceratosaurus* and *Majungatholus*.

The acetabulum is subrectangular in ventral view (Fig. 9B). Its articular surface is gently anteroposteriorly and transversely concave. The articular surface extends farther ventrally on the posterior side of the acetabulum, due to the greater length of the ischial peduncle. In lateral view, the acetabulum is overhung by the supracetabular crest, which is located posterior to its center at the base of the ischial peduncle (Fig. 9A, B). The lateral edge of the supracetabular crest is broken

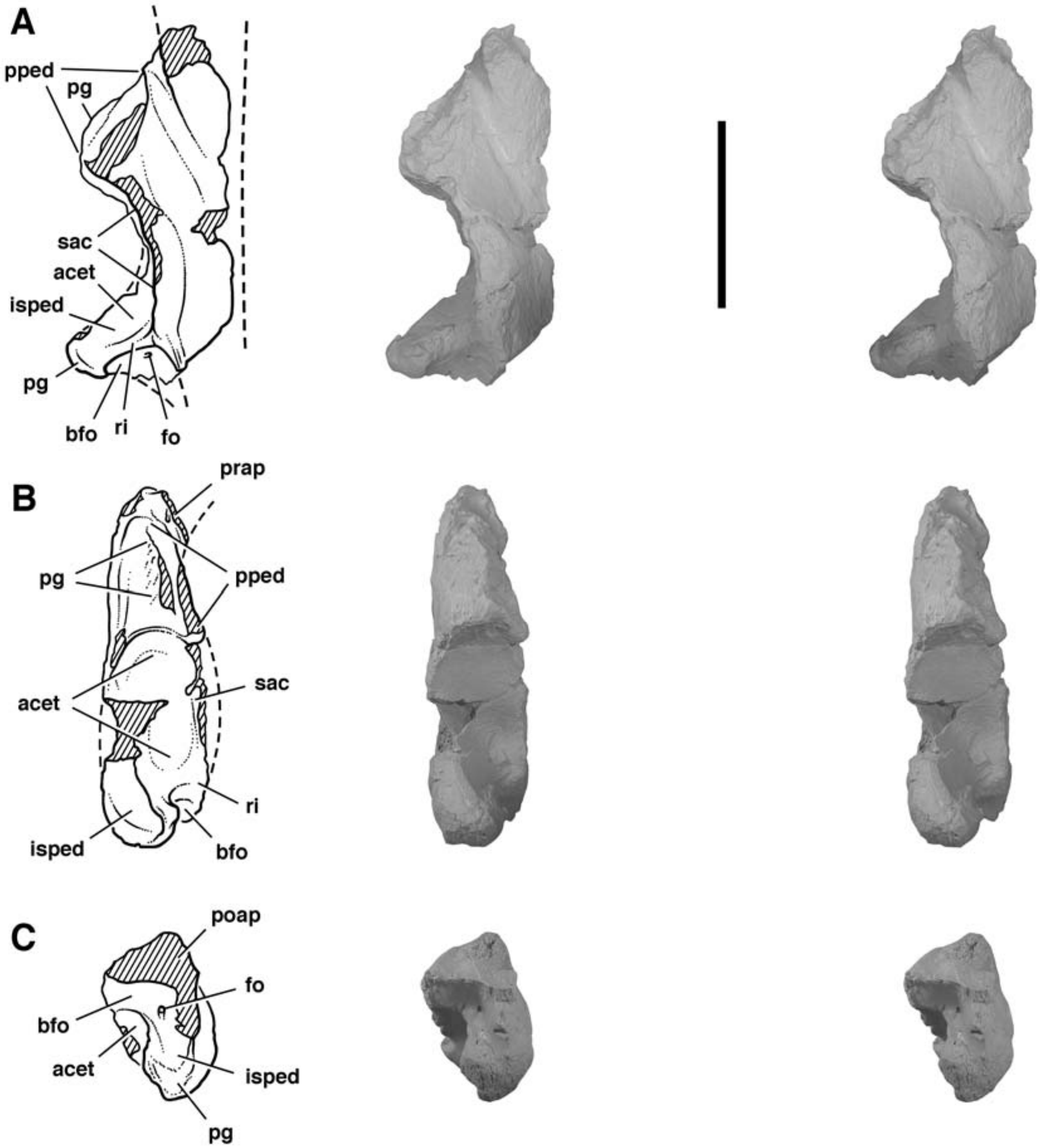

FIG. 9 — Stereopairs and line drawings of the left ilium (cast) of *Rajasaurus narmadensis* (GSI Type No. 21141/25) in A, left lateral; B, ventral; and C, posterior views. Cross-hatching indicates broken bone. Abbreviations: *acet*, acetabulum; *bfo*, brevis fossa; *fo*, foramen; *isped*, ischial peduncle; *pg*, peg; *poap*, postacetabular process; *pped*, pubic peduncle; *prap*, preacetabular process; *ri*, ridge; *sac*, supracetabular crest. Scale bar equals 20 cm.

away, but its thickness indicates it likely would have overhung the acetabulum to a greater degree, as in other ceratosaurs such as *Ceratosaurus* and *Majungatholus* (Sampson et el., 1998: fig. 2F). In ventral view, a rounded transverse ridge separates the acetabulum from the brevis fossa, which is transversely very broad (Fig. 9B, C). Unlike many tetanurans such as *Allosaurus* (Madsen, 1976), the acetabulum and brevis fossa are not completely separated by the ischial peduncle,

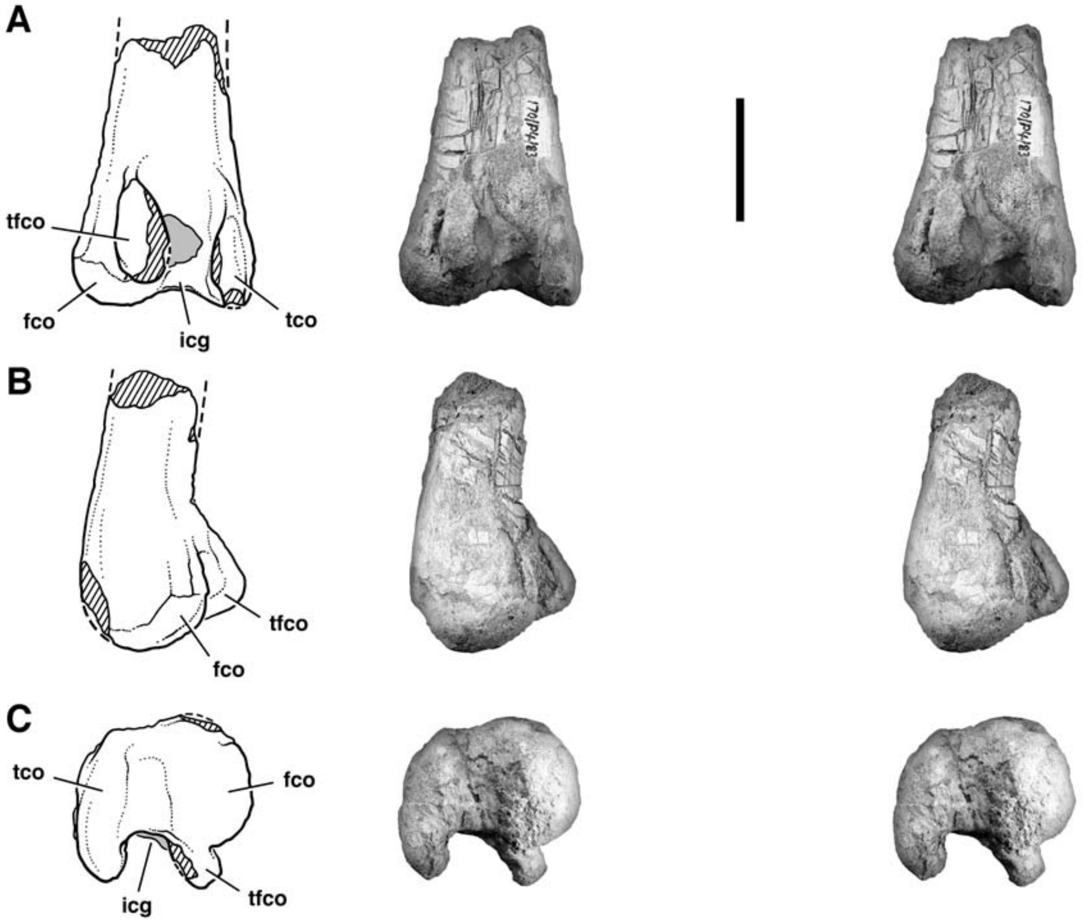

FIG. 10 — Stereopairs and line drawings of the distal portion of the left femur of *Rajasaurus narmadensis* (GSI Type No. 21141/28) in A, posterior; B, lateral; and C, distal views. Cross-hatching indicates broken bone and tone indicates matrix. Abbreviations: *fco*, fibular condyle; *icg*, intercondylar groove; *tco*, tibial condyle; *tfco*, tibiofibular condyle. Scale bar equals 10 cm.

which is inset from the lateral margin of the ilium. A foramen is located on the posterior aspect of the ischial peduncle at the proximal end of the brevis fossa (Fig. 9C).

The blade of the ilium is not preserved. The available cross-section along the dorsal margin of the left ilium, however, suggests that the blade was a relatively thin plate approximately one centimeter thick at its base (Fig. 9C). The pre- and postacetabular processes, in contrast, are seven to eight centimeters thick at their proximal ends. The preacetabular process flares laterally but is broken just beyond the base. In *Lametasaurus indicus*, the preacetabular process is laterally deflected, and its ventral margin is twisted into a near horizontal orientation (Matley, 1923: pls. 9, 10). The postacetabular process of *Lametasaurus* also flares laterally beyond the supracetabular crest and expands in width distally. How closely *Rajasaurus narmadensis* resembled *Lametasaurus* in these regards is not immediately apparent from the available portions of the right and left ilia. In medial view, there are no raised sacral attachment scars.

Pubis.— The proximal half of the left pubis was preserved in Pit 5, 4.75 meters from the sacrum. The iliac peduncle is very broad and marked by a conical pit for reception of a matching

FIG. 11 — Stereopairs and line drawing of the distal portion of the right tibia of *Rajasaurus narmadensis* (GSI Type No. 21141/29) in anterior view. Cross-hatching indicates broken bone. Abbreviation: *aasp*, articular surface for astragalar ascending process; *afi*, articular surface for fibula. Scale bar equals 10 cm.

peg on the pubic peduncle of the ilium. The acetabular and ischial surfaces are approximately one-half the length of the iliac peduncle. Below the iliac peduncle is a rugose scar marking the attachment site of the ambiens muscle. The dorsal margin of a large obturator opening is preserved. Whether this foramen was partially or completely enclosed by the pubis cannot be determined.

