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A New Tyrant Dinosaur from the Late Campanian of Mexico Reveals a Tribe of Southern Tyrannosaurs †

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Abstract: The end of the Cretaceous saw the Western Interior Seaway divide North America into two land masses, Laramidia in the west and Appalachia in the east. Laramidian dinosaurs inhabited a narrow strip of land extending from Mexico to Alaska. Within this geographically restricted area, dinosaurs evolved high diversity and endemism, with distinct species in the north and south. Here, we report a new tyrannosaurid from the Late Campanian-aged Cerro del Pueblo Formation of Coahuila, Mexico, which is part of a tribe of tyrannosaurs originating in southern Laramidia. Phylogenetic analysis recovers the new tyrannosaur as part of a clade including *Labocania anomala* from the La Bocana Roja Formation of Baja California Norte, *Bistahieversor sealeyi* from the Kirtland Formation of New Mexico, *Teratophoneus curriei* from the Kaiparowits Formation in Utah, and *Dynamoterror dynastes* from the Menefee Formation of New Mexico. Distinct frontal morphology and the younger age (~72.5–73 Ma versus >75.8 Ma for *L. anomala*) support recognition of the new tyrannosaur as a distinct species of *Labocania*, *Labocania aguillonae*. The *Labocania* clade dominated southern Laramidia at a time when the north was dominated by daspletosaurins and albertosaurines. The high endemism seen in tyrannosaurids is remarkable, given that modern apex predators have large geographic ranges and hints that the diversity of carnivorous dinosaurs has been underestimated.

Keywords: Tyrannosauridae; dinosauria; Campanian; Cretaceous; Laramidia

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1. Introduction

Tyrannosaurs dominated as apex predators in the late Cretaceous of western North America (Laramidia) [1–5]. During the Cenomanian [6] and Turonian [7] tyrannosaurs were relatively small, unspecialized, and low in diversity. By the Campanian, however, tyrannosaurs had undergone a major radiation, diversifying and producing larger, more specialized forms [1,4,5]. *Nanotyrannus* and its relatives were medium-sized predators with gracile skulls and slender limbs, suggesting specialization as pursuit predators [8,9]. The Tyrannosauridae [10,11] were larger, with highly reduced forelimbs, robust hindlimbs, and powerful jaws. The evolution of tyrannosaurids culminated at the end of the Cretaceous in the appearance of *Tyrannosaurus* [11], one of the largest, if not the largest, terrestrial predators ever to evolve [12].

As large-bodied apex predators, tyrannosaurids might be expected to have large geographic ranges. Geographic range size correlates positively with body size in extant mammals [13]; large-bodied animals such as elephants tend to have large geographic ranges. Carnivores tend to have larger geographic ranges than herbivores [13]. Lions, for example, once ranged across Africa into the Middle East and Europe [14] and tigers ranged from the Middle East into eastern Asia; wolves historically ranged throughout North America, Europe, and Asia [14].

By contrast, tyrannosaurids show a striking pattern of endemism in the late Campanian and early Maastrichtian. Species had restricted geographic ranges, and distinct

lineages occurred in northern and southern Laramidia. Canada and Montana were dominated by the subfamily Albertosaurinae and the basally-diverging tyrannosaurine tribe Daspletosaurini [15–17]. Derived tyrannosaurines dominated the American Southwest of Utah and New Mexico, including *Teratophoneus curriei* in Utah [18,19], and *Bistahieversor sealeyi* [20] and *Tyrannosaurus mcraeensis* in New Mexico [4]. These lineages are so far unknown from Alberta or Montana during this time.

Southern tyrannosaurs have remained poorly known compared to those of northern Laramidia [10,16,17,21,22], particularly those of Mexico. This is due to both preservational and study biases; northern formations tend to be more fossiliferous, but southern formations have also seen less fieldwork and study. Despite this, a number of records of Tyrannosauridae are known from the Late Cretaceous of Mexico.

Tyrannosaur teeth have been reported from the Aguja Formation of northern Coahuila [23,24]. In Sonora, tyrannosaur material has been reported dating to 86–73 mya [25]. In Baja California, the late Campanian aged El Gallo Formation has produced an isolated tyrannosaurid metatarsal [26]. From lower down, in the underlying La Bocana Roja Formation, comes the only tyrannosaur described so far from Mexico, *Labocania anomala* (IGM 5307). *Labocania* was the first carnivorous dinosaur described from Mexico [27] and, until now, the only associated large theropod. Despite this, the affinities of *Labocania anomala* have remained debated; in the original description, the animal was simply described as *Theropoda Incertae sedis*, but subsequent studies have remained ambivalent about its affinities noting affinities with Abelisauridae and Carcharodontosauridae [2]. As we show (below, and see Supplementary Materials), the anatomy of *Labocania anomala* and phylogenetic analysis definitively establish its affinities with Tyrannosauridae.

Finally, from the latest Campanian of the Cerro del Pueblo Formation of Coahuila, a number of isolated bones and teeth have previously been reported [28–30]. Associated remains are rare here, but in 2000, a partial tyrannosaurid skeleton was excavated from the Cerro Del Pueblo Formation. It has never been described until now. This specimen includes parts of the skull, vertebral column, hips and limbs and represents only the second associated tyrannosaurid from Mexico. Here, we describe this specimen and other tyrannosaur fossils from the formation as a new species of tyrannosaurine closely related to *Labocania anomala*.

Geology

The Difunta Group outcrops in northeastern Mexico in Coahuila and Nuevo León (Figure 1). Sedimentation here extends from the late Campanian to the Eocene [31–33]. The Difunta Group was deposited under deltaic conditions, with the delta draining into the ancient Gulf of Mexico to the East, and represents marsh, lagoonal, and eulittoral to shallow marine environments [34]. The upper Campanian Cerro del Pueblo Formation is the basal unit of this sequence.

Outcrops of the Cerro del Pueblo Formation in southeast Coahuila have a thickness of 162 m, with beds becoming thicker to the west, reaching a thickness of 445 m from Saltillo to Rincón Colorado [34]. The Cerro del Pueblo Formation strata here consist of shales, sandstones, and limestones deposited in a low gradient, homogeneous coastal plain [34]. Based on biostratigraphy and magnetostratigraphy, the Cerro Del Pueblo Formation is thought to date to the latest Campanian, ~72.5 Ma [34,35]. Strontium isotope dating gives an absolute age of 73 + 1 Ma for the Cerro del Pueblo Formation [36], which is in agreement with these estimates.

The stratigraphic sequence outcropping at the La Parrita locality is composed of alternating layers of sandstone, siltstone, and shale [37]. At the base of the outcrop, Bed 1 is comprised of 0.20 m of ochre-gray shales with greenish tones. Marine taxa such as the ammonite *Sphenodiscus* are associated with this layer and isolated, weathered dinosaur bones. *Sphenodiscus* is present in facies 1, corresponding to the Parras Shale [34], which is the base of the Cerro del Pueblo Formation [37]. Above the base is Bed 2, a 0.30 m layer consisting of exfoliated siltstones with a high concentration of oysters of diverse

sizes, indicating a brackish environment. The Cerro del Pueblo Formation's sandstone and siltstone deposits are, overall, characteristic of brackish conditions, as indicated by oyster banks and abundant non-ostrean bivalves and gastropods [36]. Above the siltstone lies Bed 3, a 0.90 m-thick hard, massive, coarse-grained sandstone bed with high concentrations of gastropods at the top, which indicates marine coastal environments [37]. Bed 4 is a grit layer 1 m thick, with a 0.40 m thick concentration of gastropods. Bed 5 consists of 10 m of ochre-gray shale characterized by a diverse fossil assemblage: the marine gastropods *Cerithium nodosa* and *Lissapiopsis* sp. are common, as well as oysters (*Flamingostrea* sp.), representing the most common invertebrates in this shale layer; wood fragments are also present, and vertebrate fossils [37]. De Jesus et al. [34] placed this fossil assemblage between facies 10–12. The assemblage is suggestive of overflooded coastal plains, and the marine and limnic faunal assemblages that coexist in this layer indicate an estuarine environment [36,37].

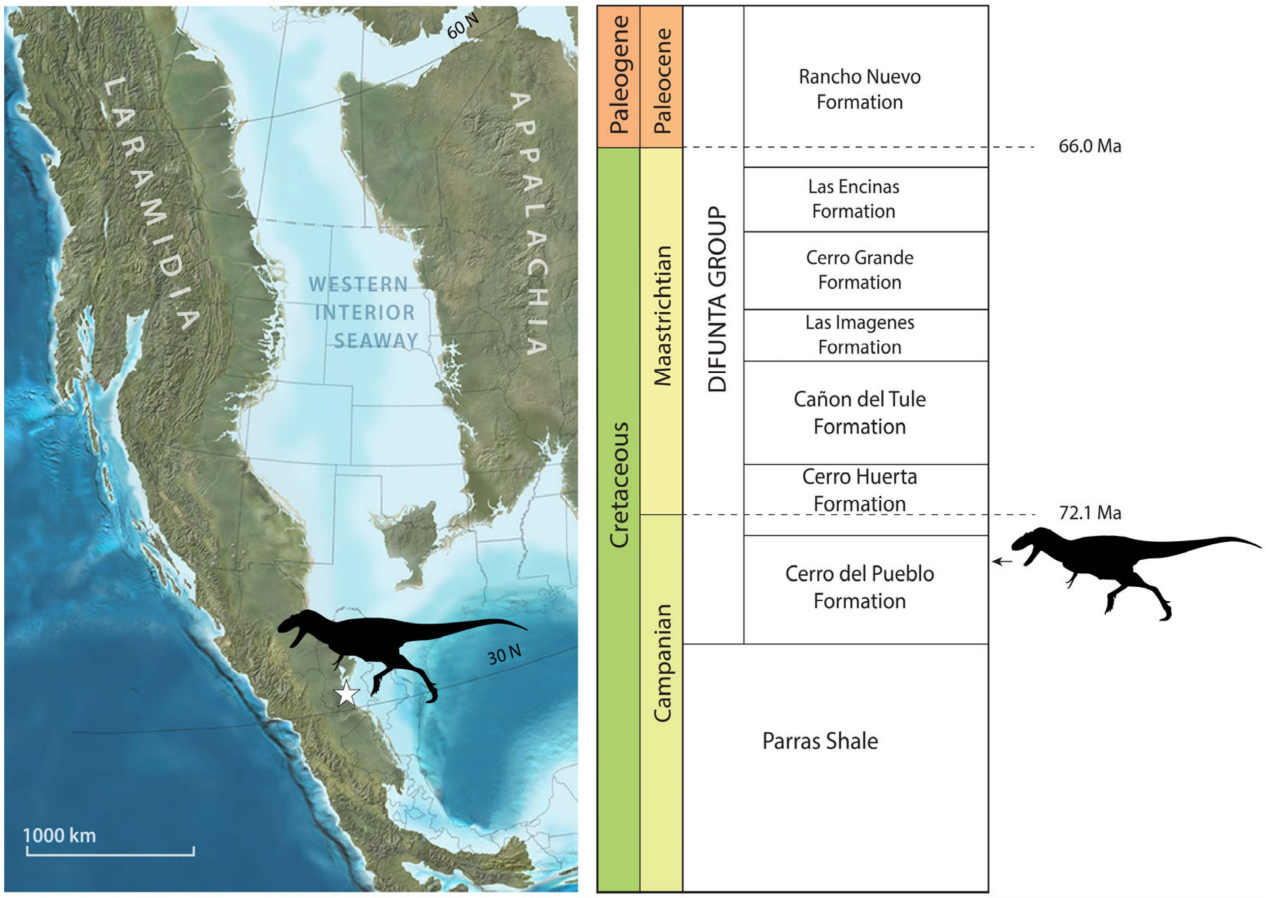


Figure 1. Left: Map showing the location of the holotype CPC 2974 in Coahuila, Mexico; Right: Stratigraphic column showing the location of the holotype CPC 2974 in the Cerro Del Pueblo Formation of Mexico.

