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FEATURED ARTICLE

BISTAHIEVERSOR SEALEYI, GEN. ET SP. NOV., A NEW TYRANNOSAUROID FROM NEW MEXICO AND THE ORIGIN OF DEEP SNOUTS IN TYRANNOSAUROIDEA

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Skeletal remains of Late Cretaceous (Campanian and Maastrichtian) tyrannosauroids are rare in southwestern North America (Carr and Williamson, 2000). Historically, the identity and diversity of southwestern tyrannosauroids was unclear because most of the fossils were isolated teeth and bones that are not diagnostic of known genera or species (Carr and Williamson, 2000). One partial skull and skeleton (OMNH 10131) from the upper Campanian of New Mexico was referred to the problematic tooth taxon *Aublysodon* cf. *A. mirandus*, a referral that was later falsified (Lehman and Carpenter, 1990; Carr and Williamson, 2004). Recently, two fairly complete skulls and skeletons were collected that enabled a review of tyrannosauroid fossils from the Campanian of New Mexico. These specimens provide the opportunity to accurately characterize Campanian tyrannosauroids of the southwest, and recover their phylogenetic relationships with well-known species (Carr and Williamson, 2000). We report the presence of a new genus and species of deep-snouted tyrannosauroid from the upper Campanian of New Mexico, represented by several specimens including the partial skeleton of an adult and a juvenile. This new taxon is part of the diversification of deep-snouted tyrannosauroids and emphasizes the high species richness of this widespread clade in the upper Campanian of western North America.

Institutional Abbreviations—**NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **OMNH**, Sam Noble Museum of Natural History, Oklahoma; **TMM**, Texas Memorial Museum, Austin; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller.

Anatomical Terminology—We follow Anglicized versions of the Nomina Anatomica Avium terminology in Baumel et al. (1993) and in Witmer (1997).

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
TYRANNOSAUROIDEA Walker, 1964

BISTAHIEVERSOR SEALEYI, gen. et sp. nov.
(Figs. 1–4, Table 1S)

Aublysodon cf. *A. mirandus*: Lehman and Carpenter, 1990:1026, figs. 1–6; OMNH 10131.
"Tyrannosaurid": Archer and Babiarz, 1992:690, fig. 1; NMMNH P-25049.
Daspletosaurus sp.: Carr and Williamson, 2000:113 figs. 5, 6A–K, 7A–F, 8, 10A–I, IIM–U, 12F–I, 13; NMMNH P-25049, OMNH 10131.
cf. *Daspletosaurus* sp.: Carr and Williamson, 2000:118, 133 fig. 7A–F; NMMNH P-27469.

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Etymology—Bistahi, place of the adobe formations (Navajo) in reference to the Bisti Wilderness Area; eversor, destroyer (Greek) in reference to the presumed predatory habits of the animal; Sealey, in reference to Mr. Paul Sealey, Research Associate at the NMMNH, in recognition of his discovery of the holotype specimen.

Pronunciation—Bis-tah-he-ee-ver-sor.

Holotype—NMMNH P-27469, an articulated skull and skeleton (Figs. 1–3) of an adult from locality L-3506, upper Campanian Hunter Wash Member, Kirtland Formation, Hunter Wash, Bisti/De-na-zin Wilderness Area, northwestern New Mexico (detailed locality information is on file at the NMMNH). At the time of this writing, the postcranial skeleton is largely unprepared.

Referred Specimens—NMMNH P-25049, an incomplete skull (Figs. 1–3) and skeleton of a juvenile from Locality L-3097, upper Campanian, Farmington Member, Kirtland Formation, Pinabete Arroyo, northwestern New Mexico; NMMNH P-32824, rostral ramus of a right lacrimal, from locality L-4010, upper Campanian, Fruitland Formation, Hunter Wash, Bisti/De-na-zin Wilderness Area, northwestern New Mexico; OMNH 10131, a partial skull and skeleton of an adult, upper Campanian, upper Fruitland or lower Kirtland formations, Ah-shi-sle-pah Wash, northwestern New Mexico.

Generic Diagnosis—As for type and only species.

Specific Diagnosis—Tyrannosauroid characterized by numerous cranial autapomorphies, including a forked palatal process of the premaxilla (Fig. 3A), supernumerary frontal processes of the nasal (Fig. 3B), lanceolate medial frontal processes of the nasal, a pneumatic foramen that pierces the supraorbital ramus of the lacrimal (Figs. 1, 2), a peaked sagittal crest (Figs. 1, 2), a dorsotemporal fossa that extends onto the lateral surface of the squamosal, a short prefrontal (Fig. 3B), a single pneumatic foramen in the palatine (Fig. 3C), a medial ridge on the angular for insertion into the surangular (Fig. 3D), a ventrolateral keel along the caudoventral margin of the mandible formed by the angular and prearticular (Fig. 3E), and a tall flange extending from the ventral margin of the rostral mylohyoid foramen of the splenial (Fig. 3F). Measurements of the holotype are provided in Table 1.

The skull of the juvenile specimen (NMMNH P-25049) is badly damaged, but it is referable to *Bistahieversor* based on the presence of two supernumerary frontal processes on each nasal and a single pneumatic foramen in the palatine. In all other tyrannosauroids, juvenile and adult, the nasal overlaps the frontal with only two processes, and they possess two pneumatic foramina in the palatine (except one specimen of *Albertosaurus sarcophagus*, TMP 86.64.1, which has one foramen; Carr et al., 2005). The juvenile does not possess any characters that support a referral to another tyrannosauroid species.

The juvenile specimen reveals that growth or size-related changes in the skull of *Bistahieversor* are consistent with differences between juveniles and adults of more derived species of tyrannosauroids, such as *Albertosaurus libratus* and *Tyrannosaurus rex* (Carr, 1999; Carr and Williamson, 2004). For

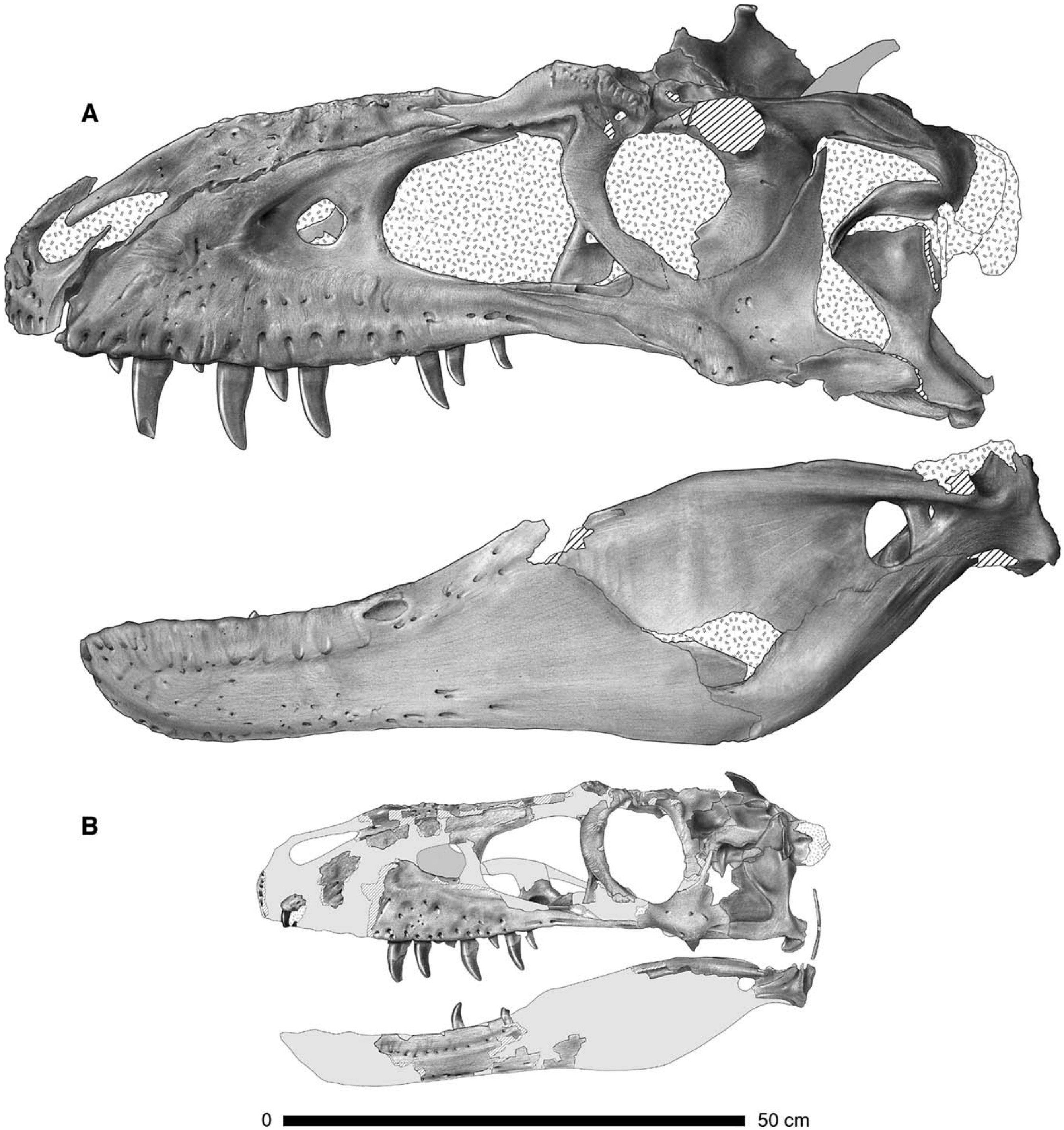

FIGURE 1. Comparison of skulls of *Bistahieversor sealeyi*, new species. The skull of the **A**, holotype (NMMNH P-27469) and **B**, juvenile (P-25049) in left lateral view (some bones reversed from the other side); scale bar equals 50 cm.

example, the cranial ornamentation is elaborated in the adult, in which the cornual processes of the lacrimals and postorbitals are grossly enlarged relative to the juvenile (Figs. 1, 2). The presence of a pneumatic foramen in the supraorbital ramus of the lacrimal in the adult, which is absent in the juvenile, is consistent with the ontogenetic increase of pneumatization that is seen in other tyrannosauroids (Carr, 1999). Individual variation might be represented by features that are not seen in the ontogeny of other tyrannosauroids, such as a pneumatic foramen above the basipterygoid process in the juvenile that is absent from the adult, and an inflated body of the ectopterygoid in the juvenile that is not seen in the adult (Carr, 1999).