Femur.— The shaft of the femur is compressed anteroposteriorly and broadens towards the distal condyles (Fig. 10). The tibial and fibular condyles are separated by a shallow intercondylar groove that is visible in both posterior and distal views (Fig. 10A, C). The tibial condyle is approximately half the breadth of the fibular condyle but is slightly longer anteroposteriorly. An ovate tibiofibular crest is present above the fibular condyle and projects posterolaterally (Fig. 10B, C).

Tibia.— A distal tibia is preserved in Pit 2, 6.5 m south of the sacrum. Its shaft is transversely broad and flattened anteriorly. Its lateral margin has a beveled surface for contact with the fibular shaft (Fig. 11). The fibular shaft maintains its lateral contact with the tibia until just before its distal end, where the fibula turns onto its anterior side. The distal end of the tibia is asymmetrically expanded, such that its lateral (fibular) malleolus is broader and projects farther distally than the medial malleolus. Consequently, the distal margin of the tibia is beveled ventrolaterally. The tibia attributed to *Lametasaurus* has a proportionately broader shaft and is slightly more transversely expanded than *Rajasaurus* (Matley, 1923: pl. 11; Table 2). A shallow triangular depression on the anterior face of the distal tibia marks the facet for the ascending process of the astragalus, which appears to have been of moderate height. The ascending process, as inferred from the articular depression, was developed as a superficial plate in *Rajasaurus narmadensis* (Fig. 11) rather than a wedge-shaped process fitted to a notch in the distal end of the tibia, as occurs in neotheropod outgroups such as *Herrerasaurus*. The lateral margin of the astragalar articular depression is nearly vertical, the apex of the facet positioned on the fibular side of the tibia. The distal tibia is very similar in form in *Ceratosaurus*, *Majungatholus*, and *Masiakasaurus*.

Fibula.— The proximal portion of the right fibula was preserved near the braincase in Pit 7 (Figs. 2, 12). As indicated on the field map, the fibula was more complete when collected, but the distal portion of the shaft is now lost. The proximal end of the fibula is laterally compressed and tapers in width posteriorly (Fig. 12C). Its medial surface, which contacts the tibia, is concave. In lateral view, the narrow posterior portion of the proximal end arches above the broader anterior portion (Fig. 12A). In medial view, a well demarcated fibular fossa is present that is deepest along its anterior margin (Fig. 12B). Here the anterior wall of the fossa is narrow and projects medially from the surface of the shaft (Fig. 12C), where it contacts the opposing fibular crest on the tibia.

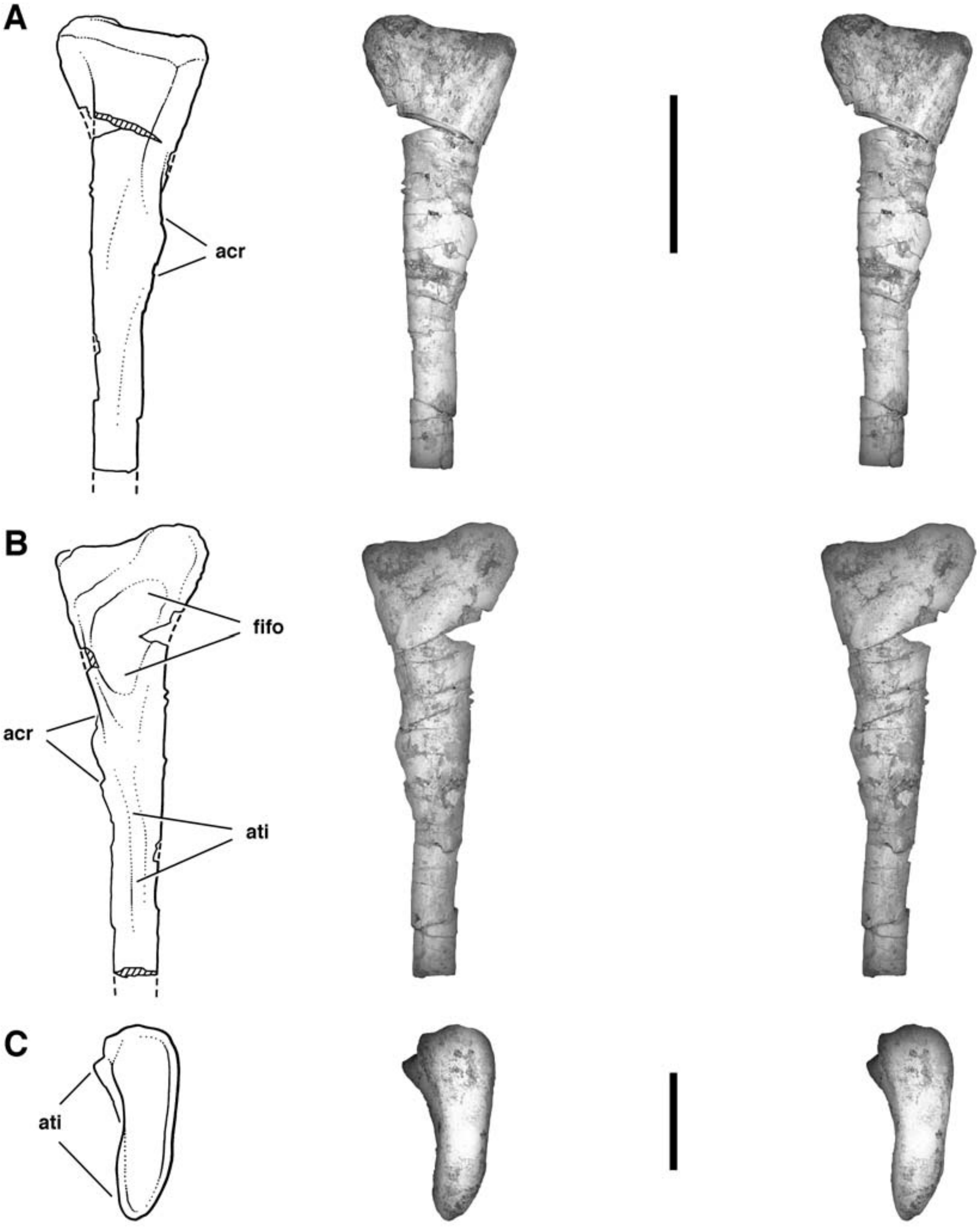

FIG. 12 — Stereopairs and line drawings of the proximal portion of the right fibula of *Rajasaurus narmadensis* (GSI Type No. 21141/30) in A, lateral; B, medial; and C, proximal views. Cross-hatching indicates broken bone. Anterior towards top in C. Abbreviations: *acr*, anterior crest; *ati*, articular surface for the tibia; *fifo*, fibular fossa. Scale bar equals 10 cm in A and B and 5 cm in C.

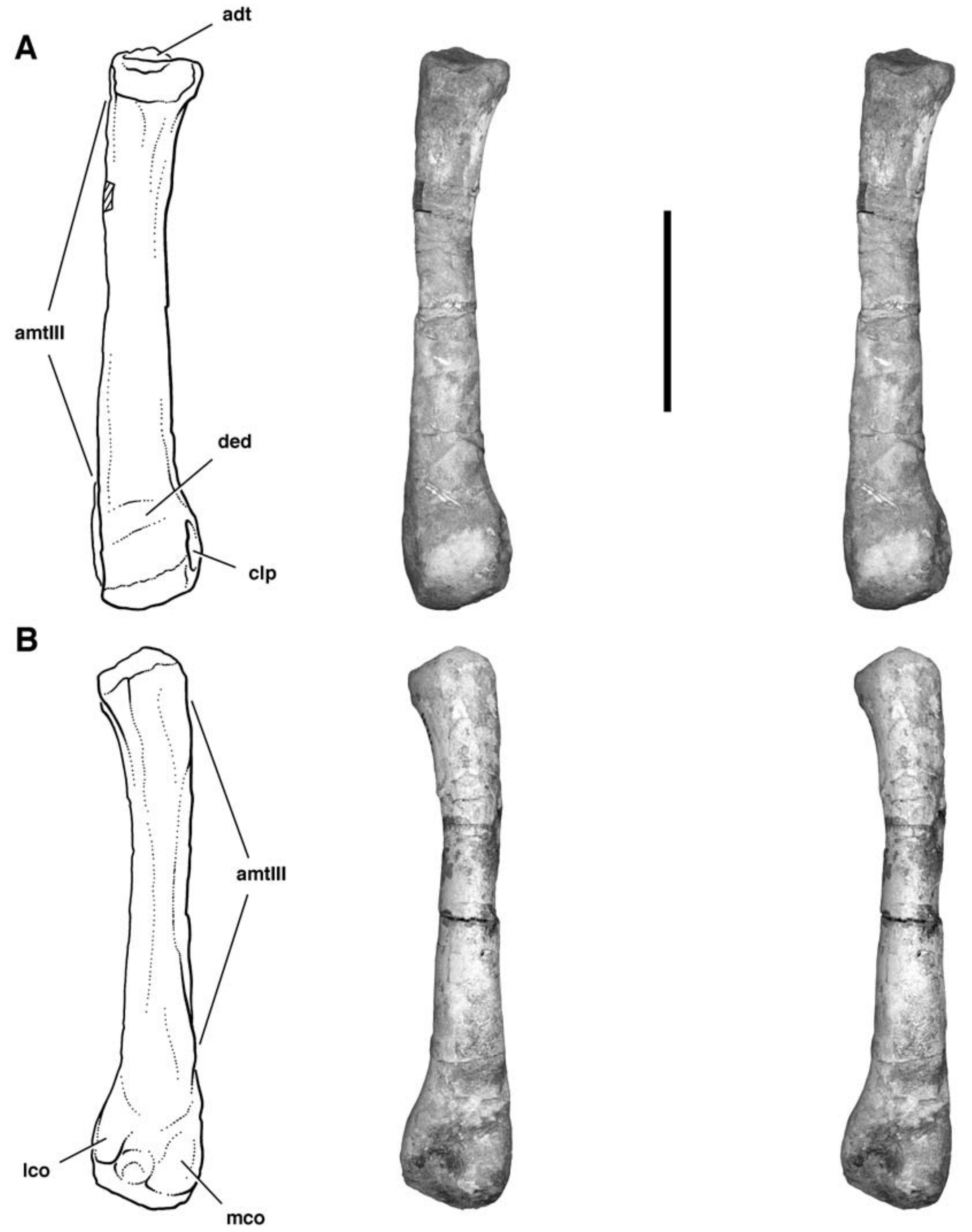

FIG. 13 — Stereopairs and line drawings of right metatarsal II of *Rajasaurus narmadensis* (GSI Type No. 21141/31) in A, anterior, and B, posterior views. Cross-hatching indicates broken bone. Abbreviations: *adt*, articular surface for distal tarsal; *amtIII*, articular surface for metatarsal III; *clp*, collateral ligament pit; *ded*, dorsal extensor depression; *lco*, lateral condyle; *mco*, medial condyle. Scale bar equals 10 cm.

