

The Anatomy of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) and a Review of Its Tyrannosauroid Affinities

STEPHEN L. BRUSATTE,^{1,2} ROGER B. J. BENSON,³
AND MARK A. NORELL^{2,4}

ABSTRACT

Although among the first theropod dinosaurs known to science, and an iconic taxon in the history of dinosaur paleontology, the large carnivore *Dryptosaurus aquilunguis* from the Late Cretaceous of New Jersey remains poorly understood. Its anatomy has been described only in brief and its phylogenetic relationships have long been the subject of debate, although recent work proposes *Dryptosaurus* as a member of the tyrannosauroid clade. Here we present a thorough osteological description of the holotype of *Dryptosaurus aquilunguis*, supplemented with photographs of all the material, and provide extensive comparisons with other theropods, especially tyrannosauroids. In concert with recent phylogenetic analyses, our description confirms the tyrannosauroid affinities of *Dryptosaurus* and supports its placement as an “intermediate” taxon bracketed between small, basal forms (e.g., *Guanlong*, *Dilong*) and the derived, Late Cretaceous tyrannosaurids (e.g., *Albertosaurus*, *Tyrannosaurus*). We identify several autapomorphies of *Dryptosaurus*, including the combination of a reduced humerus and an enlarged hand. These forelimb proportions, which differ from the uniformly large arms of basal tyrannosauroids and uniformly atrophied arms of tyrannosaurids, suggest that forelimb reduction in tyrannosauroids may not have proceeded in a uniform fashion. Functionally, *Dryptosaurus* may have used both its skull and arms as weapons for prey acquisition and processing.

¹ Division of Paleontology, American Museum of Natural History.

² Department of Earth and Environmental Sciences, Columbia University, New York, NY.

³ Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK.

⁴ Division of Paleontology, American Museum of Natural History.

INTRODUCTION

The Late Cretaceous theropod *Dryptosaurus aquilunguis* is an icon in the history of dinosaur paleontology. When it was first discovered in the Maastrichtian greensands of New Jersey in 1866 little was known about carnivorous dinosaurs, especially those from North America. Up until this time, New World theropods were represented only by isolated teeth from Montana (Leidy, 1856), but the discovery of *Dryptosaurus* offered paleontologists, and the general public alike, their first glimpse of an articulated theropod skeleton. Cope (1866) published on the specimen within a week of its discovery, christening it *Laelaps aquilunguis* at a meeting of the Academy of Natural Sciences in Philadelphia. *Laelaps* quickly gained popularity as both a poetic, evocative name (Greek for “storm wind” or “hurricane”) and an attractive wastebasket taxon for the referral of isolated theropod elements from across North America. Unfortunately, the generic name was preoccupied by a mite, and was replaced with *Dryptosaurus* in 1877 by Cope’s bitter rival, O.C. Marsh. This story long ago entered the lore of paleontological history, and has been recounted countless times in popular works and scientific papers (see review in Carpenter et al., 1997).

Despite the historical importance of *Dryptosaurus*, this taxon has remained mysterious and confusing since its initial description by Cope (1866). Early workers noted obvious similarities between *Dryptosaurus* and the handful of other large theropods known at the time, including *Megalosaurus* (e.g., Cope, 1866; Leidy, 1868; Lydekker, 1888). As more theropod fossils became known, some scientists identified features linking *Dryptosaurus* and Late Cretaceous tyrannosaurids, such as *Albertosaurus* and *Tyrannosaurus* (e.g., Gilmore, 1946; Baird and Horner, 1979). These observations were heavily challenged, however, and until recently many authors retained *Dryptosaurus* in its own monotypic family, arguing that there was no clear evidence linking it to any other theropod clade (e.g., Russell, 1970; Molnar, 1990; Carpenter et al., 1997). The discovery of basal tyrannosauroids similar in body size and morphology to *Dryptosaurus*, most importantly *Appalachiosaurus*, has recently provided strong evidence for tyrannosauroid affinity (e.g., Holtz, 2004; Carr et al., 2005; Brusatte et al., 2009, 2010; Carr and Williamson, 2010).

However, although it has become clear that *Dryptosaurus* falls within the tyrannosauroid clade, its anatomy and systematic position have received cursory attention. Although several authors have presented short papers on the anatomy of *Dryptosaurus* (e.g., Cope, 1866, 1867, 1868a, 1868b; Huene, 1932; Carpenter et al., 1997), a comprehensive osteology of this taxon and photographs of the holotype have yet to be published. Furthermore, previous authors have listed only a handful of anatomical features supporting tyrannosauroid affinity, and *Dryptosaurus* has yet to be described in a comparative framework with other tyrannosauroids. This is becoming increasingly necessary, as new basal tyrannosauroids are being discovered at an increasing pace and the phylogeny of the tyrannosauroid clade is being fleshed out in great detail (see Brusatte et al., 2010). Indeed, the most recent description of the holotype, that of Carpenter et al. (1997), presented only a brief description of each bone, made only broad comparisons with other theropods, and was unable to determine the phylogenetic placement of *Dryptosaurus*. Even a comprehensive diagnosis of *Dryptosaurus* was not possible at the time, since it was unclear exactly which theropods should serve as a basis for comparison.

Adding to the interest in *Dryptosaurus* is that it was the first large theropod, to our knowledge, to be reconstructed in a modern light. In a watercolor titled “Fighting *Laelaps*” and dated 1896, the preeminent natural history artist Charles R. Knight depicted two *Dryptosaurus*, one pouncing on the other. Prepared under the direction of E.D. Cope, this painting is unusual, and prescient, in that it portrays these animals, giant as they were, as highly active and surely reflects Cope, Knight, and Osborn’s ideas about the agility of carnivorous dinosaurs. This is in contrast to other contemporary illustrations of large carnivorous dinosaurs (predominantly *Megalosaurus*), which depict large theropods as tail-dragging behemoths. Both the original painting (fig. 1A) as well as the plaster models Knight used as reference (fig. 1B) are preserved in AMNH collections.

We present a thorough osteology of the holotype specimen of *Dryptosaurus* (ANSP 9995; AMNH 2438), with photographs of every bone and detailed comparisons with other tyrannosauroids. Our focus is on the holotype only, and we do not address the profuse material that has been referred to *Dryptosaurus* over the years, most of which cannot be confidently assigned to the taxon. We provide a diagnosis of the taxon, based on several autapomorphies, and a focused discussion of the various features that support tyrannosauroid affinities, using the recent cladistic analysis of Brusatte et al. (2010) as a guide.

Redescription of *Dryptosaurus* is timely for two reasons. First, the recent discovery of several basal tyrannosauroids allows for a more refined understanding of the anatomy and phylogenetic position of *Dryptosaurus* (e.g., Hutt et al., 2001; Xu et al., 2004, 2006; Carr et al., 2005; Benson, 2008; Brusatte et al., 2009; Ji et al., 2009; Averianov et al., 2010; Carr and Williamson, 2010; Li et al., 2010; Rauhut et al., 2010). Second, the holotype material is in poor shape, as it has suffered many generations of breaks and repairs and has been seriously degraded by pyrite disease (Spamer et al., 1995). It is critical to publish a full description and photographs before further deterioration occurs.

INSTITUTIONAL ACRONYMS

The following acronyms are used throughout this work:

AMNH FARB	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia, PA
FDRC	Fossil Research and Development Center, Gansu Bureau of Geology and Mineral Resources Exploration, Lanzhou, People’s Republic of China
IGM	Institute of Geology, Ulaan Baatar, Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People’s Republic of China
LH	Long Hao Institute of Geology and Paleontology, Hohhot, People’s Republic of China
MIWG	Museum of Isle of Wight Geology (Dinosaur Isle, Isle of Wight Museum Services, IWCMS), Sandown, England, UK
NHM	Natural History Museum, London, England, UK
OUMNH	Oxford University Museum of Natural History, Oxford, England, UK
ZPAL	Instytut Paleobiologii PAN, Warsaw, Poland



FIG. 1. The painting "Fighting Laelaps" by Charles R. Knight (1896), depicting one *Dryptosaurus* individual leaping onto another (A). A plaster model of *Dryptosaurus* that Knight used as a reference while painting his watercolor (B). Both the painting and the model are cataloged in the Division of Paleontology, American Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Coelurosauria Huene, 1914

Tyrannosauroida Osborn, 1905

Dryptosaurus Marsh, 1877*Dryptosaurus aquilunguis* Cope, 1866

HOLOTYPE: ANSP 9995. Fragmentary skeleton found associated and belonging to a single individual, including a fragment of the right maxilla, a fragment of the right dentary, a fragment of the right surangular, lateral teeth, 11 middle-distal caudal vertebrae, left and right humeri, three manual phalanges from the left hand (I-1, II-2, and an ungual), shafts of the left and right pubes, a fragment of the right ischium, left femur, left tibia, left fibula, left astragalus, midshaft fragment of metatarsal III. The neurocentral sutures are closed in all caudal vertebrae, suggesting that the holotype individual was mature or nearing maturity.

ADDITIONAL MATERIAL: AMNH FARB 2438. Left metatarsal IV, likely from the same individual as the holotype (see Carpenter et al., 1997).

CAST MATERIAL: Well-preserved, historic casts of most of the holotype, including AMNH FARB 2438, are present in the collections of the Natural History Museum in London (NHM OR50100). In some cases the casts show detail that is no longer preserved on the original specimens.

TYPE LOCALITY: West Jersey Marl Company Pit, near Barnsboro, Gloucester County, New Jersey. The *Dryptosaurus* holotype was discovered in 1866 in a unit comprised of marl and sandstone, which was defined nearly a century later as the New Egypt Formation, regarded as Maastriichtian in age (Olsson, 1960). The New Egypt Formation is a marine unit, comprised of claystone, sandstone, and marls, with frequent glauconitic and sideritic nodules (Olsson, 1963). It is up to 10.5 m thick in its type area, along Crosswicks Creek, but thins to the south, such that it is considerably thinner at the *Dryptosaurus* holotype locality (Landman et al., 2004). The New Egypt Formation conformably overlies the Navesink Formation, from which potential *Dryptosaurus* referred material has been reported, and is considered to be a deeper-water equivalent of the Tinton and Red Bank formations (Olsson, 1987). See Gallagher (1993) and Landman et al. (2004) for a more detailed description of the stratigraphy of Late Cretaceous units in New Jersey.

DIAGNOSIS: A tyrannosauroid theropod possessing the following autapomorphies: combination of a reduced humerus (humerus: femur ratio = 0.375) and a large hand (phalanx I-1: femur ratio = 0.200) (see text for numerical comparisons to other tyrannosauroids); strong mediolateral expansion of the ischial tubercle, which is approximately 1.7 times as wide as the shaft immediately distally; an ovoid fossa on the medial surface of the femoral shaft immediately proximal to the medial condyle, demarcated anteriorly by the mesiodistal crest and medially by a novel crest; proximomedially trending ridge on the anterior surface of the fibula immediately proximal to the iliofibularis tubercle; lip on lateral surface of lateral condyle of astragalus prominent and overlapping the proximal surface of the calcaneum; metatarsal IV

with a flat shaft proximally, resulting in a semiovoid cross section that is much wider medio-laterally than long anteroposteriorly.

NOMENCLATURE NOTE: In this paper we employ the clade names Tyrannosauroidae and Tyrannosauridae following the definitions of Sereno et al. (2005). Tyrannosauroidae is the most inclusive clade that contains *Tyrannosaurus rex* but not other coelurosaurs (*Ornithomimus edmontonicus*, *Troodon formosus*, *Velociraptor mongoliensis*). Tyrannosauridae is a less inclusive clade, defined as the least inclusive clade containing *Tyrannosaurus rex* and *Gorgosaurus libratus*. Therefore, Tyrannosauroidae is a larger group that includes Tyrannosauridae, as well as an array of taxa on the stem toward Tyrannosauridae, including *Guanlong*, *Proceratosaurus*, *Sinotyrannus*, *Dilong*, *Eotyrannus*, *Stokesosaurus*, *Xiongguanlong*, *Raptorex*, *Bistahieversor*, *Appalachiosaurus*, *Dryptosaurus* (following the phylogeny of Brusatte et al., 2009, 2010). Tyrannosauridae, on the other hand, is a less inclusive group of derived tyrannosauroids that includes *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, and *Tyrannosaurus*.

One further matter deserves comment. *Dryptosaurus* is included with Tyrannosauroidae, and is also the type genus for a family-level taxon, Dryptosauridae (Marsh, 1890). Dryptosauridae, in fact, was named 15 years prior to Osborn's (1905) establishment of Tyrannosauridae, and therefore has priority at all family levels by the International Code of Zoological Nomenclature Principle of Coordination, which deems all family group taxa (superfamilies, families, subfamilies, etc.) to be established upon the first use of any family group name. Thus, it may be expected that Tyrannosauroidae should be renamed using *Dryptosaurus* as an eponym. However, Article 35.5 of the Code allows for names in prevailing usage at higher rank, such as Tyrannosauroidae, to be retained in cases such as these, because a superfamily name based on *Dryptosaurus* has never (to our knowledge) been used in the literature, whereas Tyrannosauroidae is commonly used and has been for many years. A similar nomenclatural situation was recently confronted by Kammerer and Angielczyk (2009), who also invoked Article 35.5 to retain a commonly used superfamily name despite an older name being available under the Principle of Coordination.

DESCRIPTION

THE SKULL

MAXILLA: Only the anteroventral corner of the right maxilla is known (fig. 2), and this fragment is poorly preserved and has clearly been damaged since the original descriptions of Cope (1866, 1869). The fragment is 89 mm long anteroposteriorly by 77 mm deep dorsoventrally, and preserves most of the first four alveoli. It is broken ventral to the antorbital fossa, and therefore no details of the antorbital region are apparent.

The lateral surface is much better preserved than the medial surface and exhibits a unique feature (fig. 2A): a conspicuous row of neurovascular foramina situated approximately 35 mm above the alveolar margin, which is preserved as original bone surface at the anteroposterior midpoint of the fragment. Because the entire alveolar margin is not preserved, it is not possible

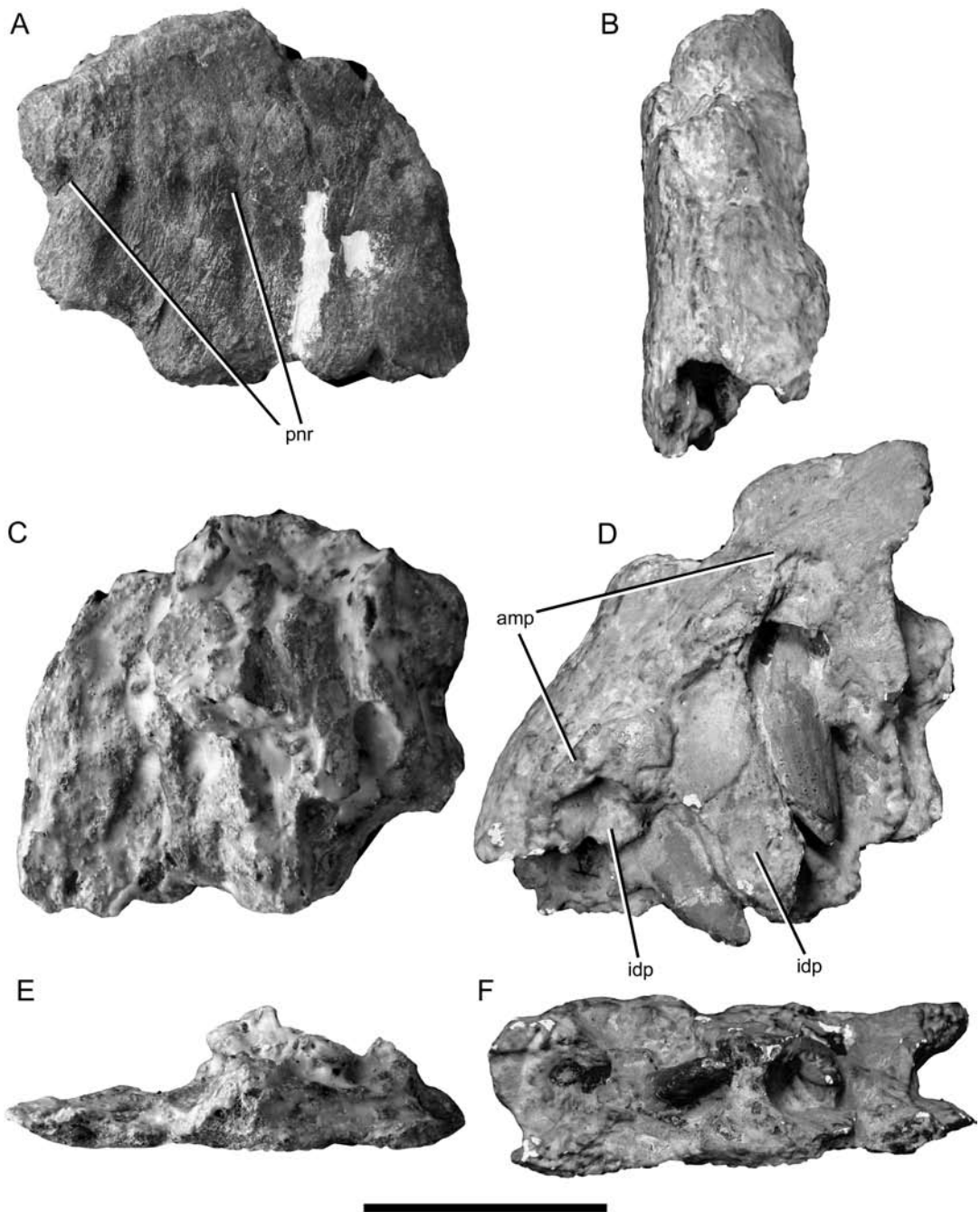


FIG. 2. Right maxilla of the holotype (original material and casts) of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A), anterior (B), medial (C, D), and ventral (E, F) views. Bones A, C, and E are original material, and B, D, and F are casts. Abbreviations: amp, anteromedial process; idp, interdental plates; pnr, primary neurovascular foramina row. Scale bar = 50 mm.

to determine whether this neurovascular row is the primary alveolar row or a secondary set of foramina occupying the midpoint of the lateral surface of the maxilla. The primary row is positioned far ventrally, usually immediately above the alveolar margin, in other tyrannosauroids, including *Albertosaurus* (Currie, 2003a: fig. 6), *Alioramus* (Brusatte et al., 2009: fig. 1), *Appalachiosaurus* (Carr et al., 2005: fig. 5), *Eotyrannus* (Hutt et al., 2001: fig. 3), *Gorgosaurus* (Currie, 2003a: fig. 2), *Guanlong* (Xu et al., 2006: fig. 2), *Proceratosaurus* (Rauhut et al., 2010: fig. 3), *Raptorex* (Serenó et al., 2009: fig. 1), *Tarbosaurus* (Hurum and Sabath, 2003: fig. 1), and *Tyrannosaurus* (Brochu, 2003: fig. 2). Therefore, if this row of foramina is the primary row in *Dryptosaurus*, then its dorsal displacement is an autapomorphy of the genus. We do not, however, recognize this as a formal autapomorphy in the diagnosis due to the uncertainty over the identification of the foramina. These foramina are deep, circular, and large, approximately 4–5 mm in diameter, and open ventrally in deep grooves that extend to the alveolar margin. The row is straight horizontally, and there are approximately two foramina per alveolus. The remainder of the lateral surface is generally smooth, without the deep grooves and ridges that are often seen on large specimens of derived tyrannosaurids (e.g., Brochu, 2003; Currie, 2003a).

The medial surface is heavily damaged and extensively covered by layers of consolidant, rendering many details apparent in the original publications of Cope (1866, 1869) impossible to ascertain (fig. 2C). Fortunately, the NHM cast preserves some important morphology (fig. 2D). First, although Carpenter et al. (1997: 562) reported “no trace of the interdental plates,” the cast shows that the interdental plates were in fact present, increased in dorsoventral depth posteriorly, and were unfused and subpentagonal (rectangular, but tapering to a ventral point) as in other tyrannosauroids (e.g., Currie, 2003a: fig. 6B). An eroded anteromedial process (= palatal process), for articulation with the vomer, premaxilla, and opposing maxilla, is present. Only the anterior region of the process is well preserved, but thick, broken bone surfaces posteriorly indicate that the process was anteroposteriorly elongate, creating an extensive palate, as is characteristic of tyrannosauroids (this is sometimes referred to as a “secondary palate,” but is not similar in morphology, composition, or position to the true secondary palate of mammals). This process is arched: it is located only slightly dorsal to the interdental plate above the first alveolus, but posteriorly it sweeps dorsally, as is characteristic of most tyrannosauroids (e.g., Carr, 1999: fig. 2K; Hurum and Sabath, 2003: figs. 4, 11). The region between the anteromedial process and the interdental plates is smooth where it is well preserved, albeit heavily eroded in places.

Few details of the dentition are apparent. The first three alveoli are preserved in full, whereas only the anterior margin of the fourth remains (fig. 2E–F). An erupted tooth is present in the second alveolus of the cast, and so much of the medial maxilla is missing above the third alveolus that a replacement tooth is exposed. The cast preserves few details, but it is clear that these teeth are ziphodont and are much thinner labiolingually than the incrassate maxillary teeth of adult tyrannosaurids, which have a width that is greater than 60% of their mesiodistal length (Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003). The labial parapet of the maxilla, formed by the lateral surface of the maxilla, extends further ventrally than the lingual parapet, formed by the interdental plates, exposing the alveoli quite widely in medial view. In

ventral view, it is clear that the first alveolus is smaller and more circular than the remaining alveoli, as originally noted by Cope (1869). This condition, in which the first maxillary tooth is small (“incisiform”) is common in tyrannosauroids, and is especially pronounced in *Alioramus* (Brusatte et al., 2009).

DENTARY: A fragment of the right dentary, broken both anteriorly and posteriorly, is present (figs. 3–4). Carpenter et al. (1997) suggested that this piece is from the anterior region of the dentary, but it is more likely that it represents the midportion, since the primary neurovascular groove is not positioned immediately ventral to the alveolar margin as occurs anteriorly in other tyrannosauroids (e.g., *Alioramus*: Brusatte et al., 2009). Five complete alveoli are preserved in the NHM cast (fig. 4), as well as portions of two others, one anterior and one posterior. As noted by Carpenter et al. (1997), the holotype specimen has been damaged since the original descriptions of Cope (1866, 1869), and much of the dorsal and posterior margins have been lost. As a result, only four complete alveoli and one partial alveolus remain in the holotype.

