Cranial pneumaticity of *Ornithomimus edmontonicus*
(Ornithomimidae: Theropoda)

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Discussion

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Computer access and software

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ABSTRACT

Modern archosaurs have extensive pneumatic invasions derived from nasal and tympanic sinuses. These are present in many fossil archosaurs, but their evolutionary history has yet to be clarified. A full description of the cranial pneumaticity of a well-preserved ornithomimid theropod is presented to help clarify the evolution of this soft tissue using CT scan data and 3D reconstruction. The cranial sinuses of *Ornithomimus edmontonicus* represent nearly all cranial sinuses of birds and add new information to the range of that of ornithomimids. Phylogenetic comparisons of cranial pneumaticity across theropods with emphasis on *O. edmontonicus* imply a novel homology between the jugal fossa or recess of non-avian theropods and the suborbital diverticulum of birds. Comparisons also establish the presence of an avian-like nasal sinus morphology at Neotetanurae and tympanic sinus morphology at Coelurosauria.

RÉSUMÉ

Les archosauriens modernes ont des invasions pneumatiques extensives dérivées de leurs sinus nasales et tympaniques. Ils sont présents dans de nombreux fossiles d'archosauriens, mais l'histoire de leur évolution demeure incertaine. Une description complète de la pneumaticité crâniens d'un théropode ornithomimidé bien préservé aide à clarifier l'évolution de ces tissues mous à l'aide de donnés d'un scanneur CT et de la reconstruction 3D. Les sinus crâniennes de *Omithomimus edmontonicus* représentent presque tous les sinus crâniens des oiseaux et rajoutent de nouvelles informations en ce qui à trait aux ornithomimidés. Les comparaisons phylogénétiques de la pneumaticité crânienne à travers les théropodes avec une emphase sur *O. edmontonicus* suggèrent une nouvelle homologie de la *jugal fossa* ou la dépression des théropodes non-aviaires et le diverticulum sous-orbital des oiseaux. Les comparaisons permettent aussi d'établir la présence de sinus nasals à morphologie aviaire au *Neotetanurae* et de sinus à morphologie tympanique au *Coelurosauria*.