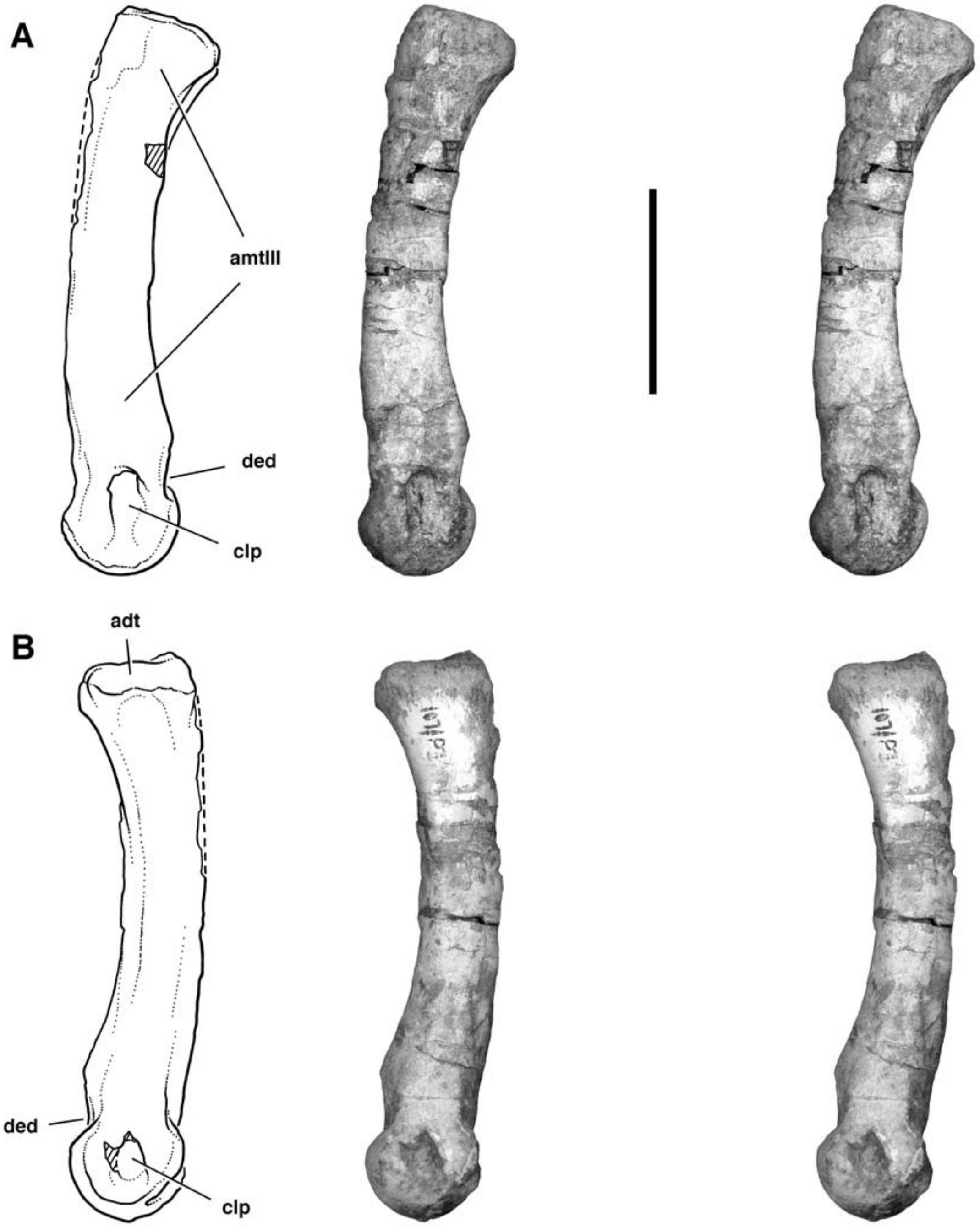

FIG. 14 — Stereopairs and line drawings of right metatarsal II of *Rajasaurus narmadensis* (GSI Type No. 21141/31) in A, lateral, and B, medial views. Cross-hatching indicates broken bone. Abbreviations: *adt*, articular surface for distal tarsal; *amtIII*, articular surface for metatarsal III; *clp*, collateral ligament pit; *ded*, dorsal extensor depression. Scale bar equals 10 cm.

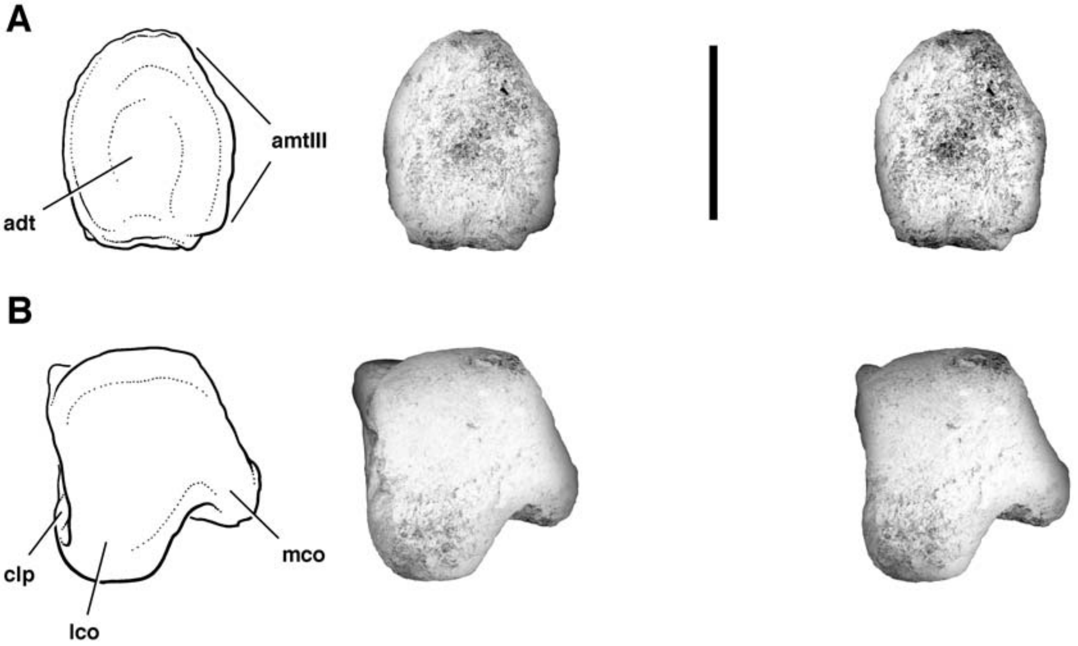

FIG. 15 — Stereopairs and line drawings of right metatarsal II of *Rajasaurus narmadensis* (GSI Type No. 21141/31) in A, proximal, and B, distal views. Abbreviations: *adt*, articular surface for distal tarsal; *amtIII*, articular surface for metatarsal III; *clp*, collateral ligament pit; *lco*, lateral condyle; *mco*, medial condyle. Scale bar equals 5 cm.

A well developed anterior crest is present distal to the fibular fossa and is visible in lateral and medial views. Distal to the anterior crest, the fibular shaft tapers in width and remains in contact medially with the tibial shaft (Fig. 12B).

Metatarsal II.— Metatarsal II is a robust metapodial similar to that in *Ceratosaurus* (Gilmore, 1920) and basal tetanurans such as *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993). The proximal shaft is not reduced in width as in noasaurids (Carrano et al., 2002). The slightly concave proximal articular surface (Fig. 15A) is oval rather than subtriangular, as in *Ceratosaurus* (Gilmore, 1920), *Allosaurus* (Madsen, 1976), and *Sinraptor* (Currie and Zhao, 1993). The convex lateral margin of its proximal surface indicates that the opposing medial margin of the metatarsal III must have been concave. The shaft of metatarsal II is flattened on its lateral side, where it contacts metatarsal III along most of its length (Figs. 13, 14A). In medial and lateral views, the shaft is bowed anteriorly (Fig. 14). In distal view, the lateral condyle is broader, extends farther distally, and is oriented more anteroposteriorly than the medial condyle, which is deflected medially (Figs. 13B, 15B). Well-developed collateral ligament pits are present medially and laterally, and there is an extensor depression on the anterior surface of the shaft, just above the distal condyle (Figs. 13A, 14).

Metatarsal IV.— A nearly complete metatarsal IV was preserved near the femur in Pit 4. Its robust proportions resemble those of metatarsal II. Its proximal articular surface is subtriangular and does not have a extended posterior apex, as is present in *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993). The distal condyles are asymmetric, with the medial condyle broader, more distally extended and less divergent than the lateral condyle.