The next layer, Bed 6, consists of 0.40 m of massive, gray, fine-grained sandstones, followed above by Bed 7, 0.50 m of dark-gray shale, and Bed 8, composed of 0.35 m of fine-grained sandstones [37]. The following Bed 9 is composed of 0.60 m of shale, then the next, Bed 10, contains 0.20 m of fractured sandstones. Above the fractured sandstone layer lies Bed 11, 32 m of shale, which is devoid of fossils. Above this shale layer, Bed 12, is a 3 m layer of massive medium-grained sandstones with high concentrations of bivalves, referred to *Inoceramus vamuxemi*, at the top of the layer. No other fossils are reported in this layer. Bed 13 consists of 18 m of t shales, and Bed 14 consists of 3 m of medium-grained sandstones. No fossils were observed in either layer [37].

Depositional at La Parrita was influenced by cyclically fluctuating paleoenvironments of intermittent shallow-marine, brackish to freshwater, or even subaerial conditions. The abundance of oysters throughout the Cerro Del Pueblo Formation suggests periodic mixing of salt- and freshwater, generating intermittent brackish environmental conditions with changing salinities [36]. This alternating sediment suggests the La Parrita locality underwent a series of events related to marine regressions and transgressions during deposition, consistent with other localities associated with the Cerro del Pueblo Formation [34].

Institutional Abbreviations. CPC, Coleccion Paleontologica de Coahuila, Museo del Desierto, Saltillo, Coahuila, Mexico; IGM, Institute de Geologia, UNAM, Ciudad Mexico, Mexico.

2. Materials and Methods

To assess the phylogenetic position of CPC 2974, the specimen was coded into an existing character-taxon matrix [4] with additional edits and codings for *Nanotyrannus* from Longrich and Saitta [9]; *Alioramus altai* and *A. remotus* were coded separately based on a previously published matrix [7]. A third state was added for Character 89 (frontal table twice as broad as long) as an ordered character, and *Nanuqsaurus* was recoded (state 3) for Character 97).

To this matrix, we added *Labocania anomala* [9] based on an extensive, first-hand restudy of the type material of IGM 5307. We added several additional characters and excluded characters 92 and 504, for a total of 517 characters. Characters were ordered where a clear evolutionary sequence can be hypothesized. Phylogenetic analysis was conducted using PAUP* 4.0 b 10 [38] using equally weighted parsimony. A second analysis was conducted, including UCM 55499, an isolated frontal from the Two Medicine Formation of Montana, previously referred to as *Daspletosaurus* [39].

3. Results

Systematic paleontology

Dinosauria—Owen 1842 [40]
Theropoda—Marsh, 1881 [41]
Coelurosauria—von Huene 1914 [42]
Tyrannosauridae—Osborn, 1906 [43]
Tyrannosaurinae—Osborn, 1906 [43]
Teratophoneini—Scherer & Voiculescu-Holvad, 2024 [44]
Labocania—Molnar 1974 [27]
L. aguillonae sp. nov.
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Etymology

The species name honors Martha C. Aguillón, discoverer of the specimen and a long-time career paleontologist of Coahuila.

Holotype

The holotype, CPC 2974 (Figures 2–9), consists of a fragment of the maxilla, left and right frontals, the ventral part of the left lacrimal, partial nasals, the posterior end of the left squamosal, fragments of a cervical vertebra, dorsal centrum, fragments of the sacrum, the posterior end of two caudal centra and a caudal neural arch, the left humerus, acetabular region of the left ilium, partial left ischium, left femur, proximal and distal ends of the left tibia, proximal end of the left fibula, left metatarsal II missing the distal end, pedal phalanges II-1, II-2, and III-3. The specimen is housed and registered in the Museo del Desierto, Saltillo, Coahuila, Mexico.

Referred specimens

Part of a left dentary, CPC 3077, including three alveoli and a replacement tooth (Figure 10); isolated teeth (Figure 11), CPC 3078-3091. These fossils do not overlap with the

holotype but are referred (albeit tentatively) to as *Labocania aguillonae* based on provenance and the autapomorphies of the dentition shared with the closely related *Labocania anomala*.

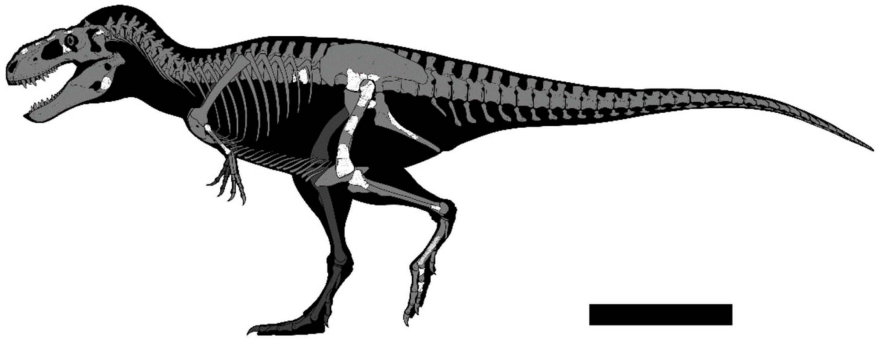


Figure 2. Skeletal reconstruction of *Labocania aguillonae* (CPC 2974) showing preserved material. Scale = 1 m.

Diagnosis

Tyrannosaurine diagnosed by the following character combination (*—autapomorphies): orbit large and circular, with a very strongly convex anteroventral margin of the lacrimal* with a prominent, strongly dorsally extended* subocular process on the lacrimal along the anteroventral margin of the orbit; strong posteroventral extension of the antorbital fossa onto the lacrimal to end below the anterior margin of the orbit; lateral ends of frontals with a very prominent, acutely triangular shape, with strong transversely expanded overlap of frontal onto lacrimal; broad anteromedial extension of supratemporal fossa extending far forward onto frontal*; strong medial projection of postorbitals behind frontals onto dorsolateral surface of postorbital process, such that frontal underlaps the postorbital anteriorly*, lateral teeth with a figure-eight basal cross-section, and deep, prominent grooves or fullers extending from the root up the labial and lingual surfaces of the crown.

Horizon and Locality

The upper part of the Cerro del Pueblo Formation, Latest Campanian; La Parrita, 54 km west of Saltillo; municipality of General Cepeda, Coahuila, Mexico (Figure 1).

Description

CPC 2974 consists of a highly fragmentary and weathered partial skeleton (Figure 2). Parts of the skull, including frontals (Figure 3), nasals, and lacrimals (Figure 4), are present, as well as postcranial elements (Figures 5–9), but many are broken or covered with desert varnish, suggesting the specimen suffered damage and loss of elements caused by prolonged exposure on the desert surface. Most of the elements are preserved for the left side only, suggesting the animal was preserved on its left side, and the elements of the right side were either eroded away or removed by scavenging prior to burial.

CPC 2974 is a relatively small animal by tyrannosaur standards (Table 1; Figure 2); it measures about 110 mm across the frontals; based on comparisons with *Bistahieversor sealeyi* [20], this suggests a skull ~775 mm in length. The preserved sections of the femur suggest the femur was ~700 mm long; assuming the proportions similar to *Teratophoneus curriei* [18], the CPC 2974 holotype was probably ~6.3 m long at the time of death.

The small size of the animal, the presence of extensive striated bone [45], and the lack of fusion between neural arches and vertebral centra [46] suggest CPC 2974 was immature at the time of death, although the relatively rugose bone of the maxilla, nasals, and lacrimal are consistent with a subadult or young adult [9]. The broken femur shaft reveals a series of concentric rings in the cortex, which appear to represent lines of arrested growth (LAGs). LAGs are relatively widely spaced near the center of the bone but more closely spaced towards the outside, suggesting decelerating growth [9].

Frontals. Both frontals are preserved (Figure 3). The left frontal is poorly preserved; the right frontal is mostly complete except for the nasal processes and parietal contact. Overall, the frontals closely resemble those of *Labocania anomala* and differ subtly in the shape of the postorbital process and in being less expanded posteriorly.

The frontals are characteristic of tyrannosaurids in being short and broad [10,18]. Both frontals are damaged anteriorly; however, the left frontal preserves a finished surface representing the nasal articulation. It is, therefore, possible to infer that the frontal table was short and broad, as in *Labocania anomala* [27], *Bistahieversor sealeyi* [20], *Teratophoneus curriei* [18], and other Tyrannosaurinae [18,47–49]. The frontals' dorsal surface is slightly concave, suggesting a median ridge anteriorly; there appears to be a sulcus here instead in *Bistahieversor*.

Table 1. Dimensions. * = incomplete.

Femur, maximum transverse diameter of shaft	69.2
Femur, maximum transverse diameter of distal end	124.1
Tibia, maximum anteroposterior width of proximal end	93.6 *
Tibia, maximum transverse width of proximal end	79.0
Tibia, maximum transverse width of distal end	115.0
Fibula, maximum anteroposterior width of proximal end	107.0
Fibula, maximum mediolateral width of proximal end	37.3
Dorsal vertebra, maximum anteroposterior length of centrum	90.0
Dorsal vertebra, maximum dorsoventral height of anterior face	88.7
Dorsal vertebra, maximum width of anterior face	71.7 *
Dorsal vertebra, maximum dorsoventral height of posterior face	74.8
Dorsal vertebra, maximum width of posterior face	74.9 *

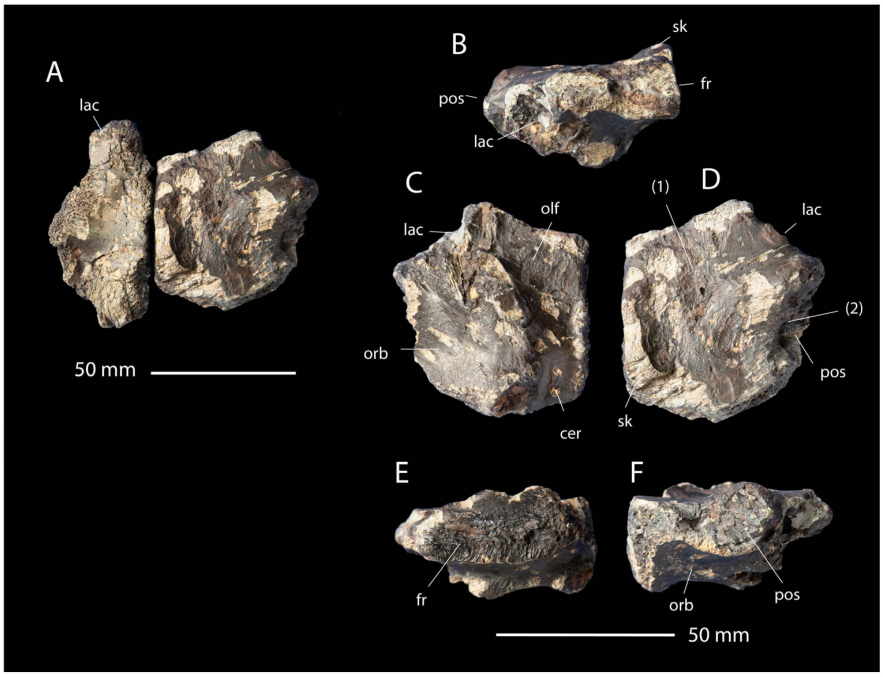


Figure 3. Frontals of *Labocania aguillonae* CPC 2974 holotype. (**A**) Paired frontals, right frontal in (**B**) anterior, (**C**) ventral, (**D**) dorsal, (**E**) medial, and (**F**) lateral views. Abbreviations: cer—cerebral fossa; fr—frontal–frontal suture; lac—lacrimal articulation; olf—olfactory fossa; orb—orbital fossa; pos—postorbital articular facet; sk—sagittal keel. Autapomorphies: (1), very strong anteromedial extension of supratemporal fossae; (2), postorbital facet dorsolaterally oriented for overlap of postorbital.