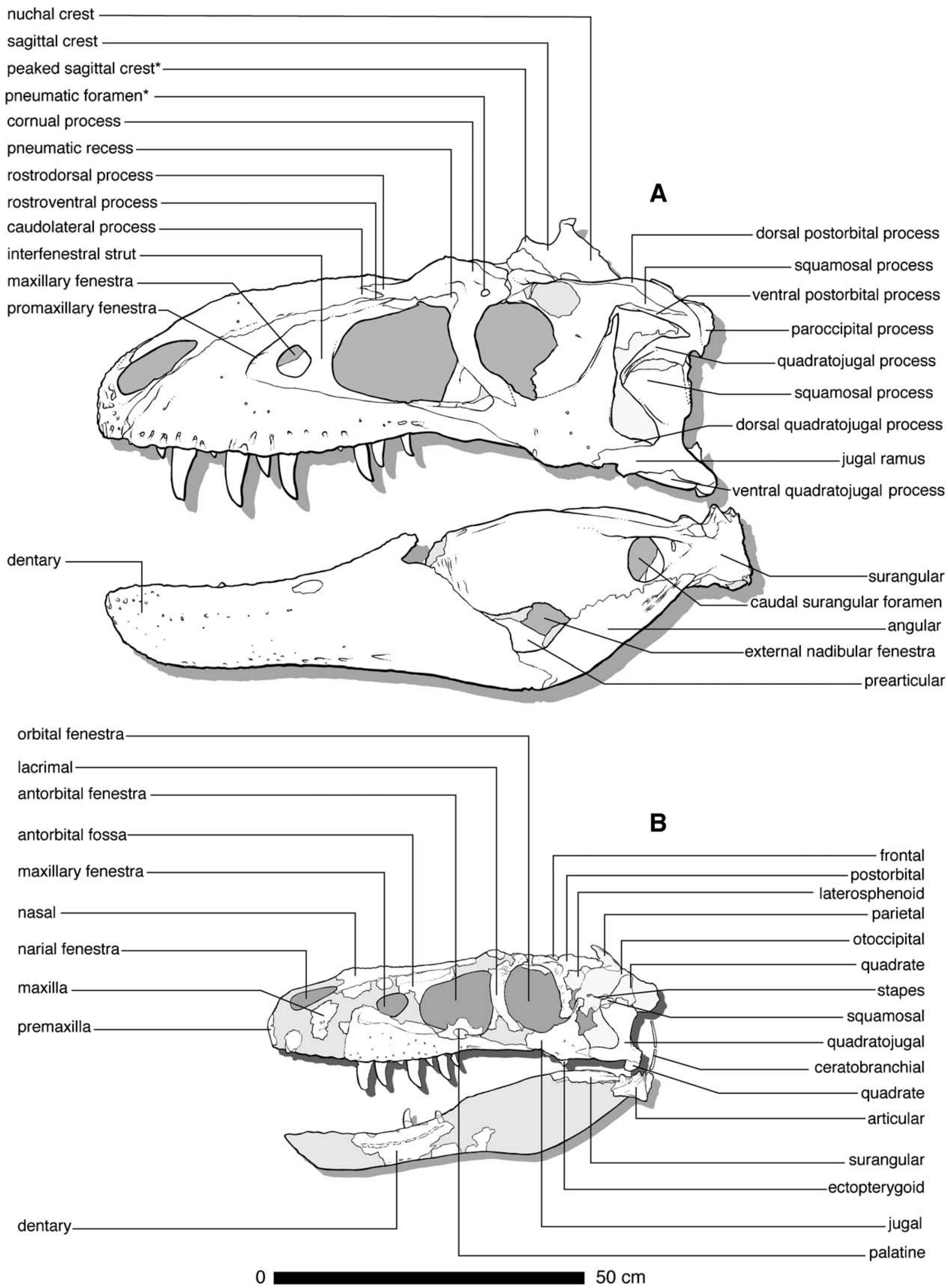

FIGURE 2. Interpretive line drawing of the holotype and juvenile skulls of *Bistahieversor sealeyi*, new species in left lateral view. The skull of the **A**, holotype (NMMNH P-27469) and **B**, juvenile (P-25049) in left lateral view (some bones reversed from the other side); scale bar equals 50 cm. Asterisks (*) indicate autapomorphies that can be seen in this view.

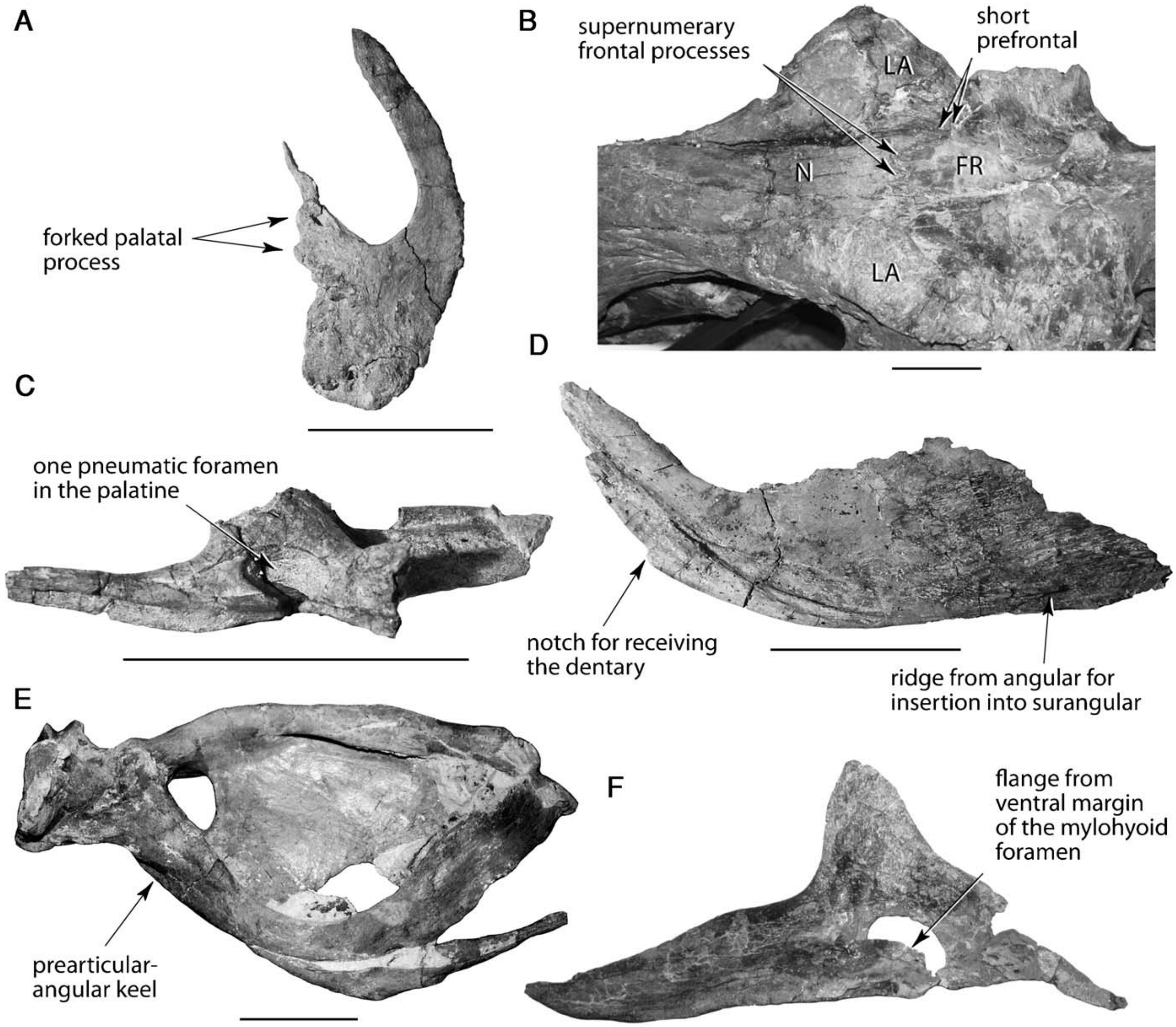

FIGURE 3. Autapomorphies of *Bistahieversor sealeyi*, new species. **A**, left premaxilla (NMMNH P-27469) in medial view; **B**, nasofrontal region (P-27469) in dorsal view; **C**, left palatine (P-25049) in lateral view; **D**, right angular (P-27469) in medial view; **E**, left articular, surangular, angular, and prearticular (P-27469) in medial view; **F**, right splenial (P-27469) in lateral view. Scale bars equal 10 cm. **Abbreviations**: **FR**, frontals; **LA**, lacrimal; **N**, right nasal.