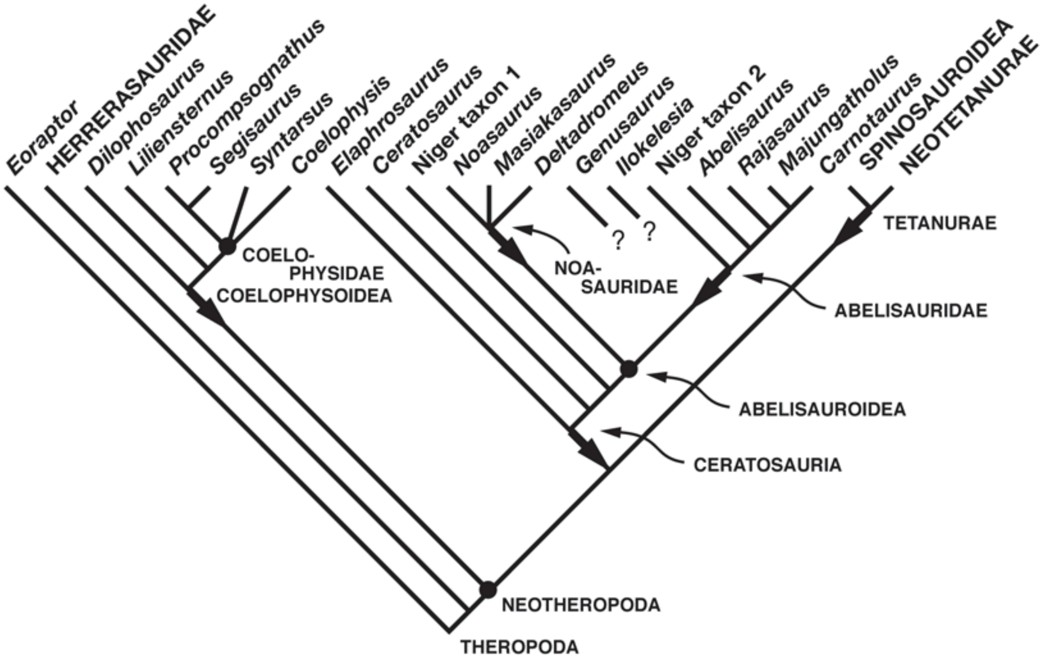

FIG. 16 — Phylogenetic relationships among ceratosaur neotheropods, based on the analysis performed by Sereno et al. (in review). Solid circles indicate node-based groups, thickened arrows indicate stem-based groups. "Niger taxon 1" and "Niger taxon 2" are informal references to two new genera described in Sereno et al. (in review). See section on Basal Neotheropod Phylogenetic Taxonomy in text for discussion of the names applied to nodes.

PHYLOGENETIC AFFINITIES

Discovery of the skull of the nearly complete skeleton of the horned *Carnotaurus sastrei* (Bonaparte, 1985) from Upper Cretaceous (Campanian-Maastrichtian; Pascual et al., 2000) rocks of Argentina revealed a new group of abelisauroid theropods that radiated on southern continents during the end of the Mesozoic. Discoveries of closely related taxa elsewhere in Argentina (e.g., Bonaparte and Novas, 1985; Bonaparte and Powell, 1980), India (Huene and Matley, 1933; Chatterjee and Rudra, 1996), and Madagascar (Sampson et al., 1998; Carrano et al., 2002) followed. Due to their Cretaceous distribution on southern landmasses, abelisauroids have figured prominently in paleobiogeographic scenarios for the breakup of Gondwana (e.g., Sampson et al., 1998; Bonaparte, 1999; Chatterjee and Scotese, 1999). Recent interest in the phylogenetic affinities among abelisauroids has resulted in a reevaluation of the higher-level relationships among basal theropods. Most cladistic analyses have united abelisauroids, *Ceratosaurus*, and *Coelophysis*-like forms as Ceratosauria, the sister-taxon of Tetanurae within Neotheropoda (e.g., Holtz, 1994, 2000; Sereno, 1999). However, recent studies have recognized that *Ceratosaurus* and abelisauroids share a more recent ancestry with Tetanurae than with *Coelophysis*-like forms (Carrano and Sampson 1999; Forster, 1999; Carrano et al., 2002; Rauhut, 2003; Sereno et al., in review).

The phylogenetic position of *Rajasaurus narmadensis* among basal neotheropods was evaluated in a maximum parsimony analysis conducted by Sereno et al. (in review). Their analysis evaluated 169 characters in 21 ingroup taxa; *Eoraptor* and Herrerasauridae were chosen as outgroup taxa (see Appendix for character list and character-taxon matrix). The tree statistics are detailed elsewhere (Sereno et al., in review), only the topology will be summarized here. The resultant topology (Fig. 16) supports the results of Carrano et al. (2002), linking *Ceratosaurus* and abelisauroids more closely to Tetanurae than to *Coelophysis*. The Sereno et al. (in review) analysis recognizes *Elaphrosaurus*, *Ceratosaurus*, and "Niger taxon 1" as successive outgroups to Abelisauroidea, which comprises Noasauridae and Abelisauridae (clade names discussed below under Basal Neotheropod Phylogenetic Taxonomy). The relationships of *Ilokelesia* and *Genusaurus* within Abelisauroidea are unresolved. Abelisauridae unites the mid-Cretaceous "Niger taxon 2" and a clade of Late Cretaceous forms that include *Abelisaurus* ("pre mid-Campanian"; Heredia and Salgado, 1999) and the carnotaurines *Rajasaurus* (Maastrichtian), *Majungatholus* (Maastrichtian; Rogers et al., 2000), and *Carnotaurus* (Campanian-Maastrichtian; Pascual et al., 2000).

Several cranial and postcranial synapomorphies support the hypothesis that *Rajasaurus narmadensis* is a derived abelisaurid closely related to *Majungatholus* and *Carnotaurus*. Synapomorphies of Ceratosauria preserved in *Rajasaurus* include the presence of a skull table with a prominent parietal crest, cervical vertebrae with two pleurocoels, iliac pubic peduncle oriented approximately 60° from the horizontal, peg-in-socket iliopubic and ilioischial contacts, and a crescentic, anteriorly invaginated medial fibular fossa. Synapomorphies of Abelisauridae include the presence of a thick parietal posteromedian process capping the nuchal wedge, which is tall and positioned posterior to occipital condyle. The presence of a thickened skull roof, fused frontal-parietal suture, and hypertrophied nuchal wedge and parietal alae further nest *Rajasaurus* within Abelisauridae. Synapomorphies of Carnotaurinae include the positioning of the posterior process of the nasal dorsal to the orbit and the presence of a frontal excrescence.

BASAL NEOTHEROPOD PHYLOGENETIC TAXONOMY

Recent efforts to stabilize the phylogenetic taxonomy of Theropoda have arranged and evaluated clade names in the context of a monophyletic Ceratosauria that included *Ceratosaurus* and *Coelophysis* (Sereno, 1998; Padian et al., 1999). However, the alternative hypothesis that *Ceratosaurus*-like forms share a more recent ancestry with Tetanurae than with *Coelophysis*-like forms (e.g., Carrano et al., 2002; Rauhut, 2003; Sereno et al., in review) has important taxonomic consequences, which we explore below in the context of presenting a revised taxonomy for basal neotheropods. Our revision focuses on applying taxon names to six clades that are currently ambiguously defined. Our proposed taxonomy aims to provide stability of constituency and Linnean rank agreement while preserving priority of definition and original intent where possible. The original definition and subsequent phylogenetic definitions for these and other basal theropod taxa are provided in Table 4.

Neotheropoda.— Unlike other names discussed here, Neotheropoda never received a definition when it was coined. It first appeared on a branching diagram of theropod dinosaurs at the node uniting theropods more derived than "podokesaurids" such as *Coelophysis* (Bakker, 1986: 459; Bakker et al., 1988: fig. 2). Herrerasaurids were not then considered to be theropod dinosaurs. Neotheropoda included "ceratosaurs" and a "Dinoaves" group composed of "allosaurs", ornithomimids, tyrannosaurs, dromaeosaurs, and birds. Although Bakker's (1986) branched diagram indicated the paraphyly of *Coelophysis*-like and *Ceratosaurus*-like animals, most other early studies of maintained the monophyly of these lineages. In these latter studies, Neotheropoda and Theropoda were synonymous (e.g., Gauthier, 1986). In the following years, newer and better materials of basal theropod dinosaurs indicated that *Herrerasaurus*-like dinosaurs were basal theropods (Sereno and Novas, 1992), and the term Neotheropoda was adopted to distinguish more derived theropods from these basal forms. These latter studies applied Neotheropoda at the node joining the *Coelophysis*-*Ceratosaurus* lineage with tetanurans (e.g., Sereno et al., 1994). Consequently, the taxonomic content of Neotheropoda shifted to include *Coelophysis*, *Ceratosaurus*, and Tetanurae.

However, disbanding of the *Coelophysis*-*Ceratosaurus* clade into successive outgroups to Tetanurae created two nodes where the name Neotheropoda can be applied. Sereno (1998) and Padian et al. (1999) provided node-based definitions that place the name Neotheropoda at these alternate nodes (Table 4). The Sereno (1998) reference taxa identify as Neotheropoda the more inclusive node, whereas those of Padian et al. (1999) identify the less inclusive node (Table 4). Although the Padian et al. (1999) definition matches the intent and taxonomic content of Bakker (1986), we propose to associate Neotheropoda with the more inclusive node, which preserves the taxonomic content that has become associated with the name, recognizes priority of phylogenetic definition, and attaches a useful name to a node diagnosed by numerous characters. Carrano et al. (2002) placed Neotheropoda at this node. We thereby maintain the Sereno (1998) definition of Neotheropoda as *Coelophysis*, Neornithes, and all descendants of their most recent common ancestor. As discussed below, we recommend leaving the more exclusive node unnamed.

Tetanurae.— Gauthier's (1986: 23) original phylogenetic definition of Tetanurae specified "birds and all other theropods that are closer to birds than they are to Ceratosauria". Subsequent phylogenetic definitions by Sereno (1998) and Padian et al. (1999) appear to specify different constituencies for Tetanurae. Padian et al. (1999) defined Tetanurae as all neotheropods more closely related to Neornithes than to *Ceratosaurus*, which matches that of Gauthier (1986). However, that of Sereno (1998) uses *Torvosaurus* as a second reference taxon, which specifies Tetanurae as a more exclusive group than that of Gauthier (1986) and Padian et al. (1999). This discrepancy resulted from a textual error that was not repeated in the Sereno (1998) figures, which place Tetanurae at the node consistent with other authors. Here we adopt Padian et al.'s (1999) definition of Tetanurae.

