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First tyrannosaurid remains from the Upper Cretaceous "El Gallo" Formation of Baja California, México

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We report a complete left fourth metatarsal collected from rocks of the Upper Cretaceous (Campanian) "El Gallo" Formation exposed along the Pacific Ocean near El Rosario, Baja California, México. The metatarsal IV was part of an arctometatarsalian metatarsus, as evidenced by a deep medial notch proximally and extensive articulation for metatarsal III. This condition, along with the U-shape of the proximal end, supports identification as tyrannosauroid. It is assigned to Tyrannosauridae based on features on the posterior surface of the shaft, but finer taxonomic resolution is not possible. Compared to other tyrannosauroids, the metatarsal is relatively short, closely resembling the proportions of the gracile *Albertosaurus sarcophagus* rather than the much more massive, robust metatarsals of *Tyrannosaurus rex*. The Baja tyrannosaurid metatarsal is shorter than almost all other tyrannosauroid fourth metatarsals, raising the possibility that it pertains to an immature individual. North American tyrannosauroids are best known from the northern coast of the Western Interior Seaway, as well as less frequently on the southern coast of the seaway in Utah and New Mexico. The new record in Baja marks the first unambiguous skeletal material of a tyrannosaurid both in México and along the Pacific coast.

Key words: Dinosauria, Tyrannosauridae, fourth metatarsal, Campanian, "El Gallo" Formation, Baja California, México.

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Introduction

During much of the Late Cretaceous, North America was covered by the Western Interior Seaway (WIS), a shallow inland sea that separated the eastern landmass Appalachia from the western landmass Laramidia (Lehman 1997). Diversity was high for large-bodied dinosaurs, such as hadrosaurids, ceratopsids, and tyrannosaurids, across Laramidia during the Late Cretaceous (Sampson et al. 2010). Fossils collected from the Western Interior Basin, which borders the WIS, suggest the presence of two biogeographic provinces within Laramidia, a northern province located around the modern day Montana/Alberta border and a southern province in Utah and New Mexico (Lehman 1981, 1997, 2001; Weil 1999; Gates et al. 2010; Sampson et al. 2010; Wilson et al. 2010). The separation of these provinces in the Maastrichtian has recently been challenged (Vavrek and Larsson 2010). Data from Laramidian localities outside of the Western Interior Basin are scarce; thus, additional data would provide valuable information with which to study broader biogeographic questions across the continent.

Compared to the Western Interior Basin, vertebrate faunas from the Pacific coast of Laramidia are poorly known. The exceptions are the La Bocana Roja and "El Gallo" formations of Baja California, México, which are Campanian in age (Renne et al. 1991). During the 1960s and 1970s, crews from the Los Angeles County Museum and Occidental College led by William J. Morris were the first to intensively prospect for vertebrate fossils in the area around the town of El Rosario, Baja California, México (Fig. 1; see Hilton 2003). Within the upper Campanian "El Gallo" Formation,

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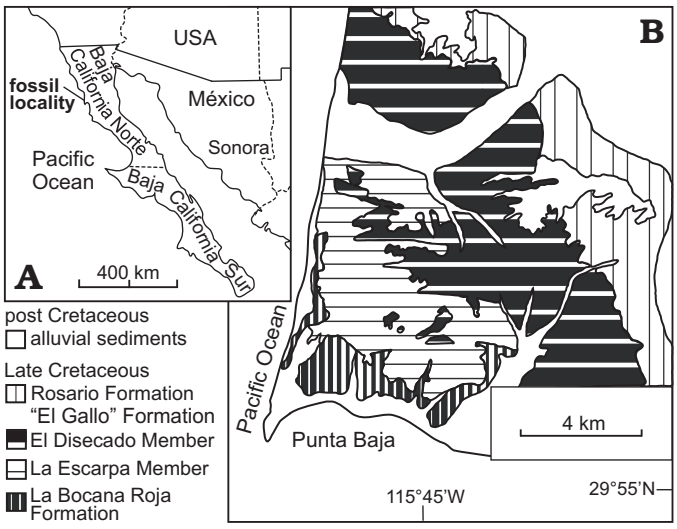


Fig. 1. Generalized geography and stratigraphy of the study area. **A**. Geographic map of southwestern North America with fossil locality marked. **B**. Stratigraphic map of the area around El Rosario. Modified from Renne et al. (1991).

they found fossil remains of mammals, turtles, lizards, crocodilians, and dinosaurs, including hadrosaurs, ankylosaurs, birds, and different-sized non-avian theropods (Morris 1968, 1973; Lillegraven 1972, 1976; Brodkorb 1976). Importantly, Morris (1967:1540) noted that large serrated teeth found in the "El Gallo", "resemble the late Cretaceous predator *Gorgosaurus*." It was suggested that the "El Gallo" fauna had close ties to those of the Western Interior of North America, but was itself unique, a combination of interior and possibly endemic forms (Morris 1967, 1973; Lillegraven 1972). The expeditions recovered additional dinosaurian fossils from the underlying La Bocana Roja Formation including hadrosaurian remains as well as pelvic and cranial material from a distinct large-bodied theropod, *Labocania anomala*, which was hypothesized to be a tyrannosaurid based on its pneumatic quadrate and ischial characters (Molnar 1974).

