The Cranial Pneumatic Sinuses of the Tyrannosaurid Alioramus (Dinosauria: Theropoda) and the Evolution of Cranial Pneumaticity in Theropod Dinosaurs

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The cranial pneumatic sinuses of the tyrannosaurid *Alioramus* (Dinosauria: Theropoda) and the evolution of cranial pneumaticity in theropod dinosaurs

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ABSTRACT

Archosaurs and mammals exhibit skeletal pneumaticity, where bone is infilled by air-filled soft tissues. Some theropod dinosaurs possess extensively pneumatic skulls in which many of the individual bones are hollowed out by diverticula of three main cranial sinus systems: the paranasal, suborbital, and tympanic sinuses. Computed tomography (CT scanning) permits detailed study of the internal morphology of cranial sinuses. But only a few theropod specimens have yet been subjected to this type of analysis. We present CT scans of the remarkably preserved and disarticulated skull bones of the long-snouted tyrannosaurid theropod *Alioramus*. These scans indicate that *Alioramus* has extensive cranial pneumaticity, with pneumatic sinuses invading the maxilla, lacrimal, jugal, squamosal, quadrate, palatine, ectopterygoid, and surangular. Pneumaticity is not present, however, in the nasal, postorbital, quadratojugal, pterygoid, or angular. Comparisons between *Alioramus* and other theropods (most importantly the closely related *Tyrannosaurus*) show that the cranial sinuses of *Alioramus* are modified to fill the long-snouted skull of this taxon, and that *Alioramus* has an extreme degree of cranial pneumaticity compared to other theropods, which may be the result of the juvenile status of the specimen, a difference in feeding style between *Alioramus* and other theropods, or passive processes. Based on these comparisons, we provide a revised terminology of cranial pneumatic structures and review the distribution, variation, and evo-

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lution of cranial pneumaticity within theropod dinosaurs. This review illustrates that most theropods possess a common "groundplan" in which the maxilla and lacrimal are pneumatized, and that various theropods modify this groundplan by pneumatizing numerous other bones of the skull. Tyrannosaurids are very pneumatic compared to other theropods, particularly in the development of extensive ectopterygoid, quadrate, and palatine sinuses, as well as a pneumatic invasion into the surangular. Tyrannosauroids seem to retain many cranial sinuses, such as the jugal and nasal recesses, which are primitive for coelurosaurs but lost or apomorphically modified in taxa more closely related to birds.

INTRODUCTION

Archosaurs and mammals are unusual among vertebrates in exhibiting skeletal pneumaticity: the invasion of bone by air-filled epithelial diverticula (e.g., Müller, 1908; King, 1966; Duncker, 1971; Witmer, 1990, 1997a, 1997b; Britt, 1993, 1997; Koppe et al., 1999; O'Connor, 2004, 2006; Benson et al., 2012; Butler et al., 2012). Among archosaurs, some theropod dinosaurs possess an extreme degree of cranial pneumaticity, where individual bones of the skull are largely hollowed out by air-filled sinuses. The complex array of theropod cranial sinuses can be organized into several major systems: the paranasal sinuses (which are diverticula of the nasal passage), the suborbital sinuses (which are closely related to the paranasal system), the tympanic sinuses (which originate from the inner ear), (Witmer, 1997b; Witmer and Ridgely, 2008; other sinuses relating to the median pharyngeal system and cervical air sacs, which pneumatize the braincase, are not discussed in detail here). The function of these sinuses is not always clear. The paranasal and suborbital sinuses may influence respiration and physiology, and the tympanic sinuses may be associated with hearing and balance, but it is also thought that the size, shape, and extent of the sinuses may largely result from opportunistic invasion of bone by soft tissue (e.g., Witmer, 1997a).

Regardless of their exact functions, cranial pneumatic sinuses often leave bony correlates on theropod skulls. These correlates include the hollowed out internal sinuses, as well as the foramina and fenestrae that lead into the sinuses and, in some cases, smooth fossae on the external bone surfaces where a soft-tissue sinus (airsac) would have lain against the bone. Because pneumatic fossae, foramina, fenestrae, and sinuses are so widespread and variable among theropods, they often form the basis for phylogenetic characters that are instrumental in elucidating the phylogenetic relationships of theropods (e.g., Turner et al., 2012). This is particularly true for the derived theropod subgroup Coelurosauria—birds and their closest relatives—because many pneumatic features originated and changed during the evolution of early birds and their theropod antecedents.

Cranial pneumaticity can often be identified on theropod specimens by observation of large foramina or fenestrae leading into internal sinuses. These observations form the basis for most morphological descriptions of theropod pneumaticity, as well as the delimitation of most phylogenetic characters. However, external observations of specimens provide little information on the size, shape, and extent of the internal sinuses. Furthermore, small pneumatic foramina or other subtle signs of pneumaticity can easily be missed if the external bone

surface is poorly preserved. This raises a pressing concern: our understanding of cranial sinus morphology may be extremely limited if we rely on external observation of specimens alone. As a result, phylogenetic character statements and scores based on such observations may be misleading or incorrect.

Computed tomography (CT) scanning is a more refined approach, allowing the internal morphology of theropod skulls to be imaged and studied in detail (e.g., Carlson et al., 2003; Witmer et al., 2008). Although CT scanning has become a standard tool in paleontology, most CT-based studies of theropod dinosaurs have focused on the morphology of the brain, inner ear, cranial nerves, and tympanic sinuses of the braincase region (e.g., Rogers, 1998; Larsson et al., 2000; Brochu, 2000, 2003; Franzosa and Rowe, 2005; Sanders and Smith, 2005; Sampson and Witmer, 2007; Balanoff et al., 2009; Norell et al., 2009; Witmer and Ridgely, 2009; Zelenitsky et al., 2009; Bever et al., 2011, 2013; Lautenschlager et al., 2012). Less work has focused on the remainder of skull, including the morphology of the paranasal, suborbital, and nonbraincase tympanic sinuses. The cranial pneumaticity of a select handful of theropods has been studied in detail (e.g., Brochu, 2003; Witmer and Ridgely, 2008, 2009; Tahara and Larsson, 2011), but additional well-preserved exemplar specimens must be subjected to CT scanning to better understand the range of sinus morphology and variation in theropods.

We use CT data to describe cranial pneumaticity in a spectacularly preserved specimen of the long-snouted tyrannosaurid theropod *Alioramus altai* (IGM 100/1844; Brusatte et al., 2009, 2012; Bever et al., 2011, 2013). The excellent preservation, relative completeness, and complete disarticulation of the cranial bones of IGM 100/1844 allow for a detailed look at the cranial sinuses and thorough comparison to other theropods that have been the subject of CT study. This specimen also offers unique insight into theropod cranial sinus morphology because it belongs to a subadult individual with a peculiar longirostrine morphology. Therefore, comparisons between the pneumatic patterns in this specimen and other theropods may inform how pneumaticity changes through ontogeny and whether taxa that have undergone extreme morphological changes (e.g., evolution of a long snout) also experience changes in internal sinus morphology.

We describe the pneumatic features of each bone of the *Alioramus altai* skull based on a series of CT scans of IGM 100/1844. We make comparisons with other taxa where CT data is available, most notably the closely related *Tyrannosaurus rex* (Brochu, 2003; Witmer and Ridgely, 2008). We then discuss the distribution and evolution of cranial pneumatic features in theropods within a phylogenetic context. This review illustrates that most theropods share a common "groundplan" in which the maxilla and lacrimal are pneumatized by diverticula from the antorbital sinus of the paranasal sinus system. Various theropods exhibit numerous variations on this architecture, including the development of sinuses invading the jugal, nasal, squamosal, palatine, ectopterygoid, quadrate, articular, and surangular. Tyrannosaurids such as *Alioramus* are among the most extensively pneumatic of all theropods, and seem to retain many cranial sinuses that are primitive for coelurosaurian theropods but lost or modified in taxa more closely related to birds.

Institutional Acronyms

AMNH   American Museum of Natural History, New York, NY
BMR   Burpee Museum of Natural History, Rockford, IL
CM   Carnegie Museum of Natural History, Pittsburgh, PA
CMNH   Cleveland Museum of Natural History, Cleveland, OH
IGM   Institute of Geology, Ulaanbaatar, Mongolia
ZPAL   Institute of Paleobiology, Polish Academy of Science, Warsaw, Poland

MATERIALS AND METHODS

The disarticulation of the skull of IGM 100/1844 allows each bone to be analyzed separately with high resolution X-ray computed tomography (CT scans). The bones were scanned in a GE phoenix v|tome|x CT scanner at the American Museum of Natural History Microscopy and Imaging Facility. In total, 13 elements were scanned with the following general settings: voltage between 140 and 210 kV, amperage between 125 and 175 µA, and a slice thickness ranging from 0.09 to 0.14 mm (for specific element scan settings, see table 1). Each element was analyzed with Visual Graphics Studio Max 2.2, and the region growing and pen tools were used to seperate out the interior pneumatic regions. Those regions were then colored, using the same color scheme as Witmer and Ridgely (2008). Each pneumatic region was compared to corresponding regions in tyrannosauroids and other theropods.

Sinus volumes were calculated using the volume calculation tool in Visual Graphics Studio Max (table 2). Many of these volumes are slightly overestimated due to the inclusion of pneumatic foramina (the external openings leading into sinuses) in the volume measurements. The antorbital sinus (which is bounded by many bones and not located within a single bone) was filled in entirely by eye, mainly as a visualization tool; however, its volume is included here for general reference. The squamosal sinus, which is located on the ventral surface of the squamosal and not entirely within the bone, was also filled in. The shape of this sinus was inferred from the deep pocket formed by the three processes of the squamosal and the location of the foramina on the ventral side of the dorsal ramus. In rare cases, as with the ectopterygoid, the bone is slightly crushed, so the volume of the internal sinus may represent an underestimate. In such cases, however, differences between the measured volumes and genuine volumes would be minimal, and we hold that the volumes presented here are accurate for the specimen as preserved and are valuable for comparison purposes.

TERMINOLOGY

In this paper, we use a consistent terminology to refer to the pneumatic space within a bone and the openings on the external surfaces of bones that lead into this internal space. The internal space is referred to as a *sinus*. For example, the space within the jugal is called the *jugal sinus*. For descriptive purposes these sinuses are sometimes also referred to as *recesses, cavities,* or *antra*, and if they are connected to a larger sinus they may be referred to as a *diverticulum*

TABLE 1. Scanning parameters for each bone of *Alioramus altai*.

Bone	Side	Voltage (kV)	Amperage (μA)	Voxel size	Number of slices
Angular	Right	155	175	0.1107	1913
Ectopterygoid	Right	170	160	0.1071	1450
Jugal	Left	155	175	0.1416	1774
Lacrimal	Left	200	170	0.1224	1804
Larcimal	Right	155	125	0.1137	1860
Maxilla	Left	190	150	0.1418	1872
Nasals	Unpaired	215	180	0.1141	3573
Palatine	Left	170	160	0.1037	1860
Pterygoid	Right	155	175	0.1348	1897
Quadrate	Left	210	150	0.1318	1276
Quadrate	Right	190	135	0.1267	1251
Squamosal + postorbital	Right	190	135	0.0903	1806
Squamosal	Left	210	150	0.0991	1381
Surangular	Left	170	160	0.1071	2422

TABLE 2. Volume of each cranial sinus in *Alioramus altai* calculated using VG Studio Max.

Bone	Sinus volume (mm³)	Sinus volume (cm³)	Sinus volume in *T. rex* (cm³)[*]
Maxillary[1]	23527	23.527	7772.5
Antorbital	229533.6	229.5	6766.1
Lacrimal (L)	11843.28	11.843	1177.1
Lacrimal (R)	15053.64	15.054	1177.1
Jugal	9059.70	9.059	1031.3
Palatine	4146.78	4.146	1082.5
Squamosal	1381.08	1.381	1377.4
Quadrate (L)	23158.917	23.159	482.1
Quadrate (R)	17955.61	17.956	–
Ectopterygoid	22184.77	22.185	1641.3

[1] Combined volume measurement for promaxillary sinus and maxillary antrum.
[*] From Witmer and Ridgely, 2008.

(for example, the jugal sinus is a diverticulum of the larger antorbital sinus). Most sinuses fill the interior of bones, but the antorbital sinus itself lies on the lateral surface of the upper jaw and the squamosal sinus is located on the ventral surface of the bone and extends only slightly into the bone interior. The external openings that lead into the sinuses are referred to as *pneumatic fenestrae* or *pneumatic foramina*. The distinction between a fenestra and a foramen is largely subjective, with a fenestra usually referring to a larger, windowlike opening and a foramen to a smaller hole. Sometimes *foramina* is specifically used to refer to passages through which structures, like blood vessels and nerves, pass, whereas *fenestra* indicates a larger open-

ing, but this distinction is often difficult to make without specific knowledge of cranial nerves and vasculature. For the sake of simplicity, the term *pneumatic* is sometimes dropped when referring to the fenestrae and foramina in this paper (for instance, we use the term *maxillary fenestra* not *maxillary pneumatic fenestra*).

This terminology is generally consistent to that used by Witmer (1997a, 1997b), Witmer and Ridgely (2008), and previous authors who have studied the cranial sinuses of archosaurs. However, there is some confusion in the literature, especially with the term *recess*. For example, the Theropod Working Group research team (TWiG) has sometimes written phylogenetic characters in which the external fenestra leading into a sinus has been called a *recess* (e.g., Brusatte et al., 2010a: char. 67). Usually these characters relate to the position or shape of the fenestra and not to the position or shape of the internal sinus itself, so they can be particularly confusing. We rectify this situation here with consistent terminology.

Regions of pneumaticity in the skull take two general forms (Witmer, 1997a). First, some pneumatic air sacs lie against the external surface of the bone, and leave a characteristic fossa or depression on the bone surface. An example of this is the antorbital sinus, which abuts the lateral surface of the snout, within the broad antorbital fossa. Second, and more common, are internal sinuses within bones that are connected to the bone exterior via one or more fenestrae or foramina. These sinuses may have one or multiple chambers and are sometimes finely divided by internal laminae. An example of this is the sinus within the quadrate. These regions of pneumaticity are identified by the characteristic morphology of large external fenestrae or foramina leading into an interior cavity. This is also the diagnostic combination that allows for the unequivocal identification of postcranial skeletal pneumaticity in the vertebrae, ribs, and other bones of archosaurs (e.g., Britt, 1993; O'Connor, 2006; Wedel, 2007; Benson et al., 2012; Butler et al., 2012).

RESULTS

General Skull

The antorbital sinus—one of the major anatomical features shared by archosaurs—is a large paranasal air sinus positioned between the orbit and the external naris (Witmer, 1997a, 1997b). In *Alioramus*, as in most other theropods and many other archosaurs, this sinus is an extensive feature that occupies much of the lateral aspect of the snout. The antorbital sinus is not enclosed within bone, but rather is located between the maxilla, lacrimal, jugal, and palatine. It would have been covered laterally by skin (and perhaps other soft tissues) in life, as is normal for most archosaurs (Witmer, 1997a, 1997b).

The position of the sinus is marked by the antorbital fossa, as the antorbital air sac (paranasal air sinus) would have sat against the smooth surface of the fossa in life. The shape of the fossa, and thus the antorbital sinus, mirrors the elongation of the snout in being dorsoventrally low and rostrocaudally elongate. The fossa covers much of the lateral surface of the maxilla, including much of the region rostral to the antorbital fenestra and much of the ascending ramus dorsally and main (alveolar) body ventrally. Therefore, the maxilla would have formed the rostral and much of the dorsal and ventral borders of the antorbital sinus. Ventrally, on the main body of the bone, the antorbital fossa is deeply invaginated as a channel that extends

rostrocaudally. Thus, the ventral part of the sinus would have sat within this channel in life. The fossa also extensively excavated much of the rostral ramus and main body of the lacrimal and the rostral region of the jugal. Correspondingly, the lacrimal would have comprised its caudoventral border. Finally, much of the lateral surface of the palatine is covered by the antorbital fossa, meaning that this bone would have comprised some of the medial and ventral border of the antorbital sinus.