Frontals are almost entirely excluded from the orbits, forming a narrow slot between the prefrontal and postorbital contacts, as in other Tyrannosauridae [10,18,47,48]. The contact between the frontal and the lacrimal is oblique, such that the lateral tips of the frontals are triangular, where they project laterally between the prefrontals and postorbitals. A similar triangular shape of the postorbital processes is seen in *Labocania anomala* [27] and *Bistahieversor sealeyi*, although not developed to the same degree (Figure 12); it results from an anterior extension of the frontal over the lacrimal. An incipient version of this feature seems to occur in the Aguja tyrannosaurid, where a convex tab of the frontal projects over the lacrimal but does not extend medially [50]. By contrast, in other tyrannosaurids such as *Gorgosaurus* [10], *Teratophoneus*, and *Lythronax* [18], the frontal–lacrimal suture forms an L- or V-shaped notch with limited overlap of the frontal onto the lacrimal.

Posteriorly, the postorbitals projected inward behind the orbital notch, as in other tyrannosaurines. The postorbital suture is divided into a pair of facets: a deep anterior facet and a long posterior facet. The anterior facet is canted posteriorly and oriented dorsolaterally, rather than laterally, in contrast to other tyrannosaurines where it faces more laterally [47,48] so that the postorbital suture is strongly directed upwards and the postorbitals would overlap onto the frontals. This feature is an autapomorphy of *L. aguillonae*, although it appears to be approached by *L. anomala*. Posterior to this, there is a second facet where the postorbitals lap onto the dorsal surface of the frontal lateral to the supratemporal fossae, as in other tyrannosaurids.

As in other tyrannosaurids [10,18,47,48], there is a large supratemporal fossa where jaw adductor muscles extended forward to anchor to the frontals. The anterior margin of the adductor fossa is strongly sinusoidal, as typical of tyrannosaurines [18,47,48] and unlike the straighter margin seen in Albertosaurinae [10]. The adductor fossa extends strongly anteriorly and inward, limiting the contribution of the frontal table to the skull roof. This condition is approached in *Teratophoneus* [18] (although the anteromedial extension is narrower here), *Nanuqsaurus* [47,51], and Tyrannosaurini [48] but not in *Daspletosaurus* [52] or Albertosaurinae [10]. However, the strong anteromedial extension of the supratemporal fossae seen in *L. aguillonae* appears to be absent in other Teratophoneini, and so appears to be diagnostic.

The frontals rise up where the adductor fossae approach the midline, creating a large sagittal keel of the frontals, again as in Tyrannosaurinae. The supratemporal fossae extend almost horizontally behind the postorbital process, a primitive condition shared with *Labocania anomala*, whereas the supratemporal fossae slope posteriorly in *Nanuqsaurus* [47,51] and Tyrannosaurini [48].

In the medial view, the frontal is thick and massive, with a deep interfrontal suture where it contacts the other frontal. The thickened frontal and deep frontal articulation are shared with other teratophoneins, including *Labocania anomala* [27], the Aguja tyrannosaurid [50], *Teratophoneus curriei* [53], and *Dynamoterror dynastes* [49]; thick frontals also occur in *Tarbosaurus* [48]. Thickened frontals appear to be a tyrannosaurine apomorphy. Thickening of the frontals also appears to be size-related: juvenile *T. rex* have thin frontals [9] whereas large animals like *Labocania anomala* [27] and *Dynamoterror* [49] have massive frontals. Frontals of Albertosaurinae [10] show an intermediate condition, being thicker than those of small theropods such as dromaeosaurids and troodontids [54] but not as massive as in tyrannosaurines.

The frontal suture has a strongly convex ventral margin, with the frontal bulging down between the orbits. This strong ventral convexity of the frontal is shared with *Labocania anomala*, *Teratophoneus curriei* [53] the Aguja tyrannosaurid [50], and *Dynamoterror dynastes* [49]; this character appears to represent a synapomorphy of Teratophonei. Ventral convexity is present but much more weakly developed in other tyrannosaurids such as *Tarbosaurus* and Albertosaurinae [10], where the underside of the frontal is gently convex in medial view.

The inter-frontal articular surface bears a series of ridges and grooves arranged in a series of nested "V" or "U"s. These ridges would imbricate with the grooves of the other

frontal. This distinctive suture pattern is seen in *Labocania anomala* and other Tyrannosauridae [10,49,50,53] but not in other coelurosaurs [54]; it appears to represent a specialization of the tyrannosaurid skull and presumably reduced shearing movements between the frontals.

The frontal bears a pair of robust ventral flanges, which help form the lateral surface of the endocranial cavity and the medial surface of the orbit. There is a large socket-like articulation for the orbitosphenoid, similar to other tyrannosaurids. The development of these ventral flanges is comparable to *Labocania anomala*, *Teratophoneus curriei* [53], and the Aguja tyrannosaur [50], being reduced relative to the condition in *Albertosaurus* (in which these flanges contribute extensively to the endocranial cavity) but the orbital flanges are not reduced to the same degree as in *Tarbosaurus* [48].

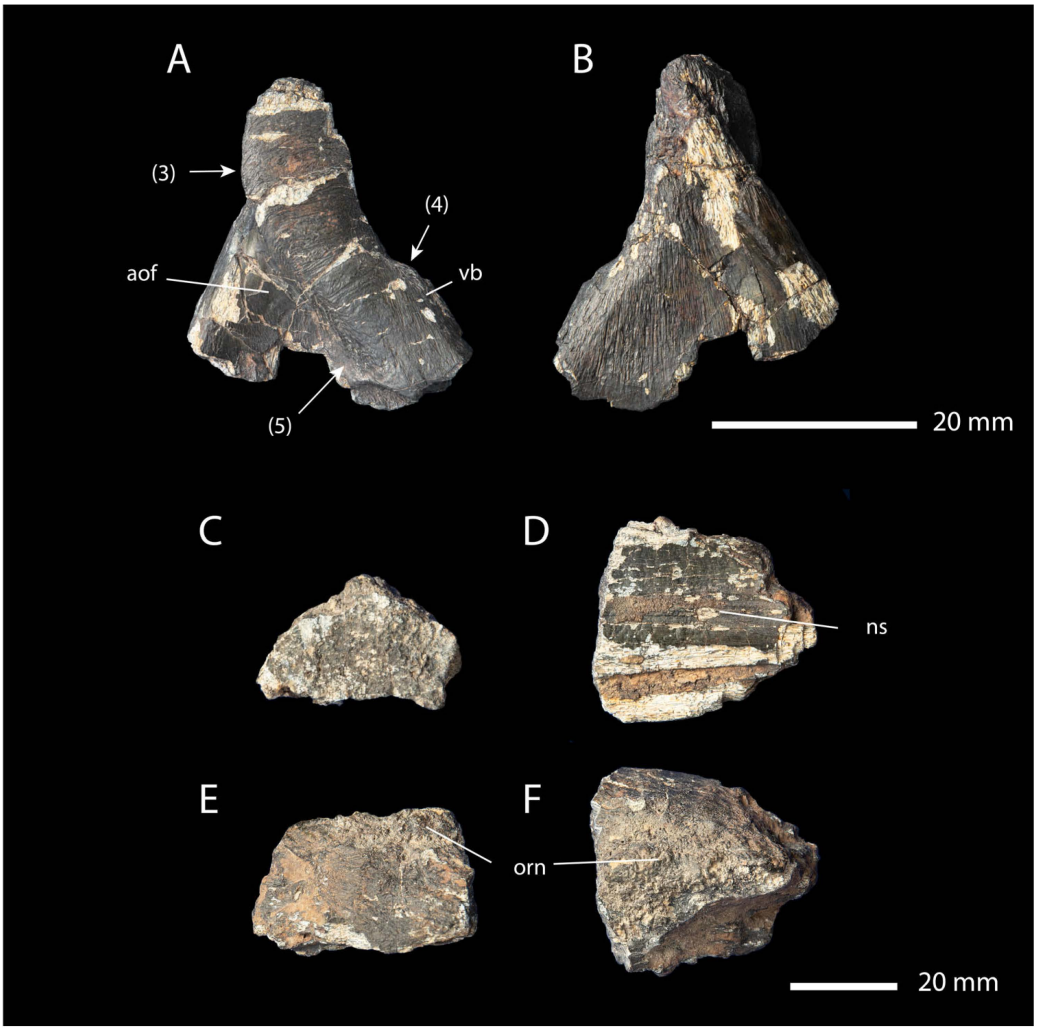


Figure 4. Left lacrimal of *Labocania aguillonae* CPC 2974 holotype in (**A**) lateral view, (**B**) medial view, nasals in (**C**) anterior view, (**D**) ventral view, (**E**) right lateral view, and (**F**) dorsal views. Abbreviations: aof—antorbital fossa; ns—nasal suture; orn—nasal ornament; vb—ventral boss. Autapomorphies: (3) strongly convex anterior margin of lacrimal, (4) dorsal extension of the ventral boss, (5) strong anteroventral extension of antorbital fossa.

Nasals. Several fragments of the nasals are preserved (Figure 4). Nasals are fused as in other tyrannosaurids and have the rugose dorsal surface that characterizes tyrannosaurids [10]. The cross-section of the nasals is D-shaped, with the nasals being very tall relative to their width. Strong transverse arching of the nasals characterizes the Tyrannosaurinae, including *Daspletosaurus* [17], *Lythronax* [18], *Bistahieversor* [20], *Tarbosaurus* [55]

and *Tyrannosaurus* [11]. The nasals are lower, wider, and less arched in Albertosaurinae [10], *Nanotyrannus* [8], and *Alioramus* [56].

Lacrimal. The ventral part of the left lacrimal is well-preserved (Figure 4). The anterior margin of the lacrimal is very strongly convex, to a greater degree than *Bistahieversor* [20] or other tyrannosaurines; this character represents an autapomorphy of *L. aguillonae*. The shape of the lacrimal suggests a relatively circular orbit, similar to *Bistahieversor* [20] and, to a lesser degree, *Teratophoneus* [18], and unlike the dorsoventrally elongated orbit of *Tarbosaurus* [55], *T. rex* [11], and *Daspletosaurus* [57]. A similar circular orbit is seen in Albertosaurinae [10] and *Nanotyrannus* [8,9].

The lacrimal becomes very broad ventrally, with the anteroventral surface of the bone being broadly covered by the posteroventral extension of the antorbital fossa. A well-developed antorbital fossa is shared with *Bistahieversor* [20], *Teratophoneus* [19], and *Daspletosaurus* [17]; the antorbital fossa has a highly reduced exposure on the lacrimal in *Tarbosaurus* [55] and *Tyrannosaurus* [11]. The antorbital fossa extends posteriorly far beneath the preorbital bar of the lacrimal [20], with the antorbital fossa ending just below the orbit's anterior margin. This posteroventral extension of the antorbital fossa is a derived feature of *L. aguillonae* that is shared with *Teratophoneus* and *Bistahieversor*. However, this feature is better developed in *Bistahieversor* than in *L. aguillonae* or *Teratophoneus*, with the antorbital fossa extended behind the anterior margin of the orbit in that species [20]. *Bistahieversor* is also unique in that the antorbital fossa extends inside the lacrimal to excavate it posteriorly rather than lying on its external surface. In *Teratophoneus*, other Tyrannosaurinae, and Albertosaurinae, the antorbital fossa of the lacrimal ends ahead of the external orbit.

