THE APPENDICULAR SKELETON OF *MAJUNGASAURUS CRENATISSIMUS* (THEROPODA: ABELISAURIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—The appendicular skeleton of the abelisaurid theropod *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955 is described for the first time. The available materials include an incomplete pectoral girdle and forelimb, along with the ilium and a nearly complete hind limb. These materials display a number of ceratosaur, abelisauroid, and abelisaurid synapomorphies, supporting the phylogenetic placement of *Majungasaurus* based previously on cranial anatomy. As in *Ceratosaurus* and *Carnotaurus*, the scapular blade is relatively wide and has a pronounced dorsal lip over the glenoid. The humerus is short and bears a globular head, but is more slender than in *Carnotaurus*. The ilium has a preacetabular hook, a strong supraacetabular crest, a notched posterior margin, and peg-and-socket articulations with both the pubis and ischium. Hind limb elements are proportionally stocky, as in some other abelisaurids. The femur lacks a trochanteric shelf, the tibia has a greatly enlarged cnemial crest, and the fibula bears a deep, posteriorly facing medial fossa. The abelisaurid astragalocalcaneum is described here in detail for the first time, and is more similar to that of tetanurans than to those of coelophysoids. Taken together, these materials illustrate that the appendicular skeleton of abelisaurids was specialized over the typical condition in basal theropods, particularly through the development of enlarged muscle attachment processes.

MALAGASY ABSTRACT (FAMINTINANA)—Sambany izao no namelabelabelarin'i Lavocat tamin'ny 1955 ny momban'ny taolan-drambon'ny abelisaurid theropod *Majungasaurus crenatissimus* (Depéret, 1896). Ireo karazan-taolana nisy tamin'ireo dia maro ny ceratosaur sy abelisauroid ary abelisaurid synapomorphies, izay nanamarina ny toerana phylogenetic –n'ny *Majungasaurus* izay tamin'ny bikan'ny karan-doha ny nametrahana azy. Toy ny an'ny *Ceratosaurus* sy *Carnotaurus* dia azo ambara fa mivelatra ny taolan-tsoroka ary iny faritra ambonin'ny glenoid iny dia misy molony aoriana mivoitra mazava tsara. Fohy ny taolan-tsandry ary borobory ny lohany, saingy marotsadrotsaka raha ampitahaina ny an'i *Carnotaurus*. Ny ilium dia ahitana faingoka alohan'ny acetabular, ny tampony supraacetabular matanjaka, misy faingoka aoriana amin'ny sisiny, ary lavaka fitoerana miaro vohitra mahatazona ny fifanohizan'ny taolana izay miaraka amin'ny pubis sy ischium. Ny taolan-tongotra dia mitovitovy ny fahafohezany, toy ireo sasany amin'ny abelisaurids. Tsy ahitana trochanteric self ny taolam-pe, ny tibia (taolan-dranjo iray) dia misy vohitra cnemial mivelatra be, ary ny fibula (taolan-dranjo iray hafa) dia mitondra lavaka lalina manatrika aoriana. Ny abesilaurid astragalocalcaneum dia novelabelarina volalohany tamin'ny antsipirihiny eto, izay toy ny natao tamin'ny tetanurans ka mihoatra ny natao tamin'ny coelophysoids. Rehefa nojerena miaraka dia tsapa fa ireo taolana ireo dia manazava fa ny taolan-damosin'ny abelisaurids dia voatokana manokana tamina fisehoan-javatra izay tsy mahazatra teo amin'ny faritra ambany amin'ny vatan'ny theropods, indrindra indrindra ny fisian'ny fivelaran'ny toerana fipetrahan'ny hozatra.

INTRODUCTION

The first theropod materials in Madagascar were discovered by French military personnel in the 1890s and subsequently described by Charles Depéret (1896a, b). As was common in 19th-century dinosaur paleontology, Depéret allocated these fragmentary theropod elements from the Upper Cretaceous Maevarano Formation to a species of *Megalosaurus* (*M. crenatissimus*), and subsequently to the genus *Dryptosaurus* (Depéret and Savornin, 1928). Although Lavocat (1955) later referred a dentary to this form, separating it from *Megalosaurus* as *Majungasaurus crenatissimus*, its anatomy and broader phylogenetic relationships remained obscure.

Two decades after Depéret described the Malagasy remains, Matley (1921) reported the presence of at least two 'megalosaurians' from the Upper Cretaceous Lameta Formation of India. He later removed some of these materials—including ilia, tibiae, a sacrum, and a number of scutes—and placed them into a new stegosaur taxon, *Lametasaurus indicus* (Matley, 1924). *Lametasaurus* was later recognized as a theropod by Chakravarti (1934, 1935) and Walker (1964), thus 're-associating' it with the original Lameta theropod materials. Huene and Matley (1933) named two additional theropods from the same deposit (*Indosaurus matleyi* and *Indosuchus raptorius*), along with *Dryp-*

tosauroides grandis. Like Depéret and Lavocat, however, Huene and Matley did not appreciate the distinctive nature of their taxa at the suprageneric level, and referred them to the Allosauridae. Chatterjee (1978) later explicitly supported the notion of two distinct large theropods in the Lameta Beds by suggesting that *Indosuchus* was a tyrannosaurid.

The peculiar morphological specializations of the Indian and Malagasy theropods went unappreciated until the discovery and description of the more complete South American forms *Abelisaurus comahuensis* (Bonaparte and Novas, 1985) and *Carnotaurus sastrei* (Bonaparte, 1985; Bonaparte et al., 1990). These taxa were recognized as distinct from allosaurids, 'megalosaurs,' and tyrannosaurids, instead having shared a closer phylogenetic history with the unusual North American theropod *Ceratosaurus nasicornis* (and possibly with *Indosaurus* and *Indosuchus*; Bonaparte and Novas, 1985). In particular, the abelisaurid skull and vertebral column were noted as being highly derived, differing markedly from those of tetanurans. The appendicular skeleton also appeared to be very specialized, but was comparatively incompletely known.

With these South American examples in hand, several authors (Bonaparte et al., 1990; Molnar, 1990) suggested that the Malagasy and Indian theropods were probably also members of the Abelisauridae. Unfortunately, these remained fragmentary and

therefore poorly understood. More recently, however, Sampson and colleagues (1996, 1998) described new, more complete theropod materials from the Maevarano Formation of Madagascar. They regarded *M. crenatissimus* as a nomen dubium because it was not distinguishable on morphological grounds from other abelisaurids. Instead they referred the newly discovered materials to *Majungatholus atopus*, which originally had been described as a pachycephalosaurid (Sues and Taquet, 1979). However, as detailed elsewhere (Krause et al., this volume), new materials have made it clear that: (1) *Majungasaurus* can be distinguished from other abelisaurids; (2) only one large abelisaurid is present in the Maevarano Formation; and (3) this taxon should be referred to as *Majungasaurus crenatissimus*, with *M. atopus* as a junior synonym.

Majungasaurus is now known from numerous specimens that preserve nearly the entire skull and vertebral column, as well as most of the appendicular skeleton, making it one of the best-known abelisaurids (Fig. 1). Although only portions of the forelimb have been recovered, much of the hind limb skeleton is preserved. This is in contrast to nearly all other abelisaurids, where this region of the skeleton is either incomplete (e.g., *Carnotaurus*, *Xenotarsosaurus*, *Lametasaurus*, *Ekrixinatosaurus*) or entirely unknown (e.g., *Abelisaurus*, *Indosaurus*, *Indosuchus*). Although the holotype of *Aucasaurus garridoi* includes nearly complete hind limb materials, these have been only preliminarily described (Coria et al., 2002).

In this article, I describe the appendicular materials of *Majungasaurus* and discuss their relevance to phylogenetic and functional interpretations of this taxon and other abelisaurids. Because many major theropod clades are diagnosed by features of the hind limb, understanding these structures in abelisaurids significantly affects assessments of their phylogenetic position. In a broader sense, these features also bear on the placement of abelisauroids and neoceratosaurs relative to coelophysoids and tetanurans (i.e., the monophyly or paraphyly of Ceratosauria sensu Gauthier, 1986). Finally, the apomorphic nature of the abelisaurid appendicular skeleton highlights several potential functional specializations in this unusual theropod clade.

Institutional Abbreviations—**DGM**, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **FMNH**, Field Museum of Natural History, Chicago, IL; **FSL**, Faculté des Sciences, Université de Lyon, France; **GSI**, Geological Society of India, Kolkata, India; **HMN**, Humboldt Museum für Naturkunde, Berlin, Germany; **ISI**, Indian Statistical Institute, Kolkata, India; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; **MCF-PVPH**, Museo "Carmen Funes," Plaza Huincul, Argentina; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MPCA-PV**, Museo Provincial "Carlos Ameghino," Cipoletti, Argentina; **MWC**, Museum of Western Colorado, Fruita, CO; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **UMNH VP**, Utah Museum of Natural History, Salt Lake City, UT; **UNPSJB-PV**, Universidad Nacional de Patagonia "San Juan Bosco," Comodoro Rivadavia, Argentina; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Comparative Taxa and Specimens—The following specimens were examined for the comparisons mentioned in this paper. When literature illustrations were used, the appropriate reference is given below. Abelisauridae indet. (GSI 296, K27/525, 539, 558, 560, 568-570, 620, 653-654, 658-659, 671, Huene and Matley, 1933; ISI R91/1); *Aucasaurus garridoi* (MCF-PVPH 236); *Carnotaurus sastrei* (MACN-CH 895); Ceratosauria indet. (HMN 37, 69); *Ceratosaurus nasicornis* (MWC 1.1; UMNH VP 5278, USNM 4735); *Elaphrosaurus bambergi* (HMN Gr. S. 38-44); *Genusaurus sisteronis* (MNHN Bev-1); *Ilokelesia aguadagrandensis* (MCF-PVPH 35); *Lametasaurus indicus* (GSI uncat., Matley, 1924); *Masiakasaurus knopfleri* (FMNH PR 2112, 2114-2119, 2129-2132, 2120-2123, 2134-2136, 2143, 2146-2155, 2158-2161, 2167, 2169, 2171-2176, 2205-2106, 2208, 2214-2119, 2223-2225, 2227, 2234, 2236; UA 8681, 8683-8684, 8686, 8693-8694, 8700, 8710-8711, 8713-8714); *Pycnonemosaurus nevesi* (DGM 859-R, Kellner and Campos, 2002); *Quilmesaurus curriei* (MPCA-PV 100); *Rajasaurus narmadensis* (GSI 21141/1-33, Wilson et al., 2003); *Tarascosaurus salluvicus* (FSL 330 201-3); *Xenotarsosaurus bonapartei* (MACN 1468, cast of UNPSJB-PV 184/PVL 612).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAUROIDEA (Bonaparte and Novas, 1985)
ABELISAURIDAE Bonaparte and Novas, 1985
MAJUNGASAURUS Lavocat, 1955
MAJUNGASAURUS CRENATISSIMUS (Depéret, 1896)
Lavocat, 1955

Type Specimen—MNHN MAJ-1, nearly complete right dentary of subadult individual (Lavocat, 1955).

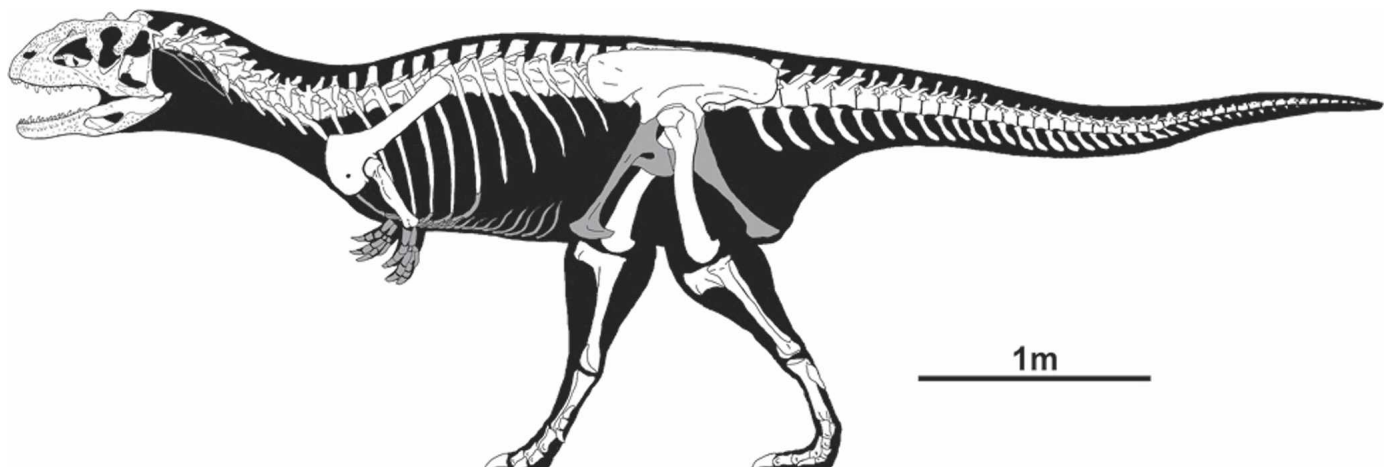**Referred Specimens**—See complete listing in Krause et al. (this volume).