CHAPTER 1. INTRODUCTION AND LITERATURE REVIEW

1.1. Introduction

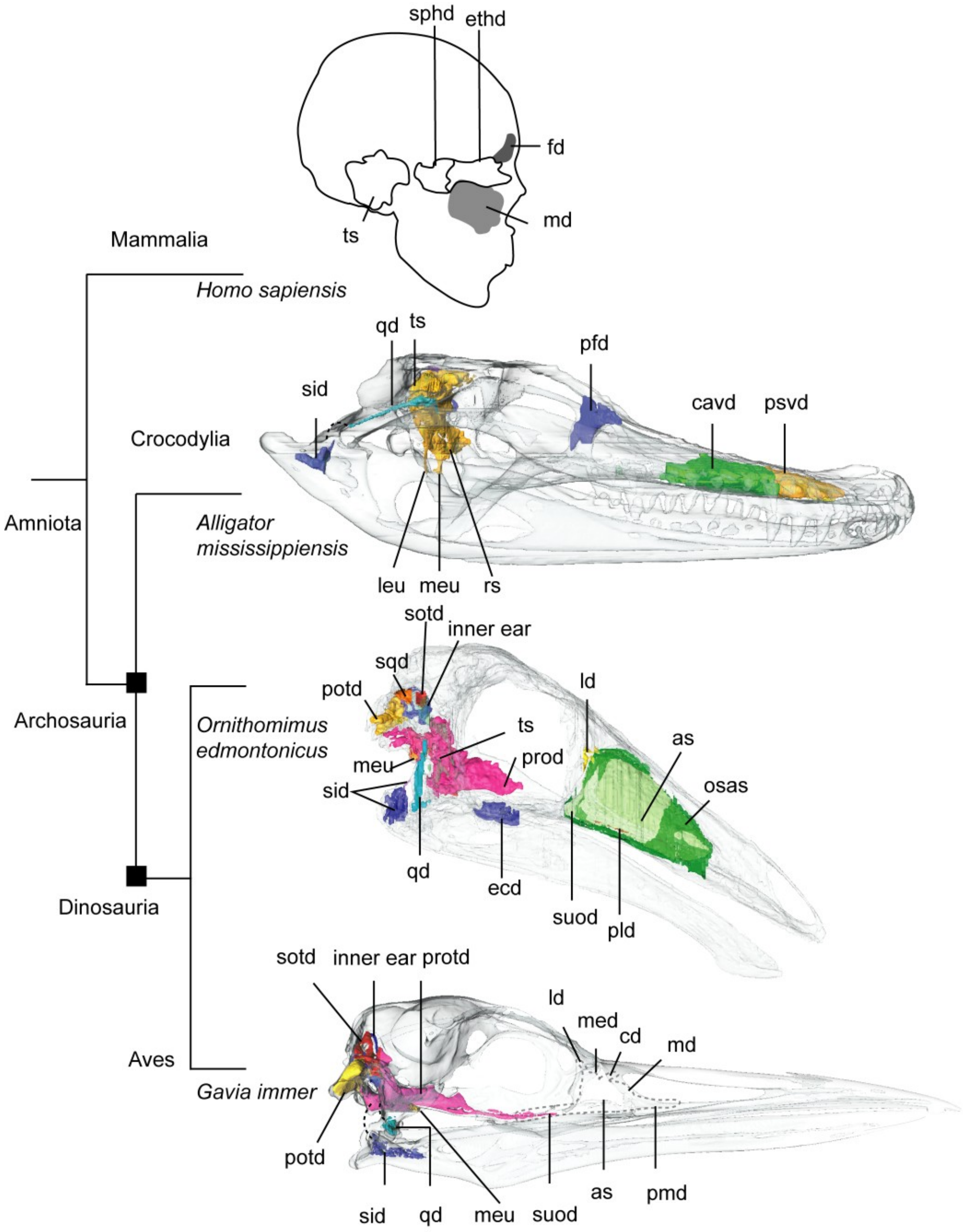
Dinosauria originated approximately 225 million years ago and dominated terrestrial ecosystems for the next 150 million years (Sereno, 1999). Their long history and diversity within a geographic wide range of habitats are reflected in much complex morphologies. Recently much attention has been paid toward the internal cranial anatomy of dinosaurs thanks to computed tomographic (CT) imaging and computer-aided three-dimensional reconstructions. Cranial pneumatic morphology, in particular, has received recent attention because of its complex morphology and putative functions of reducing head density, increasing relative bone strength, and physiological processes such as cooling.

Pneumaticity is a condition where diverticula, epithelial outgrowths of the sinuses, penetrate into soft and/or bony tissues. I use the terms of 'sinus' and 'diverticulum' to refer to only soft tissues in this thesis to differentiate from bony anatomy, such as recesses, because often these terms have been used in reference to the same morphologies.

When these diverticula enter bones, they do so via foramina that pass into internal chambers or simply as blind fossae on the bone surfaces. These osteological signatures are used to determine the presence and extent of pneumaticity. Of course, there may be numerous pneumatic diverticula that only penetrate soft tissues, such as a number of nasal diverticula in modern birds, but only those that leave an osteological signature can be mapped with some degree of certainty in fossil taxa.