In 2004, crews from the University of California Museum of Paleontology, Universidad Autónoma de Baja California, and Universidad Nacional Autónoma de México led by two of us (GPW and MM) resumed collection of vertebrate fossils in the "El Gallo" and La Bocana Roja formations. Field work, which has also included crews from the Denver Museum of Nature & Science and now includes crews from the University of Washington, is ongoing and has led to the recovery of new material, including mammals (Wilson et al. 2011), a scincomorph lizard (Montellano et al. 2005), and the tyrannosaurid described herein.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BHI, Black Hills Institute, Hill City, South Dakota, USA; BMRP, Burpee Museum of Natural History, Rockford, Illinois, USA; CMI, Children's Museum of Indianapolis, Indianapolis, Indiana, USA; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IGM, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, México; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Los Angeles County Museum, Los Angeles, California, USA; LH, Long Hao Institute of Geology and Paleontology, Hohhot, China; MIWG, Museum of Isle of Wight Geology, Isle of Wight, England, United Kingdom; MOR, Museum of the Rockies, Bozeman, Montana, USA; MPC, Mongolian Paleontological Center, Ulaan Bataar, Mongolia; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RMM, Red Mountain Museum, Birmingham, Alabama, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

Within Baja California most Cretaceous vertebrate remains have been recovered from the "El Gallo" Formation (Morris 1973; Fig. 1). Kilmer (1963) coined the formational name "El Gallo" as a part of an unpublished Ph.D. dissertation, and so the name remains an informal designation that will appear in quotation marks hereafter. The "El Gallo" Formation, which ranges from 500 to 1300 meters in thickness, is underlain by the non-marine La Bocana Roja Formation and overlain by the marine Rosario Formation. All three formations are a part of the Rosario embayment of the Late Cretaceous Peninsular Range forearc basin complex (Renne et al. 1991). Kilmer's dissertation partitioned the "El Gallo" Formation into the La Escarpa, El Disecado, and El Castillo members (Fig. 2). Renne et al. (1991) analyzed sanidine crystals from four tuffs within La Escarpa and El Disecado members using $^{40}Ar/^{39}Ar$ geochronology. The statistically distinct age determinations range from 75.21 ± 0.07 Ma and 74.55 ± 0.09 Ma (Renne et al. 1991; published ages here converted using 28.201 Ma for the Fish Canyon Sanidine from Kuiper et al. 2008). This confirms a late Campanian age for the "El Gallo" Formation, which had been inferred from fossil evidence (Morris 1967). Vertebrate fossils, including dinosaurs and mammals, have been recovered from the El Disecado Member between the two upper tuffs that were sampled by Renne et al. (1991).

The El Disecado Member, up to ca. 1150 m thick, is composed of inter-fingering layers of massive light brown sandstone and gray siltstone thought to represent tidal/beach and sandy low-sinuosity fluvial systems, respectively (Renne et al. 1991). The sandstone is well sorted and contains wa-

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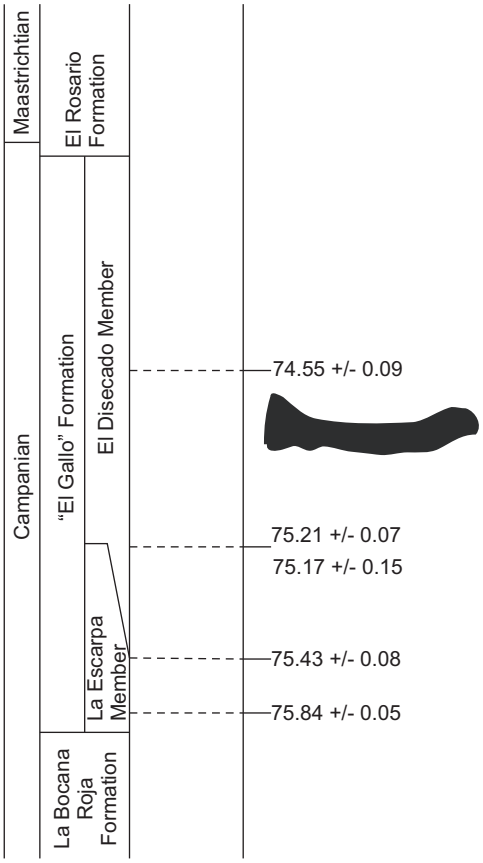


Fig. 2. Stratigraphic column of the La Bocana Roja, "El Gallo", and El Rosario formations in the area of El Rosario, Baja California, México. $^{40}Ar/^{39}Ar$ ages are from tuffs dated by Renne et al. (1991), but updated based on more recent data from Kuiper et al. 2008. See text for details. Bone icon indicates stratigraphic height of IGM 6130.

terborne wood and bone, which is interpreted as evidence for a beach environment (Morris 1973). The Baja coastline during the upper Campanian must have been relatively stable, because sandstone containing ammonites and other marine invertebrates is inter-fingered with siltstone containing the remains of terrestrial vertebrates (Morris 1973).

