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Abelisaurid pedal unguals from the Late Cretaceous of India

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Abstract. The ungual phalanges of theropod dinosaurs discovered in the Lameta Formation (Maastrichtian), central India, exhibit distinctive characters unknown in other theropods. Hence, their taxonomic identification remained obscure since their original description in 1933. Recent discoveries of abelisaurid theropods in Patagonia indicate that the phalanges from India belong to the foot of these dinosaurs. New information on the foot skeleton of this group of Cretaceous Gondwanan predators is included herein.

Key words. Theropoda. Abelisauridae. Unguals. Cretaceous. Gondwana.

Introduction

The Late Cretaceous (Maastrichtian) Lameta Formation of central India has yielded dissociated elements of a variety of predatory dinosaurs. The materials were described by Frederich von Huene (in Huene and Matley, 1933), who recognized nine theropod species from a fossil quarry at Bara Simla Hill (Madhya Pradesh, India). They are: *Indosuchus raptorius* Huene, *Indosaurus matleyi* Huene, *Compsosuchus solus* Huene, *Laevisuchus indicus* Huene, *Jubbulpuria tenuis* Huene, *Coeluroides largus* Huene, *Dryptosauroides grandis* Huene, *Ornithomimoides mobilis* Huene, and *Ornithomimoides* (?) *barasimlensis* Huene. Huene also described a considerable amount of theropod hindlimb bones (*e.g.*, femora, tibiae, metatarsals, and pedal phalanges) that he could not refer to any of these species. On the contrary, such bones were vaguely interpreted by him as corresponding to "allosaurid" or "coelurosaurid" theropods (Huene and Matley, 1933).

Phylogenetic relationships of the Indian theropods has been unknown since then, and virtually no progress has been attained about the systematic allocation of the abundant post-cranial remains (*e.g.*, Romer, 1956; Walker, 1964; Chatterjee, 1978; Molnar, 1990; Norman, 1990). Fortunately, the last 15 years has been highly prolific in discoveries of abelisaurid theropods in Upper Cretaceous beds from Patagonia (*e.g.*, *Abelisaurus*, *Carnotaurus*, *Xenotarsosaurus*; Bonaparte and Novas, 1985; Martínez *et al.*, 1986; Bonaparte *et al.*, 1990), India (*Indosuchus*; Chatterjee and Rudra, 1996), and Madagascar (*Majungatholus*; Sampson *et al.*, 1998). This considerable amount of information about abelisaurid anatomy has served as a valuable guide to resolve confusing taxonomic aspects of the Indian theropods.

Currently, *Indosuchus*, *Indosaurus*, and also *Laevisuchus*, are interpreted as members of Abelisauridae (Bonaparte and Novas, 1985; Molnar, 1990; Chatterjee and Rudra, 1996; Sampson *et al.*, 1998; Novas and Bandyopadhyay, 1999). Moreover, the controversial taxa "*Compsosuchus*", "*Dryptosauroides*", "*Ornithomimoides*", and "*Jubbulpuria*" are represented by vertebrae corresponding to different regions of the neck and tail that also exhibit abelisaurid features (Novas and Bandyopadhyay, 1999).

Now, abelisaurid material from the Upper Cretaceous rocks from NW Patagonia settles the long standing confusion about the theropod unguals from India, and establishes its abelisaurid affinity.

Abbreviations

AMNH, American Museum of Natural History, New York; GSI, Geological Survey of India, Calcutta; MCA, Museo "Carlos Ameghino", Cipolletti; SUNY, State University of New York, Stony Brook; YPM, Yale Peabody Museum, New Haven.

Morphology of abelisaurid pedal unguals from Patagonia and India

The new abelisaurid specimen (MCA 56) includes two pedal unguals (figure 1) apparently from digit