The antorbital sinus sends numerous diverticula into the surrounding elements (Witmer, 1997a, 1997b; Witmer and Ridgely, 2008). These accessory sinuses often hollow out large portions of these bones. Among these are two discrete sinuses in the maxilla (the promaxillary sinus and the maxillary antrum), a chamber within the lacrimal (which may be confluent with a second, smaller medial lacrimal sinus), the jugal recess, and a sinus within the palatine (which is a caudal extension of the maxillary antrum). Additionally, as discussed by Witmer (1997a, 1997b) and Witmer and Ridgely (2008), there is probably a suborbital sinus that extends caudally and ventrally from the antorbital sinus into the orbit. This sinus is difficult to confirm, much less describe, because it likely was bounded almost entirely by soft tissue. However, it is possible that the suborbital sinus may be the source of diverticula leading into the squamosal and/or ectopterygoid (Witmer and Ridgely, 2008).

Maxilla

Both left and right maxillae are preserved as disarticulated bones in the IGM 100/1844, but only the left maxilla was CT scanned here, as it is more complete, better preserved, and substantially less deformed than the right (fig. 1; Brusatte et al., 2012). The left maxilla is nearly complete, and even retains most of the thin, fragile medial bounding wall of the maxillary antrum and promaxillary sinus (the two main accessory chambers of the antorbital sinus that extend into the maxilla, rostral to the antorbital fenestra: Witmer, 1997a, 1997b). In contrast, this thin, bony flange is eroded or broken in nearly every other known tyrannosaurid maxilla (Witmer and Ridgely, 2008). Because this wall encloses the maxillary antrum and promaxillary sinus medially, the shape and volume of these sinuses can uniquely be studied in complete detail in IGM 100/1844.

As in *Tyrannosaurus* and most other nonavian tetanuran theropods, *Alioramus* possesses two separate diverticula extending from the antorbital sinus into the interior of the maxilla. These are the promaxillary sinus and maxillary antrum, which together are often referred to as the maxillary sinus (Witmer, 1997a, 1997b). More basal theropods, on the other hand, possess only a very small, single sinus within the maxilla. This condition is exemplified by the large abelisaurid *Majungasaurus* (Sampson and Witmer, 2007; Witmer and Ridgely, 2008). In *Alioramus*, *Tyrannosaurus*, and most other nonavian tetanurans, the diverticulum leading into the promaxillary sinus passes through the promaxillary fenestra and the connection with the maxillary antrum passes through the maxillary fenestra.

The promaxillary and maxillary fenestrae are features characteristic of the maxilla in most tetanurans and usually are small, subsidiary openings within the antorbital fossa, rostral to the antorbital fenestra (Witmer, 1997a). Their presence indicates that the promaxillary sinus and maxillary antrum, or some homologous feature, is also present even if CT data are not available

FIGURE 1. Left maxilla in lateral (A), medial (B), dorsal (C), and ventral (D) views. Left column shows antorbital sinus in approximate life position, with maxilla semitransparent. Middle column shows maxilla semitransparent without the antorbital sinus. Right column shows isolated maxillary sinus. Scale bar = 45 mm.

to confirm this. *Alioramus* has large, distinctive promaxillary and maxillary fenestrae (Brusatte et al., 2012), as do other tyrannosauroids (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003; Hurum and Sabath, 2003). Therefore, all known tyrannosauroids likely possess a promaxillary sinus and maxillary antrum, based on their possession of the corresponding fenestrae. The size, shape, and position of the fenestrae are highly variable among tyrannosauroids. This variability has been differentiated into several characters used in phylogenetic analyses (e.g., Holtz, 2001; Currie et al., 2003; Holtz, 2004; Sereno et al., 2009; Brusatte et al., 2010a; Carr and Williamson, 2010). These characters are not reviewed in detail here, but are discussed more thoroughly in Brusatte et al. (2012).

The promaxillary sinus of *Alioramus* is a large space occupying much of the interior of the maxilla rostral to the antorbital fossa. There is a wall of bone dorsal to the roots of the maxillary teeth that prevents the promaxillary sinus from communicating with the tooth crypts. From the dorsal edge of that bone wall, the promaxillary sinus extends dorsally, following the dorsal curvature of the maxilla until it reaches the interfenestral strut. The sinus is rostrocaudally broad, extending caudally from the rostral margin of the maxilla to the rostral edge of the antorbital fossa, where the promaxillary fenestra is positioned. Therefore, the promaxillary sinus is located strictly rostral and medial to the promaxillary fenestra. The medial surface of the rostral margin of the maxilla curves as it projects dorsally and is a very thin bone layer that has many medial openings. These openings may allow the promaxillary sinus to send narrow extensions into the premaxilla or the nasal passage. Neither premaxilla is preserved in IGM 100/1844, so any potential extensions of the promaxillary sinus into the premaxilla can only be inferred.

The long and extensive maxillary antrum is located ventral and caudal to the promaxillary sinus. The ventralmost edge of this sinus appears to penetrate the root of each tooth, extending into the alveoli in many cases along the tooth row. This may be an artifact of CT scanning, however, where adjacent structures look continuous. Therefore, the maxillary antrum may terminate prior to each tooth root. This is similar to the condition in *Tyrannosaurus*, in which "interalveolar recesses" extend ventrally from the maxillary sinus between the tooth crypts (Witmer, 1997a; Witmer and Ridgely, 2008). Ventrally, the maxillary antrum continues along the tooth row until the last maxillary tooth, penetrating into each alveolus. The maxillary antrum extends through the medial surface of the maxilla through an opening above the rostromedial process (which currently is unnamed), and also through an open channel ventromedial to the antorbital fossa.

Nasals

The nasals (fig. 2) are elongate and fused into a single, vaulted unit, as is normal for tyrannosaurids (e.g., Holtz, 2001; Snively et al., 2006). The ventral face forms the dorsal surface of the nasal airway. Both the internal and external morphology of the bone, however, demonstrate that the antorbital sinus and any associated diverticula were not associated with the nasal. The internal region of the bone lacks any pneumatic pockets, chambers, or sinuses. The external surface lacks any extension of the smooth antorbital fossa and any foramina or fenestrae (Brusatte et al., 2012). Both of these conditions are generally shared with other tyrannosaurids. Brochu (2003) and Witmer and Ridgely (2008) used CT data to confirm the lack of any internal
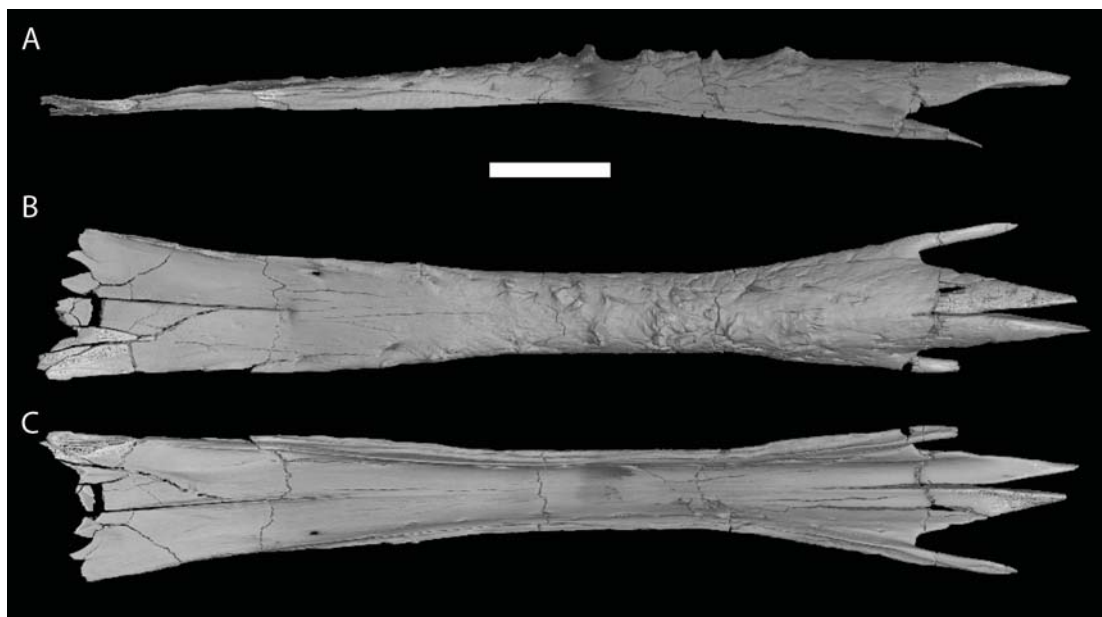
FIGURE 2. Nasals in lateral (A), dorsal (B), and ventral (C) views. Scale bar 45 mm.

cavities within the nasal of *Tyrannosaurus*. Most tyrannosaurid nasals also lack any trace of the antorbital fossa on the external surface, although some juvenile tyrannosaurids do exhibit a very narrow extension of the fossa (Carr, 1999).

The condition in more basal tyrannosauroids, however, is drastically different. The basal (non-tyrannosaurid) taxa *Dilong* (Xu et al., 2004), *Eotyrannus* (Hutt et al., 2001), *Guanlong* (Xu et al., 2006), and *Yutyrannus* (Xu et al., 2012) exhibit pneumatized nasals with internal cavities. These cavities communicate with the antorbital sinus via one or more pneumatic fenestrae, which are housed within an extension of the antorbital fossa that excavates part of the lateral surface of the nasal. The basal tyrannosauroid *Proceratosaurus* also appears to have internal nasal pneumaticity, based on CT data presented by Rauhut et al. (2010). Nasal pneumaticity is rare in coelurosaurs, but present in many non-coelurosaurian outgroups, such as allosauroids (e.g., *Allosaurus*: Madsen, 1976; *Neovenator*: Brusatte et al., 2008; *Sinraptor*: Currie and Zhao, 1993), ceratosaurs (e.g., *Majungasaurus*: Sampson and Witmer, 2007; Witmer and Ridgely, 2008), and *Monolophosaurus* (Brusatte et al., 2010b). The distribution of pneumaticity in theropod nasals indicates that it evolved early in theropod evolution and was secondarily lost in tyrannosauroids around the base of Tyrannosauridae (see Discussion). This indicates that the lack of pneumaticity in more-derived coelurosaurs is an independent loss and not primitive for Coeulurosauria.

Lacrimal

The lacrimal (figs. 3, 4) is extensively pneumatized internally by a single, large chamber, the lacrimal sinus (Witmer, 1997a, 1997b; Witmer and Ridgely, 2008). Numerous foramina on the lateral surface lead into this recess, including several within the antorbital fossa on the rostral ramus (the portion of the lacrimal roofing the antorbital fenestra, and thus the antorbital sinus

itself). The largest of these communicating foramina is a deep funnellike opening at the corner where the rostral and ventral rami of the lacrimal join, which would have been the caudodorsal corner of the antorbital fossa in life. This enormous opening is often called the *lacrimal recess* (e.g., Brusatte et al., 2012), although we have corrected this terminology here (see Terminology above).

The internal lacrimal sinus extends rostrally into the dorsal ramus to occupy at least half the length of the bone. The sinus tapers rostrally and mirrors the tapering of the dorsal ramus. The sinus also extends caudally into the small caudal ramus, a conical projection of bone that articulated against the frontal above the orbit. Ventrally, the lacrimal sinus descends for only a few millimeters below the lacrimal recess. Therefore, the majority of the ventral ramus is not hollowed out by an internal sinus. The ventral ramus of the left lacrimal does not enclose any sinuses whatsoever, although the bone becomes trabecular two thirds of the way down. This trabecular region terminates before the ventral edge of the element.

The morphology of the right lacrimal (fig. 3) is peculiarly different, as in this bone the ventral ramus contains a ventral projection of the lacrimal sinus. In other words, the lacrimal sinus extends further ventrally, deep into the ventral ramus, on the right side. This may indeed be an extension of the lacrimal sinus proper, or it could represent a modified medial lacrimal sinus, a separate diverticulum of the antorbital sinus that has been observed in CT scans of *Tyrannosaurus* by Brochu (2003) and Witmer and Ridgely (2008). If this is the medial lacrimal sinus, then *Alioramus* would exhibit two unusual conditions: (1) development of the medial lacrimal sinus on one side of the skull only; and (2) the merging of the medial lacrimal sinus with the lacrimal sinus. These variations in a single individual suggest caution should be used in diagnosing specimens based on these characters or using them in phylogenetic analyses.

Jugal

The jugal (fig. 5) is hollowed out by the jugal sinus (= "main posterior chamber" of Brusatte et al., 2012). This cavity is present in all known tyrannosauroids and many non-coelurosaurian theropods, but is generally rare among coelurosaurs (see Discussion). In *Alioramus* and other theropods with a jugal sinus, the sinus communicated with the antorbital fossa via the enlarged jugal foramen on the lateral surface of the bone. This foramen is located at the caudoventral corner of the antorbital fossa and has a complex shape that is described in detail by Brusatte et al. (2012). The jugal sinus extends caudally from the foramen to hollow out almost the entire rostrocaudal length of the bone, but is only about two thirds of the dorsoventral height. The sinus continues dorsally to the midpoint of the dorsal ramus and caudally toward the dorsal and ventral prongs of the caudal ramus. The jugal sinus is thin mediolaterally, reflecting the narrow morphology of the jugal compared to other tyrannosaurids (Witmer and Ridgely, 2008; Brusatte et al., 2012). Medioventral to the attachment point of the jugal horn, the ventral edge of the jugal sinus descends into the cornual process briefly before rising back to meet the more horizontal contour of the caudal process.