FIGURE 1. Skeletal reconstruction of *Majungasaurus crenatissimus* in left lateral view, showing known skeletal elements in white, unknown elements in gray.

Revised Diagnosis—See Krause et al. (this volume).

Age and Distribution—Appendicular materials of *Majungasaurus* were found at several localities (MAD93-01, 93-18, 93-19, 93-20, 93-32, 93-33, 93-35, 93-73, 95-14, 95-16, 96-01, 96-07, 96-18, 96-21, 99-26, 99-32, 99-33, and 01-05) near the village of Berivotra, in the Mahajanga Basin of northwestern Madagascar (Krause et al., 1997; Sampson et al., 1998). Most materials of *Majungasaurus* derived from the Anembalemba Member, the uppermost white sandstone stratum of the Maevarano Formation (Maastrichtian, Upper Cretaceous) (Rogers and Hartman, 1998; Rogers et al., 2000, this volume).

Described Material—FMNH PR 2423 (right humerus), UA 9031 (left humerus), UA 8678 (left and right ilia), UA 9032 (left tibia), FMNH PR 2424 (left tibia), UA 9077 (left tibia and fibula), UA 9078 (right fibula), FMNH PR 2425 (left astragalocalcaneum), UA 9033 (right astragalocalcaneum), UA 9082 (astragalus), UA 9034 (left metatarsal II), UA 9079 (left metatarsal III), UA 9035 (left metatarsal IV), UA Bv 532 (left pedal phalanx I-2), UA Bv 1658 (left pedal phalanx I-2), UA 9036 (left pedal phalanx II-1), FMNH PR 2426 (right pedal phalanx II-1), UA Bv 1260 (right pedal phalanx II-1), FMNH PR 2428 (right pedal phalanx II-1, left pedal phalanx II-3 and III-2), FMNH PR 2427 (right pedal phalanx II-2), UA 9037 (right pedal phalanx II-2), UA 9038 (left pedal phalanx II-3), UA Bv 1265 (left pedal phalanx III-1), FMNH PR 2429 (left pedal phalanx III-1), UA 9039 (right pedal phalanx III-1), UA 9042 (left pedal phalanx III-2), UA 9081 (right pedal phalanx III-1 or III-2), FMNH PR 2430 (right pedal phalanx IV-1), UA 9040 (right pedal phalanx IV-1), FMNH PR 2431 (left pedal phalanx IV-3), UA 9041 (right pedal phalanx IV-2), FMNH PR 2432 (left pedal phalanx IV-4), FMNH PR 2433 (right pedal phalanx IV-4), FMNH PR 2434 (left pedal phalanx IV-5), UA 9043 (pedal phalanx IV-5), and FSL 92.290 (pedal ungual phalanx).

FMNH PR 2278 is an associated skeleton that includes cranial, axial, and appendicular elements from site MAD99-26. Among the latter have been identified a left scapulocoracoid, partial left ilium, left femur, left and fragmentary right tibiae, left and partial right fibulae, left astragalocalcaneum, left metatarsals II-IV, right pedal phalanges II-1 and IV-2, and left pedal phalanges IV-2 and IV-3.

Specimens UA 9031, 9033-9037, 9040-9041, 9077-9079, 9081-9082, and FMNH PR 2430 come from a single quarry horizon (site MAD99-33), along with a nearly complete skull. Although there is some duplication of elements (notably two right pedal IV-2 phalanges and two right premaxillae), most of the materials are consistent with having been derived from a single subadult individual.

DESCRIPTION AND COMPARISONS

Pectoral Girdle

The pectoral girdle of *Majungasaurus* is represented only by a single, incomplete scapulocoracoid (FMNH PR 2278). The clavicles and sternum are not known.

Scapulocoracoid—FMNH PR 2278 includes an incomplete, coossified scapulocoracoid (FMNH PR 2278; Fig. 2). The scapular blade is long, with nearly parallel anterodorsal and posteroventral edges where they are complete (approximately the ventral one-third). Although the anterodorsal edge of the distal end is missing, the posteroventral edge does not flare appreciably, thus resembling the condition in tetanurans and *Herrerasaurus* more than that in coelophysoids and *Eoraptor*. Unlike the condition in tetanurans, however, the blade is relatively wide anteroposteriorly, as in abelisauroids (*Masiakasaurus*, *Carnotaurus*, *Aucasaurus*), *Ceratosaurus*, and more primitive taxa. Only the base of the acromial process is preserved. The posteroventrally-facing glenoid has prominent lips both dorsally and ven-

trally, with the former being the most pronounced. The posteroventral process appears to have been relatively deep dorsoventrally, with a moderately concave notch between it and the glenoid. In general shape and proportions, this element is most similar to the scapulocoracoids of *Masiakasaurus*, *Carnotaurus*, and *Aucasaurus*.

On the lateral surface, the scapulocoracoid suture is faintly visible as a roughened ridge that passes anteriorly from the glenoid along a slightly undulating line. A large, elliptical rugosity sits ventral to this, just anterior to the glenoid and dorsal to the coracoid foramen (Fig. 2). The coracoid foramen faces ventrally in lateral view, and opens into a dorsally directed channel that passes through the bone to the medial side. A small, faint tu-
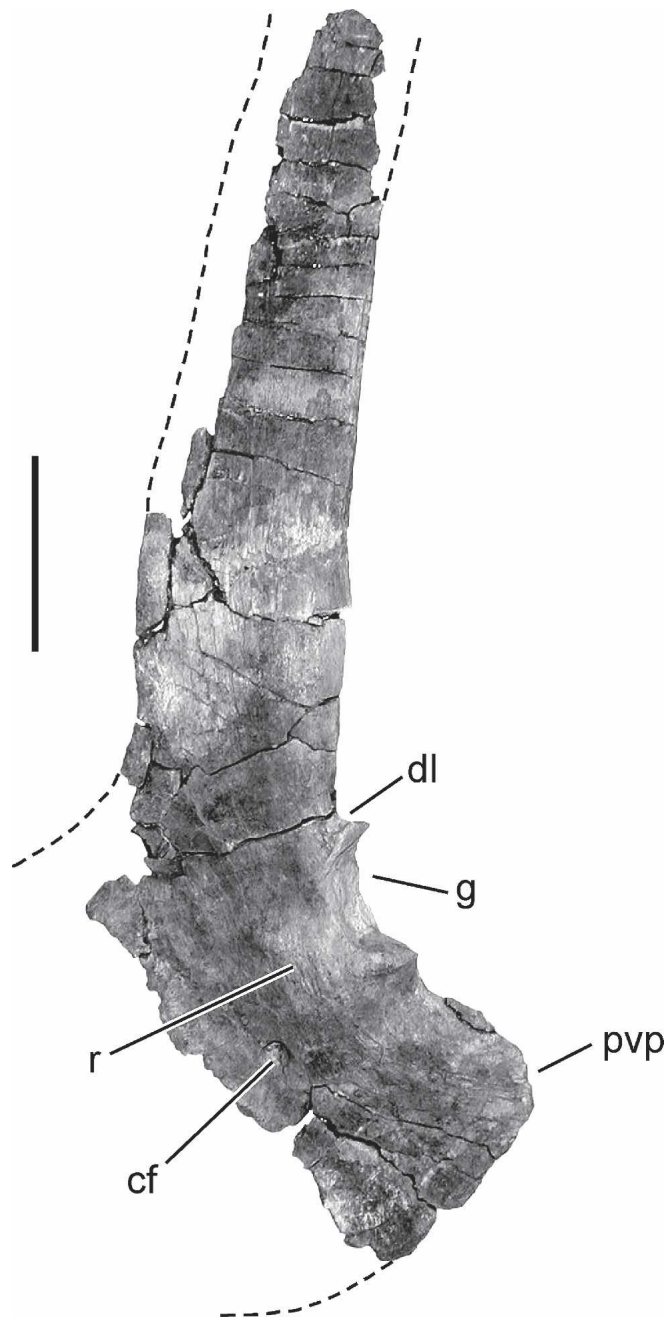

FIGURE 2. Left scapulocoracoid of *Majungasaurus crenatissimus* (FMNH PR 2278) in lateral view. **Abbreviations**: **cf**, coracoid foramen; **dl**, dorsal lip; **g**, glenoid; **pvp**, posteroventral process; **r**, rugosity. Dashed lines indicate reconstructed outlines of element. Scale bar equals 10 cm.

bercle is visible ventral to the glenoid, between it and the posteroventral process; this may have been associated with the origination for M. biceps (Ostrom, 1974; Welles, 1984, Carpenter and Smith, 2001; Jasinoski et al., 2006) and/or M. coracobrachialis brevis (Osmólska et al., 1972; Walker, 1977; Jasinoski et al., 2006). The lateral surface of the scapular blade is smooth.

The medial surface of the scapular blade is more poorly preserved and illuminates few additional details. In posterior view, the blade can be seen to curve broadly, with its concave face directed medially (against the ribcage). Its thickness decreases from proximal to distal, as well as from posteroventral to anterodorsal. The glenoid is approximately reniform, with a slightly longer dorsal (scapular) component. The scapulocoracoid suture between these two components is unclear. Additionally, there is a deep fossa just dorsal to the glenoid that exaggerates the prominence of the dorsal lip, as in other ceratosaurs.

Forelimb

The forelimb of *Majungasaurus* is represented only by the humerus. All remaining elements (radius, ulna, carpus, and manus) are unknown and cannot be compared to the highly derived corresponding elements of the abelisaurids *Carnotaurus* and *Aucasaurus*. These elements are also largely unknown in other abelisauroids (with the exception of individual manual phalanges in *Noasaurus* and *Masiakasaurus*; Carrano et al., 2004), and thus are currently of limited use in phylogenetic assessments of these taxa. The forelimb materials known for *Ceratosaurus* are relatively short compared to those of other theropods, but lack the peculiar derived morphology seen in abelisaurids.

Humerus—The humerus is short but not particularly stocky (Fig. 3; Table 1), similar in proportions to the same bone in adult tyrannosaurids (Carpenter and Smith, 2001; Currie, 2003). The long axes of the proximal and distal ends are slightly twisted relative to each other in *Majungasaurus* and other abelisaurids, more than in coelophysoids but less than in tetanurans. The humeral shaft is nearly straight in anteroposterior view (Fig. 3B, D), bowed anteroposteriorly, and flares as it approaches the distal end. The proximal end is dominated by a large, rounded head, and the accompanying internal tuberosity and greater tubercle are comparatively small. The humeral head and internal tuberosity both expand anteroposteriorly from the shaft.

The deltopectoral crest is a low, rugose ridge that curves from the lateral surface (proximally) onto the anterior midshaft. It
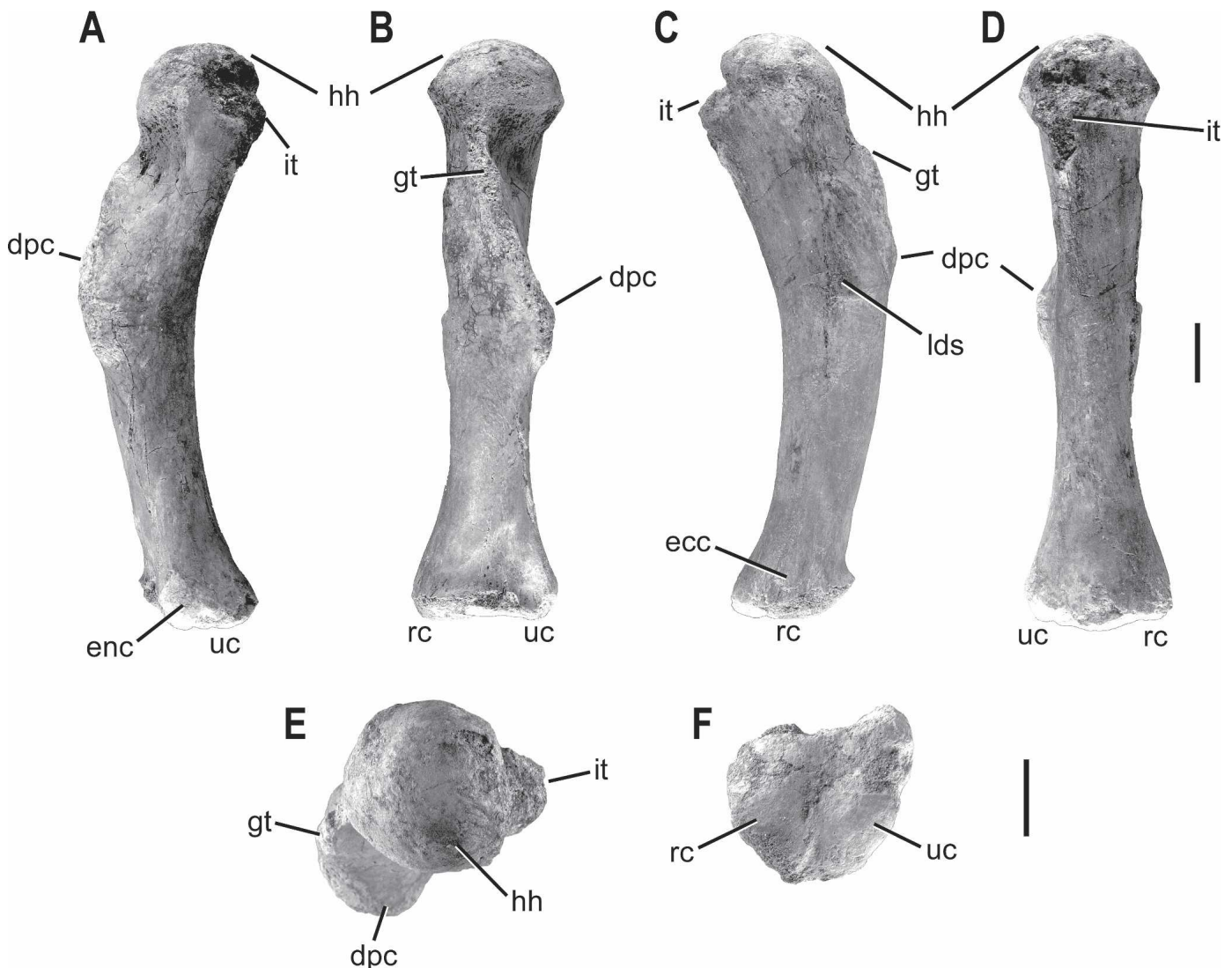

FIGURE 3. Right humerus of *Majungasaurus crenatissimus* (FMNH PR 2423). **A**, anteromedial view; **B**, anterolateral view; **C**, posterolateral view; **D**, posteromedial view; **E**, proximal view; **F**, distal view. **Abbreviations**: **dpc**, deltopectoral crest; **ecc**, ectepicondyle; **enc**, entepicondyle; **gt**, greater tubercle; **hh**, humeral head; **it**, internal tuberosity; **lds**, scar for M. latissimus dorsi; **rc**, radial condyle; **uc**, ulnar condyle. Scale bar equals 10 cm.