The lateral surface of the dentary is convex and the medial surface subtly concave, resulting in an approximately D-shaped cross section. The lateral surface is generally smooth and lacks the deep grooves, ridges, and other rugosities of large tyrannosaurids (e.g., Molnar, 1991). There are two primary rows of foramina: a primary (alveolar) and a ventral row. The primary row is located approximately 22 mm ventral to the dorsal margin of the bone, and because this margin is eroded, would have been even further separated from the true alveolar margin. The foramina are large, 5–6 mm in diameter, circular, and lie in a shallow groove. This groove is distinct, but is not sharp and deep as in *Guanlong* (Xu et al., 2006), *Proceratosaurus* (Rauhut et al., 2010), and *Sinotyrannus* (Ji et al., 2009). Each individual foramen opens anteriorly into the groove, and together they comprise an approximately linear row. The most anterior foramen is positioned approximately five mm dorsal to the remainder of the row, and probably represents part of the transition as the row sweeps from a dorsal position anteriorly to become situated closer to the center of the dentary posteriorly. This profile, with the row located close to the alveolar margin anteriorly and deflecting ventrally as it continues posteriorly, is present in all other tyrannosauroids (e.g., Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003; Xu et al., 2004, 2006; Brusatte et al., 2009; Rauhut et al., 2010).

The ventral row of foramina is present along the ventral margin of the lateral surface, and occupies the corner where the lateral and ventral surfaces meet. This row occupies the entire preserved length of the bone, and therefore was anteroposteriorly elongate as in all other tyrannosauroids (e.g., Brochu, 2003; Currie, 2003a; Brusatte et al., 2009; Rauhut et al., 2010). The individual foramina face laterally and ventrally, and vary more widely in morphology than the more uniform foramina of the primary row. The anterior foramina are larger, deeper, and more anteroposteriorly elongate, but posteriorly they become smaller, rounded, and less deeply inset. They are not set into a groove. The more circular posterior foramina are unusual, because in other tyrannosauroids the posterior foramina become progressively more anteroposteriorly elongate (e.g., Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003; Brusatte et al., 2009; Rauhut et al., 2010). More circular posterior foramina are also figured in the holotype of *Appalachiosaurus* (Carr et al., 2005: fig. 5), but this specimen is poorly preserved in this region. It

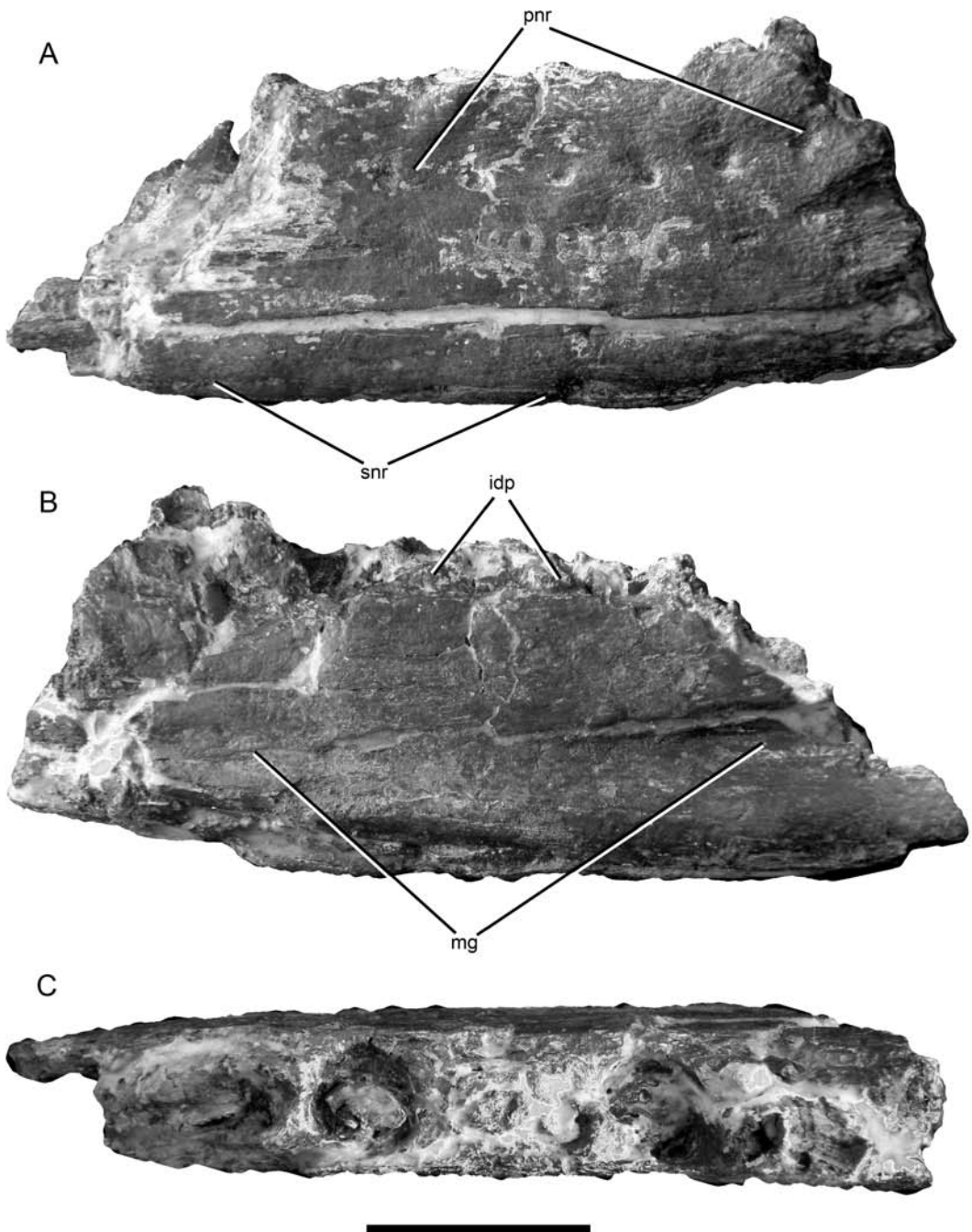


FIG. 3. Right dentary of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A), medial (B), and dorsal (C) views. Abbreviations: idp, interdentary plates; mg, Meckelian groove; pnr, primary neurovascular foramina row; snr, secondary neurovascular foramina row. Scale bar = 50 mm.

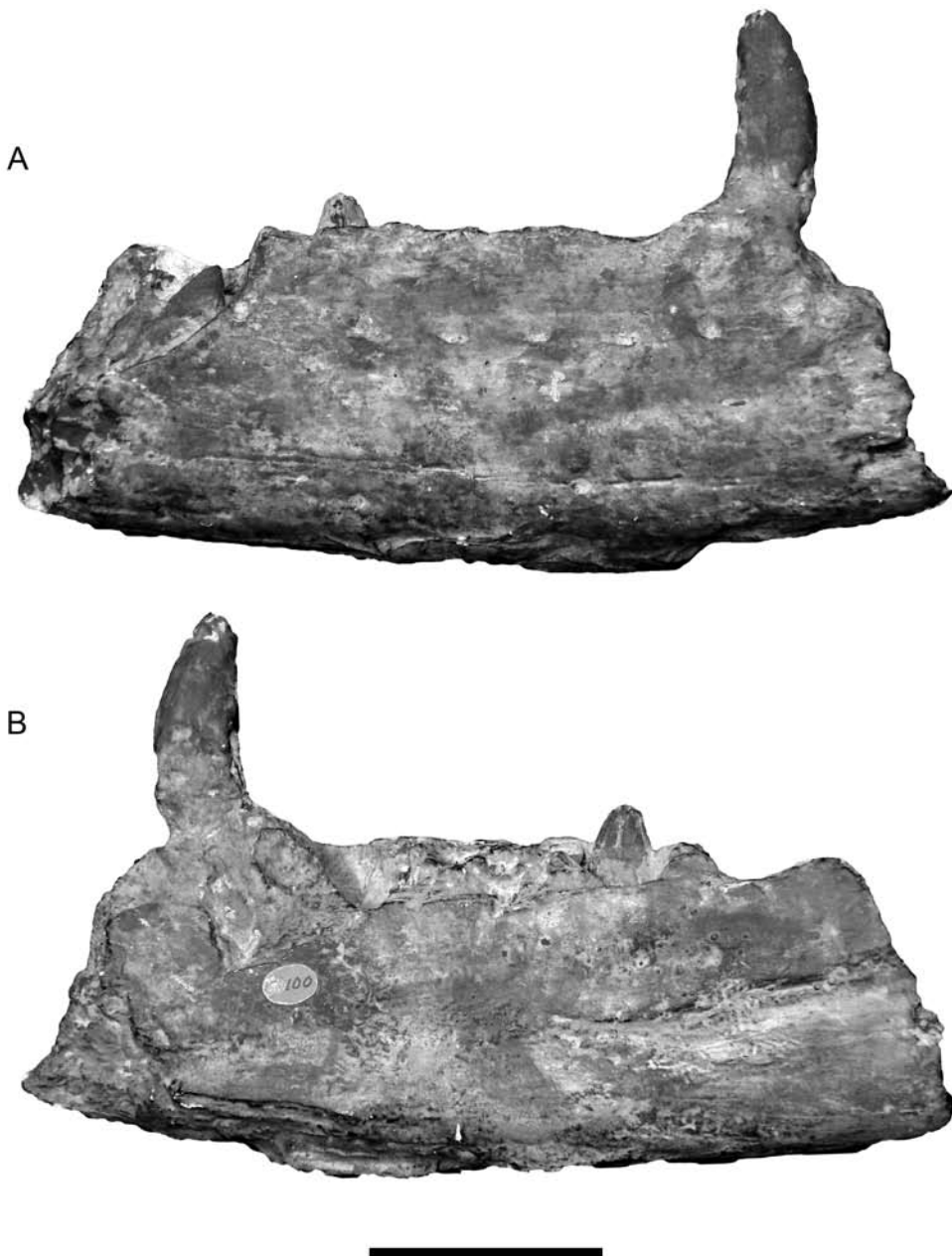


FIG. 4. Casts of the right dentary of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A) and medial (B) views. Scale bar = 50 mm.

is possible that circular posterior foramina are either an autapomorphy of *Dryptosaurus* or a synapomorphy of *Dryptosaurus* and *Appalachiosaurus*, but because the ventral row is easily affected by preservation, and perhaps individual variation, we hesitate to place too much emphasis on this feature.

On the medial surface, the Meckelian groove is shallow, similar to the condition in *Eotyrannus* (MIWG 1997.550) and basal coelurosaur outgroups (e.g., Peyer, 2006), but unlike the condition in more derived tyrannosauroids, including *Raptorex* (LH PV18), in which the groove is deeply inset into the bone. The groove is essentially nonexistent anteriorly, where it is dorsoventrally shallow and not inset into the bone, such that it is medially flat. Posteriorly it funnels out in depth and becomes slightly more inset. The groove is positioned closer to the ventral margin and, as a result, the lingual bar above the groove is dorsoventrally deeper than the region below the groove. However, the groove is not located immediately above the ventral margin as in most other coelurosaurs (e.g., Ostrom, 1969; Kobayashi and Barsbold, 2005; Peyer, 2006; Norell et al., 2009). This more centered position of the groove is also present in other tyrannosauroids (e.g., *Alioramus*: IGM 100/1844; *Daspletosaurus*: Currie, 2003a: fig. 33; *Eotyrannus*: MIWG 1997.550; *Raptorex*: LH PV18; *Tarbosaurus*: Hurum and Sabath, 2003: fig. 19; *Tyrannosaurus*: Brochu, 2003: figs. 40–41), as well as the closest coelurosaur outgroups (e.g., Madsen, 1976; Brusatte et al., 2008).

Small remnants of the interdental plates are preserved. The plates are clearly unfused, short dorsoventrally, and somewhat triangular in shape, as is characteristic of the posterior interdental plates of tyrannosauroids (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003) and many other theropods (e.g., Madsen, 1976; Bever and Norell, 2009). There is a shallow groove between the interdental plates and the lingual bar; the groove is sharp and thin, and demarcates a pronounced step between the two regions. It is likely that an ossified supradentary element fit against the interdental plates medially and filled the pronounced step, as in other tyrannosauroids (e.g., Brochu, 2003; Currie, 2003a).

The alveoli are difficult to interpret in the holotype (fig. 3C), but comparison with the NHM cast reveals some anatomical features. The best preserved alveoli are ovoid, longer mesiodistally than wide labiolingually. They are not figure-eight shaped, due to a labiolingual constriction at midlength, as in some tyrannosauroids (most prominent in *Alioramus*: IGM 100/1844). Erupted teeth are present in the first and fourth preserved alveoli in the cast, but these have broken off in the holotype; these teeth are similar to the maxillary teeth in morphology, and are not labiolingually thickened as is typical of adult tyrannosaurids. Two replacement teeth are still visible in the first alveolus of the holotype. The first is erupting medial to the erupted tooth, whereas the second, smaller tooth is located ventromedial to the first replacement tooth, as described by Carpenter et al. (1997).

SURANGULAR: The posterodorsal region of the right surangular is present (fig. 5). This bone was first identified by Cope (1869) as a “malar,” or zygomatic arch, a bone that is not present in dinosaurs. Carpenter et al. (1997) pointed out Cope’s (1869) misinterpretation but could not identify the fragment with any certainty, and tentatively suggested that it was a prearticular or an angular. As a result, they only provided a measurement and an unlabelled figure of the bone,

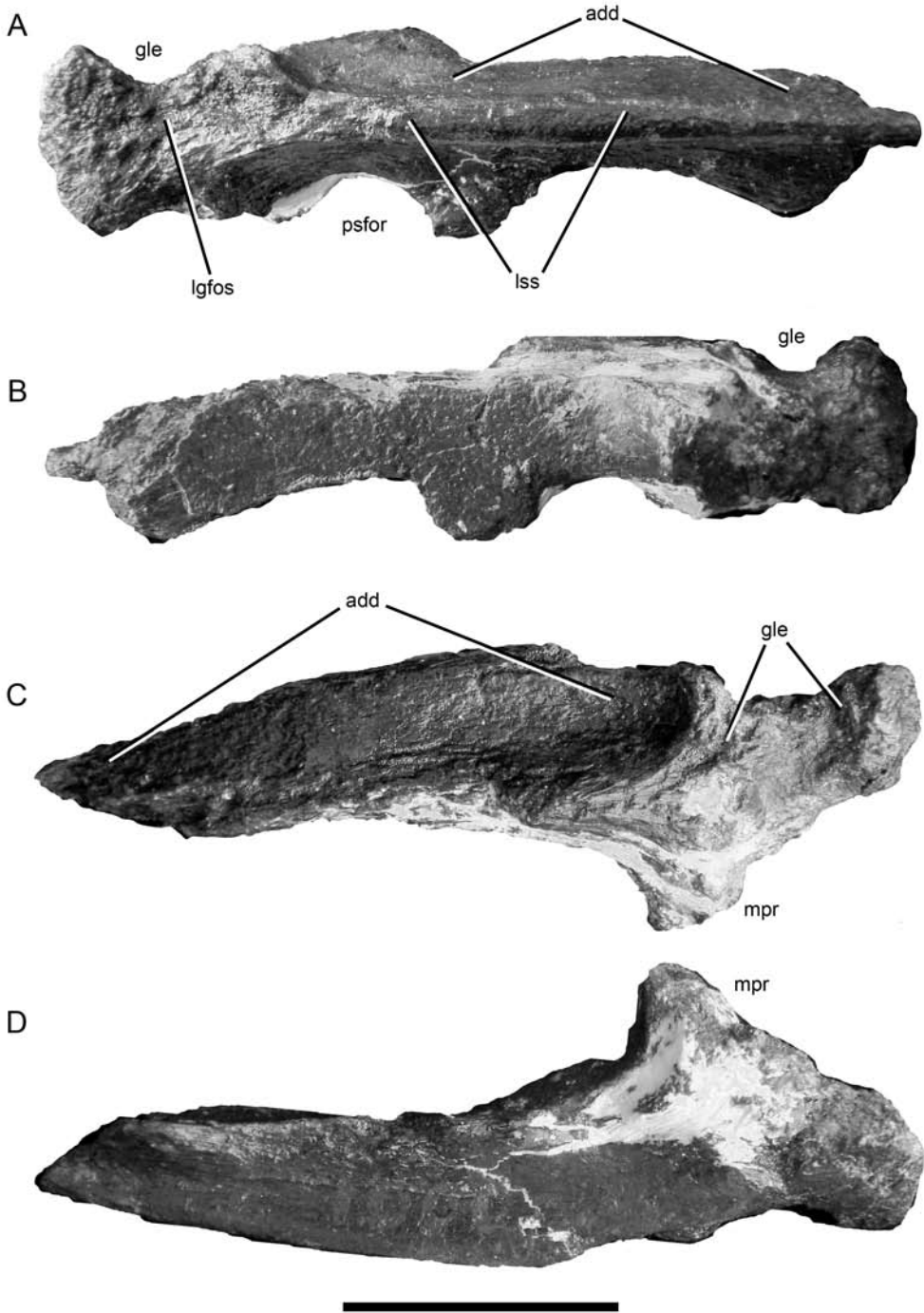


FIG. 5. Right surangular of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A), medial (B), dorsal (C), and ventral (D) views. Abbreviations: add, adductor muscle attachment; gle, glenoid; lgfossa, lateral fossa below the glenoid; lss, lateral surangular shelf; mpr, medial process; psfor, posterior surangular foramen. Scale bar = 50 mm.

and did not describe or compare it in detail. Carr et al. (2005) correctly identified this specimen as a right surangular, and noted that it possesses a characteristic tyrannosauroid feature, a large posterior surangular foramen. However, this bone has yet to be fully described and compared to the surangulars of other tyrannosauroids.

The surangular fragment is heavily eroded and 159 mm long anteroposteriorly as preserved. As reported by Carpenter et al. (1997), it has been slightly broken since Cope's (1869) original description, such that it is now shorter. On the lateral surface, the surangular shelf is robust: it is thick dorsoventrally (11 mm) and laterally overhangs the remainder of the bone by 24 mm at its midpoint (fig. 5A). Shelves of similar prominence are seen in other tyrannosauroids more derived than *Dilong* (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003a). The shelf is most prominent immediately dorsal to the posterior surangular foramen and becomes progressively less offset anteriorly. It projects straight laterally and does not project ventrolaterally to overhang the posterior foramen. This condition is shared with most other tyrannosauroids with a prominent shelf, including *Albertosaurus* (Currie, 2003a), *Alioramus* (Brusatte et al., 2009), *Eotyrannus* (MIWG 1997.550), and *Raptorex* (Serenó et al., 2009), whereas the derived tyrannosaurines *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* possess the ventrolaterally overhanging morphology (Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003). Furthermore, the shelf is oriented nearly horizontally in lateral view, as in tyrannosauroids more derived than *Eotyrannus* (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003a; Sereno et al., 2009).

Above the surangular shelf, the attachment surface for the jaw adductor muscles is prominent (fig. 5A). This scar is mediolaterally broad (32 mm immediately in front of the glenoid) and has a smooth and deeply concave surface that becomes progressively flatter anteriorly. This attachment site faces almost equally dorsally and laterally, as in many tyrannosauroids, including *Albertosaurus* (Currie, 2003a), *Alioramus* (Brusatte et al., 2009), *Daspletosaurus* (Currie, 2003a), *Eotyrannus* (MIWG 1997.550), *Gorgosaurus* (Currie, 2003a), and *Raptorex* (Serenó et al., 2009). In contrast, the scars of *Tarbosaurus* and *Tyrannosaurus* face nearly entirely laterally, resulting in a dorsoventrally deep surangular (Molnar, 1991; Brochu, 2003; Hurum and Sabath, 2003), whereas those of more basal taxa such as *Guanlong* (Xu et al., 2006) and *Proceratosaurus* (Rauhut et al., 2010) face almost entirely dorsally.

Immediately below the surangular shelf, the dorsal margin of the posterior surangular foramen is present (fig. 5A). The foramen is enormous: its broken ventral edge is 25 mm long anteroposteriorly, but the diameter of the foramen would have been much larger in life. The enlarged foramen has long been recognized as a tyrannosauroid hallmark, and it is present in all taxa more derived than *Eotyrannus* (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003; Brusatte et al., 2009; Sereno et al., 2009). Unfortunately, erosion posterior to the posterior surangular foramen makes it difficult to assess the presence or absence of a pneumatic pocket, which is present in all tyrannosauroids more derived than *Eotyrannus* and especially deep and invaginated in some derived taxa such as *Alioramus* (Brusatte et al., 2009). Anterior to the posterior surangular foramen, and ventral to the prominent shelf, there is a small preserved region of the ventral ramus of the surangular. This region is sheetlike and measures only 6 mm in mediolateral thickness. However, it is still more robust than in the

holotype of *Alioramus altai*, which measures 1.5 mm thick (IGM 100/1844).

The glenoid and retroarticular region is heavily eroded and few comparisons can be made with other tyrannosauroids. However, one important tyrannosauroid feature is apparent: there is a smooth fossa on the lateral surface of the surangular immediately ventral to the glenoid, as in all tyrannosauroids more derived than *Eotyrannus* (Brusatte et al., 2010).

DENTITION: Several disarticulated lateral teeth are preserved (fig. 6), as is a complete replacement tooth in the dentary (fig. 7). These are transversely narrow, recurved, and serrated, similar to those of most other theropods, but unlike the laterally incassate lateral teeth of tyrannosaurids (see description of maxilla above; Brochu, 2003; Currie, 2003a; Hurum and Sabath, 2003). The distal carina is well preserved on two disarticulated teeth and bears 17 denticles/cm, measured at the middle of the carina. The denticles diminish in size adjacent to the apex and base of the tooth. The mesial carina is preserved on one disarticulated tooth. It extends to the base of the tooth and bears 18 denticles/cm. Subtle, bandlike enamel wrinkles are present on the labial and lingual tooth surfaces, extending between the mesial and distal carinae as apically concave undulations of consistent relief over their mesiodistal length. These are widespread among tetanuran theropods, including tyrannosaurids (Brusatte et al., 2007). Interdenticular sulci (sensu Smith, 2007; “blood grooves” of Currie et al., 1990) extend a short distance onto the tooth from between the denticles of the distal carina. These are approximately as long as the denticles are high and are horizontal, not inclined basally. Interdenticular sulci are widespread among theropods including tyrannosaurids (Currie et al., 1990), ceratosaurs (Smith, 2007) and basal tetanurans (Benson, 2009).

