Prootic anatomy of a juvenile tyrannosauroid from New Jersey and its implications for the morphology and evolution of the tyrannosauroid braincase

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Among the most recognizable theropods are the tyrannosauroids, a group of small to large carnivorous coelurosaurian dinosaurs that inhabited the majority of the northern hemisphere during the Cretaceous and came to dominate large predator niches in North American and Asian ecosystems by the end of the Mesozoic era. The clade is among the best-represented of dinosaur groups in the notoriously sparse fossil record of Appalachia, the Late Cretaceous landmass that occupied the eastern portion of North America after its formation from the transgression of the Western Interior Seaway. Here, the prootic of a juvenile tyrannosauroid collected from the middle-late Campanian Marshalltown Formation of the Atlantic Coastal Plain is described, remarkable for being the first concrete evidence of juvenile theropods in that plain during the time of the existence of Appalachia and the only portion of theropod braincase known from the landmass. Phylogenetic analysis recovers the specimen as an “intermediate” tyrannosauroid of similar grade to *Dryptosaurus* and *Appalachiosaurus*. Comparisons with the corresponding portions of other tyrannosauroid braincases suggest that the Ellisdale prootic is more similar to Turonian forms in morphology than to the derived tyrannosaurids of the Late Cretaceous, thus supporting the hypothesis that Appalachian tyrannosauroids and other vertebrates were relict forms surviving in isolation from their derived counterparts in Eurasia.

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Abstract.

Among the most recognizable theropods are the tyrannosauroids, a group of small to large carnivorous coelurosaurian dinosaurs that inhabited the majority of the northern hemisphere during the Cretaceous and came to dominate large predator niches in North American and Asian ecosystems by the end of the Mesozoic era. The clade is among the best-represented of dinosaur groups in the notoriously sparse fossil record of Appalachia, the Late Cretaceous landmass that occupied the eastern portion of North America after its formation from the transgression of the Western Interior Seaway. Here, the prootic of a juvenile tyrannosauroid collected from the middle-late Campanian Marshalltown Formation of the Atlantic Coastal Plain is described, remarkable for being the first concrete evidence of juvenile theropods in that plain during the time of the existence of Appalachia and the only portion of theropod braincase known from the landmass. Phylogenetic analysis recovers the specimen as an “intermediate” tyrannosauroid of similar grade to *Dryptosaurus* and Appalachiosaurus. Comparisons with the corresponding portions of other tyrannosauroid braincases suggest that the Ellisdale prootic is more similar to Turonian forms in morphology than to the derived tyrannosaurids of the Late Cretaceous, thus supporting the hypothesis that Appalachian tyrannosauroids and other vertebrates were relict forms surviving in isolation from their derived counterparts in Eurasia.

Introduction.

During the Campanian Stage of the Late Cretaceous, taxa from the clade Tyrannosauroidea had emerged as dominant large predators of terrestrial ecosystems in the northern hemisphere (e.g., Holtz, 2004; Brusatte et al., 2010; Holtz, 2012; Loewen et al., 2013 Brusatte and Carr, 2016; Carr et al., 2017). In western North America, members of the derived Tyrannosauridae inhabited the Campanian landmass Laramidia, whereas intermediate-grade species did so on Appalachia (e.g, Schwimmer, 1997; Holtz, 2004; Carr et al., 2005; Brusatte et al, 2011; Brusatte and Carr, 2016; Carr et al., 2017). The latter are among the best-represented dinosaurs in Appalachian faunas, with comparatively abundant teeth and bones assignable to them described from many deposits in the American East (e.g., Baird & Horner, 1979; Schwimmer et al., 1993; Schwimmer, 1997; Carr et al., 2005; Brusatte et al., 2011; Ebersole & King, 2011; Schwimmer et al., 2015; Brownstein, 2017). The majority of recently described tyrannosauroid material has come from Campanian deposits in the southeastern United States, including the holotype juvenile partial skeleton and other elements assigned to *Appalachiosaurus* (Schwimmer et al., 1993; Carr et al., 2005; Ebersole & King, 2011; Schwimmer et al., 2015). Schwimmer (2002) and Schwimmer et al. (2015) noted the abundance of definite and likely small/juvenile tyrannosauroid elements from southeastern sites, the former proposing that the large crocodylian *Deinosuchus* may have actively been competing with tyrannosaurs for prey. Southeastern deposits have also preserved the remains of juvenile nodosaurids and hadrosauroids (e.g, Burns & Ebersole, 2016; Prieto-Márquez et al., 2016a, 2016b), evincing a possible preservation bias towards juvenile individuals in such geological units.