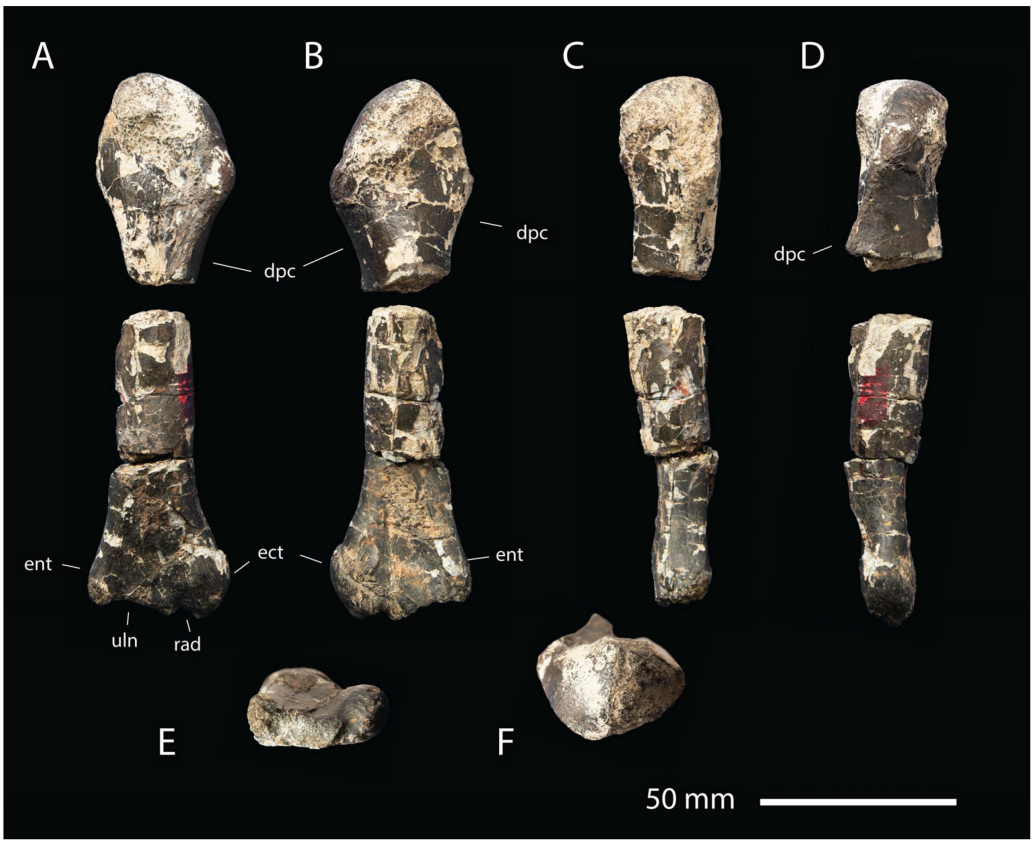


Figure 5. Left humerus of *Labocania aguillonae* CPC 2974 holotype in (**A**) anterior view, (**B**) posterior view, (**C**) lateral view, (**D**) medial view, (**E**) distal view, and (**F**) proximal views. Abbreviations: dpc—deltopectoral crest; ect—ectepicondyle; ent—entepicondyle; rad—radial condyle; uln—ulnar condyle.

There is a very prominent tubercle on the caudoventral margin of the lacrimal, which would have projected into the anteroventral part of the orbit. A similar tubercle is present

in *Bistahieversor* [20] but absent in *Teratophoneus* [19] and other tyrannosaurines [11,55,57]. The tubercle extends more dorsally in CPC 2974 than in *Bistahieversor*, an autapomorphy of *L. aguillonae*.

Vertebrae. A prezygapophysis and postzygapophysis come from a cervical vertebra or vertebrae. The postzygapophysis bears a prominent epipophysis as in other tyrannosaurids [11]. Otherwise, little can be said. A relatively well-preserved dorsal centrum is present. It is relatively elongated, and the anterior and posterior articular surfaces are tall. Fragments of the sacrum, including the sacral centra and the base of two fused neural arches are also preserved.

Humerus. The humerus (Figure 5) is well-preserved, but a small part of the shaft and part of the distal end are missing. The proximal end is bulbous and strongly projects proximally, similar to *T. rex* [11]. The shaft is massive, and the distal end is expanded, as in *T. rex*; the humerus of *Albertosaurus* is much more slender and reduced distally [58].

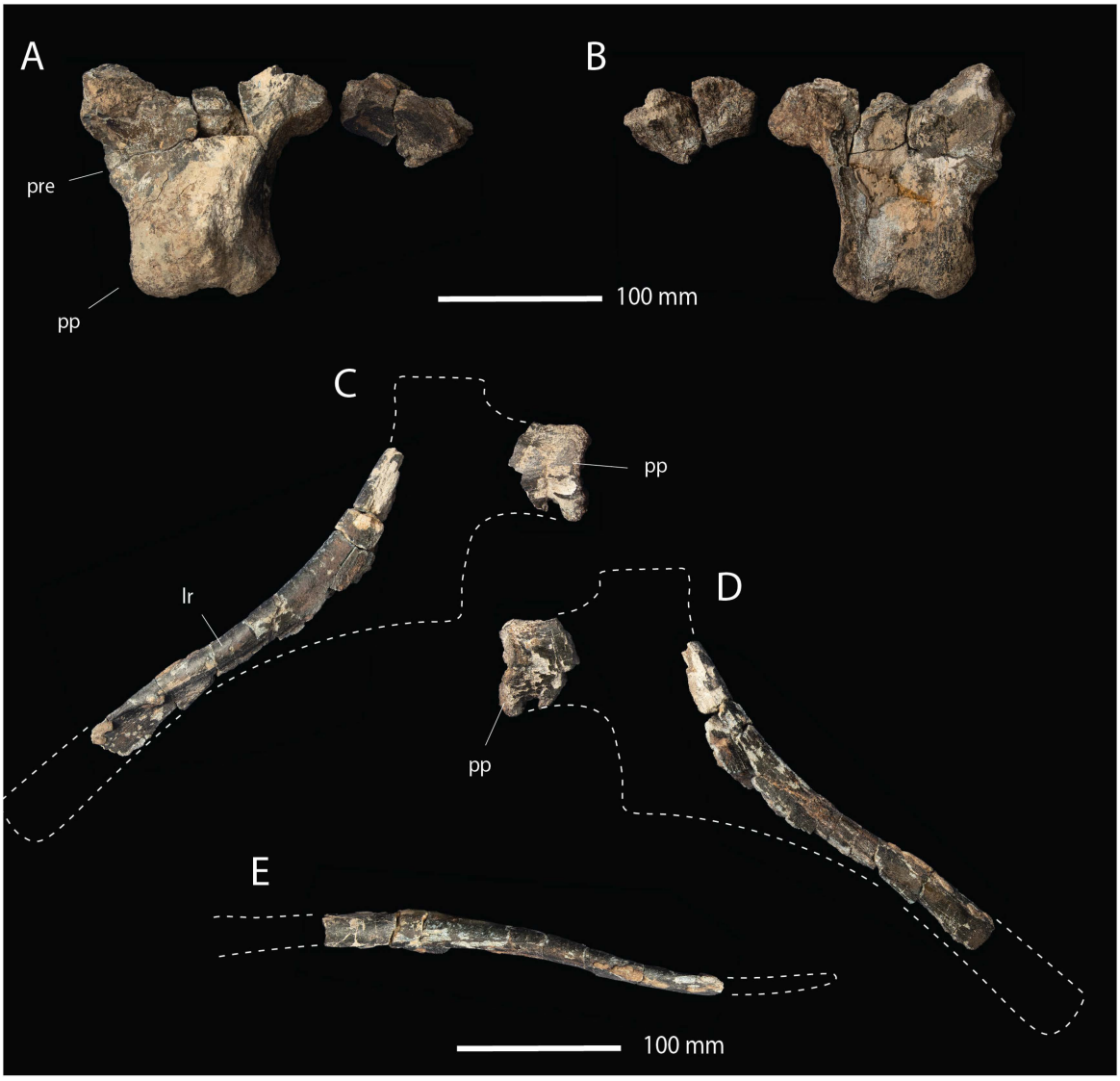


Figure 6. Left ilium of *Labocania aguillonae* CPC 2974 holotype; in (**A**) lateral view, (**B**) medial view, right ischium in (**C**) lateral view, (**D**) medial view, and (**E**) dorsal view. Pp—pubic peduncle, pre—preacetabular process, lr—lateral ridge.

Ilium. The ilium (Figure 6) is fragmentary, preserving only the pubic peduncle and the dorsal margin of the acetabulum. The pubic peduncle is distinctive in being rectangular in shape. Here, it closely resembles the pubic peduncle of *Teratophoneus* [18]. By contrast, the

pubic peduncle is anteroposteriorly expanded in other tyrannosaurs, e.g., *Tyrannosaurus* [11] and *Albertosaurus* [58], and the anteroventral margin of the pubic peduncle is inclined anteriorly, giving it a more triangular shape. The rectangular pubic peduncle and vertical orientation of the anterior margin seem to be a synapomorphy of Teratophoneini, although, unfortunately, the pelvis is unknown for most species.

Ischium. The ischiadic peduncle and the posterodorsal margin of the ischium are preserved (Figure 6). The posterodorsal margin of the ilium forms a thickened lip, while the main body of the ischium below this lip forms a thin plate, as in other tyrannosaurids. The posterodorsal margin of the ischium is distinctly curved upwards. A dorsally curved ischium is seen in *Labocania anomala* (IGM 5307) and *Teratophoneus* [18] but not other tyrannosaurines [11] or albertosaurines [58]. The curved shaft of the ischium appears to be a teratophonein synapomorphy.



Figure 7. Left femur of *Labocania aguillonae*, holotype CPC 2974 in (**A**) anterior view, (**B**) posterior view.

Femur. The femur (Figure 7) is missing the head and parts of the condyles, but otherwise, most of the femur is preserved. It was around 700 mm in length. A series of LAGs are present, widely spaced towards the inside of the cortex and more closely spaced towards the outside, suggesting decelerating growth. The femur is slender compared to that of the highly robust *T. rex* [11] and, in this respect, is more similar to *Teratophoneus* and *Albertosaurus* [58].



Figure 8. Left fibula *Labocania aguillonae* CPC 2974, holotype, proximal end in (**A**) proximal view, (**B**) medial view, (**C**) lateral view; distal end in (**D**) medial view, (**E**) anterior view, (**F**) lateral view. Distal left tibia in (**G**) posterior view, (**H**) anterior view, (**I**) distal view. Abbreviations: fos—fossa.

Tibia. The tibia's proximal and distal ends (Figure 8) are present but damaged; the shaft is missing. The proximal articular surface is sub-triangular in outline. The cnemial crest projects above the level of the proximal articular surface. It arises from the distal half of the bone and curves laterally, forming a broad antero-lateral fossa. Its lateral tip has an oval expansion with a broad notch to receive the proximal end of the fibula. Distally to the expanded tip, the cnemial crest continues onto the tibial shaft. The tibia's distal end is platelike and narrow, as in *Albertosaurus* [58], and unlike the strongly expanded distal tibia of *T. rex* [11].

Fibula. The proximal and distal ends of the left fibula (Figure 8) are well-preserved. The fibular head is crescentic in proximal view, and the proximal articular surface is concave in lateral view, in contrast to the notched articular surface of *T. rex* [11]. The posterior

end of the head is rounded versus angular in *T. rex* [11]. The slender shaft is D-shaped in cross-section, and the distal end is slightly expanded versus strongly expanded in *T. rex* [11].