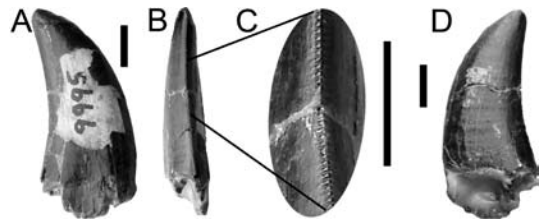


FIG. 6. Lateral tooth of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in labial/lingual (A, D), and distal (B, C) views. Scale bars = 10 mm.

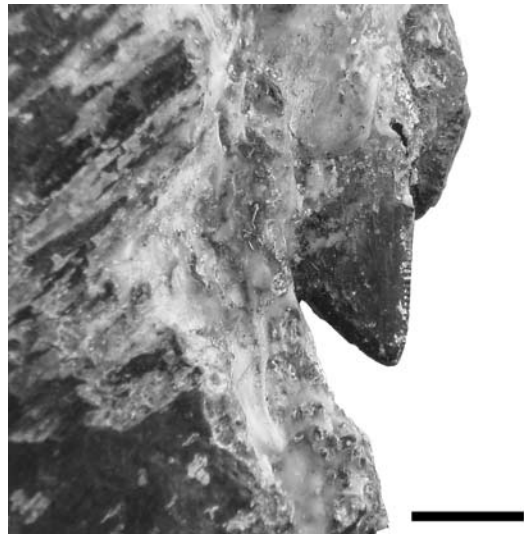


FIG. 7. Replacement tooth in the dentary of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lingual view. Scale bar = 10 mm.

AXIAL SKELETON

CAUDAL VERTEBRAE: Eleven caudal vertebrae are preserved (figs. 8–10). The neurocentral sutures are firmly joined, but still visible, in all elements, indicating likely adult ontogenetic

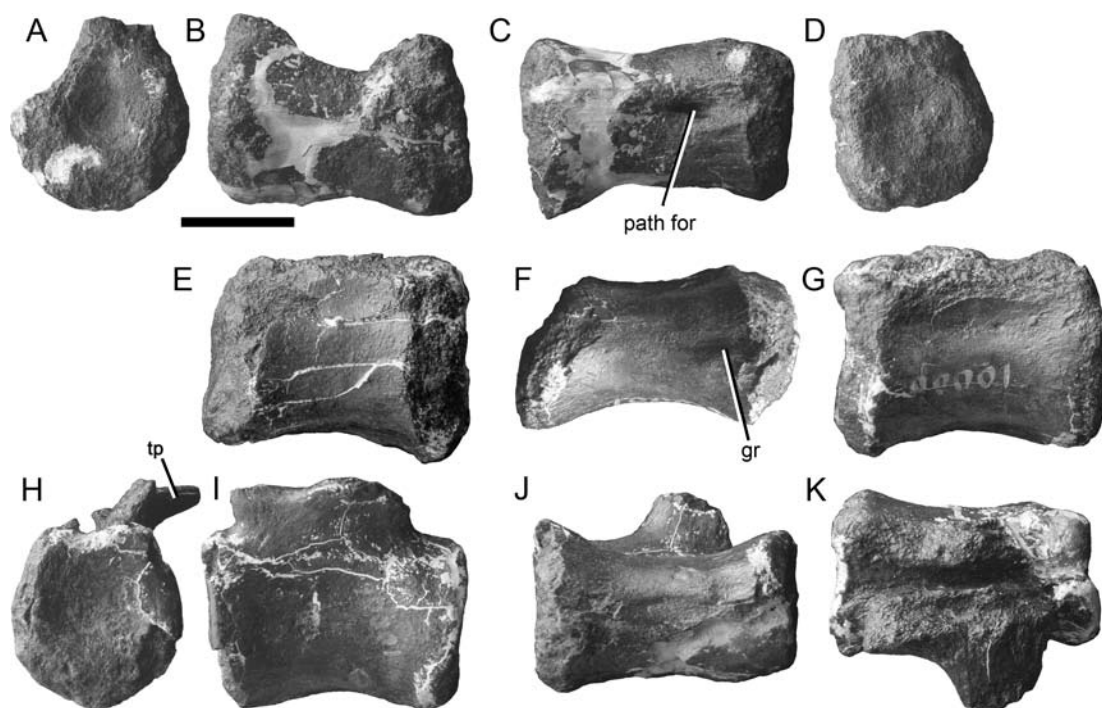


FIG. 8. Middle caudal vertebrae the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A, H), left lateral (B, E, I), ventral (C, F, J), posterior (D), right lateral (G), and dorsal (K) views. Abbreviations: path for, pathological foramen; tp, transverse process. Scale bar = 50 mm.

status (see Irmis, 2007, for a discussion of the utility of this feature in assessing ontogenetic stage in archosaurs). Three of the vertebrae have substantially larger articular surfaces than the others (fig. 8). One of these preserves an incomplete neural arch, which bears the broken base of a dorsolaterally inclined transverse process (fig. 8H–K). The anteroposteriorly elongate proportions (table 1) and the presence of a transverse process in these three larger vertebrae indicates that they are middle caudal vertebrae. The remaining vertebrae are smaller and lack transverse processes, indicating that they are distal caudal vertebrae. Six of these represent anterior or middle distal caudal vertebrae (fig. 9; note that one is very poorly preserved and not figured). The two smallest vertebrae are the most distal and are much smaller than the others (fig. 10). One is poorly preserved, but the other is represented by a centrum and partial neural arch.

All the caudal vertebrae of *Dryptosaurus* are proportionally longer relative to their height than the equivalent bones in *Tyrannosaurus* (table 1; Brochu, 2003). All vertebrae are amphicoelous. The ventral rim of the posterior surface is thickened, so that the ventral part of the articular surface is convex and forms a poorly defined, posteroventrally facing chevron facet. A broad, but shallow, longitudinal groove is present on the ventral surface of all preserved centra. This is more pronounced posteriorly than anteriorly in the middle caudal elements (fig. 8), but is developed both anteriorly and posteriorly on the distal caudal centra, in which the middle section of the “groove” forms a flattened strip (fig. 9). The proximalmost preserved

TABLE 1. Measurements of vertebrae (in millimeters) of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995). Abbreviations: i, measurement of incomplete specimen; *, measurement estimated from slightly incomplete specimen. Two additional vertebrae were too incomplete to provide measurements.

Caudal vertebra	Length	Minimum width	Anterior dv	Anterior ml	Posterior dv	Posterior ml
Middle (fig. 8A–D)	110i	56	82i	76i	77i	69i
Middle (fig. 8E–G)	115	51	86i	65i	85i	65i
Middle (fig. 8H–K)	115	54	85*	80*	81i	63i
Distal (fig. 9A–E)	118	51	68	74	68	65i
Distal (fig. 9F–J)	118	48	63*	70*	65*	67i
Distal (fig. 9K–O)	113	42	60*	65*	61*	64i
Distal (fig. 9P–R)	108	39	?	?	57i	55i
Distal (fig. 9S–W)	104	36	48	53	44i	51i
Distal (fig. 10A–F)	72	22	23*	30*	24*	28i

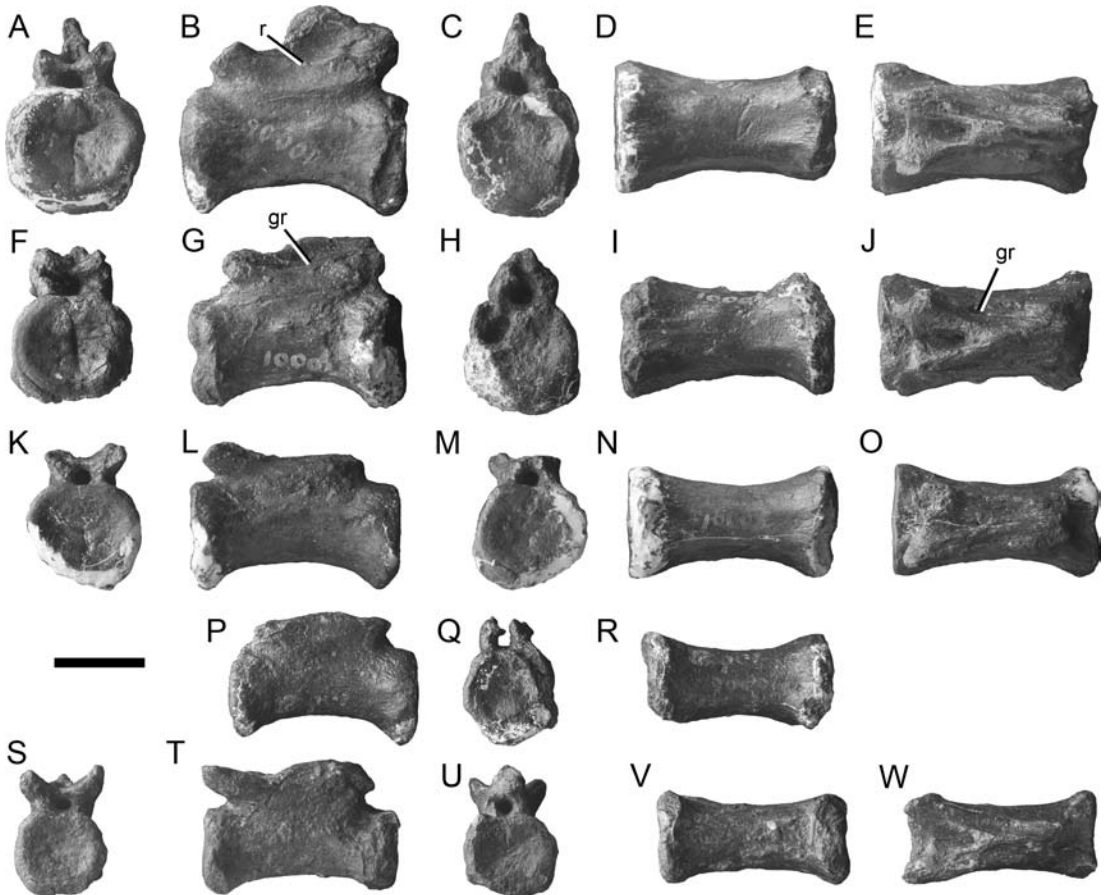


FIG. 9. Anterior-middle distal caudal vertebrae of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A, F, K, S), left lateral (B, G, L, P, T), posterior (C, H, M, Q, U), ventral (D, I, N, R, V), and dorsal (E, J, O, W) views. Abbreviations: gr, groove; r, ridge. Scale bar = 50 mm.



FIG. 10. Posterior distal caudal vertebrae of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A, G), left lateral (B, H), posterior (C), right lateral (D), dorsal (E), and ventral (F) views. Scale bar = 50 mm.

centrum bears a large foramen on the ventral surface posteriorly and to the left side (fig. 8A–D). This slight asymmetry in location suggests that this foramen is pathological. The anterior surface of the centrum is offset dorsally relative to the posterior surface of the centrum in the middle caudal vertebrae, a characteristic of more proximal caudal vertebrae in theropods. The distal caudal centra have articular surfaces that are not offset from each other and are wider transversely than they are tall dorsoventrally (figs. 9–10).

Although the distal caudals lack transverse processes, in the proximalmost preserved distal caudal an angular ridge is present on the lateral surface of the neural arch in the position of the transverse process of more proximal vertebrae (fig. 9B). In the succeeding vertebra, this ridge is modified into a longitudinal groove (fig. 9G, J) that may be autapomorphic as it is absent in *Tyrannosaurus* (Brochu, 2003). However, as the distal caudal vertebrae of most tyrannosauroids are poorly documented, we do not formally designate this feature as an autapomorphy of *Dryptosaurus*. A second angular ridge, which is longer anteroposteriorly, is located more ventrally on the lateral surface of the neural arch, just dorsal to the neurocentral suture. This is pronounced in the more proximal distal caudal vertebra, but is weak or absent in succeeding elements.

The prezygapophyses of the distal caudal vertebrae project anterolaterally from a common origin immediately dorsal to the neural canal. They extend only slightly further anteriorly than the centrum and have dorsomedially facing facets. This differs from the situation in *Appalachiosaurus* and *Tyrannosaurus* (Brochu, 2003; Carr et al., 2005), in which the distal caudal vertebrae have much longer prezygapophyses that project anteriorly, approximately half the length of the centrum. Postzygapophyses are not preserved in any of the caudal vertebrae of *Dryptosaurus*. Although broken in all specimens, the neural spine is approximately half the anteroposterior length of the centrum and is located posteriorly. It is transversely narrow and sheetlike.

APPENDICULAR SKELETON

HUMERUS: Both humeri are known, but each is heavily abraded and missing substantial portions (fig. 11; table 2). The left humerus is more complete and better preserved, but its proximal and distal ends are abraded (fig. 11A–E). In overall shape, the humerus is subcylindri-

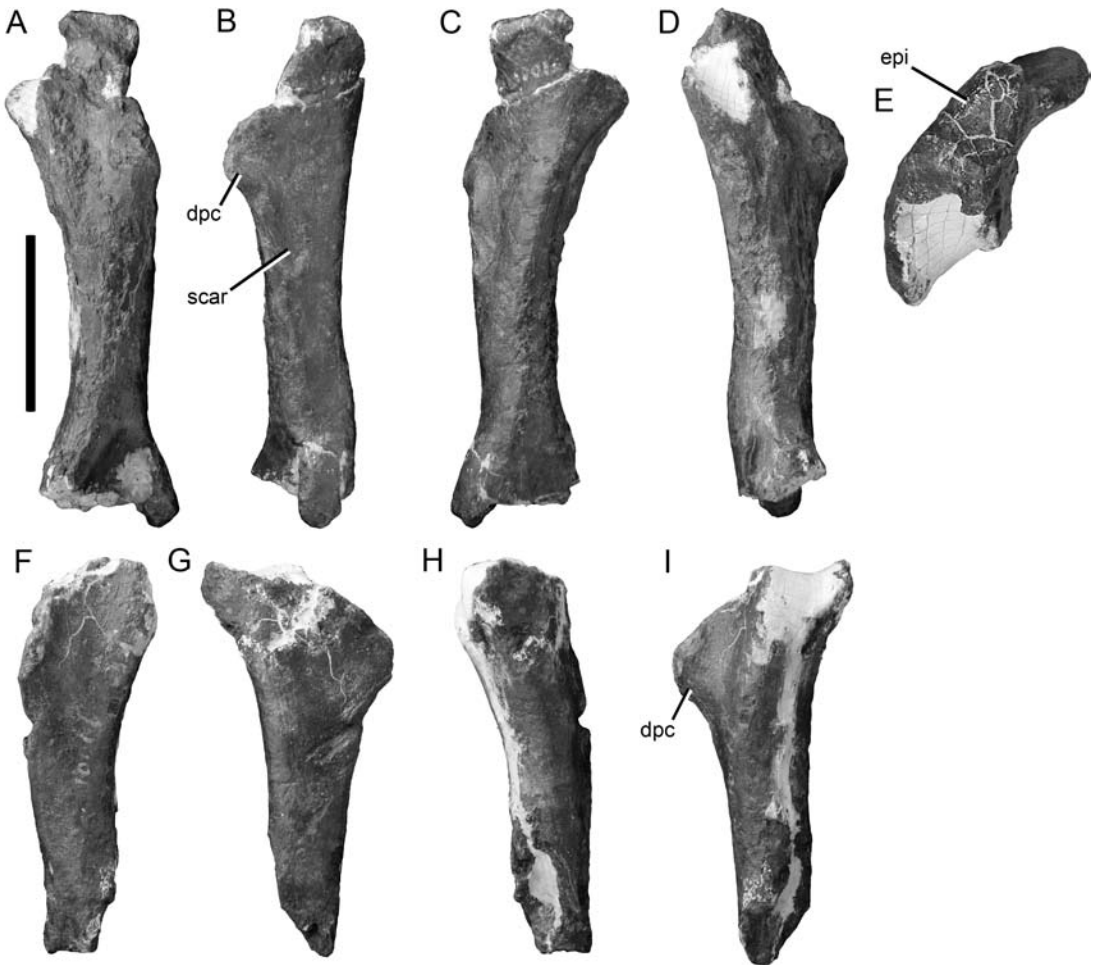


FIG. 11. Left (A–E) and right (F–I) humeri of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A, F), lateral (B, G), posterior (C, H), medial (D, I), and proximal (E) views. Abbreviations: dpc, deltopectoral crest; epi, lateral epicondyle; scar, muscle attachment scar. Scale bar = 100 mm.

cal. The proximal half is inclined proximomedially and the distal condyles are inclined antero-distally, contributing to the appearance of a sigmoidal curvature to the otherwise straight shaft. The distal condyles are rotated by approximately 50° relative to the plane of the proximal end so that the medial (ulnar) condyle is located anteromedially. Such rotation is present in basal tyrannosauroids such as *Dilong* (IVPP V14242) and *Guanlong* (IVPP V14531), but the long axes of the proximal and distal ends are essentially parallel, due to a lack of rotation, in *Eotyrannus* (MIWG 1997.550), *Raptorex* (LH PV18), and tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003).

The proximal end of the humerus is damaged, but several details are visible (fig. 11E). The humeral head and medial epicondyle are broken off and, thus, only part of the lateral epicondyle is well preserved. Although the head is broken off, the profile of the break and the morphology of the remainder of the proximal end suggest that a hemispherical humeral head was not pres-

TABLE 2. Measurements of appendicular bones (in millimeters) of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995 and AMNH FARB 2438). Asterisk indicates incomplete measurement due to damage.

Humerus (left element)	Femur (left element)
Proximodistal length: 282* (300 estimated)	Proximodistal length: 781
Proximal end, anteroposterior: 27*	Distal end, anteroposterior: 90
Proximal end, mediolateral: 85 estimated	Distal end, mediolateral: 160
Minimum shaft circumference: 143	Minimum shaft circumference: 275
Manual Phalanx I-1	Tibia (left element)
Proximodistal length: 148* (160 estimated)	Proximodistal length: 759
Shaft, minimum anteroposterior: 32	Proximal end, anteroposterior: 184*
Shaft, minimum mediolateral: 31	Proximal end, mediolateral: 125*
Minimum shaft circumference: 111	Distal end, anteroposterior: 191
	Distal end, mediolateral: 65
	Minimum shaft circumference: 260
Manual Phalanx II-2	Fibula (left element)
Proximodistal length: 126	Proximal end, anteroposterior: 138*
Proximal end, anteroposterior: 45	Proximal end, mediolateral: 48*
Proximal end, mediolateral: 43	
Distal end, anteroposterior: 41	
Distal end, mediolateral: 46	
Minimum shaft circumference: 114	
Manual Ungual	Astragalus (left element)
Proximodistal length: 176	Condyle region, mediolateral width: 161
Proximal end, anteroposterior: 73	Condyle region, anteroposterior length at midpoint: 63
Proximal end, mediolateral: 40	
	Metatarsal IV (left element)
	Proximodistal length: 396
	Proximal end, anteroposterior: 66
	Proximal end, mediolateral: 78
	Distal end, anteroposterior: 77
	Distal end, mediolateral: 54
	Minimum shaft circumference: 138

ent. The hemispherical condition—in which the head is bulbous, approximately as broad anteroposteriorly as mediolaterally, and overhangs both the anterior and posterior surfaces of the humerus—is present in *Raptorex* (Serenó et al., 2009) and tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003). In *Dryptosaurus*, on the contrary, it appears as if the head was longer transversely than anteroposteriorly, as in most other theropods, including basal tyrannosauroids such as *Dilong* (IVPP V14243), *Guanlong* (Xu et al., 2006), and *Eotyrannus* (Hutt et al., 2001). We emphasize, however, that this interpretation is based on the shape of broken surfaces, so it cannot be absolutely ruled out that *Dryptosaurus* possessed a hemispherical head.

The deltopectoral crest is low and emerges anterolaterally from the shaft. The most prominent portion of the crest terminates 102 mm from the proximal surface, just over one-third the length of the humerus. The extent of the deltopectoral crest exhibits phylogenetically informative variation in tyrannosauroids, and in general more derived taxa (i.e., those progressively more closely related to tyrannosaurids) possess a progressively shorter crest. Basal taxa such as *Dilong* (IVPP 14243) and *Guanlong* (IVPP V14531) possess a crest that extends 40%–50% of the length of the humerus, *Eotyrannus* (MIWG 1997.550) and *Dryptosaurus* exhibit a crest that is approximately 30% of the length of the humerus, and *Raptorex* (Serenó et al., 2009) and

tyrannosaurids (e.g., Brochu, 2003) possess a short crest that is less than 25% of the humeral length. The posterolaterally facing surface of the deltopectoral crest and the adjacent part of the shaft are weakly concave. A suboval depression, marked by rugose surface texture, is located on the lateral surface of the shaft at the distal end of the deltopectoral crest. This may correspond to both the first and second humeral tuberosity of Brochu (2003, fig. 85E), as it is located at the same position as portions of both structures in *Tyrannosaurus*. However, the scars of *Tyrannosaurus* and close relatives are larger and more rugose than the potentially corresponding structure in *Dryptosaurus*.

Much of the shaft is present, but heavily damaged in places. Unfortunately, the distal end is only partially preserved on the left humerus and completely missing on the right bone. The posterior surface of the distal humerus is flat up to the point at which it is broken. By contrast, the anterior surface of the distal humerus is concave.

MANUS: Parts of the left hand are preserved, including two nonungual phalanges and one large ungual (fig. 12; table 2). The two elongate nonungual phalanges likely represent phalanges I-1 and II-2 (Parks, 1928; Russell, 1970). The least well preserved of these (fig. 12A–D) is identified as phalanx I-1 due to its marked lateral curvature, as seen in phalanx I-1 of *Tyrannosaurus* and closely related taxa (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003). In tyrannosaurids, this curvature is related to asymmetry in the distal articular surface of metacarpal I, which has paired dorsoventrally curving distal condyles. Characteristically, the lateral condyle projects further distally than the medial condyle (Brochu, 2003). This also indicates that the left side of the *Dryptosaurus* phalanx I-1 is the lateral side, affirming that these phalanges represent the left hand. Our identifications therefore differ from those of Carpenter et al. (1997) who identified our phalanx I-1 as phalanx II-2 and vice versa.