TABLE 1. Measurements (in cm) of appendicular elements of *Majungasaurus crenatissimus*. **Abbreviations**: **4t**, distance from proximal end to fourth trochanter; **AP**, anteroposterior diameter; **C**, circumference; **e**, estimated; **GH**, glenoid height; **GW**, glenoid width; **L**, left; **ML**, mediolateral diameter; **TL**, total length. Dashes indicate where measurements could not be taken; plus signs (+) indicate that some length is missing from the element as preserved.

Specimen	Element	TL	AP	ML	C	4t	GW	GH
FMNH PR 2278	L scapulocoracoid	645	111	21.7			39.7	64.3
	R femur	568+	—	80.5	—	205+		
	L tibia	455++	55.2	70.2	218			
	L fibula	(406)e	32.8	18.9	84			
	R fibula	(406)e	31.8	19.5	84			
	MT II	198.9	32.4	24.3	105			
	MT III	250.0	35.2	39.5	132			
	MT IV	207.7	24.8	35.1	93			
UA 9077	L fibula	406.4	33.4					
UA 9036	L II-1	88.0	30.0	26.0				
UA 9037	R II-2	45.0	19.0	23.0				

likely served as the insertion point for Mm. pectorales (Dilkes, 2000, 2001; Carpenter and Smith, 2001; Jasinoski et al., 2006). The crest is widest at its distal end, and approximately half again as high as the shaft is wide. A large fossa located just distal to the humeral head on the anterior surface may mark the insertion of M. coracobrachialis (Carpenter and Smith, 2001; Jasinoski et al., 2006).

The cross-section of the proximal shaft is elliptical, whereas that of the distal half is nearly circular. At the distal end, a faint ridge runs obliquely proximomedially away from the radial condyle, delineating the lateral border of the shallow intercondylar depression. The medial border is more pronounced, and runs more directly proximally from the weakly convex ulnar condyle. The convexity of the radial condyle is particularly evident in posteromedial view (Fig. 3D).

In anteroposterior view, the humeral head appears more asymmetrically rounded than in mediolateral view. A large, oval, rugose ridge extends roughly parallel to the distal deltopectoral crest on the posterolateral side of the bone, with a small fossa between them proximally. An additional fossa is positioned adjacent to this second ridge, separating it from a rounded, rugose bump more posteriorly; this probably represents the insertions of M. latissimus dorsi and part of M. deltoideus (Fig. 3C; Dilkes, 2000, 2001; Carpenter and Smith, 2001; Jasinoski et al., 2006).

In proximal view (Fig. 3E), the humeral head is rounded and bulbous, with no clear long axis. The internal tuberosity is visible as a triangular medial projection, but the greater tubercle is indistinct from the deltopectoral crest, which descends from the greater tubercle as a ridge. The distal end is unusual in lacking prominent, convex condyles for the radius and ulna, instead bearing nearly flat articular surfaces. In distal view (Fig. 3F), this end is irregularly shaped, with two slightly concave swellings that represent the articular surfaces for the radius and ulna. A small central depression separates these indistinct condyles.

The humerus of *Majungasaurus* is strikingly similar to those of *Carnotaurus* and *Aucasaurus*, the only other abelisaurids for which this bone is known. In all three taxa, this bone is proportionally short, lacks significant mediolateral curvature, and bears a globular head and flattened distal condyles. Of the two, the humerus of *Majungasaurus* more closely resembles that of *Aucasaurus* than the bulkier element of *Carnotaurus*. The humeri of *Masiakasaurus* and *Elaphrosaurus* also share several features with that of *Majungasaurus* (Carrano et al., 2002), but are relatively longer and more slender.

Pelvic Girdle

The pelvic girdle of *Majungasaurus* is represented only by the ilium; the pubis and ischium are not known.

Ilium—The ilium is considerably longer than tall (Fig. 4; Table 1), and greatly resembles the same element in *Carnotaurus*, *Au-*

casaurus, *Lametasaurus*, *Rajasaurus*, and *Genusaurus*. As in other neotheropods, the ilium is elongated anteroposteriorly past the pubic and ischial peduncles, and bears an extensive, largely concave lateral surface (Fig. 4). In lateral view, the anterior blade is lobate, curving ventrally below its point of origin on the pubic peduncle. This flat surface bears several weak longitudinal crenulations and is angled out ventrolaterally. The ventralmost point of the postacetabular blade (Fig. 4A) forms a "hook" that is located midway between the pubic peduncle and the anteriormost edge, demarcating the anterior edge of the gap for passage of M. puboischiofemoralis internus 2. The origination fossa for M. puboischiofemoralis 1, on the anterior surface of the pubic peduncle, is faint. The central portion of the lateral face is slightly concave with a straight dorsal margin. Along the dorsal edge, a faint band of parallel, dorsoventrally-oriented lines marks the origination of Mm. iliotibiales. As in most theropods, there is no clear division between the origins of M. iliofemoralis and M. iliofibularis.

More posteriorly, the dorsal edge curves ventrally, meeting the posterior border at a distinct corner. As in other abelisauroids, the posterior border itself is unusual in having an undulating margin, concave in its dorsal third and convex below. Ventrally, the posterior iliac blade is concave, and the thick, rounded edge is rugose along its posterior third. The blade is concave in this region as well, a feature exaggerated by the lateral position of the ventral border, which marks the lateral extent of the brevis fossa. Medial to this edge, the brevis fossa both widens and deepens posteriorly as in other ceratosaurs. The acetabulum is tall, open medially, and has a parabolic outline. Dorsolaterally, it is roofed by a well-developed and somewhat pendant supraacetabular shelf. The shelf extends ventrolaterally to form a lobate extension over the posterior half of the acetabulum.

As in tetanurans, the ischial peduncle is smaller than the pubic peduncle. In *Majungasaurus* (as in *Masiakasaurus* and *Giganotosaurus*), it is developed into a ventrally extending projection that presumably lodged into a corresponding fossa in the iliac peduncle of the ischium. The peduncle is oriented posteroventrally, and the process occupies only the anterior half of its ventral contact surface. The pubic peduncle is more unusual; it is larger than the ischial peduncle (as in tetanurans), but also bears a distinct peg that is extended ventrally below the remainder of the peduncle. This peg is presumed to have lodged into a corresponding socket in the pubis, although this bone is unknown in *Majungasaurus*. This is similar to the condition in *Masiakasaurus* (Sampson et al., 2001; Carrano et al., 2002), *Lametasaurus* (Matley, 1924), *Rajasaurus* (Wilson et al., 2003), and *Ceratosaurus* (Britt et al., 1999, 2000).

Medially, the contact points for at least four sacral vertebrae are evident as paired dorsal and ventral rugosities; only a single
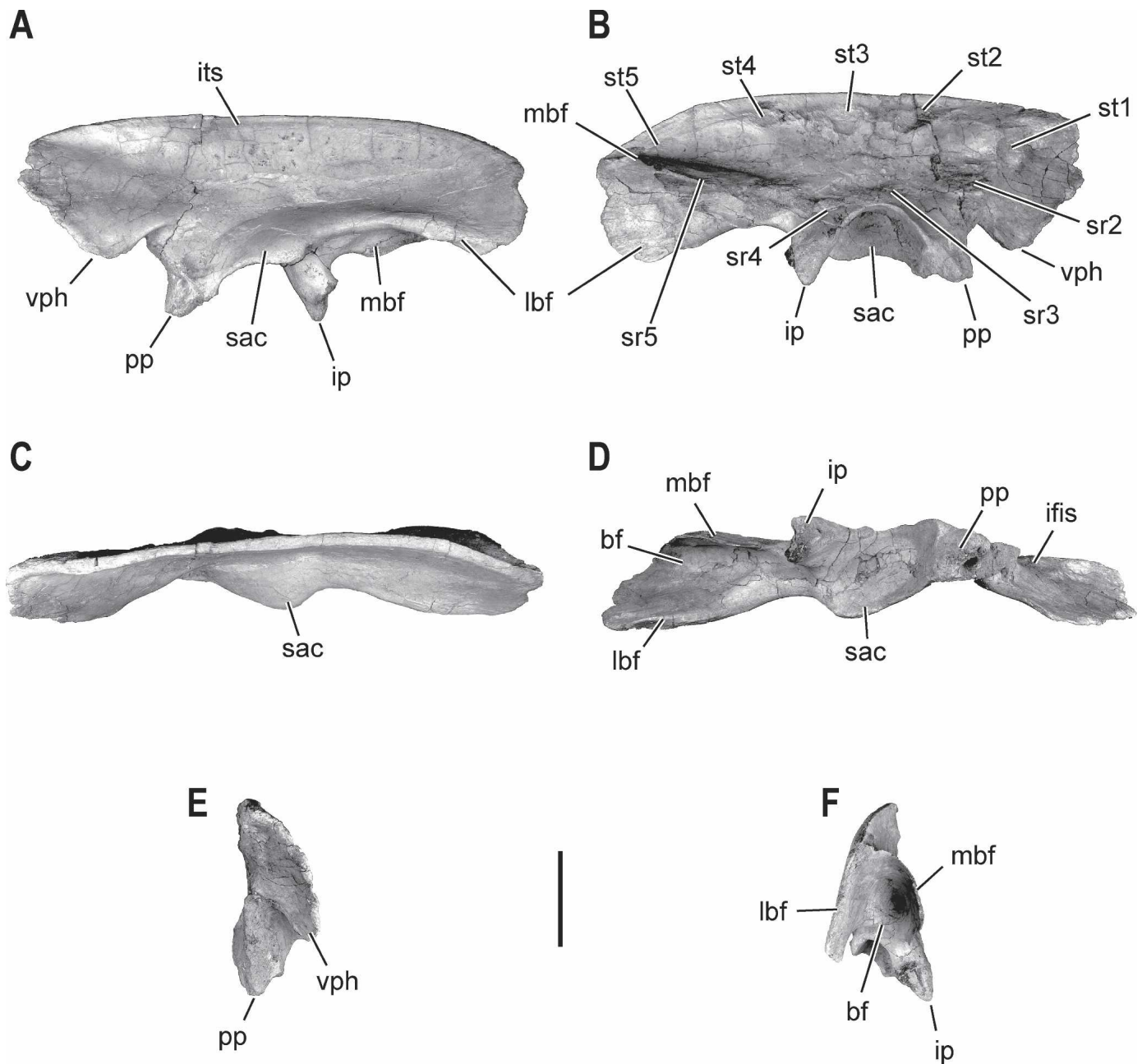
FIGURE 4.   Left ilium of *Majungasaurus crenatissimus* (UA 8678). **A**, lateral view; **B**, medial view; **C**, dorsal view; **D**, ventral view; **E**, anterior view; **F**, posterior view. **Abbreviations**: **bf**, brevis fossa; **ifis**, scar for M. iliofibularis; **ip**, ischial peduncle; **its**, scar for Mm. iliotibiales; **lbf**, lateral wall of brevis fossa; **mbf**, medial wall of brevis fossa; **pp**, pubic peduncle; **sac**, supraacetabular crest; **sr2-5**, attachment surfaces for sacral ribs 2-5; **st1-5**, attachment surfaces for transverse processes of sacral vertebrae 1-5; **vph**, ventral preacetabular hook. Scale bar equals 10 cm.

contact is present for the first sacral (Fig. 4B). Along the dorsal margin, long, parallel dorsoventral ridges run along nearly the entire length of the bone. The brevis fossa is inset medially to a considerable degree, forming a distinct medial shelf whose ventral border turns from convex to strongly concave as it approaches the ischial peduncle. The pegs of both peduncles are more prominent in medial view, appearing to extend directly from the medial wall of the bone. The anterior blade diverges laterally from the midline, beginning at a point just anterior to the base of the pubic peduncle. The medial edge of the dorsal acetabulum is thin.