One of the most unusual features of *Alioramus* is the large, lateral, conical horn that extends laterally from the external surface of the jugal below the orbit (Brusatte et al., 2009; 2012). The jugal sinus expands ventral to the lateral jugal horn, but does not pneumatize the jugal horn itself. On the medial surface of the jugal there is another set of foramina: one large opening near the
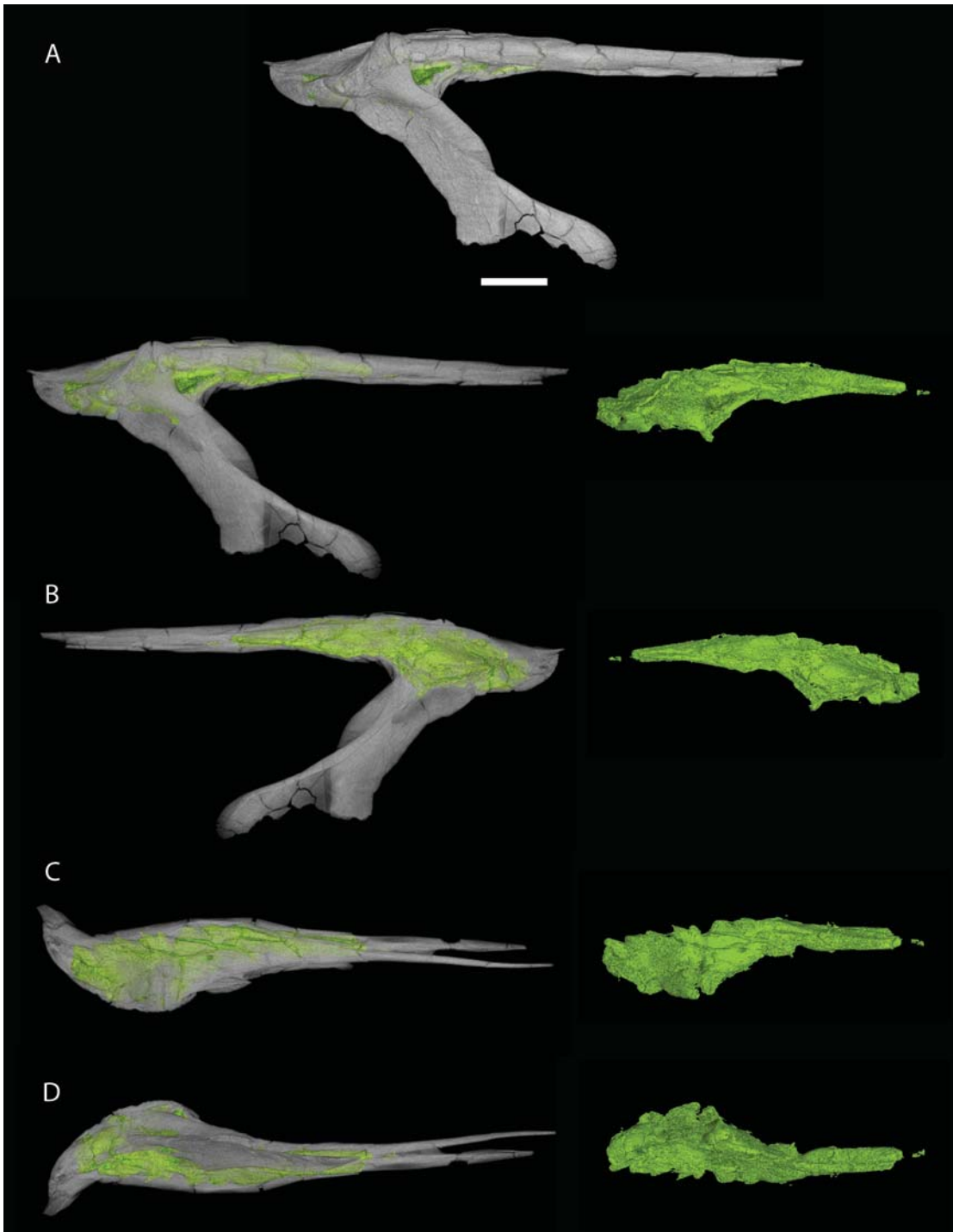
FIGURE 3. Right lacrimal in lateral (A), medial (B), dorsal (C), and ventral (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 25 mm.
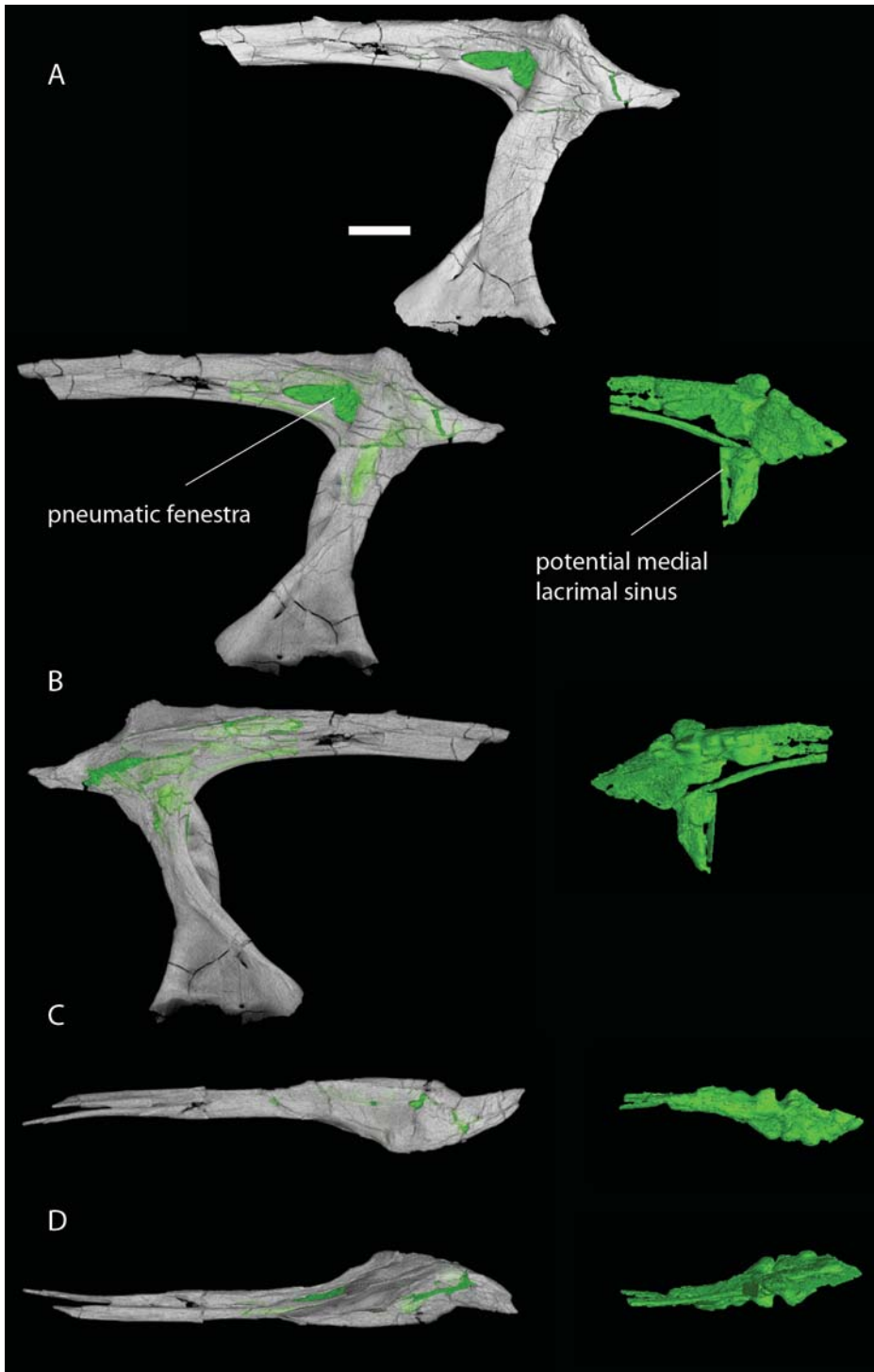
FIGURE 4. Left lacrimal (A), medial (B), dorsal (C), and ventral (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 25 mm.
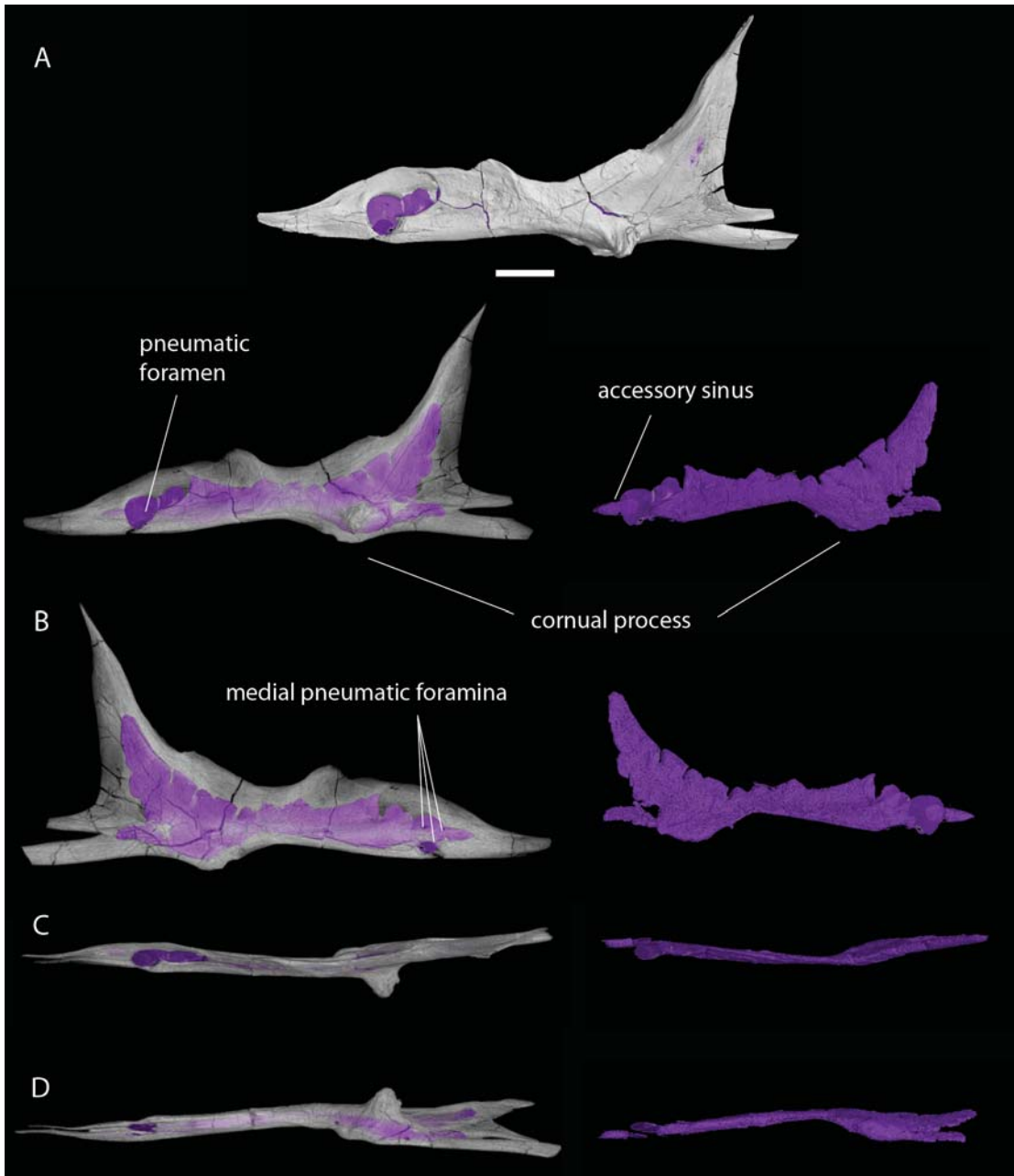
FIGURE 5. Left jugal in lateral (A), medial (B), dorsal (C), and ventral (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 25 mm.

rostral end of the element that is angled medioventrally, with a slight rostral tilt, and two smaller openings above the larger one, which sit on the shelf of bone on the medial surface of the jugal, ventral to the orbit. These foramina lead into the jugal sinus and have not been noted in other studies of tyrannosaurid cranial pneumaticity (Brochu, 2003; Witmer and Ridgely, 2008).
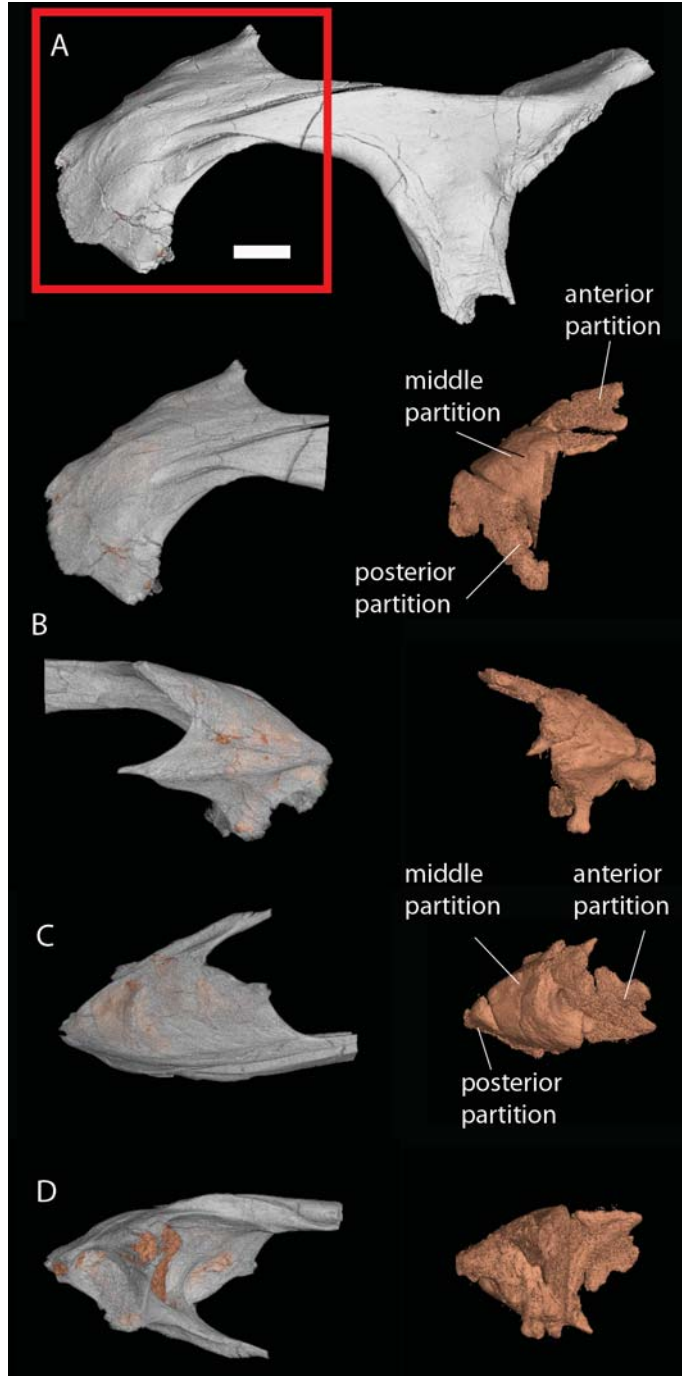
FIGURE 6. Squamosal and postorbital in lateral (A), medial (B), dorsal (C), and ventral (D) views. Red box in (A) shows location of images in (B), (C), and (D). Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 15 mm.

An accessory sinus proceeds from the jugal foramen rostrally into a small, shallow pocket. Because this accessory sinus is located rostral to the jugal foramen, it is not continuous with the jugal sinus proper. However, as both the main jugal sinus (caudally) and the accessory sinus (rostrally) are separated by the large pneumatic foramen, it is clear that they are both part of the same diverticulum from the antorbital sinus. The presence of an accessory rostral sinus is rare among tyrannosauroids, as reviewed by Brusatte et al. (2012), and does not appear to be present in *Tyrannosaurus* based on the CT scans of Witmer and Ridgely (2008), at least as a well-defined space that is clearly separated from the jugal sinus proper.

Postorbital

The postorbital (fig. 6) is surrounded by several highly pneumatic bones, including the lacrimal, squamosal, and jugal. However, the postorbital itself shows only a slightly trabecular interior, not a hollow sinus. This trabecular region is not connected to the external surface of the bone via any pneumatic foramina or fenestrae. This is not unexpected, as all known nonavian theropods lack postorbital pneumaticity (see Discussion).

Squamosal

The squamosal (fig. 6) has one, multilobed internal chamber: the squamosal sinus. This chamber is typical of many other tyrannosaurids (e.g., Brochu, 2003; Witmer and Ridgely, 2008; Brusatte et al., 2010a, 2012), but is unusual among theropods and its source is unclear (e.g., Currie and Zhao, 1993b; Witmer, 1997a, 1997b; Witmer and Ridgely, 2008; Tahara and Larsson, 2011). The sinus is housed mainly in the main body (dorsal portion) of the squamosal, and spreads laterally nearly to the postorbital contact. The sinus is divided into three main partitions, with the rostral section comprising three sublobes itself. The middle partition is the largest and the caudal section spreads into the caudal processes of the squamosal. The rostral partition is the most complex section of the sinus. Each of its three lobes is transversely oriented. Of the two caudalmost lobes, one extends laterally and one extends medially from their central meeting point. The rostralmost lobe extends rostrally, but also divides into two smaller lobes, with one extending rostrally, and the other extending medially.

There are three small pneumatic openings lying in the squamosal recess. The lateralmost opening is triangular and is located in the rostrodorsolateral area of the squamosal recess. It opens rostrally and leads into the rostral lobe. The second opening is larger and circular and opens dorsally into the middle lobe of the sinus. The third foramen is rectangular and also leads to the middle sinus lobe. Some erosion of the caudal process shows two passages from the caudal lobe of the squamosal sinus, which in life would have continued caudally to pneumatize the caudal process.