Unfortunately, the record of juvenile dinosaurs in the Campanian of northeastern North America is limited. Gallagher (1995) described teeth from the Ellisdale site that he referred to juveniles of the tyrannosauroid *Dryptosaurus*, as well as several very small specimens of hadrosauroids. However, these teeth, all from the Ellisdale site, are either assignable to large dromaeosaurids or only to Theropoda indet. (pers. obs.). The few specimens of possible hadrosauroids described from the Campanian of the Atlantic Coastal Plain (ACP) are less problematic, being at least an order of magnitude smaller than inferred adult material from the same deposits (Gallagher, 1995). Moreover, cranial material from Appalachian dinosaurs is also extremely rare compared to its frequency in Laramidian fossil record, with only a handful of specimens known from the eastern United States (Langston, 1960; Carpenter et al., 1995; Schwimmer, 1997; Fix & Darrough, 2004; Carr et al., 2005; Prieto-Márquez et al., 2006; Brusatte et al., 2011; Schwimmer et al., 2015; Burns & Ebersole, 2016; Prieto-Márquez et al., 2016a, 2016b).

In June 1994, a skull element was collected from the Campanian-age deposits of the Ellisdale site of New Jersey, a locality notable for producing an extensive vertebrate microfauna (e.g., Grandstaff et al., 1992; Denton & O'Neill, 1995, 1998; Weishampel & Young, 1996; Denton et al., 2011). The fossil (NJSM 22738), identified as the prootic of a juvenile tyrannosauroid here, is especially well-preserved among dinosaur materials from the ACP. The prootic is the first definite occurrence of a juvenile theropod in the Atlantic Coastal Plain and the first element of a theropod braincase known from Appalachia.

Methods.

Permits.

No permits were required for this study. Access to the collections of the NJSM was given by David Parris.

Photography.

The specimen was photographed using a Canon G-12 camera and figures were cropped in Apple Preview.

Institutional Abbreviations.

NJSM, New Jersey State Museum collections, Trenton, NJ, United States; YPM VPPU, Princeton University collection in the Division of Vertebrate Paleontology, Yale Peabody Museum, New Haven, CT, United States.

Phylogenetic analysis.

In order to provide support for the assignment of NJSM 22738 to Tyrannosauroidea among Coelurosauria and test its relationships in detail among the former clade, the prootic was coded for and included in phylogenetic analyses using both the Theropod Working Group matrix of Brusatte et al. (2014) and the tyrannosauroid matrix of Carr et al. (2017). The parsimony analysis was run in TNT v. 1.5 with standard parameters for ratchet, tree drift, tree fuse, and sectorial search (Goloboff and Catalano, 2016). The most parsimonious trees (MPTs; 100 (overflow) in both) found were then subjected to traditional TBR branch swapping. Clade support was quantified by bootstrap values (100 replicates in TNT v. 1.5; Goloboff and Catalano, 2016) and Bremer supports.

Results

Systematic Paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tyrannosauroidea Osborn, 1905

Tyrannosauroidea indet.

Material: NJSM 22738 (Fig. 1), prootic of a juvenile tyrannosauroid dinosaur.

Geological Setting: NJSM 22738 was recovered from the Campanian Marshalltown Formation at the Ellisdale site in New Jersey. The Marshalltown Formation is Campanian in age (e.g., Miller et al., 2004), dated at 76.4-79.6 million years old at Ellisdale (Denton & Tashjian, 2012). The

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site has most recently been interpreted as an assemblage of both proximal and distal faunas deposited in the same area by storms (Denton & Tashjian, 2012).