In posterior view (Fig. 4F), the brevis fossa can be seen to expand both medially and laterally beneath the main iliac blade.

Longitudinal striations are visible on most of the internal surface of the fossa. Its lateral wall extends farther ventrally than medially. In anterior view (Fig. 4E), the lateral deviation of the anterior iliac blade is quite evident, which creates a distinct passage for M. puboischiofemoralis internus 2. A well-defined fossa at the junction of the blade and pubic peduncle marks the beginning of this passage. The anteriormost end of the iliac blade is thinner and rougher than the other edges.

Hind Limb

Most of our knowledge of the hind limb of *Majungasaurus* is derived from one specimen, FMNH PR 2278, a partial skeleton

that includes most of the hind limb elements. This specimen indicates that the hind limb is unusually short relative to other skeletal elements (Fig. 1; Table 1). This stockiness is especially apparent in the tibia and metatarsals, which are robust for their size, but even the femur is relatively short (although not particularly robust).

Nearly the entire hind limb of *Majungasaurus* is known, with the exception of metatarsals I and V, and pedal phalanges I-1 and III-4. Among abelisaurids only *Aucasaurus* has a more completely preserved hind limb (Coria et al., 2002).

Femur—The femur is known only from parts of two damaged elements, both pertaining to FMNH PR 2278. The head, neck, and much of the anterolateral surface have been weathered away in even the most complete specimen (Fig. 5). The exposed internal structure reveals a large central cavity that permeated the entire femoral shaft, as is typical for theropods. Proximally, the base of the lesser trochanter is preserved, as well as the deepest portion of the sulcus between it and the main femoral shaft. This sulcus indicates that the lesser trochanter was elevated, probably comparable to the condition in *Carnotaurus*, *Xenotarsosaurus*, *Tarascosaurus*, *Genusaurus*, and *Ceratosaurus*. The preserved portion of the lesser trochanter is extremely rugose. Near its base, but more distolaterally positioned, a rounded bump marks the insertion of M. iliofemoralis externus. These two structures result from complete separation of the primitive trochanteric shelf (Hutchinson, 2001), as in tetanurans but not coelophysoids. A flat, longitudinally striated facet marks the lateral edge of the greater trochanter, and represents the insertion of Mm. puboischiofemorales externi (Hutchinson, 2001).

Still farther distally, the posteromedial surface shows a well-preserved, ridge-like fourth trochanter (for Mm. caudofemorales) situated approximately two-fifths of the way down the shaft. A rugose region extending proximally onto the posterior

shaft surface represents the additional insertion area for M. caudofemoralis brevis. Compared to the other prominent limb muscle attachment sites, the fourth trochanter appears to be surprisingly small, although the relevance of this to actual muscle size is questionable (e.g., Bryant and Seymour, 1990). The insertion of M. adductor femoris 1 cannot be identified with certainty because the posteromedial side of the distal shaft is damaged. However, M. adductor femoris 2 insertion is complete and located about two-thirds down the shaft, along its lateral edge; the insertion is flat and longitudinally elliptical.

The shaft exhibits bowing in both the anteroposterior and mediolateral planes, being slightly concave posteriorly and medially. Both distal condyles are present but poorly preserved. The fibular condyle is approximately twice as wide mediolaterally as the tibial, but the two extend the same distance distally (Fig. 5A, C). In distal view, the fibular condyle is expanded and bulbous, as in *Masiakasaurus*, *Carnotaurus*, and *Xenotarsosaurus*. The deep, broad posterior intercondylar sulcus contains no marked longitudinal ridges for attachment of the knee flexors. A mediolaterally narrow tibiofibular crest is separated from the main fibular condyle by a broad, shallow groove. The medial edge of the bone is battered, so the presence of a prominent entepicondylar crest (as in *Masiakasaurus* and *Genusaurus*; Carrano et al., 2002) cannot be ascertained.

Tibia—The tibia of *Majungasaurus* is known from five specimens, two isolated (UA 9032, FMNH PR 2424), one provisionally associated with a skull and partial skeleton at MAD93-33 (UA 9077), and a pair belonging to another partial skull and skeleton (FMNH PR 2278). As in other abelisauroids (including *Genusaurus* and *Quilmesaurus*), the well-developed cnemial crest of *Majungasaurus* extends far anteriorly and bears a prominent extensor groove on its lateral face (Fig. 6). In proximal view, the cnemial crest extends in a broad arch from the main body of
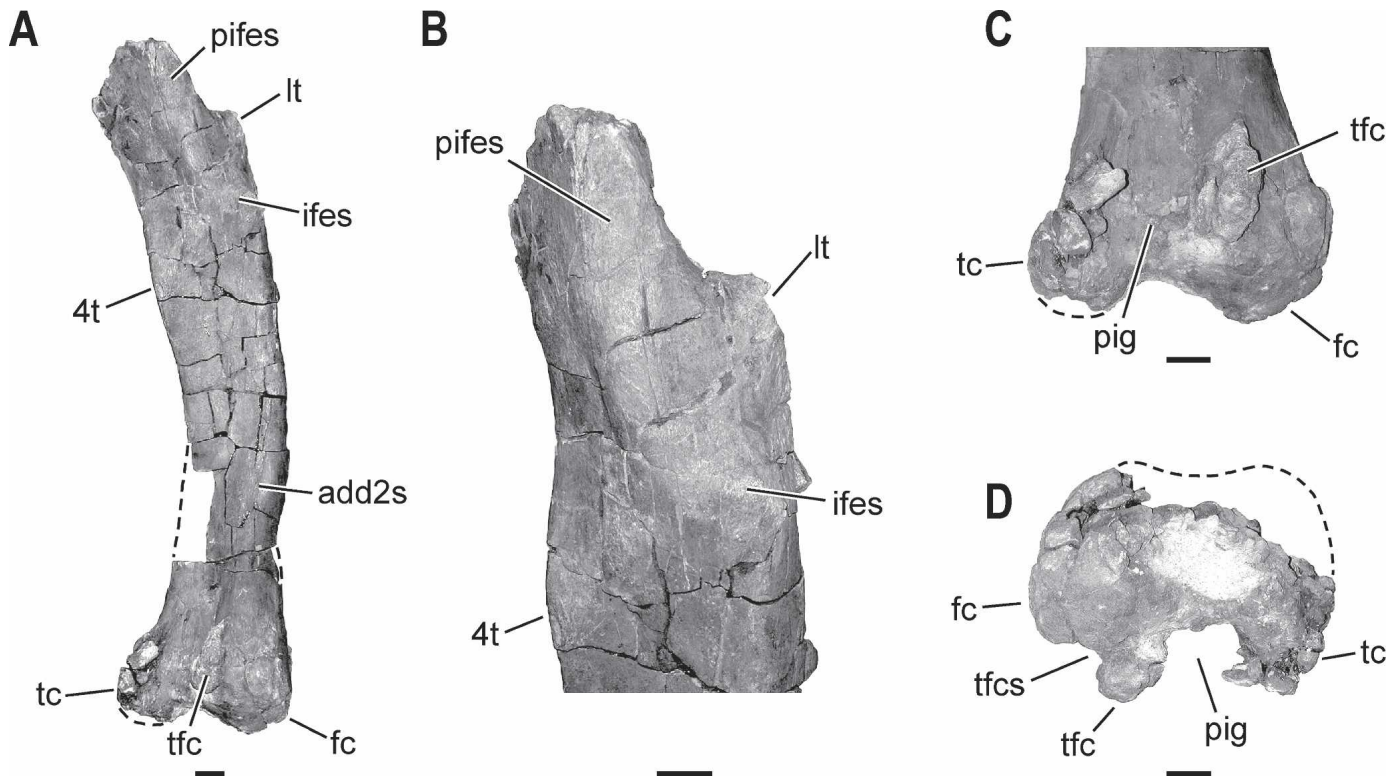

FIGURE 5. Right femur of *Majungasaurus crenatissimus* (FMNH PR 2278). **A**, posterolateral view; **B**, posterolateral view of proximal end; **C**, posterior view of distal end; **D**, distal view. **Abbreviations**: **4t**, fourth trochanter; **add2s**, scar for M. adductor femoris 2; **fc**, fibular condyle; **ifes**, scar for M. iliofemoralis externus; **lt**, lesser trochanter; **pifes**, scar for M. puboischofemoralis externus; **pig**, posterior intercondylar groove; **tc**, tibial condyle; **tfc**, tibiofibularis crest; **tfcs**, tibiofibularis sulcus. Dashed lines are reconstructed outlines. Scale bars equals 5 cm.
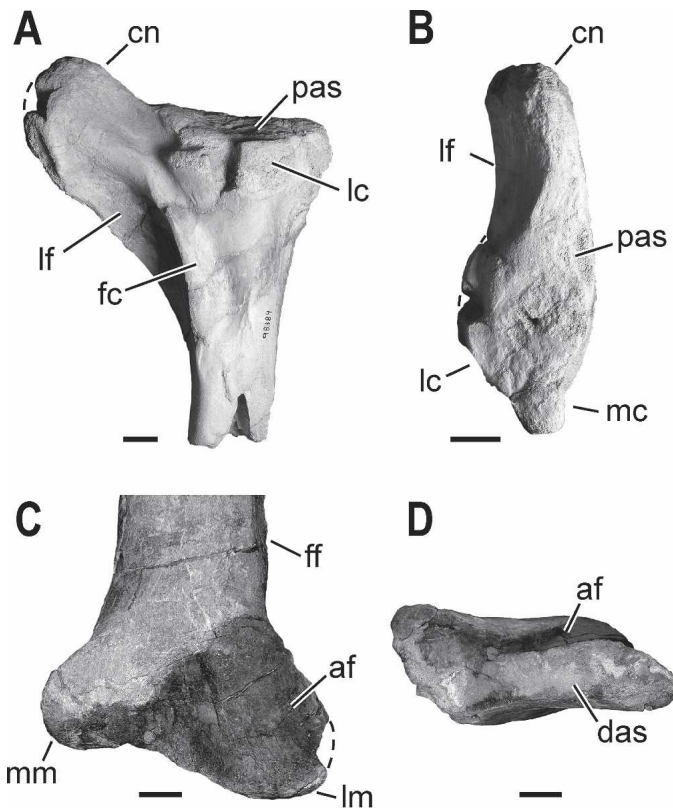
FIGURE 6.   Left tibia of *Majungasaurus crenatissimus*. Proximal end of FMNH PR 2424 in **A**, lateral view and **B**, proximal view. Distal end of FMNH PR 2278 in **C**, anterior view and **D**, distal view. **Abbreviations**: **af**, astragalar facet; **cn**, cnemial crest; **das**, distal articular surface; **fc**, fibular crest; **ff**, fibular facet; **lc**, lateral condyle; **lf**, lateral fossa; **lm**, lateral malleolus; **mc**, medial condyle; **mm**, medial malleolus; **pas**, proximal articular surface. Dashed line in **B** indicates reconstructed outline of element. Scale bars equals 1 cm.

the bone, with a wide lateral concavity that does not resemble the distinct notch of forms such as *Allosaurus*, *Sinraptor*, and many coelurosaurs. In lateral view (Fig. 6A), the cnemial crest exhibits a strong dorsal curvature such that a substantial portion of this structure occurs dorsal to the lateral and medial condyles. The anteriormost portion of the cnemial crest is slightly expanded mediolaterally, with a distinct sulcus (presumably for the knee extensor tendons) visible along the lateral edge. The two proximal condyles are similarly sized and separated by a weak notch. In addition, the posterior edge of the tibia is angled obliquely relative to the mediolateral axis, as evident in proximal view (Fig. 6B).

The lateral fossa between the cnemial crest and the tibial shaft is also correspondingly well-developed. In addition, the terminus of the cnemial crest is expanded both proximally and distally, and does not taper to a rounded point as in most theropods. This structure is thin and delicate, and is completely preserved (or nearly so) only in UA 9077. More posteriorly, the lateral tibia bears a stout ridge, the fibular crest, which runs for approximately one-fourth of the bone's length and articulates with the fibula. A short gap sits distal to the crest, and a large foramen is located posterior to it. Farther distally, the long, flat fibular facet runs to a point just proximal to the expansion of the lateral malleolus. This facet is exceptionally rugose and wide, as in other abelisaurids, contrasting with the thinner, fainter structure of most other theropods.

The anterior aspect of the tibia is relatively smooth and flattened, with a rounded anteromedial edge. At the distal end (Fig. 6C), a triangular facet for the astragalar ascending process can be observed, bounded proximally by an obliquely oriented buttress. In this view, the lateral malleolus is clearly larger and descends farther distally than the medial. The medial malleolus bears a short proximal ridge. Medially, the tibial surface is smooth and largely featureless, with a broadly rounded cross-section throughout most of its length. The distal end shows the same 'torsion' relative to the proximal end as do most theropod tibiae; that is, the long axis of the distal end is oriented perpendicular to that of the proximal end. The posterior shaft is also rounded and fairly smooth, with a modest distal ridge that terminates at the sulcus between the two malleoli.