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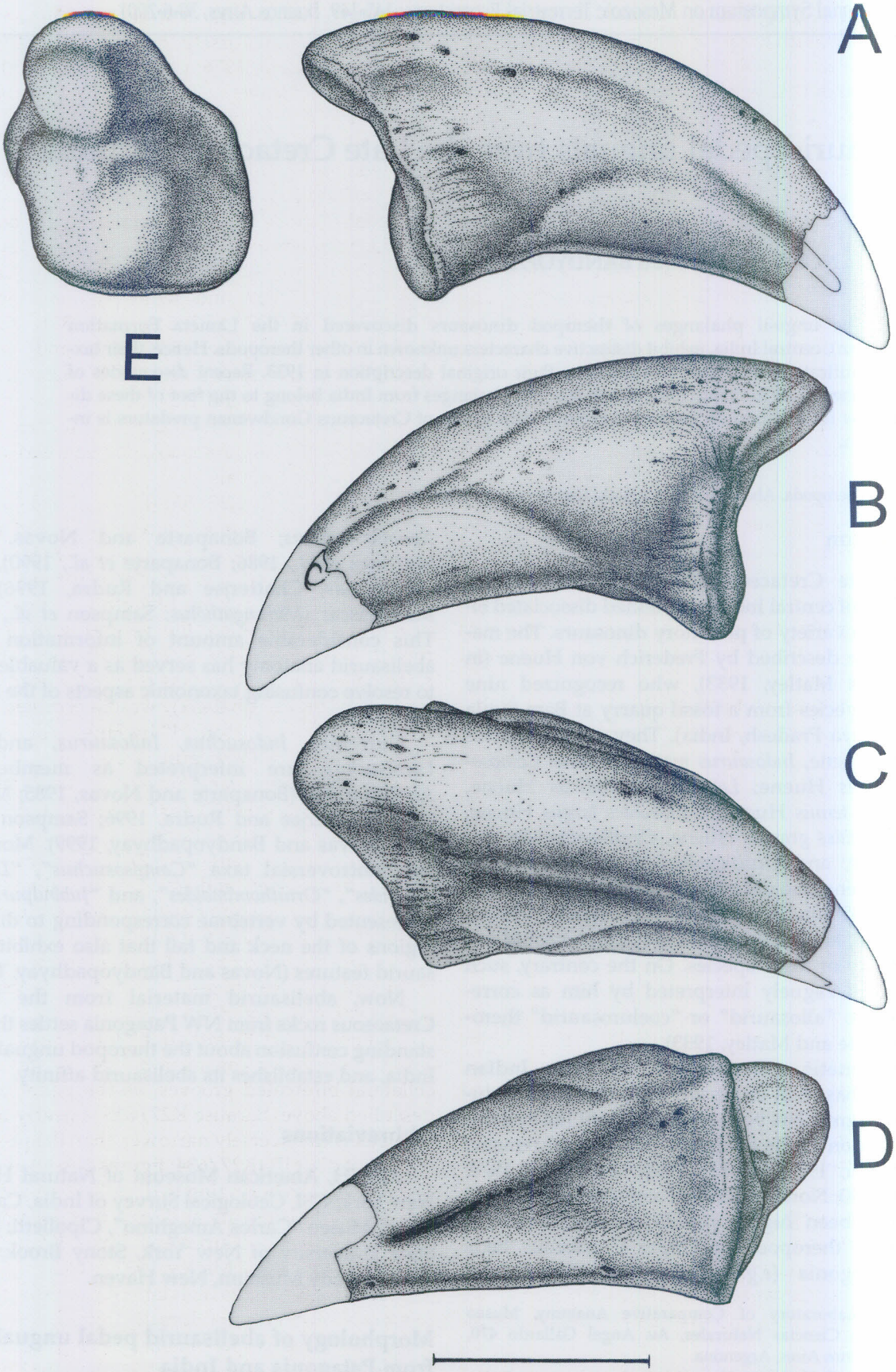

Figure 1. A-E, digit IV ungual, presumably of the left foot, of an indeterminate abelisaurid (MCA 56) from the Río Limay Formation, northwestern Patagonia, in **A,** medial, **B,** lateral, **C,** dorsal, **D,** ventral, and **E,** proximal views. Scale bar: 2 cm.

IV of the left and right feet. The unguals were found in association with other hindlimb elements and dermal skull bones that show a characteristic pattern of ornamentation (*e.g.*, anastomosed grooves delimiting a mosaic pattern of raised areas) found in other abelisaurids (*e.g.*, *Carnotaurus*, *Abelisaurus*, *Majungatholus*); distal caudal vertebrae were also collected, the morphology of which fits well with that of *Majungatholus* (specimen 93161-14 at SUNY) and *Indosuchus* (AMNH 1957, 1958).

The unguals, nearly 6.5 cm when complete, are blunt and asymmetrical. They are arched (presumably medially), with the lateral surface strongly convex and the internal surface almost flat. As a result of this asymmetry, the medial surface of the ungual is also exposed dorsally. Both lateral and medial surfaces have wide canals that show a distinct, proximally bifurcated, "Y"-shaped pattern. The bifurcation is at mid-length. The grooves are deeper on the lateral rather on the medial side of ungual. The "Y"-shaped groove of the lateral surface bounds a conspicuous, triangular bump. There is no proximoventral flexor tubercle. The ventral surface of the ungual, instead, is proximally flat, but has a narrow and deep groove centrally. The proximal articular contour is triangular, and the proximodorsal lip is prominent and tongue-shaped.