Evidence from paleomagnetism (Dickinson and Butler 1998; Gehrels et al. 2002), lithology (Gehrels et al. 2002), vertebrate paleontology (Lillegraven 1972), and micropaleontology (Helenes and Téllez-Duarte 2002) supports the claim that Baja California was positioned near its present location in northwest México from at least the Campanian onward. Dinoflagellates and planktonic foraminiferal microfossils place Baja California in the Central Temperate Zone (i.e., north of the Tropic of Cancer) during the upper Campanian, where it remains today (Helenes and Téllez-Duarte 2002). The current coastline is also roughly where it was in the upper Campanian (Durham and Allison 1960; Carreño and Smith 2007). However, because the Baja California plate did not begin rifting west- and northward until the Miocene (Atwater 1970), the Upper Cretaceous non-marine deposits near El Rosario were formed when the region was contiguous with mainland Mexico.

Systematic paleontology

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Coelurosauria Huene, 1914
Tyrannosauroidea Osborn, 1905
Tyrannosauridae Osborn, 1905
Tyrannosauridae gen. et sp. indet.

Material.—IGM 6130, a left metatarsal IV (Fig. 3) from locality Arroyo del Rosario, outside the town of El Rosario, Baja California, México (Fig. 1). An overbank deposit in the sandstone/siltstone El Disecado Member of the "El Gallo" Formation, which is bracketed by age determinations of 75.21 ± 0.07 Ma and 74.55 ± 0.09 Ma (late Campanian; Renne et al. 1991).

Remarks.—Two features support this referral: the proximal articular surface of metatarsal IV bears a deep, pointed medial notch that articulates with the crescent-shaped proximal end of metatarsal III; and the posterior surface of the shaft is slightly concave between the facet for metatarsal III on the medial surface of the shaft and the M. gastrocnemius lateralis insertion site on the posterior surface of the shaft (see Discussion below).

Description.—IGM 6130 is a complete left fourth metatarsal (Fig. 3). Its total length is 391 mm, and its circumference is 150 mm at midshaft. The minimum circumference (140 mm) is present in two regions of the shaft: above the proximal point of the teardrop articulation for metatarsal III and just above the distal condyle (Table 1). The bone has excellent preservation of surface detail, but there is moderate damage to the perimeter of the proximal end and posterior portion of the distal condyle. The shaft is relatively straight, with the exception of its distal one-fifth, which sharply angles laterally approximately 10º as in *Tyrannosaurus rex* (FMNH PR2081). The lateral divergence of the distalmost portion of the shaft is not noticeable in lateral or medial view, in which the shaft appears straight.

The proximal surface of metatarsal IV is shaped like a U (Fig. 3E). The rounded portion of the U faces laterally, and

Table 1. Length, circumference, and width measurements (in mm) of IGM 6130, a tyrannosaurid left fourth metatarsal.

Length of metatarsal IV	391.0
Proximal surface, circumference	240.0
Proximal surface, anteroposterior width	76.8
Proximal surface, mediolateral width	69.2
Midshaft, circumference	150.0
Midshaft, anteroposterior width	43.2
Midshaft, mediolateral width	42.7
Distal surface, circumference	193.0
Distal surface, anteroposterior width	47.4
Distal surface, mediolateral width	60.5

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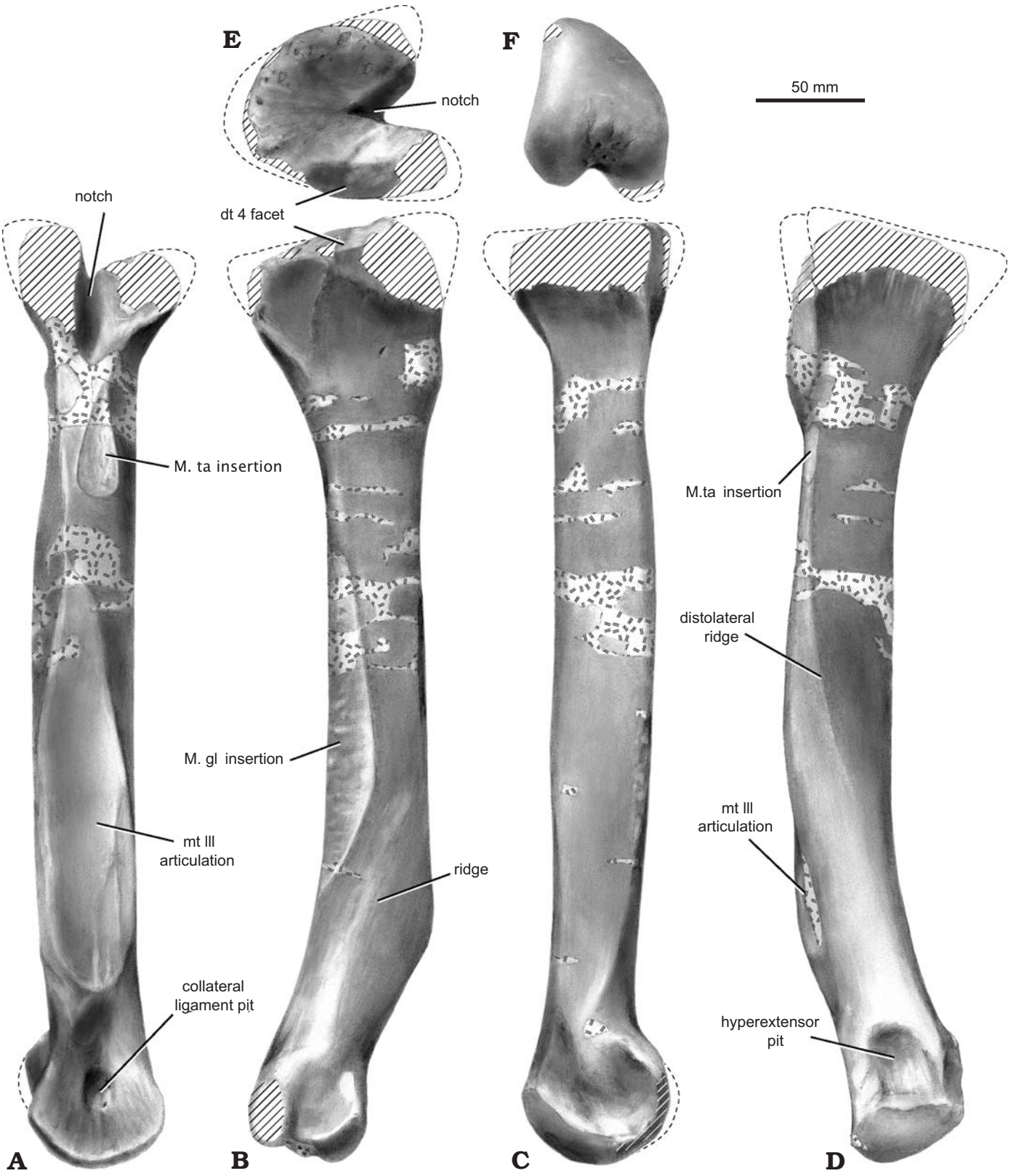