In distal view (Fig. 6D), the tibia of *Majungasaurus* more closely resembles those of tetanurans than those of coelophysoids or *Herrerasaurus*. The expanded lateral malleolus and distal ridge lend an elongate shape to the distal tibia, in contrast to the rectangular or circular form of more primitive taxa. The astragalar facet invaginates the anterior profile opposite the posterior distal ridge. The outer ends of both malleoli are tapered.

The tibia of *Majungasaurus* is relatively short and stocky (Fig. 7; Table 1), as are those of *Lametasaurus* (Matley, 1924), other Indian theropod tibiae (GSI K19/579, K27/568; Huene and Matley, 1933), *Quilmesaurus*, and a large ceratosaurian from the Tendaguru Formation of Tanzania (HMN 37, 69). In contrast, the tibiae of *Rajasaurus*, *Xenotarsosaurus* and *Aucasaurus* are more slender than that of *Majungasaurus*. The tibia of *Carnotaurus* is incomplete, but given its general similarity to those of the latter two taxa, it was probably proportionally longer than that of *Majungasaurus* but still shorter than originally reconstructed (Bonaparte et al., 1990).

Fibula—The fibula is correspondingly short but not proportionally stocky (Fig. 8; Table 1). Its lateral face is generally smooth and rounded. The anterolateral edge below the proximal end bears a roughened, bulbous expansion that is elevated above the rest of the concave proximal surface. This tubercle, the insertion of M. iliofibularis (Romer, 1923; Carrano and Hutchinson, 2002), is more prominent than in most other theropods, but similar to those of *Ceratosaurus*, *Xenotarsosaurus*, *Genusaurus*, *Carnotaurus*, *Rajasaurus*, and *Aucasaurus*. Farther distally, the posterior edge is expanded into a prominent, obliquely oriented trochanter whose thin, ridge-like proximal half yields to a broader, slightly concave distal surface. Both anterior and posterior edges of the fibular shaft are acute but rounded. At the distal end, the shaft flares out laterally and anteroposteriorly, terminating in a rugose calcaneal articulation. The anterior edge of the shaft at this point bears a roughened flange that (based on FMNH 2278) abutted against the lateral edge of the astragalar ascending process. The distal articular surface is convexly rounded in mediolateral view.

The medial face is shallowly concave near the proximal end (Fig. 8D) in a manner that approximately corresponds to the curvature of the lateral tibia. A raised ridge extends distally down the proximal one-third of the anterior shaft edge, probably marking the attachment of the interosseus membrane. Just posterior to this ridge, the fibula is excavated into a wide, deep medial fossa that occupies most of the proximal third of the bone. The fossa is more open anteriorly than posteriorly (giving it an L-shape in cross-section), and the posterior portion of the bone is expanded medially to create a thin but prominent wall. This medial fossa is unlike the much deeper excavation of derived coelurosaurs, the narrow incisure of coelophysoids (Rowe and Gauthier, 1990), or the broadly shallow surface of spinosauroids, but instead closely resembles the condition in *Ceratosaurus*, *Rajasaurus*, *Xenotarsosaurus*, and *Genusaurus*. Nonetheless, all these structures are likely homologous, representing the in-
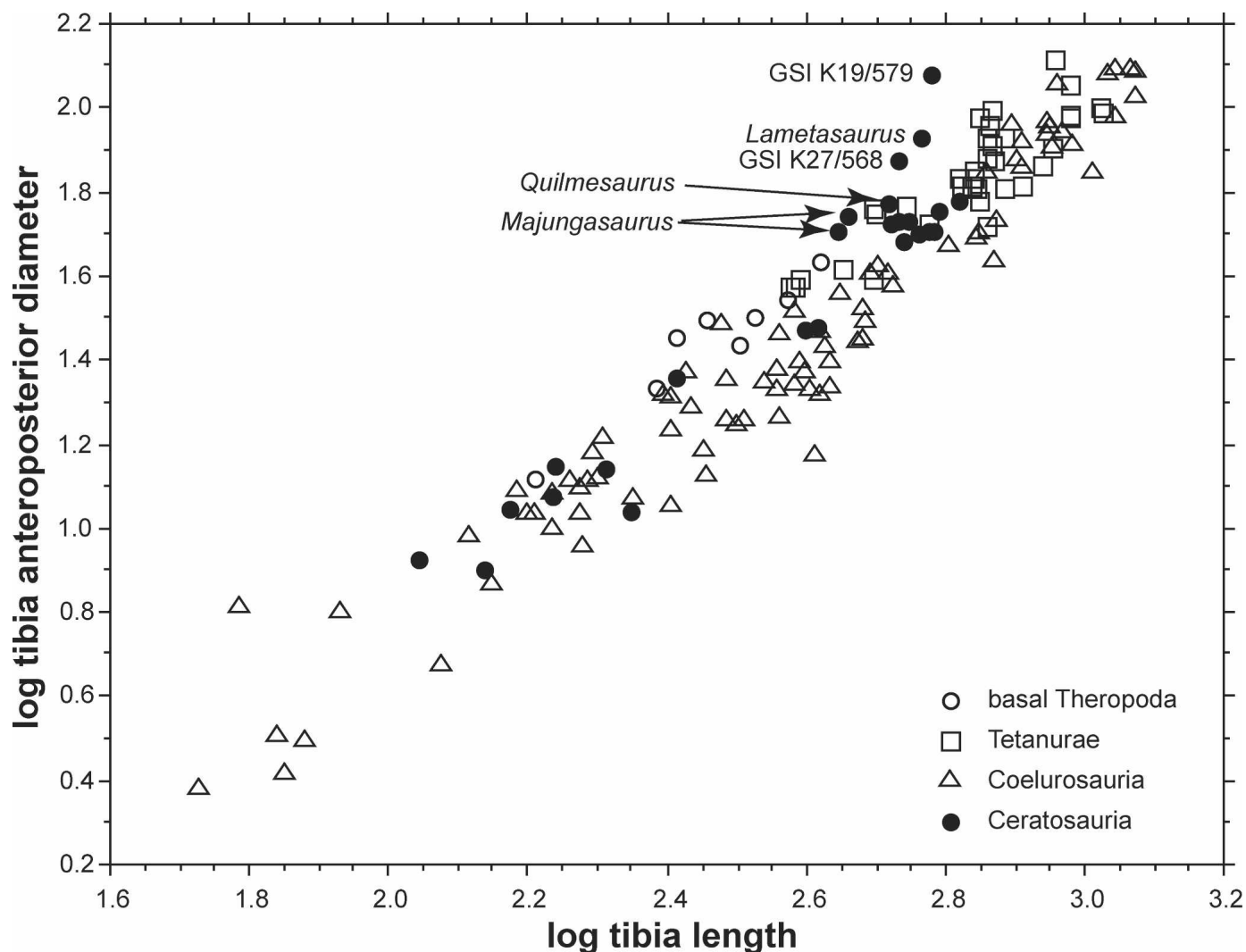
FIGURE 7.   Tibial proportions within non-avian Theropoda. Log-log plot of tibial anteroposterior midshaft diameter versus tibial length (both measured in millimeters), showing relatively robust proportions of some ceratosaur taxa.

sertion of M. popliteus (Carrano and Hutchinson, 2002). Distal to the fossa, the fibula is flattened medially near midshaft and becomes increasingly concave farther distally.

As in all neotheropods, the fibula was aligned closely with the tibia for much of its length, contacting directly at the fibular crest and via an interosseous membrane along the lengthy fibular facet. The distal fibula lodges into a concave fibular facet that spans both proximal tarsals. The distalmost one-fifth of the medial surface would have contacted the broad lateral malleolus of the tibia.

Astragalus—Representative elements of the tarsus of *Majungasaurus* are limited to the astragalus and calcaneum; the distal tarsals are not known. In anterior view, the astragalus bears two distinct and asymmetrical condyles separated by a shallow central sulcus (Fig. 9). On the anterior face, a (presumably vascular) groove runs horizontally, parallel to the ventral condylar edge. A large, oval fossa sits at the base of the ascending process and extends somewhat onto it. It contains two foramina, the larger of which passes through the base of the ascending process to the tibial facet, whereas the smaller disappears into the interior of the bone. Laterally, the astragalus bulges anteriorly near its calcaneal contact, marking the beginning of the fibular facet.

The most complete ascending process is present in UA 9033. It is taller and more laminar than those of coelophysoids, *Herrerasaurus*, and *Ceratosaurus*. Although incomplete, the medial edge is oblique and lodged beneath a similarly oriented buttress on the anterior distal tibia. Rising perpendicularly to about one-eighth the length of the tibia, the ascending process tapers but remains wide proximally. This conformation more closely resembles that of *Xenotarsosaurus* (Martínez et al., 1986) and *Masiakasaurus* (Carrano et al., 2002) than it does the acuminate process of *Dilophosaurus* and most tetanurans. The lateral edge of the process runs nearly vertically down to the calcaneal contact, where it connects to two distinct ridges. The first runs a short distance to merge with the anterolateral edge of the fibular facet, and the second crosses to the posterolateral corner of the calcaneum and divides its fibular and tibial facets.

The calcaneal contact is largely intact in UA 9033, preserving a complex facet with concave and convex portions that suggest an interlocking articulation. The tibial facet is deep and acute in lateral view, facing mostly posteriorly. In this view, it is apparent that the astragalar condyles face anteroventrally (as in tetanurans) rather than ventrally (as in more primitive theropods). Posteriorly, the astragalus rises obliquely from lateral to medial, reaching a peak near the medial border; it simultaneously ex-
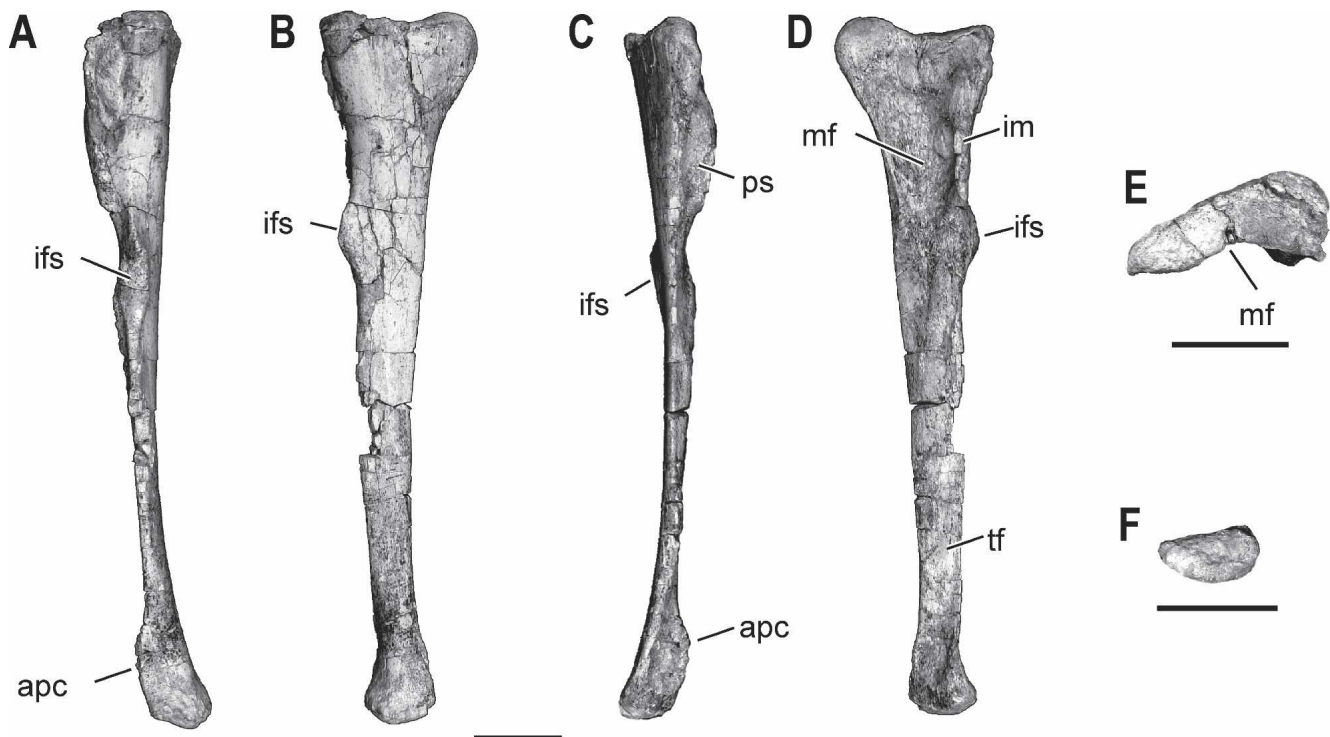
FIGURE 8.   Left fibula of *Majungasaurus crenatissimus* (UA 9077). **A**, Anterior view; **B**, lateral view; **C**, posterior view; **D**, medial view; **E**, proximal view; **F**, distal view. **Abbreviations**: **apc**, contact for the astragalar ascending process; **ifs**, scar for M. iliofibularis; **im**, ridge for attachment of interosseus membrane; **mf**, medial fossa; **tf**, tibial facet. Scale bars equals 5 cm.

pands anteroposteriorly, forming a rounded bulge at this peak. A small fossa is visible near the calcaneal contact. In medial view, the astragalar surface is broad, reniform, and faintly concave. The medial malleolar facet faces proximomedially and flanks the medial ascending process. The anteromedial corner is blunt.