Brochu (2003) commented on the deep nature of the squamosal recess in the *Tyrannosaurus* specimen FMNH PR2081 and observed a single, oval perforation within it, but mentioned that no other tyrannosaurid seemed to show this opening. Therefore, *Alioramus* is unique among tyrannosaurids in having three small openings in the squamosal recess. The origin of the squamosal sinus is still unknown (Witmer, 1997a), and it is unclear whether it is a diverticulum of the tympanic or suborbital sinus, making morphological variation in this sinus shape among tyrannosaurids difficult to assess.
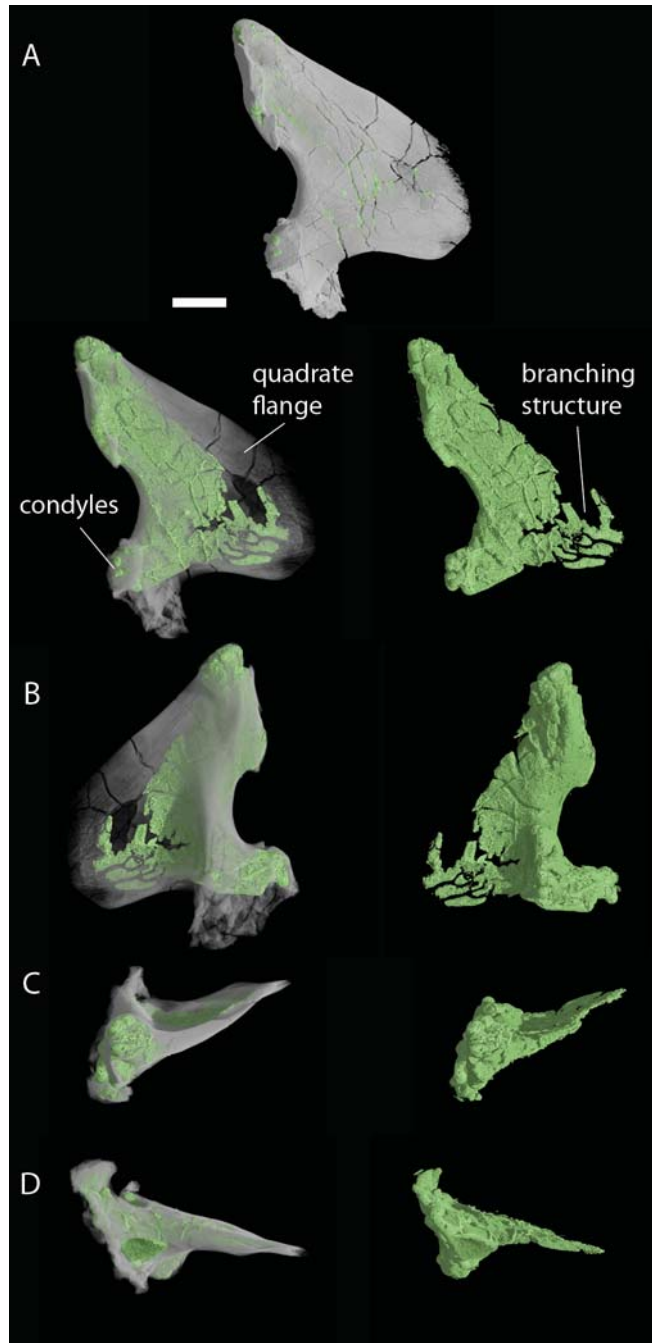
FIGURE 7. Right quadrate in lateral (A), medial (B), dorsal (C), and ventral (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 20 mm.

Quadrate

The quadrate (fig. 7) is extensively hollowed out by a series of interconnected chambers, which together comprise the quadrate sinus. This sinus is a diverticulum of the mandibular arch tympanic sinus (Witmer, 1990; Tahara and Larsson, 2011). The complexity of this sinus in *Alioramus* was described briefly by Brusatte et al. (2012), who based their descriptions on what was visible through the large external pneumatic opening leading into the sinus. This funnellike opening, which is sometimes confusingly referred to as the *quadrate recess* (see our Terminology section for standard nomenclature), is located on the rostral surface of the quadrate, immediately dorsal to the condyles and at the base of the rostral (pterygoid) flange. It projects strongly rostrally, but also opens somewhat medially, and is displaced toward the medial side of the rostral surface of the bone. This ovoid opening leads into the ventral portion of the quadrate sinus. Several partitioned internal chambers are visible within this opening, as noted by Brusatte et al. (2012: fig. 23).

The CT scans show that the complexity of the ventral chambers is merely one small component of the extensive and intricate quadrate sinus as a whole. Almost the entire quadrate is hollow, except where the rostral flange is the thinnest (a small region at approximately midheight of the flange, positioned approximately one third of the rostrocaudal length of the quadrate from the front of the bone). Dorsal to this region, the internal structure of the bone is trabecular. Rostral to the thinnest portion of the flange, the quadrate sinus is extremely thin and separates into a branching structure, with each tip extending rostrally. This feature does not appear to be the result of physical damage as the exterior of the bone does not show a similar fracturing pattern. This portion of the sinus nearly reaches the dorsorostral edge of the element. Caudally, the sinus fills the quadrate head. More ventrally the sinus closely follows the shape of the element, reaching and filling the ventral and lateral condyles.

Alioramus has a larger quadrate sinus than a similarly sized juvenile tyrannosaurid, CMNH 7541 (Witmer and Ridgely, 2010). In CMNH 7541, the sinus extends throughout the full height of the quadrate, but does not expand into the quadrate flange as it does in *Alioramus* (Witmer and Ridgely, 2010). Witmer and Ridgely (2010) mention that the sinus is better preserved on the right side of CMNH 7541, but do not illustrate it, nor do they mention whether the sinus is more expansive on the right (see their fig. 10). Brochu (2003) noted some asymmetries in the quadrate sinus of the *Tyrannosaurus* specimen FMNH PR2081, namely that the sinus on the right forms two isolated chambers while the left sinus forms a single continuous cavity. Witmer and Ridgely (2008) did not comment on the quadrate sinus of FMNH PR2081, which they illustrated as part of the larger paratympanic system instead of as a separate chamber.

Quadratojugal

The quadratojugal is a flat, thin bone. It was not scanned as part of this project, because it has no external signs of pneumaticity (e.g., a discrete foramen or fenestra leading inside the bone). The thin nature of the bone is consistent with its apneumatic state. Some juvenile tyrannosaurids possess a large pneumatic fenestra on the lateral surface of the quadratojugal that leads into an internal recess. This is present on the juvenile tyrannosaurid skulls CMNH 7541 and BMR P2002.4.1 from North America (Bakker et al., 1988; Witmer and Ridgely, 2010).

These specimens are likely juvenile specimens of *Tyrannosaurus rex* (e.g., Carr, 1999), although some authors regard them as belonging to a separate taxon, *Nanotyrannus*, closely related to *T. rex* (e.g., Bakker et al., 1988; Currie, 2003; Larson, 2008). A pneumatic quadratojugal is not present, however, in any known adult tyrannosaurid specimens (e.g., Brochu, 2003; Witmer and Ridgely, 2008), nor the tiny juvenile *Tarbosaurus* skull recently described by Tsuihiji et al. (2011), which is much less than half the size of IGM 100/1844. If a pneumatic quadratojugal is a feature of juvenile tyrannosaurids, it may have been limited to *Tyrannosaurus rex* or a small subset of taxa from North America, as no pneumatic fenestra is present in juvenile specimens of the Asian *Alioramus* or in *Tarbosaurus*.

Palatine

The interior of the palatine is hollowed out by a single, extensive, internal palatine sinus (fig. 8). There are two distinct routes leading from the external surface of the palatine into the sinus. First, there is an enormous, windowlike opening on the lateral surface of the bone, in the area where the maxillary and jugal processes meet (Brusatte et al., 2012). This fenestra is sometimes referred to as the palatine recess, although it is more properly a fenestra (see Terminology, above), and it opens directly medially into the sinus. Second, there is a broad region of smooth antorbital fossa on the maxillary process of the palatine. Although the fossa appears to be separated from the palatine sinus in lateral view by a stout pillar, there is a small internal foramen caudal to the pillar that links the caudal edge of the fossa with the sinus. This foramen is a separate, rostral entry into the palatine sinus and is distinct from the broad, lateral opening afforded by the recess itself.

Consequently, it appears as if the palatine recess and antorbital fossa are separate pneumatic regions that would have been invaded by discrete diverticula. The sources of these diverticula, however, are unclear. The palatine most likely formed part of the ventral and medial border of the antorbital sinus itself. Moreover, as described by Witmer and Ridgely (2008), the maxillary antrum—a diverticulum of the antorbital sinus—would have sent an additional diverticulum caudally to invade the palatine. Therefore, both the antorbital sinus proper and the maxillary antrum likely pneumatized the palatine. It may be that the antorbital fossa region of the palatine was strictly pneumatized by the antorbital sinus, but this is uncertain because the caudally extending maxillary antrum diverticulum would have also passed through this area.

It is also possible that the antorbital sinus and maxillary antrum would have jointly pneumatized the palatine through one or both of the external openings (i.e., the sinus and antrum both entered the palatine recess laterally). Or it is possible that the antorbital sinus proper only approached the palatine and did not invade it, and therefore both routes into the palatine where invaded by the maxillary antrum. Finally, it is also possible that the jugal sinus sent a small diverticulum through the foramina on the medial surface of the jugal to pneumatize the palatine rostrally. At a minimum, it is clear that there are two main routes into the palatine sinus and that the maxillary antrum, and most likely the antorbital sinus, pneumatized the bone.

Regardless of its precise sources of pneumatization, the palatine sinus is an expansive cavity that expands into each ramus of the palatine to varying degrees. The sinus excavates only the caudal third of the maxillary process, where it both sits against the antorbital fossa externally
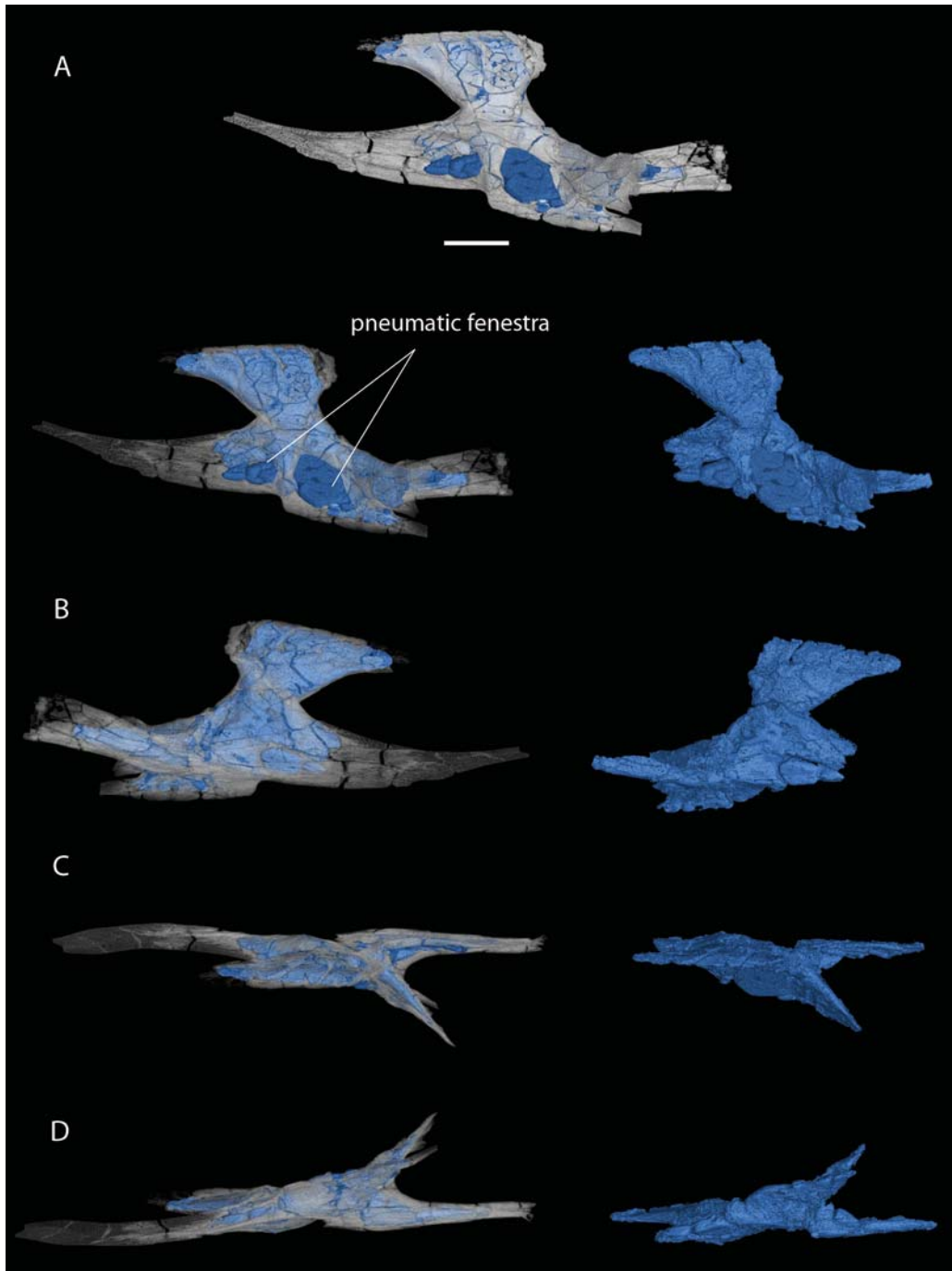
FIGURE 8. Left palatine in lateral (A), medial (B), dorsal (C), and ventral (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 15 mm.

and also slightly invades the bone. The jugal process is hollow almost to its caudal margin. The medial process houses the sinus only in its rostral portion; the sinus extends caudally to approximately the same level as the caudal edge of its invasion into the jugal process. Finally, the sinus fills nearly the entire vomeropterygoid process and mirrors its anvil shape.

In addition to the two primary routes into the palatine sinus described above, there is also a series of pits on the jugal and medial processes leading into the same palatine sinus. These small openings were noted by Brusatte et al. (2012) and hypothesized as accessory openings into the sinus, and we confirm this with CT data here. The sources for these openings are not immediately clear, but it is likely that they derive from either the antorbital sinus itself or the caudal extension of the maxillary antrum. Given their position, it is also possible that they are rostral extensions of the suborbital sinus. These accessory foramina are limited to the jugal and medial processes, and the medial and ventral portions of the palatine sinus do not communicate externally through any similar foramina.

Witmer and Ridgely (2010) described the juvenile tyrannosaurid CMNH 7541 as possessing two separate palatine sinuses. These are equivalent in position to the antorbital fossa and palatine fenestra portions of the palatine of *Alioramus*, with the only difference being that they do not merge internally via the small foramen at the caudal end of the antorbital fossa described above. Instead, there is a solid wall of bone between them (Witmer and Ridgely, 2010: fig. 12). Their separation in CMNH 7541, if genuine and not an artifact of preservation, lends support to the hypothesis that the antorbital fossa and palatine recess regions of *Alioramus* (and other tyrannosaurids) are pneumatized by distinct diverticula.

Other differences between *Alioramus* and CMNH 7541 are also apparent. As noted by Brusatte et al. (2012), the palatine recess in *Alioramus* is positioned far rostrally compared to most other tyrannosaurid specimens, as it is located entirely rostral to the caudal end of the vomeropterygoid process. The recess of CMNH 7541 extends further caudally. Also, the palatine sinus in *Alioramus* expands to the dorsal edges of the vomerpterygoid process, whereas in CMNH 7541 the sinus terminates prior to reaching the edge of the element. In adult *Tyrannosaurus,* Brochu (2003) also observed a large vacuity in the palatine that fills most of the vomeropterygoid process, more similar to *Alioramus* than CMNH 7541.

Pterygoid

The pterygoid (fig. 9) is exceptionally thin in *Alioramus* (Brusatte et al., 2012). Even though all of the bones surrounding this bone are pneumatic, the preserved portions of the pterygoid lack internal pneumaticity. This is not surprising, given that pterygoid pneumaticity is rare or absent in other nonavian theropods, although it is present in both living birds and crocodylians, but derived from different sources (Witmer and Ridgely, 2008).