Description: NJSM 22738 (Fig. 1A-C) is the prootic of an intermediate-grade tyrannosauroid dinosaur. Two unambiguous features support this referral: the presence of a deepened fossa on the lateral portion of the bone and the extension of the tympanic recess onto it (e.g., Brusatte et al., 2010; Brusatte et al., 2014; Brusatte & Carr, 2016; Carr et al., 2017). NJSM 22738 is assignable to a juvenile theropod dinosaur based on the presence of unfused sutures on all sides. The prootic is small, measuring less than 20 mm on its greatest axis (Table 1). The prootic is elongate dorsoventrally, and the articular surfaces for the parietal, blasisphenoid, and opisthotic-exooccipital are all present and unfused, evincing that the prootic came from a juvenile tyrannosauroid dinosaur. It is likely that the animal to which NJSM 22738 belonged was very young, as the prootic is much smaller than the corresponding element in tyrannosauroids of similar size to *Appalachiosaurus* and *Dryptosaurus* (Brochu, 2003; Bever et al., 2013). The caudal process of the prootic, though not as developed as in *Alioramus* and other derived tyrannosauroids (e.g., Bever et al., 2013), is preserved and triangular in morphology (Fig. 1A). The otosphenoidal crest is preserved, with a rounded lateral edge (Fig. 1A). It is unclear whether the otosphenoidal crest runs along the caudal process in NJSM 22738. The presence of a "dull" otosphenoidal crest differentiates NJSM 22738 from the sharpened condition of the lateral surface of the crest in adult specimens of *Daspletosaurus* and *Tyrannosaurus* and was suggested by Bever et al. (2013) as a mark of immaturity. The preotic pendant (Fig. 1A) is present as in large tyrannosauroids and other theropods (e.g., Currie, 1997; Chure & Madsen, 1998; Norell et al., 2006; Sampson & Witmer, 2007; Bever et al., 2013). The superficial lamina appears as two eroded caudal processes (Fig. 1A), allying NJSM 22738 with derived tyrannosauroids rather than with *Dilong* and *Guanlong*, the prootics of which lack the feature (Bever et al., 2013). The confluence of the dorsal of the two processes of the superficial lamina and the caudal process is not as sharp as in *Alioramus* (Bever et al., 2013). As in other tyrannosauroids, the lateral surface bears a deepened prootic fossa that sits between the caudal process and preotic pendant and houses both the foramen for the maxillomandibular branch of the trigeminal ($V_{2/3}$) nerve and that for the facial (VII) nerve (Fig. 1A)(e.g, Witmer & Ridgely, 2009; Bever et al., 2013; Brusatte et al., 2014; Brusatte et al., 2016). The trigeminal ($V_{2/3}$) nerve bifurcates within the prootic (Fig. 1A-B) as in the intermediate-grade tyrannosauroid *Timurlengia*, but unlike the condition in derived tyrannosauroids where the nerve arrives in two separate branches from the endocast (Witmer & Ridgely, 2009; Bever et al., 2013; Brusatte et al., 2016). As observed in the braincase of *Alioramus*, two small foramina associated with the rostral tympanic sinus sitting in the prootic fossa dorsoventrally between the foramina for the openings of the trigeminal ($V_{2/3}$) and facial (VII) nerves are present (Bever et al., 2013). Another foramen associated with the rostral middle cerebral vein and the rostral tympanic sinus that is present on the caudal process of *Alioramus* (Bever et al., 2013) is also identifiable on the caudal process of NJSM 22738 (Fig. 1A)/ The trigeminal ($V_{2/3}$) nerve openings are large and rounded and contained in a larger, slight ovoid fossa, whereas that for the facial nerve is elliptical and deep. The tympanic recess projects slightly into the prootic. The medial surface is smooth with one exit point for the trigeminal ($V_{2/3}$) nerve, and the entirety of the original bone surface is preserved (Fig. 1B). The dorsal tympanic recess, which sits on the lateral surface of the braincase just dorsal to the prootic (e.g., Witmer, 1997; Rauhut, 2004; Bever et al., 2013) is inferred present based on a smooth, concave portion of bone on the dorsomedial surface of the caudal process of the prootic (Fig.1B). This feature unites the Ellisdale prootic with basal and intermediate-grade tyrannosauroids, such as *Dilong*, *Guanlong*, and *Timurlengia* (e.g., Bever et al., 2013; Brusatte et al., 2016).

Discussion.

Placement within Tyrannosauroidea.

NJSM 22738 was resolved as a basal tyrannosauroid in the analysis of the bone in the matrix of Brusatte et al. (2014)(Fig. 2A), providing support for this referral (tree length = 3306, consistency index = 0.327, retention index = 0.757). NJSM 22738, when included in the matrix of Carr et al. (2017) for phylogenetic analysis among Tyrannosauroidea, was recovered as the sister taxon to all other tyrannosauroids more derived than *Dilong* (tree length = 782, consistency index = 0.571, retention index = 0.803; Fig. 2B). This corresponds to the results of previous phylogenetic analyses that have found Appalachian tyrannosauroids as of intermediate grade between basal taxa like *Dilong*, *Eotyrannus*, and the proceratosaurids and the derived tyrannosaurids and their closest relatives (e.g., Holtz, 2004; Carr et al., 2005; Brusatte et al., 2010; Brusatte et al., 2011; Brusatte et al., 2014; Brusatte & Carr, 2016; Brownstein, 2017; Carr et al., 2017). The results of the phylogenetic analyses on NJSM 22738 undertaken herein also further support the hypothesis that Appalachia was a refugium for dinosaurs and other vertebrates (e.g, Grandstaff et al., 1992; Denton and O'Neill, 1995, 1998; Schwimmer, 1997; Schwimmer, 20002; Kiernan & Schwimmer, 2004; Carr et al., 2005; Brusatte et al., 2011; Prieto-Márquez et al., 2016a, 2016b).