The separate left dentary and surangular of the holotype of *Bistahieversor* reveals that the rostral (dentary + splenial) and caudal (surangular + articular + prearticular + angular) sections of the mandible are securely united by a deep tongue-in-groove joint between the dentary and angular (Fig. 3D). Thus, *Bistahieversor* can be counted with *Tyrannosaurus bataar* as a tyrannosauroid with an intermandibular 'locking' mechanism (Hurum and Currie, 2000). Based on this evidence, dorsoventral flexion between rostral and caudal sections, as proposed for basal and derived theropods, did not occur in these tyrannosauroids (Hurum and Currie, 2000). Also, the squamous contacts between the sections in *Bistahiversor* consist of interleaving grooves and ridges between the dentary and surangular, angular and dentary, and prearticular and splenial. These tight contacts indicate the absence of vertical motion along the entire intraramal hinge, which requires reconsideration of the function of the smooth contact between the intermandibular processes of the dentary and surangular (Hurum and Currie, 2000). However, streptognathy (flexion in the horizontal plane at the junction between the rostral and caudal sections of the mandibular ramus), as observed in living birds (Zusi and Warheit, 1993), is not necessarily ruled out for tyrannosauroids.

To hypothesize the phylogenetic position of *Bistahieversor*, a data matrix was compiled in MacClade 3.0 (Maddison and Maddison, 1992) for a cladistic analysis in PAUP 4.0b 10 (Swofford, 2002). The data set consists of 274 characters among 21 ingroup

TABLE 1. Skull measurements (in millimeters; left side) of the holotype of *Bistahieversor sealeyi* (gen. et. sp. nov.), NMMNH P-27469.

Skull length	~ 1070.0
Preorbital skull height	310.0
Length naris	148.2
Depth naris	51.6
Total length of the antorbital fossa	~ 327.0
Length of the antorbital fenestra	203.8
Depth of the antorbital fenestra	175.7
Depth of the orbital fenestra	167.3
Length of the orbital fenestra	133.0
Ratio orbit length:orbit depth	0.8
Depth of skull in front of orbital fenestra	~ 318.0
Depth of the laterotemporal fenestra	219.4
Maximum skull depth through laterotemporal fenestra	~ 330.0
Length of snout from rostral edge of the lacrimal	~ 580.0
Length of snout from caudal edge of the lacrimal	~ 627.0
Ratio snout length:skull length	0.54, 0.60
Width across apices of the lacrimal horns	~ 195.2
Depth skull through jugal horn	~ 315.0

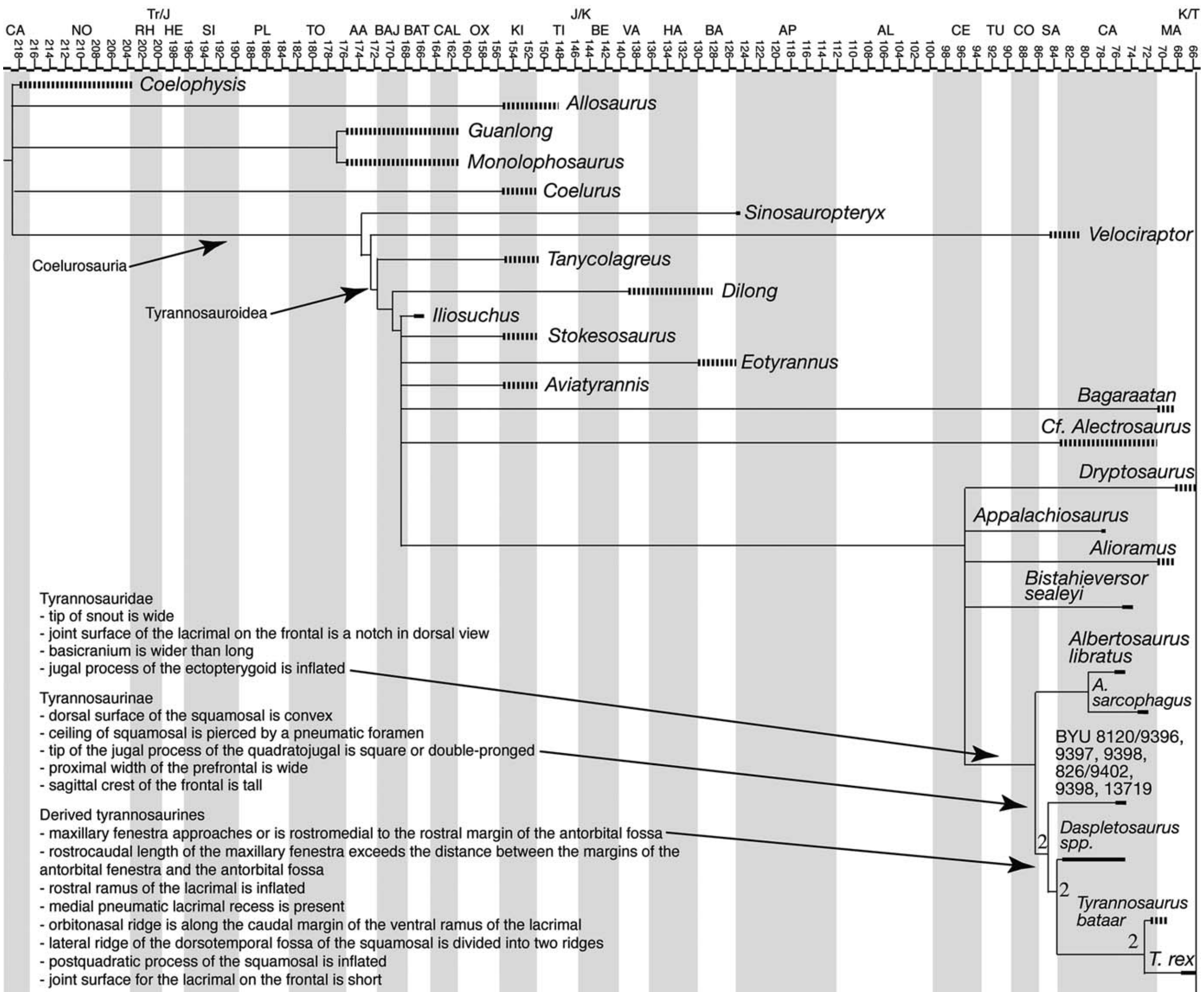

FIGURE 4. Time-calibrated phylogeny (strict consensus tree) of tyrannosauroid relationships and unambiguously resolved synapomorphies. Time scale is after Ogg et al. (2004). Synapomorphies were obtained under ACCTRAN optimization. Dashed lines indicate estimated time ranges. Decay indices are indicated by the numbers above the nodes.

species and five outgroup taxa (Appendices 1, 2). This analysis differs from previous studies in that it includes purported basal tyrannosauroids that have not been previously analyzed together: *Dilong*, *Guanlong*, *Tanycolagreus*, *Coelurus*, *Iliosuchus*, *Stokesosaurus*, *Aviatyrannis*, and *Eotyrannus* (Madsen, 1974; Galton, 1976; Chure and Madsen, 1998; Hutt et al., 2001; Rauhut, 2003; Xu et al., 2004, 2006; Carpenter et al., 2005a, 2005b; Senter, 2007). *Monolophosaurus* was included in the outgroup because of features in its crest that are also seen in *Guanlong*. All of the basal taxa were scored from the literature, as well as *Bagaraatan* and cf. *Alectrosaurus* (Perle, 1977; Osmólska, 1996). The phylogenetic characters were selected from Carr (1999, 2004), Currie et al. (2003), Carpenter et al. (2005a, 2005b), Holtz (2001), Holtz et al. (2004), and Xu et al. (2004, 2006). The matrix was run under a heuristic search, for 100 replicates. All the characters were treated as unordered and equally weighted. We obtained 840 most parsimonious trees, each tree has a length of 652 steps, CI = 0.59, HI = 0.41, and RC = 0.42. The strict consensus tree recovered *Bistahieversor* in an unresolved polytomy with *Appalachiosaurus*, *Alioramus*, *Dryptosaurus*, and Tyrannosauridae. Tyrannosauridae is monophyletic, and *Albertosaurus* is the sister taxon of Tyrannosaurinae. Within the latter clade, *Tyrannosaurus* is monophyletic, and its successive outgroups are *Daspletosaurus* and a new taxon from Utah. These results are not robust, and most nodes collapse with the addition of one step. Stronger support is found for the interrelationships of derived tyrannosaurines, which collapse with two extra steps. Outside of derived tyrannosauroids, the taxa cf. *Alectrosaurus*, *Bagaraatan*, *Aviatyrannis*, *Eotyrannus*, *Stokesosaurus*, and *Iliosuchus* are in a polytomy, and basal to these are *Dilong* and *Tanycolagreus*. Unlike Senter (2007), we do not recover *Coelurus* as a tyrannosauroid. The phylogenetic relationship of the purported basal tyrannosauroid *Guanlong* is reconstructed as the sister species of *Monolophosaurus*, outside of Coelurosauria.