Cranial pneumaticity is known to have evolved independently in both Archosauria and Mammalia (Fig. 1). Nasal diverticula are common to most mammals and invade many facial bones. Extensive pneumatic diverticula from the nasal and tympanic sinuses are found in all modern archosaurs (crocodiles

FIGURE 1. The distribution of the cranial pneumaticity in amniote phylogeny. As representatives of extant archosaurs, the cranial pneumaticities of *Alligator mississippiensis* (TMM M-983) and *Gavia immer* (TCWC 13, 300) and an extinct archosaur, *Ornithomimus edmontonicus* (RTMP 95.110.1) were reconstructed in this study. Skull is oriented with the horizontal semicircular canal in the horizontal plane. The human figure is modified from Witmer and Ridgely (2008). Pneumatic structures not visible in the CT data are illustrated as dashed lines. **Abbreviations**: **as**, antorbital sinus; **cavd**, caviconchal diverticulum (=antorbital sinus); **cd**, conchal diverticulum; **ecd**, ectopterygoid diverticulum; **ethd**, ethmoid diverticulum ; **fd**, frontal diverticulum; **ld**, lacrimal diverticulum; **leu**, lateral eustachian tube; **md**, maxillary diverticulum; **med**, mesethmoid diverticulum; **meu**, median eustachian tube; **osas**, osteological correlates of the antorbital sinus; **pfd**, prefrontal diverticulum; **pld**, palatine diverticulum; **pmd**, premaxillary diverticulum; **potd**, postotic diverticulum of the periotic sinus (=CTR, caudal tympanic recess); **protd**, preotic diverticulum of the periotic sinus (=ATR, anterior tympanic recess); **psvd**, postvestibular diverticulum; **rs**, rhomboidal sinus; **sid**, siphoneal diverticulum; **sphd**, sphenoid diverticulum; **sotd**, supraotic diverticulum of the periotic sinus (=DTR, dorsal tympanic recess); **sqd**, squamosal diverticulum; **suod**, suborbital diverticulum; **qd**, quadrate diverticulum; **ts**, tympanic sinus. Figures are not scaled.


sphd
ethd
fd
md
ts
Mammalia
Homo sapiensis
qd
ts
pfd
sid
cavd
psvd
Crocodylia
Amniota
Alligator mississippiensis
leu
meu
rs
sotd
inner ear
sqd
potd
ld
ts
as
Archosauria
Ornithomimus edmontonicus
prod
meu
osas
sid
qd
ecd
Dinosauria
suod
pld
sotd
inner ear
protd
ld
med
cd
md
Aves
Gavia immer
potd
sid
qd
meu
suod
as
pmd

and birds). Osteological signatures of early evolution of this pneumaticity can be found in all known fossil Archosauriformes (Witmer, 1997a). Similarities of cranial pneumatic morphologies between crocodile and bird were used erroneously to support a close evolutionary relationship between the two clades by assuming that details of this anatomy were homologous between these taxa (Walker, 1972, 1990; Whestone and Martin, 1979; Whestone and Whybrow, 1983). These errors were symptomatic of the poor understanding of the evolution of this complex cranial pneumatic anatomy. Witmer (1990, 1995, 1997a, 1997b) has since clarified many issues surrounding the evolution and morphology of the cranial sinuses of archosaurs.

Sufficient cranial pneumatic morphology of extinct archosaurs closely related to birds has recently been described through the use of CT imaging and three-dimensional visualizations to begin revealing the evolution of this soft tissue anatomy (e.g., Kundrát and Janáček, 2007; Sampson and Witmer, 2007; Starck, 1995; Witmer, 1997a, 1997b; Witmer and Ridgely, 2008; Witmer et al., 2008). However, descriptions of this anatomy along the avian stem lineage have been restricted to taxa within Coelophysoidea, Abelisauroidea, Allosauroidea, Tyrannosauroidea, Oviraptorosauria, Troodontidae, and Dromaeosauridae.

The goal of this thesis is to examine the pneumatic anatomy of an ornithomimid to assess the evolution of this complex anatomy throughout the avian stem lineage. I describe the cranial pneumatic anatomy of a well-preserved *Ornithomimus edmontonicus* based on CT scan data using computer-assisted three-dimensional visualizations.