Phalanx II-2 (fig. 12E–J) is much better preserved than phalanx I-1, which is heavily abraded and missing much of the distal articular surface. Phalanx II-2 is slightly more robust than I-1, and the ventral surfaces of both phalanges are flat. The distal articular surface of II-2 consists of paired, dorsoventrally oriented condyles divided by a dorsoventral trough. The medial condyle is slightly taller dorsoventrally than the lateral condyle. Suboval ligament pits are present on the lateral and medial surfaces of the bone adjacent to the distal end. The proximal articular surface consists of paired depressions separated by a dorsoventrally oriented angular ridge. The left (lateral) depression is deeper and slightly broader.

An ungual phalanx may represent either phalanx I-2 or II-3 of the left hand (fig. 12K–N). As in many theropod ungual phalanges, it has pronounced posterodistal curvature and tapers to a point at its distal end. Expansive longitudinal grooves curve anteromedially along the lateral and medial surfaces of the phalanx. The flexor tubercle is comparable in relative size to those of *Raptorex* (Serenó et al., 2009) and tyrannosaurids (e.g., Parks, 1928; Brochu, 2003), but less prominent than the discrete, rugose tubercles of *Guanlong* (IVPP V14531), *Dilong* (IVPP V14243), and *Eotyrannus* (MIWG 1997.550). The proximal articular surface bears a dorsoventrally oriented angular ridge that is slightly offset medially, similar to the asymmetry seen in the articular surfaces of the well-preserved phalanx II-2. Although the identity of the ungual phalanx is uncertain, the ungual phalanges of the two digits of derived tyrannosauroids

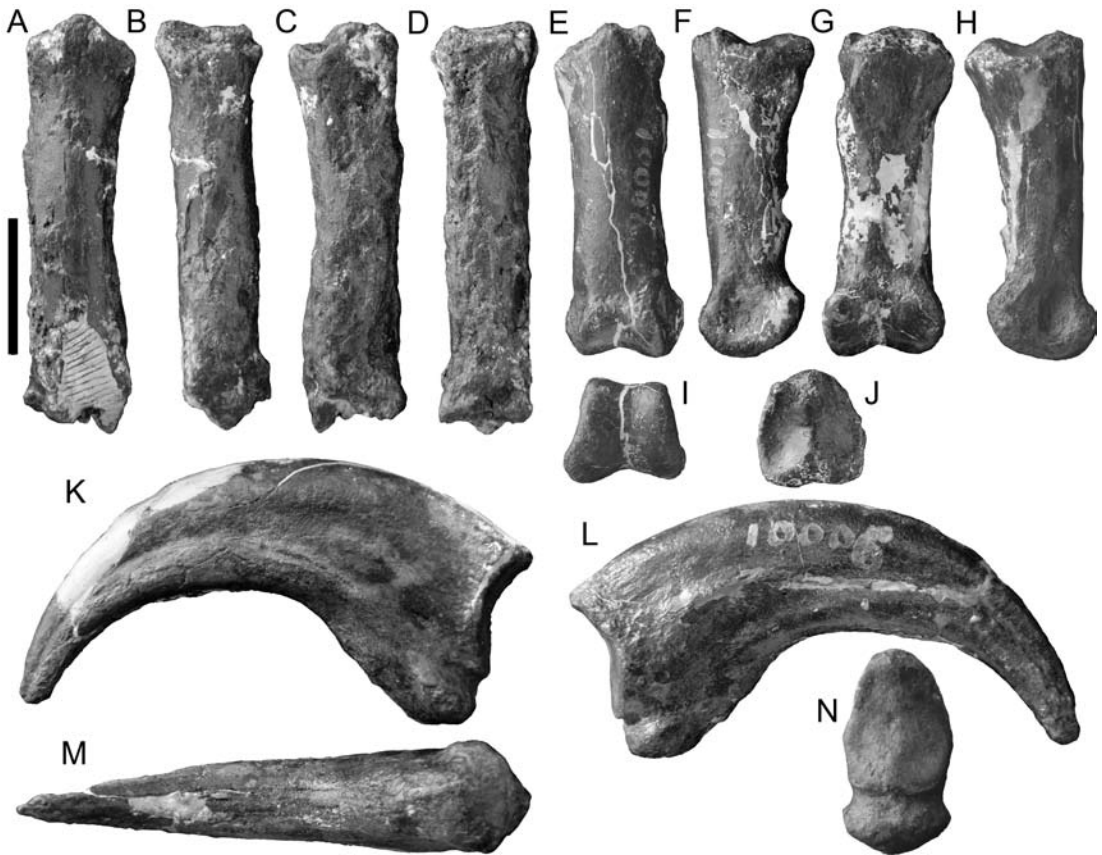


FIG. 12. Left manual elements of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995). Phalanges I-1 (A–D) and II-2 (E–J), and an unguis phalanx (K–N) in anterior (A, E), lateral (B, F, K), ventral (C, G, M), medial (D, H, L), distal (I), and proximal (J, N) views. Scale bar = 50 mm.

are of approximately equal length. An estimate of the length of digit I can therefore be obtained by adding the length of the unguis phalanx (176 mm) to the length of first phalanx (160 mm) and an estimate of the length of metacarpal I based on comparison with other derived tyrannosauroids (~96 mm: Parks, 1928; Brochu, 2003).

PUBIS: Much of the shafts of both pubes are present (fig. 13). The preserved region of the left shaft is approximately 450 mm long, whereas that of the right is 465 mm. Unfortunately, the distal region, which is expanded into a boot in other tyrannosauroids, is not preserved in either specimen.

The proximal obturator region is completely missing on the left pubis, but eroded remnants of both peduncles are present on the right specimen. These are not sufficient to infer the shape and size of the peduncles, but it is clear that there was no enclosed obturator foramen or a discrete obturator notch, as the widely open region where the ischial peduncle and shaft diverge is preserved as original bone surface. This condition is shared with most other tyrannosauroids, whereas the basal taxa *Guanlong* (Xu et al., 2006) and *Stokesosaurus* (Benson, 2008) possess

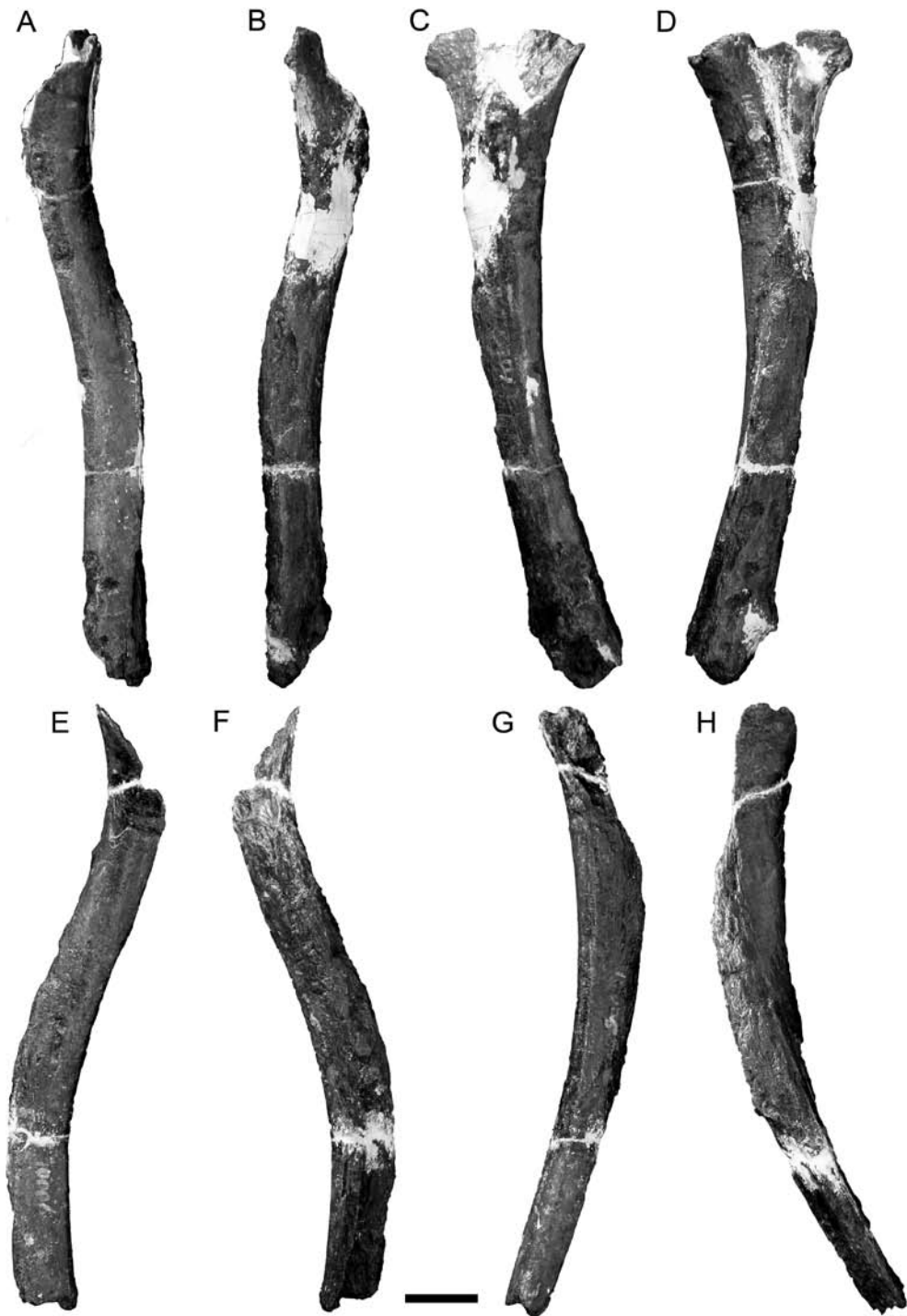


FIG. 13. Pubes of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995). Right pubis in anterior (A), posterior (B), lateral (C), and medial (D) views; left pubis in anterior (E), posterior (F), lateral (G), and medial (H) views. Scale bar = 50 mm.

discrete, inset notches that are demarcated ventrally by extensive obturator flanges. This ventral flange is clearly absent in *Dryptosaurus*, a strong indication that a notch is absent.

The pubic shafts are heavily damaged and most of the external surface is poorly preserved, making it difficult to identify muscle attachment sites and other subtle surface details. The shafts are concave anteriorly and convex posteriorly, the “bowed posteriorly” condition identified by Carr and Williamson (2010) and Brusatte et al., (2010) as a synapomorphy of derived tyrannosauroids including *Dryptosaurus*, *Appalachiosaurus*, and tyrannosaurids. Interestingly, this feature is not present in *Raptorex* (LH PV18; Sereno et al., 2009) or a putative tyrannosauroid pubis from the Aptian or Albian of Australia (Benson et al., 2010a), which have more of a straight pubic shaft as in more basal taxa such as *Guanlong* (Xu et al., 2006) and *Stokesosaurus* (Benson, 2008). All tyrannosauroids with an anteriorly concave pubic shaft possess an enlarged pubic boot that is at least 60% of the shaft length, with a prominent anterior process. Thus, it is reasonable to hypothesize that *Dryptosaurus* would have also possessed this feature and the concomitant enlarged femoral extensors that attached here (Carrano and Hutchinson, 2002).

Carpenter et al. (1997: fig. 7D) reconstructed the medial contact between the pubic shafts as lacking the flangelike medial apron that is common among theropods, and instead showed the shafts making contact by simply lying against each other. However, the medial surfaces of both pubes, especially the left, are heavily eroded, so it is unclear whether a thin apron arose from the shaft. It is possible, however, to trace a helical broken surface, which arises from the open obturator notch and then curves onto the medial surface of the pubic shaft. It is likely that this surface represents the apron. If so, the pubic apron is proximodistally elongate, and the contact between the pubes was extensive. Extensive contact is seen in basal tyrannosauroids such as *Guanlong* (IVPP V14531), *Dilong* (IVPP V14243), *Stokesosaurus* (Benson, 2008), and a tyrannosauroid from the Aptian-Albian of Australia (Benson et al., 2010a), but not more derived taxa such as *Tyrannosaurus* (Brochu, 2003), in which contact begins at approximately the mid-shaft of the pubis. The shafts begin to diverge slightly immediately above the distal broken surface, which probably represents the pubic fenestra between the two pubes within the distal part of the apron. If correct, the fenestra faces anteroposteriorly (i.e., opens straight anteriorly and posteriorly), as is normal for tetanurans (e.g., Rauhut, 2003; Benson et al., 2009).

ISCHIUM: A heavily eroded fragment of the proximal right ischium is present (fig. 14). This piece was correctly identified by Carpenter et al. (1997), who recognized it as an ischium based on the presence of an ovoid, rugose scar on the posterior margin: the ischial tubercle for attachment of the flexor tibialis musculature (fig. 14F; Hutchinson, 2001; Carrano and Hutchinson, 2002). However, Carpenter et al. (1997: 565) provided only measurements and a small illustration of this bone, feeling that “too little of it remains for meaningful comparison with other theropods.” The identity of *Dryptosaurus* as a tyrannosauroid, as well as the discovery of several new tyrannosauroid taxa in recent years, now allow for a more focused comparison with other taxa.

The lateral surface of the ischium is highly convex and the medial surface flat. Only the proximal portion of the shaft is preserved, but it clearly tapered distally. Unfortunately, the pubic and iliac peduncles, the obturator process, and the acetabular margin are not preserved

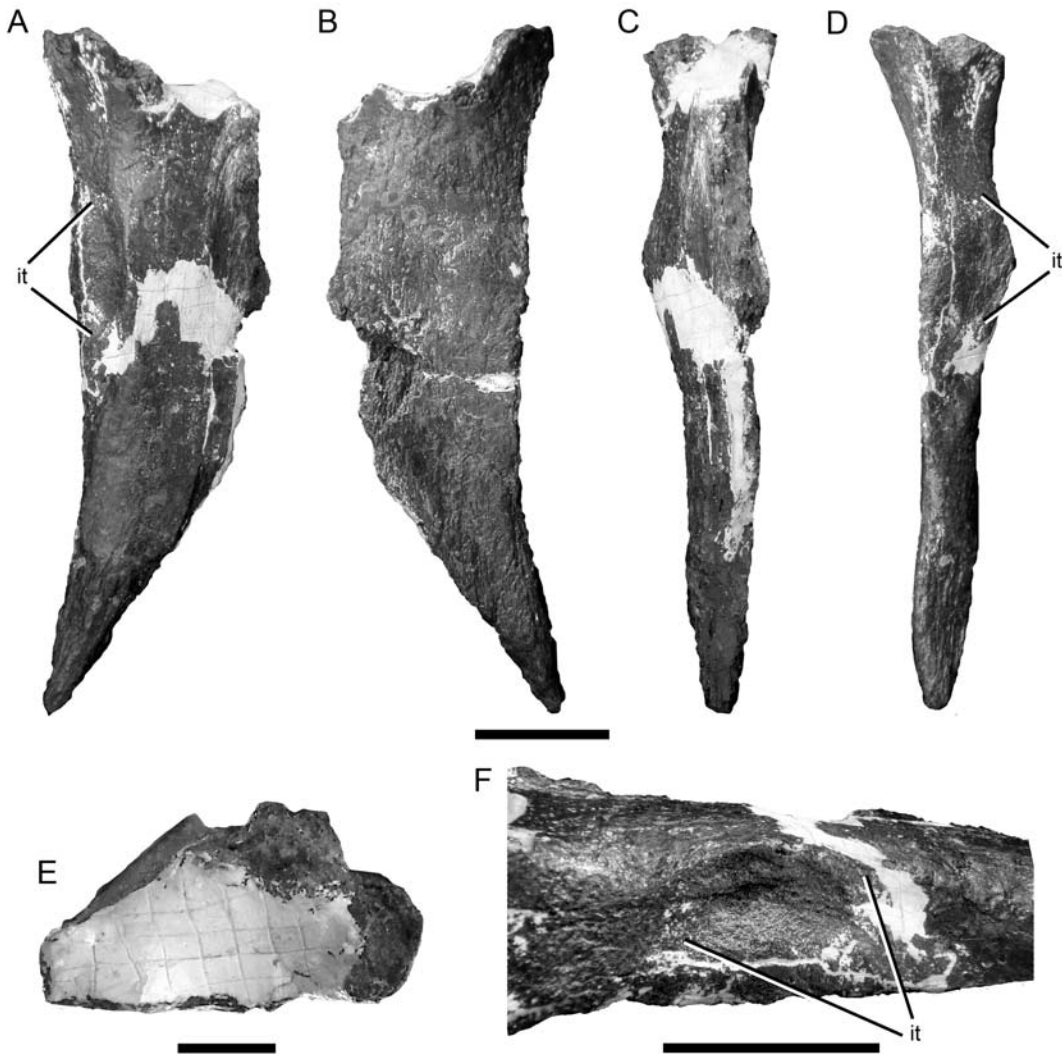


FIG. 14. Right ischium of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A), medial (B), anterior (C), posterior (D), and proximal (E) views, with a closeup of the ischial tubercle in posterior view (F). Abbreviations: it, ischial tuberosity. Scale bars = 50 mm.

(fig. 14E). However, the base of the acetabulum is partially preserved proximally, and the ischium is swollen both laterally and medially in this region. The most conspicuous feature of the bone is the rugose ischial tubercle identified by Carpenter et al. (1997). The scar is present as an expanded ovoid eminence, 64 mm proximodistally by 40 mm mediolaterally, on the corner where the posterior and lateral surfaces meet (fig. 14F). It is smoothly concave at its center and is surrounded by a swollen and rugose rim. The anterior rim is much more prominent than the posterior rim, and forms a sharp lip that separates the scar from the lateral surface of the bone.

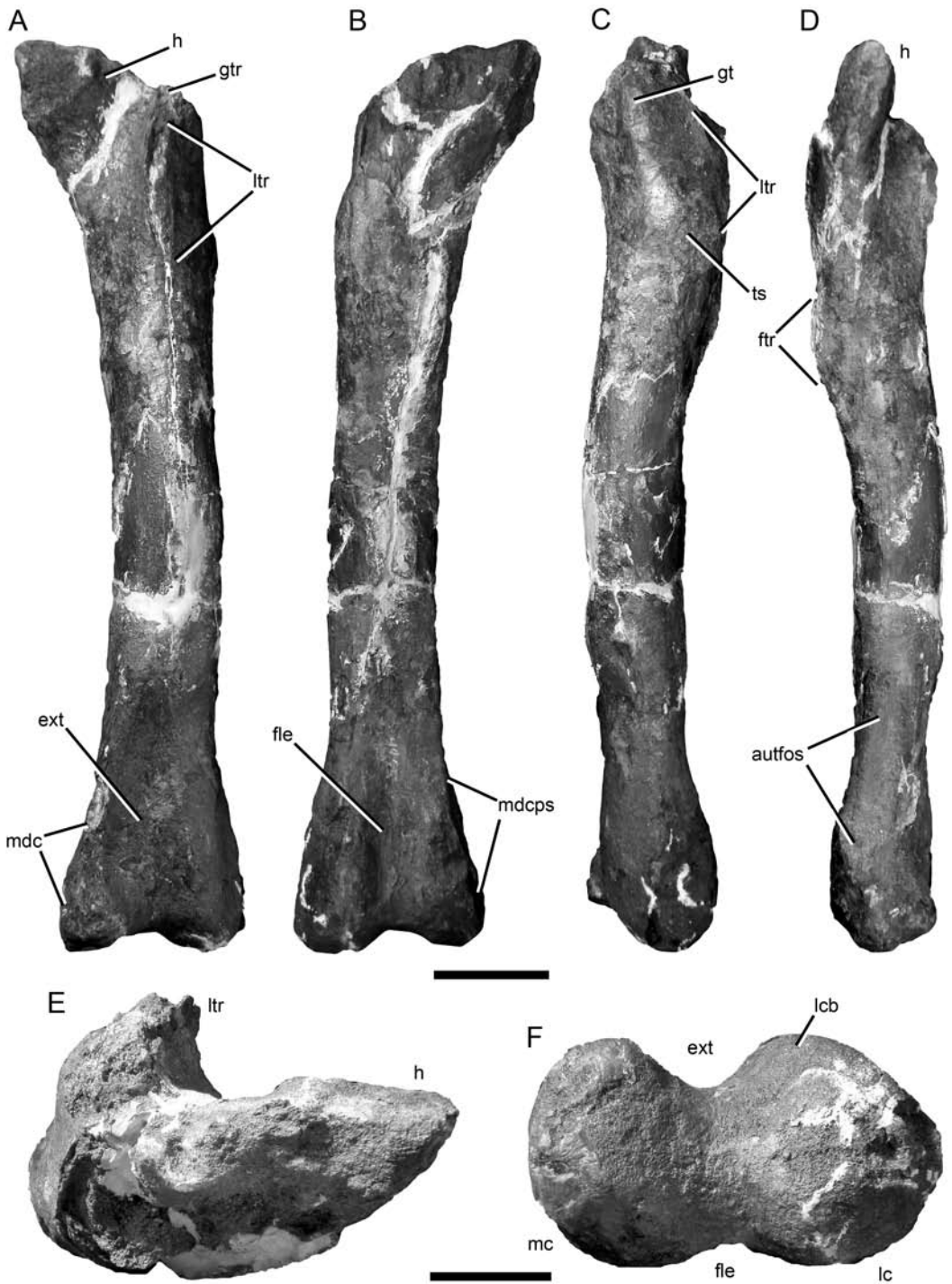
Carpenter et al. (1997: 565) stated that the scar is “not as prominent as in tyrannosauroids.” Although the ischial tubercle does become more swollen and rugose in extremely large individuals of derived tyrannosaurids (e.g., Brochu, 2003), the morphology in *Dryptosaurus* is broadly similar to that of other tyrannosauroids more derived than *Stokesosaurus*. Whereas the tubercle is expressed as a subtle groove in *Guanlong* (Xu et al., 2006) and a convex bulge on the posterior surface of the ischium in *Stokesosaurus* (Benson, 2008), in *Dryptosaurus*, *Appalachiosaurus*, *Raptorex*, and tyrannosaurids it takes the form of a rugose flange whose central surface is depressed relative to the remainder of the bone. In *Dryptosaurus* the tubercle does not project far posteriorly as a discrete flange in lateral view, but is more expanded in the mediolateral direction (and thus most visible in posterior view as a swollen, enlarged structure). A similar morphology appears to be present in *Appalachiosaurus* (Carr et al., 2005) and may be a synapomorphy of these two taxa. However, the strong mediolateral expansion of the tubercle, which is approximately 1.7 times as wide as the shaft immediately distally, is here regarded as an autapomorphy of *Dryptosaurus*, pending further study of *Appalachiosaurus*. In contrast, other tyrannosauroids with a prominent tubercle exhibit a scar that projects posteriorly as a discrete flange, often triangular, that is only slightly mediolaterally expanded relative to the remainder of the ischium (e.g., Brochu, 2003).