With geographic distribution considered, the topology indicates a difference in the depth of the horizontal ramus of the maxilla, especially the dentigerous region; this region is deep in *Bistahieversor* and tyrannosaurids (Fig. 4), but it is shallow in *Dilong*, *Appalachiosaurus*, *Alioramus*, and in outgroup species. It appears that the shallow condition is primitive for tyrannosauroids, as seen in North American, European, and Asian species from the Early Cretaceous, and in relatively primitive Late Cretaceous species from eastern North America and Asia. The deep condition is present in relatively primitive species (e.g, *Bistahieversor*) and tyrannosaurids from the American west and Asia. We hypothesize that the deep condition first evolved in the common ancestor of Late Cretaceous tyrannosauroids from western North America after emplacement of the Western Interior Seaway, before they later dispersed to Asia. A description of the distinction between the deep and shallow conditions is in Appendix 3. The deep condition of the dentigerous region evolved independently in abelisaurids, carcharodontosaurids, and *Monolophosaurus* (Sampson and Witmer, 2007; Sereno et al., 1996; Zhao and Currie, 1993). If the phylogenetic reconstruction is accurate, then tyrannosauroids tended to be small predators during the Jurassic and Early Cretaceous. The largest species (ilium or femur length >500 mm) evolved by the Late Cretaceous and they were present in Asia and North America.

Large tyrannosauroids had a near holarctic distribution during the Late Cretaceous, during which they were the largest terrestrial predators. A significant morphological dichotomy distinguishes tyrannosauroids with shallow maxillae from Asia and eastern North America, and tyrannosauroids with deep maxillae from western North America and Asia. We hypothesize that large derived tyrannosauroids primitively had shallow maxillae and had attained a wide distribution in North America before the emplacement of the Western Interior Seaway (WIS) in the Albian. This hypothesis is consistent with recent discoveries of basal and shallow-snouted tyrannosauroids, such as *Dilong*, from the Early Cretaceous of China (Xu et al., 2004, 2006). The inception of the WIS created a barrier to dispersal for tyrannosauroids to and from eastern North America, and tyrannosauroids there (e.g., *Appalachiosaurus*) retained the primitive condition of a shallow maxilla.

The dichotomy in maxilla depth may reflect a difference in hunting strategy. Small basal shallow-snouted forms, such as *Dilong*, had a long and slender manus with raptorial claws (Xu et al., 2004), in contrast to the smaller forelimbs of large deep-snouted species, such as *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus*. It is conceivable that the forelimb was the primary weapon of predation in basal tyrannosauroids, whereas the deep upper jaw of derived species took that role. Thus, it may be hypothesized that the size of the forelimb and cranium are correlated in tyrannosauroids, in which the forelimbs were reduced in concert with hypertrophy of the jaws and teeth. Therefore, we predict that the forelimbs of *Bistahieversor* will be small, as in tyrannosaurids, should those bones be found among the unprepared postcranial skeleton.

The presence of a new genus and species of tyrannosauroid from the upper Campanian of New Mexico reinforces the difference in tyrannosauroid diversity between the upper Campanian and Maastrichtian in western North America. Every distinct upper Campanian intermontane basin that yields diagnostic tyrannosauroids contains different species or genera; however, this distribution does not necessarily support a distinct division into northern and southern faunal provinces (Lehman, 2001). In contrast to the upper Campanian pattern, only one species of tyrannosauroid, *Tyrannosaurus rex* (including TMM 41436-1, TDC pers. observ.), is distributed throughout western North America in the upper Maastrichtian (Carr and Williamson, 2004).

Several fossils referred to *Bistahieversor sealeyi* were previously identified as another taxon; Carr and Williamson (2000) referred the juvenile and OMNH 10131 to *Daspletosaurus* sp., a view that is cited in the literature (e.g., Farlow and Pianka, 2002; Currie, 2003; Holtz, 2004; Sullivan and Lucas, 2006). We later revised our identification of these fossils to a new, but unnamed, genus (Carr and Williamson, 2004); this decision was based on new information from the holotype. In summary, the southernmost occurrence of *Daspletosaurus* is Montana (Holtz, 2004), whereas *B. sealeyi* is the only upper Campanian tyrannosauroid from New Mexico.

The fossils of *Bistahieversor sealeyi* add to the discovery of upper Campanian tyrannosauroids of western North America and clarify the previously insufficient record of this clade in the southwestern United States. All diagnostic tyrannosauroid bones from the upper Campanian of the San Juan Basin of New Mexico are referable to *Bistahieversor*; this low diversity differs from the north, where sympatric genera occur in the upper Campanian of Montana and Alberta. *Bistahieversor* provides evidence of a lengthy and complex history of tyrannosauroids in the west following the emplacement of the WIS in the Albian, and indicates that the morphology of a deep maxilla is a relatively new evolutionary novelty for the clade.

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APPENDIX 1. List and description of 274 characters, and their character states, used to resolve the ingroup relationships of Tyrannosauroidea.

Skull

(1) Maximum postorbital skull width: less than one half premaxilla-occipital condyle length (0), more than two-thirds premaxilla-occipital condyle length causing orbits to face forward (1; Holtz, 2001, in Currie et al., 2003).
(2) Mediolateral width of snout at the caudal end of the tooth row: twice or less width of nasals (0), approximately three times the width of nasals (1; Holtz, 2001, in Currie et al., 2003).
(3) Occipital region orientation: caudally (0), caudoventrally (1; Holtz, 2001, in Currie et al., 2003).

Premaxilla

(4) Rostral margin in lateral view: extends caudodorsally (0), extends vertically (1).
(5) Nasal processes: diverge distally (0), apposed throughout their entire length (1).
(6) Nasal process, large foramen in lateral surface of base: absent (0), present (1; Carpenter et al., 2005a).
(7) Depth of body of bone in lateral view: shallow (0), deep (1).
(8) Snout tip in dorsal view: narrow (0), wide (1; Carr, 1999).
(9) Maxillary process, external surface in lateral view: faces laterodorsally (0), faces dorsally (1).
(10) Length of body of bone in lateral view: long (0), short (1).
(11) Orientation of tooth row in ventral view: more anteroposteriorly than mediolaterally oriented (0), more mediolaterally than anteroposteriorly oriented (1; Holtz, 2001, in Currie et al., 2003).
(12) Interdental plate fusion: fused (0); unfused (1).

Maxilla

(13) Promaxillary fenestra in lateral view: absent (0), obscured by the ascending ramus of maxilla (1), visible (2; Russell, 1970, in Currie et al., 2003); absent (2).
(14) Maxillary fenestra rostrocaudal position in lateral view A: absent (0), rostromedial to rostral margin of antorbital fossa (1), caudal to rostral margin of antorbital fossa (2; modified after Carr et al., 2005).
(15) Maxillary fenestra rostrocaudal position in lateral view B: absent (0), approaches or rostromedial to rostral margin of antorbital fossa (1); midway in position (2; modified after Carr et al., 2005).
(16) Maxillary fenestra, rostrocaudal length compared to distance between rostral margins of antorbital fossa and fenestra in adults: absent (0), less than half (1), more than half (2; Currie et al., 2003).
(17) Maxillary fenestra, dorsoventral position in lateral view: absent (0), dorsal (1), ventral (2; modified after Carr et al., 2005).
(18) Maxillary antorbital fossa in lateral view: length from rostral margin of antorbital fossa to rostral margin of antorbital fenestra is less than 40% the length of the entire antorbital fenestra (0), 40% or greater length of antorbital fenestra (1; Holtz, 2004).
(19) Antorbital fossa, contact with nasal suture in lateral view: reaches suture (0), does not reach suture (1).
(20) Antorbital fossa, extent of contact with nasal in lateral view: extensive (0), limited or does not reach suture (1).
(21) Interfenestral strut width in lateral view: absent (0), wide (1), narrow (2; Carpenter, 1992).
(22) Horizontal ramus depth in lateral view: shallow (0), deep (1; modified after Carr et al., 2005).
(23) Horizontal ramus, rostral margin in lateral view: sloping (0), square (1).
(24) Antorbital fossa, height over horizontal ramus in lateral view: diminishes (0), uniform (1).
(25) Subcutaneous flange in lateral and dorsal views: absent (0), present (1; modified after Carr et al., 2005).
(26) Proximal region of antorbital fossa in dorsal view: narrow (0), wide (1).
(27) Dorsolateral process, coverage by antorbital fossa in lateral view: process absent (0), subcutaneous surface entirely (1), ventral half covered by antorbital fossa (2), excluded (3).
(28) Texture rostral to the antorbital fossa: absent (0), present (1).

(29) Ventral margin of lateral alveolar process in lateral view: straight (0), convex (1).
(30) Joint surface for palatine in medial view: shallow, does not obscure the tooth root bulges from view (0); deep, obscures the tooth root bulges from view (1; Carr, 1999, in Currie et al., 2003).
(31) Length of vomer contact in ventral view: one half or less length of tooth row (0), greater than three quarters length of tooth row (1; Holtz 2001, in Currie et al., 2003).
(32) Interdental plates: not fused to each other (0), fused with each other (1; Currie et al., 2003).
(33) Tooth row, position of last tooth: below orbital fenestra (0), ahead of orbital fenestra (1).