Ectopterygoid

The single, external ectopterygoid foramen, which opens on the ventral surface of the bone, leads into an extensive ectopterygoid sinus (fig. 10). This configuration, with a ventrally opening and extensive sinus, is seen in many theropods, but its source is unclear. It is most likely
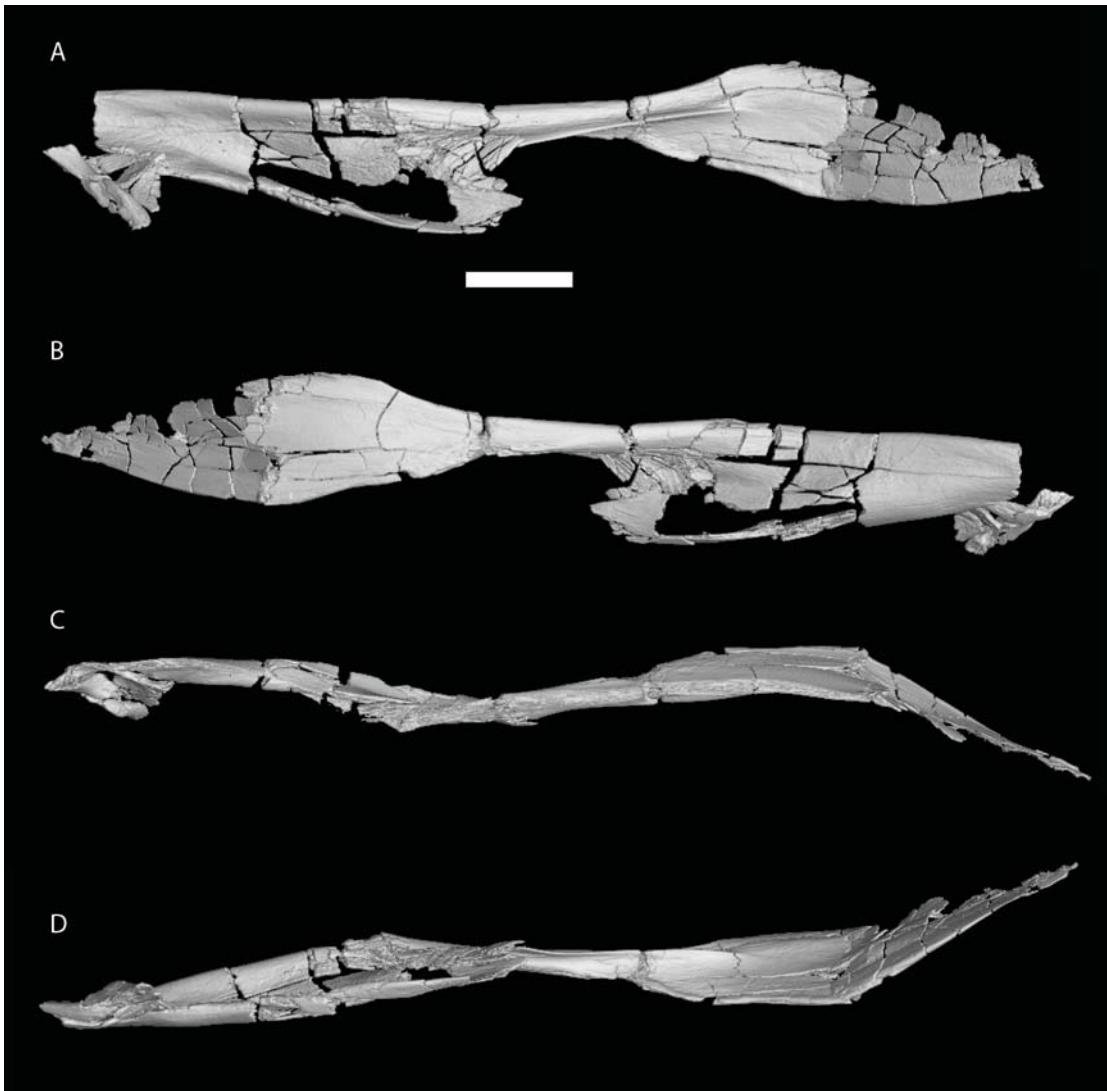
FIGURE 9. Right pterygoid in lateral (A), medial (B), dorsal (C), and ventral (D) views. Scale bar = 25 mm.

derived from either the medial pharyngeal sinus or the rostral tympanic sinus (e.g., Witmer, 1997a; Witmer and Ridgely, 2008; Tahara and Larsson, 2011). In *Alioramus*, the ectopterygoid sinus is divided by a few internal bony struts. The complex shape of the ectopterygoid is echoed by the sinus, which extends into the hooklike jugal process, leaving only the distal fourth of the hook apneumatic. The medial projection of the caudal end of the main body is also excavated by the ectopterygoid sinus. Brochu (2003) observed an asymmetry in the ectopterygoid recess of the *Tyrannosaurus* specimen FMNH PR2081, where the left side contains two sinus openings, but the right has only a single opening. Because only the right ectopterygoid is preserved in the IGM 100/1844, it is uncertain whether it also possessed asymmetrical ectopterygoid pneumaticity.
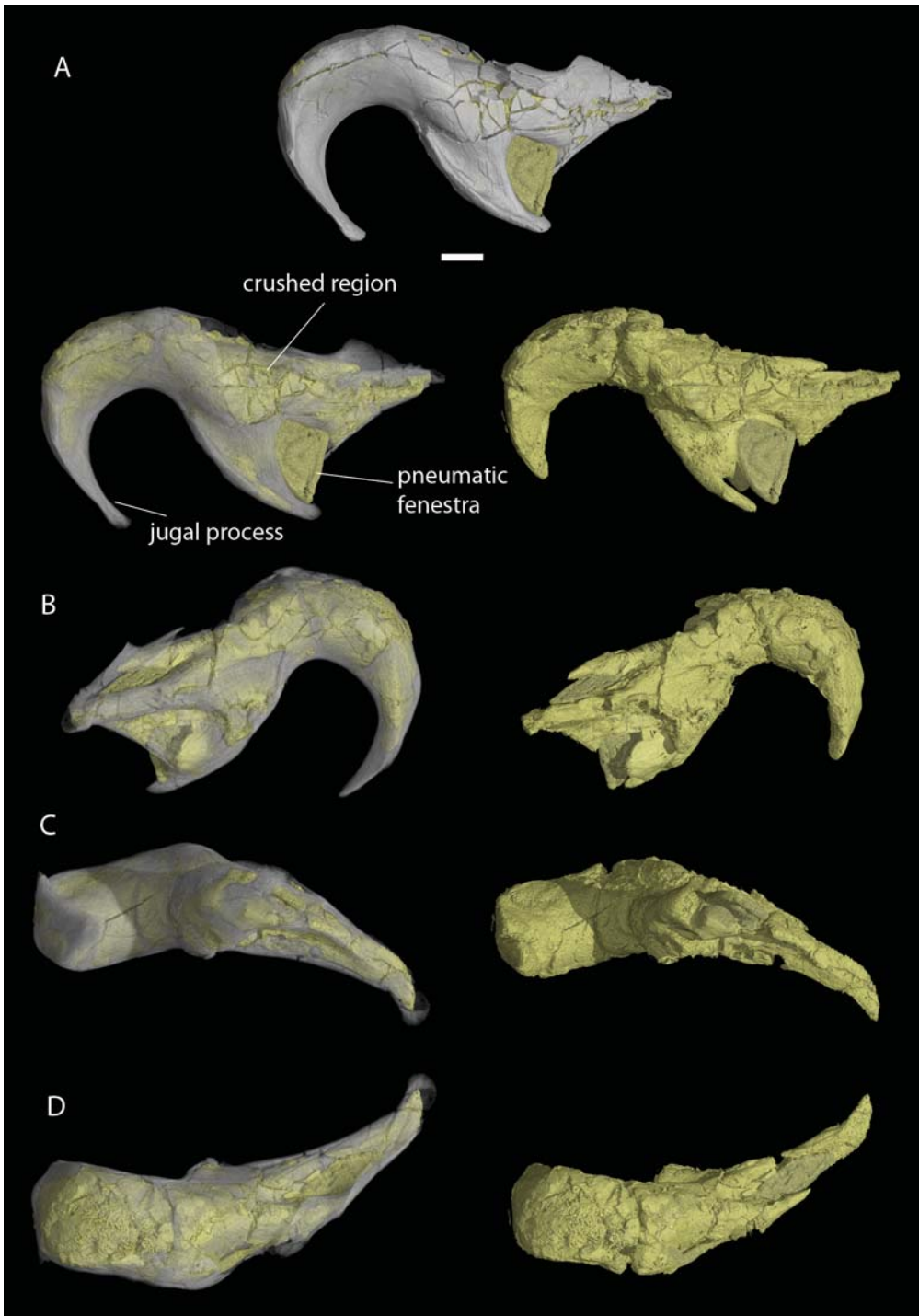
FIGURE 10. Right ectopterygoid in ventral (A), dorsal (B), lateral (C), and medial (D) views. Left column shows renders the bone semitransparent, right column shows the isolated sinus. Scale bar = 10 mm.

FIGURE 11. Left surangular in lateral (A), medial (B), dorsal (C), and ventral (D) view. Scale bar = 30 mm.

Surangular

The surangular is mostly apneumatic (fig. 11). Several interior regions are constructed of trabecular bone, which is most prevalent where the surangular is the thickest. Trabecular bone occurs within much of the dorsal region of the bone that comprises the robust lateral surangular shelf, which was a jaw adductor muscle-attachment site. The trabecular structure begins caudal to the rostral two fifths of the dorsal part of the bone and continues caudally to the caudal tip of the bone. Ventrally, the surangular is trabecular below the midpoint of the suran-

gular foramen and this structure continues caudally to the end of the bone. Caudal to the surangular foramen, the entire bone is trabecular. However, the area directly ventral to the surface that articulates with the upper jaw is solid.

There is only one small area of pneumaticity within the surangular: a shallow fossa located caudal to the caudal margin of the surangular foramen. This fossa—referred to as the *pneumatic pocket* by Brusatte et al. (2012)—contains a small, rostrally opening foramen leading into a shallow chamber (fig. 12). Instead of hollowing out a large portion of the caudal portion of the surangular, the pneumatic pocket dissipates into trabecular bone.

A similar pneumatic fossa is present in other tyrannosaurids, including *Tyrannosaurus* (Brochu, 2003). CT scans of *Tyrannosaurus* show that the foramen within the fossa extends through the surangular and into the articular (the "articular antrum"; Brochu, 2003). A complete passage through the surangular is not present in IGM 100/1844, as the foramen leads into trabecular bone and not a discrete channel (fig. 12). Given the juvenile status of IGM 100/1844, it is possible that complete communication between the surangular fossa and articular antrum developed later in ontogeny, sometime between the subadult stage of IGM 100/1844 and the adult stage of the *Tyrannosaurus* studied by Brochu (2003). Unfortunately, the articular was not preserved in IGM 1844/100, so any possible pneumatic opening or channels confluent with the surangular cannot be assessed.

The source of surangular pneumaticity in tyrannosaurids is not immediately clear, but the association between the surangular pneumatic pocket and the articular antrum in *Tyrannosaurus* suggests that the surangular sinus is a diverticulum of the mandibular arch tympanic system, which pneumatizes the articular in birds and many nonavian theropods (Witmer, 1990; Tahara and Larsson, 2011). If indeed there is no internal (through bone) communication between the articular antrum and surangular sinus in *Alioramus*, as described above, then it is plausible that a diverticulum from the articular passed laterally through the large surangular foramen and then, once external to the surangular, turned caudally to invade the pneumatic pocket.

ANGULAR

The angular (fig. 13) is not pneumatic, and the internal structure of this bone is only slightly trabecular. Even though there is a small pore on the lateral aspect, it does not lead into the interior of the element. Therefore, there is no internal communication to the exterior of this bone.

DISCUSSION

Cranial Pneumaticity and Snout Elongation in *Alioramus*

Alioramus is immediately distinguished from other tyrannosaurids by its proportionally long snout (Kurzanov, 1976; Brusatte et al., 2009, 2012). The long-snouted nature of *Alioramus* is caused primarily by elongation of the rostrum, including the maxilla, nasals, lacrimals, jugals, and the palatine bones. This elongation is mirrored in the sinuses housed within the affected
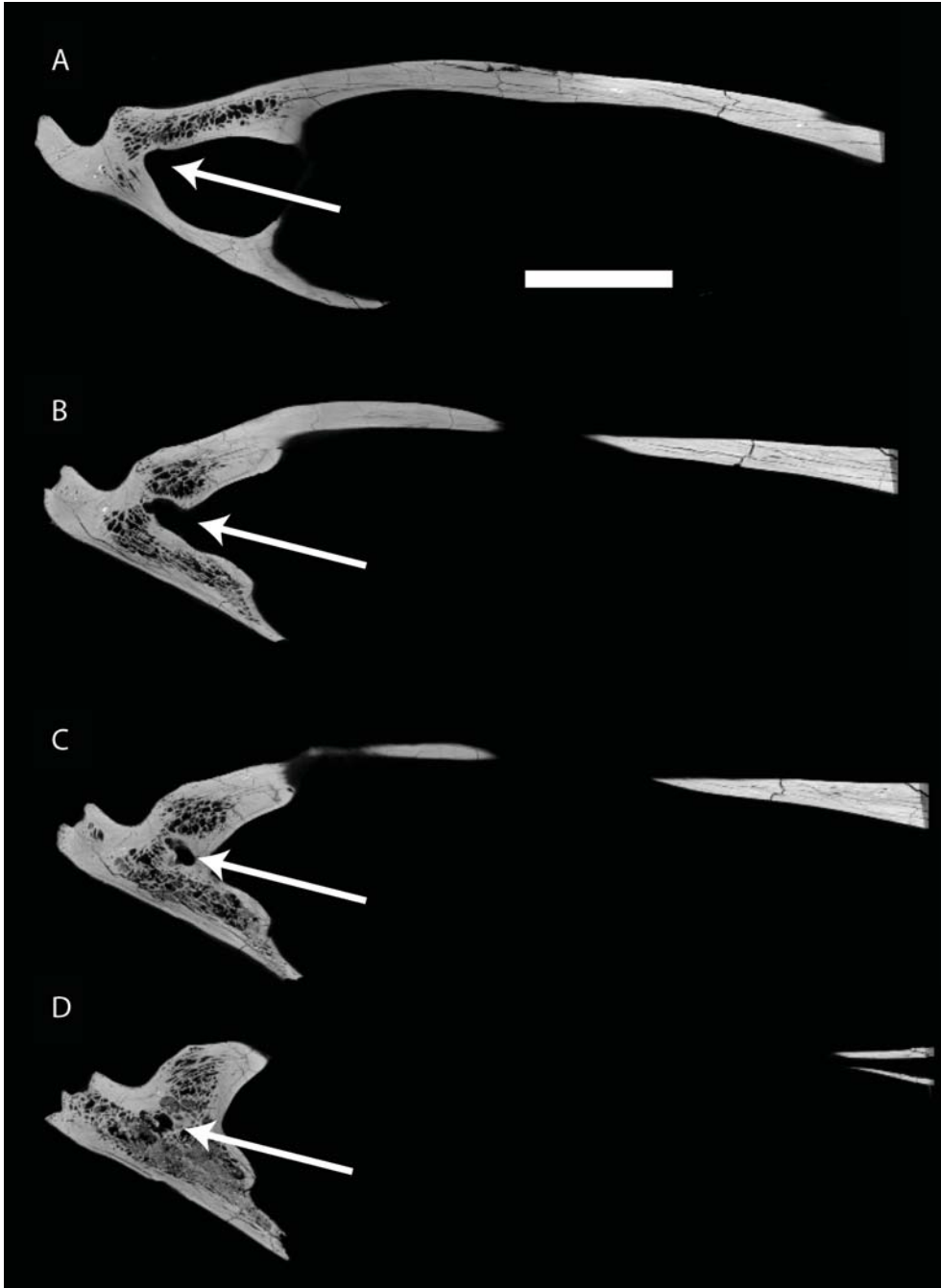
FIGURE 12. Surangular pocket shown in sagittal slices from most lateral (A) to most medial (D). Arrow points to pneumatic pocket. Pocket can be seen dissipating into the trabecular bone of the surangular. Scale bar = 40 mm.
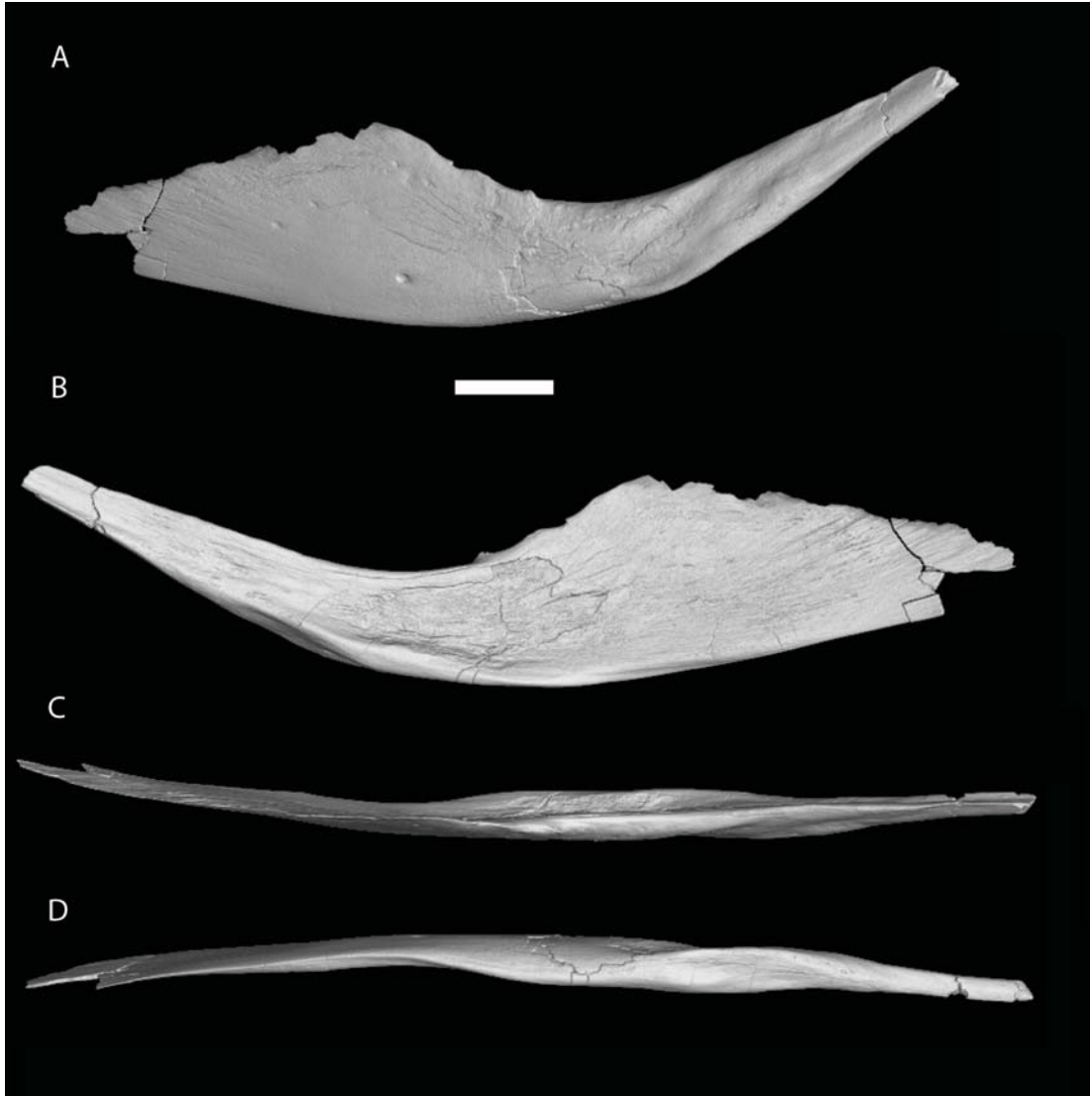
FIGURE 13. Right angular in lateral (A), medial (B), dorsal (C), and ventral (D) views. Scale bar = 20 mm.