FEMUR: The left femur is nearly complete but heavily damaged in places, and the surface texture is poorly preserved across the entire bone (fig. 15; table 2). Much of the head, greater trochanter, and lesser trochanter are eroded, precluding accurate measurements and descriptions of these features. The same is true of portions of the distal end, including the crista tibiofibularis. Therefore, we are conservative in our description, and are unable to verify some of the features of the proximal and distal ends identified by Carpenter et al. (1997).

The shaft is bowed anteriorly, which appears to be a genuine feature and not a product of deformation. The anterior surface of the shaft is highly convex and the lateral and medial surfaces more subtly so, whereas the posterior surface is nearly flat. Surface texture is poorly preserved, and in many places the surface is caked with preservative and glue. This makes it impossible to identify most of the muscle attachment sites identified by Hutchinson (2001), Carrano and Hutchinson (2002), and Brochu (2003), including the anterior intramuscular line, which is usually a prominent feature in well-preserved theropod femora of this size.

The proximal end is heavily weathered, but it is clear that the head projects medially and not at all anteriorly (fig. 15E). Unfortunately, it is not possible to determine whether the head was also projected proximally, the “elevated” condition present in most tyrannosauroids (e.g., Brochu, 2003). Carpenter et al. (1997: 565) stated that a “sufficient” amount of the head was

FIG. 15. Left femur of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A), posterior (B), lateral (C), medial (D), proximal (E), and distal (F) views. Abbreviations: autfos, autapomorphic fossa on medial surface of distal end; ext, extensor groove; fle, flexor groove; ftr, fourth trochanter; gtr, greater trochanter; h, head; lc, lateral condyle; lcb, bulge on anterior surface of lateral condyle; ltr, lesser trochanter; mc, medial condyle; mdc, mesiodistal crest; mdcps, mesiodistal crest posterior surface; ts, trochanteric shelf. Scale bar for A–D = 100 mm, for E–F = 50 mm.



present to “show that it is of the elevated type,” but this cannot be determined with certainty because the entire proximal surface of the head is eroded. Additionally, it is difficult to describe the morphology of the greater trochanter, including systematically informative characters relating to its separation from the head and lesser trochanter (Brusatte et al., 2010).

The lesser trochanter is prominent, and in proximal view is seen to extend far anterior relative to the head, curving medially as it continues anteriorly (fig. 15E). It is thick mediolaterally, and its rugose lateral surface is one of the better-preserved regions of original bone texture on the femur. This surface is highly convex anteriorly, where it is covered with a series of fine striations for muscle attachment, and is concave posteriorly. This concavity, which forms a proximodistally elongate trough, is also covered by fine, rugose striations. Medially, the trochanter is separated from the head by a deep, smooth fossa. Unfortunately, the broken anterior margin makes it difficult to identify and describe the accessory trochanter, but the NHM cast (fig. 16) suggests that this structure was reduced to a subtle convexity as in *Appalachiosaurus* (Carr et al., 2005), *Raptorex* (LH PV18), and all other tyrannosauroids more derived than *Xiongguanlong* (Li et al., 2010). The trochanteric shelf is well preserved on the lateral surface of the shaft, and takes the form of a highly convex bulge, beginning approximately 105 mm distal to the proximalmost preserved margin of the head (figs. 15–16). The bulge is ovoid, 60 mm proximodistally by 40 mm anteroposteriorly, and is separated from the lesser trochanter by a smooth, concave margin.

The fourth trochanter is heavily eroded but visible as a mediolaterally thick, proximodistally elongate ridge on the posterior surface of the femur, paralleling the medial margin of the shaft and beginning immediately distal to the distal end of the trochanteric shelf (fig. 15D).

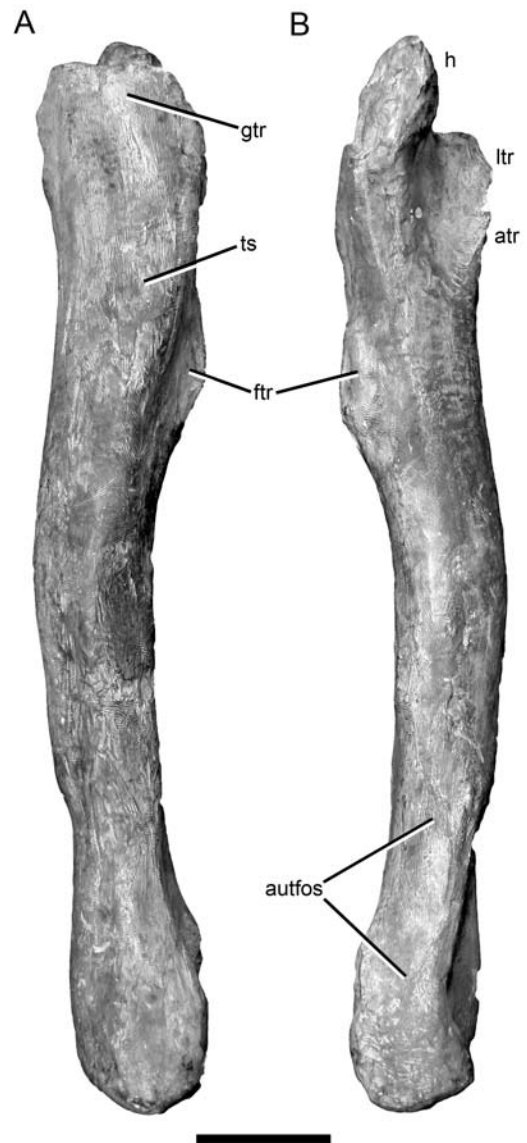


FIG. 16. Cast of the left femur of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in lateral (A) and medial (B) views. Abbreviations: atr, accessory trochanter; autfos, autapomorphic fossa on medial surface of distal end; ftr, fourth trochanter; gtr, greater trochanter; h, head; ltr, lesser trochanter; ts, trochanteric shelf. Scale bar = 100 mm.

The position of the distal end of the trochanter is estimated at less than 35% of the femoral length. This condition is present in *Appalachiosaurus* and more basal tyrannosauroids, whereas tyrannosaurids have a more elongate trochanter that extends to a point more than 40% of the length of the shaft (Brusatte et al., 2010). Distal to the fourth trochanter, on the posterior surface of the bone, *Dryptosaurus* lacks the prominent circular scar of *Tarbosaurus* and *Tyrannosaurus* (Brochu, 2003; Carr and Williamson, 2010).

The distal end is damaged: the crista tibiofibularis is completely missing and fine details of both condyles, such as which projected further ventrally, are not apparent (fig. 15F). However, in distal view, it is evident that the lateral and medial condyles are separated by a deep, antero-posteriorly oriented groove, which is continuous with the extensor groove on the anterior surface but separated from the flexor groove on the posterior surface by a lip of bone. It is possible that a lip was also present anteriorly but has been eroded. The lateral condyle is 88 mm long anteroposteriorly by 71 mm mediolaterally, whereas the medial condyle measures 81 by 59 mm. These are likely underestimates due to slight amounts of surface erosion, but the general shapes of the condyles appear genuine. The lateral condyle, for instance, preserves a discrete bulge along the midpoint of its anterior surface, a subtle feature also present in other tyrannosauroids more derived than *Dilong* (Brusatte et al., 2010).

The extensor groove is deep. It is defined by the lateral and medial condyles, both of which have remarkably convex anterior surfaces. As a result, in distal view, the groove is expressed as a discrete, U-shaped notch between the anterior surfaces of the condyles (fig. 15F). Because the lateral condyle is mediolaterally wider than the medial condyle, the groove is displaced somewhat medially from the midpoint of the femur. A deep notch is seen in all tyrannosauroids more derived than *Xiongguanlong*, including *Raptorex* and tyrannosaurids (Brusatte et al., 2010). In contrast, the extensor groove of *Stokesosaurus* is expressed as a shallower, more broadly concave margin in distal view (Benson, 2008). In *Guanlong* (IVPP V14531) and *Dilong* (IVPP V14243) the extensor grooves are so shallow that the anterior surface between the condyles is essentially flat. In addition, the condition in derived tyrannosauroids differs from that in large-bodied basal tetanurans, such as allosauroids, in which the medial condyle is flat anteriorly and gently slopes into the groove, giving the groove an asymmetrical, wedgelike shape in distal view (e.g., Madsen, 1976; Brusatte et al., 2008; Benson et al., 2009; Benson, 2009, 2010).

In anterior view, the extensor groove is smoothly concave and extends dorsally and medially to abut the mesiodistal crest, which is sharp and strongly overhangs the medial surface of the femur (fig. 15A). Most of the crest is broken here, but it was clearly extensive, measuring approximately 160 mm in proximodistal length. This is similar to the condition in *Tyrannosaurus* (Brochu, 2003) and other tyrannosauroids, in which the crest is robust and visible in posterior view as a medially extended flange. The crest extends laterally as it continues proximally, eventually merging with the shaft. Proximal to where these two regions merge the extensor groove ceases to exist as a discrete depression.

The flexor groove is deep, but it is difficult to measure its true depth since the crista tibiofibularis, which forms its lateral bounding wall, is missing (fig. 15F). The groove is smooth and concave where it is well preserved on the posterior surface of the distal femur, and it extends

proximally while gradually merging with the shaft, such that it is no longer present as a discrete depression at the same level where the extensor groove disappears.

The femur exhibits an autapomorphic feature on the medial surface of the distal end: an ovoid fossa (150 mm in proximodistal extent) on the shaft immediately proximal to the medial condyle (figs. 15–17). The fossa is defined anteriorly by the mesiodistal crest, which forms an enlarged flange that overhangs the medial surface anteriorly as is normal for tyrannosauroids and most other theropods. However, the medial margin of the posterior surface also thins into a much weaker crest, which serves to define the fossa posteriorly (fig. 17). This posterior crest is unknown in other tyrannosauroids (e.g., Brochu, 2003),

and its presence, in conjunction with the standard mesiodistal crest, serves to define the autapomorphic fossa. Unfortunately, erosion makes it impossible to discern whether the mesiodistal crest bifurcates distally when it reaches the medial condyle, as is the case in some tyrannosaurines (e.g., *Alioramus*, *Tarbosaurus*, *Tyrannosaurus*; Brusatte et al., 2010). However, it is clear that the medial surface of the medial condyle faces completely medially, and is not largely visible in anterior view as in *Tyrannosaurus* (Brochu, 2003: fig. 95). This latter condition may be an autapomorphy of *Tyrannosaurus*, as it is absent in closely related taxa such as *Alioramus* (IGM 100/1844) and *Tarbosaurus* (ZPAL MgD/I-09), which have an identical morphology to that of *Dryptosaurus*.

TIBIA: The left tibia is preserved in a comparable condition to the femur (fig. 18; table 2). The bone is nearly complete, but fine surface details have been obliterated over most of the specimen, and the proximal and distal ends are slightly eroded. The proximodistal length of the tibia is slightly less than that of the femur, a derived feature shared with large-bodied tyrannosauroids such as *Appalachiosaurus* (Carr et al., 2005) and tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003). In contrast, the small-bodied, more basal tyrannosauroids, including *Raptorex* (Serenó et al., 2009), possess a tibia that is longer than the femur, a condition also present in outgroup coelurosaurian taxa (e.g., Kobayashi and Lu, 2003; Carpenter et al., 2005a, 2005b; Peyer, 2006; although note that the relative length of the femur is positively allometric compared to the tibia: Russell, 1970; Currie, 2003b). The anterior surface of the shaft is flat to slightly convex in places, whereas the posterior, lateral, and medial surfaces are more strongly convex.

The proximal end is generally well preserved but is damaged in some regions, especially anteriorly and on the proximal articular surface (fig. 18E). The cnemial crest is large and stout,

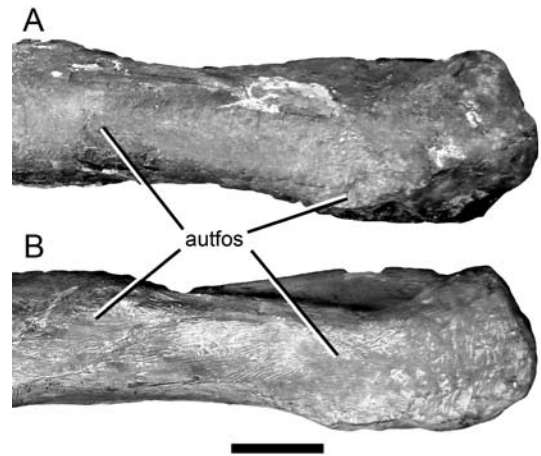


FIG. 17. Left femur of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in medial view: original material (A) and cast (B). Abbreviations: autfos, autapomorphic fossa on medial surface of distal end. Scale bar = 50 mm.

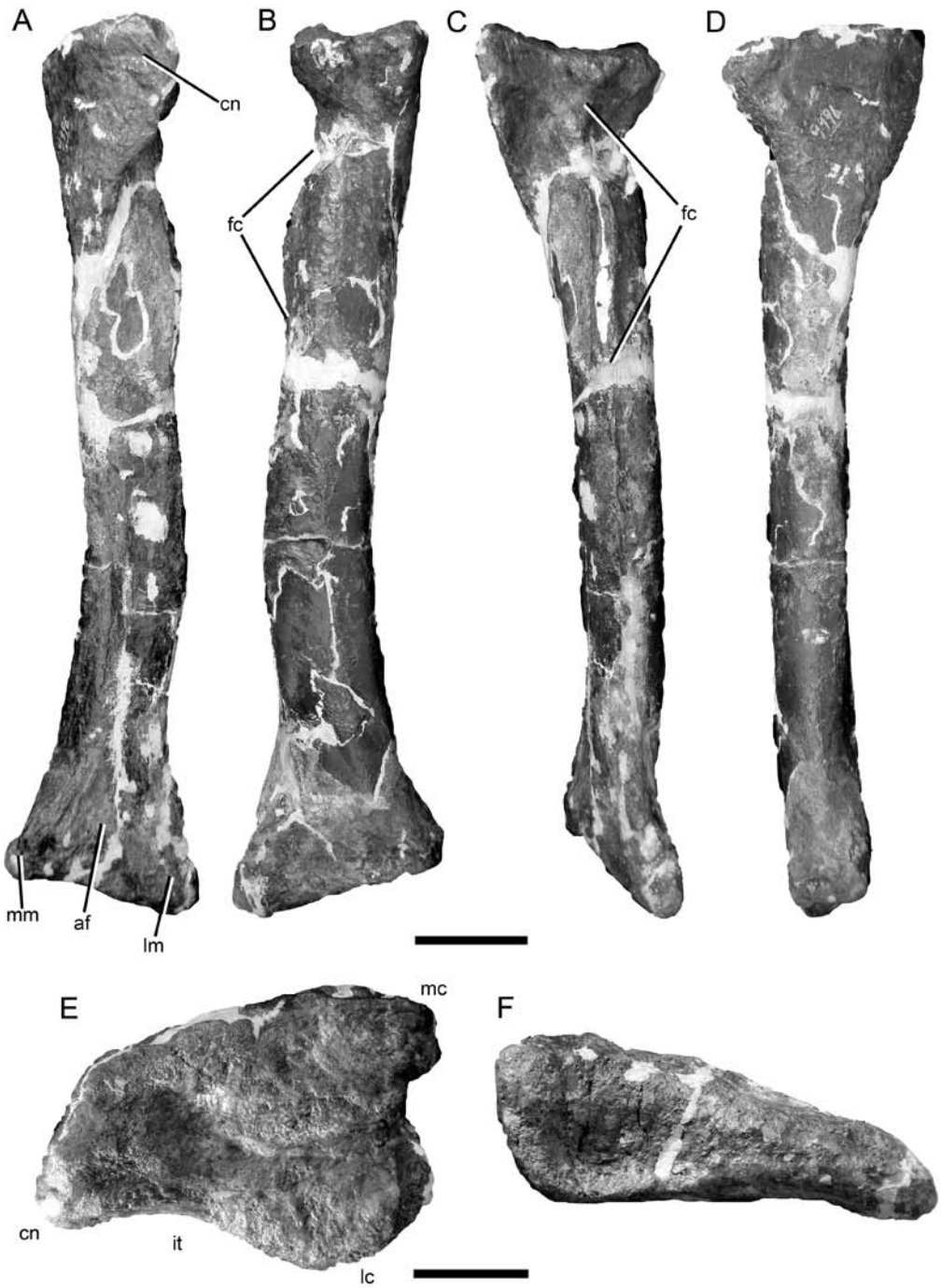


FIG. 18. Left tibia of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A), posterior (B), lateral (C), medial (D), proximal (E), and distal (F) views. Abbreviations: af, astragalus facet; cn, cnemial crest; fc, fibular crest; it, incisura tibialis; lc, lateral condyle; lateral malleolus; mc, medial condyle; mm, medial malleolus. Scale bar for A–D = 100 mm, for E–F = 50 mm.

and curves laterally as it continues anteriorly. The crest appears somewhat triangular in proximal view and its base is thick mediolaterally, almost as wide as the posterior condyles. As a result, there only appears to be a subtle incisura tibialis, the depression between the crest and lateral condyle on the lateral surface, which led Carpenter et al. (1997) to consider *Dryptosaurus* as lacking the deep notch of tyrannosaurids. However, because the anterior surface of the cnemial crest is broken, and it is likely that the crest would have extended further anteriorly in life, a deeper and more defined incisura tibialis was almost certainly present. Because of erosion, it is not possible to determine the presence or absence of an anterior process projecting into the incisura from the anterior surface of the lateral condyle, contra Carr et al. (2005) who described the absence of this process as a diagnostic difference between *Dryptosaurus* and *Appalachiosaurus*. However, if this process had been present, it is clear that it was not confluent with the fibular crest. Although the crest approaches the proximal end of the tibia, there is a small region of smooth, concave original bone on the lateral surface of the tibia, between the crest and the eroded region that may have housed the anterior process.

Posteriorly on the proximal end, separate lateral and medial condyles are divided by a deep, concave notch. Unfortunately, it is not possible to determine which condyle extended further posteriorly, as both are eroded. The medial surface of the medial condyle is gently convex, and smoothly merges with the medial surface of the cnemial crest to form a single, sweeping medial margin of the proximal tibial. The lateral surface of the lateral condyle, on the other hand, is strongly convex, forming the posterior wall of the incisura tibialis. Although the proximal articular surface is subtly eroded, it appears as if the lateral condyle was slightly convex posteriorly and concave anteriorly, with a slight lip on its lateral margin. The medial condyle and cnemial crest are nearly flat and together slope laterally, combining with the morphology of the lateral condyle to define a depression at the middle of the proximal articular surface.

There is a pronounced fibular crest on the lateral surface of the proximal end of the tibia (fig. 18B–C). The lateral surface of the crest is broken, but original bone surfaces on the anterior and posterior margins are heavily rugose. The broken profile of the crest clearly indicates that this structure was elongate and robust. It extends for approximately 190 mm proximodistally, terminating only a few millimeters below the proximal edge of the tibia, and is approximately 26 mm thick anteroposteriorly at its midpoint. Such thickness indicates that the crest extended as a robust flange, visible as a discrete rectangular sheet in anterior view, as in other tyrannosauroids (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003). However, in comparison to other tyrannosauroids, the crest of *Dryptosaurus* is proportionally elongate, as its broken outline nearly reaches the proximal articular surface of the tibia. Comparisons with other tyrannosauroids are hampered by the poor preservation of the crest in *Dryptosaurus*, but if the extreme proximal extent of the crest is a genuine feature, it is unusual among tyrannosauroids. Most other taxa possess a crest that terminates further distally, often 5–15 mm from the proximal end in individuals of similar size or larger than the *Dryptosaurus* holotype (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003; Carr et al., 2005). The only exception is *Stokesosaurus langhami*, which possesses an even more extreme condition in which the fibular crest extends to the proximal end of the tibia (Benson, 2008).

The distal end of the tibia is flattened anteriorly to back the ascending process of the astragalus. However, surface texture is so poorly preserved that it is impossible to measure the height of the astragalus facet, contra Carpenter et al. (1997), who provided a measurement of the ascending process based on a perceived tibial articular surface that we could not identify. In distal view the tibia is triangular (fig. 18F). Its anteroposterior dimension is longest medially, and laterally the bone thins to a rounded point. The medial region of the distal surface is excavated by a deep, ovoid concavity, which was likely even deeper and more distinct in life since its surface is eroded.

The lateral malleolus extends further distally than the medial malleolus, and also projects laterally from the shaft as a discrete flange. The distal expansion of the lateral malleolus is a tyrannosauroid feature also present in *Guanlong* (IVPP V14531), *Stokesosaurus* (Benson, 2008), *Eotyrannus* (MIWG 1997.550), *Appalachiosaurus* (Carr et al., 2005), and tyrannosaurids (e.g., Parks, 1928; Lambe, 1917; Brochu, 2003). In contrast, basal coelurosaur outgroups possess lateral and medial malleoli that extend to roughly the same level distally (e.g., Carpenter et al., 2005a, 2005b; Kobayashi and Barsbold, 2005; Rauhut and Xu, 2005; Gohlich and Chiappe, 2006) (note, however, that several more basal tetanuran outgroups also possess a distally expanded lateral malleolus, which may be a deeper theropod plesiomorphy retained in tyrannosauroids).