Nasal

(34) Internasal suture: unfused (0), fused (1; Holtz 2001, in Currie et al., 2003).
(35) Premaxillary process: cleft present (0), cleft absent (1).
(36) Dorsal surface cross-section: flat for most of length (0), dorsally convex (1, Currie et al., 2003).
(37) Rostral half cross-section: D-shaped (0), flat or uniformly convex (1).
(38) Pneumatic recesses: present (0), absent (1; Holtz, 2000, in Currie et al., 2003).
(39) Caudolateral process presence: present (0), absent (1).
(40) Frontal process width in dorsal view: unconstricted (0), constricted (1; Russell, 1970).
(41) Lateral frontal process in dorsal view: not covered by the lacrimal (0); covered by the lacrimal (1).
(42) Medial frontal process length in dorsal view: absent (0), long (1), short (2).
(43) Paired medial frontal processes, form in dorsal view: absent or transverse (0), lanceolate (1), taper distally (2).
(44) Supernumerary frontal processes in dorsal view: absent (0), present (1).
(45) Lateral frontal process length in dorsal view: short (0), long (1).
(46) Frontal process dorsum: flat (0); convex (1).
(47) Dorsal surface: smooth (0); rough (1).
(48) Nasal crest: absent or unpaired (0); paired nasal crest present (1; Xu et al., 2004).

Snout Crest

(49) Snout crest, presence: absent (0), present (1).
(50) Snout crest, form: absent or paired (0), sagittal (1).
(51) Snout crest, fenestrae: absent or not fenestrate (0), fenestrate (1).
(52) Snout crest, extent: absent or limited to front of snout (0), extends along entire length of snout (1).

Bony Naris

(53) Bony naris length in lateral view: short (0); long, extends caudally to level of antorbital fossa (1).

Lacrimal

(54) Shape in lateral view: 7 shaped (0), T shaped (1; modified after Carr et al., 2005).
(55) Cornual process presence: absent (0), present (1).
(56) Cornual process apex presence: cornual process absent (0), apex present (1), apex absent (2; modified after Carr et al., 2005).
(57) Cornual process apex offset: cornual process absent (0), apex offset (1), apex not offset (2).
(58) Position of apex of cornual process: cornual process or apex absent (0), apex above ventral ramus (1), apex rostral to ventral ramus (2; modified after Carr et al., 2005).
(59) Length of pneumatic recess in lateral view: fossa or recess absent (0), large (1), small (2; modified after Carr et al., 2005).
(60) Height of pneumatic recess in lateral view: fossa or recess absent (0), tall (1), short (2; modified after Carr et al., 2005).
(61) Lacrimal recess and subcutaneous surface of ventral ramus in lateral view: fossa bounded laterally by web, merges or is marginally separate (0), widely separate (1).
(62) Antorbital fossa rostral to recess in lateral view: separate (0), recess absent (1), blend (2).
(63) Rostral ramus: not inflated (0), inflated (1; modified after Carr et al., 2005).
(64) Rostrodorsal process length in lateral view: absent (0), short (1), long (2).
(65) Maxillary process position in lateral view: ventral to dorsal margin (0), reaches dorsal margin (1), absent (2).
(66) Position of the accessory pneumatic recess in lateral view: absent (0), proximal (1), distal (2; Carr et al., 2005).
(67) Medial pneumatic recess presence in medial view: absent (0), present (1).
(68) Position of orbitonasal ridge in medial view: rostral to caudal margin of ventral ramus (0), close to or reaches caudal margin (1).
(69) Subocular process in lateral view: absent (0), present (1).
(70) Supraorbital ramus cornual process, presence in lateral view: absent (0), present (1).
(71) Rostroventral lamina in lateral view: more than half the height of the ventral ramus (0), less than half ramus height or absent (1).

Jugal

(72) Maxillary ramus depth in lateral view: shallow (0), rostrodorsally expanded (1).
(73) Maxillary ramus, jugal recess: absent (0), present (1).
(74) Maxillary ramus, edge of jugal recess in lateral view: antorbital fossa absent (0), edge is undercut and continues caudodorsal to the secondary fossa (1), fossa edge does not extend past the secondary fossa (2; Russell, 1970).
(75) Maxillary process, jugal recess position relative to ventral ramus of lacrimal in lateral view: recess absent (0), recess beneath ventral ramus (1), recess rostral to ventral ramus (2).
(76) Maxillary process, contribution to the antorbital fenestra in lateral view: does not reach the fenestra (0), restricted between maxilla and lacrimal to a small surface (1), forms the corner (2; Carr, 1999).
(77) Pneumatic recess: recess is absent (0), axis of relatively small foramen is horizontal (1), axis of foramen inclined at an angle of 45 degrees to the ventral skull margin (2; Currie et al., 2003).
(78) Secondary fossa in lateral view: absent (0), present (1).
(79) Maxillary ramus, secondary fossa extent in lateral view: absent (0), ventral (1), dorsal (2).
(80) Maxillary ramus, angle of the caudal half of the lacrimal suture in lateral view: low (0), steep (1).
(81) Postorbital ramus, concavity depth in lateral view: absent or shallow (0), deep (1).
(82) Postorbital ramus in lateral view: tapering contact with postorbital (0), horizontal, interlocking notch for postorbital (1; Currie et al., 2003).
(83) Cornual process, presence in lateral view: absent (0), present (1).
(84) Cornual process, width in ventral view: cornual process absent (0), narrow (1), wide (2; Carr, 1999).
(85) Cornual process, flange in lateral view: flange absent (0), present (1).

(86) Rostral extent of the joint surface for the quadratojugal, extent in lateral view: caudal to rostral margin of laterotemporal fenestra (0), reaches rostral margin of fenestra (1), extends ahead of rostral margin of fenestra (2), quadratojugal absent (3).
(87) Position of the ventral margin of the joint surface for the quadratojugal in lateral view: caudal (0), rostral (1; modified after Carr, 1999).
(88) Joint surface for the quadratojugal, slope in lateral view: low (0); steep (1; Carr, 1999).
(89) Dorsal quadratojugal process, orientation in lateral view: horizontal (0); caudodorsal (1).

Postorbital

(90) Cornual process, dorsal ridge position in lateral view: absent or undifferentiated rugosity (0), ridge dorsal to ventral boss (1), ridge caudal to boss (2).
(91) Position of cornual process relative to laterotemporal fenestra in lateral view: absent (0), does not approach fenestra (1), approaches fenestra (2).
(92) Position of cornual process relative to dorsal margin of bone in lateral view: absent (0), approaches or exceeds dorsal margin (1), does not approach dorsal margin (2).
(93) Position of cornual process relative to orbit in lateral view: absent (0), at orbit margin (1), caudal to orbit margin (2).
(94) Cornual process, presence of a crease in lateral view: process or crease absent (0), crease present (1).
(95) Cornual process, undercut in dorsal view: cornual process is absent (0), undercut is absent (1), undercut is present (2).
(96) Joint surface for squamosal in lateral view: at or ahead of rostral margin of the fenestra (0), caudal to rostral margin of laterotemporal fenestra (1; Carr, 1999).
(97) Squamosal process, caudodorsal margin in lateral view: uninterrupted arc (0), emarginated by squamosal (1).
(98) Squamosal process, length in lateral view: reaches caudal margin of the laterotemporal fenestra (0), stops short of caudal margin of fenestra (1; modified after Carr et al., 2005).
(99) Subocular process, presence in lateral view: absent (0), present (1; Carr, 1999).
(100) Subocular process, position in lateral view: process absent (0), distal (1), proximal (2).
(101) Orbit margin in lateral view: concave (0), vertical (1).
(102) Postorbitolacrimal osteoderms: osteoderms absent (0), present (1).

Squamosal

(103) Dorsotemporal fossa, extension onto lateral surface presence: absent (0), present (1).
(104) Lateral ridge of dorsotemporal fossa in dorsal view: undivided or dorsotemporal fossa is absent (0), divided into two or more ridges (1).
(105) Dorsotemporal fossa in dorsal view: fossa absent or flat (0), convex (1).
(106) Quadratojugal process, presence: present (0), absent (1).
(107) Depth of quadratojugal process in lateral view: shallow (0), absent (1), deep (2).
(108) Tip of quadratojugal process in lateral view: point (0), absent (1), square (2).
(109) Orientation of the quadratojugal process in lateral view: rostroventral (0), horizontal (1), process absent (2).
(110) Flange of articular surface for the quadratojugal in lateral view: shallow (0), deep (1).
(111) Pneumatic foramen in ceiling of bone in ventral view: absent (0), present (1).
(112) Inflation of postquadratic process in lateral view: not inflated (0), inflated (1).
(113) Postquadratic process in lateral view: long (0), short (1).

Squamosoquadratojugal Flange

(114) Flange present and constricts the laterotemporal fenestra in lateral view: absent (0), present (1; Holtz, 2001, in Currie et al., 2003).

Quadratojugal

(115) Extent of ridge on squamosal process in lateral view: ridge absent or fades distally (0), ridge extends distally (1).
(116) Notch of squamosal process in lateral view: absent (0), present (1).
(117) Flange of squamosal process in lateral view: absent (0), present (1).
(118) Position of the dorsal quadratojugal process of the jugal in lateral view: does not approach base of the vertical ramus of the quadratojugal (0), reaches the base of the vertical ramus (1).
(119) Jugal process, shape in lateral view: tapers anteriorly (0), squared off or double pronged (1; Currie et al., 2003).
(120) Ventral quadratojugal process (= T-shaped quadratojugal of Carpenter et al., 2005a), presence in lateral view: absent (0), present (1).

Quadrate

(121) Truncation of the dorsal margin of the pterygoid process in lateral view: distal (0), proximal (1).
(122) Medial margin of articular surface for the quadratojugal in caudal view: dorsolateral (0), dorsomedial or vertical (1).
(123) Paraquadrate foramen, size in caudal view: absent or small and enclosed by the quadrate (0), large and between the quadratojugal and quadrate (1; Holtz, 2000, in Currie et al., 2003).
(124) Pneumaticity in rostral view: apneumatic (0), pneumatic (1; Molnar, 1991, in Currie et al., 2003).