Because NJSM 22738 is the first portion of a tyrannosauroid braincase known from Appalachia, it could not be compared morphologically with the other taxa from the landmass and is thus referred to Tyrannosauroidea indet. Fortunately, however, the braincase of the intermediate-grade tyrannosauroid *Timurlengia* is known (Brusatte et al., 2016). As noted, NJSM

22738 shares with *Timurlengia* a trigeminal ($V_{2/3}$) nerve that bifurcates within the prootic (as opposed to the endocast)(Brusatte et al., 2016). Because NJSM 77238 was resolved as a close relative of other Appalachian tyrannosauroids in the phylogenetic analysis performed, it is likely that the prootic is to an extent representative of the general morphology of Appalachian genera. The prootic described herein also shows that many of the features of the same element in derived tyrannosauroids were already developed among tyrannosauroids of intermediate grade. These features include the presence of the superficial lamina as two caudal oriented processes. However, the prootic also shows that Appalachian tyrannosauroids retained many similarities with basal taxa in their braincase, such as the divergence of the two branches of the trigeminal ($V_{2/3}$) nerve within the prootic and the presence of the tympanic recess (Bever et al., 2011; Bever et al., 2013; Brusatte et al., 2016).

Taphonomic implications.

NJSM 27738 can be confidently identified as the prootic of a juvenile dinosaur based on the unfused sutures present on its borders with other portions of the braincase, its small size, and its reduced otosphenoidal crest (e.g., Bever et al., 2013). The prootic is thus important for being the first specimen of a dinosaur identifiable as a juvenile theropod from the the Atlantic Coastal Plain. In the southeastern United States, juvenile tyrannosauroids are represented by at least two immature specimens, the holotype of *Appalachiosaurus* and a partial metatarsal IV from the Blufftown Formation of Georgia assignable to a juvenile individual of that taxon based on its smaller size than the metatarsal IV of the holotype (Schwimmer et al., 1993; Carr et al., 2005). Schwimmer et al. (2015) reported teeth and other elements of *Appalachiosaurus* from the mid-Campanian Coachman Formation of South Carolina that they suggested to be material from juveniles of the taxon based on size. Gallagher (1993, 1995) reported teeth from the Ellisdale site

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he assigned to juveniles of the genus *Dryptosaurus*, though none can be confidently referred to any particular ontogenic stage. It should be noted that in the case of the majority of these reports of juvenile animals, the specimens come from microfossil sites (Grandstaff et al., 1992; Gallagher, 1993, 1995; Denton and O'Neill, 1995, 1998; Schwimmer et al., 2015). Nevertheless, it is intriguing that 50% of reported Conacian-Maastrichtian Appalachian dinosaur specimens that include cranial material (n = 14) are juveniles (n = 7)(Langston, 1960; Carpenter et al., 1995; Schwimmer, 1997; Fix & Darrough, 2004; Carr et al., 2005; Prieto-Márquez et al., 2006; Brusatte et al., 2011; Schwimmer et al., 2015; Longrich, 2016; Prieto-Márquez et al., 2016a, 2016b; Burns & Ebersole, 2017; this paper). Juvenile dinosaurs are very well-represented in the Appalachian fossil record (e.g., Carpenter et al., 1995; Schwimmer, 1997; Prieto-Márquez et al., 2016a, 2016b), and the fact that this pattern stands true for all groups of dinosaurs known from Appalachia suggests against competition with *Deinosuchus* being the maturation-restricting factor (thought indeed this could account for the somewhat smaller size of Appalachian tyrannosauroids (e.g., Schwimmer, 2002; Schwimmer et al., 2015)). Schwimmer (1997) proposed a "bloat and float" model for the preservation of Appalachian dinosaur specimens, which he divided into three groups of preservation. The results of this study are certainly not at odds with that model, rather suggesting that the factor of being a juvenile was perhaps important in the preservation of Appalachian dinosaurs.