The lateral expansion of the lateral malleolus is normal for theropods, but is subtle when compared to the condition in many other tyrannosauroids. In taxa such as *Raptorex* (LH PV18), *Appalachiosaurus* (Carr et al., 2005), and all tyrannosaurids except for *Alioramus* (IGM 100/1844), the mediolateral dimension of the lateral malleolus is greater than 40% of the mediolateral width of the adjacent shaft. *Dryptosaurus* retains the primitive, less expanded condition, which is also present in *Guanlong* (IVPP V14531), *Dilong* (IVPP V14243), *Eotyrannus* (MIWG 1997.550), and *Stokesosaurus* (Benson, 2008). In *Dryptosaurus*, the fibular articular facet on the lateral malleolus faces almost entirely anteriorly, as is typical for theropods with even a subtly expanded malleolus. The medial surface of the medial malleolus is eroded, but appears to have been smoothly confluent with the tibial shaft, and thus did not project as a lobate structure. The two malleoli join each other distally to form a concave distal margin of the tibia in anterior and posterior views.

FIBULA: The proximal end of the left fibula is present (fig. 19; table 2). Assuming that the fibula is approximately the same length as the tibia, it is estimated that slightly more than half of the fibula is preserved. The proximal region is expanded relative to the shaft, which tapers distally, as is normal for theropods. The lateral surface of the bone is convex, as are the anterior and posterior surfaces.

The medial surface of the proximal region is invaded by a deep, ovoid fossa (fig. 19D). Both the proximal and anterior walls of the fossa are nearly perpendicular to the medial surface, and thus form an abrupt separation between the fossa and the remainder of the medial surface of the fibula. As a result, the anteroproximal corner of the fossa is most deeply inset. Posteriorly and distally, however, the fossa becomes gradually shallower to become confluent with the remainder of the medial fibula. Posterior to the fossa, much of the fibula is missing, and a large broken surface is present. This break is also present on the NHM cast, in which it appears as

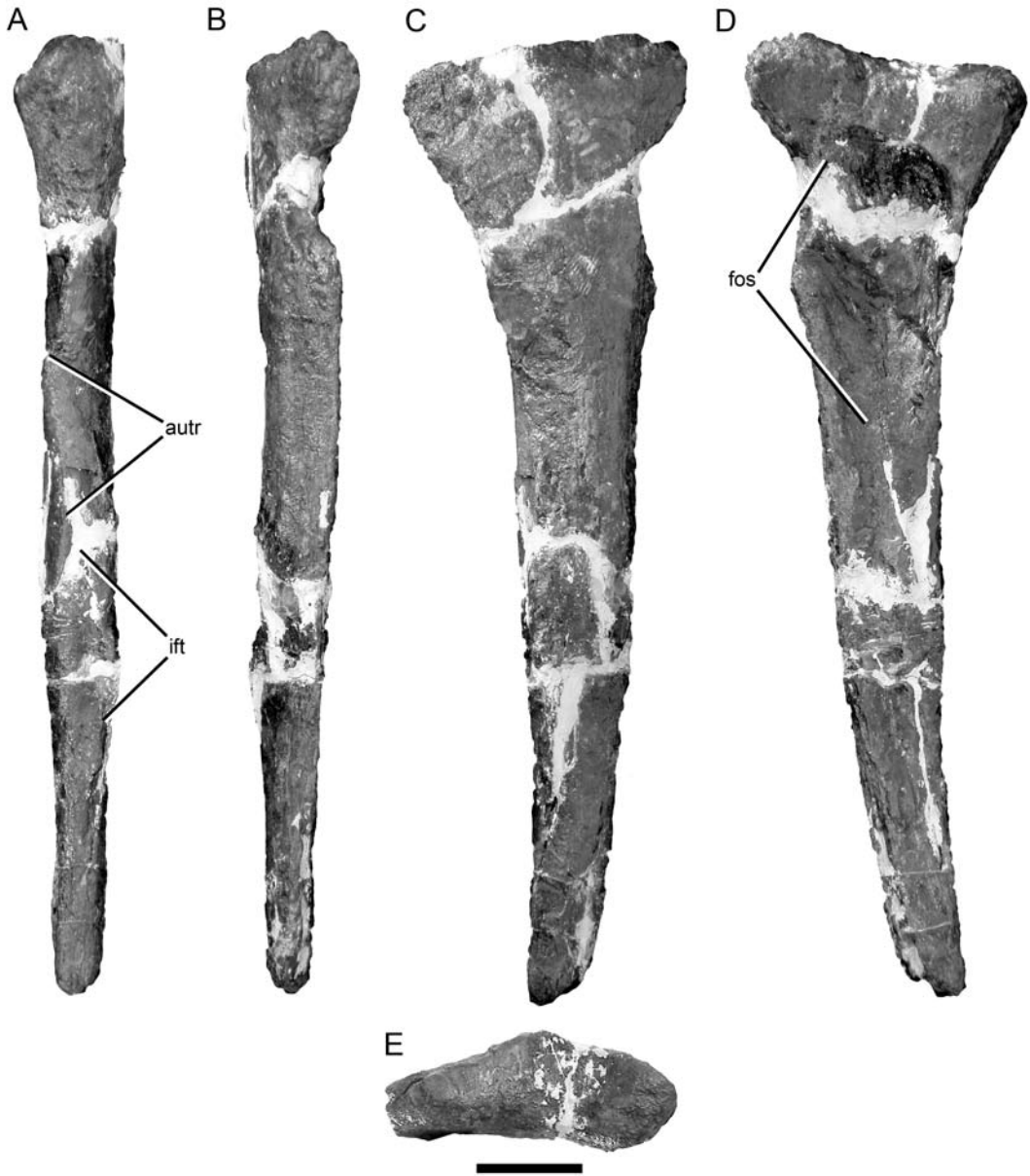


FIG. 19. Left fibula of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A), posterior (B), lateral (C), medial (D), and proximal (E) views. Abbreviations: autr, autapomorphic ridge; fos, medial fossa; ift, iliofibularis tubercle. Scale bar = 50 mm.

a smooth notch that could easily be mistaken for original morphology. Distal to the fossa, the medial surface is flat.

The fibula is mediolaterally thickened dorsal to the fossa, and the proximal articular surface is crescentic (fig. 19E). Its lateral margin is convex, its medial margin concave, and it tapers in mediolateral width as it extends posteriorly. The articular surface for the distal femur is trochlear, with a smooth concave region between anterior and posterior convexities. The entire proximal surface slopes medially.

The most conspicuous feature of the fibula is a pronounced muscle scar on the margin where the anterior and lateral surfaces meet, slightly proximal to the broken distal edge of the bone (fig. 19A). This scar, the iliofibularis tubercle, is large, prominent, rugose, and elongate proximodistally, and its long axis trends proximolaterally-distomedially. Importantly, the tubercle is bifurcated: it is comprised of lateral and medial crests that are separated by a depressed fossa. This morphology is especially clear in anterior view. Bifurcated iliofibularis tubercles are present in *Appalachiosaurus* (Carr et al., 2005) and tyrannosaurids (e.g., Brochu, 2003), but are absent in basal tyrannosauroids such as *Guanlong* (IVPP V14531) and *Dilong* (IVPP V14243). The bifurcated tubercle of *Dryptosaurus* was first recognized by Carr et al. (2005), who described it as a derived feature shared with tyrannosaurids.

Immediately proximal to the tubercle, the anterior margin of the fibula is marked by an accessory ridge that trends proximomedially (fig. 19A). This ridge is nearly as swollen, rugose, and prominent as the ridges that define the iliofibularis tubercle itself. Although this region of the fibula is poorly preserved, the ridge appears to be a genuine structure. It is absent in other tyrannosauroids (e.g., Brochu, 2003; Carr et al., 2005) and is here considered an autapomorphy of *Dryptosaurus*. Unlike the iliofibularis tubercle, this crest is a single structure and does not bifurcate to enclose a smooth fossa.

ASTRAGALUS: The left astragalus is well preserved distally but is missing most of its ascending process (fig. 20; table 2). As in other coelurosaur, the distal condyles are positioned on the anterior surface of the tibia when the two bones are articulated. Therefore, the condyles project mostly anteriorly rather than cupping the tibia ventrally, and in proximal view the ascending process and condyles form a smooth, single articular surface that lies against the anterior surface of the tibia.

Only the base of the ascending process is preserved, but it is clear that the process was essentially as wide as the condylar region of the bone, unlike the condition in *Guanlong* in which the ascending process is reduced to a discrete, tongue-like flange (IVPP V14531, V14532). The anterior surface of the ascending process is invaded by a deep, discrete, ovoid fossa immediately above the condyles (fig. 20A). The fossa clearly continued up the ascending process for some distance, as it is still present at the broken proximal margin of the astragalus. Fossae are common on the anterior surface of the ascending process in theropods, but derived tyrannosauroids exhibit a unique condition in which the fossa is especially deep, well defined, centered on the astragalus, and surrounded by a second, more extensive broad fossa that covers most of the ventral region of the ascending process. This morphology is present in *Raptorex* (Sereno et al., 2009), *Appalachiosaurus* (Carr et al., 2005), and tyrannosaurids (e.g., Lambe, 1917; Parks,

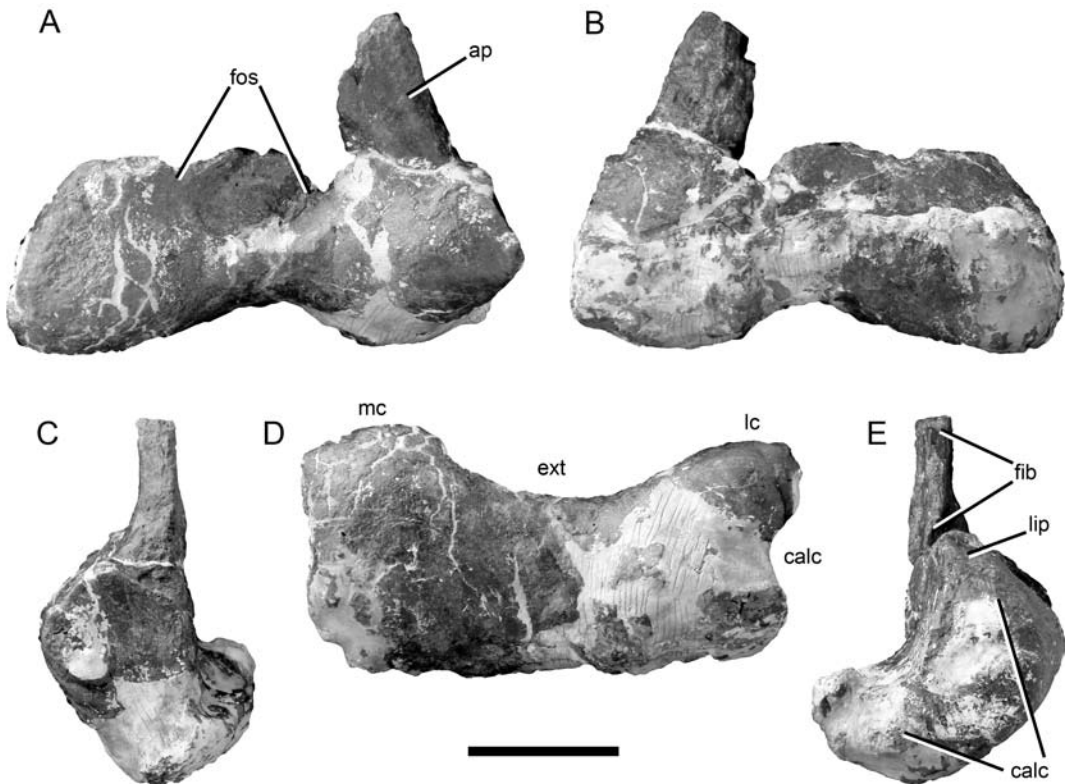


FIG. 20. Left astragalus of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (A), posterior (B), medial (C), distal (D), and lateral (E) views. Abbreviations: ap, ascending process; calc, calcaneum articulation; ext, extensor groove; fib, fibula articulation; fos, fossa on anterior surface; lip, lip separating fibula and calcaneum articulations; lc, lateral condyle; mc, medial condyle. Scale bar = 50 mm.

1928; Brochu, 2003). In contrast, the basal tyrannosauroids *Guanlong* (IVPP V14531, V14532) and *Dilong* (IVPP V14243) exhibit only a shallow, subtle fossa, comparable to that in close coelurosaurian outgroups (e.g., Carpenter et al., 2005a, b; Kobayashi and Barsbold, 2005; Rauhut and Xu, 2005). In *Dryptosaurus*, the lateral edge of the ascending process projects somewhat proximomedially, unlike the more proximodistally vertical morphology in *Appalachiosaurus* (Carr et al., 2005) and tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Brochu, 2003). As only the base is preserved, however, it is unknown whether this trend continued proximally or whether the lateral margin straightened out.

Distally, the medial condyle is more strongly convex both distally and anteriorly, and therefore appears expanded relative to the lateral condyle (fig. 20D). The medial condyle is 82 mm long anteroposteriorly at its midpoint and 64 mm wide mediolaterally, and its long axis is antero-medially oriented. The lateral condyle is 81 by 55 mm with a straight anteroposterior long axis. This condyle would have been larger in life, however, since the calcaneum would have formed its lateral margin. The distal surface of the astragalus is smooth and deeply inset as a trochlear surface between the two condyles. As a result, the distal margin of the astragalus is concave in

anterior and posterior views, more so than figured by Carpenter et al. (1997: fig. 9A). In proximal view, the condyles are marked by a trochlear surface where they sit against the anterior face of the tibia.

The medial surface of the astragalus is crescent shaped and mostly flat, although some regions are gently convex (fig. 20C). The lateral surface exhibits a heavily damaged facet for the calcaneum ventrally (fig. 20E), and this articulation is expressed in distal view as a concave notch on the lateral surface of the lateral condyle (fig. 20D). It is clear that the fibula made contact with only the lateral surface of the astragalus, including the lateral surface of the ascending process, as there is no discrete fibular cup on the proximal surface of the astragalus. Contact between the fibula and astragalus is more extensive in basal theropods, in which the astragalus cups the tibia and fibula distally (e.g., Welles and Long, 1974; Madsen, 1976).

Unfortunately, because the lateral surface is broken distally in *Dryptosaurus*, it is difficult to trace the sutural relationships between the astragalus, fibula, and calcaneum here. However, there is a pronounced lip that separates the ascending process from the condyles on the lateral surface (fig. 20E). Dorsal to this lip is a broad, smooth contact site for the fibula on the lateral surface of the ascending process, which faces strongly laterally and slightly anteriorly. It is likely that this lip would have separated the articular facets for the fibula and calcaneum, and therefore the calcaneum would have articulated with the entire lateral surface of the lateral condyle itself. The lip is sharp and pronounced, and projects as an anterolaterally oriented corner at its anterior point. Its dorsal surface is punctured by a deep pit, which forms the bottom of the fibular articulation on the ascending process. This pit, although reduced, is probably homologous to the more extensive fibular cup on the proximal surface of the astragalus in more basal theropods. Ventral to the lip, there is no discrete socket on the lateral surface of the condyle, which is present and receives a peg from the calcaneum in *Appalachiosaurus* and tyrannosaurids (Carr et al., 2005). On the contrary, in *Dryptosaurus* the lip on the astragalus overlaps the calcaneum proximally, which is an autapomorphy among tyrannosauroids because it is absent in other taxa such as *Appalachiosaurus* (Carr et al., 2005), *Tarbosaurus* (ZPAL MgD-I/29), and *Tyrannosaurus* (Brochu, 2003).

Carr et al. (2005: 134) described the ventrolateral buttress, the ridge defining the anterodistal corner of the fibular articulation, as “weakly developed” in *Dryptosaurus*. In comparison, *Appalachiosaurus* was described as having a more prominent buttress, a difference used to support the taxonomic separation of these two genera. *Dryptosaurus* does appear to have a weaker buttress in comparison to the sharp, pronounced ridge in *Appalachiosaurus* (Carr et al., 2005: fig. 18A). This region of the astragalus has been abraded in *Dryptosaurus*, however, and its apparently weaker buttress may be artifactual.

METATARSALS: Two metatarsals are preserved (figs. 21–22), including a complete left metatarsal IV (AMNH FARB 2438, the only bone of the holotype not cataloged under ANSP 9995) and a fragmentary metatarsal III that has not hitherto been described.

The left **metatarsal IV** is long and gracile, with convex anterior, lateral, and medial surfaces (fig. 22; table 2). The posterior surface, on the contrary, is flat proximally before becoming convex distally. As a result, the proximal cross section of the shaft is semiovoid, much wider

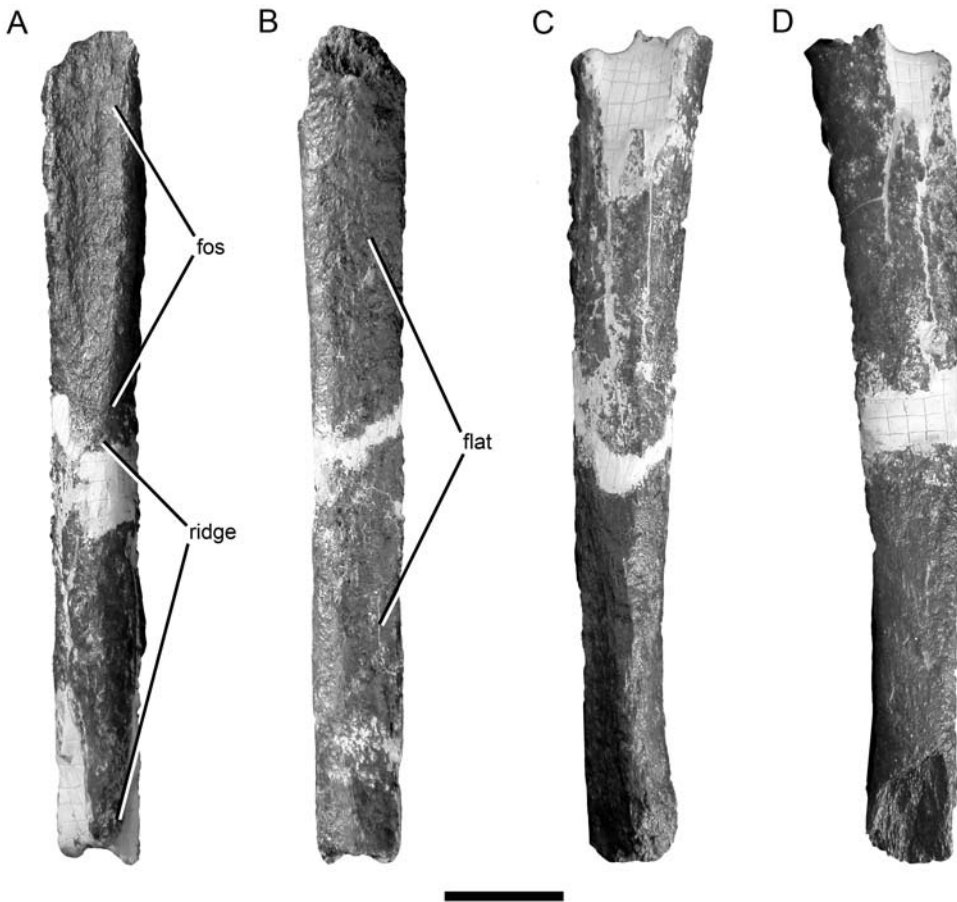


FIG. 21. Metatarsal III (left or right) of the holotype of *Dryptosaurus aquilunguis* (ANSP 9995) in anterior (= extensor) (A), posterior (= flexor) (B), lateral or medial (C), and opposite lateral or medial (D) views. Abbreviations: flat, flat posterior surface; fos, fossa; ridge, anterior surface reduced to thin ridge. Scale bar = 50 mm.

mediolaterally than anteroposteriorly, with the lateral and medial surfaces reduced to thin, pronounced crests. Unfortunately, little original bone surface is preserved in this region, raising the possibility that the posterior surface was not so extremely flat in life. However, the few preserved regions of original bone are flat, so we tentatively identify the flattened posterior surface, and the associated mediolateral thickening of the shaft relative to its anteroposterior thickness, as an autapomorphy of *Dryptosaurus*. Other tyrannosauroids, such as *Guanlong* (IVPP V14531), *Eotyrannus* (MIWG 1997.550), *Appalachiosaurus* (Carr et al., 2005), and *Tyrannosaurus* (Brochu, 2003), have a much more convex posterior surface, resulting in a more ovoid or triangular cross section of the shaft at its midpoint.