Ceratosauria.— Although Gauthier (1986) provided a definition of Tetanurae, he did not define Ceratosauria, which he included in his analysis as a terminal taxon consisting of *Ceratosaurus*, *Syntarsus*, *Coelophysis*, *Segisaurus*, *Sarcosaurus*, and *Dilophosaurus*. Gauthier (1986: 35) regarded Ceratosauria as "a modified version of Marsh's Ceratosauria…the sister-group of a new taxon, Tetanurae". Later, Rowe (1989: 132) presented what may be interpreted as a stem-based definition of Ceratosauria, listing only one reference taxon: "Tetanurae includes those theropods more closely related to birds (and includes birds), whereas Ceratosauria includes taxa more closely related to *Ceratosaurus nasicornis*." Despite their previous stem-based concepts of the group, Rowe and Gauthier (1990: 153) later provided an explicitly node-based definition for Ceratosauria as "the group including *Ceratosaurus nasicornis*, *Dilophosaurus wetherilli*, *Liliensternus liliensterni*, *Coelophysis bauri*, *Syntarsus rhodesiensis*, *Syntarsus kayentakatae*, *Segisaurus halli*, *Sarcosaurus woodi*, and all other taxa stemming from their most recent common ancestor." Both Sereno (1998) and Padian et al. (1999) have provided stem-based definitions of Ceratosauria that reflect its original conception as the sister stem-lineage to Tetanurae. However, because these authors used different reference taxa to specify this lineage, their definitions specify distinct constituencies in the context of the alternate phylogeny accepted here (Fig. 16; Table 4). Whereas the Sereno (1998) definition of Ceratosauria includes *Dilophosaurus* and coelophysids (thereby overlapping with Coelophysoidea), that of Padian et al. (1999) includes *Ceratosaurus* and abelisaurs. To preserve the original phylogenetic meaning of the term, we propose adoption of the Padian et al. (1999) definition of Ceratosauria as the stem-grouping of all neotheropods more closely related to *Ceratosaurus* than to Neornithes, which includes *Rajasaurus* and other abelisauroids.

Ceratosauria + Tetanurae.— As discussed above, we have chosen not to apply any of the available names to this node, which is comparatively weakly supported in the analysis of Sereno et al. (in review). The phylogenetic definitions proposed by Sereno (1998) and Padian et al. (1999) specify two redundant stem-based names and third, node-based name that could be applied here. The node-based Neotheropoda proposed by Padian et al. (1999) was not applied to this node because it was found to be more appropriately placed at a more inclusive node as defined by Sereno (1998). The two redundant stem-based names have the same phylogenetic definitions – all taxa more closely related to *Carnotaurus* than to *Coelophysis*, which Sereno (1998) and Padian et al. (1999) referred to as Ceratosauroidea and "Neoceratosauria", respectively. Ceratosauroidea, attributed to Marsh (1884a) by the Principle of Coordination (ICZN, Article 36) was first applied

TABLE 4 — Original definitions and subsequent phylogenetic definitions for neotheropod clades discussed in text, listed chronologically. Definitions are followed by a letter (in parentheses) indicating the definition type. Traditional definitions are followed by included taxa, phylogenetic definitions are followed by reference taxon. Node-based definitions specify a clade by the most recent common ancestor of the reference taxon and all its descendents. Stem-based definitions specify a clade as all taxa more closely related to the first reference taxon than to the second. Abbreviations: *N*, node-based definition; *S*, stem-based definition; *T*, traditional definition. Asterisk (*) indicates definition in which only one reference taxon was listed.

Taxon	Original definition – included taxa	Phylogenetic definition – reference taxa
Ceratosauria	Marsh 1884b (T) – monotypic	*Rowe 1989 (S) – Tetanurae Rowe & Gauthier 1990 (N) – *Ceratosaurus*, *Dilophosaurus*, *Syntarsus*, *Liliensternus*,
Coelophysis,		
		Syntarsus, *Segisaurus*, *Sarcosaurus* *Rowe et al. 1997 (S) – *Ceratosaurus* Sereno 1998 (S) – *Coelophysis*, Neornithes Padian et al. 1999 (S) – *Ceratosaurus*, Neornithes
Noasauridae	Bonaparte & Powell 1980 (T) – monotypic	This analysis (S) – *Noasaurus*, *Carnotaurus*
Abelisauridae	Bonaparte & Novas 1985 (T) – monotypic	Novas 1997 (N) – *Abelisaurus*, *Carnotaurus*, *Xenotarsosaurus*, *Indosaurus*, *Indosuchus*, *Majungasaurus* Rowe et al. 1997 (S) – *Carnotaurus*, *Elaphrosaurus* Sereno 1998 (N) – *Abelisaurus*, *Carnotaurus* Padian et al. 1999 (N) – *Abelisaurus*, *Carnotaurus*
Neotheropoda	Bakker 1986 (T) – ‘ceratosaurs’, ‘Dinoaves’ (=‘allosaurs’, ornithomimids, tyrannosaurs, dromaeosaurs, birds)	Sereno 1998 (N) – *Coelophysis*, Neornithes Padian et al. 1999 (N) – *Ceratosaurus*, Neornithes
Tetanurae	Gauthier 1986 (S) – Ceratosauria, Aves	Sereno 1998 (S) – Neornithes, *Torvosaurus* Padian et al. 1999 (S) – Neornithes, *Ceratosaurus*
Ceratosauroidea	Bonaparte et al. 1990 (T) – Ceratosauridae, Abelisauridae, Noasauridae	Sereno 1998 (S) – *Carnotaurus*, *Coelophysis*
Abelisauroidea	Bonaparte 1991 (T) – Abelisauridae, Noasauridae	Rowe et al. 1997 (S) – Abelisauridae, *Ceratosaurus* Padian et al. 1999 (S) – *Carnotaurus*, *Ceratosaurus*
Abelisauria	Novas 1992 (T) – Abelisauridae, *Noasaurus*	Novas 1997 (N) – Abelisauridae, *Noasaurus*

TABLE 4 (continued).

Taxon	Original definition – included taxa	Phylogenetic definition – reference taxa
Neoceratosauria	Novas 1992 (T) – *Ceratosaurus*, *Noasaurus*, Abelisauridae	Padian et al. 1999 (S) – *Ceratosaurus*, *Coelophysis*
Coelophysoidea	Holtz 1994 (T) – *Coelophysis*, *Dilophosaurus*	Sereno 1998 (S) – *Coelophysis*, *Ceratosaurus* Padian et al. 1999 (S) – *Coelophysis*, *Ceratosaurus*
Carnotaurinae	Sereno 1998 (S) – *Carnotaurus*, *Abelisaurus*	Sereno 1998 (S) – *Carnotaurus*, *Abelisaurus*
Abelisaurinae	Sereno 1998 (S) – *Abelisaurus*, *Carnotaurus*	Sereno 1998 (S) – *Abelisaurus*, *Carnotaurus*

by Bonaparte (1991) to the group formed by *Ceratosaurus*, Abelisauridae, and Noasauridae. That same year, Novas (1991) named Neoceratosauria for the same constituency in an abstract, a concept he more fully developed the following year (Novas, 1992). Later phylogenetic definitions anchored Ceratosauroidea and Neoceratosauria with the same reference taxa, *Carnotaurus* and *Coelophysis*, which were hypothesized to bracket a monophyletic Ceratosauria. Because coelophysoids and ceratosaurs are here considered successive sister taxa to Tetanurae, these definitions encompass a much more inclusive group of ceratosaurs and tetanurans. We regard Ceratosauroidea as an inappropriate name to apply to this node because its Linnean rank is equal to or below many of the groups it supposedly includes. Neoceratosauria is similarly inappropriate because its name implies “new Ceratosauria”, which suggests that it should refer to a subclade of Ceratosauria. However, if applied at this node, it would include Ceratosauria as a subgroup rather than the opposite. We suggest that these names be abandoned and no name applied to this node at present.

Abelisauroidea.— Bonaparte (1991) defined Abelisauroidea to include *Noasaurus* and Abelisauridae. The following year, Novas (1992) created the taxon “Abelisauria” to encompass the same taxa. Although neither presented phylogenetic definitions, these and subsequent studies indicate the utility of naming this group. Rowe et al. (1997) employed a stem-based definition for Abelisauroidea as all taxa more closely related to Abelisauridae than to *Ceratosaurus*. Padian et al. (1999) echoed this definition, specifying as a reference taxon *Carnotaurus* instead of Abelisauridae. These stem-based definitions specify all Ceratosauria but *Ceratosaurus*, which broadens the original taxonomic content of Abelisauroidea. We suggest that the name Abelisauroidea be tied to the clade specified by *Carnotaurus*, *Noasaurus*, their most recent common ancestor, and all descendants. This node-based definition of Abelisauroidea preserves the specified taxonomic content of the original definition of Bonaparte (1991), anchors a node-stem triplet (see below), and provides a useful name to describe the small and large-bodied ceratosaurs that were widespread on southern landmasses during the Cretaceous.

Abelisauridae.— Bonaparte and Novas (1985) coined this monotypic family to accommodate their new genus *Abelisaurus*. *Carnotaurus* was later included in the group (Bonaparte, 1985), which was first phylogenetically defined by Novas (1997) as the node-based group including *Abelisaurus*, *Carnotaurus*, *Xenotarsosaurus*, *Indosaurus*, *Indosuchus*, and *Majungasaurus*. The definitions of both Sereno (1998) and Padian et al. (1999) also defined Abelisauridae as a node-based group specified as all descendants of the most recent common ancestor of *Carnotaurus* and *Abelisaurus*. In contrast, Rowe et al. (1997) defined Abelisauridae as the stem-based group including all taxa more closely related to *Carnotaurus* than to *Elaphrosaurus*.

The configuration of the sister-clades Abelisauridae and Noasauridae within Abelisauroidea provides an opportunity to apply a node-stem triplet to stabilize the nomenclature within the group. We therefore agree with the Rowe et al. (1997) stem-based concept of Abelisauridae, but modify its definition to include all abelisauroids more closely related to *Carnotaurus* than to *Noasaurus*. A complement to this grouping is provided by the reflexive stem-based definition of Noasauridae as all abelisauroids more closely related to *Noasaurus* than to *Carnotaurus*.

Summary.— Phylogenetic definitions for Neotheropoda and some of its subclades are provided below. Node-based definitions appear in boldface type, whereas stem-based definitions appear in regular type. The original author is referenced first, and the author of the phylogenetic definition adopted here is listed second. These phylogenetic definitions anchor traditional taxon names to stable nodes, preserving priority and reflecting traditional usage where possible. We propose a new node-stem triplet within Abelisauroidea:

Neotheropoda (Bakker, 1986; Sereno, 1998) – the least inclusive clade containing *Coelophysis bauri* and Neornithes.
Tetanurae (Gauthier, 1986; Padian et al., 1999) – the most inclusive clade including Neornithes but not *Ceratosaurus nasicornis*.
Ceratosauria (Marsh, 1884b; Padian et al., 1999) – the most inclusive clade containing *Ceratosaurus nasicornis* but not Neornithes.
Abelisauroidea (Bonaparte, 1991; this paper) – the least inclusive clade containing *Carnotaurus sastrei* and *Noasaurus leali*.
Abelisauridae (Bonaparte and Novas, 1985; this paper) – the most inclusive clade containing *Carnotaurus sastrei* but not *Noasaurus leali*.
Noasauridae (Bonaparte and Powell 1980; this paper) – the most inclusive clade containing *Noasaurus leali* but not *Carnotaurus sastrei*.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Rajasaurus narmadensis is the first Indian theropod preserving associated cranial and postcranial remains. As such, *Rajasaurus* has the potential to resolve associations among previously described isolated remains (Huene and Matley, 1933) and perhaps to offer insight into theropod diversity in the Late Cretaceous of India. Our preliminary results suggest that the eleven named species from the Lameta Formation of India actually represent at least three large-bodied theropods (*Rajasaurus*, *Indosuchus*, *Indosaurus*) and a fourth, small-bodied theropod (*Laevisuchus*), pending a full description of the unnamed form described by Chatterjee and Rudra (1996) and re-study of the GSI collection (Sereno and Wilson, in preparation). This result agrees with those reached by Novas and Bandyopadhyay (1999). The phylogenetic affinities of these four Indian theropods have important implications for the paleobiogeographic history of Indo-Pakistan. Based on the presence of abelisauroids and titanosaurian sauropods, the biota of the infratrappean sediments of the Lameta Formation traditionally have been interpreted as sharing closest affinities to taxa from other Gondwanan landmasses, though to no one landmass in particular (e.g., Bonaparte, 1999; Chatterjee and Scotese, 1999).