bones, which are rostrocaudally expanded and dorsoventrally low compared to other tyrannosauroids. Therefore, *Alioramus* shows that extreme modifications in cranial shape and proportion also cause changes in the shape and proportion of the cranial sinuses. At least in this case, cranial sinuses do not retain their plesiomorphic shape in the face of major cranial restructuring. This corresponds well with Witmer's (1997a) argument that cranial sinuses opportunistically expand in size and shape when possible, rather than remain as fixed entities of well-defined shape, size, and position.

ASYMMETRY OF CRANIAL PNEUMATICITY IN *ALIORAMUS*

Pneumaticity is often asymmetrically expressed in the skeletons of archosaurs (e.g., Witmer, 1997a; Witmer and Ridgely, 2010; Brochu, 2003). These asymmetries can be reflected in the size, location, and number of pneumatic foramina leading into a sinus, or the connectivity, size, and shape of the sinus (Brochu, 2003). Some skull bones of IGM 100/1844 are preserved on only one side, but where left and right elements are present some asymmetry is expressed. The quadrates show a similar amount of sinus space in each element, although the shape of the sinus is slightly different on each side. Even more striking are differences in the size and shape of the right and left lacrimal sinuses (figs. 3 and 4, respectively). The left lacrimal exhibits a projection of the sinus into the ventral ramus, which may either be an extension of the lacrimal sinus or a medial lacrimal sinus that has merged with the lacrimal sinus. Regardless of what this space represents, it is not present on the right lacrimal. We interpret this as a genuine difference, but acknowledge that it may also be taphonomic in nature. The right lacrimal shows some signs of taphonomic damage (e.g., its lateral side is slightly crushed), so this may be affecting the shape of the sinus.

THE EVOLUTION OF CRANIAL PNEUMATICITY IN THEROPODS

Alioramus is a good example of the extensive, and in some cases extreme, cranial pneumaticity of theropod dinosaurs. Nonavian theropods display a wide array of pneumatic sinuses within the bones of the skull, most of which are diverticula from the antorbital and tympanic sinuses. Although the size, shape, and position of cranial sinuses differ among theropods, a common "groundplan" seen in most theropods has been well described (Witmer, 1997a, 1997b; Sampson and Witmer, 2007; Witmer and Ridgely, 2008; Tahara and Larsson, 2011). The central components of this groundplan are the maxillary sinus, comprising one or two main chambers, and one or two lacrimal sinuses, all of which are extensions of the antorbital sinus. Variations on this architecture, which are seen in only some theropods, include antorbital sinus diverticula excavating the jugal, nasal, and/or palatine. Additionally, some theropods have pneumatic quadrates, articulars, and squamosals, which are likely all pneumatized by diverticula of the tympanic sinus system. Many theropods also possess a pneumatic ectopterygoid, but the source of this pneumaticity is unclear.

Although a common groundplan of theropod cranial pneumaticity has been described, Witmer (1997a, 1997b) and other authors have also noted incredible variability in the morphology of cranial sinuses among theropods. Furthermore, only some theropods possess the various nasal, jugal, palatine, quadrate, articular, squamosal, and ectopterygoid sinuses, and in some cases one taxon possesses a sinus whereas a different ontogenetic stage, close relative, or even sister taxon lacks it (Witmer and Ridgely, 2008). Clearly, the distribution and evolution of cranial sinuses in theropods is complex, which is not surprising given that Witmer (1997a) has hypothesized that cranial pneumaticity in theropods may not be closely related to biomechanical or physiological demands, but results chiefly from opportunistic invasion of bone by soft tissues. Regardless of the source of cranial sinus variation, differences in morphology of sinuses, as well as their presence

or absence, are some of the most striking distinctions in skull anatomy among theropods. Therefore, pneumatic characters are often employed in phylogenetic analyses.

In the following discussion, we briefly review the distribution of cranial sinuses among coelurosaurian theropods, make general comments on discrete morphological differences in sinus morphology among taxa, and propose phylogenetically grounded hypotheses of cranial sinus evolution. As a framework, we utilize the phylogenetic dataset from Brusatte's Ph.D. thesis (Brusatte, 2013), which includes numerous characters relating to cranial pneumaticity. This dataset is the latest iteration of the Theropod Working Group (TWiG) project and is largely a combination of the hitherto most recent TWiG matrix (Turner et al., 2012) and the tyrannosauroid-specific dataset of Brusatte et al. (2010a). The entire dataset is not presented here as it is the corpus of a developing project, but the pneumatic characters are discussed in detail. Our evolutionary hypotheses are largely based on phylogenetic character optimization and presented in general terms, but in the future we anticipate that a more quantitative study of theropod cranial sinus evolution will be feasible, similar to the phylogenetic comparative study of theropod axial column pneumaticity published recently by Benson et al. (2012).

MAXILLA: The maxillary sinus is part of the common "groundplan" of theropod cranial pneumaticity (Witmer, 1997a, 1997b; Witmer and Ridgely, 2008). Basal, non-tetanuran theropods usually possess a single maxillary sinus chamber, while the majority of tetanuran theropods exhibit separate chambers, referred to as the promaxillary sinus and maxillary antrum (Witmer, 1997a). These are connected to the antorbital fossa, and therefore the antorbital sinus, by the promaxillary and maxillary fenestrae, respectively. Most coelurosaurs possess both promaxillary and maxillary fenestrae, and therefore the presence of a promaxillary sinus and maxillary antrum can be confidently inferred without the use of CT data. Based on character optimization, both a promaxillary sinus and maxillary antrum are primitive for Coelurosauria, and any absences of these sinuses are most likely reversals.

Although most coelurosaurs possess a bipartite maxillary sinus with the two associated fenestrae, there is considerable variation in the size and position of the fenestrae. It is unclear how this variation may relate to variation in the size and position of the corresponding sinuses themselves, as most theropod specimens have yet to be CT scanned and many are known from inadequate material. This variation will not be discussed further here, although it is encapsulated by several characters in the TWiG matrix (e.g., Turner et al., 2012) and the Brusatte et al. (2010a) tyrannosauroid phylogenetic analysis.

Some nonavian coelurosaurs are considered to lack the promaxillary fenestra, and have been scored to this effect in the TWiG matrix (Turner et al., 2012), including the dromaeosaurids *Austroraptor* (Novas et al., 2009) and *Shanag* (Turner et al., 2007), the troodontids *Saurornithoides* and *Zanabazar* (Norell et al., 2009), and many oviraptorosaurs (e.g., Balanoff et al., 2009). Some of these character scores, however, may be incorrect. Most oviraptorosaurs possess two accessory fenestrae in front of the antorbital fenestra, as in most coelurosaurs, but the homologies of these openings have been treated as uncertain (e.g., Balanoff et al., 2009). This is because the more rostral one, in the position of the promaxillary fenestra in other theropods, is much larger than the more caudal one, which is in the position of the maxillary fenestra. In

almost all other theropods, by contrast, the promaxillary fenestra is much smaller than the maxillary fenestra. Balanoff and Norell (2012) recently reviewed the maxillary sinus morphology of oviraptorosaurs, and concluded that positional similarity between the two fenestrae of oviraptorosaurs and the promaxillary and maxillary fenestrae of other theropods is reasonable evidence for primary homology. With that said, they do consider the caenagnathid oviraptorosaur *Chirostenotes* to genuinely lack a promaxillary fenestra, along with a maxillary fenestra (Sues, 1997). The conditions in the aforementioned dromaeosaurids and troodontids are less clear, and it is possible that erosion or poor preservation has obscured a promaxillary fenestra in some of these taxa (e.g., *Shanag*). *Austroraptor* genuinely possesses a single, enlarged accessory fenestra in front of the antorbital fenestra, which Novas et al. (2009) described as a maxillary fenestra. Observation of the specimen, however, confirms that there is a swollen "bulla"-like structure on the medial surface of the maxilla in the region of the anteromedial process, in front of the antorbital fenestra (MML 195). Similar structures are present in many other theropods and appear swollen because they are invaded by the promaxillary sinus (Witmer, 1997a). Although CT data would be needed for confirmation, we suggest that *Austroraptor* possesses a promaxillary sinus and a maxillary antrum, and that the single large "maxillary fenestra" is a derived feature that may have received the diverticula leading to both of these sinuses.

All coelurosaurs with well-preserved maxillae possess a maxillary fenestra, with the exception of the caenagnathid *Chirostenotes* (Sues, 1997) and therizinosauroids, as exemplified by *Erlikosaurus*, the only member of this group with a described well-preserved skull (Clark et al., 1994). It is unclear whether the lack of a maxillary fenestra in these taxa corresponds to an absent maxillary antrum, or whether the antrum may have been pneumatized by another source, because the antorbital regions of these specimens have not been studied in detail using CT. New CT data for *Erlikosaurus*, which has recently been used to study the endocranial cavity and inner ear, could help address this issue (Lautenschlager et al., 2012). Assuming that both *Chirostenotes* and *Erlikosaurus* do genuinely lack a maxillary antrum, this could represent a derived character shared by oviraptorosaurs and therizinosaurs, but then later reversed in more derived oviraptorosaurs such as *Khaan*. If so, this may be a feature uniting therizinosauroids and oviraptorosaurs into a clade. Such a clade was commonly recovered in earlier versions of the TWiG dataset (e.g., Turner et al., 2007, and earlier iterations), but is not found in more recent iterations because many of the characters once thought to unite these two clades are now reconstructed as convergences shared by derived members, but not basal taxa, of each group (e.g.., Senter, 2007; Zanno et al., 2009; Turner et al., 2012). This realization is largely due to the inclusion and better description of more primitive taxa along the oviraptorosaur and therizinosaur lineages.

Nasal: *Alioramus* and other derived tyrannosauroids do not possess any pneumatic sinuses within the nasal. This is the normal condition among coelurosaurs, although a select handful of coelurosaurs do possess pneumatizied nasals, as do many coelurosaurian outgroups (e.g., *Allosaurus*: Madsen, 1976; *Majungasaurus*: Sampson and Witmer, 2007; Witmer and Ridgely, 2008; *Monolophosaurus*: Zhao and Currie, 1993, Brusatte et al., 2010b; *Neovenator*: Brusatte et

al., 2008; *Sinraptor*: Currie and Zhao, 1993). Among coelurosaurs, there are two general conditions of nasal pneumaticity. First, most oviraptorosaurs exhibit a large pneumatic opening on the lateral surface of the nasal, above the antorbital fenestra and immediately caudodorsal to the external naris, which is within the narial fossa and surrounded by several small pneumatic foramina (e.g., Balanoff et al., 2009; Balanoff and Norell, 2012). Second, some basal tyrannosauroids possess a clear extension of the antorbital fossa onto the lateral surface of the nasal, which houses two or three discrete pneumatic foramina that lead into an internal chamber. This condition is seen in *Dilong* (Xu et al., 2004), *Eotyrannus* (Hutt et al., 2001; MIWG 1997.550), *Guanlong* (Xu et al., 2006), and *Yutyrannus* (Xu et al., 2012), and is likely present in *Proceratosaurus* based on CT data (Rauhut et al., 2010). Finally, it is important to note that Witmer (1997a) described nasal pneumaticity in the dromaeosaurid *Deinonychus*, but this taxon is scored as lacking nasal pneumaticity in the TWiG dataset.

Because the form and position of the pneumatic openings is similar in tyrannosauroids and close coelurosaurian outgroups (e.g., *Allosaurus*), Brusatte (2013) hypothesized primary homology between these conditions. However, he considered the oviraptorosaurian condition as nonhomologous to that of tyrannosauroids and outgroups, because of distinct differences in the position of the external pneumatic openings (caudodorsal rim of naris vs. midpoint of bone) and the form of the pneumatic openings (several pneumatic openings caudodorsal to the rim of the naris and within the narial fossa vs. two or three discrete pneumatic openings centered in an extension of the antorbital fossa). The nonhomology of the tyrannosauroid and oviraptorosaurian conditions is corroborated by the great phylogenetic separation between these two clades, and the homology of the tyrannosauroid and outgroup conditions may be corroborated by the position of tyrannosauroids as basal coelurosaurs (i.e., nasal pneumaticity of the tyrannosauroid variety may be primitive for Coelurosauria and later independently lost in derived tyrannosaurids and coelurosaurs more derived than Tyrannosauroidea).

It is striking that basal tyrannosauroids possess extensive nasal pneumaticity, but large-bodied tyrannosauroids do not. Based on phylogenetic character optimization on the recent cladogram of Brusatte et al. (2010a), tyrannosauroids secondarily lost pneumatic nasals sometime around the origin of Tyrannosauridae. Whether this is associated with the origin of large body size, the expansion of other cranial sinuses, the development of vaulted nasals, or something else awaits future research. Given that the vaulted nasals of tyrannosaurids likely increased skull strength, enabled stronger bite forces, and were an integral component of the unusual style of "puncture-pull" feeding (Rayfield, 2004; Snively et al., 2006), it is tempting to hypothesize that the loss of nasal pneumaticity may be related to the development of nasal vaulting. However, *Eotyrannus* possesses both nasal pneumaticity and vaulted nasals (Hutt et al., 2001). With that being said, *Eotyrannus* is much smaller than *Alioramus*, *Tyrannosaurus*, and other tyrannosaurids that lack nasal pneumaticity but exhibit vaulted nasals. It may be that the possession of vaulted nasals at large body size triggered the loss of nasal pneumaticity, as only large-bodied taxa like *Tyrannosaurus* likely employed potent bite forces and puncture-pull feeding (e.g., Erickson et al., 1996; Meers, 2003; Bates and Falkingham, 2012).

LACRIMAL: Witmer and Ridgely (2008: 1374) described the lacrimal sinus as "among the most consistent paranasal sinuses in theropods," because it is part of the common pneumatic "groundplan" seen in many taxa (Witmer, 1995; 1997a, 1997b). In the handful of nonavian theropods that have been subjected to CT scanning, an internal lacrimal sinus is invariably present (e.g., oviraptorosaurs: Balanoff and Norell, 2012; *Majungasaurus*: Witmer and Ridgely, 2008; *Ornithomimus*: Tahara and Larsson, 2011; *Tyrannosaurus*: Brochu, 2003, Witmer and Ridgely, 2008; *Zanabazar* Norell, personal obs.). In many other theropods that have yet to be studied using CT, a lacrimal sinus is clearly observable due to the presence of a large external pneumatic fenestra, sometimes referred to confusingly as the *lacrimal recess,* that leads into the sinus (figs. 14A, 15A–B). This is the case, for example, in non-coelurosaurs such as *Zupaysaurus* (Ezcurra and Novas, 2007) and *Sinraptor* (Currie and Zhao, 1993a), the dromaeosaurid *Austroraptor* (Novas et al., 2009), the basal coelurosaurs *Ornitholestes* (AMNH FARB 619) and *Tanycolagreus* (Carpenter et al., 2005), and many tyrannosauroids (e.g., Currie, 2003).