The proximal end of the metatarsal is expanded relative to the shaft. In proximal view, its lateral margin is strongly convex and its anterior and posterior margins more weakly so (fig. 22E). The medial margin is interrupted by a small, discrete, concave notch, against which

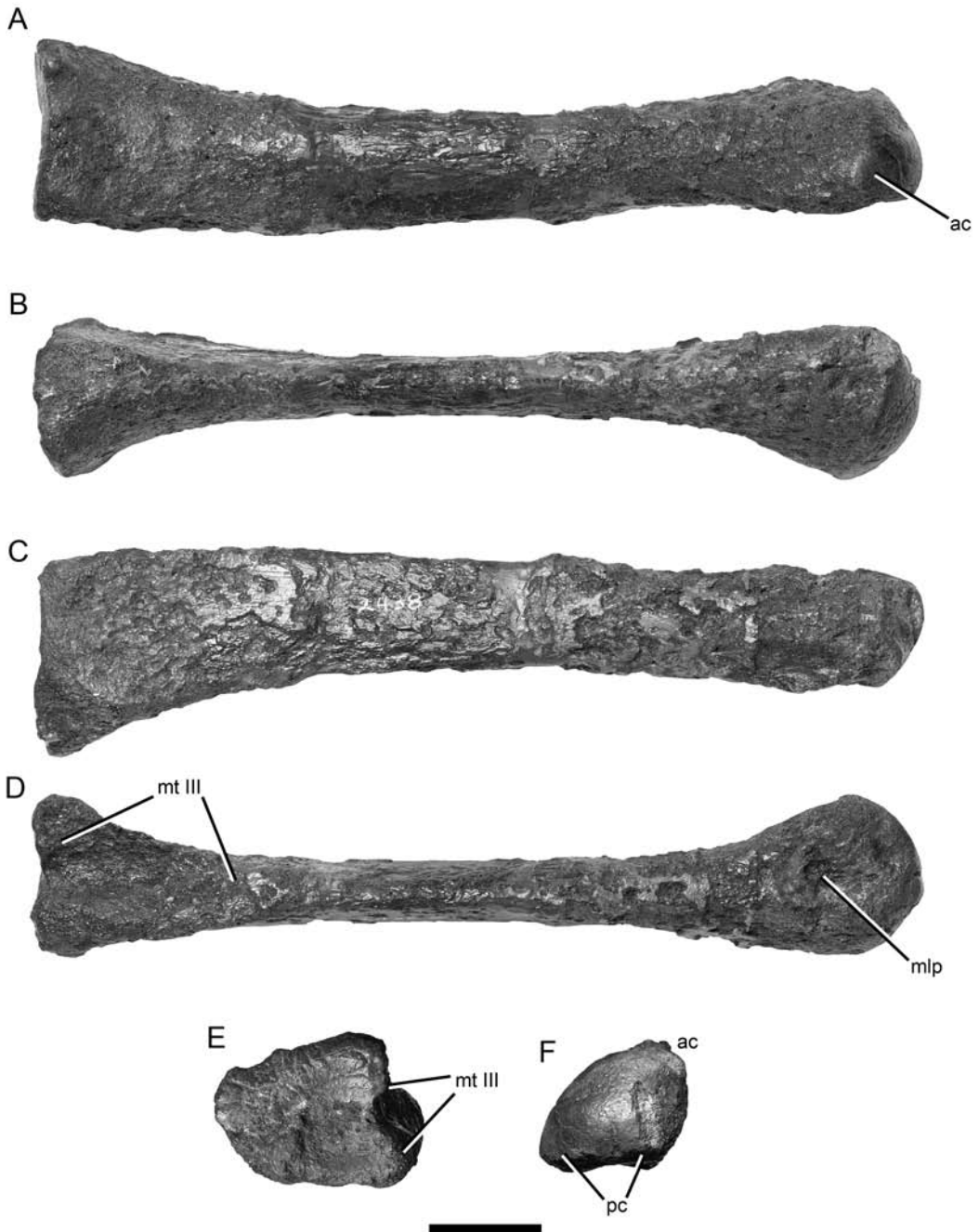


FIG. 22. Metatarsal IV of the holotype of *Dryptosaurus aquilunguis* (AMNH 2438) in anterior (= extensor) (A), lateral (B), posterior (= flexor) (C), medial (D), proximal (E), and distal (F) views. Abbreviations: ac, anterior condyle; mlp, medial ligament pit; mt III, articular facet for metatarsal III; pc, posterior condyles. Scale bar = 50 mm.

metatarsal III articulated. The notch continues distally on the medial surface of the shaft as a concave fossa, which quickly expands in anteroposterior width before gradually tapering and becoming less inset into the medial surface distally.

The shape of the proximal articular surface, especially the shape and size of the notch for metatarsal III, is nearly identical to that of derived tyrannosauroids such as *Albertosaurus* (Holtz, 1995), *Appalachiosaurus* (Carr et al., 2005), *Gorgosaurus* (Lambe, 1917), *Raptorex* (Serenó et al., 2009), *Tarbosaurus* (Maleev, 1974), and *Tyrannosaurus* (Brochu, 2003), all of which have an arctometatarsalian pes in which metatarsal III is “pinched” between metatarsals II and IV (see Holtz, 1995; Snively et al., 2004 for more details). In contrast, more basal tyrannosauroids without an arctometatarsalian pes, such as *Eotyrannus* (MIWG 1997.550), exhibit a more planar medial margin of the proximal fourth metatarsal, as in large-bodied basal tetanurans (e.g., Brusatte et al., 2008). In sum, the morphology of the proximal metatarsal IV suggests that *Dryptosaurus* possessed an arctometatarsalian pes, which is borne out by the morphology of metatarsal III (see below). Carpenter et al. (1997) noted that the presence of a proximal notch for metatarsal III is a characteristic of arctometatarsalian taxa, but argued that *Dryptosaurus* was not arctometatarsalian, at least in the style of derived tyrannosaurids, because it lacks the flat, expanded facet on the medial surface distally that articulates with metatarsal III, as well as the laterally kinked distal end of metatarsal IV that accommodates the expanded distal end of metatarsal III. However, we note that the medial surface is heavily eroded distally, and very little original bone surface remains. Thus, the presence or absence of the medial facet cannot be determined. Additionally, although the distal end is not sharply kinked, it is curved laterally relative to the proximal end.

Distally, metatarsal IV is heavily eroded and the posterior condyles are missing (fig. 22F). The anterior condyle is teardrop shaped and curves medially as it continues anteriorly, such that its medial surface is nearly flat whereas its lateral surface is broadly convex. Anteriorly the condyle tapers to a thin point, as in *Eotyrannus* (MIWG 1997.550) and *Appalachiosaurus* (Carr et al., 2005), but unlike the more gently rounded condition in *Albertosaurus* (Parks, 1928), *Gorgosaurus* (Lambe, 1917), *Tarbosaurus* (ZPAL MgD-I/206), and *Tyrannosaurus* (Brochu, 2003), in which the anterior surface is nearly flat. In concert with this morphology, the distal surface is more elongate anteroposteriorly relative to its mediolateral width in *Dryptosaurus* and basal tyrannosauroids than it is in tyrannosaurids (Brusatte et al., 2010: character 305). The distal articular surface itself is smooth and highly convex, and the medial ligament pit was evidently large, deep, and set in a broad fossa. The corresponding region is eroded on the lateral side, but if present, the lateral pit would have been much smaller.

A very poorly preserved bone appears to represent the midshaft region of **metatarsal III**, although it is difficult to determine whether this is a left or right element (fig. 21). Importantly, one surface of this fragment is reduced to a thick ridge, whereas the opposite surface is flat and one of the remaining (either lateral or medial) surfaces is marked by an elongate, concave fossa. These details match well with the morphology of metatarsal III of arctometatarsalian tyrannosauroids, in which the anterior surface is reduced to a ridge where it fits between metatarsals

II and IV, the posterior surface is flat and extensively contributes to the palmar surface of the metatarsus, and the lateral and medial surfaces tightly brace against the surrounding metatarsals (e.g., Brochu, 2003: fig. 100). This morphology, especially the triangular cross section of the bone due to the thick ridge, would not be expected in a fibula (another possible identification for a long, thin bone fragment), which in tyrannosauroids has a more crescentic cross section without a conspicuous ridge.

DISCUSSION

DRYPTOSAURUS SYSTEMATICS: HISTORICAL OVERVIEW

When Cope (1866, 1867, 1868a, 1868b, 1869) first described the holotype of *Dryptosaurus*, it was among the most complete skeletons of a large theropod dinosaur known to science. With little comparative material at hand, Cope and other contemporary paleontologists noted similarities between *Dryptosaurus* and other fragmentary remains of large theropods, including *Megalosaurus* from the United Kingdom (e.g., Cope, 1866; Leidy, 1868; Lydekker, 1888). *Dryptosaurus* was often allied with *Megalosaurus* and *Deinodon*, both wastebasket genera that subsumed material from what are now known as numerous theropod taxa widely spread in time and space, in the family Megalosauridae or Deinodontidae (e.g., Osborn, 1902; Hay, 1902; Gilmore, 1920; Huene, 1926; Romer, 1956, 1966; Kuhn, 1965). Other authors, however, argued that *Dryptosaurus* was unusual enough to warrant its own family, Dryptosauridae, which in time became a wastebasket taxon for fragmentary theropod remains from across North America (e.g., Marsh, 1890, 1896). This concept has remained in favor until relatively recently, as Carpenter et al. (1997) retained a monotypic Dryptosauridae after they were unable to confidently place *Dryptosaurus* within any other theropod clade.

Beginning in the middle of the 20th century, and especially gaining steam in the 1970s, paleontologists began to recognize similarities between *Dryptosaurus* and the characteristic Late Cretaceous tyrannosaurids *Albertosaurus* and *Tyrannosaurus* from western North America (e.g., Gilmore, 1946; Steel, 1970; White, 1973). Baird and Horner (1979) formally referred *Dryptosaurus* to Tyrannosauridae, but this was based on the tyrannosaurid affinities of a femur from North Carolina that was tentatively referred to *Dryptosaurus*, not the holotype. Molnar (1980) regarded *Dryptosaurus* as an “albertosaur,” an informal term used to group this genus with the tyrannosaurids *Albertosaurus* and *Daspletosaurus*. However, despite these referrals, the tyrannosaurid affinities of *Dryptosaurus* remained controversial. Russell (1970) disputed any connection between *Dryptosaurus* and Late Cretaceous tyrannosaurids, arguing that the larger hand and more gracile femur of *Dryptosaurus* precluded assignment to Tyrannosauridae. Carpenter et al. (1997: 571) followed suit, asserting that the teeth and astragalus of *Dryptosaurus* differed in morphology from those of tyrannosaurids, thus “cast(ing) doubt on the affinity of *Dryptosaurus* with the tyrannosaurids.” In his review of problematic large theropods, Molnar (1990) noted a few features shared between *Dryptosaurus* and tyrannosaurids, but concluded that *Dryptosaurus* could not be placed into any currently known theropod clade.

One of the primary problems confronting theropod paleontologists, from the time of Cope (1866) until the more recent redescription of Carpenter et al. (1997), was poor sampling, specifically the lack of basal tyrannosauroid taxa—species intermediate in phylogenetic position, body size, and morphological features between generalized coelurosaurs and the derived, colossal Late Cretaceous tyrannosaurids. Authors such as Russell (1970), Molnar (1990), and Carpenter et al. (1997) were correct in identifying both similarities between *Dryptosaurus* and tyrannosaurids, as well as differences. This confounded many researchers, including Carpenter et al. (1997), who used a typological argument to exclude *Dryptosaurus* from Tyrannosauridae based only on the absence of characters, ignoring shared derived features that unite these taxa. The discovery of numerous basal tyrannosauroids during the first decade of the 21st century, which have been studied in a rigorous phylogenetic context, illuminate an important pattern: the mixture of similarities and differences between *Dryptosaurus* and tyrannosaurids are expected in an “intermediate” tyrannosauroid taxon on the stem toward the large-bodied Tyrannosauridae. In other words, *Dryptosaurus* shares many derived characters with tyrannosaurids not seen in non-tyrannosauroid coelurosaurs and some basal tyrannosauroids such as *Guanlong*, *Dilong*, and *Eotyrannus* (Hutt et al., 2001; Xu et al., 2004, 2006). It lacks other characters that unite taxa such as *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus* into Tyrannosauridae proper. Therefore, it possesses a mixture of primitive and derived features, which in the context of a phylogenetic analysis support the placement of *Dryptosaurus* on the tyrannosaurid “stem” (e.g., Holtz, 2004; Brusatte et al., 2009, 2010; Carr and Williamson, 2010).

The first authors to recognize this emerging pattern were Holtz (2004) and Carr et al. (2005). The discovery of the Campanian tyrannosauroid *Appalachiosaurus*, also a midsized taxon from eastern North America showing both similarities and differences with derived tyrannosaurids, was a key to realizing the tyrannosauroid affinities of *Dryptosaurus*. Carr et al. (2005: 139) argued that *Dryptosaurus* was a tyrannosauroid based on the possession of two unique, derived characters seen only in this clade: an enlarged posterior surangular foramen and a bifurcated iliofibularis scar on the fibula. In addition, the generalized morphology of metatarsal IV was described as “comparable” to that of tyrannosaurids. Carr et al. (2005) also included *Dryptosaurus* in a phylogenetic analysis, which placed it as the most basal tyrannosauroid (however, it is worth noting that other basal tyrannosauroids such as *Eotyrannus*, *Dilong*, and *Guanlong* were not included, and several recently described basal tyrannosauroids were unknown at the time). Holtz (2004), who based his analysis on the characters discussed in a prepublication version of Carr et al. (2005), also included *Dryptosaurus* in a phylogenetic analysis, finding it in a comparable basal tyrannosauroid position. More recently, Brusatte et al. (2009, 2010) and Carr and Williamson (2010) have recovered similar results. These latter studies include a full array of basal tyrannosauroids, and place *Dryptosaurus* as intermediate between basal taxa (i.e., *Guanlong*, *Proceratosaurus*, *Dilong*, *Eotyrannus*) and Tyrannosauridae proper (i.e., *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, *Tyrannosaurus*). Contemporary theropod paleontologists, therefore, have reached a consensus: *Dryptosaurus* is an intermediate-grade tyrannosauroid (fig. 23).

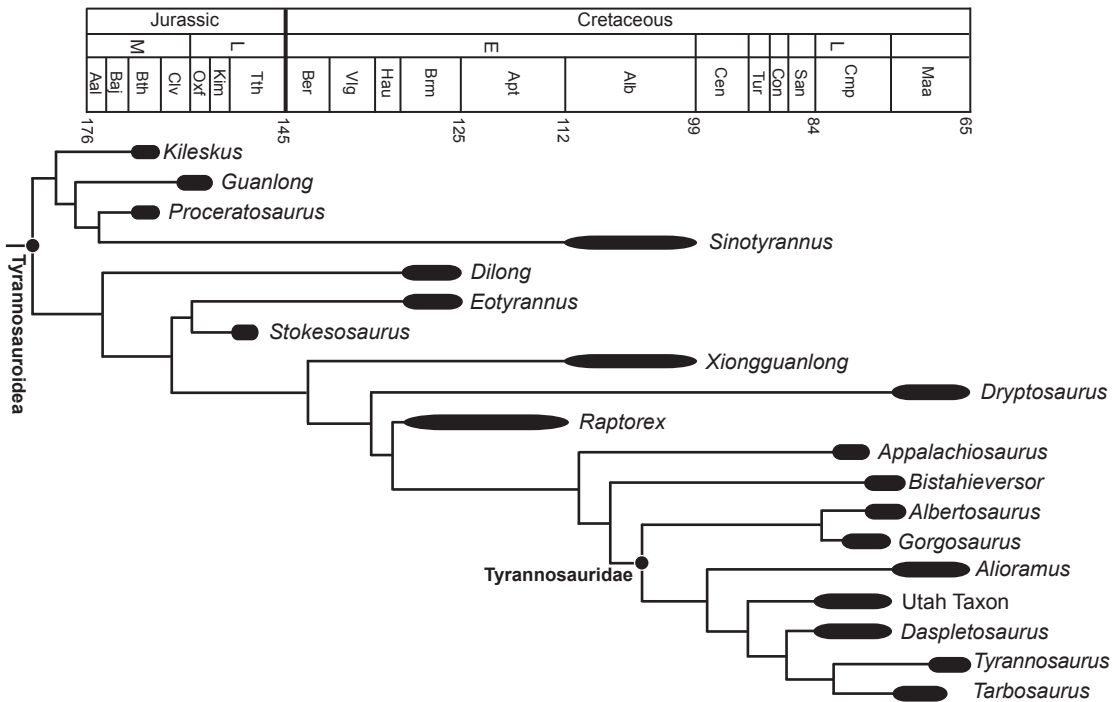


FIG. 23. Phylogenetic relationships of tyrannosauroids, based upon the cladistic analysis of Brusatte et al. (2010). *Dryptosaurus* is an “intermediate” tyrannosauroid that is more derived than basal taxa such as *Guanlong* and *Dilong*, but outside of the derived Tyrannosauridae that includes *Tyrannosaurus*, *Albertosaurus*, and other colossal Late Cretaceous taxa.

THE TYRANNOSAURID AFFINITIES OF *DRYPTOSAURUS*

Although the work of Carr et al. (2005) and others has made it clear that *Dryptosaurus* is a tyrannosauroid, the specific characters supporting this placement have been only briefly discussed in the literature. Carr et al. (2005) and Holtz (2004) noted the two synapomorphies listed above, and Carr et al. (2005) also included specific comparisons between *Dryptosaurus* and *Appalachiosaurus* in their osteological description of the latter taxon. Other features that place *Dryptosaurus* within the tyrannosauroid clade have been encoded in phylogenetic datasets, but have been listed only in data matrices and not discussed or described in detail. Here, we review numerous features of the skeleton that support the tyrannosauroid affinities of *Dryptosaurus*. Most of these characters are included in the phylogenetic analysis of Brusatte et al. (2010), and many of them in the earlier analyses of Brusatte et al. (2009) and Carr and Williamson (2010), and thus explicitly support the tyrannosauroid placement of *Dryptosaurus* in numerical cladistic studies (fig. 23). In the following discussion, we rely explicitly on the phylogenetic dataset and analysis of Brusatte et al. (2010).

Dryptosaurus possesses three characters that currently optimize as synapomorphies of the tyrannosauroid clade (i.e., present in all members of the clade, including basal forms such as

Guanlong and *Dilong*). The anteromedial process (= palatal process) of the maxilla is elongate and extends posteriorly at least to the level of alveolus 4, forming an extensive “secondary palate” (e.g., Holtz, 2004). The mesiodistal crest of the femur is robust and medially expanded, such that it is visible in posterior view as a pronounced flange. The lateral malleolus of the tibia is expanded distally relative to the medial malleolus. This character is seen in all tyrannosauroids except for *Dilong* (IVPP V14243) and *Alioramus* (IGM 100/1844; Brusatte et al., 2009), and is optimized as a tyrannosauroid synapomorphy lost in these two taxa. Finally, a fourth character is also seen in other tyrannosauroids. The ventral neurovascular row on the dentary is anteroposteriorly elongate, extending far posterior to the midlength of the bone. This is not an unequivocal tyrannosauroid character, as it is also present in *Compsognathus* (Ostrom, 1978) and some dromaeosaurs (e.g., Norell et al., 2006), but shorter rows are present in most other coelurosaurs, including ornithomimosaurs (e.g., Ji et al., 2003; Kobayashi and Barsbold, 2005), compsognathids (Hwang et al., 2004), and troodontids (e.g., Makovicky et al., 2003; Norell et al., 2009).

Dryptosaurus also possesses several ingroup tyrannosauroid characters, which are not present in basal taxa such as *Guanlong*, *Proceratosaurus*, and *Dilong* and thus unite *Dryptosaurus* with *Eotyrannus*, *Stokesosaurus*, *Appalachiosaurus*, *Raptorex*, *Xiongguanlong*, and Tyrannosauridae as a more derived clade. The surangular shelf is robust and prominently offset laterally, and it is positioned directly above the posterior surangular foramen and projects solely laterally. More basal tyrannosauroids, in contrast, have a subtle shelf that is located far dorsal to the foramen (e.g., Xu et al., 2004, 2006). In distal view, the anterior surface of the lateral condyle of the femur is marked by a discrete bulge. This character is absent in *Guanlong* (IVPP V14531) and *Dilong* (IVPP V14243), in which the anterior surface of the condyle is a single, broadly convex margin, but present in *Stokesosaurus* (OUMNH J.3311: Benson, 2008), *Xiongguanlong* (FRDC-GS JB16-2-1), *Raptorex* (LH PV18), and tyrannosaurids (e.g., Brochu, 2003).

Additionally, *Dryptosaurus* possesses an intermediate condition for three ordered characters in the analysis of Brusatte et al. (2010), supporting a phylogenetic placement between basal tyrannosauroids such as *Guanlong* and *Dilong* and more derived taxa such as *Raptorex* and tyrannosaurids. The adductor muscle scar on the surangular faces almost equally dorsally and laterally, intermediate between the dorsal condition of *Guanlong* and *Proceratosaurus* and the lateral condition of *Tarbosaurus* and *Tyrannosaurus*. The humerus is approximately 38% of the length of the femur, intermediate between the 50%–70% ratio of *Guanlong* and *Dilong* and the 25%–30% ratio of *Raptorex* and Tyrannosauridae (even though the ends of both bones are eroded in *Dryptosaurus*, only small regions are missing, meaning that *Dryptosaurus* confidently falls within the two end-member ratios). Similarly, the apex of the deltopectoral crest is located between 25%–35% of the length of the humerus, intermediate between the 40%–50% ratio in *Guanlong* and *Dilong* and the 25% or less ratio in *Raptorex* and Tyrannosauridae. In both features of the humerus, *Eotyrannus* shares the intermediate condition with *Dryptosaurus*, thus supporting both taxa as intermediately positioned between basal tyrannosauroids and tyrannosaurids.

Several other characters support a progressively more derived phylogenetic position, placing *Dryptosaurus* closer to *Raptorex* and tyrannosaurids than to taxa such as *Eotyrannus*, *Stokes-*

osaurus, and *Xiongguanlong*. The enlarged, fenestralike posterior surangular foramen, first noted by Carr et al. (2005), is also seen in *Raptorex* (Serenó et al., 2009) and tyrannosaurids (e.g., Molnar, 1991; Brochu, 2003), whereas it is only a small foramen in *Eotyrannus* (MIWG 1997.550), *Dilong* (IVPP V14243), *Guanlong* (IVPP V14532), *Kileskus* (Averianov et al., 2010), and *Proceratosaurus* (Rauhut et al., 2010). The surangular shelf is oriented horizontally, not anterodorsally or anteroventrally as in more basal taxa, and there is a discrete fossa on the lateral surface of the surangular below the glenoid, whereas this region is bare in more basal taxa. On the manus, the overall similarity in phalangeal shape with derived tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Maleev, 1974; Brochu, 2003) suggests that *Dryptosaurus* most likely had only two functional digits, as in *Raptorex* and tyrannosaurids; however, this cannot be determined conclusively. Also in common with these taxa, the flexor tubercle and overall degree of curvature of the manual unguals are reduced, which likely relate to a loss of grasping ability in concert with the reduced length of the arm and number of digits. The ischial tubercle is expressed as a rugose flange, not a subtle convexity or groove as in more basal taxa such as *Guanlong* (IVPP V14531) or *Stokesosaurus* (Benson, 2008), and the accessory trochanter of the femur is reduced to a subtle mound, unlike the more discrete, flangelike morphology in *Guanlong* (IVPP V14531) and *Xiongguanlong* (Li et al., 2010). The iliofibularis tubercle is bifurcated as in *Appalachiosaurus* and tyrannosaurids, as noted by Carr et al. (2005), and the anterior surface of the ascending process of the astragalus is marked by a deep, discrete fossa, as in *Raptorex* (Serenó et al., 2009), *Appalachiosaurus* (Carr et al., 2005), and tyrannosaurids (e.g., Brochu, 2003).

Two characters suggest that *Dryptosaurus* and tyrannosaurids share a more recent common ancestor relative to *Raptorex*, even though the most parsimonious phylogenetic topology places *Raptorex* closer to tyrannosaurids (Brusatte et al., 2010). Regardless of their exact optimization, these characters also support a more derived tyrannosauroid placement for *Dryptosaurus*, and include a pubis that is concave anteriorly and a femur that is longer than the tibia. Both conditions are seen in *Appalachiosaurus* (Carr et al., 2005) and tyrannosaurids (e.g., Lambe, 1917; Parks, 1928; Maleev, 1974; Brochu, 2003), whereas more basal taxa have a straight or anteriorly convex pubis and a tibia that is longer than the femur.