The results of our analysis and that of Sereno et al. (in review) strongly support the hypothesis that the Indian form *Rajasaurus* shares a closer ancestry with *Majungatholus* and *Carnotaurus* than it does with African forms (Fig. 16). As such, carnotaurines are restricted to India, Madagascar, and South America, and their outgroups are present on Africa. The area cladogram implied by these phylogenetic relationships offers apparent support for the hypothesis that Africa broke away from other Gondwanan landmasses before land connections were severed between India, Madagascar, and South America. However, uneven temporal sampling among these four landmasses strongly cautions against this interpretation. India, Madagascar, and South America are the only three southern landmasses with adequately known Maastrichtian faunas, and these share several tetrapod sister-taxa (e.g., Sampson et al., 1998; Krause et al., 1999). Latest Cretaceous horizons are poorly known in Africa, though some bones have been described (Rauhut and Werner, 1997). Conversely, among these four landmasses only Africa and South America preserve well characterized Early Cretaceous vertebrate faunas, and these share many archosaurian sister-taxa (e.g., Buffetaut and Taquet, 1977, 1979; Sereno et al., 1996, 2001). Pre-Maastrichtian Cretaceous vertebrates are almost unknown in Madagascar and scarcely known in India (Khosla et al., in review). Thus the temporal sampling pattern is presently inadequate to resolve the paleobiogeographic relationships among these landmasses. Further evaluation of this pattern will require sampling of pre-Maastrichtian horizons in India and Madagascar and of latest Cretaceous horizons on Africa.

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APPENDIX

Character list.— Codings for the 169 characters (66 cranial, 5 dental, 36 axial, 62 appendicular) used in the analysis of Sereno et al. (in review) are listed below. There are 6 multistate characters, 5 of which were ordered (47, 78, 83, 84, 91). The first cladistic use of each character appears in parentheses after the character. Characters with no such citation are new to the analysis of Sereno et al. (in review).

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1. Skull length: less (0), or more (1), than 3 times posterior skull height. (Sereno, 1999)
2. Skull, general external texture: smooth (0); sculptured (1). (Sampson et al., 1998)
3. Skull roof (frontal, nasal, lacrimal, postorbital), thickness: platelike (0); considerably thickened (1). (Novas, 1997)
4. Premaxilla, shape ventral to external naris: longer than deep (0); deeper than long (1). (Holtz, 1994)
5. Premaxilla, medial premaxillary foramen: absent (0); present (1).
6. Premaxilla posterolateral process, length: 2-3 times (0), or subequal to (1), transverse width at midlength. (modified from Carrano et al., 2002)
7. Premaxilla posterolateral process, form of articulation with maxilla: overlapping maxillary edge or anteromedial process (0); inserting into narrow slot between maxillary edge and anteromedial process (1). (modified from Carrano et al., 2002)
8. Premaxilla, palatal process: present (0); absent (1).
9. Premaxilla-maxilla arched diastema: absent (0); present (1). (Rowe, 1989)
10. Premaxilla-maxilla alveolar suture (portion of contact below premaxillary posterolateral process): present (0); absent (1). (Sereno, 1999)
11. Premaxilla-maxilla suture, form of upper portion (immediately ventral to the premaxillary posterolateral process): butt joint (0); separated by pneumatic spaces (1).
12. Premaxilla-nasal suture, form: V-shaped (0); W-shaped (1).
13. Maxilla, promaxillary fenestra and antrum: absent (0); present (1).
14. Maxilla, position of principal row of labial neurovascular foramina: displaced dorsal to (0), or immediately above (1), the alveolar margin.
15. Maxilla, position of articular facet for distal end of anteroventral process of nasal: anterior or slightly anterolateral (0); lateral (1).
16. Maxilla, form of articular surface for nasal anteroventral process, and form of nasal anteroventral process: shallow facet, tapered anteroventral process (0); trough with terminal pit, blunt-tipped anteroventral process (1).
17. Maxilla, contact with ventral process of lacrimal: present (0); absent (1). (modified from Coria and Salgado, 2000)
18. Maxilla, form of articular surface for jugal posteroventral to antorbital fossa: partially (0), or entirely (1), laterally facing.
19. Maxilla, articular surface for jugal, width: 15% or less (0), or 25% or more (1), of the length of the suture. (modified from Sampson et al., 1998)
20. Lacrimal canal, position of anterior (internal) foramen: at midlength (0), or at proximal base (1), of ventral process.
21. Lacrimal canal, position of posterior (external) foramen: at midlength (0), or at proximal base (1), of ventral process.
22. Lacrimal antorbital pneumatic recess (into central body of lacrimal): absent (0); present (1). (Novas, 1992)
23. Lacrimal antorbital pneumatic recess, orientation: laterally partially exposed (0); laterally covered (by rim of fossa) (1).
24. Lacrimal-postorbital contact: absent (0); present (1). (Novas, 1992)
25. Lacrimal brow, form: horizontal shelf (0); ventrolaterally beveled surface (1).
26. Lacrimal-jugal articulation, form: jugal overlaps lacrimal (0); jugal overlaps lacrimal and inserts into a slot in lacrimal near orbital margin (1). (modified from Sereno et al., 1994)
27. Lacrimal ventral process, shape of distal end: flange-shaped, broadening distally (0); subtriangular, tapering distally (1). (modified from Sereno, 1999)
28. Nasal, form of narial margin (lateral view): asymmetrical U-shape (0); symmetrical C-shape (1).

29. Nasal-nasal suture, form: open (0); fused anteriorly (1). (Forster, 1999; Sereno, 1999)
30. Nasal posterolateral process: absent (0); present (1). (Sereno, 1999)
31. Nasal posterior process, position of distal end: offset lateral (0), or adjacent (1), to the midline.
32. Nasal posterior process, anteroposterior position of distal end: anterior (0), or dorsal (1), to the orbit.
33. Jugal, antorbital pneumatic recess (anterior ramus): present (0); absent (1).
34. Antorbital fossa, size (anteroposterior diameter): greater than anteroposterior diameter (0), or any diameter (1), of other skull openings. (modified from Rowe, 1989)
35. Antorbital fossa, position of anterior end: posterior (0), or ventral (1), to posterior end of external naris. (Sereno, 1999)
36. Antorbital fossa on ventral ramus of maxilla: present (0); absent (1). (modified from Lamanna et al., 2002)
37. Antorbital fossa, form of ventral margin on maxilla: rounded edge (0); raised, rounded rim (1). (modified from Rowe, 1989)
38. Antorbital fossa, external rim on anterior process of lacrimal: present (0); absent (1).
39. Antorbital fossa on ventral ramus of lacrimal: present (0); absent (1).
40. Postorbital orbital process, shape and dorsoventral position: rounded, posterodorsal orbital margin (0); triangular flange, posterior orbital margin (1).
41. Postorbital orbital process, continuity: continuous with (0), or inset from (1), remainder of ventral ramus. (modified from Sampson et al., 1998)
42. Postorbital posterior process, shape: elongate (0), or equilateral (1), triangle.
43. Squamosal anterior process, form of postorbital articulation: tongue-and-groove (0); squamous (1).
44. Squamosal anterior process, orientation (lateral view): anterior (0); anterodorsal (1). (Sereno, 1999)
45. Supratemporal fossa, postorbital participation: present (0); absent (1). (Sereno, 1999)
46. Frontal-parietal suture, form: open (0); fused (1). (Forster, 1999; Sereno, 1999)
47. Frontal-parietal skull table, shape (dorsal view): hourglass (0); subtriangular (1); frontal triangle with parietal sagittal crest (2) (ordered).
48. Frontal horn(s): absent (0); present (1). (modified from Novas, 1997)
49. Parietal posteromedian process (capping nuchal wedge): absent or rudimentary (0); present and thickened (1).
50. Parietal alae, orientation: posterolateral (0); lateral (1).
51. Quadrate lateral flange, maximum width: approximately 50 % of (0), or subequal to (1), transverse width of distal condyles. (modified from Forster, 1999)
52. Quadrate foramen, position: mid height (opening anteriorly) (0), or closer to quadrate head (opening posterodorsally) (1). (modified from Holtz, 2000)
53. Quadrate distal condyles, flattened or slightly concave anterior facet: absent (0); present (1).
54. Palatine anterior process, shape: tapered distally (0); expanded distally (1). (Sereno, 1999)
55. Supraoccipital nuchal wedge, position: anterior (0), or posterior (1), to occipital condyle.
56. Supraoccipital nuchal wedge, length from foramen magnum to summit: subequal to (0), or more than twice (1), vertical diameter of the occipital condyle. (modified from Forster, 1999)
57. Supraoccipital nuchal wedge and parietal alae, position of dorsal extremity: slightly (0), or considerably (1), above frontoparietal skull table. (modified from Sampson et al., 1998)
58. Exoccipital-opisthotic, participation in basal tubera: absent (0); present (1). (Sereno, 1999)
59. Laterosphenoid head, location of articular socket: split between the frontal and postorbital (0); postorbital only (1). (Sereno, 1999)
60. Basisphenoid fontanelle: absent (0); present (1). (Forster, 1999; Sereno, 1999)
61. External mandibular fenestra, position of anterior end: posterior (0), or ventral (1), to last dentary tooth. (Sereno, 1999)
62. Dentary anterior end, shape: rounded (0); expanded dorsoventrally (1). (Forster, 1999; Sereno, 1999)
63. Dentary-surangular articulation, form: narrow V-shaped notch (0); broad U-shaped socket (1). (modified from Carrano et al., 2002)
64. Dentary, medial articular prong for surangular (separate from dorsal prong that is exposed laterally): absent (0); present (1).
65. Dentary posteroventral process, length: long (0); short (1), extending only as far posteriorly as the dentary posterodorsal process. (Sereno, 1999)
66. Prearticular-angular foramen: absent (0); present (1). (Sereno, 1999)