In the first chapter, I review the cranial pneumaticity in archosaurs and mammals. I summarize the origin and evolution of nasal pneumaticity in archosaurs in a phylogenetic framework derived from previous literature. The second chapter describes the materials and methods that were applied to the reconstructions of the skull, braincase, and cranial sinuses in *Ornithomimus edmontonicus*, *Alligator mississippiensis*, and *Gavia immer*. The reliability of osteological recess of cranial pneumaticity in *O. edmontonicus* was accessed using the CT data and reconstructions of modern archosaurs. I then describe the three-dimensional reconstructions of the cranial pneumaticity of *O. edmontonicus* as reconstructed from the CT scan data and 3D software. The results are discussed in the third chapter with emphasis on the evolution of cranial pneumatic morphologies along the non-avian theropod to avian transition. The evolutionary implications are then discussed by comparisons of cranial sinuses across this major evolutionary transition.

1.2. Overview of cranial pneumaticity

Cranial pneumaticities are derived from the nasal and tympanic sinuses. Although turtles and squamate lepidosaurs have extracapsular diverticula, only the extracapsular diverticula present in Archosauria and Mammalia tend to pneumatize surrounding bones (Witmer, 1999). A significant anatomical difference between these clades is that mammalian cranial diverticula are completely enclosed by bones whereas archosaurian cranial diverticula are often contained only within soft tissues (Witmer, 1995) (Fig. 1). Among mammals, the human nasal sinus has been examined in greatest detail (e. g., Koppe et al., 1999; Paul et al., 1995).

Contrary to the detailed knowledge of cranial sinuses, particulary human, functions of the sinuses remain enigmatic (e.g., Blaney, 1990; Blanton and Biggs, 1969). Their putative roles in mammals and archosaurs have been explored and summarized by Witmer (1997a). The proposed functions of cranial sinuses range from vocal resonators, localization of sounds, thermal insulation, humidification, flotation devices, facial architecture, weight reduction, to suggestions they may have no function at all (see detail in Witmer (1997a)). The only experimental study for a specific function in an extant taxon demonstrated that pneumatic structures may have aided in supporting the long sauropod neck (Schwarz-Wings and Frey, 2008). Because no definitive function which can be applied across all taxa has yet been identified, Witmer (1997a; pp. 57) proposed that a novel interpretation for the function of sinuses is "simply to expand and to promote pneumatization". Recently Witmer and colleagues (2008) suggested that the possible function for tympanic sinus as resonance effects compared by the extension of tympanic diverticula and length of cochlea. The length of cochlea has been generally treated as a rough proxy for the hearing capability and was confirmed by testing their relationships by Walsh et al. (2009).

Nasal diverticula of mammals are derived only from the nasal cavity proper, which is defined by Parson (1970) as the middle part of the nasal cavity. He divided the nasal cavity into three regions, from anterior to posterior: the vestibule, nasal cavity proper, and nasopharyngeal duct. Human nasal diverticula extensively pneumatize the maxilla, ethmoid, frontal, and sphenoid bones and occupy large portions of the head.

In contrast, nasal diverticula of archosaurs are more diverse because they probably originate from all three partitions of the nasal cavity. The diverse and extensive nasal diverticula of extant archosaurs are associated with an antorbital cavity in crocodiles, and an antorbital fenestra and cavity in birds.

Crocodylia

Huxry (1869) and Parker (1883) were among the first to examine the cranial pneumatic systems in crocodylians. More recent studies addressed the morphology of the antorbital cavity and the evolution of the closure of the antorbital fenestra within Crocodylomorpha (Busbey, 1995; Witmer, 1997a). CT scanning has aided in revealing the internal cranial cavities and accessory cavities in *Alligator mississippiensis* (Rowe et al., 1999). In addition, Witmer (1995, 1997a) documented crocodylian and avian antorbital sinuses based on dissections and previous literature. Diverticula of the tympanic sinus are described in individual extinct and extant taxa by Busbey and Gow (1984), Colbert (1952), Crompton and Smith (1980), Iordansky (1973), Nash (1975), Tarsitano (1985), Tarsitano et al. (1989), Tykoski et al. (2002), and Wu et al. (1994). Hechet and Tarsitano (1983) noted that the presence of diverticula indicate informative characters defining each suborder. The tympanic sinuses of Sphenosuchians, such as *Sphenosuchus* and *Dibothrosuchus,* are most thoroughly described and have been compared to those of modern crocodiles and birds (Walker, 1990; Wu and Chatterjee, 1993).