These unguals exhibit the following peculiar features distinguishing them from other theropods (*e.g.*, *Allosaurus*, *Sinraptor*, Tyrannosauridae, Ornithomimidae, Troodontidae, Dromaeosauridae, Alvarezsauridae):

1) **Grooves bifurcated proximally** (figure 1.B). Most tetanurines (*e.g.*, *Allosaurus* AMNH 680, 5750; *Sinraptor*; Currie and Zhao, 1993; *Alectrosaurus* AMNH 6554) have a simple groove along both lateral and medial surfaces. Although some coelurosaurian theropods have "Y"-shaped grooves (*e.g.*, *Patagonykus*; Novas, 1997; *Troodon* AMNH 2137), the bifurcation is more proximal than in abelisaurids. Moreover, current phylogenetic hypotheses (*e.g.*, Novas, 1992; Sampson *et al.*, 1998) depict abelisaurids as Cretaceous ceratosaurs, suggesting that bifurcated grooves on the pedal unguals were independently acquired in different theropod groups (*e.g.*, Abelisauridae, *Patagonykus*, *Troodon*).

2) **Presence of a rounded bump on the lateral side of pedal unguals** (figure 1.B). In abelisaurid unguals the upper and lower branches of the bifurcated lateral groove bound a triangular prominence, not found in other theropods. In coelurosaurs with "Y"-shaped grooves, this region is less prominent or almost flat.

3) **Ventral surface excavated or with a narrow and deep furrow** (figure 1.D). This character seems to be unique of abelisaurid theropods. In most theropods, the ventral surface of the ungual is smooth and transversely convex (*e.g.*, *Allosaurus*, *Sinraptor*; Madsen, 1976; Currie and Zhao, 1993) or flat (*e.g.*, *Deinonychus* YPM 5205). Interestingly, *Noasaurus*, the purported sister group of Abelisauridae (Novas, 1992, 1997) also has a ventrally excavated ungual, although it is located in a more proximal position (Bonaparte and Powell, 1980).

Pedal unguals of indeterminate theropods from the Lameta Formation (Huene and Matley, 1933) were sorted into two subsets: "allosaurid" manual (specimen K27/633) and pedal unguals (specimens K27/524, K27/537, K27/543, K27/551, K27/634, K27/635, K27/636, and K20/399), and "coelurosaurid" pedal unguals (*e.g.*, K27/625, K27/629, K27/630, K27/631, and K27/632). We were able to access only K27/634, K27/632, K27/633, and K27/524, which are amenable for comparison with the Patagonian unguals.

Ungual phalanx K27/634 (figures 2.A-D) is transversely wide and almost symmetrical, and may be from the central toe (digit III). As in abelisaurid unguals from Patagonia, it has deep furrows on both sides that bifurcate at mid-length and bounding a prominent bump. Also, the ventral surface is furrowed. Ungual phalanx K27/524 (figures 2.E-F; the same collection number was originally used as well for a non-ungual phalanx), was interpreted as belonging to a "coelurosaurid" by Huene, but may belong to pedal digit IV because it resembles the ungual of this digit of *Sinraptor* (Currie and Zhao, 1993).

Ungual phalanx K27/632 (Huene and Matley, 1933) has the same characters as in K27/634. However, because ungual K27/632 is more compressed transversely and asymmetrical than the other unguals described by Huene, it may correspond to digit I. It is the smallest of all the available unguals. Also, it has a strongly keeled dorsal margin, in agreement with the first ungual of other theropods (*e.g.*, *Sinraptor*; Currie and Zhao, 1993).

Phalanx K27/633, although notably compressed transversely, has a conspicuous ventral furrow and collateral bifurcated grooves, as the pedal unguals described above. Because K27/633 is nearly as large as, albeit is transversely narrower, than the presumed ungual of digit III (K27/634; figures 2.A-D), we interpret K27/633 as belonging to digit II. It is the deepest of the available unguals, and resembles the ungual of digit II of *Sinraptor* (Currie and Zhao, 1993). Ungual K27/635 (Huene and Matley, 1933, pl. XIX, fig. 10) resembles K27/633 in its high lateral profile and asymmetry, although it is not dorsally keeled.

Another ungual presumably belongs to digit IV. Phalanx K27/537 (Huene and Matley, 1933, pl. XIX, fig. 12) shows the same curvature in lateral view, and has a similar profile in cross-section. Ungual K27/629