67. Premaxillary tooth row, position of posterior end: ventral (0), or anterior (1), to the external naris. (Sereno, 1999)
68. Maxillary tooth row, position of posterior end: ventral (0), or anterior (1), to the ventral ramus of the lacrimal. (modified from Gauthier, 1986))
69. Crown height (largest maxillary crowns): 20-30% (0), or 10-15% (1), of height of snout at midlength. (modified from Martinez et al., 1993)
70. Tooth rows, transverse curvature: minor (0); marked (1). (Sereno, 1999)
71. Dentary tooth 3, size: subequal (0), or enlarged (1), relative to dentary tooth 2. (Sereno, 1999)
72. Axial intercentrum length: 25-35% (0), or 40-70% (1), axial centrum length. (Sereno, 1999)
73. Axial anterior pleurocoel: absent (0); present (1). (Rowe, 1989)
74. Axial neural canal, vertical diameter: more (0), or less (1), than 30% vertical diameter of centrum. (Sereno, 1999)
75. Axial spinopostzygapophyseal lamina, form: straight or gently concave (0); deeply notched (1). (modified from Gauthier, 1986)
76. Axial prezygapophyses, form: raised facet (0); anteriorly-projecting shelf (1). (modified from Sereno, 1999)
77. Axial transverse process, size: rounded prominence (0); cylindrical process (1). (modified from Sereno, 1999)
78. Mid cervical (C3-C6) centrum length: less than 3 (0), 3 (1), or more than 4 (2), times centrum height (ordered). (Sereno, 1999)
79. Postatlantal cervical centra, form of articular surfaces: amphicoelous (0); marked opisthocoely (1). (Sereno, 1999)
80. Postaxial cervical centra, pleurocoel (anterior): absent (0); present (1). (Rowe, 1989)
81. Postaxial presacral vertebrae, posterior pleurocoel: absent (0); present (1). (Sereno et al., 1994)
82. Postaxial presacral vertebrae, posterior pleurocoel, form: open fossa (0); partially sharp-rimmed and invaginated (1).
83. Cervical epipophyseal-prezygapophyseal ridge/lamina, form and distribution: absent (0); rounded ridge in mid cervicals C4-C6 (1); prominent crest or lamina in all postaxial cervicals (2) (ordered). (modified from Coria and Salgado, 2000)
84. Cervical epipophyses, form: ridgelike or subconical if extended (0); mid cervical epipophyses anteroposteriorly extended with anterior corner (1); all anteroposteriorly extended (2) (ordered). (modified from Bonaparte et al., 1990)
85. Cervical epipophyses, height (dorsoventral distance from edge of postzygapophyseal facet): less (0), or more (1), than 50% of height of the posterior centrum face. (modified from Novas, 1997)
86. Postatlantal cervical vertebrae, pneumatic fossa on neural arch ventral to postzygapophysis: absent (0); present (1).
87. Mid cervical (C4-6) neural spines, orientation: vertical (0); posterodorsally inclined (1).
88. Dorsal centrum length: subequal to (0), or more than 2.5 times (1), centrum height. (Sereno, 1999)
89. Mid dorsal parapophyses, form: short process (0); process with cylindrical shaft (1).
90. Posterior dorsal parapophyses, position: anteroventral to diapophysis and ventral to prezygodiapophyseal lamina (0); anterior to diapophysis and joined with prezygodiapophyseal lamina (1).
91. Sacral number: 3 (primordial sacral pair, 1 dorsosacral) (0); 5 (primordial sacral pair, 1 dorsosacral, 2 caudosacrals) (1); 6 (primordial sacral pair, 2 dorsosacrals, 2 caudosacrals) (2) (ordered). (modified from Bonaparte, 1991)
92. Sacrum shape, dorsal view: subrectangular (0); subtriangular (1). (Sereno, 1999)
93. Mid sacral centra, ventral margin: horizontal (0); dorsally arched (1). (Sereno, 1999)
94. Mid sacral centra, transverse dimensions: similar to adjacent sacrals (0); strongly constricted (1). (Sereno, 1999)
95. Sacral transverse processes, relations: separate (0); fused (1). (Rowe, 1989)
96. Sacral neural spines, relations: separate (0); fused (1). (Rowe, 1989)
97. Sacral neural arches, development of paramedian fossae: poorly developed (0); divided by vertical septa (1).
98. Anterior caudal transverse processes, form: subrectangular or distally tapering (0); distally expanding (1). (Coria and Salgado, 2000)
99. Anterior caudal neural spines, anterior flange for interspinous articulation: absent (0); present (1). (Sereno, 1999)
100. Distal caudal centrum length: 3 to 4 (0), or approximately 7 (1), times centrum height. (Sereno, 1999)
101. Distal caudal prezygapophyses, maximum length: at least 30% or less (0), or at least 40% (1), overlap of preceding centrum. (Sereno, 1999)

102. Cervical ribs, pneumatic recesses near rib articular processes: absent (0); present (1). (Sampson et al., 1998)
103. Mid cervical (C4-8) ribs, lateral process for articulation with successive rib spine: absent (0); present (1).
104. Mid cervical (C4-8) ribs, form of lateral process for articulation with successive rib spine: ridge (0); flange (1).
105. Caudosacral ribs, attachment position: ventral margin (0), or angled toward posterodorsal corner (1), of postacetabular process. (Sereno, 1999)
106. Chevron base, paired anterior and posterior processes: absent (0); present (1). (Sereno et al., 1994)
107. Anterior chevrons, midshaft shape: transversely flattened (0); rod-shaped (1).
108. Scapular glenoid, shape: approximately twice as long as (0), or subequal to (1), its transverse width.
109. Coracoid posterior process, shape: hook-shaped (0); rounded corner (1). (Sereno et al., 1996)
110. Humeral head, shape and size: subcylindrical, approximately 50% of maximum width of proximal end (0); subspherical, approximately 70% or more of maximum width of the proximal end (1). (modified from Coria et al., 2000)
111. Humeral lateral tuberosity, position: proximal (0), or distal (1), to medial tuberosity.
112. Humeral deltopectoral crest, size (measured from the anterior margin of midshaft): subequal to (0), or less than (1), anteroposterior shaft diameter at midshaft. (modified from Carrano et al., 2002)
113. Humeral shaft axis, form: sigmoid (0); straight (1). (Holtz, 1994)
114. Humeral distal condyles, form: convex, rounded anteriorly (0); nearly flat (1). (Carrano et al., 2002)
115. Distal carpal 1, distal articulation: metacarpal I (0); metacarpals I and II (1). (Gauthier, 1986)
116. Manual digits and metacarpals, longest: digit III, metacarpal III (0); digit II, metacarpal II (1). (Sereno, 1999)
117. Metacarpal I length: longer (0), or shorter (1), than phalanx 1 or ungual of digit I. (Sereno, 1999)
118. Metacarpal III, mid shaft transverse diameter, and III-ungual length: subequal to digit II (0); diameter 55% or less metacarpal II, ungual length less than 70% II-ungual (1). (modified from Sereno et al., 1994)
119. Manual digit V: present (0); absent (1). (Gauthier, 1986)
120. Pelvic girdle sutures, form: open (0); fused (1). (Rowe, 1989)
121. Iliac length: shorter (0), or longer (1), than femoral length. (modified from Novas, 1991)
122. Iliac supracetabular crest, form: shelf-like with straight edge in lateral view (0); pendant with convex margin in lateral view (1). (Gauthier, 1986)
123. Iliac preacetabular process, position of anteroventral corner: anteroventral extremity of process (0); proximal to the anterior margin of the process (1).
124. Iliac postacetabular process, form of posterior margin: convex (0); concave (1). (Sereno, 1999)
125. Iliac postacetabular process, form of lateral attachment scar: subtle (0); pronounced scar (1). (Sereno, 1999)
126. Iliac pubic peduncle, orientation of distal articular end: approximately 45° (0), or 60° (1), from the horizontal. (modified from Sereno, 1999)
127. Iliac pubic peduncle, anterodorsal margin: present (0); rudimentary or absent (1).
128. Iliopubic contact, form: butt joint (0); peg-in-socket (1). (Sampson et al., 2001)
129. Ilioischial contact, form: butt joint (0); peg-in-socket (1).
130. Ilioischial articulation, width of distal end: subequal to (0), or smaller than (1), iliac-pubic articulation (1). (Sereno et al., 1994)
131. Pubic fenestra: absent (0); present (1). (Rowe, 1989)
132. Pubic shaft axis, form: straight (0); bowed anteriorly (1). (Rowe, 1989)
133. Pubic shaft, distal half, transverse width of blade-shaped medial portion: subequal to (0), or twice the width of (1), rod-shaped lateral portion. (Sereno, 1999)
134. Pubic foot: present (0); absent (1). (Holtz, 1994)
135. Pubic foot, symphyseal area: absent or restricted to distal margin (0); broad median contact (1). (Sereno, 1999)
136. Pubic foot, anteroposterior length: longer (0), or shorter (1), than ischial foot. (Sereno, 1999)
137. Ischial antitrochanter, form of nonarticular acetabular margin: concave (0); concave so as to undercut the antitrochanter (1).
138. Ischial antitrochanter, size: less (0), or subequal to or greater (1), than adjacent articular surface for ilium. (Sereno, 1999)
139. Ischial obturator notch (or foramen): absent (0); present (1). (Sereno et al., 1994)
140. Ischial shaft, cross-sectional shape (paired): broad contact, rod-like (0); separated dorsally, V-shaped. (Sereno, 1999)
141. Ischial foot: absent (0); present (1). (Bonaparte et al., 1990)
142. Femoral anterior trochanter, form: sigmoid (0); blade-shaped (1). (Sereno et al., 1994)