Jaw Joint

(125) Position of jaw joint in lateral view: rostral to the paroccipital process (0), caudal to the paroccipital process (1; Holtz et al., 2004).

Prefrontal

(126) Proximal width in dorsal view: bone absent or narrow (0), wide (1; Carr, 1999).
(127) Proximal margin in dorsal view: caudal to lateral frontal process of nasal (0), lateral to process (1), prefrontal absent (2).
(128) Rostral extent in dorsal view: distal to the frontal processes of the nasals (0), intermediate (1), proximal to division of the frontal processes (2), prefrontal absent (3).
(129) Prefrontal and lacrimofrontal contact in dorsal view: separates lacrimal and frontal (0), lacrimal and frontal contact each other behind the prefrontal (1), prefrontal is absent (2).
(130) Contribution to mediodorsal margin of the preorbital bar in lateral view: well developed and forms a large part of the bar (0), reduced or absent (1; Gauthier, 1986, in Currie et al., 2003).

Frontal

(131) Length of forehead in dorsal view: long (0), short (1).

(132) Length of nasal process in dorsal view: long (0), short (1).
(133) Width of nasal process in dorsal view: wide (0), narrow (1).
(134) Extent of dorsotemporal fossa in dorsal view A: covers less than half (0), covers half the length or greater than half the length of the frontal (1).
(135) Extent of dorsotemporal fossa in dorsal view B: covers less than half or half the length of the frontal (0), covers greater than half the length of the frontal (1).
(136) Presence of crest along rostral margin of dorsotemporal fossa in dorsal view: absent (0), present (1).
(137) Sagittal crest, division in dorsal view: absent or undivided (0), paired (1).
(138) Sagittal crest, height in lateral view: absent or low (0), tall (1).
(139) Sagittal crest, length in lateral and dorsal views: absent or short (0), long (1).
(140) Joint surface for the lacrimal, length in dorsal view: no contact or long (0), short (1; Carr, 1999).
(141) Joint surface for the lacrimal, width in dorsal view: no contact or narrow (0), wide (1; Carr, 1999).
(142) Margin of the articular surface for the lacrimal, form in dorsal view: lacrimal articulates with prefrontal (0), rostromedial (1), notch (2).
(143) Joint surface for the postorbital in lateral view: little distinction between anterior and posterior parts of suture (0); suture vertical anteriorly, but is a distinct horizontal shelf posteriorly (1; Currie et al., 2003).

Frontoparietal Contact

(144) Pointedness of sagittal crest in lateral view: crest absent or present and not pointed (0), pointed (1).

Parietal

(145) Form of frontoparietal suture in dorsal view: transverse (0), wedge (1).
(146) Sagittal crest in dorsal view: absent (0), present (1; Holtz, 2001, in Currie et al., 2003).
(147) Nuchal crest height in lateral view: as low or lower than the dorsal surface of the interorbital region (0), taller than interorbital region (Holtz, 2001).
(148) Dorsal surface: flat with two parallel sagittal crests that extend onto the frontal (0), paired sagittal crests absent (1; modified after Xu et al., 2006).
(149) Transverse crest within dorsotemporal fossa: present (0), absent (1, Xu et al., 2006).

Laterosphenoid

(150) Transverse scar in dorsal view: absent (0), present (1).
(151) 151: Laterosphenoidoparietal suture: flat (0), raised into a sharp ridge (1).
(152) Parietal suture: laterosphenoid is flat above suture (0), laterosphenoid curves dorsomedially to the suture (1).
(153) Ventrolateral shelf in lateral view: absent (0), present (1).

Otoccipital

(154) Caudal tympanic recess in lateral view: absent or caudal to prootic (0), close to prootic (1).
(155) Ventral extension in caudal view: notch separates basal tuber from more anteroventral extension of exoccipital-basisphenoid suture (0), notch absent (1; Currie et al., 2003).
(156) Contribution to the foramen magnum in caudal view: no contact between left and right sides (0), contact above the foramen magnum (1; Harris, 1998, in Currie et al., 2003).
(157) Curvature of the paroccipital process in caudal view: curving ventrally, pendant (0); directed laterally (1; Currie et al., 2003).

Basisphenoid

(158) Pneumatic recess above basipterygoid process in lateral view: absent (0), present (1).
(159) Recess associated with carotid foramen in lateral view: present (0), absent (1).
(160) Tuberosity lateral to basal tuber in caudal view: absent (0), present (1).
(161) Restriction of the basisphenoid recess in ventral view: absent or open (1), restricted or closed (2).
(162) Closure of the basisphenoid recess in ventral view: absent or open (0), closed (1).
(163) Recess in lateral and caudal views: oriented ventrally (0), oriented posteroventrally (1; Harris, 1998, in Currie et al., 2003).
(164) Inflation of ceiling of basisphenoid recess in ventral view: recess absent or not inflated (0), inflated (1).
(165) Fossae around pneumatic recesses in ventral view: recesses absent (0); recesses present and without fossae (1); fossae present around recesses (2; Carr, 1999).

Basisphenoidobasioccipital Contact

(166) Subcondylar recess depth in caudal view: absent or deep (0), shallow (1).

Basicranium

(167) Basicranium, rectangle defined by positions of both basal tubera and both basipterygoid processes in ventral view: anteroposteriorly longer than wide (0), mediolaterally wider than long (1; Currie et al., 2003).

Basioccipital-Otoccipital

(168) Distance across basal tubera in ventral view: less than the transverse width of condyle (0), greater than transverse width of occipital condyle (1; Holtz, 2000, in Currie et al., 2003).

Supraoccipital

(169) Width of dorsal process in caudal view: narrow (0), wide (1).
(170) Dorsal process of supraoccipital in caudal view: undivided (0), forked (1).
(171) Median ridge in caudal view: absent (0), present (1; Holtz, 2000, in Currie et al., 2003).
(172) Pair of tab-like processes in caudal view: absent (0), present (Bakker et al., 1988, in Currie et al., 2003).

Palate

(173) Shelf-like primary palate, presence in ventral view: absent (0), present (1; modified after Currie et al., 2003).

Vomer

(174) Shape of anterior end, dorsal or ventral view: lanceolate (lateral margins parallel-sided) (0), diamond (1; Carr, 1999).

Epipterygoid

(175) Ventral margin in lateral view: undivided (0); forked (1).

Ectopterygoid

(176) Inflation of the body of the bone in ventral view: not inflated (0), inflated (1; modified after Carr et al., 2005).
(177) Length of jugal process in dorsal or ventral view: short (0), long (1; modified after Carr et al., 2005).
(178) Perforation of jugal process in caudal view: imperforate (0), perforate (1; Carr et al., 2005).
(179) Inflation of jugal process in dorsal or ventral view: rostral margin not inflated (0), rostral margin inflated (1; modified after Carr et al., 2005).
(180) Inflation of the pterygoid process in ventral view: not inflated (0), inflated (1).
(181) Shape of pneumatic recess in ventral view: recess absent (0), slot (1), round (2).
(182) Extent of pneumatic foramen in ventral view: absent (0), extends medially (1), restricted laterally (2; modified after Carr et al., 2005).
(183) Surface adjacent to pneumatic recess in ventral view: recess absent (0), flat (1), lip (2; modified after Carr et al., 2005).
(184) Strut from the dorsal articular surface for the pterygoid: absent (0), present (1).

Palatine

(185) Height of the dorsal process in lateral view: tall (0), low (1; modified after Carr et al., 2005).
(186) Length of dorsal process in lateral view: narrow (0), long (1; modified after Carr et al., 2005).
(187) Dorsal process in lateral view: inclined rostrodorsally (0), extends vertically (1).
(188) Choanal process position in lateral view: dorsal (0), ventral (1).
(189) Number of pneumatic recesses in lateral view: zero (0), one (1), two (2; Carr et al., 2005).
(190) Pattern of pneumatic recesses in lateral view: recess absent (0), caudal foramen only (1), caudal foramen and rostral fossa (2).
(191) Size and shape of caudal pneumatic recess in lateral view: recess absent (0), small and angular (1), large and round (2).
(192) Position of the caudal palatine recess in lateral view A: absent (0), extends beyond caudal margin of dorsal process (1), does not reach the caudal margin of the process (2; modified after Carr et al., 2005).
(193) Position of caudal recess in lateral view B: absent (0), extends ahead of rostral margin of dorsal process (1), restricted ventral or caudal to rostral edge of process (2).
(194) Position of the articular surface for the lacrimal in lateral view: no contact (0), proximal (1), distal (2; modified after Carr et al., 2005).
(195) Slot of the articular surface for the maxilla in lateral and ventral views: absent (0), present (1; modified after Carr et al., 2005).
(196) Lateral extension in dorsal view: absent (0), present (1).
(197) Inflation of the lacrimal process in lateral view: uninflated (0), inflated (1).

Mandibular Ramus

(198) Depth in lateral view: shallow (0), deep (1).

Articular

(199) Depression for depressor mandibulae in caudal view: oriented more dorsally than posteriorly (0), oriented mostly posteriorly (1; Currie et al., 2003).
(200) Pneumaticity: apneumatic (0), pneumatic (1; Currie et al., 2003).
(201) Retroarticular process, length in lateral view: long (0), short (1; Xu et al., 2006).