Fig. 3. Left metatarsal IV of the Campanian tyrannosaurid (IGM 6130) from Baja California, México, in medial (**A**), posterior (**B**), lateral (**C**), anterior (**D**), proximal (**E**), and distal (**F**) views. Anterior is toward the top of the page in E and F. Diagonal line pattern indicates broken bone surface; hatching pattern indicates reconstructed areas; dashed lines indicate inferred extent of the bone. Inferred attachment sites for M. gastrocnemius lateralis (M. gl) and M. tibialis anterior (M. ta) based on reconstruction of *Tyrannosaurus* hindlimb musculature by Carrano and Hutchinson (2002).

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there is a deep notch on its medial side. In tyrannosauroids such as *Tyrannosaurus*, the medial notch receives the crescentic proximal end of metatarsal III (Brochu 2003; Holtz 2004), and the anteromedially-directed arm of the U contacts metatarsal II anterior to metatarsal III, which is a feature of the arctometatarsalian complex (Holtz 1994). Weathering has removed evidence for this articulation from the Baja metatarsal (IGM 6130). The posteromedial corner of the proximal surface is also weathered, though less severely. The posteromedial portion of the proximal surface of metatarsal IV bears a well-marked articulation for distal tarsal 4, which was not recovered. The anterolateral rim of the proximal surface is pitted with many small openings that are a few millimeters in diameter.

The medial side of the shaft of metatarsal IV has an elongated, teardrop-shaped articular facet for metatarsal III (Fig. 3A). This facet, which is oriented with the point directed proximally, starts roughly one-third of the way down the shaft and extends to where the axis of the shaft diverges laterally near its distal end. The edges of the facet are raised on the anterior margin around the midpoint of the metatarsal, but on the posterior margin more distally, and the interior of the facet bears a roughened texture. Between the proximal notch for metatarsal III and the teardrop articular facet is an ovoid rugosity that is roughly twice as long as it is wide. This rugosity marks the insertion site for M. tibialis anterior (Carrano and Hutchinson 2002).

The posterior surface of the shaft of metatarsal IV is flat transversely and is set off from the medial and lateral margins of the shaft by sharp corners (Fig. 3B). The most noticeable feature of the posterior surface of the shaft is a sharply pointed, elliptical rugosity, about 120 mm long, lying along its lateral border. The rugosity is centered on the midpoint of the shaft and is well textured, most heavily along the lateral border. This rugosity represents the insertion site for M. gastrocnemius lateralis (Carrano and Hutchinson 2002). The area between this rugosity and the teardrop articular facet for metatarsal III on the medial side of the shaft is slightly concave. A low ridge rises from the medial margin of the midshaft and reaches a maximum thickness of ca. 10 mm before merging with the distal condyle. A similar distolaterally-trending ridge is present on the anterior surface but disappears at the lateral flaring of the distal fifth of the bone.

The shaft is pinched anteroposteriorly above the distal condyle to 140 mm, 10 mm less than the midshaft circumference. This feature is most prominent in lateral view and least prominent in posterior view. The articular surface itself, when viewed distally, is asymmetrical with the medial condyle broader transversely and anteroposteriorly longer than the lateral condyle (Fig. 3F). Between the two condyles open a dozen or so pits similar to those on the proximal surface of the metatarsal. The lateral collateral ligament pit, which is weakly developed, and the anterior hyperextensor pit are connected distally by a depression, together creating a larger roughly U-shaped depression just above the distal condyle (Fig. 3C, D). This U-shaped depression lies just dorsal to the distal articular surface on the shared anterolateral face of the shaft. This depression can be seen in *Tyrannosaurus rex* (FMNH PR2081), although it is much more compressed proximodistally. The collateral ligament pit on the medial side of the distal shaft is well marked and ovoid in shape. It is deep, with vertical walls on three sides and a gentle slope proximally that extends towards the teardrop articulation for metatarsal III.