143. Femoral anterior trochanter, dimorphism: absent (0); present (1). (Rowe, 1989)
144. Tibial cnemial crest, width (lateral view): tapers distally, or less than 50% of proximal end (0); expands distally, or more than 50% of proximal end (1), distally. (cnemial crest measured from anterior margin of shaft)
145. Tibial cnemial crest, lateral fossa: absent (0); present (1).
146. Tibial proximal end, tibiofibular crest: absent (0); present (1). (Forster, 1999; Sereno, 1999)
147. Tibial midshaft proportions, transverse versus anteroposterior: subequal (0); transverse width 135-150% of anteroposterior width (1). (Sereno, 1999)
148. Tibiofibular shaft contact distal to tibiofibular crest: absent (0); present (1).
149. Tibial crest (distal to tibiofibular crest) with flattened articular edge for fibular shaft: absent (0); present (1). (Martinez et al., 1986)
150. Tibial distal end, lateral extension of posterolateral flange (= calcaneum, posterior articular facet for tibial posterolateral flange): partially (0), or nearly completely (1), backs the distal end of fibula and calcaneum. (modified from Sereno et al., 1994)
151. Fibular fossa: absent (0); present (1). (Rowe, 1989)
152. Fibular fossa, form: oval, opens medially (0); crescentic, invaginated anteriorly, opens posteromedially (1).
153. Fibular shaft ventral to tibiofibular crest, position relative to tibial shaft: lateral (0); anterior (1).
154. Fibular midshaft, anteroposterior width: 40% (0), or 10-25% (1), of anteroposterior width of the proximal end. (Sereno, 1999)
155. Astragalar ascending process, thickness: wedge-shaped, dorsal margin inserting into tibia (0); low plate, 3-4 times taller than thick anteroposteriorly at midpoint (1); tall plate, more than 5 times taller than thick at midpoint (2). (modified from Gauthier, 1986)
156. Astragalar posterolateral crest (ascending process to posterolateral corner): absent (0); present (1). (Sereno, 1999)
157. Astragalar posteromedial crest (dorsal aspect of posteromedial corner): absent (0); present (1). (Sereno, 1999)
158. Astragalar distal articular surface, orientation: ventrally directed (0); anteroventrally directed (1). (Sereno et al., 1994)
159. Calcaneal articular surface for distal end of fibula, size: approximately 40-60% (0), or 90% (1), of distal articular cup for fibula.
160. Distal tarsal 3 and metatarsals II and III, contact: open (0); fused (1). (modified from Gauthier, 1986)
161. Metatarsal I length: more (0), or less (1), than 50% metatarsal II length. (modified from Gauthier, 1986)
162. Metatarsal I, location on metatarsal II: medial side of proximal end (0); posteromedial side halfway down shaft (1). (Sereno, 1999)
163. Metatarsal II, width of proximal shaft: subequal to III (0); strongly transversely compressed (1). (Bonaparte, 1991)
164. Metatarsal III, shape and area of proximal articular surface: subrectangular, with minimum transverse width subequal to, or greater than, either metatarsals II or IV (0); hourglass-shaped, with minimum transverse width less than either metatarsals II or IV (1); subrectangular, with maximum transverse width less than either metatarsals II or IV (2); vestigial, with metatarsals II and IV contacting anteriorly (3). (modified from Sereno et al., 1994)
165. Metatarsal III, mid-shaft shape: subrectangular (0); wedge-shaped (anterior overlap on metatarsals II and IV). (modified from Sereno et al., 1994)
166. Metatarsal IV distal condyles and opposing base of proximal phalanx, proportions: broader than tall (0); taller than broad (1). (Sereno, 1999)
167. Metatarsal IV, width of distal condyles: subequal (0), or less than 50% width of distal condyles of metatarsal II (1).
168. Metatarsal V shaft axis, form: straight (0); curved or sigmoid (1). (Sereno, 1999)
169. Metatarsal V shaft width: robust (0); slender (1). (Sereno, 1999)

Character-taxon matrix. — The scorings for 169 characters in 21 ingroup taxa from the analysis of Sereno et al. (in review) are listed below. The two suprageneric ingroup taxa were scored on the basis of well known included genera (Spinosauroidea: *Suchomimus*, *Baryonyx*, *Torvosaurus*; Tetanurae: *Allosaurus*, *Sinraptor*). Character code abbreviations: *a*, 0 or 1; *b*, 1 or 2; *c*, 2 or 3.

	010	020	030	040	050	060
Eoraptor	0000000000	000000000?	00X0X00000	0000000000	0000000000	0000000000
Herrerasaurus	0000000000	000000000?	00X0X00000	0000000000	0000000000	0000000000
Dilophosaurus	1000100111	X11000000?	?0X0X00001	0001000000	0001000000	0001000111
Liliensternus	10??????1?	??00??????	??????????	??01?01???	???1??????	0001??????
Procompsognathus	??????????	??????????	??????????	??????????	??????????	??????????
Segisaurus	??????????	??????????	??????????	??????????	??????????	??????????
Syntarsus	1000100111	X100000000	00X0X00001	0001101000	0001100000	0001000111
Coelophysis	1000100111	X10000000?	00X0X00001	0001101000	0001100000	0001000111
Elaphrosaurus	??????????	??????????	??????????	??????????	??????????	??????????
Ceratosaurus	0001110000	0110000000	0100X00111	0011000000	0001001000	1101000111
Niger taxon 1	??????????	??????????	??????????	??????????	??????????	??????????
Genusaurus	??????????	??????????	??????????	??????????	??????????	??????????
Deltadromeus	??????????	??????????	??????????	??????????	??????????	??????????
Masiakasaurus	00????0?00	0?1?10??0?	??????????	?????00?0?	??????????	??????????
Noasaurus	00????0?00	0?0???????	??????????	?????00?0?	??01??????	1?0???????
Ilokelesia	?1????????	??????????	???1??????	?????????1	110???????	1?1???????
Niger taxon 2	0101111100	1111111111	1101001111	00?1010011	0???002011	?0??110?1?
Abelisaurus	011111?100	1?11???11?	???10?1?1?	01?1010?11	0111112011	????110???
Rajasaurus	0111111100	111111111?	??????????	1111010???	?????12111	????11011?
Majungatholus	0111111100	1111111111	1111101111	1110010111	1111112111	1111111111
Carnotaurus	0111111100	111111111?	1111101111	1110010111	1111112111	11111111?1
SPINOSAUROIDEA	0010110000	0110000000	0100X10001	0001000000	0001100000	0001000111
NEOTETANURAE	0010110000	0110000000	0100X10001	0001000000	0001100000	0001000111

	070	080	090	100	110	120
Eoraptor	0000000000	0000000000	0X00000000	0000000000	000X000000	0000000000
Herrerasaurus	0000000000	0000000000	0X00000000	0000000000	000X000000	0000000000
Dilophosaurus	0100011000	1001010011	1000010001	?000000010	000X110110	0000111010
Liliensternus	010?0???00	1??????111	100XX10001	?0000??0?0	0???1?0110	000011???0
Procompsognathus	??????????	???????211	100XX?010?	??????????	??????????	??????1?1?
Segisaurus	??????????	??????????	???????1??	??????????	??????????	?????????1
Syntarsus	01000?1000	1001010211	??0XX10101	1100110001	000X11??10	0000111011
Coelophysis	0100011000	1?01010211	100XX10101	1100110001	000X110?10	0000111011
Elaphrosaurus	??????????	???????211	1000010001	20110100?0	1???0??100	0111?????1
Ceratosaurus	0000010000	0111011011	1110010011	201101?010	110X011?10	0111?11011
Niger taxon 1	??????????	???????011	1121010011	????010???	?110??????	??????????
Genusaurus	??????????	??????????	??????????	??????????	????0?????	?????????1
Deltadromeus	??????????	??????????	??????????	?????????0	1????1?101	1111??????
Masiakasaurus	10??1???00	0??????011	11200100??	?011011?10	1????????1	111???????
Noasaurus	??11????0?	???????0??	??2b010???	??????????	?110??????	??????????
Ilokelesia	??????????	???????011	112211001?	??????????	?111?11???	??????????
Niger taxon 2	??????0011	??????????	??????????	??????????	??????????	??????????
Abelisaurus	??????0?11	??????????	??????????	??????????	??????????	??????????
Rajasaurus	10????0011	0??????0??	?1?????0??	??010?????	??????????	?????????0
Majungatholus	1011110011	0111011011	1122110011	201101111?	?11101??01	1111??????
Carnotaurus	1011110011	0111011011	1122110011	2011011110	?111011?01	1111???0?1
SPINOSAUROIDEA	0000010100	0111111011	0X00011000	1000000010	110X010100	0000111110
NEOTETANURAE	0000010100	0111111011	0X00011000	1000000010	110X010100	0000111110

Character-taxon matrix (continued).

	1	1	1	1	1
	3	4	5	6	6
	0	0	0	0	9
Eoraptor	0000000000	0001X00000	0000000000	0X00000000	000000000
Herrerasaurus	0000000000	0000000000	0000000000	0X00000000	000000000
Dilophosaurus	0101000001	0000110000	1a10010100	0X11011000	110001011
Liliensternus	0101010001	0000010000	11?0010100	0X11011000	??00010??
Procompsognathus	01???000??	1011XX????	?0?0???10?	??110??0?1	110???0??
Segisaurus	?1????????	1011XX1?00	00?0????0?	???1??????	110???0?1
Syntarsus	0101100??1	1101X11100	1a10010100	0X11011001	110001011
Coelophysis	0101100??1	1100111100	1a10010100	0X11011001	110001011
Elaphrosaurus	01?1000001	000???0010	11?0111111	1101110?0	??001????
Ceratosaurus	0111011111	0000100010	1101111111	1101111000	??00110??
Niger taxon 1	??????????	??????????	??????????	??????????	?????????
Genusaurus	111101???1	000???????	???111?11?	1101??????	?????????
Deltadromeus	??????????	?0001????0	?1?1011??1	11?11??000	??0011111
Masiakasaurus	???????1??	00001?????	??01111111	??0?1??0?0	??10111??
Noasaurus	??????????	??????????	??????????	?????????0	??1??????
Ilokelesia	??????????	??????????	??????????	??????????	?????????
Niger taxon 2	??????????	??????????	??????????	??????????	?????????
Abelisaurus	??????????	??????????	??????????	??????????	?????????
Rajasaurus	????011111	??????????	???11??111	1101?????0	??0?1?0??
Majungatholus	1111011111	??????????	???1111111	1101111000	??01110??
Carnotaurus	1111011??1	0000100010	11??111111	1101???0??	??0??????
SPINOSAUROIDEA	0000000001	0000100011	110?011101	1011211110	110211011
NEOTETANURAE	0000000001	0000100011	110?011101	1011211110	110c11011