Metatarsal II. The second metatarsal (Figure 9) is relatively complete except for the distal end. It is relatively gracile, flattened mediolaterally, and slightly bowed. It is gracile, more similar to *Albertosaurus* [58], than the robust metatarsus of *T. rex* [11].

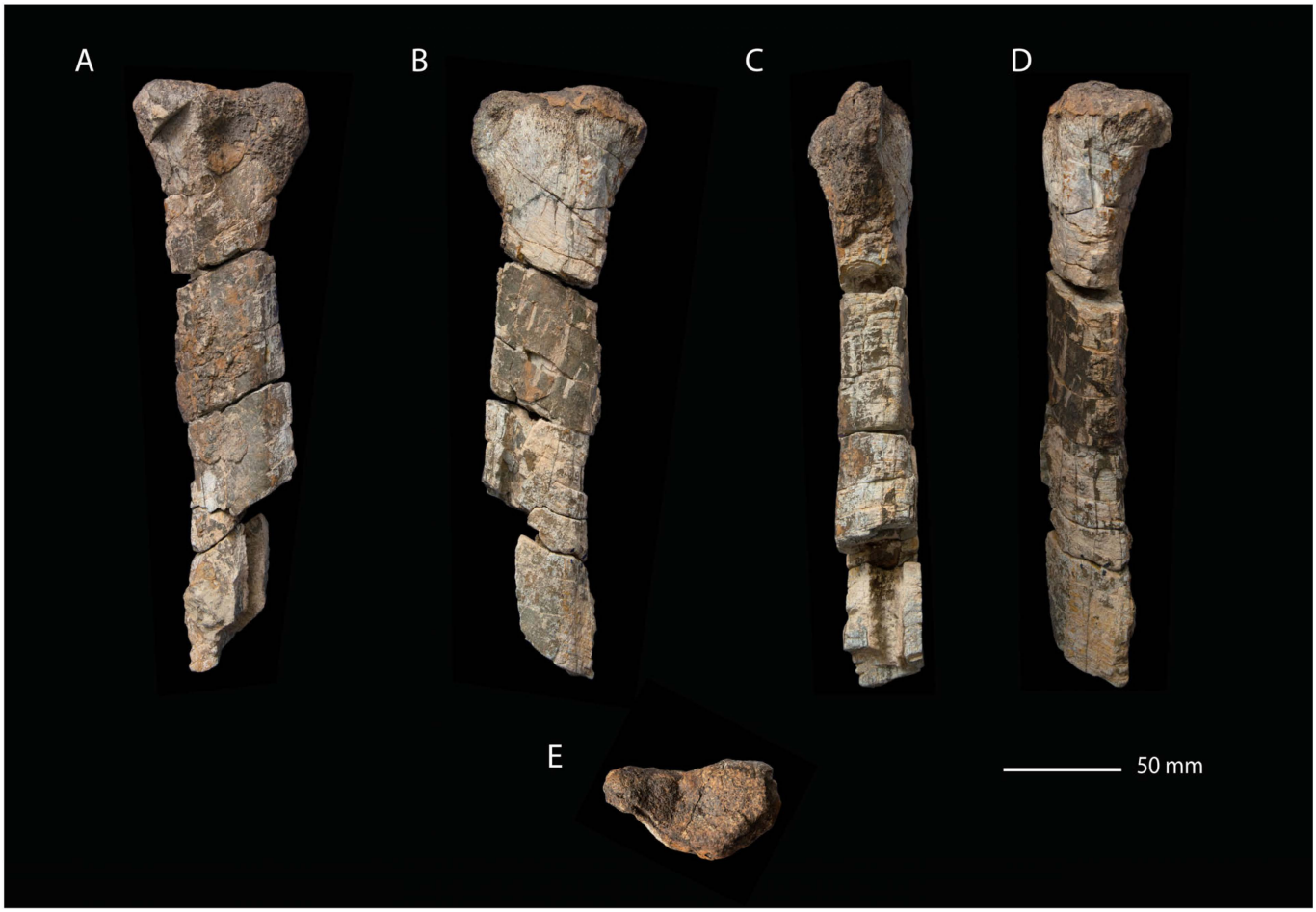


Figure 9. Left metatarsal II of *Labocania aguillonae* CPC 2974 holotype, in (**A**) medial view, (**B**) lateral view, (**C**) posterior view, (**D**) anterior view, and (**E**) distal view.

Pedal phalanges. Pedal phalanges II-1, II-2, and III-3 are preserved but do not differ appreciably from those of other tyrannosaurs.

Referred dentary. A partial dentary (CPC 3077) comes from a much larger animal than the holotype (Figure 10). Alveoli are ~40 mm in anteroposterior diameter. For comparison, the largest tooth *of Labocania anomala* measures 37 mm in FABL (fore-aft basal length); the largest tooth of *Bistahieversor sealeyi* [20] has a FABL of ~40 mm.

The dentary fragment came from an animal that approached *Bistahieversor* and *Labocania anomala* in size. *Bistahieversor* is estimated to have grown to approximately 8 m in length and had an estimated mass of 2.5 tons [59]; *Labocania anomala* may have been comparable in size.

The alveolus is not oval but instead pinched, suggesting a figure-eight-shaped section to the tooth crown, as seen in referred teeth of *L. aguillonae* (seen below) and *Labocania anomala* (IGM 5307). The lack of overlap between the CPC 3077 and the holotype makes a definitive referral impossible, but based on provenance, it seems more likely than not to represent *L. aguillonae*. The unusual shape of the alveoli suggests affinities between CPC 3077 and *Labocania anomala*, consistent with referral to *Labocania*.

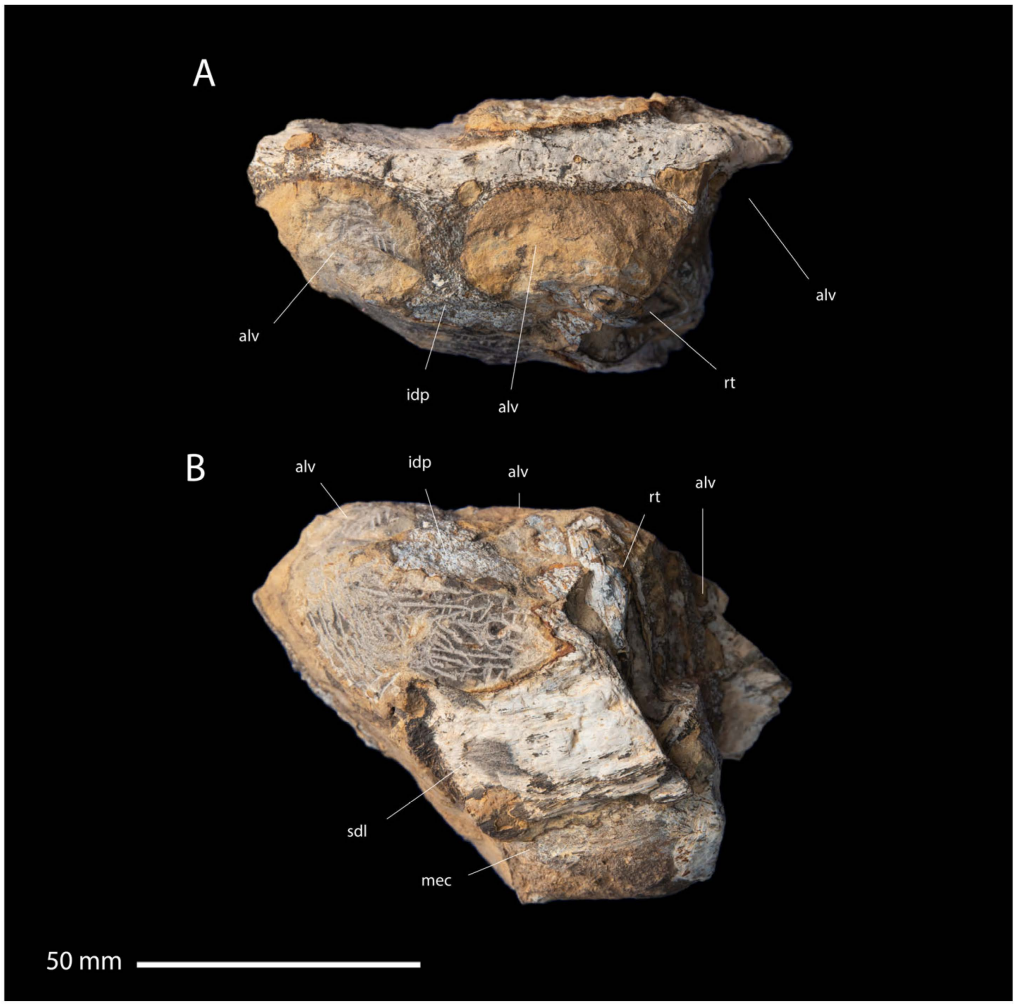


Figure 10. Left dentary fragment (CPC 3077) of cf. *Labocania aguillonae.* (**A**) Dorsal view and (**B**) medial view. Abbreviations: alv—alveolus, idp—interdental plate, mec—Meckelian groove, rt—replacement tooth; sdl—subdental lamina.

Referred teeth. Numerous isolated tyrannosaurid teeth have been recovered from the Cerro Del Pueblo Formation (CPC 3078-CPC 3091) (Figure 11). These teeth suggest a medium-sized tyrannosaurid; the maximum fore-aft basal length (FABL) of the largest teeth is 30–31 mm, somewhat smaller than the alveoli of the referred jaw. Based on size and provenance, they are tentatively referred to *L. aguillonae*.

The teeth are unusual in having deep grooves or fullers running up the crown (Figure 11). As a result, the base of the crown is distinctly pinched in ventral view, giving it a figure-8 shape. This feature is unusual among theropods. A slight pinching of the crown is seen in dromaeosaurids [60], but tyrannosaurids typically have either a rectangular section to the crown [61] or, in the case of *T. rex*, an inflated, ovoid section [61]. The strong pinching and fullers are uniquely shared with *Labocania anomala* (IGM 5307), consistent with the referral of these teeth to *Labocania*.

Phylogenetic Analysis

Phylogenetic analysis using maximum parsimony recovered 1260 most-parsimonious trees (Treelength = 1867 steps; Consistency index = 0.3664; Retention index = 0.7601). The Cerro del Pueblo tyrannosaurid is recovered as a sister to *Labocania anomala*—both are members of Tyrannosaurinae and Tyrannosaurinae and are recovered as part of the tribe Teratophoneini; the strict consensus topology is shown in Figure 12. The relatively large number of trees reflects the poor resolution of the highly fragmentary Aguja Formation and

Two Medicine tyrannosaurines, whose incompleteness means their phylogenetic position is difficult to resolve, but overall resolution is good.

Teratophoneini here includes *Labocania anomala*, *Bistahieversor sealeyi*, a tyrannosaurine frontal from the Two Medicine Formation, UCM 55499, and *Teratophoneus curriei* and *Dynamoterror dynastes* (Figure 13). *Labocania anomala* was strongly supported as a member of Tyrannosauridae; despite the incompleteness of the specimen, forcing it into Allosauridae required an additional 14 steps—forcing it into Ceratosauria required an additional 15 steps.