Aves

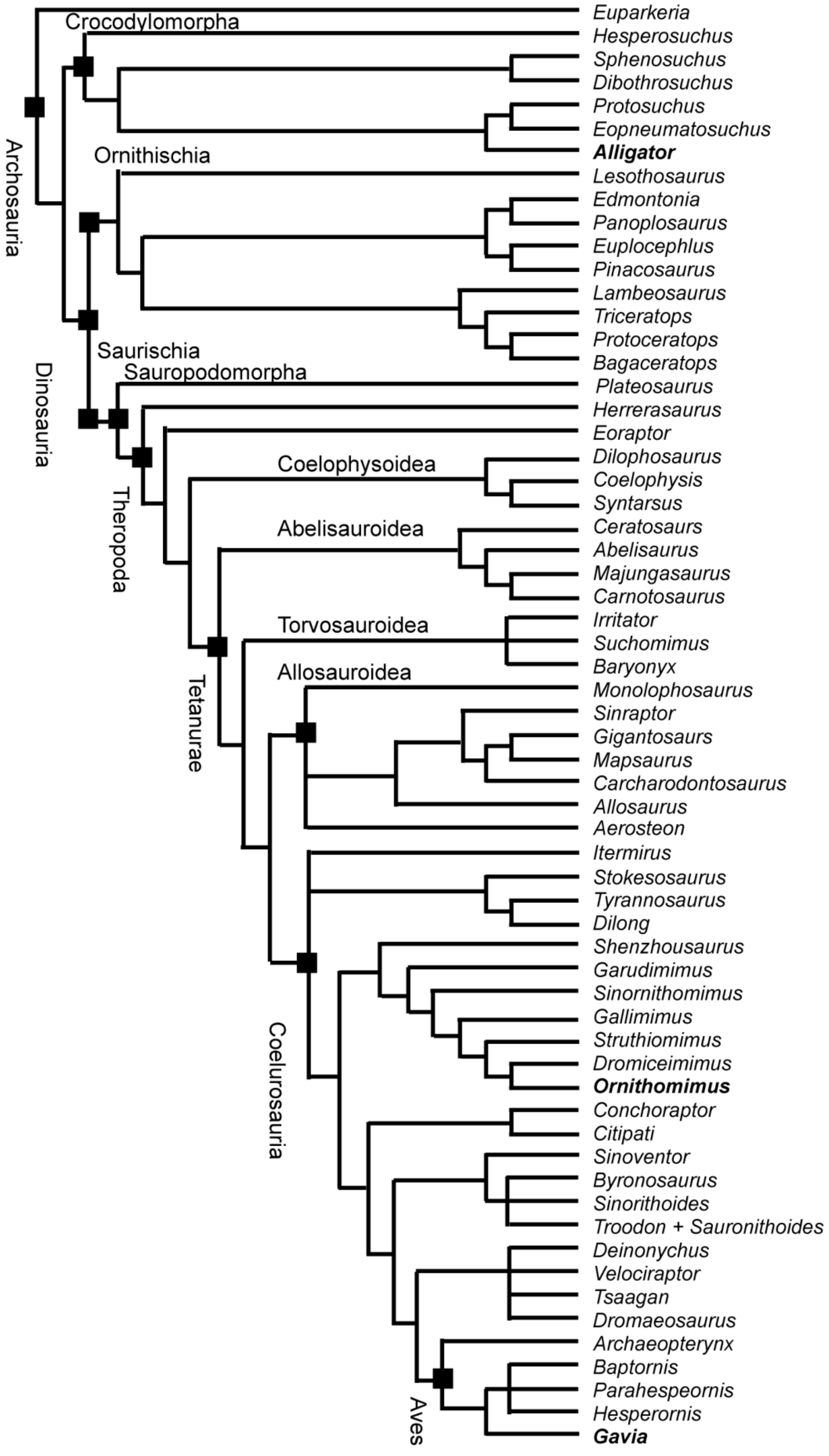
Hunter (1774) was likely the first to note the presence of cranial pneumaticity in birds. Since then, the avian skull has been recognized as being extensively pneumatized (e.g., de Beer, 1937; Winkler, 1985). The majority of researches on avian cranial pneumaticity have focused on descriptive anatomy (e.g., Norberg, 1978; Saiff, 1974, 1976, 1978, 1981, 1982, 1988) or development studies of extant taxa (e.g., Bremer, 1940; Hogg, 1990; Jollie, 1957; T. J. Parker 1891; W. K. Parker, 1866, 1869). Starck (1995) reconstructed several avian tympanic sinuses (Rhea, Tinamou, Emu, Cassowary, Kiwi, Ostrich, and Quail) based on CT scans for anatomical comparisons with quantitative data of tympanic air spaces. He implied the functional resonance effects for the large air space in the middle ear of birds but admitted that the physiological data is lacking.