Discussion

Identification of the Baja tyrannosaurid.—IGM 6130 is a tyrannosaurid dinosaur, based on the presence of synapomorphies of that and more inclusive clades. The presence of a medial notch on the proximal end of metatarsal IV to accommodate metatarsal III is an important characteristic of the arctometatarsalian metatarsus (Holtz 1994), which is present in ornithomimosaurs, troodontids, caenagnathid oviraptorosaurs, and a subset of tyrannosauroids, including Tyrannosauridae, *Dryptosaurus* (AMNH 2438) and *Raptorex* (LH PV18). Two features associated with the arctometatarsus indicate that IGM 6130 is a tyrannosauroid. In most tyrannosauroids, the proximal end of metatarsal III is crescentic and a pointed medial notch on metatarsal IV accommodates one point of that crescent (Holtz 2004). The rest of the crescent curves posteriorly toward the posteromedial corner of metatarsal IV. No metatarsal III was recovered for IGM 6130, but tyrannosaurids such as *Tyrannosaurus rex* (FMNH PR2081) have a pointed notch morphology nearly identical to IGM 6130. Ornithomimosaurs also have the arctometatarsalian condition, but metatarsal III is oval-shaped proximally, not crescentic. Therefore, the corresponding notch on metatarsal IV is not pointed, but smoothly curved (Holtz 1994, 2004). Another feature of the tyrannosauroid arctometatarsus that IGM 6130 possesses is the pronounced lateral divergence of the distal ends of both metatarsals II and IV (Brusatte et al. 2010: character 302), though IGM 6130 does not include metatarsal II. This feature is not present in caenagnathids, ornithomimosaurs, or troodontids. For example, metatarsal II of *Chirostenotes elegans* (MOR 752) is relatively straight in anterior and posterior view, with the distal end curving away from metatarsal III only slightly (Varricchio 2001). Furthermore, size likely precludes IGM 6130 being identified as a troodontid, because a metatarsal IV length of 391 mm is substantially larger than the known size range for that clade. This morphology allows us to assign IGM 6130 to Tyrannosauroidea among coelurosaurs with an arctometatarsalian metatarsus.

To further refine the phylogenetic position of IGM 6130 within Tyrannosauroidea, we scored and included it the matrix of Brusatte et al. (2010). The taxonomic scope of that analysis was Tyrannosauroidea, of which 19 genera were included along with four outgroup taxa. Nearly two-thirds of the characters are cranial features, and we could score IGM 6130 for only 5 out of the 307 characters (2%

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Table 2. Comparative lengths (in mm) of the long axis of tyrannosauroid fourth metatarsals (Philip J. Currie, personal communication 2012). IGM 6130 is referred to as the Baja tyrannosaurid.

Taxon	Number	mt IV length
Albertosaurus sp.	MOR 553	390
Albertosaurus sp.	MOR 657	485
Albertosaurus sarcophagus	AMNH 5233	426
Albertosaurus sarcophagus	CMN 11315	422
Albertosaurus sarcophagus	TMP 1999.50.24 - .26	448
Albertosaurus sarcophagus	AMNH 5234	452
Albertosaurus sarcophagus	TMP 1986.64.1	439
Albertosaurus sarcophagus	TMP 1985.98.1	465
Albertosaurus sarcophagus	AMNH 5231	510
Albertosaurus sarcophagus	AMNH 5232	521
Albertosaurus sarcophagus	TMP 1981.10.1	530
Albertosaurus sarcophagus	ROM 807	563
Albertosaurus sarcophagus	TMP 2003.45.34	250
Albertosaurus sarcophagus	TMP 2004.56.47	350
Albertosaurus sarcophagus	AMNH 5229	394
Albertosaurus sarcophagus	TMP 2004.56.43, 44, 45	440
Albertosaurus sarcophagus	AMNH 5228	465
Albertosaurus sarcophagus	TMP 1988.16.22	477
Albertosaurus sarcophagus	TMP 2002.45.47	480
Albertosaurus sarcophagus	UALVP 52074	480
Albertosaurus sarcophagus	AMNH 5235	486
Alectrosaurus olsoni	AMNH 6554	475
Appalachiosaurus montgomeriensis	RMM 6670	469
Baja tyrannosaurid	IGM 6130	391
Bistahieversor sealeyi	NMMNH P-25049	375
Daspletosaurus torosus	MOR 590	466
Daspletosaurus torosus	TMP 85.62.1	530
Daspletosaurus torosus	UALVP 11	490
Dilong paradoxus	IVPP V11579	108
Dilong paradoxus	IVPP V14243	112
Dryptosaurus aquilunguis	AMNH 2438	392
Eotyrannus lengi	MIWG 1997.550	260
Gorgosaurus	FMNH PR 2211	311
Gorgosaurus	CMI 2001.89.1	495
Gorgosaurus	BMRP R4279	445
Gorgosaurus libratus	AMNH 5423	426
Gorgosaurus libratus	TMP 91.36.500	435
Gorgosaurus libratus	TMP 99.33.1	490
Gorgosaurus libratus	ROM 1247	470
Gorgosaurus libratus	TMP 73.30.1	490
Gorgosaurus libratus	CMN 350	500
Gorgosaurus libratus	UALVP 10	515
Gorgosaurus libratus	TMP 94.12.602	515
Gorgosaurus libratus	AMNH 5432	545
Gorgosaurus libratus	CMN 11593	550
Gorgosaurus libratus	CMN 2120	574
Guanlong wucaii	IVPP 14531	185
Nanotyrannus lancensis	BMRP CC 2002.004.001	518
Raptorex kriegsteini	LH PV18	266
Tarbosaurus baatar	MPC-D107/05	351
Tarbosaurus baatar	ZPAL MgD-I/29	364
Tarbosaurus baatar	MPC 940823-Bgt-1	385
Tarbosaurus baatar	MPC-D	420
Tarbosaurus baatar	MPC-D100/61	445
Tarbosaurus baatar	MPC-D100/60	470
Tarbosaurus baatar	MPC-D107/02	490
Tarbosaurus baatar	ZPAL MgD-I/206	485
Tarbosaurus baatar	MPC-D100/63	505
Tarbosaurus baatar	MPC-D100/64	520
Tarbosaurus baatar (*efremovi*)	PIN 551-2	510
Tarbosaurus baatar (*novojilovi*)	PIN 552-2	395
Tyrannosaurus rex	UCMP 137539	570
Tyrannosaurus rex	CMI 2001.90.1	560
Tyrannosaurus rex	TMP 81.6.1	540
Tyrannosaurus rex	MOR 009	559
Tyrannosaurus rex	TMP 81.12.1, NMC 9950	605
Tyrannosaurus rex	MOR 555	608
Tyrannosaurus rex	BHI 6230	620
Tyrannosaurus rex	CMNH 9380 (AMNH 973) type specimen	600
Tyrannosaurus rex	FMNH PR2081	624
Tyrannosaurus rex	TMP 88.16.66	485