Although a lacrimal sinus is standard for theropods, there is some variation in the size of the fenestra that opens into the sinus. The TWiG matrix includes a character specifying the presence or absence of an "enlarged foramen or foramina opening laterally at the angle of the lacrimal above the antorbital fenstra" (e.g., Turner et al., 2012: char. 38). Essentially, this character scores for the presence or absence of a large and discrete lacrimal fenestra, not the presence or absence of the lacrimal sinus itself. The only taxa scored for the presence of the fenestra are the outgroups *Allosaurus* and *Sinraptor*, the dromaeosaurid *Austroraptor*, oviraptorosaurs, and some tyrannosauroids. Brusatte (2013) noted that a few other coelurosaurs also possess an enlarged external fenestra, including *Ornitholestes* and *Tanycolagreus*.

Other coelurosaurs, by contrast, do not possess anything more than a small pneumatic foramen on the external surface of the bone that leads into the lacrimal sinus. This is the case, for example, in *Ornithomimus*, in which CT scans confirm the presence of a large internal lacrimal sinus connected to the external surface of the lacrimal by only a very tiny foramen (Tahara and Larsson, 2011). The condition in *Ornithomimus* starkly demonstrates that the absence of a lacrimal sinus cannot be inferred from the absence of a large lacrimal fenestra, or even the absence of any external foramina, as these may often be subtle. CT data are properly needed to assess the presence and shape of the lacrimal sinus of most taxa.

There is also a second discrete chamber within the lacrimal of some theropods: the medial lacrimal sinus (Witmer and Ridgely, 2008). This is present in *Allosaurus*, *Majungasaurus*, *Tyrannosaurus*, and *Albertosaurus* and in these taxa it is fed by a small foramen located on the medial surface of the lacrimal (Sampson and Witmer, 2007; Witmer and Ridgely, 2008; Carr, 2010). A chamber is located in a similar position in *Alioramus*, but as described above, this is apparently confluent with the lacrimal sinus, and therefore it is unclear whether it is a discrete medial lacrimal sinus or simply a portion of the lacrimal sinus. Additionally, a comparable chamber is present in *Ornithomimus*, but it connects to the lateral surface of the lacrimal via a small foramen, not the medial surface (Tahara and Larsson, 2011). Because the medial lacrimal sinus is usually small and pneumatized by a small, subtle foramen, it is almost impossible to assess its presence or absence based on external examination of the lacrimal. Therefore, CT

data are essential, and it is hoped that the distribution and evolution of this sinus will become better understood as more theropods are analyzed with CT.

JUGAL: Some theropods possess an internal jugal sinus, which is linked to the antorbital sinus via a large pneumatic fenestra or foramen on the lateral surface of the jugal. The sinus is a common feature of non-coelurosaurian theropods close to the root of Coelurosauria, such as allosauroids (e.g., *Sinraptor*: Currie and Zhao, 1993) and *Monolophosaurus* (Brusatte et al., 2010b), but is rarely seen in coelurosaurs. It is present, however, in all known tyrannosauroids, including basal forms such as *Guanlong* (Xu et al., 2006) and *Dilong* (Xu et al., 2004), and more derived taxa like *Eotyrannus* (MIWG 1997.550) and all tyrannosaurids (e.g., Witmer and Ridgely, 2008). It is also present in the basal ornithomimosaur *Pelecanimimus* (LH 7777), but apparently not other ornithomimosaurs (see below). The presence or absence of the external pneumatic fenestra is scored in the TWiG matrix (e.g., Turner et al., 2012: char. 33). Additional characters in the tyrannosauroid-specific analysis of Brusatte et al. (2010a) refer to variation in the location and orientation of the fenestra, and these were incorporated into the TWiG dataset by Brusatte (2013). Character optimization suggests that the jugal pneumatic fenestra (and thus sinus) was a primitive feature of coelurosaurs retained in all tyrannosauroids and *Pelecanimimus*, but lost in all other coelurosaurs. The retention of the jugal sinus in tyrannosauroids is one of many features supporting the basal coelurosaurian position of this clade.

The condition in other ornithomimosaurs deserves further comment, based on the CT data of Tahara and Larsson (2011). All ornithomimosaurs other than the basal taxon *Pelecanimimus* apparently lack an internal jugal sinus, based on the lack of external pneumatic foramina and the absence of any noticeable swelling of the jugal. Additionally, the CT scans of Tahara and Larsson (2011) confirm that *Ornithomimus* lacked an internal sinus. With that being said, Tahara and Larsson (2011) described *Ornithomimus* as possessing a jugal diverticulum of the antorbital sinus, which extends caudoventrally from the antorbital sinus and along the external surface of the jugal and does not penetrate the bone (Tahara and Larsson, 2011). This condition is inferred from the presence of "a shallow triangular fossa (that) covers the external surface of the jugal from the caudoventral corner of the antorbital fossa" (Tahara and Larsson, 2011: 133). If this conclusion is correct, then at least some theropods may have possessed a jugal diverticulum that did not pneumatize the interior of the jugal. However, it is also possible that the small fossa on the jugal of *Ornithomimus* was simply excavated by the antorbital sinus itself, not a separate diverticulum. CT data from other ornithomimosaurs, especially other basal forms like *Shenzhousaurus* (Ji et al., 2003) will be particularly useful in better answering this question.

POSTORBITAL: Postorbital pneumaticity is unknown in other tyrannosauroids, and indeed, in other nonavian dinosaurs (e.g., Brochu, 2003; Witmer and Ridgely, 2008; Tahara and Larsson, 2011). It is possible that some examples of postorbital pneumaticity may have gone unnoticed because so few specimens have yet been subjected to CT scans. But any such examples would necessarily be subtle, as all known nonavian theropod postorbitals lack the large and obvious external pneumatic openings commonly seen on the nasal, jugal, lacrimal, maxilla, and other bones that allow pneumaticity to be easily observed without the use of CT data. The noted lack of postorbital pneumaticity among theropods is intriguing, especially as so many
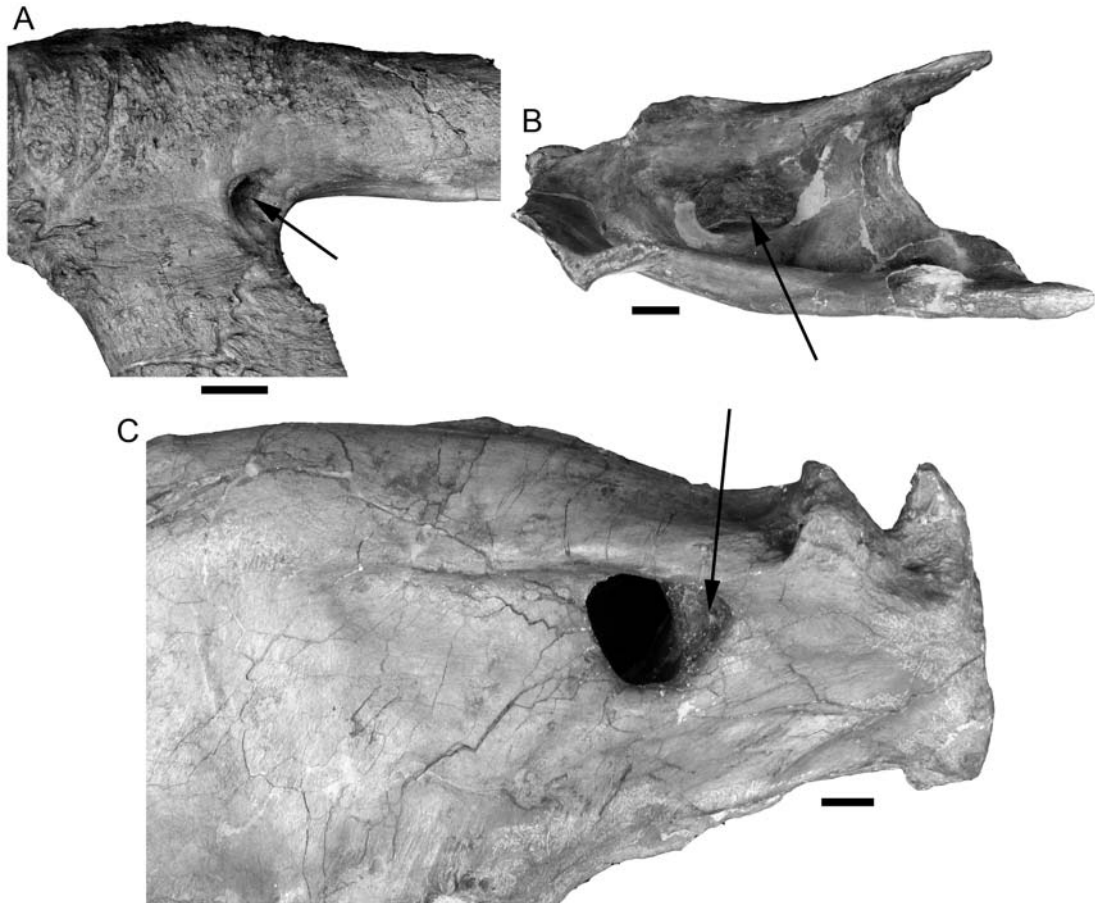
FIGURE 14. Pneumatic features on selected cranial bones of *Tyrannosaurus rex* (CM 9380). Right lacrimal in lateral view (A), left squamosal in ventral view (B), and left surangular in lateral view (C). Scale bars = 3 cm. Arrows denote external pneumatic features (foramina and fenestrae).

adjacent diverticula are available to pneumatize the bone, and deserve further study using biomechanical, histological, and developmental data. One hypothesis is that the postorbital may serve a vital biomechanical role in strengthening the skull, especially during biting. This is hinted at by the strong association between orbit shape and skull strength (Henderson, 2002). Perhaps postorbital pneumatiziation may compromise cranial strength, a hypothesis that could be tested using Finite Element Analysis or related biomechanical methods (e.g., Rayfield, 2007).

The lack of postorbital pneumaticity among nonavian theropods is also surprising because crown-group avians have an enormous fronto-ethmoidal sinus that pneumatizes the frontal immediately caudodorsal to the orbit, in the same region of the large postorbital of nonavian theropods (Witmer, 1990, 1995; Witmer and Ridgely, 2008). If there is a functional reason for an apneumatic region caudodorsal to the orbit in nonavian theropods, this constraint must have been lifted at some point during the early evolution of avians. Alternatively, it may be that something intrinsic to the development of the postorbital itself prohibits pneumaticity, and

birds were only able to develop a large fronto-ethmoidal sinus caudodorsal to the orbit after the postorbital was apomorphically reduced and/or lost entirely.

SQUAMOSAL: Pneumaticity of the squamosal is rare among nonavian theropods, but is present in *Troodon* (Currie and Zhao, 1993b), tyrannosaurids (Brochu, 2003; Witmer and Ridgely, 2008), and potentially in ornithomimosaurs (Witmer, 1997a; Tahara and Larsson, 2011). It is likely that additional examples will emerge when other theropod skulls are subject to CT scanning. The source of the squamosal diverticulum is unclear, but the antorbital sinus and paratympanic sinus are the most likely candidates (Witmer, 1997a, 1997b; Witmer and Ridgely, 2008).

It is also uncertain whether the conditions in *Troodon*, ornithomimosaurs (if they possesses a squamosal recess), and tyrannosaurids are homologous. The squamosal recess of *Troodon* was described by Currie and Zhao (1993b) as associated with the dorsal tympanic recess, a sinus that mostly invades the prootic and other portions of the lateral braincase. This is also the case in *Zanabazar* (Norell et al., 2009). This recess, however, is absent in tyrannosaurids, as confirmed by CT scans (e.g., Witmer and Ridgely, 2008). The condition in ornithomimosaurs is difficult to compare to both *Troodon* and tyrannosaurids. Witmer (1997a) identified a cavity in the squamosal of an ornithomimid specimen, which funnels out to open broadly into the lateral temporal fenestra. He interpreted this as a pneumatic recess, but Tahara and Larsson (2011), who described a similar opening within the squamosal of *Ornithomimus* using CT, were unable to confirm whether it was pneumatic in origin or a muscle attachment site. If a pneumatic sinus, this chamber differs from the sinus of some tyrannosaurids because it is limited to the main body of the squamosal and does not extend into the caudal process.

The squamosal sinus of tyrannosaurids is unusual and likely a derived feature of Tyrannosauridae or a slightly more inclusive clade. Any sign of squamosal pneumaticity is absent in the basal tyrannosauroids *Dilong* (IVPP V14343) and *Guanlong* (IVPP V14531), but a distinct sinus is seen in *Albertosaurus*, *Gorgosaurus*, *Alioramus*, *Teratophoneus*, *Daspletosaurus*, *Tarbosaurus* (fig. 15D), and *Tyrannosaurus* (fig 14B; see review in Brusatte et al., 2012). With the exception of *Albertosaurus* and *Gorgosaurus* (T.D. Carr, personal commun.), the ventral surface of the squamosal (which opens ventrally into the lateral temporal fenestra) of these taxa is deeply hollowed out, so that the squamosal is cuplike. Although jaw muscles do attach in this region, the pneumatic nature of this space is confirmed by the presence of large pneumatic foramina leading into the bone, as well as CT data for *Alioramus* (this paper) and *Tyrannosaurus* (Brochu, 2003; Witmer and Ridgely, 2008). In *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* there is usually one single, enormous pneumatic foramen within the center of the cuplike excavation that leads deep into the bone (e.g., Witmer, 1997a: fig. 34C). In these three taxa that sinus is so large that it extends caudally into the squamosal caudal process; this is a derived feature of the *Daspletosaurus* + *Tarbosaurus* + *Tyrannosaurus* clade (Brusatte et al., 2010a; Carr and Williamson, 2010).

QUADRATE: Quadrate pneumaticity is fairly common among coelurosaurs, as it is present in many tyrannosauroids (e.g., Brochu, 2003), ornithomimosaurs (e.g., Tahara and Larsson, 2011), therizinosauroids (e.g., *Falcarius*: Zanno, 2010), oviraptorosaurs (e.g., Balanoff et al.,
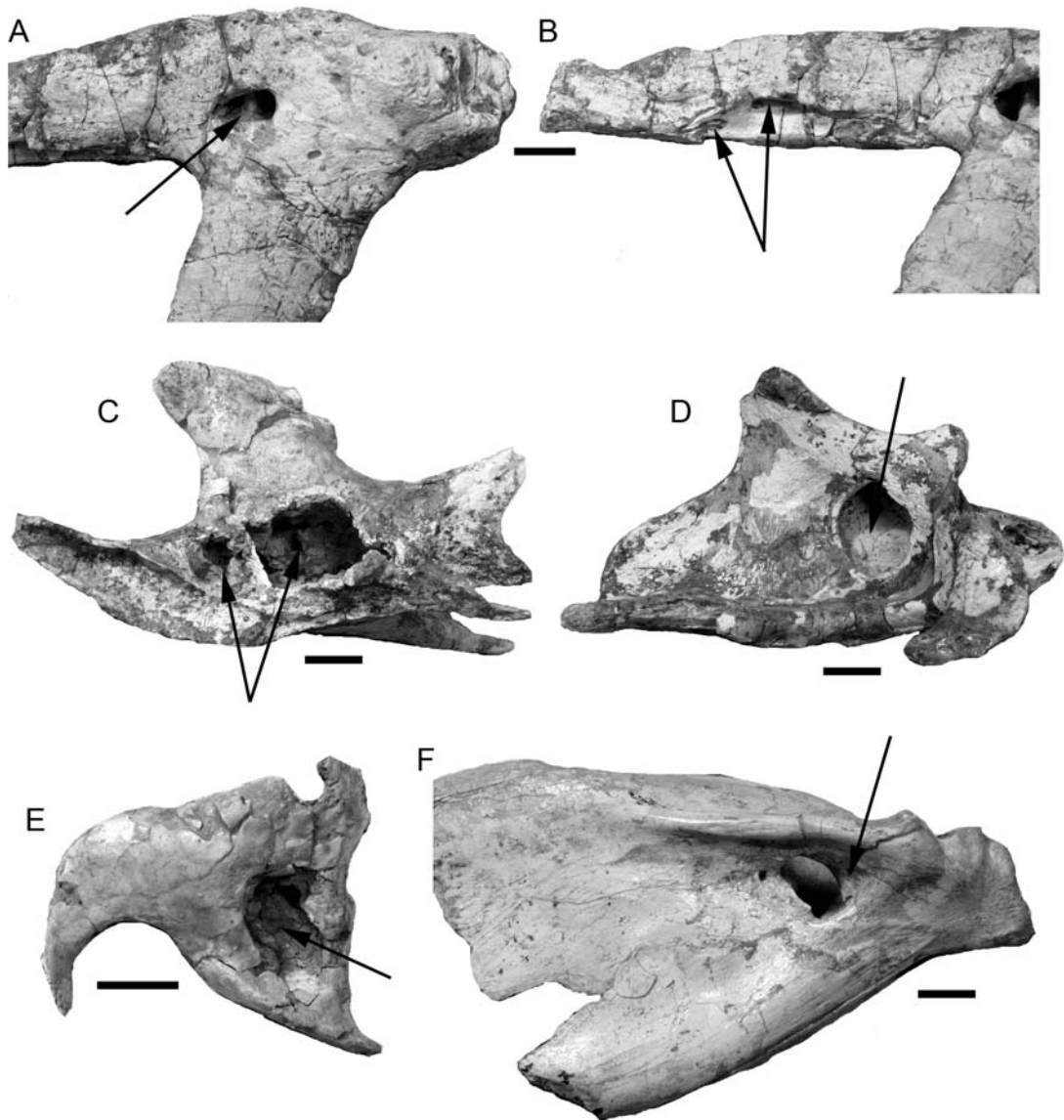
FIGURE 15. Pneumatic features on selected cranial bones of *Tarbosaurus bataar* (ZPAL collection). Main body of left lacrimal ZPAL MgD-I/4 in lateral view (A), anterior ramus of left lacrimal ZPAL MgD-I/4 in lateral view (B); left palatine ZPAL MgD-I/4 in lateral view (C), right squamosal ZPAL MgD-I/4 in ventral view (D), right ectopterygoid ZPAL MgD-I/34 in ventral view (E); left surangular ZPAL MgD-I/3 in lateral view (F). Scale bars = 3 cm. Arrows denote external pneumatic features (foramina and fenestrae).