Witmer (1990) has reexamined the osteological recesses present in several Mesozoic avian taxa and was the first to interpret avian cranial pneumaticity in an evolutionary context. Chatterjee (1991) reported several avian-like pneumatic morphologies in the braincase of a putative Triassic stem bird, *Protoavis* and shed light on the origin of Aves by comparing avian pneumatic features between birds and theropod dinosaurs. The validity of this taxon has since been disputed but, nevertheless, the extraordinary degree of cranial pneumaticity in the braincase of this Triassic archosaur remains.

Non-avian Dinosauria

Ornithischian and saurischian dinosaurs are monophyletic sister clades within Dinosauria (Fig. 2). The most basal ornithischian, *Lesothosaurus* and nearly all other ornithischians have an antorbital fenestra and thus probably would have had some degree of nasal pneumatic diverticula (Witmer, 1997a). The fenestra is generally small within the clade. Witmer (1997a, 1997b) suggested the reduced antorbital cavity and fenestra of ornithischian dinosaurs may be related to their specialized feeding apparati. However, some ornithischians have rare invasions of pneumatic diverticula into bones

FIGURE 2. The phylogenetic relationships of the taxa relevant to the text. The phylogeny of crocodylomorphs, basal theropods, and theropods are referred to Wu et al. (2001), Smith et al. (2007), and Norell et al. (2006), respectively. Bold taxa were reconstructed in this study.

Euparkeria
Crocodylomorpha
Hesperosuchus
Sphenosuchus
Dibothrosuchus
Protosuchus
Eopneumatosuchus
Alligator
Archosauria
Ornithischia
Lesothosaurus
Edmontonia
Panoplosaurus
Euplocephlus
Pinacosaurus
Lambeosaurus
Triceratops
Protoceratops
Bagaceratops
Saurischia
Sauropodomorpha
Dinosauria
Plateosaurus
Herrerasaurus
Eoraptor
Coelophysoidea
Dilophosaurus
Coelophysis
Syntarsus
Theropoda
Abelisauroidea
Ceratosaurs
Abelisaurus
Majungasaurus
Carnotosaurus
Torvosauroidea
Irritator
Suchomimus
Baryonyx
Allosauroidea
Tetanurae
Monolophosaurus
Sinraptor
Gigantosaurs
Mapsaurus
Carcharodontosaurus
Allosaurus
Aerosteon
Itermirus
Stokesosaurus
Tyrannosaurus
Dilong
Shenzhousaurus
Garudimimus
Sinornithomimus
Gallimimus
Struthiomimus
Dromiceimimus
Ornithomimus
Coelurosauria
Conchoraptor
Citipati
Sinoventor
Byronosaurus
Sinorithoides
Troodon + Sauronithoides
Deinonychus
Velociraptor
Tsaagan
Dromaeosaurus
Archaeopterynx
Baptornis
Parahespeornis
Hesperornis
Aves
Gavia

surrounding the nasal diverticula. Basal ceratopsians, such as *Protoceratops* and *Bagaceratops,* would have had a prominent maxillary sinus that has communicated with the antorbital fossa (Osmólska, 1986).