Conclusions.

The Ellisdale prootic is the first unambiguous occurrence of a juvenile theropod in the Late Cretaceous of the Atlantic Coastal Plain and the first portion of a theropod braincase known from Appalachia. The prootic has implications for the evolution of the braincase among

Tyrannosauroidea, showing that those of Appalachian tyrannosauroids shared features with both the derived tyrannosaurids and with more basal taxa. Finally, the prevalence of juvenile dinosaur remains in many Appalachian deposits suggests that the factor of being a juvenile was influential in the taphonomy of eastern North American specimens from the Late Cretaceous.

Acknowledgements.

I thank David Parris for allowing me to access the collections of the New Jersey State Museum, and Robert Denton for our discussions on the Ellisdale site. I also acknowledge the Willi Hennig society for sponsoring the phylogenetics software TNT (Goloboff and Catalano, 2016), which was used herein.

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Figure 1(on next page)

Prootic of a juvenile tyrannosauroid

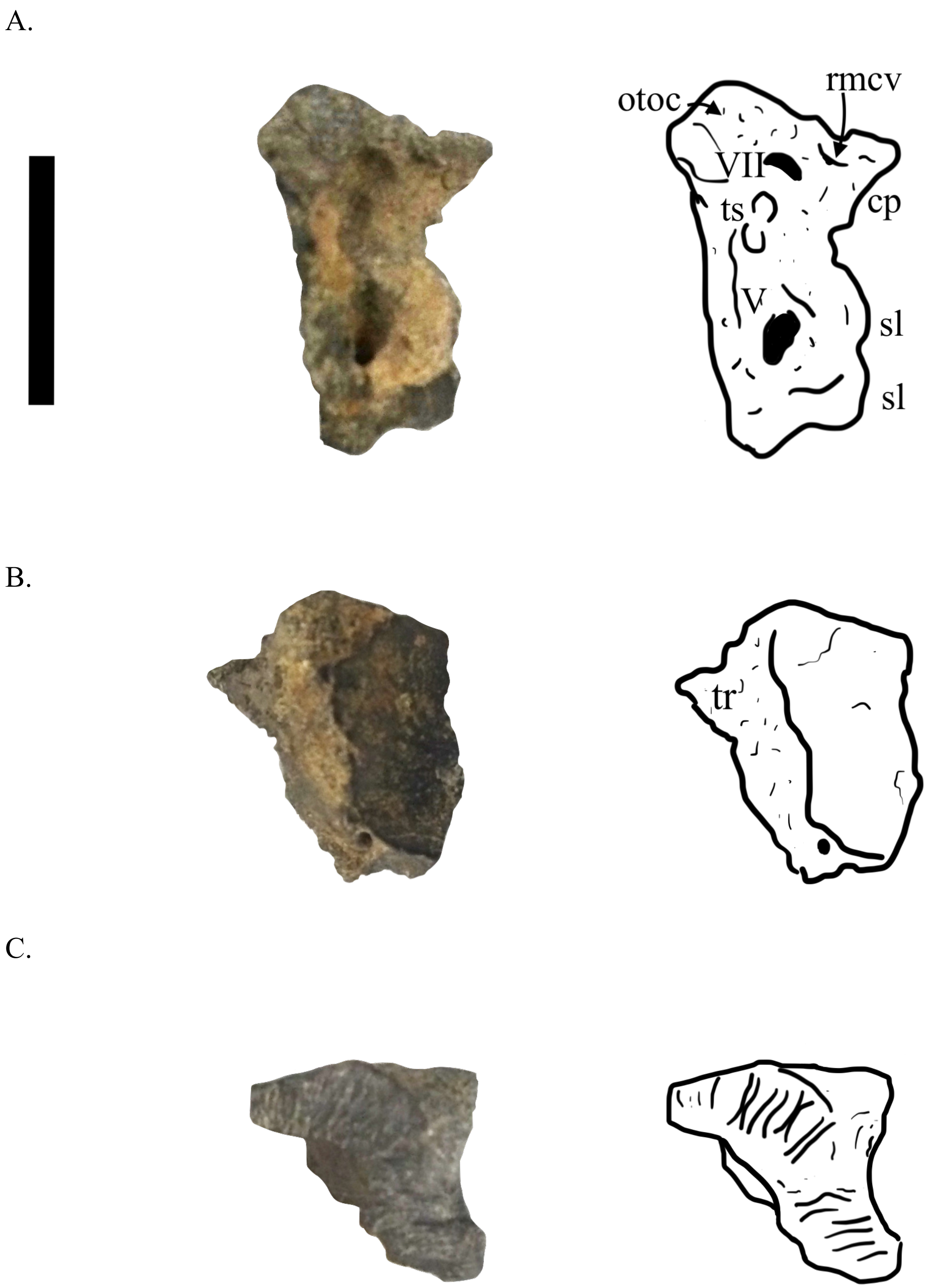