scored; characters 299[1], 302[1], 303[1], 304[1], 305[1] ordered). Characters 303 and 304 concern metatarsal II, but refer to character data that apply to metatarsal IV within an arctometatarsus. Despite the high level of missing data, IGM 6130 was resolved as the sister taxon to Tyrannosauridae in the analysis (tree length = 555; Consistency Index = 0.5476; Retention Index = 0.6107). However, we assign IGM 6130 to Tyrannosauridae based on features pertaining to the posterior surface of metatarsal IV and its robusticity that were not included in the Brusatte et al. (2010) matrix (see *Comparison* below). In non-tyrannosaurid tyrannosauroids, the area between the medial teardrop facet for metatarsal III and the posterior elliptical rugosity for insertion of the M. gastrocnemius lateralis is flat, as in *Dryptosaurus aquilunguis* (AMNH 2438), but in tyrannosaurids it is either concave or ridged. The early Campanian tyrannosauroid *Appalachiosaurus montgomeriensis* (RMM 6670) also displays the flat condition, whereas the Campanian–Maastrichtian tyrannosaurids *Gorgosaurus libratus* (AMNH 5423, 5432), *Albertosaurus sarcophagus* (ROM 1247), and *Daspletosaurus torosus* (NMC 8506) have a distinct ridge that follows the long axis of the bone. This area in IGM 6130 is slightly concave, much like in the tyrannosaurids *Teratophoneus curriei* (UMNH VP 16690) and *Tyrannosaurus rex* (FMNH

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PR2081). At this point, no assignment can be made beyond the level of Tyrannosauridae.

Comparison to other tyrannosauroids.—It has been noted by Holtz (2004), among others, that most synapomorphies of Tyrannosauridae are cranial in nature, though recent work (Brusatte et al. 2010) has put more emphasis on postcranial characters. This pattern holds for other late Campanian taxa as well, such as Ceratopsidae and Hadrosauridae, in which cranial elements have been sourced more frequently for character data than have postcranial elements. Although we cannot diagnose IGM 6130 beyond Tyrannosauridae, we can make meaningful comparisons to other tyrannosauroid metatarsals (Table 2).

Tyrannosauroids transitioned from small- to medium-sized mesopredators during the Jurassic and Early Cretaceous to enormous-sized apex predators in the Late Cretaceous (Madsen 1974; Xu et al. 2004, 2006; Sereno et al. 2009; Rauhut et al. 2010; Brusatte et al. 2010, but see Brusatte et al. 2011). The Baja tyrannosaurid (IGM 6130) is part of this transition, because its metatarsal IV is longer than all pre-Late Cretaceous tyrannosauroid taxa measured, including *Dilong paradoxus* (IVPP P11579, IVPP P14243), *Raptorex kriegsteini* (LH PV18), and *Eotyrannus lengi* (MIWG 1997.550). IGM 6130 is shorter than most Late Cretaceous tyrannosauroid genera, although its ontogenetic stage remains unknown. Larger taxa include forms from earlier in the Campanian, such as the poorly known *Alectrosaurus olsoni* (AMNH 6554) of Asia and *Appalachiosaurus montgomeriensis* (RMM 6670) of eastern North America (Appalachia), and Maastrichtian taxa such as *Albertosaurus sarcophagus* (AMNH 5233, ROM 807), *Tarbosaurus bataar* (PIN 551-2), and *Tyrannosaurus rex* (FMNH PR2081). The Baja tyrannosaurid metatarsal IV (IGM 6130) is most similar in length to that of the Maastrichtian tyrannosaurid *Albertosaurus sp.* (MOR 553) and the tyrannosauroid *Dryptosaurus aquilunguis* (AMNH 2438) from eastern North America.