Dorsally, the astragalus bears two distinct facets for the tibial malleoli (Fig. 9C). The medial facet is divided from the lateral by a low ridge that runs from the ascending process to the posteromedial bulge. The lateral edge of this ridge is sharper than the medial, and borders a discrete fossa. The lateral facet is also deeper and narrower than the medial, and contains several fossae as well as the internal counterpart to the medial foramen on the external ascending process. This lateral facet is continuous with the calcaneal facet for the tibia, and includes two large foramina that enter into mediolateral channels, which themselves are confluent with two large calcaneal foramina. The anterolateral corner of the astragalus extends anteriorly beyond the ascending process, marking the beginning of the fibular articulation. Thus the tibia articulates partly posterior to the fibula, as in tetanurans but not more primitive theropods. The fibular facet contains several small foramina, as well as an additional small fossa lodged within its medial corner. Ventrally, the astragalus is obliquely hourglass-shaped, due to the enlargement of the anteromedial corner relative to the anterolateral corner.

Several astragali are known: one isolated (UA 9082), two connected to their respective calcanea (FMNH PR 2425, UA 9033), and a fourth articulated with both the tibia and calcaneum (FMNH PR 2278). None of these specimens show evidence of having been directly fused to the tibia or fibula, although all of the ascending processes show some breakage along the potential fibular contact surface.

Calcaneum—The three known calcanea (FMNH PR 2278, 2425, UA 9033) are fused to their astragali (Fig. 9), obscuring the medial surface in these specimens. Anteriorly, the fibular facet is slightly visible where it rises at its posterolateral corner, and contains numerous small foramina. The anterior wall is raised and obscures the tibial facet from anterior view. Laterally the calcaneum has a broad, slightly concave face that is rounded except for two triangular projections, one marking the anterolateral edge of the fibular cup, and the second its posterolateral edge.

The bone is smooth and convex in posterior view, with a low, concave proximal ridge that bounds the tibial facet posteriorly. This ridge descends to a low point at the (faintly visible) astragalocalcaneal suture. Much of the tibial facet can be viewed posteriorly. Ventrally, the calcaneum shows a slightly pitted, convex articular condyle that is continuous with that of the astragalus. The contact between the two runs nearly directly anteroposteriorly, and the horizontal groove on the anterior surface of the astragalus is continued onto the anteroventral part of the calcaneum. The anterior bulge beneath the fibular cup of the astragalus also has a counterpart on the calcaneum, just above the horizontal groove.

In dorsal view, the calcaneum shows two distinct articular facets. The concave fibular facet is a rounded triangle with its most acute apex directed posterolaterally. About one-fifth of the facet is on the astragalus. This facet is separated from the more posterior tibial facet by the sharp ridge that runs from the lateral edge of the ascending process to the posterolateral corner of the calcaneum. This corner is the highest point of the calcaneum. Behind it, the concave tibial facet contains two small lateral foramina as well as two larger foramina situated just at the astragalocalcaneal junction. The calcaneal portion of the tibial facet forms a narrow triangle with its apex (the shallowest portion) directed laterally.

Metatarsals—Metatarsals I and V remain unknown, but all three central elements are preserved. They are typical of theropod metatarsals in being tightly articulated proximally but diver-
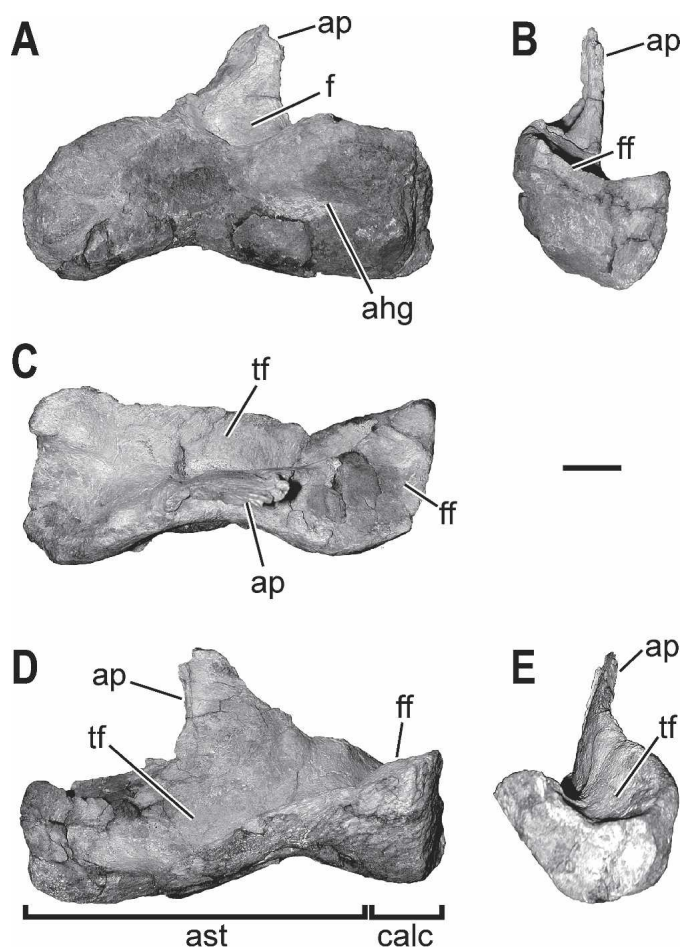
FIGURE 9. Left astragalocalcaneum of *Majungasaurus crenatissimus* (FMNH PR 2278). **A**, anterior view; **B**, lateral view; **C**, proximal view; **D**, posterior view, showing approximate mediolateral dimensions of astragalus (**ast**) and calcaneum (**calc**); **E**, medial view. **Abbreviations**: **ahg**, anterior horizontal groove; **ap**, ascending process; **f**, fossa; **ff**, fibular facet; **tf**, tibial facet. Scale bar equals 1 cm.
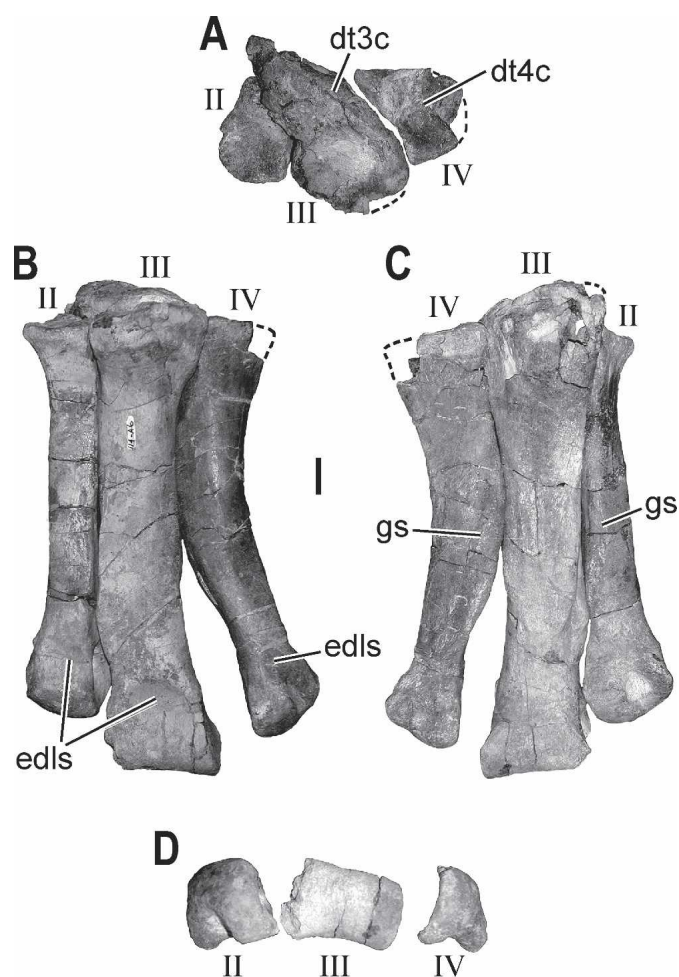

FIGURE 10. Articulated left metatarsals II-IV of *Majungasaurus crenatissimus* (FMNH PR 2278). **A**, proximal view (anterior toward the bottom); **B**, anterior view; **C**, posterior view; **D**, distal view (anterior toward the top). **Abbreviations**: **II**, metatarsal II; **III**, metatarsal III; **IV**, metatarsal IV; **dt3c**, contact surface for distal tarsal 3; **dt4c**, contact surface for distal tarsal 4; **edls**, fossa for insertion of M. extensor digitorum longus; **gs**, scar for M. gastrocnemius. Scale bar equals 1 cm.

gent distally, particularly metatarsal IV (Figs. 10, 11). They have similar general proportions to the metatarsals of non-coelurosaur tetanurans such as *Allosaurus*, although there are several important differences.

Metatarsal II is known from two specimens, FMNH PR 2278 and UA 9034, the former of which is complete (Fig. 10; Table 1). The bone is almost straight, with a narrow shaft that widens steadily from proximal to distal. The proximal articulation is typical for a theropod, being flat and relatively featureless (Fig. 10A); its proximal profile is a narrowly rounded triangle with the apex directed posteriorly. The distal articulation bears two condyles for contact with phalanx II-1 (Fig. 10D). The lateral condyle is much larger than the medial and is flattened on its ventral surface, whereas the medial condyle is acuminate. The two condyles are separated by a deep fossa. Both collateral ligament pits are present, but the lateral is much deeper than the medial, which is merely a faint fossa. The 'hyperextensor' pit ("oblique ligament fossa" of Snively et al., 2004) is extremely shallow. The flat lateral surface of the shaft indicates that this bone was closely appressed to that of metatarsal III for most of its length. Indeed, articulating metatarsals II and III (FMNH PR 2278) indicates that only the distal one-third of metatarsal II is divergent. The shaft is otherwise rounded in cross-section around the anterior, medial, and posterior surfaces, forming a

D-shape overall. A longitudinally striated facet is present along the middle third of the posterior surface, representing the insertion for M. gastrocnemius pars medialis (Carrano and Hutchinson, 2002). A flat area on the medial surface, adjacent to the proximal end, marks the likely articulation site for metatarsal I (Tarsitano, 1983).

Metatarsal III is known only from FMNH PR 2278 (Fig. 10). It is proportionally robust, being noticeably larger in all dimensions than either metatarsal II or IV (Table 1). The straight shaft shows a distinct lateral deviation along its distal third, in opposition to the 'medial deflection' seen in many theropods (Snively et al., 2004). The proximal articulation is rectangular but not distinctly hourglass-shaped, lacking the deep lateral notch for metatarsal IV present in tetanurans. Instead, the markedly smaller proximal end of metatarsal II contacts within a broad curved fossa on the medial edge of proximal metatarsal III. As the posterior edge of this surface is damaged, it cannot be determined whether metatarsal III is expanded in this direction as in *Elaphrosaurus* and *Ceratosaurus*. The facet for metatarsal IV is rugose and extends over a broadly concave surface. The proximal surface itself is damaged as well, but it appears to have been convex posteriorly and flat anteriorly. The distal articulation is
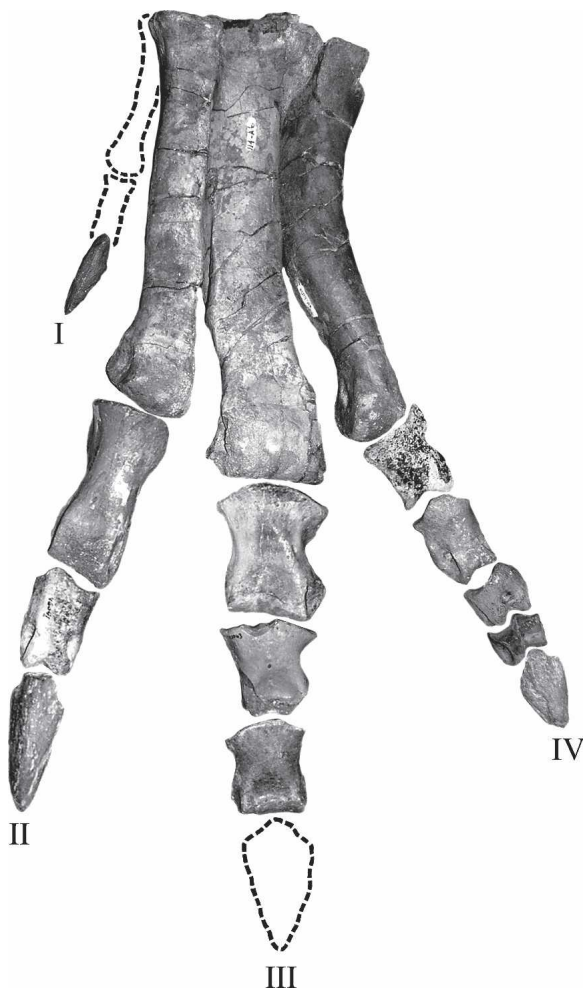
FIGURE 11.   Reconstructed left pes of *Majungasaurus crenatissimus* in anterodorsal view. Metatarsals and phalanx IV-2 and is from FMNH PR 2278; the remaining phalanges are from the following specimens: UA Bv-532 (I-2), FMNH PR 2426 (II-1), FMNH PR 2427 (II-2), UA 9038 (II-3), FMNH PR 2429 (III-1; reversed), UA 9042 (III-2), UA 9039 (III-3), FMNH PR 2430 (IV-1; reversed), FMNH PR 2431 (IV-3), FMNH PR 2432 (IV-4), and FMNH PR 2434 (IV-5). This composite demonstrates the general morphology and approximate proportions of the pes; note that images of many phalanges have been scaled up to correspond with the sizes of metatarsals II-IV. **Abbreviations**: **I**, digit I; **II**, digit II; **III**, digit III; **IV**, digit IV. Dashed lines indicate approximate size and position of metatarsal I and phalanges I-1 and III-4, based on *Aucasaurus garridoi*.

broad and roller-like, with only a very faint central sulcus. Along the medial shaft, a large, flat facet indicates the articulation with metatarsal II; it occupies nearly two-thirds of the length of the bone.