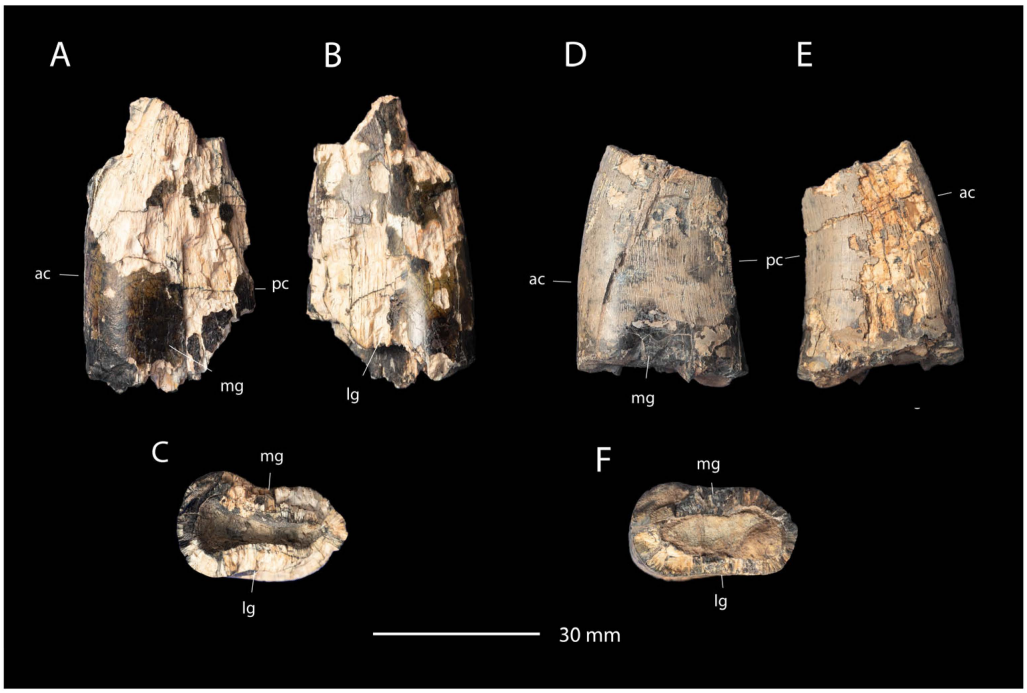


Figure 11. Teeth of cf. *Labocania aguillonae* CPC 3078 in (**A**) labial view, (**B**) lingual view, and (**C**) basal view, and CPC 3079 in (**D**) labial view, (**E**) lingual view, and (**F**) basal view. Abbreviations: ac—anterior carina, lg—lateral groove, mg—medial groove, pc—posterior carina.

4. Discussion

4.1. Ontogenetic Status

CPC 2974 appears to be immature and was probably a subadult or young adult. Neural arches and centra are found dissociated. Some bones exhibit striated textures (e.g., the lacrimal medial surface), suggestive of rapid growth [62], although striated bone can persist until relatively late in ontogeny [9]. Where the tibia has been broken, LAGs are visible, and the spacing appears to increase and then decrease again towards the surface of the bone, suggesting growth had begun to slow.

The jaw fragments and teeth seem to come from significantly larger animals. Assuming these do represent the same species, *Labocania aguillonae* grew much larger than the holotype; a large adult may have been comparable to *L. anomala* and *Bistahieversor sealeyi* in size. Although the holotype was immature, the size of the animal suggests it represents a subadult or a young adult, at which point most species-level diagnostic features are present [9] and therefore the type is diagnostic.

4.2. Systematics

The anatomy of CPC 2974 suggests it represents a tyrannosaurine, with affinities with Teratophoneini, and specifically *Labocania anomala*. Affinities with Tyrannosaurinae are indicated by the S-shaped anterior margin of the supratemporal fossa and well-developed frontal, sagittal crest, as well as the robusticity of the frontal. Within Tyrannosaurinae, CPC 2974 is recovered as sister to *Labocania anomala* from the La Bocana Roja Formation of Baja

California, *Bistahieversor sealeyi* from the Kirtland Formation of New Mexico, *Teratophoneus curriei* from the Kaiparowits Formation of Utah, and *Dynamoterror dynastes*. This clade has previously been named Teratophonei [44].

Labocania aguillonae and *L. anomala* are united by the shape of the frontal, specifically the broad and oblique frontal–lacrimal contact, and the distinctive upturned dorsal margin of the ischium (shared with *Teratophoneus*). The frontal–lacrimal contact is oblique rather than transverse, such that the frontal lateral ala has a triangular shape, a characteristic shared with *Bistahieversor* and *Labocania anomala*. The frontal has a more L-shaped margin where it contacts the lacrimal in other tyrannosaurines such as *Teratophoneus*, *Daspletosaurus*, *Lythronax*, and *Tarbosaurus* (Figure 12). Assuming the referred teeth do belong to *L. aguillonae*, the prominent 'figure-eight' shaped tooth bases, with prominent lateral sulci on the crowns, support affinities with *L. anomala* to the exclusion of *Bistahieversor sealeyi*, which appears to lack this character.

Labocania aguillonae also resembles *Bistahieversor sealeyi* [20] in the strong posteroventral extension of the antorbital fossa beneath the orbit and the subocular flange along the anteroventral margin of the orbit. Both characters are absent in *Teratophoneus* [18] but, unfortunately, cannot be assessed in *Labocania anomala*.

The strongly circular orbit of *L. aguillonae* is shared with *Bistahieversor* [20] but is not preserved in *Labocania anomala*. In *Teratophoneus,* the orbit is ovate [18], but it is not as highly circular. The transition from an ovoid to a more circular orbit from *Teratophoneus* to *Bistahieversor* suggests that teratophoneins reverted to a more primitive orbit shape. The distinctive square shape of the pubic peduncle in *L. aguillonae* is shared with *Teratophoneus* [18], but the ilium is unknown for either *Labocania anomala* or *Bistahieversor*.

Phylogenetic analysis recovers the Cerro del Pueblo tyrannosaurine, *Labocania anomala*, *Bistahieversor sealeyi*, the Aguja Formation tyrannosaur, *Teratophoneus curriei*, and *Dynamoterror dynastes* as members of a clade. This clade would be called Teratophoneini (Figure 12), corroborating a previous study suggesting the existence of a southern clade [44] but its membership is somewhat different from that originally conceived when the group was named [44]. Although many of these species are known from incomplete specimens, they share striking similarities in the skull, dentition, and pelvis.

Characters diagnosing teratophoneins include the shape of the lacrimal (posteroventral extension of the antorbital fossa), pubis (vertical anterior margin) and ischium (bowed ischium); characters of the frontals and teeth diagnose more exclusive clades within teratophoneins. The phylogeny recovered here, therefore, suggests the existence of a tribe of tyrannosaurines emerging from Mexico and the American Southwest. This clade is so far absent or rare from Alberta (Figure 12), but we note the existence of an isolated frontal from the Two Medicine Formation of Montana, previously referred to as *Daspletosaurus* [39], which closely resembles the Teratophonei and specifically *Labocania*. This raises the possibility that Teratophonei dispersed as far north as Montana, but if so, it appears that the group's diversity is still primarily southern and that the earliest members of the clade appear in the south. The group may not have been entirely endemic to the south, and yet may still have emerged from and diversified in the south.

Our analysis was able not just to replicate the finding of a distinct clade of *Teratophoneus*-like animals but also to find new characters that provide support for this phylogenetic hypothesis. However, given that most species are known from incomplete remains and that no species is known from a reasonably complete specimen, additional and more complete fossils and restudy of known teratophoneins are needed to test this hypothesis.

4.3. Diagnosis and Recognition of L. aguillonae

Despite the similarities seen here, a number of characters differentiate *L. aguillonae* from related Teratophoneini. *L. aguillonae* differs from *L. anomala* in having a more triangular, laterally projecting postorbital process of the frontal and in having a strong overlap of the postorbital onto the postorbital process, an autapomorphy of *L. aguillonae* (Figure 13).

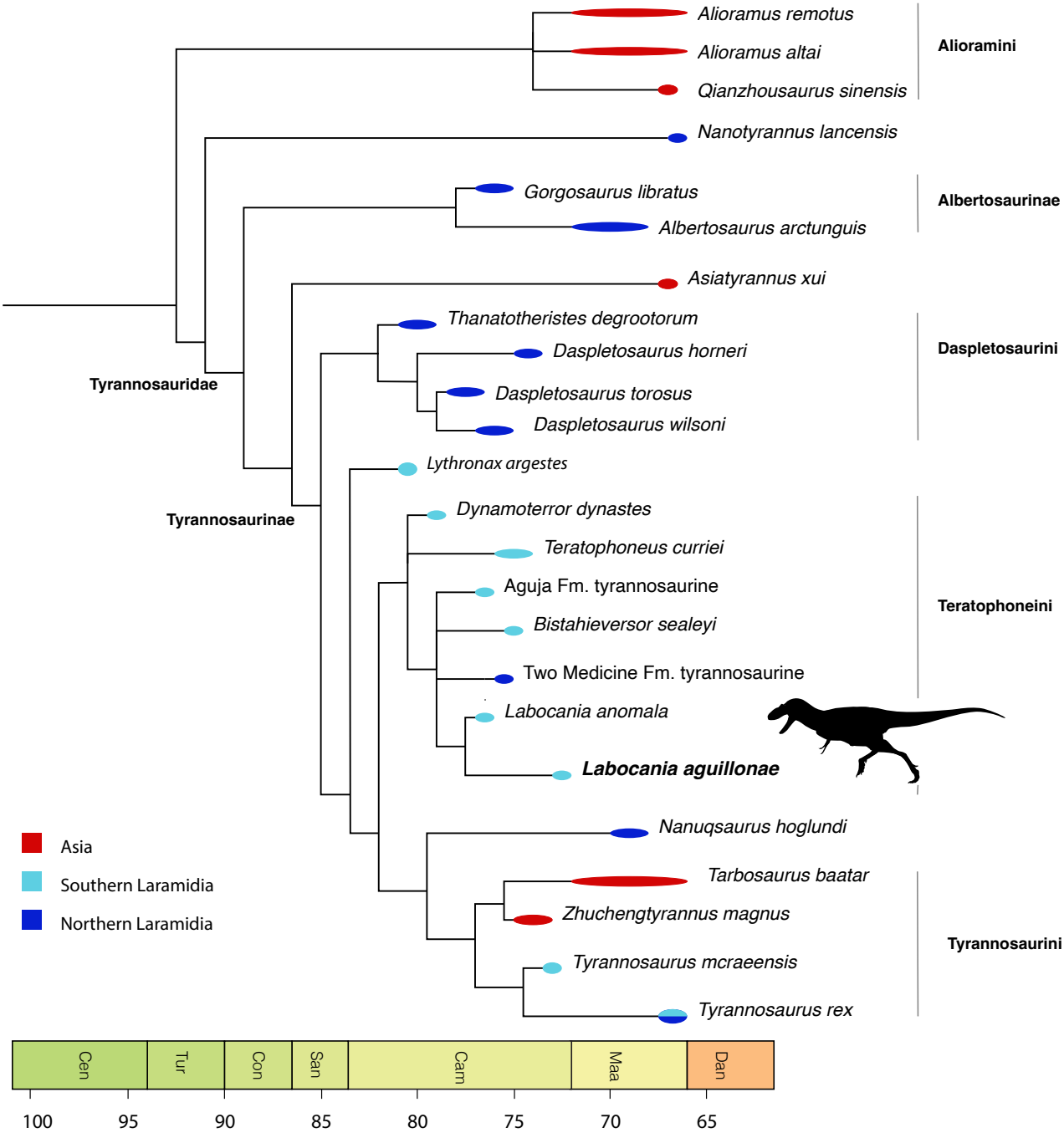


Figure 12. Phylogenetic analysis showing the placement of *Labocania aguillonae* in Teratophoneini. Strict consensus of 2160 most-parsimonious trees.