The relatively small size of the Baja tyrannosaurid metatarsal raises the possibility that it is either a young individual or a new, small-bodied tyrannosaurid genus. Currently, there is not enough additional skeletal material available to rule out either of these hypotheses, which are not mutually exclusive.

Recent work on tyrannosauroid growth has demonstrated substantial ontogenetic changes that include an increase in the robusticity of the hind limbs as well as a lengthening and relative deepening of the skull (Carr 1999; Currie 2003; Currie et al. 2003; Carr and Williamson 2004; Holtz 2004). Adult tyrannosauroid hind limbs are, however, more gracile than other large-bodied theropod predators, such as spinosauroids and allosauroids (Carrano 1998; Currie 2000, 2003; Holtz 2004). Table 3 lists the robusticity index (RI = mid-shaft circumference/total length) of the metatarsal IVs of eight tyrannosauroid species. The RI of IGM 6130 is within the range of the albertosaurine tyrannosaurids *Albertosaurus* and *Gorgosaurus* measured and not with gracile non-tyrannosaurid tyrannosauroids. It is important to note that in addition to being similarly proportioned, IGM 6130 shares morphological features with tyrannosaurids to the exclusion of *Appalachiosaurus* (RMM 6670) and *Dryptosaurus* (AMNH 2438). It is especially interesting that *Appalachiosaurus* (RMM 6670) is less robust than IGM 6130 because its metatarsal is much longer. *Tyrannosaurus rex* (FMNH PR2081) is substantially more robust than the others. We hypothesize similar RI values between IGM 6130 and albertosaurine tyrannosaurids have phylogenetic significance related to increased robusticity in the hindlimbs of tyrannosaurids relative to non-tyrannosaurid tyrannosauroids.

Before the discovery of IGM 6130, the only non-dental evidence of large theropods reported from México was from *Labocania anomala*, which consists of a few massive skull bones and fragmentary postcranial remains that include an ischium collected from the La Bocana Roja Formation, which underlies the "El Gallo" Formation (Molnar 1974). Unfortunately, a metatarsal IV was not found with *Labocania*, although the distal end of a damaged metatarsal (LACM

Table 3. Robusticity indices (RI) for metatarsal IV of tyrannosauroids. RI is the ratio of the circumference at midshaft (in mm) and length (in mm). Measurements for *Dryptosaurus aquilunguis*, *Bistahieversor sealeyi*, and *Appalachiosaurus montgomeriensis* taken from Brusatte et al. (2011), Carr and Williamson (2010), and Carr et al. (2005), respectively.

Taxon	Number	Length	Circumference	RI
Alectrosaurus olsoni	AMNH 6554	477.0	133.0	0.2788
Bistahieversor sealeyi (juvenile)	NMMNH P-25049	374.8	111.4	0.2972
Albertosaurus sp.	AMNH 5229	381.0	123.0	0.3228
Dryptosaurus aquilunguis	AMNH 2438	392.0	130.0	0.3316
Appalachiosaurus montgomeriensis	RMM 6670	468.7	162.7	0.3471
Albertosaurus sp.	AMNH 5232	558.0	196.0	0.3513
Gorgosaurus libratus	AMNH 5432	542.0	193.0	0.3561
Albertosaurus sp.	AMNH 5233	440.0	157.0	0.3568
Baja tyrannosaurid	IGM 6130	391.0	150.0	0.3836
Albertosaurus sp.	AMNH 5235	496.0	197.0	0.3972
Albertosaurus sarcophagus	ROM 807	563.3	231.3	0.4106
Tyrannosaurus rex	FMNH PR 2081	624.0	316.0	0.5064

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6755/20877), likely metatarsal II, was preserved. It is slightly larger and more robust than the IGM 6130, but too fragmentary and poorly preserved to make more detailed comparisons. *Labocania* is enigmatic in that it has a number of tyrannosauroid-like features (e.g., pneumatic quadrate, semicircular scar on the posterolateral surface of the proximal ischium, triangular obturator process on the ischium; Holtz 2004) but also has tetanuran-like features (e.g., thick frontals, caudoventral angling of the quadrate; Molnar 1974). Holtz (2004: 133) remarked that these features are similar to the condition seen in some abelisaurid ceratosaurians, whereas other workers have noted that the combination of pneumatic quadrates and thick frontals is shared in some carcharodontosaurid allosauroids (Currie and Carpenter 2000; Coria and Currie 2006). The phylogenetic affinities of *Labocania* remain ambiguous and are beyond the scope of this work.