Distal to this point, the marked lateral offset displaces the distal end of metatarsal III away from that of metatarsal II. Here a prominent ridge runs distally down the anteromedial edge of the shaft. The lateral facet for metatarsal IV is similarly pronounced but extends only to the midshaft. Posteriorly, two oval rugosities may mark additional insertion points for Mm. gastrocnemii, adjacent to the articulations for metatarsals II and IV. The collateral ligament pits are equally pronounced, and the 'hyperextensor' pit is deep and mediolaterally wide.

Metatarsal IV, known from two specimens (FMNH PR 2278, UA 9035), is approximately the same length as metatarsal II

(Fig. 10; Table 1). The proximal end is D-shaped, although the medial edge is slightly concave where it contacts metatarsal III. The weak projection at the posteromedial corner is smaller than the extended process seen in most tetanurans. The proximal articulation is concave, with thicker rims along the postero-medial and lateral edges. A small triangular rugosity along the posterolateral edge marks the contact with metatarsal V. The distal end is convex and bears two unequal condyles for articulation with phalanx IV-1; its shape is typical of most theropods. The lateral surface bears a flat, faintly ridged contact for metatarsal III that extends approximately to the midshaft. Here the shaft diverges strongly laterally, a feature most clearly observed in anterior view. The shaft is rounded along the other edges, again forming a D. Two rugose, flat ridges run down the length of the shaft along the posteromedial and posterior faces, probably marking the insertion of M. gastrocnemius pars lateralis (Carrano and Hutchinson, 2002). The shaft narrows both mediolaterally and anteroposteriorly just before reaching the distal articulation. Both collateral ligament pits are weakly present, but the lateral one is particularly shallow, present only as a fossa.

Phalanges—Most of the pedal phalanges are represented. Presuming the typical theropod phalangeal formula of 2-3-4-5-x, this collection includes all but I-1 and III-4 (Fig. 11). However, subtle proportional differences can be detected among the phalanges, suggesting that some dimorphism may have been present, as in the limb bones of *Masiakasaurus* (Carrano, et al., 2002). Because of these variations, similarly shaped phalanges can be difficult to distinguish as isolated specimens. Thus some of the following identifications should be considered tentative. This is especially true for the digit III phalanges (e.g., III-2 and III-3).

Only the ungual phalanx (I-2) from digit I is known (UA Bv 532, 1658). Unlike the other pedal unguals, this element is nearly symmetrical, straight, and strongly laterally compressed. The proximal articular surface is tall, narrow, and concave but lacks a central ridge. Ventrally there is no flexor tubercle, but rather a shallow, flattened fossa. Vascular grooves are present but irregular on both lateral and medial surfaces, with numerous large foramina and distinct grooves near the tip. A pair of vascular grooves is apparent on one side only.

Digit II is known in its entirety. Both non-ungual phalanges bear a large dorsal tubercle and two prominent, flattened ventral heels. Of these, the lateral is approximately twice as large as the medial and extends farther distally as an elongate ridge. Both are rugose, although the medial heel is flatter. The remainder of the phalangeal shaft is rounded but taller than wide. A distinct hyperextensor pit is visible on the dorsal surface. The distal articular surface bears two rounded condyles separated by a deep sulcus. The condyles appear to diverge ventrally and terminate in flat ventral heels: they are subequal in size, although the medial is slightly larger. Both collateral ligament pits are deep, but the lateral pit is larger and more rounded. II-1 (UA 9036, FMNH PR 2426; UA Bv 1260) is the longest and tallest pedal phalanx, with a concave, dorsoventrally oval proximal articular surface. Pedal phalanx II-2 (FMNH PR 2427, UA 9037) is about half as long as II-1. Its proximal surface forms a rounded triangle, with two facets separated by a weak vertical ridge. The medial facet is slightly larger than the lateral, corresponding to the morphology of the distal condyles of II-1. The hyperextensor pit is deeper and more pronounced on II-1 than on II-2, bounded distally by the dorsal margin of the distal articular surface.

The ungual phalanx of digit II (II-3; FMNH PR 2428, UA 9038) is markedly asymmetrical. On the triangular proximal surface, the long axis is tilted so that the apex appears to lean laterally. The two similarly sized articular facets are separated by a wide, low ridge and bear numerous large vascular foramina. The dorsal tubercle is pronounced, but ventrally there is no

flexor tubercle. Instead, a deep, longitudinal ventral fossa is flanked by marked lateral and medial ridges. Numerous foramina within this fossa appear to lead to a distally directed channel, and the fossa may also be confluent with the lateral and medial vascular grooves. The medial surface is relatively flat, with a distinct ventral groove that wraps onto the ventral surface near the proximal end. Its ventral edge forms the larger of the two grooves bounding the ventral fossa. The lateral surface is more rounded, with a distinct triangular arrangement of grooves. The ventral groove is the most distinct and connects with the large fossa on the ventral surface. It contains several large foramina, the distalmost leading into a tunnel within the bone and emerging again near the tip.

The first three phalanges of digit III are known in *Majungasaurus*. These non-ungual phalanges are remarkably short and wide, with broad, flat articular condyles and correspondingly shallow articular facets (Fig. 12). Indeed, the proximal articular surface lacks a vertical ridge entirely, making it difficult to distinguish even III-1 from the remaining phalanges. As with digit II phalanges, the medial condyle tends to be slightly larger than the lateral. The 'hyperextensor' pit is triangular, wide, and deep, with a marked border where it abuts the distal articular surface. Both collateral pits are deep and rounded, with little difference in size and shape between lateral and medial. The proximal and distal ends each bear a pair of distinct, flat ventral heels that are separated by a shallow fossa. The lateral distal heel is abruptly demarcated from the shaft at its proximal edge, creating a ridge and furrow that run between the ventral and lateral surfaces. The proportional breadth of these elements increases distally from III-1 to III-3.

All of the phalanges of digit IV are known. They are remarkably short and blocky, with a very short shaft between the proximal and distal ends. The proximal surface is taller than wide, with nearly equal dorsal and ventral midline tubercles. The distal articular surface is composed of two prominent, rounded condyles that are separated by a deep sulcus. Because the lateral distal condyle is smaller than the medial, the corresponding proximal articular facets differ in size accordingly. Whereas the two proximal ventral heels are flat and nearly confluent with one another, the distal ventral heels bear distinct proximal edges and are widely separated by the articular sulcus. A hyperextensor pit is present on all phalanges. In contrast to digit II, the medial collateral pit is markedly deeper than the lateral pit on digit IV phalanges. The proximal surface of IV-1 (FMNH PR 2430, UA 9040) is taller than wide, concave, but shallow. The lateral collateral pit of IV-1 is elliptical, whereas those of the other phalanges are rounded. These phalanges become progressively shorter up to IV-3 and IV-4, which are little more than closely attached proximal and distal articular surfaces.

The ungual phalanx of digit IV (IV-5; FMNH PR 2434, UA 9043; Fig. 13) is asymmetrical but in a manner opposite to that of digit II, as with the phalanges. The proximal end is a rounded triangle whose two facets are separated by a weak ridge. A ventral tubercle is lacking, replaced instead by a deep fossa containing several foramina. The fossa appears to be confluent with the ventral vascular grooves on the lateral and medial surfaces. A triangular arrangement of grooves can be seen on the medial surface, but on the lateral side only a ventral groove is apparent. The lateral surface is flatter than the medial, terminating below
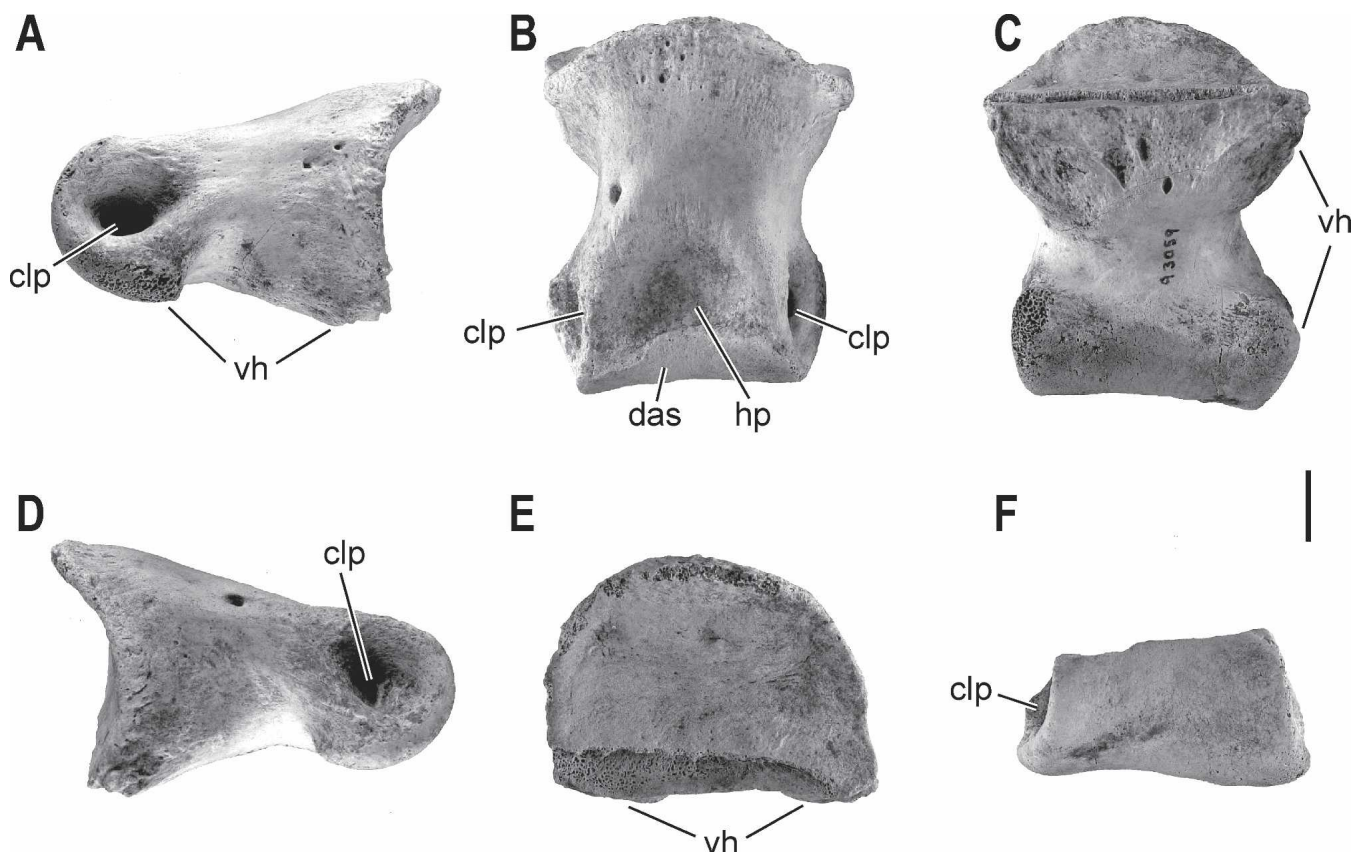