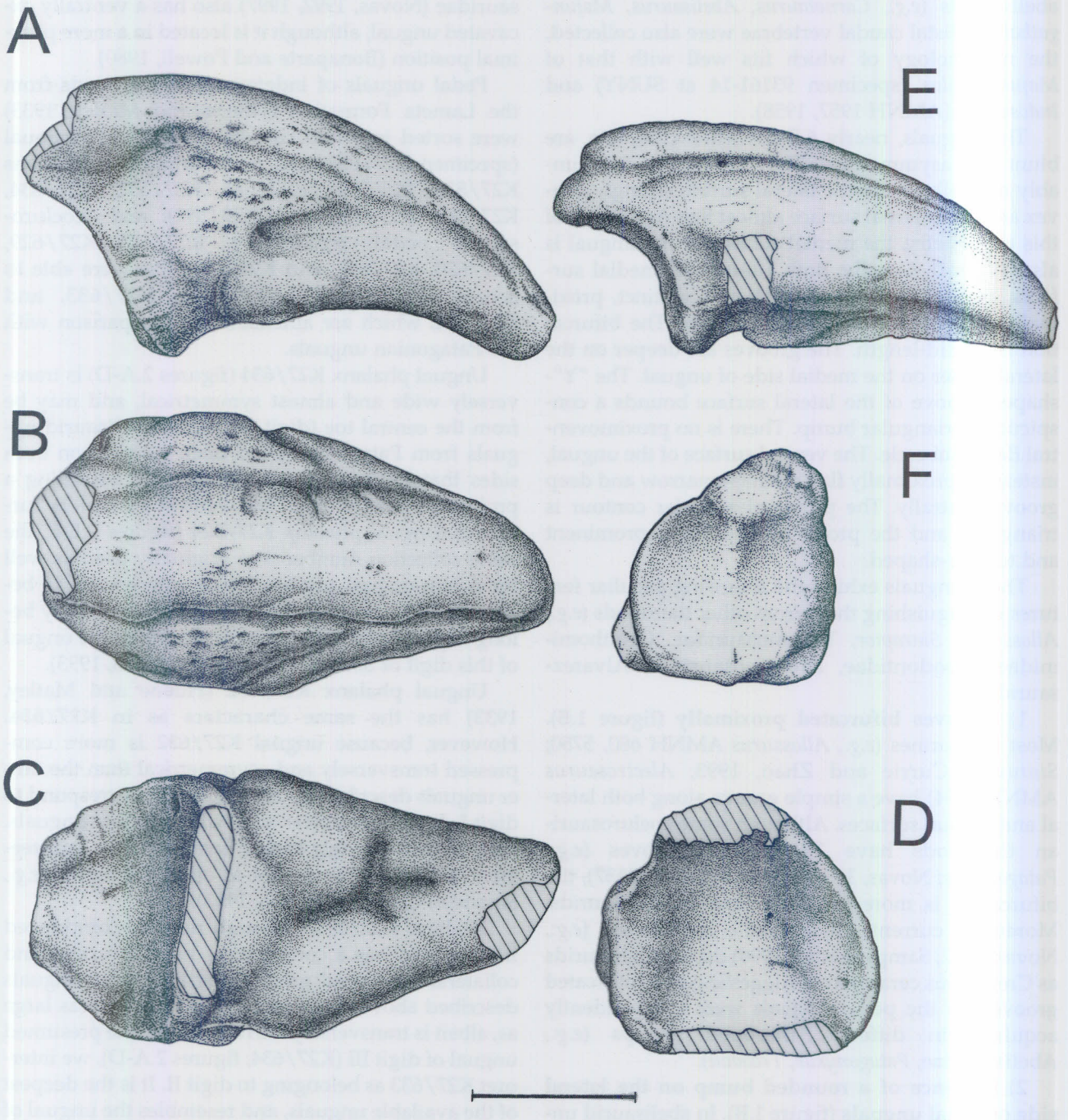

Figure 2. A-F, abelisaurid unguals from the Lameta Formation (Maastrichtian) of Central India. **A-D,** pedal ungual (K27/634) presumably corresponding to digit III, and **E-F,** pedal ungual (K27/524) presumably corresponding to digit IV. **A** and **E,** lateral, **B,** dorsal, **C,** ventral, and **F** and **D,** proximal views. Scale bar: 2 cm.

(Huene and Matley, 1933, pl. XXIV, fig. 20) may also belong to digit IV.

Conclusions

Peculiar theropod pedal unguals from the Lameta Formation are different from those of other theropods (*e.g.*, *Allosaurus*, *Sinraptor*, Tyrannosauridae, Ornithomimidae, Troodontidae, Dromaeosauridae, Alvarezsauridae) in the presence of proximally bifurcated grooves, a rounded bump on the lateral side of pedal unguals, and a narrow and deep furrow on the ventral surface. This set of derived features is shared with a new Patagonian abelisaurid (MCA 56), suggesting that the unguals originally described by Huene (in Huene and Matley, 1933) belong to Abelisauridae. This evidence is consistent with the remarkable abundance of abelisaurid remains documented in the same quarry at Bara Simla Hill (Chatterjee and Rudra, 1996; Novas and Bandyopadhyay, 1999).

Differences in absolute size, degree of axial asymmetry, transverse width, dorsoventral height, and depth of the ventral furrow that were originally noted for the Indian unguals (Huene and Matley, 1933), may represent different pedal digits of individuals of different size. At this moment, we are not able to determine if the unguals from Bara Simla Hill correspond to a single abelisaurid species.

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