Late Campanian paleobiogeography in western North America.—On the basis of taxonomic differences among vertebrate faunas, Lehman (1997) hypothesized that during the late Campanian (Judithian) there was a northern and a southern biogeographic province in the Western Interior of North America. Taxonomic differences have been noted in a broad range of taxa, including chondrichthyans, actinopterygians, turtles, squamates, crocodilians, dinosaurs (Lehman 1997, 2001), and mammals (Weil 1999), though sister taxa occurring in separate "provinces" cloud this interpretation. Additional sampling in deposits like the Kaiparowits Formation of Utah and the Fruitland and Kirtland formations of New Mexico (Carr and Williamson 2010; Carr et al. 2011; Zanno et al. 2011) has improved the fossil database of late Campanian vertebrates from the Western Interior, such that rigorous tests of this paleobiogeographic hypothesis are possible. However, the fossiliferous formations of the Campanian Western Interior are not all contemporaneous (Roberts et al. 2005), so broad scale analyses of Campanian biogeography need to be done carefully to avoid comparison between non-coeval faunas, and therefore imprecise conclusions.

The vertebrate fauna from the "El Gallo" Formation, including the new tyrannosaurid material described here, adds new information to the late Campanian biogeographic layout of western North America, such as the occurrence of tyrannosaurids along the Pacific coast. The "El Gallo" Formation is from nearly as far south as the Aguja Formation of Texas. However, because of its location on the Pacific west coast of Laramidia and its relative geographic isolation from Western Interior basins, the "El Gallo" fauna might have a taxonomic composition distinctive from the Western Interior. Preliminary results from parsimony analysis of endemicity (PAE), parsimony analysis of endemicity with progressive character elimination (PAE-PCE), and cluster analysis (UPGMA) on non-mammalian microvertebrate fossil localities show that the "El Gallo" vertebrate fauna is more similar to the northern (Horseshoe Canyon) and central (Kaiparowits, Williams Fork) fluvial associations of the Western Interior than to the Terlingua local fauna of Texas (Romo de Vivar 2011). It must be acknowledged that temporal differences among Judithian faunas may also contribute to these results; the "El Gallo" local fauna is possibly three to six million years younger than the Terlingua local fauna (Wilson et al. 2010: fig. 1b).

In addition to the Baja tyrannosaurid described here, the "El Gallo" vertebrate fauna includes several other taxa. The large hadrosaurid *Lambeosaurus laticaudus* (Morris 1967, 1981) has recently been assigned to a unique genus, *Magnapaulia*, and found to be sister to *Velafrons coahuilensis*, which is known from northern México (Prieto-Marquez et al. 2012). Most other non-avian dinosaur remains are not identifiable beyond suprageneric levels. These include hadrosaurid bones and teeth, an ankylosaurid scute, tyrannosauroid-sized teeth, and smaller theropod teeth attributed to dromaeosaurids, troodontids and *Richardoestesia* (Hilton 2003; Romo de Vivar 2011). Among the mammalian taxa from the "El Gallo" fauna, the multituberculates *Mesodma* cf. *M. formosa*, *Cimolodon* sp. (Wilson et al. 2011), and the metatherian *Pediomys* (Lillegraven 1972) are known from northern and southern localities along the Western Interior. The multituberculate ?*Stygimys* (Lillegraven 1972) has only otherwise been reported from the Paleogene of the northern interior, whereas the lone eutherian, *Gallolestes pachymandibularis* (Lillegraven 1976; Clemens 1980), has a congener (*G. agujaensis*) from the Terlingua local fauna of Texas (Rowe et al. 1992; Cifelli 1994). The scincomorph lizard *Dicothodon bajaensis* (Nydam 1999, Nydam et al. 2007), which is now known from partial skulls and skeletons from the "El Gallo" Formation (Montellano et al. 2005), has congeners (*D. moorensis* and *D. cifellii*) from younger beds from Utah, further implying connections between the "El Gallo" and other areas of the Western Interior.

The occurrence of diagnostic tyrannosaurid postcrania in Baja California supports what had previously inferred from isloated teeth. A preliminary look at the taxonomic composition of the "El Gallo" fauna provides a unique paleobiogeographic signal relative to contemporaneous associations of the Western Interior, perhaps due to its geographic position along the Pacific.

Note added in proof

After this manuscript became available online, an unpublished tyrannosauroid metatarsal II also from the upper Campanian "El Gallo" Formation in the area around El Rosario was brought to our attention (Ralph Molnar, personal communication 2012). This bone, which was recovered by teams led by William Morris from the Los Angeles County Museum and Occidental College in the early 1970s, was originally accessioned to the L.A. County Museum but is now housed in Universidad Nacional Autónoma de México. The specimen (IGM 6260, formerly LACM 28237) has poor surface preservation, and the proximal one-fourth of the bone is badly damaged. Anatomical details, such as the posterolaterally directed notch for metatarsal III proximally, are very similar

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to the conditions seen in other tyrannosauroid metatarsal IIs (e.g., FMNH PR 2081, *Tyrannosaurus rex*) and corroborate Molnar's taxonomic assignment. The metatarsal II (IGM 6260) collected by Morris generally resembles the metatarsal IV (IGM 6130) described herein, but it is longer (480 mm vs. 391 mm) and less robust (RI = 0.3271 vs. 0.3836). Because instances of sympatry among Late Cretaceous tyrannosauroid species are rare and because of the morphological similarities of the two metatarsals, we hypothesize that the metatarsals probably pertain to the same taxon. The size difference suggests that IGM 6260 represents a larger and likely more mature individual than does IGM 6130.

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