Surangular

(202) Size of the caudal surangular foramen in lateral view: small foramen or absent (0), large (1; Carr et al., 2005).
(203) Size of the caudal surangular foramen in lateral view: small foramen or absent (0), small fenestra (1), large fenestra (2; modified after Carr et al., 2005).
(204) Rostral margin of caudal surangular foramen in lateral view: caudoventral or vertical (0), rostroventral (1), absent (2).
(205) Anteroventral extension, presence in lateral view: extension is absent (0), present and encloses external mandibular fenestra by contacting the angular rostrally (1; Currie et al., 2003).
(206) Surangular shelf in lateral view: does not overhang caudal surangular foramen (0), overhangs caudal surangular foramen (1; Carr, 1999, in Holtz, 2001).
(207) Surangular shelf in lateral view: a low ridge (0), a prominent ridge (1; Xu et al., 2006).

Splenial

(208) Rostral mylohyoid foramen, size in lateral or medial view: small (0), large (1).
(209) Rostral process in lateral or medial view: short and shallow (0), long and deep (1).
(210) Anterodorsal margin of the bone in lateral or medial view: smoothly tapering (0); abrupt step anterior to contact with intercoronoid (1; Currie et al., 2003).

Dentary

(211) Position of Meckelian groove in medial view: at the mid-height of the bone (0), close to ventral margin of bone (1).
(212) Rostral extent of lingual bar in medial and dorsal views: medial to first alveolus (0), medial to second (or further caudal) alveolus (1).
(213) Position of the transition point between the ventral and rostroventral margins of the dentary in lateral view: below alveoli 1-3 (0); below alveolus 4 (1).
(214) Interdental plates in medial view: unfused (0); fused (1).

External Mandibular Foramen

(215) External mandibular foramen in lateral view: large (0), small (1).

Dentition

(216) Premaxillary: smaller than maxillary teeth (0), same size as maxillary teeth (1).
(217) Premaxillary: not D-shaped in cross section or absent (0), D-shaped in cross section (1).
(218) Maxillary: 13 or more alveoli (0); less than 13 alveoli (1).
(219) Dentary: 15 or more alveoli (0); less than 15 alveoli (1).

Cervical Vertebrae

(220) Cervical centra: amphicoelous (0); opisthocoelous, cranial surface is flat or convex (1).

Dorsal Vertebrae

(221) Dorsal centra: amphicoelous (0), opisthocoelous cranial dorsals (1) platycoelous or amphiplatyan (2; Carpenter et al., 2005b).

(222) Dorsal vertebrae pneumaticity: apneumatic (0), pneumatic (1).
(223) Dorsal vertebrae, length of spinous process: long, overhangs centrum caudally (0); short, does not overhang centrum caudally (1).
(224) Dorsal vertebrae, ratio of centrum height:length: less then 75% (long and low; 0), greater than 75% (short and tall; 1; Carpenter et al., 2005a).

Sacral Vertebrae

(225) Sacral vertebrae pneumaticity: pneumatic (0), apneumatic (1).

Caudal Vertebrae

(226) Prezygapophyses, length A: short (0); elongate, exceeds the length of the preceding vertebra (1).
(227) Prezygapophyses, length B: less then one-third of centrum length (0), one-third centrum length or greater (1; Carpenter et al., 2005).
(228) Transverse processes: on more than 15 caudals (0), on 15 or fewer caudals (1; Holtz, 2004).

Furculum

(229) Hypocleidium: absent (0), present (1; Lipkin et al., 2007).

Scapula

(230) Angle between acromion process and shaft in lateral view: greater than 90 degrees (0), approaches or equals 90 degrees (1).

Forelimb

(231) Size of manus and arm: not reduced (0), reduced (1).

Humerus

(232) Humerus, form of shaft: straight (0), sigmoid (1; Carpenter et al., 2005a).

Radius

(233) Radius, form: straight (0), bowed (1; Carpenter et al., 2005b).

Carpus

(234) Semilunate carpal: present (0), absent (1; Xu et al., 2006).

Manus

(235) Manus, number of digits: three or more (0), less than three (1).
(236) Metacarpal II: more robust than metacarpal I (0), same width or narrower than metacarpal I (1).
(237) Metacarpal III: same length as metacarpal II (0), shorter than metacarpal II (1; Holtz, 2004).
(238) Manus, D III: not reduced or absent (0), thin (1).
(239) Metacarpal IV: present (0), absent (1).

Ilium

(240) Rostrodorsal notch in lateral view: absent (0), present (1).
(241) Preacetabular ilium in lateral view: short (0), long (1).
(242) Ridge above acetabulum in lateral view: absent (0), present (1; Rauhut, 2003).
(243) Orientation of ridge above acetabulum in lateral view A: absent or posterodorsal (0), vertical (1; Rauhut, 2003).
(244) Orientation of ridge above acetabulum in lateral view B: absent or vertical (0), posterodorsal (1; Rauhut, 2003).
(245) Anterior hook in lateral view: absent (0), present (1; Rauhut, 2003).
(246) Anterior margin of the pubic peduncle in lateral view: straight or convex (0), concave (1; Xu et al., 2006).
(247) Ilium: almost the same length as the femur (0), significantly shorter than the femur (1; Xu et al., 2004).

Pubis

(248) Shaft in lateral view: straight or bowed rostrally (0), bowed caudally (1).
(249) Obturator foramen in lateral view: present (0), absent or notch (1).
(250) Obturator foramen in lateral view: absent or foramen (0), notch (1).
(251) Pubic tubercle in lateral view: absent (0), present (1).
(252) Rostral boot in lateral view: absent (0), present (1).
(253) Rostral boot in lateral view: absent or short (0), long (1).
(254) Rostral boot in lateral view: absent or long (0), short (1).
(255) Ventral margin of boot in lateral view: boot absent (0), convex (1), straight (2; Carpenter et al., 2005a).
(256) Pubic apron in caudal or rostral view: foramen absent (0), present (1; Carpenter et al., 2005a).

Ischium

(257) Semicircular scar in lateral view: absent (0), present (1).
(258) Obturator foramen in lateral view: absent or notch (0), present (1).
(259) Obturator foramen in lateral view: notch (0), absent or foramen (1).
(260) Distal end in lateral view: dilated (0), not dilated distally (1).
(261) Ischial shaft compared with pubic shaft in lateral view: as thick or thicker than pubis (0), ischium thinner than pubis (1).

Femur

(262) Femoral shaft form, cranial and caudal views: straight (0), sigmoid (1; Carpenter et al., 2005a).
(263) Femoral head elevation in cranial or caudal views: not elevated (0), elevated (1).
(264) Oval scar for M. caudifemoralis longus in caudal view: absent or medial to caudal midline (0), on caudomedial medial edge of shaft (1; modified after Carr et al., 2005).
(265) Lesser trochanter in cranial or caudal views: lower than the greater trochanter (0), as tall as the greater trochanter (1; Xu et al., 2004).

Tibia

(266) Cranial process of the lateral cnemial process in dorsal view: present (0), absent (1; Molar et al., 1994).

Fibula

(267) Bipartite scar in cranial view: absent (0); present (1).

Astragalus

(268) Ascending process, width in cranial view: half the width of the bone (0), greater than half the width of the bone (1; Carpenter et al., 2005b).
(269) Ascending process, basal fossa in cranial view: basal fossa is absent (0), basal fossa is present (1; Carpenter et al., 2005b).
(270) Distal condyles in cranial view: horizontal groove present (0), horizontal groove absent (1; Carpenter et al., 2005b).

Metatarsus

(271) Arctometatarsus: absent (0), present (1; Holtz, 1994).

(272) Metatarsals II and III, length relative to humerus: less than 1.74 times length of humerus (0), greater than 1.74 times length of humerus (1; Carpenter et al., 2005a).

Body Size

(273) Ilium or femur: less than 50 cm long (0), greater than 50 cm long (1).

Integument

(274) Integument: scales (0), feathers (1).

APPENDIX 2. The data matrix used to resolve the ingroup relationships of Tyrannosauroidea.

Dryptosaurus aquilunguis

?????????? ?????????? ?0???????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?12???1??? 0????????? ?????0???? 00???????? ???????1?? ??????1??? ???0?111?1 ??1?

Appalachiosaurus montgomeriensis

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Bistahieversor sealeyi

00?1011001 0122212111 110001101? ?011111110 02111010000 0001220220 000010?001 01112?0000 0110100011 1212000110 010000000? ?010001010 1110002110 0010101011 1111111000 0?0??1(01)100 0101?01??? ???0010001 2110000111 1211011111 1210011010 ?1000100?? ????011?1? ?????????1 ?????????? ?????????? ?01?1??1?1 1?1?

Albertosaurus libratus

0001011101 11222121(01)(01) 1101001010 0011011110 0220101000 0000111211 0(02)00010000 1011122111 0011020001 1210(12)0111(01) (01)000000010 0001000001 0011001110 00010(01)0101 121(01)111100 0100101010 000110?110 1110100010 1211111022 1221101111 11(12)0001101 00100010(01)1 0101?01111 1001101011 1110110110 11102?1001 001010111? 1110

Albertosaurus sarcophagus

0011011101 11222121(01)1 2101001(01)10 0011?111(01)0 0110011000 000011(12)212 0(02)(01)(01)01??00 1011122111 001(12)(01)20102 1210101111 001000001? ??01001001 1011000210 00010(01)0101 1210111100 00?0111010 0011(12)011(01)0 1110?0(01)0(01)0 1211111(01)(12)(12) 2(12)(12)(12)001111 1120001101 0010?01(01)01 0??1?0??11 100110?011 1110110110 01102?1001 001?101111 1?1?

New genus from Utah

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Daspletosaurus spp.