DRYPTOSAURUS AND APPALACHIOSAURUS: EASTERN NORTH AMERICAN TYRANNSAUROIDS

During most of the Late Cretaceous, eastern and western North America were separated by the Western Interior Seaway, a continental sea that stretched from the present-day Gulf of Mexico to the Arctic Ocean (Smith et al., 1994). Therefore, *Dryptosaurus* and its contemporary fauna would have had little, if any, faunal connection with the tyrannosaurid-dominated ecosystems of western North America during the Maastrichtian. This is also true of the slightly older (Campanian), eastern North American tyrannosauroid *Appalachiosaurus*. In light of this information, our current understanding of tyrannosauroid phylogeny is congruent with the physical geography of terminal Cretaceous North America: *Dryptosaurus* and *Appalachiosaurus*

are not particularly close relatives of coeval western North American tyrannosaurids such as *Albertosaurus* and *Tyrannosaurus*.

The Campanian-Maastrichtian western North American tyrannosauroids form a clade, Tyrannosauridae, which also includes Asian members. It is tempting to consider whether eastern North American tyrannosauroids also form a clade. Indeed, *Dryptosaurus* and *Appalachiosaurus* are extremely similar in body size and general morphology. However, there is currently no strong evidence that they form a unique eastern clade. No such clade is recovered in the phylogenetic analysis of Brusatte et al. (2010), which instead places *Dryptosaurus* and *Appalachiosaurus* as successively closer outgroups to Tyrannosauridae. Furthermore, the two eastern tyrannosauroids are not proximal outgroups on the tyrannosaurid “stem,” but *Raptorex* falls out in between them.

With this said, it is notable that there is minimal overlapping material between *Dryptosaurus* and *Appalachiosaurus*, and many of the overlapping bones are poorly preserved in both taxa. *Appalachiosaurus* is known from a decently preserved skull, whereas little cranial material is present in *Dryptosaurus*. Conversely, the forelimb of *Dryptosaurus* is reasonably well known, but is completely unknown in *Appalachiosaurus*. Therefore, we consider the exact phylogenetic relationships of these two taxa as equivocal. It is clear that neither is a tyrannosaurid and that both are close outgroups to Tyrannosauridae, but whether they form a unique eastern clade can be confidently tested only with the discovery of additional material from eastern North America. It would not surprise us if such discoveries eventually illuminate a clade of tyrant dinosaurs restricted to eastern North America.

FORELIMB PROPORTIONS OF *DRYPTOSAURUS*

Derived tyrannosauroids are well known for their highly reduced forelimb (e.g., Lambe, 1917; Parks, 1928; Russell, 1970; Carpenter and Smith, 2001; Brochu, 2003; Lipkin and Carpenter, 2009). This feature is first known, both temporally and phylogenetically, in the small-bodied (femur length = 338 mm) tyrannosauroid *Raptorex* from the Hauterivian-Barremian. In contrast, more basal tyrannosauroids, such as *Guanlong* (IVPP V14531) and *Dilong* (IVPP V14243), possess much larger forelimbs similar to those of other coelurosaurian theropods. In general, the entire forelimb of *Raptorex* and tyrannosaurids is reduced: the humerus, radius and ulna, and hand are all proportionally short (relative to the femur or other comparative bones), reflecting a reduction in the overall range of motion, grasping ability, and presumably predatory function, of the entire limb (e.g., Lipkin and Carpenter, 2009).

Interestingly, the forelimb proportions of *Dryptosaurus* are unlike those of other tyrannosauroids (table 3). The humerus is short relative to the femur (humerus: femur length ratio = 0.375). Although it is not as reduced as those of tyrannosaurids and *Raptorex* (ratio = 0.268–0.344), the *Dryptosaurus* humerus is substantially shorter than in basal tyrannosauroids such as *Guanlong* (ratio = 0.597). The ratio of humerus length to femur length is used as an ordered multistate character in the analysis of Brusatte et al., (2010), and *Dryptosaurus* is scored for the intermediate condition. However, the hand of *Dryptosaurus* is proportionally large. Phalanx I-1

TABLE 3. Comparative measurements (in mm) of fore- and hind limbs of theropod dinosaurs, illustrating the unique morphology of *Dryptosaurus aquilunguis* (ANSP 9995) in which the humerus is proportionally reduced but the hand is large.

		Femur	Humerus	Phalanx I-1	Ungual I-2	Phalanx II-2	Humerus: Femur	Phalanx I-1: Femur	Ungual I-2: Femur
Tyrannosauroidae									
<i>Albertosaurus</i>	Parks, 1928	1020	303	85	92	70	0.30	0.083	0.090
<i>Tarbosaurus</i>	Maleev, 1974	1011	271	54	33	45	0.27	0.053	0.033
<i>Raptorex</i>	Sereno et al., 2009	338	99	26	18	22	0.29	0.077	0.053
<i>Gorgosaurus</i>	Parks, 1928	1040	324	98	80	83	0.31	0.094	0.077
<i>Daspletosaurus</i>	Russell, 1970	655	225	63	46	40	0.34	0.096	0.070
<i>Guanlong</i>	IVPP V14531	352	210	80	74	75	0.60	0.227	0.210
<i>Dryptosaurus</i>	ANSP 9995	800	300	160	176	126	0.38	0.200	0.220
Outgroups									
<i>Chilantaisaurus</i>	Benson and Xu, 2008	1190	580	—	250	—	0.49	—	0.210
<i>Suchomimus</i>	MNN GDF 500	1075	560	—	260	—	0.52	—	0.242

is more than twice as long relative to the femur as those of tyrannosaurids and *Raptorex*, closer to the proportions in long-armed basal tyrannosauroids like *Guanlong* (table 3). This combination of a large hand and short humerus is unusual among theropods. Other theropods have large hands and correspondingly enlarged manual ungual phalanges (Rauhut, 2003), including spinosaurids (Charig and Milner, 1997), the megalosaurid *Torvosaurus* (Galton and Jensen, 1979) and neovenatorid allosauroids (Benson and Xu, 2008; Benson et al., 2010b) (table 3). However, all of these taxa also have proportionally elongate forelimbs with long humeri, unlike those of *Dryptosaurus* and tyrannosaurids. Therefore, the combination of a proportionally short humerus and a large hand is considered an autapomorphy of *Dryptosaurus* among theropods.

We hypothesize that forelimb reduction in tyrannosauroids may not have proceeded in a uniform fashion, but rather that the humerus (and perhaps radius and ulna) were shortened prior to the reduction in manus size. Although current character optimizations support such a scenario, it is difficult to rigorously test this hypothesis at present, since complete (or near-complete) forelimbs of other “intermediate tyrannosauroids” phylogenetically proximal to *Dryptosaurus* are unknown (e.g., *Appalachiosaurus*, *Eotyrannus*, *Xiongguanlong*).

Similarly, the function of the bizarre forelimb proportions of *Dryptosaurus* is mysterious. At the most basic level, it appears as if both the skull and hands were important weapons for prey acquisition and processing in *Dryptosaurus*, unlike the condition in coeval western North American tyrannosaurids in which only the skulls were likely used as predatory armaments (e.g., Lipkin and Carpenter, 2009). However, it is worth noting that much of the skull is unknown in *Dryptosaurus*, and the few skull fragments exhibit some features unlike those of large-skull, short-armed tyrannosaurids (e.g., ziphodont teeth, more delicately constructed maxilla and dentary). Similarly, although the hand of *Dryptosaurus* is large, the ungual flexor tubercles and degree of curvature are reduced compared to more basal tyrannosauroids, indicating a loss of some grasping ability. In sum, neither the skull nor hands of *Dryptosaurus* were

as well developed for predatory function as in derived tyrannosaurids and basal tyrannosauroids, respectively. Regardless, it is clear that *Dryptosaurus* possessed a different set of predatory features than contemporary derived tyrannosaurids, which may suggest a difference (perhaps subtle) in ecology between these animals. It is hoped that future discoveries of related taxa and more detailed biomechanical studies may shed light on the unusual forelimb and ecology of *Dryptosaurus*.

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REFERENCES

- Averianov, A.O., S.A. Krasnolutskii, and S.V. Ivantsov. 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute RAS* 314: 42–57.
- Baird, D., and J. Horner. 1979. Cretaceous dinosaurs (Reptilia) of North Carolina. *Brimleyana* 2: 1–18.
- Benson, R.B.J. 2008. New information of *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology* 28: 732–750.
- Benson, R.B.J. 2009. An assessment of variability in theropod dinosaur remains from the Bathonian (Middle Jurassic) of Stonesfield and New Park Quarry and taxonomic implications for *Megalosaurus bucklandii* and *Iliosuchus incognitos*. *Palaeontology* 52: 857–877.
- Benson, R.B.J. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* 158: 882–935.
- Benson, R.B.J., and X. Xu. 2008. The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashuikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People's Republic of China. *Geological Magazine* 145: 778–789.
- Benson, R.B.J., S.L. Brusatte, S. Hutt, and D. Naish. 2009. A new large basal tetanuran (Dinosauria: Theropoda) from the Wessex Formation (Barremian) of the Isle of Wight, England. *Journal of Vertebrate Paleontology* 29: 612–615.
- Benson, R.B.J., P.M. Barrett, T.H. Rich, and P. Vickers-Rich. 2010a. A southern tyrant reptile. *Science* 327: 1613.

- Benson, R.B.J., M.T. Carrano, and S.L. Brusatte. 2010b. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97: 71–78.
- Bever, G.S., and M.A. Norell. 2009. The perinate skull of *Byronosaurus* (Troodontidae) with observations on the cranial ontogeny of paravian theropods. *American Museum Novitates* 3657: 1–51.
- Brochu, C.A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir* 7: 1–138.
- Brusatte, S.L., R.B.J. Benson, T.D. Carr, T.E. Williamson, and P.C. Sereno. 2007. The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology* 24: 1052–1056.
- Brusatte, S.L., R.B.J. Benson, and S. Hutt. 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Monograph of the Palaeontographical Society* 162 (631): 1–166.
- Brusatte, S.L., T.D. Carr, G.M. Erickson, G.S. Bever, and M.A. Norell. 2009. A long-snouted, multi-horned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences (USA)* 106: 17261–17266.
- Brusatte, S.L., et al. 2010. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329: 1481–1485.
- Carpenter, K., and M. Smith. 2001. Forelimb osteology and biomechanics of *Tyrannosaurus rex*. In D.H. Tanke and K. Carpenter (editors), *Mesozoic vertebrate life*: 90–116. Bloomington: Indiana University Press.
- Carpenter, K., C. Miles, and K. Cloward. 2005a. New small theropod from the Upper Jurassic Morrison Formation of Wyoming. In K. Carpenter (editor), *The carnivorous dinosaurs*: 23–48. Bloomington: Indiana University Press.
- Carpenter, K., C. Miles, J. H. Ostrom, and K. Cloward. 2005b. Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. In K. Carpenter (editor), *The carnivorous dinosaurs*: 49–71. Bloomington: Indiana University Press.
- Carpenter, K.D., D. Russell, D. Baird, and R. Denton. 1997. Redescription of the holotype of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) from the Upper Cretaceous of New Jersey. *Journal of Vertebrate Paleontology* 17: 561–573.
- Carr, T.D. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology* 19: 497–520.
- Carr, T.D., and T.E. Williamson. 2010. *Bistahieversor sealeyi*, gen. et sp. nov. a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidea. *Journal of Vertebrate Paleontology* 30: 1–16.
- Carr, T.D., T.E. Williamson, and D.R. Schwimmer. 2005. A new genus and species of tyrannosauroid from the Late Cretaceous (Middle Campanian) Demopolis Formation of Alabama. *Journal of Vertebrate Paleontology* 25: 119–143.
- Carrano, M.T., and J.R. Hutchinson. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology* 253: 207–228.
- Charig, A.J., and A.C. Milner. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum London (Geology)* 53: 11–70.
- Cope, E. 1866. Remarks on the remains of a gigantic extinct dinosaur from the Cretaceous Greensand of New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia* 18: 275–279.

- Cope, E. 1867. Remarks on extinct reptiles which approach birds. *Proceedings of the Academy of Natural Sciences of Philadelphia* 19: 234–235.
- Cope, E. 1868a. On some Cretaceous Reptilia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 30: 233–242.
- Cope, E. 1868b. On the genus *Laelaps*. *American Journal of Science* 46: 415–417.
- Cope, E. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society* 14: 1–252.
- Currie, P.J. 2003a. Cranial anatomy of tyrannosaurid dinosaurs from the late Cretaceous Alberta, Canada. *Acta Palaeontologica Polonica* 48: 191–226.
- Currie, P.J. 2003b. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences* 40: 651–665.
- Currie, P.J., J.K. Rigby, Jr., and R.E. Sloan. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In K. Carpenter and P.J. Currie (editors), *Dinosaur Systematics: Perspectives and Approaches*: 107–125. Cambridge: Cambridge University Press.
- Gallagher, W.B. 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coastal Plain. *The Mosasaur: Journal of the Delaware Valley Paleontological Society* 5: 75–155.
- Galton, P.M., and J.A. Jensen. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geology Studies* 26: 1–12.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8: 1–55.
- Gilmore, C.W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* 60: 1–154.
- Gilmore, C.W. 1946. A new carnivorous dinosaur from the Lance Formation of Montana. *Smithsonian Miscellaneous Collections* 106: 1–19.
- Göhlich, U.B., and L.M. Chiappe. 2006. A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* 440: 329–332.
- Hay, O. 1902. Bibliography and catalogue of the fossil vertebrates of North America. *U.S. Geological Survey Bulletin* 179: 1–868.
- Holtz, T.R. 1995. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology* 14: 480–519.
- Holtz, T.R. 2001. The phylogeny and taxonomy of the Tyrannosauridae. In D.H. Tanke and K. Carpenter (editors), *Mesozoic vertebrate life*: 64–83. Bloomington: Indiana University Press.
- Holtz, T.R. 2004. Tyrannosauroidae. In D. B. Weishampel, P. Dodson, and H. Osmólska (editors), *The Dinosauria*, 2nd ed.: 111–136. Berkeley: University of California Press.
- Huene, F. von. 1914. Das natürliche System der Saurischia. *Zentralblatt Mineralogie, Geologie, und Palaeontologie B* 1914: 154–158.
- Huene, F. von. 1926. The carnivorous Saurischia in the Jura and Cretaceous formations principally in Europe. *Revista del Museo de La Plata* 29: 35–167.
- Huene, F. von. 1932. Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* (Ser. 1) 4: 1–361.
- Hurum, J.H., and K. Sabath. 2003. Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica* 48: 161–190.
- Hutchinson, J.R. 2001. The evolution of pelvic osteology and soft tissue on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131: 123–168.

- Hutt, S., D.W. Naish, D.M. Martill, M.J. Barker, and P. Newberry. 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research* 22: 227–242.
- Hwang, S.H., M.A. Norell, Q. Ji, and K.-Q. Gao. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaeontology* 2: 13–30.
- Irmis, R.B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* 27: 350–361.
- Ji, Q., S.-A. Ji, and L.-J. Zhang. 2009. First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. *Geological Bulletin of China* 28: 1369–1374.
- Ji, Q., et al. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. *American Museum Novitates* 3420: 1–19.
- Kammerer, C.F., and K.D. Angielczyk. 2009. A proposed higher taxonomy of anomodont therapsids. *Zootaxa* 2018: 1–24.
- Kobayashi, Y., and R. Barsbold. 2005. Reexamination of a primitive ornithomimosaur, *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences* 42: 1501–1521.
- Kobayashi, Y., and J.-C. Lu. 2003. A new ornithomimid dinosaurian with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica* 48: 235–259.
- Kuhn, O. 1965. Saurischia. *Fossilium Catalogus* 109: 1–94.
- Lambe, L.M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus*. *Memoirs of the Geological Survey of Canada* 100: 1–84.
- Landman, N.H., R.O. Johnson, and L.E. Edwards. 2004. Cephalopods from the Cretaceous/Tertiary boundary interval on the Atlantic coastal plain, with a description of the highest ammonite zones in North America. Part 2. Northeastern Monmouth County, New Jersey. *Bulletin of the American Museum of Natural History* 287: 1–107.
- Leidy, J. 1856. Notice of remains of extinct reptiles and fishes discovered by Dr. F. V. Hayden in the badlands of the Judith River, Nebraska Territory. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 72–73.
- Leidy, J. 1868. Remarks on a jaw fragment of *Megalosaurus*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 18: 197–200.
- Li, D., M.A. Norell, K. Gao, N.D. Smith, and P.J. Makovicky. 2010. A longirostrine tyrannosauroid from the Early Cretaceous of China. *Proceedings of the Royal Society Series B* 277, 183–190.
- Lipkin, C., and K. Carpenter. 2009. Looking again at the forelimb of *Tyrannosaurus rex*. In P. Larson and K. Carpenter (editors), *Tyrannosaurus rex: the tyrant king*: 167–190. Bloomington: Indiana University Press.
- Lydekker, R. 1888. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part 1. 309 pp.
- Madsen, J.H. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin* 109: 1–163.
- Makovicky, P.J., M.A. Norell, J.M. Clark, and T. Rowe. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402: 1–32.
- Maleev, E.A. 1974. [Gigantic carnivores of the family Tyrannosauridae]. *Joint Soviet-Mongolian Palaeontological Expedition Transactions* 1: 132–191. [in Russian, English summary]
- Marsh, O.C. 1877. Notice of a new and gigantic dinosaur. *American Journal of Science* 114: 87–88.

- Marsh, O.C. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science (Ser. 3) 21: 417–423.
- Marsh, O.C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. American Journal of Science 39: 418–426.
- Marsh, O.C. 1896. The dinosaurs of North America. U.S. Geological Survey, 16th Annual Report: 133–230.
- Molnar, R.E. 1980. An albertosaur from the Hell Creek Formation of Montana. Journal of Paleontology 54: 102–108.
- Molnar, R.E. 1990. Problematic Theropoda. In D. B. Weishampel, P. Dodson, and H. Osmólska (editors), The Dinosauria: 306–317. Berkeley: University of California Press.
- Molnar, R.E. 1991. The cranial morphology of *Tyrannosaurus rex*. Palaeontographica Abteilung A Palaeozoologie-Stratigraphie 217: 137–176.
- Norell, M.A., et al. 2006. A new dromaeosaurid theropod from Ukhaa Tolgod (Ömnögov, Mongolia). American Museum Novitates 3545: 1–51.
- Norell, M.A., et al. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). American Museum Novitates 3654: 1–63.
- Olsson, R.K. 1960. Foraminifera of latest Cretaceous and earliest Tertiary age in the New Jersey coastal plain. Journal of Paleontology 34: 1–58.
- Olsson, R.K. 1963. Latest Cretaceous and earliest Tertiary stratigraphy of New Jersey coastal plain. American Association of Petroleum Geologists Bulletin 47: 643–665.
- Olsson, R.K. 1987. Cretaceous stratigraphy of the Atlantic coastal plain, Atlantic highlands of New Jersey. Geological Society of America Centennial Field Guide–Northeastern Section: 87–90.
- Osborn, H.F. 1902. On the Vertebrata of the mid-Cretaceous of the Northwest Territory. Distinctive characters of the mid-Cretaceous fauna. Contributions to Canadian Palaeontology 3: 1–21.
- Osborn, H.F. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. Bulletin of the American Museum of Natural History 21 (14): 259–265.
- Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Bulletin of the Peabody Museum of Natural History 30: 1–165.
- Ostrom, J.H. 1978. The osteology of *Compsognathus longipes* Wagner. Zitteliana 4: 73–118.
- Parks, W.A. 1928. *Albertosaurus arctunguis*, a new species of theropodous dinosaur from the Edmonton Formation of Alberta. University of Toronto Studies Geological Series 25: 3–42.
- Peyer, K. 2006. A reconsideration of *Compsognathus* from the Upper Tithonian of Canjuers, southeastern France. Journal of Vertebrate Paleontology 26: 879–896.
- Rauhut, O.W.M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69: 1–213.
- Rauhut, O.W.M., and X. Xu. 2005. The small theropod dinosaurs *Tugulusaurus* and *Phaedrolosaurus* from the Early Cretaceous of Xinjiang, China. Journal of Vertebrate Paleontology 25: 107–118.
- Rauhut, O.W.M., A.C. Milner, and S. Moore-Fay. 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. Zoological Journal of the Linnean Society 158: 155–195.
- Romer, A.S. 1956. Osteology of the reptiles. Chicago: University of Chicago Press.
- Romer, A.S. 1966. Vertebrate paleontology. Chicago: University of Chicago Press.
- Russell, D.A. 1970. Tyrannosauroids from the Late Cretaceous of western Canada. National Museum of Natural Science (Ottawa) Publications in Paleontology 1: 1–34.

- Sereno, P.C., S. McAllister, and S.L. Brusatte. 2005. TaxonSearch: a relational database for documenting taxa and their phylogenetic definitions. *Phyloinformatics* 8: 1–21.
- Sereno, P.C., et al. 2009. Tyrannosaurid skeletal design first evolved at small body size. *Science* 326: 418–422.
- Smith, A.G., D.G. Smith, and B.M. Funnell. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge: Cambridge University Press.
- Smith, J.B. 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* 8: 103–126.
- Snively, E., A.P. Russell, and G.L. Powell. 2004. Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric and phylogenetic approaches. *Zoological Journal of the Linnean Society* 142: 525–553.
- Spamer, E.E., E. Daeschler, and L.G. Vostreys-Shapiro. 1995. A study of fossil vertebrate types in the Academy of Natural Sciences of Philadelphia. Special Publication 16, Academy of Natural Sciences of Philadelphia.
- Steel, R. 1970. Saurischia. *Handbuch der Paläoherpetologie* 16: 1–84.
- Welles, S.P., and R.A. Long. 1974. The tarsus of theropod dinosaurs. *Annals of the South African Museum* 64: 191–218.
- White, T. 1973. Catalogue of the genera of dinosaurs. *Annals of Carnegie Museum* 44: 117–155.
- Xu, X., et al. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431: 680–684.
- Xu, X., et al. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* 439: 715–718.

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