FIGURE 12. Right pedal phalanx III-1 of *Majungasaurus crenatissimus* (UA Bv-1265). **A**, medial view; **B**, dorsal view; **C**, ventral view; **D**, lateral view; **E**, proximal view; **F**, distal view. **Abbreviations**: **clp**, collateral ligament pit; **das**, distal articular surface; **hp**, 'hyperextensor' pit; **vh**, ventral 'heel.' Scale bar equals 1 cm.
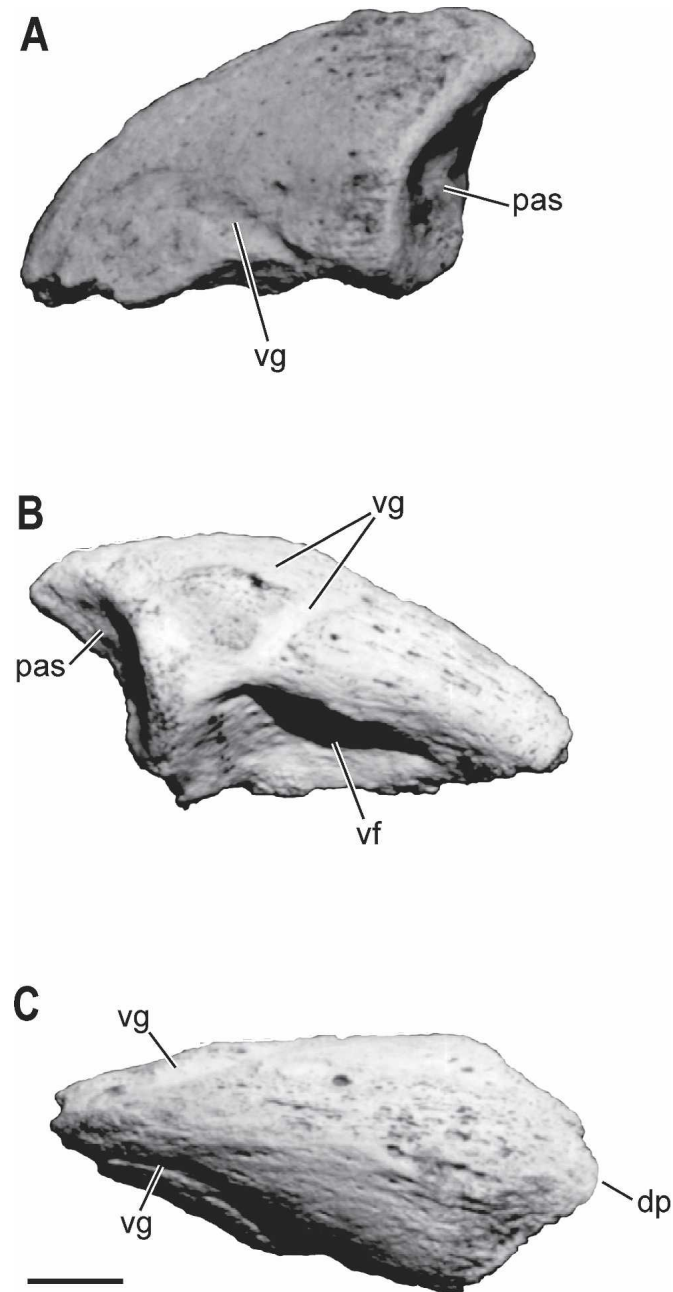
FIGURE 13.   Left pedal phalanx IV-5 of *Majungasaurus crenatissimus* (FMNH PR 2434). **A**, lateral view; **B**, medial view; **C**, dorsal view. **Abbreviations**: **dp**, dorsal process; **pas**, proximal articular surface; **vf**, ventral fossa; **vg**, vascular groove. Scale bar equals 1 cm.

in a large ventral ridge that helps bound the fossa on the ventral surface.

In general morphology, the pedal phalanges are quite similar to, although more robust than, the corresponding bones in *Aucasaurus* and *Masiakasaurus*. Specifically, these taxa share a relatively broad digit III, pronounced collateral pits, flat ventral heels, and remarkably shortened individual IV phalanges. The pedal unguals are unusual in being highly asymmetrical (on II and IV), lacking flexor tubercles, and bearing a triangular arrangement of vascular grooves. These features are also seen in isolated abelisaurid phalanges from India and South America (Novas and Bandyopadhyay, 2001; Novas et al., 2004).

DISCUSSION

Forelimb Specializations of Abelisaurids

The unusual abelisaurid forelimb is one of the most distinctive morphological hallmarks of this group. The remarkable parallels between abelisaurids and tyrannosaurids in this regard have been noted (Bonaparte et al., 1990), although close examination reveals that the forelimbs in these two groups differ in certain important details. In particular, abelisaurids, like other basal theropods, apparently retained four functional manual digits with primitive phalangeal size proportions (e.g., *Carnotaurus*, Bonaparte et al., 1990; *Aucasaurus*, Coria et al., 2002).

Nonetheless, there are notable similarities to the independently reduced forelimbs of tyrannosaurids (Carpenter and Smith, 2001; Currie, 2003). In particular, although both groups show manus reduction (digit number in tyrannosaurids, digit length in abelisaurids), both also retain manus functionality along with all of the primitive theropod pectoral and forelimb musculature. It has been suggested that forelimb reduction is largely an allometric effect visible in giant theropods (Currie, 2003), but differences in forelimb size and development between abelisaurids and tyrannosaurids versus spinosaurids imply that important functional convergences (and divergences) were also at work.

The scapulocoracoid of *Majungasaurus* differs from that of most other theropods in the broad, rounded shape of the coracoid and the pronounced dorsal lip of the glenoid. It is very similar to the same element in *Carnotaurus* and *Aucasaurus*, as well as those of *Masiakasaurus*, *Elaphrosaurus*, and *Deltadromeus*. The short humerus bears a globular head flanked by small medial and lateral tubercles. The long deltopectoral crest attached to a M. pectoralis that was likely large, which in turn would have originated partly on the expansive ventral coracoid. The distal humeral condyles are unusually flattened, and their articulation with the bizarre radius and ulna (as in *Carnotaurus* and *Aucasaurus*) are not well understood. Still, the rounded humeral head and distal radius/ulna suggest that both the shoulder and elbow joints enjoyed a wide range of mobility in abelisaurids.

The manual elements of *Carnotaurus* originally appeared to be so specialized that their precise homologies and morphologies were difficult to determine (Bonaparte, 1985; Bonaparte et al., 1990). As a result, it has been exceedingly difficult to identify potential manual elements from among the isolated epipodial materials referred to *Majungasaurus*. A few unusual phalanges probably pertain to the manus, but without adequate articulated or comparative materials, more specific identifications are not possible.

Nevertheless, the manus of *Carnotaurus* may not be as bizarre as originally described. Both left and right manus are present, although they are disarticulated, damaged, and incomplete. Re-examination of MACN-CH 895 suggests that several typical theropod manual elements are represented, including unguals. These were probably arrayed among four digits, as in *Aucasaurus*, *Ceratosaurus*, and other primitive theropods, but beyond this little can be said concerning their particular arrangement. At present *Carnotaurus* alone does not provide convincing evidence for anything radically unusual in the abelisaurid manus aside from its extremely short length. Further preparation and description of the nearly complete *Aucasaurus* forelimb (Coria et al., 2002) will undoubtedly shed light on the general morphology of the abelisaurid manus.

Hind Limb Specializations of Abelisaurids

Not surprisingly, the abelisaurid hind limb shows far fewer morphological deviations from the basic theropod design than the forelimb. Nevertheless, the hind limb elements are somewhat unusual in their relatively stocky proportions (Figs. 1, 7). In par-

ticular, the tibia is short relative to other hind limb elements, and the entire limb appears to be short relative to body length (although the incomplete nature of most abelisaurid skeletons makes this difficult to determine precisely). It is interesting to note that a subset of abelisaurids—notably *Majungasaurus*, *Lametasaurus*, *Quilmesaurus*, GSI K19/579, and GSI K27/568—have stocky tibiae even compared to other members of this clade. In contrast, *Aucasaurus*, *Xenotarsosaurus*, ISI R91/1, and perhaps *Carnotaurus* appear to have tibial proportions that are closer to those of other theropods (Novas et al., 2004).

Where they can be identified, pelvic and hind limb muscle attachment points appear to be consistent with those seen in other basal theropods (e.g. Hutchinson, 2001). Like coelophysoids and some tetanurans, abelisaurids lack coelurosaur synapomorphies such as a marked accessory trochanter at the base of the lesser trochanter (insertion of M. puboischiofemoralis internus 2), a well-defined fossa on the anterior pubic peduncle of the ilium (origin of M. puboischiofemoralis internus 1), and a fibular fossa restricted to the medial surface only (insertion of M. popliteus). No shifts in muscle attachment positions associated with these morphologies are therefore inferred to have occurred in these taxa.

However, the abelisaurid hind limb is also derived relative to those of coelophysoids and more primitive taxa. The insertion for M. popliteus, composed largely of the medial fibular fossa, has moved to occupy most of the medial surface of the proximal fibula, unlike in coelophysoids where it originates from a shallow posterior sulcus. The lesser trochanter is more elevated and accompanied by a distinct bump for insertion of M. iliofemoralis, indicating that the deep dorsal muscles were more similar to the avian condition than to those of primitive theropods (Hutchinson, 2001). In addition, the tarsus has achieved the tetanuran condition, with a mediolaterally expanded distal tibia that partially backs the fibula and articulates with the calcaneum.

The pronounced cnemial crest is associated with a prominent medial femoral epicondyle in other abelisauroids, and such a structure may also have been present in *Majungasaurus*. This marks part of the origin of Mm. femorotibiales, which contributed to the knee extensor tendon(s) that inserted on the cnemial crest. The possible elaboration of Mm. femorotibiales, but not other, more proximal knee extensors (such as Mm. iliotibiales and M. ambiens) suggests enhancement of the knee extension moment. The extensive lateral fossa on the proximal tibia may have housed a large M. tibialis anterior as well.

Consolidation of the tarsus into a single, block-like structure has been cited as a synapomorphy of Ceratosauria (sensu Gauthier, 1986; Rowe, 1989), but recent phylogenetic work (e.g., Carrano et al., 2002; Rauhut, 2003) suggests that this is convergent between coelophysoids and abelisauroids. Further differences in detail between the fusion patterns in these groups support this hypothesis (see below). Regardless, although some degree of immobility obviously would have been conferred by such fusion, it is not clear what effect this might have had on tarsal function because little mobility is inferred between these elements in theropods where they remain unfused.

The abelisauroid pes is also unusual in bearing markedly asymmetrical unguals at the ends of relatively broad, shortened digits. The digits themselves also appear to be more strongly curved and bear pronounced, flattened ventral tendon attachments. The metatarsals are fairly tightly appressed, not diverging from one another until rather close to their distal ends. The prominence of metatarsal III appears to be a common feature of abelisauroids, although the particular breadth exhibited by *Majungasaurus*, for example, may characterize only abelisaurids.

Phylogenetic Implications

The appendicular morphology of *Majungasaurus*, particularly the tarsus, strongly suggests closer affinities with tetanurans than with coelophysoids and other more primitive theropods. For example, the distal tibia has a flat lateral malleolus that backs the fibula, lodging within an elongate tarsal facet that overlaps the dorsal surfaces of both the astragalus and calcaneum. The calcaneal facet for the tibia faces slightly medially. The tibial distal end is mediolaterally elongate (Novas, 1996), with a centrally-placed buttress marking the articulation with the astragalar ascending process (Molnar et al., 1996). This process is tall and plate-like rather than triangular and peg-like (Sereno, 1999), and sits superficially on the anterior tibia without being inset. In these features the abelisaurid hind limb shows similarities with tetanurans and not with coelophysoids. Likewise, the enlarged femoral lesser trochanter (accompanied by a distinct M. iliofemoralis externus insertion) is more derived than that of coelophysoids and other primitive theropods, resembling the condition in spinosauroids and other basal tetanurans (Hutchinson, 2001).

In other aspects, the appendicular morphology of *Majungasaurus* is more similar to those of more primitive theropods, including coelophysoids. These features include an anteromedially oriented femoral head (Bonaparte, 1991), a femoral lesser trochanter well below the level of the femoral head (Novas, 1991), flattened (rather than elliptical) unguals on pedal digits II-IV (Russell and Dong, 1993), and a relatively broad scapular blade (Gauthier, 1986). It is important to note, however, that these represent symplesiomorphies and not synapomorphies of *Majungasaurus* and coelophysoids. Only one appendicular feature—fusion between the astragalus and calcaneum—can be observed that appears to be synapomorphic (or homoplastic) between these two taxa. Even this characteristic, however, shows some differences in detail. In abelisauroids (*Majungasaurus*, *Xenotarsosaurus*, *Masiakasaurus*), the astragalus and calcaneum are fused to each other, with the ascending process occasionally fused to the medial fibula and the anterior tibia. By contrast, in coelophysoids (*Coelophysis*, *Syntarsus*, *Dilophosaurus*, *Liliensternus*), the astragalus and calcaneum tend to fuse together but with little direct involvement of the tibia or fibula.

Thus, the morphology of *Majungasaurus* is consistent with the results of previous phylogenetic analyses (Sampson et al., 2001; Carrano et al., 2002; Rauhut, 2003; Wilson et al., 2003) in indicating a closer relationship between abelisauroids (and *Ceratosaurus*) and tetanurans than between abelisauroids and coelophysoids. Particular similarities in the tarsus suggest that many 'tetanuran' morphological innovations actually diagnose a more inclusive clade, and therefore must have appeared considerably earlier in theropod evolution than had been previously appreciated (Carrano et al., 2002; Rauhut, 2003).

CONCLUSIONS

The appendicular morphology of the abelisaurid theropod *Majungasaurus crenatissimus* is described. Abelisaurid appendicular materials have not been well documented, and several relatively complete specimens of this Late Cretaceous Malagasy theropod greatly clarify this region of the skeleton in these theropods.

The forelimb of *Majungasaurus* is similar to those of other abelisaurids and includes a short, highly modified humerus. Numerous abelisaurid and abelisauroid synapomorphies are also found in the pelvis and hind limb. In addition, the pelvis and hind limb display a combination of features that strongly suggest a close affinity between abelisauroids and tetanurans. Functionally, the abelisaurid forelimb remains obscure and its interpretation must await more complete materials. The hind limb ap-

pears to show specializations for strong knee extensors, as well as unusual modifications of the metatarsus and pes that may have additional locomotor implications.

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