0011011111 1112122111 1101002111 0011111101 0120101000 0001111(12)22 12121(12)1101 1112221120 11120(12)(01)001 2121110012 1001(01)02211 1101100011 0111010010 01(01)1(01)00202 1211011101 10101111(01)0 0010101110 1110010011 2221(01)(01)0022 1122101111 1120011101 0010001001 ?101?01111 1001101011 1110110110 01102?1001 0?1?1????? 1?1?

Daspletosaurus sp. **(MOR 590)**

0????????? ??12122?11 110100211? ??11?11101 ??????1000 0000111022 ?012111101 1112221121 1112010001 1121110012 1001?02211 1101???1?1 ??1?0???1? 0?????0??? ??111?1??1 1?10111??0 001??0??11 ?????11?11 222100102? 1121??11?? ?120??110? 0010???00? ?????????? ?????????? ?????????? ?????????? ?01?10?1?? 1?1?

Tyrannosaurus rex

1111(01)11111 111122100 (12)10(01)0(01)(13)011 1011111111 12(02)0101000 0001020022 0210021110 1112(12)1112(01) 011(12)021011 1120100012 01(01)1102211 1111(01)10111 0111000(01)11 1(01(01)1(01)01(12)12 211(01)011101(01) (01)011111101 1110111111 1111(01)1(01)(01)11 2120000022 1122111111 11(12)001110(01) 0(01)10001111 0101101001 10?101011 1110110110 1110211001 0011101111 1110

Tyrannosaurus bataar

0011011111 1111122100 1100103011 0011?111(01)1 0220101000 0001020022 0212021100 1112221120 111101(01)011 1120100?12 0101102?11 11?1000011 0111010010 1001101212 2111011100 0011111??1 1010?11111 1111?11111 212?000022 1122?11111 1??(01)01110(01) 0(01)10001101 01011010?1 1001101011 1110110110 ?1102??001 0011101111 1110

Cf. *Alectrosaurus* (GIN 100/50, 100)

????11??1 1??22111?? 100?????1? ?????????? ??????0000 000??????? ?????????? ?????????0 ?????1000? ??????0000 1????0???? ???1???001 ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???????1?? ?????????? ??1??0?00? ?????????0 ?????????? ?????????? ?????????? ?????????? 1???

Alioramus remotus

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Bagaraatan ostromi

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Aviatyrannis jurassica

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Dilong paradoxus

00000111?0 1?22121011 10010??01? ?011?01110 0000??0000 0010000022 ??0??0??0? 101122?11? 001?000000 0000010000 100??1110? ??10?0000? ???10???00 01?00?000? ???001001? ?????01??? 001???00?? 1????????? ?????????? ???????011 10020010?? ??0?001111 001??00??0 0???001111 00000?101? 00002??000 1???0????? 0001

Guanlong wucaii

00?10011?0 1?22211000 10110?000? ?011?1?010 ??????0111 1110000022 ??00?0??00 011122?120 0?1?00?000 ?????00100 000??1110? ??00000001 ????0???01 ???00?000? ???000000? ?????11??? 000???01?? ?????????? ?????????? ???????0?? 1002000??? ??0?101010 ?0??001??0 0100011001 011?010000 11011?0110 0???0????? 0?0?

Eotyrannus lengi

???1??10?1 1????????? ?00????00? ?0?1?111?0 ??????1000 00???????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? 1??1?????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? 0??0??1??1 11??1????0 00??00???? ?????????? ?????????? ?????????? ?00?

Stokesosaurus clevelandi

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Iliosuchus incognitus

?????????? ?101?1???? ?????????? ?????????? ????

Tanycolagreus topwilsoni

???0?110?1 00???????? ?????????? ???0?1???? ??????0000 00?0000011 0?0???0000 1????????? ?????????0 000001??12 00???????? ????000?01 ?110?????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? 1??????0?? ?????????? 0001001??0 001000110? ???????0?? ?10121???? ?00?010111 000?

Coelurus fragilis

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Monolophosaurus jiangi

00?1001000 0?21122000 211100000? ??10?11010 0000001011 1110000000 010100??00 011212?001 000002?000 0000000011 10??01110? ??00000001 011?111000 10000?0000 00?000000? ????00??0 000????010 10??1????? ????100100 0001?000?? ?00?000000 0000110001 1001?0???? ?????????0 000011?000 0?????0110 0????????? ??1?

Allosaurus fragilis

0000000000 0011111000 1011000000 01100000(01)0 0121000110 0010111111 0(02)00000000 1100(01)?1(01)00 00000(01)0(01)00 111010000(02) 1000011100 0000000001 0000100000 (01)000000000 0000000000 ???0000(01)00 0000000000 00000000?0 1110000000 0000000000 0000101001 1001010001 1101001010 0100000110 0000000110 0101110000 1000000000 0?1?

Velociraptor mongoliensis

00?0?00010 0?22211100 100100?01? ?110?10100 0000000000 0001122112 1002?00000 101122?00? 000002?000 0000010000 0000000000 ?000000101 ??10002321 0100000000 01??0????0 00011011?0 1001?01110 1011??0?0? ????110011 221??1001? 100??110?? 1?010101(01)0 2101011110 00?001111? 0000101010 1001?10011 000?0??11? 0?01

Sinosauropteryx prima

0??1??00?0 0?0???21?? 100??????? ??1???1??0 0????00000 00??000000 ?10??0???0 ?????????? 0?000????0 00000???00 00???0000? ??1??????? ???1001000 ?????????? ?0???????? ?????????? ?????????? ?????????? ?????????? ???????0?? ?????????? ??0??100?0 ?011?000?0 0000011010 10001111?? ?1011?0000 100?0??111 0?01

Coelophysis bauri

00?00000?0 0?0????000 ?0000???0? ?000?0?000 0000000000 0000000000 0?0??0??00 00???0???? 000000?000 000000??00 00???0000? ???0???000 ??0?0????? ?????????? ?????????? ?????????? ?????????? ???????0?? 000?0?0100 000???00?? ?????????? ??0?000000 0000000000 000?000000 00000(01)1000 0000000000 000?0??000 000?

APPENDIX 3. The distinction between the shallow and deep conditions of theropod maxillae.

Relative snout depth is in reference to the depth of the dentigerous region of the horizontal ramus of the maxilla below the antorbital fenestra in lateral view. Externally, the dorsal extent of the teeth in theropods coincides with the ventral margin of the antorbital fossa. The dentigerous region is indicated by the subcutaneous surface below the fossa, which is wider than the fossa presumably to accommodate the teeth.

In shallow-snouted tyrannosauroids, such as *Dilong* and *Appalachiosaurus*, the dentigerous region is twice the depth or less than the antorbital fossa above it (Xu et al., 2004; Carr et al., 2005). In shallow-snouted theropods, the dentigerous region is usually shallower than the longest tooth below it, with the exception of therizinosauroids and troodontids where the teeth are small (Clark et al., 2004; Makovicky and Norell, 2004). Because of its incompleteness, the maxilla of *Dryptosaurus* could not be characterized as either shallow or deep. In ornithomimosaurians and oviraptorosaurians, the maxilla is a shallow bar below the antorbital fenestra, although the antorbital fossa may be shallower or deeper than the subcutaneous surface below it, or absent (Makovicky et al., 2004; Osmólska et al., 2004).

In deep-snouted tyrannosauroids, such as *Bistahiversor*, *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus*, the dentigerous region is greater than twice the depth of the antorbital fossa above it. This character is somewhat variable, where the dentigerous region may only be twice as deep as the fossa or less in small juvenile specimens (CMNH 7541, TMP 85.11.3, TMP 86.144.1), and some subadults (AMNH 5477) where the dentigerous may only be twice the depth of the fossa. Regardless, it is evident in those specimens that the dentigerous region is deep in comparison with the length of the bone, and it is as deep or deeper than the longest teeth below it.

The shallow-snouted condition is also present in most other theropods, except for *Herrerasaurus*, *Eoraptor*, abelisaurids, *Monolophosaurus*, *Carcharodontosaurus*, *Acrocanthosaurus*, and *Dromaeosaurus*, where the dentigerous region is twice or more the depth of the antorbital fossa above it (Langer, 2004; Tykoski and Rowe, 2004; Holtz et al., 2004; Norell and Makovikcy et al., 2004). In other theropods such as *Dilophosaurus*, *Ceratosaurus*, and *Allosaurus*, the antorbital fossa is several times deeper than the dentigerous region (Tykoski and Rowe, 2004; Holtz et al., 2004). Although this condition produces a deep horizontal ramus of the maxilla it is not equivalent to the condition in other deep-snouted theropods, because the dentigerous region is shallow.

ADDENDUM

Recently a new genus and species of tyrannosauroid, *Raptorex kriegsteini*, from the Early Cretaceous of China has been found to be the sister taxon of Tyrannosauridae (Sereno et al., 2009). This taxon is significant because it is thought to be a small-bodied tyrannosauroid, in contrast to the much larger tyrannosaurids, and it has a reduced forelimb as is seen in its sister clade. The holotype and only specimen of *R. kriegsteini* is a subadult, in which the dentigerous region of the maxilla is shallow; the condition of the bone in adults is presently unknown, but we hypothesize that it will be deep, if that character state is correlated with the small forelimb size. If so, then the adaptation of a deep snout originated much earlier than the Campanian, and it evolved in Asia instead of western North America.

LITERATURE CITED

Sereno, P. C., L. Tan, S. L. Brusatte, H. J. Kriegstein, X. Zhao, and K. Cloward. 2009. Tyrannosaurid skeletal design first evolved at small body size. Science 326(5951):418–422.