L. aguillonae also resembles *Bistahieversor sealeyi* but differs in the more strongly sinusoidal margin of the supratemporal fossa and stronger anterolateral expansion of the frontal postorbital process where it contacts the lacrimal (Figure 13). The lacrimal also differs in that its anteroventral margin is more strongly convex, and the suborbital process that projects into the orbit is more dorsally extended. The antorbital fossa extends less far posteriorly than in *Bistahieversor*; excavation of the antorbital fossa is more weakly developed; by contrast, it deeply excavates the lacrimal in *Bistahieversor*. *Teratophoneus* lacks a strong expansion of the frontal where it contacts the lacrimal and has a less sinuous margin of the supratemporal fossa (Figure 12); *Teratophoneus* also lacks the strongly convex anteroventral

margin of the lacrimal and the strong posteroventral expansion of the antorbital fossa onto the lacrimal.

The morphological differences seen here are relatively subtle, but tyrannosaurid species are typically diagnosed by relatively subtle differences [4]. Furthermore, CPC 2974 is unlikely to be referable to any known species, given that it is markedly younger than *Bistahieversor* or *Teratophoneus*. *Bistahieversor* comes from the Hunter Wash Member in the lower Kirtland Formation, and so dates to at least 73.04 Ma, based on a radiometric date from the top of the Kirtland, and younger than 75.56 based on a date for the underlying Fruitland Formation [63]. *Teratophoneus,* meanwhile, comes from the middle member of the Kaiparowits Formation, roughly 75.5 to 76.5 Ma in age [18]. *Labocania anomala*, which appears to represent the sister taxon of *L. aguillonae*, comes from the La Bocana Roja Formation of Baja California [27]. Radiometric dates constrain the base of the overlying El Gallo Formation to 75.84 Ma [26], so *Labocania anomala* is presumably older and as much as two or three million years older than *L. aguillonae*.

Although geologic age is not a diagnostic character, *per se*, dinosaur species turn over rapidly in the Late Cretaceous of Laramidia [64]. This appears to be true of tyrannosaurids as well. Three species of *Daspletosaurus* have been described from Montana and Alberta and succeed each other within a period spanning 77–75.5 Ma [16], a period of around 1.5 million years. Variation within *Tyrannosaurus* also suggests turnover within the latest Maastrichtian [65], although this idea remains controversial [66]. It would therefore seem unlikely that the Cerro Del Pueblo tyrannosaurine could be referred to as an older species.

4.4. Affinities and Age of Labocania anomala

The relationships of *Labocania* have long been unclear, and its age is poorly constrained. In the original description, Molnar remained ambivalent about the animal's affinities [27], comparing it to tyrannosaurids, carcharodontosaurs, and abelisaurids, and emphasizing supposedly unusual features of *Labocania,* including the thickened frontals, absence of well-demarcated supratemporal fossae and a shelf on the dentary. Since then, *Labocania* has often been ignored in studies of tyrannosaurs, and its affinities have been considered or uncertain; a recent study classified *Labocania* as a carcharodontosaur [67]. As part of this study, we re-examined the holotype of *Labocania* and can confirm that in all aspects of the morphology, its anatomy is consistent with Tyrannosauridae, and specifically with that of Teratophonei; the age of *Labocania* remains uncertain. Below, we present a summary of our conclusions; a more detailed examination of these problems is contained in Supplementary Materials.

The frontals of *Labocania* are not unusually thick but comparable to other large tyrannosaurines, such as *Dynamoterror* [49] and *Tarbosaurus* [48]. The supratemporal fossae are not absent; instead, the bone's dorsal surface is simply eroded, and the preserved frontal morphology is almost identical to that of other teratophoneins. Maxillae lack the rugosity or fused interdental plates of carcharodontosaurs or abelisaurids, and the 'lateral shelf' of the 'dentary' is the palatal shelf of the maxilla. The quadrate is broad, as in Tyrannosauridae. Teeth are typical of tyrannosaurids. Ischia has a large proximodorsal muscle scar as in Tyrannosaurinae and [27] are bowed as in teratophoneini [18]; the tibia's tall, wide astragalus scar is characteristic of coelurosaurs; the gracile metatarsal is typical of tyrannosaurids. We found no characters that would reject tyrannosaurid affinities and could not confirm the presence of any abelisaurid or carcharodontosaurid characters that are not found in tyrannosaurids. The evidence for tyrannosaur affinities is definitive; affinities with either archarodontosaurs or abelisaurs are, at best, implausible given the morphology of the bones. The phylogenetic analysis presented here, which includes a wide range of taxa, including allosauroids and ceratosaurs, found no evidence for a basal position in the tree as would be expected if *Labocania* was a non-tyrannosaurid; codings are entirely consistent with its placement as a teratophonein tyrannosaurine. As discussed above, placement of *Labocania* in either Allosauroidea or Ceratosauria increases treelength (an increase of 14 and 15 steps, respectively) relative to a position in Teratophoneini, even though it can only be

coded for relatively few elements; the anatomical characters are highly incongruent with placement outside Tyrannosauridae.

The age of *Labocania*, which is reported as coming from the La Bocana Roja Formation [27] (but see below), is poorly constrained. The stratigraphy of the area is also complicated; the La Bocana Roja Formation forms an angular unconformity with the overlying El Gallo Formation and is incut and overlain by submarine canyon fills of the Punta Baja Formation [68]. Radiometric dates of tuffs in the overlying El Gallo Formation suggest a minimum age of 75.84 ± 0.05 Ma for the La Bocana Roja Formation [26]. Detrital zircons from the La Bocana Roja Formation provide an age of 93 93.6 ± 1.1 Ma [68] but because detrital zircons are reworked from older sediments, this is only a maximum age. If source sediments are significantly older than the host rocks, detrital zircons may overestimate the age of the host rocks. Microfossils and detrital zircon dating of the interfingering Punta Baja Formation suggest a Santonian-Coniacian age for the Punta Baja [68], but bivalves and ammonites instead suggest a late middle Campanian age [68].

The dinosaur fossils reported from the La Bocana Roja Formation suggest a mid-to-late Campanian age. As discussed above, *Labocania* is referable to the Teratophoneini, a clade known only from the Campanian, and it closely resembles teratophoneins from the Late Campanian of Utah, New Mexico, and Coahuila (Figure 13), implying a Late Campanian age. A lambeosaur ischium collected from the same beds resembles and may be referable to the Late Campanian genus *Magnapaulia*, again implying a Campanian age. The dinosaur fauna therefore strongly argues for a mid- or late Campanian age.

The situation is therefore complicated, with detrital zircons, dated ash beds, microfossils, fossil invertebrates and vertebrates providing discordant dates. The complex stratigraphy—the La Bocana Roja Formation meets the overlying El Gallo in an angular unconformity so that the age of the uppermost La Bocana Roja differs from north to south- is another issue. There is also the possibility, in the absence of a detailed stratigraphic column, that *Labacania* and the lambeosaurs come from the lower part of the El Gallo Formation and that the dinosaurs have been assigned to the wrong formation, as sometimes occurs [69].

Data for the type locality, site LACM 7257, are conflicting. It is reported as part of the La Bocana Roja Formation, but LACM records state that "LACM 6755 is now incorporated into this locality. Site LACM 6755 is reported as "El Gallo Fm. (El Diseado [sic] member)". If Labocania does instead come from the El Disecado Member of the El Gallo Formation, this would put *Labocania* between 75.84 Ma (the age of the base of the El Disecado Member) based on radiometric dating of tuffs and 71.9 ± 1.7, based on radiometric dating of detrital zircons from the top of the El Gallo Formation [68].

Biogeography

The phylogeny recovered here finds a high diversity of tyrannosaurine lineages in Mexico and the American Southwest and recovers a distinct southern clade, including *Labocania anomala*, *Bistahieversor*, *Teratophoneus*, and *Dynamoterror* (Figure 13). A tyrannosaurid from the Aguja Formation of Texas [50] is recovered within this clade. Along with the presence of Tyrannosaurini in the south, including *Tyrannosaurus mcraeensis* in New Mexico [4] and *Tyrannosaurus* sp. in the Maastrichtian of the Javelina Formation Texas [70], southern Laramidia appears to be a major center of tyrannosaurine diversification.

Further north, distinct, basally diverging tyrannosaur lineages occur in the northern Great Plains of Montana and southern Canada. Albertosaurines and Daspletosaurini dominated in the Dinosaur Park Formation [15], Oldman Formation [71], and Foremost Formation [52] of southern Canada, and in the Judith River [16] and Two Medicine [17] formations of Montana. Albertosaurines persisted into the latest Campanian and early Maastrichtian [72] in Alberta.

The endemicity among tyrannosaurs in the Campanian and early Maastrichtian is striking. Modern large carnivores such as wolves, tigers, mountain lions, and lions have large geographic ranges [14], so it is surprising that far larger dinosaurian predators have small geographic ranges. Whether this reflects different environmental conditions that

prevailed in the Cretaceous or different patterns of speciation in dinosaurs versus mammals is unknown.

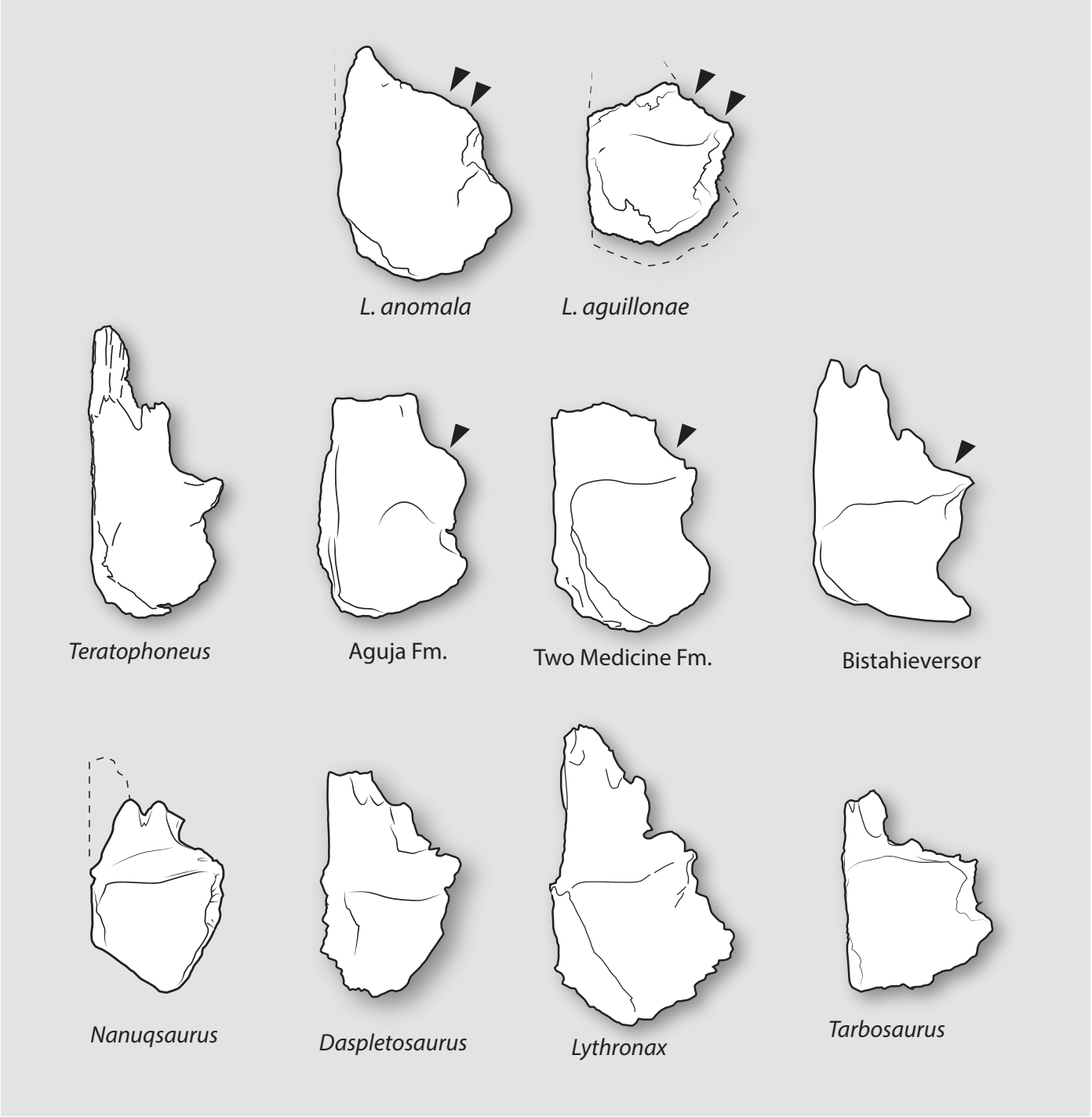


Figure 13. Frontals of *Labocania aguillonae* compared with other Teratophoneini (above) and Tyrannosaurinae (below). Arrows indicate anterolateral overlap of the frontal onto the lacrimal (single arrow) and its anteromedial extension to create an oblique contact with the lacrimal (second arrow). *Teratophoneus* after UMNH 16690, Aguja Fm. Tyrannosaur after TMM, 45905-1 [50], Two Medicine tyrannosaurine after [39], *Bistahieversor sealeyi* after NMMNH P-27469; *L. anomala* after IGM 5307, *L. aguillonae* after CPC 2974, *Nanuqsaurus* after DMNH 21461 [51], *Daspletosaurus* after TMP 2001.036.0001 [52], *Lythronax* after UMNH 20200, and *Tarbosaurus* after MPC-D 107/22 [48].