2009; Balanoff and Norell, 2012), and some, but not all, troodontids and dromaeosaurids (e.g., *Buitreraptor*: Makovicky et al., 2005; *Sinovenator*: Xu et al., 2002). It is not present in some very basal coelurosaurs such as *Zuolong* (Choiniere et al., 2010) and *Bicentenaria* (Novas et al., 2012), or some close coelurosaurian outgroups such as *Sinraptor* (Currie and Zhao, 1993a), but it is present in some carcharodontosaurian allosauroids (e.g., Coria and Currie, 2006; Sereno

et al., 2008). The presence or absence of quadrate pneumaticity is scored in the TWiG matrix (e.g., Turner et al., 2012: char. 299).

There is variation, however, in the type of quadrate pneumaticity present among taxa. The TWiG character scores for the simple presence or absence of an internal sinus. This sinus communicates with the external surface of the quadrate in two distinct ways (e.g., Tahara and Larsson, 2011). Most coelurosaurs have a small foramen, usually on the midshaft of the caudal surface of the quadrate, that leads into the sinus. Derived tyrannosauroids, on the other hand, possess a large, deep, funnellike pneumatic opening on the rostral surface of the quadrate where the pterygoid wing and mandibular condyles meet. A similar condition is also seen in the therizinosauroid *Falcarius* (Zanno, 2010), but is not apparent in *Erlikosaurus* (Clark et al., 1994). Both of these conditions are likely homologous at some level, as they are both present in the basal tyrannosauroid *Dilong* (IVPP V14243). Most taxa possess either one or the other condition, however. That said, it is possible that the small caudal foramen has not been identified in some tyrannosauroid taxa with big rostral funnellike openings, due to the small size of the caudal foramen, which may be easily damaged by breakage or not visible without CT. This does not appear to be the case in *Alioramus*, as the rostral funnel is clearly present, but no caudal foramen is visible either externally or in CT scans.

Brusatte (2013) divided quadrate pneumaticity into several separate characters. One character follows the original TWiG character denoting simple presence or absence of quadrate pneumaticity, and all theropods with any form of a quadrate internal sinus or external pneumatic openings were scored for the present condition. An additional character referred to the foramen on the caudal or caudomedial surface of the shaft, which was also originally included in the TWiG matrix (e.g., Turner et al., 2012: char. 301). This foramen is present in the aforementioned dromaeosaurids and troodontids, as well as some (but not all) oviraptorosaurs, all ornithomimosaurs with quadrate pneumaticity, and the basal tyrannosauroid *Dilong*. It is absent in the therizinosauroid *Falcarius* and in all other tyrannosauroids with quadrate pneumaticity.

Finally, a third character, originally included in the tyrannosauroid cladistic dataset of Brusatte et al. (2010a: char. 106), denotes the presence or absence of the funnellike external opening on the rostral surface of the quadrate, above the condyles. This is present in derived tyrannosauroids, including *Dilong*, *Eotyrannus* (MIWG 1997.550), and tyrannosaurids, as well as the therizinosauroid *Falcarius*. It is absent, however, in the very basal tyrannosauroids *Guanlong* (IVPP V14531) and *Proceratosaurus* (NHMUK R4850). It is also absent in the non-tyrannosaurid tyrannosauroid *Xiongguanlong* (Li et al., 2010), although the phylogenetic placement of this taxon as intermediate between *Dilong* and *Eotyrannus,* on the one hand, and tyrannosaurids, on the other, indicates that its lack of a rostral funnellike opening on the quadrate is a reversal (Brusatte et al., 2010a).

There is also another character relating to quadrate pneumaticity in the TWiG dataset, which concerns a cluster of small pneumatic foramina on the caudal surface of the tip of the dorsal process of the bone (e.g., Turner et al., 2012: char. 300). This character is currently very difficult to score in many taxa, as these small foramina cannot easily be observed in small specimens, poorly preserved or prepared specimens, and in the absence of CT.

PALATINE: Palatine pneumaticity is variably present among theropods (Witmer, 1997a; Tahara and Larsson, 2011). Among non-coelurosaurian theropods, pneumatic palatines are seen in taxa such as *Acrocanthosaurus* (Eddy and Clarke, 2011), *Majungasaurus* (Sampson and Witmer, 2007), *Monolophosaurus* (Zhao and Currie, 1993; Brusatte et al., 2010b), *Neovenator* (Brusatte et al., 2008), and *Sinraptor* (Currie and Zhao, 1993). It is likely, therefore, that palatine pneumaticity is primitive for Coelurosauria. Among coelurosaurs, such pneumaticity has been described in some dromaeosaurids (e.g., *Deinonychus* and *Velociraptor*: Witmer, 1997a) and troodontids (e.g., *Saurornithoides*: Witmer, 1997a), various ornithomimosaurs (e.g., *Garudimimus*, *Ornithomimus*, *Shenzhousaurus*: Tahara and Larsson, 2011; *Pelecanimimus*: LH 7777), and most tyrannosauroids (e.g., Witmer, 1997b). Most of these taxa are scored for pneumatic palatines based on external observation of the bone, but CT data has confirmed the presence of internal palatine sinuses in *Ornithomimus* (Tahara and Larsson, 2011) and tyrannosaurids (e.g., Brochu, 2003; Witmer and Ridgely, 2008; this paper). CT data suggest that pneumaticity was limited to the external surface of the palatine, and did not expand into an internal sinus, in *Saurornithoides* (Norell et al., 2009; Norell, personal obs.).

Although a disparate sample of theropods exhibit palatine pneumaticity, the form of this pneumaticity varies. Dromaeosaurids, troodontids, and most ornithomimosaurs exhibit a deep fossa on the dorsal surface of the palatine, which Witmer (1997a) described as pneumatic in nature, based largely on the fact that a small pneumatopore within this fossa leads into a small internal chamber in *Deinonychus*. Tyrannosauroids, on the other hand, possess a windowlike palatine fenestrae that leads into a large internal chamber, which hollows out much of the palatine. This condition is present in the basal tyrannosauroid *Eotyrannus* (MIWG 1997.550), as well as the larger and more derived taxa *Appalachiosaurus* (Carr et al., 2005), *Bistahieversor* (Carr and Williamson, 2010), *Albertosaurus* (Carr, 2010), *Gorgosaurus*, and *Daspletosaurus* (Currie, 2003), *Tarbosaurus* (Hurum and Sabath, 2003), *Tyrannosaurus* (Molnar, 1991; Brochu, 2003; Witmer and Ridgely, 2008), and *Alioramus* (Brusatte et al., 2012; this paper). A similar condition is also present in the basal ornithomimosaur *Pelecanimimus* (LH 7777) and the more derived *Ornithomimus*, as confirmed by CT scans (Tahara and Larsson, 2011). It is also present in close coelurosaurian outgroups such as *Sinraptor* (Currie and Zhao, 1993a).

In addition to the large fenestra, there is a second route into the internal palatine sinus in some tyrannosauroids: a small foramen at the caudal end of the antorbital fossa on the maxillary process of the palatine. It is present in *Alioramus*, as described above. It is also present in all other tyrannosaurids for which palatines are known, including *Albertosaurus* (Carr, 2010), *Daspletosaurus* (Currie, 2003), *Tarbosaurus* (Hurum and Sabath, 2003), and *Tyrannosaurus* (Molnar, 1991). It is not present, however, in more basal tyrannosauroids, including *Bistahieversor* (Carr and Williamson, 2010.), as well as in all other non-tyrannosauroid theropods with palatine pneumaticity that we are aware of. Brusatte et al. (2010a: char. 137) utilized a phylogenetic character to differentiate between the single fenestra of most theropods and the derived condition of two openings in some tyrannosauroids. However, they scored only *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* for the double openings, when this condition is present in all tyrannosaurids.

Based on character optimization, palatine pneumaticity is primitive for Coelurosauria and retained in most coelurosaurs. A large internal palatine sinus connected to the bone exterior via a windowlike fenestra is mostly likely primitive for Coelurosauria, retained in tyrannosauroids and most ornithomimosaurs, and then lost in more derived coelurosaurs. It is worth noting that the basal tyrannosauroid *Proceratosaurus* lacks both internal and external evidence of palatine pneumaticity, based on CT scans, making it the only example of a tyrannosauroid that lacks both palatine pneumaticity generally and the extensive internal sinus specifically (Rauhut et al., 2010). Both of these absences optimize as isolated reversals based on the recent tyrannosauroid phylogeny of Brusatte et al. (2010a). These hypotheses are likely to change, however, as more taxa are CT scanned. As originally noted by Witmer (1997a), and still true today, the vast majority of theropods lack well preserved palatines, and most theropods with palatines have yet to be CT scanned.

Ectopterygoid: The ventral (palatal) surface of the ectopterygoid is excavated by a pneumatic fossa in most theropods (Gauthier, 1986), as well as many other archosaurs (Witmer, 1997a). In many taxa there is a large pneumatic fenestra within this fossa that leads into an internal chamber, the ectopterygoid sinus. This fenestra is large in all known coelurosaurs, as is denoted by a character in the TWiG matrix (char. 59 in the Turner et al., 2012, analysis). Turner et al. (2012) scored *Albertosaurus* and *Gorgosaurus* as the only two coelurosaurs lacking a large fenestra, but this is incorrect, as the condition in these taxa is essentially identical to that in other tyrannosaurids such as *Alioramus* and *Tyrannosaurus*, which are correctly scored for a large fenestra. Therefore, all known coelurosaurs possess a large fenestra leading into an ectopterygoid sinus, and the presence of this condition in outgroups strongly suggests that it is primitive for not only Coelurosauria, but at a much deeper node in Theropoda (or Archosauria).

There is some variation in the size and extent of the ectopterygoid sinus in coelurosaurs, and several unusual features are restricted to derived tyrannosaurids. Most of these have to do with the size of the sinus in large-bodied tyrannosaurids. In *Alioramus*, *Daspletosaurus*, *Tarbosaurus* (fig. 15E), and *Tyrannosaurus*, the sinus is so enlarged that it visibly inflates the body of the ectopterygoid and the pterygoid process, resulting in an ectopterygoid that appears "puffy" (Brusatte et al., 2010a: char. 129, and references therein). In *Bistahieversor*, *Tarbosaurus*, and *Tyrannosaurus*, there are large pneumatic foramina on the external surface of the jugal process that lead into the ectopterygoid sinus (Brusatte et al., 2010a: char. 130; Carr and Williamson, 2010). The jugal process itself is visibly inflated by the sinus in *Albertosaurus*, *Gorgosaurus*, *Alioramus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* (Brusatte et al., 2010a: char. 131; Carr and Williamson, 2010). Finally, the pneumatic fenestra on the ventral surface of the bone is slotlike in most theropods, but an enormous ovoid fenestra in *Alioramus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* (Brusatte et al., 2010a: char. 132; Carr and Williamson, 2010).

Witmer (1997a) also described a second ectopterygoid pneumatic sinus that is apparently restricted to a subset of derived dromaeosaurids (e.g., *Deinonychus*, *Saurornitholestes*). This sinus excavates the dorsal surface of the ectopterygoid, and it and the ventral sinus (which is also present in these dromaeosaurids) are likely pneumatized from distinct diverticula, perhaps

from two very different cranial sinus systems. The dorsal sinus is not present in *Alioramus*, nor in any other known tyrannosauroid, non-paravian coelurosaur, or non-coelurosaurian outgroup. CT scans, however, may show that it is more widely distributed among theropods (especially derived birdlike taxa) than currently realized. The dorsal sinus is atomized as a separate character in the TWiG dataset (Turner et al., 2012: char. 60).

Surangular: Surangular pneumaticity is extremely unusual among nonavian theropods. As far as we know, it is present only in derived tyrannosauroids, in which there is a deep pneumatic pocket immediately caudodorsal to the surangular foramen. This pocket is certainly pneumatic, because the CT scans of *Tyrannosaurus* presented by Brochu (2003) show that it extends inside the surangular, passes through the bone, and continues into the articular. The pocket is present in *Bistahieversor*, *Albertosaurus*, *Gorgosaurus*, *Alioramus*, *Daspletosaurus*, *Tarbosaurus* (fig. 15F), and *Tyrannosaurus* (fig. 14C; see review in Brusatte et al., 2012).

Intriguingly, the presence of a pneumatic pocket in the surangular is exactly correlated with the presence of an enlarged surangular foramen in those tyrannosauroids that can be scored for both characters. The surangular foramen, as this term is used here, does not necessarily refer to a pneumatic opening. It is an opening on the lateral surface of the surangular that perforates the bone, thereby connecting the lateral surface of the skull and the region medial to the jaws. It is present in most theropods, including many that do not have obvious signs of surangular pneumaticity. It has long been noted that derived tyrannosaurids are unique in possessing a very large surangular foramen that is approximately 30% of the dorsoventral height of the surangular, as opposed to the tiny openings of other theropods, which are very small (rarely larger than a centimeter in diameter, even in large-bodied theropods like *Allosaurus*) (Holtz, 2001, 2004; Currie et al., 2003; see review in Brusatte et al., 2012). As far as we know, the function of such an enlarged surangular foramen has never been discussed with certainty.

We hypothesize here that the enlargement of the surangular foramen of derived tyrannosauroids is associated with the development of surangular pneumaticity. It could be that the enlarged foramen transmitted a pneumatic diverticulum from the region medial to the lower jaws to the exterior surface of the surangular (or in the opposite direction). Perhaps this diverticulum would then have swept caudally along the lateral surface of the surangular to invade the pneumatic pocket. Or, if the direction was reversed, perhaps the diverticulum began in the articular, passed through the surangular, then swept rostrally along the lateral surface of the surangular before diverting medially through the large surangular foramen. CT scans of additional theropods should reveal whether surangular pneumaticity is perhaps more widespread than currently considered, and therefore maybe present in non-tyrannosauroids that do not possess enormous surangular foramina. Additional CT scans should also help confirm the source of surangular pneumaticity in tyrannosauroids. Brochu's (2003) discovery of a pneumatic conduit between the surangular and the articular in *Tyrannosaurus* makes it plausible that the articular, a bone that is commonly pneumatic in theropods, was the source of surangular pneumaticity. But this needs to be tested with additional data.

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