Figure 1. Prootic NJSM 22738 in lateral (A), medial (B), and dorsal (C) views. Scale bar = 10 mm. Abbreviations: otoc, otosphenoid crest; rmcv, rostral middle cranial nerve foramen; VII, foramen for facial nerve VII; ts, tympanic sinus foramina, cp, caudal process; V, foramina for branches of the trigeminal ($V_{2/3}$) nerve; sl, superficial lamina; tr, space for tympanic recess.

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Figure 2(on next page)

Results of phylogenetic analyses including NJSM 22738

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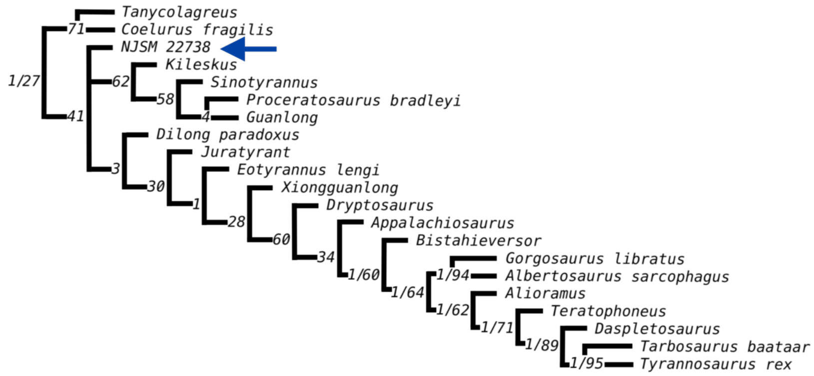
A.



B.

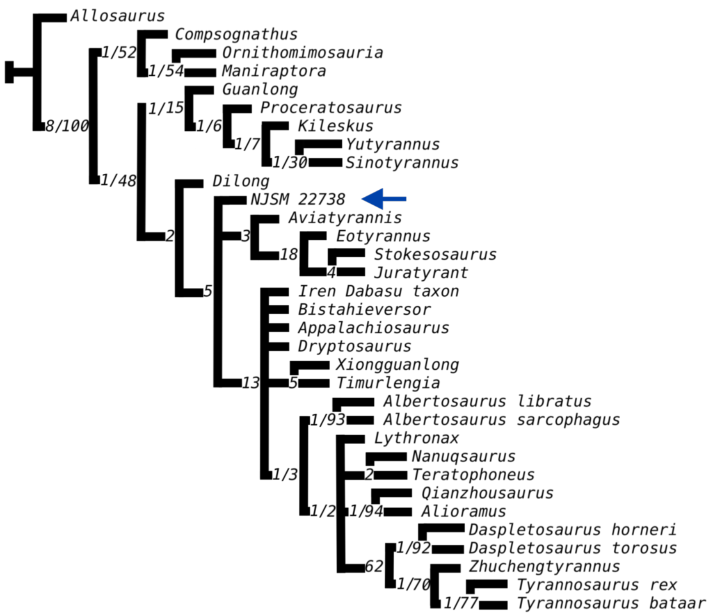


Figure 2. Results of phylogenetic analysis of Coelurosauria and Tyrannosauroidea including NJSM 22738. Strict consensus topology for the analysis of NJSM 22738 in Coelurosauria (Brusatte et al., 2014)(A), strict consensus topology for the analysis of NJSM 22738 in Tyrannosauroidea (Carr et al., 2017)(B). Numbers to the left of slashes are Bremer support values. Blue arrows indicate resolved position of NJSM 22738.

Table 1(on next page)

Measurements of NJSM 22738

Table 1. Measurements of NJSM 27738.

Measurement (in mm)	
Dorsoventral length	23
Proximodistal width (dorsal end)	15
Proximodistal width (confluence of caudal process and superficial lamina)	8
Proximodistal width (ventral end)	8
Mediolateral width (dorsal end)	10
Mediolateral width (ventral end)	7

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