Regardless, given the small geographic ranges of the tyrannosaurs, it seems that Laramidia must have supported a far higher diversity of tyrannosaurs than our geographically restricted sampling would suggest. If tyrannosaurs had small ranges, then extensive sampling would be needed to find all known species. Therefore, many undiscovered species may have existed in poorly known areas of Laramidia, including Mexico, the Pacific coast, and the Arctic.

The dinosaur fauna of the Cerro del Pueblo Formation (Figure 14) as a whole is also distinct from those of more northern assemblages, particularly the coeval Horseshoe Canyon Formation of Alberta [72]. Lehman [73,74] argued that the Late Campanian dinosaur faunas were not homogeneous, but changed as one moved from Canada to Mexico. Lehman identified provinciality and specifically suggested the existence of two distinct faunas: a northern fauna including Alberta, Saskatchewan, Montana, Wyoming, and northern Colorado, and a southern fauna encompassing southern Colorado, New Mexico, Texas, and Mexico. While it remains unclear whether Laramidian dinosaurs form discrete faunal provinces [75], further studies of southern horned dinosaurs [76–79], hadrosaurs [80–82], and tyrannosaurs [18,20] have broadly upheld the hypothesis that dinosaur faunas were highly heterogenous, with high endemism, and distinct species occurring in different formations [75].

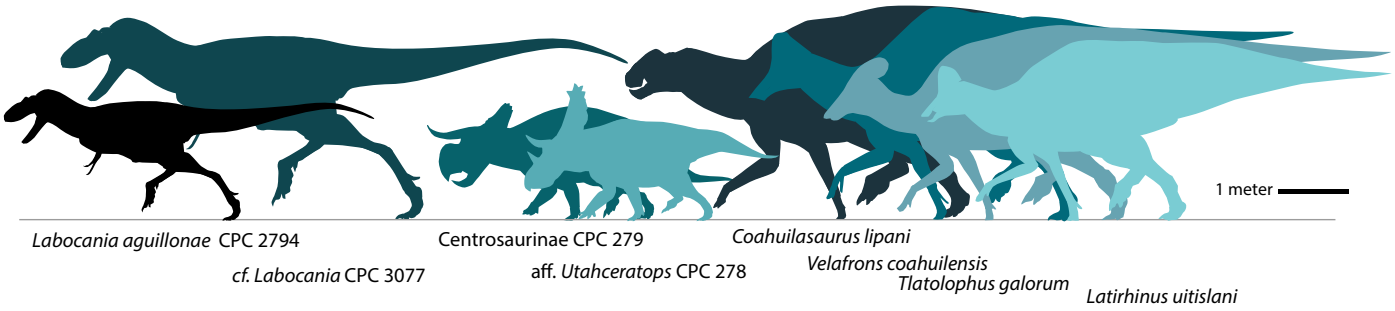


Figure 14. Cerro del Pueblo Formation dinosaur fauna. CPC 2974, the holotype of *Labocania aguillonae* (subadult or young adult), is reconstructed with a 710 mm long femur, implying an animal ~6.3 m long. A referred dentary fragment, CPC 3077, and teeth come from larger, more mature individuals.

Some genera are shared between northern and southern assemblages, notably *Parasaurolophus* [83,84], *Gryposaurus* [81,85] and *Pentaceratops* [86–88]. However, in each case, these genera are represented by distinct species in the north and south. The existence of geographically widespread dinosaur genera shows that dispersal between the north and south was possible and did occur; there do not seem to have been geographic barriers to dispersal. However, because distinct species exist, dispersal of species appears to have been followed by genetic isolation of the populations and rapid allopatric speciation. As a result, few dinosaur species are shared between the northernmost faunas in Alberta and Montana and the southern faunas in Utah, New Mexico, and Mexico [75].

Endemicity is also seen at higher taxonomic levels. Among herbivorous dinosaurs, for example, *Centrosaurus*-like ceratopsids occur exclusively in the north [89–92], *Nasutuceratops* primarily occur in the south [93–95], and giant triceratopsins are exclusively found in the south [76] at least during the Campanian and early Maastrichtian. This pattern of clade-level endemicity is perhaps even more striking among tyrannosaurs. As discussed above, Albertosaurinae [96,97] and Daspletosaurini [16] are so far found only in the north, while teratophoneins [19,20,27] and tyrannosaurins [4] are so far exclusively found in the south.

The factors driving dinosaurian endemicity remain unknown. As shown by the existence of widespread genera, no geographic barriers seem to have existed [73,75] to prevent dispersal along the coastal plain of the Western Interior Seaway. Latitude may play a role. Strikingly, while Laramidia was relatively small in terms of land area, it extended across a huge latitudinal range, from the north, in Alaska and Canada, south to the tropics

of Mexico [75]. Different regions must have seen marked variations in climate in terms of mean annual temperature and seasonality [75], precipitation [75], and also in day length.

Curiously, at least some lineages seem to persist in the south after disappearing in the north, e.g., kritosaurins [98,99] and lambeosaurins [100] persist in the southwest after disappearing from Alberta and Canada [3,72]. This occurs coincident with Campanian-Maastrichtian cooling [101] and might indicate that the range of dinosaur species is directly or indirectly affected by temperature.

Seasonality and climate likely drove differences in the flora, as distinct floral provinces are seen in Laramidia in the Campanian. Laramidia's northern coastal plain was part of an *Aquilapollenites* floral province that extended into eastern Asia [102]. Further south, palynomorphs corresponding to the *Normapolles* province occur in the Aguja Formation of south Texas [102] and in northeastern Mexico [103].

Plant macrofossils show major regional differences, although discrete floral provinces are hard to identify. The most conspicuous regional difference is the dominance of conifers at higher latitudes versus angiosperms at lower latitudes. The Cerro Del Pueblo Formation and Olmos Formation of Coahuila are characterized by subtropical and tropical angiosperms [104] such as palms (Arecaceae) and bananas (Musaceae) [104]. The forests were angiosperm-dominated, as indicated by the presence of laurels (Lauraceae), beeches (Fagaceae) and magnolias (Magnoliaceae), and fossilized angiosperm wood [104]. Aquatic species like *Pistia* and lotus (Nelumbaceae) are common [104]. Further north, the Aguja Formation of Texas is interpreted as preserving a dicot-dominated riparian community and conifer-dominated forest distal to the rivers, with adaptations to periodic dry spells [105]. The flora of the McRae Formation of New Mexico consists of angiosperms and rarer conifers, with adaptations such as drip tips and lianas suggesting a tropical rainforest ecosystem [104]. The Kirtland and Fruitland Formations are dominated by dicots [104,106,107]; palms [106] and conifers occur as well [104]; thick coals and fluvial sandstones suggest large rivers and wet, swampy lowlands. The Kaipairowits Formation has a diverse dicot community but conifers among trees [108]. The Two Medicine Formation of Montana is dominated by conifers, including auracarias and cypress [107]. The Dinosaur Park Formation is low in diversity. Conifers, including cypress, podocarps, and ginkgos, are diverse, and conifers dominate the fossil wood; angiosperms are rare [109].

These regional differences in vegetation could drive the endemicity seen in herbivores. Carnivores were presumably less constrained because the duckbill and ceratopsid species in different regions will not differ greatly in food value or in terms of the techniques used to hunt and feed on them. However, different habitat types, e.g., open savannahs and woodlands or closed forests, presumably favor predators with different hunting strategies, and the relative abundance of different species, e.g., ceratopsids versus hadrosaurids, and so vegetation types could indirectly affect predators' geographic ranges.

Even accounting for these differences in flora and fauna, it is still unclear why endemicity is so pronounced in the absence of geographic barriers [75] to prevent species from expanding their ranges. Without large bodies of water to prevent dispersal, it seems likely that a biotic barrier to dispersal existed, i.e., competition between competing species of dinosaur limited dispersal [88]. In modern ecosystems, birds exhibit high endemism, especially in the tropics, despite having excellent dispersal ability. Studies of modern birds show that it is primarily the presence of competing species that prevents species from expanding their ranges [110]. The same was likely true of dinosaurs. After dinosaurs became specialized for local climates, flora, and fauna, they would have had a competitive advantage against immigrants and prevented competitors from invading, at least until the climate, flora, or fauna changed. Environmental disruptions could have then disrupted these biotic barriers and allowed species to disperse into new habitats, then become adapted to these new habitats, creating endemism once again.

The endemism seen in Laramidia in the Campanian persists until at least the mid-late Maastrichtian, at which point southern lineages, including *Tyrannosaurus* [4,70] and tricer-atopsins [70,76] move north in the late Maastrichtian. This suggests a possible decrease in

endemism. In particular, *T. rex* appears to have been widespread in the Late Maastrichtian, extending from at least as far south as Utah [111] north into Saskatchewan [112] and Alberta [10]. However, sampling of late Maastrichtian assemblages in the south [70,113] remains poor, and the persistence of lambeosaurins, kritosaurins, and titanosaurs into the latest Maastrichtian in the south (but not the north) suggests endemism persists into the Maastrichtian. Further study of tyrannosaurs and other dinosaurs from the late Maastrichtian of the southwest and Mexico is needed.

5. Conclusions

CPC 2974 represents a new species of tyrannosaurid, *Labocania aguillonae*, closely related to *Labocania anomala*, *Bistahieversor sealeyi*, and *Teratophoneus curriei*. It adds to the diversity of the Cerro del Pueblo Formation and shows that endemicity existed within tyrannosaurs in the Late Campanian, with distinct species and clades inhabiting the northern Great Plains in the north and the American Southwest and Mexico in the south. Given the limited geographic sampling, many tyrannosaur species likely remain undiscovered. Competition between species likely helped to enforce endemism among dinosaurs. Why large dinosaurs seem to have such unusually high levels of endemism compared to modern mammals remains unclear.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fossils2040012/s1, Affinities and Age of *Labocania anomala*.

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Abbreviations

CPC—Colección Paleontológica de Coahuila, Museo del Desierto, Mexico; IGM—Instituto de Geología de la UNAM, Mexico; MUDE—Museo del Desierto, Mexico; MPC—Mongolian Paleontological Center, Ulaanbaatar, Mongolia; TMM—Texas Memorial Museum, University of Texas, Austin, Texas, USA; TMP—Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; UCM—University of Colorado Museum, Boulder, Colorado, USA.

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