Although Ankylosauridae secondarily close an antorbital fenestra, the clade was thought to have had large sinuses within their ornamented domed skulls. Witmer and Ridgely (2008) investigated the internal anatomy of *Panoplosaurus* and *Euoplocephalus* and suggested that there were no nasal sinuses in either taxon. Instead these have complicated narial pathways with no diverging diverticula. However, the pneumatic morphology of ankylosaurs may be more variable because a paranasal aperture in the premaxilla has been reported in *Pinacosaurus grangeri* (Hill et al., 2003) and *Edmontonia rugosidens* (Vickaryous, 2006).

Complex nasal pathways similar to those of Ankylosauridae are present in lambeosaurine hadrosaurs, such as *Lambeosaurus*. *Lambeosaurus* possess a high domed cranial crest composed of primarily a posterodorsally elongate premaxillary bone. The narial chamber within this crest extends to lateral diverticula rostrally and a median chamber caudolaterally. These diverticula have been suggested to have a function as resonating chambers for vocalization (Evans, 2006; Weishampel, 1981).

The antorbital fenestra of Ceratopsidae is greatly reduced but the antorbital sinus in the maxilla would have been present in all taxa in this family. In addition, the nasal diverticula would have invaded the premaxilla in chasmosaurine ceratopsids and is particularly elaborated in *Triceratops* (Sampson and Witmer, 1999). Ceratopsids are also characterized by a supracranial cavity which is often referred to as a “frontal sinus” (e.g., Farke, 2006; Sampson, 1997). However, due to its location and development, the pneumatic origin of this cavity is undetermined (Witmer, 1997b). No elaboration of the tympanic sinus appears to have been present in ornithischians (Witmer, 1997b).

Among the saurischian dinosaurs, sauropodomorphs do not appear to have had extensive diverticular invasions. The antorbital fenestra of this clade is generally reduced much like the condition in ornithischians (Witmer, 1997a). Prosauropods possess an antorbital fossa bounding the antorbital fenestra similar to the condition in early theropods. Prosauropods, such as *Plateosaurus,* also possess foramina for nasal diverticula to penetrate into the nasal, thus Witmer (1997a) suggested this pneumatic condition might be homologous to similar anatomies found in theropods. The tympanic diverticula of sauropodomorphs do not appear to have invaded the braincase with the exception of the preotic recess in the prosauropod, *Plateosaurus* (Witmer, 1997b).

Non-avian theropods, in contrast, appear to have had extensive invasions of nasal and tympanic sinuses into surrounding bones (Witmer 1997a, 1997b; Witmer and Ridgely, 2008; Witmer et al., 2008). The high degree of cranial pneumaticity in this clade has been described by numerous authors for a number of taxa. These include basal theropods such as *Herrerasaurus* (Sereno and Novas, 1993) and *Eoraptor* (Sereno et al., 1993), Coelophysoidea, such as *Coelophysis bauri* (Colbert, 1989), *Syntrasus rhodsiensis* (Raath, 1985), and *Syntarsus kayentakatae* (Rowe, 1989; Tykoski, 1998), Abelisauroidea, such as *Majungasaurus* (Sampson and Witmer, 2007), *Ceratosaurus* (Madsen and Welles, 2000), and *Carnotosaurus sastrei* (Bonaparte et al., 1990), Torvosauroidea, such as *Irritator challengeri* (Sues et al., 2002), *Baryonyx walkeri* (Charig and Milner, 1997), and *Suchomimus tenerensts* (Sereno et al., 1998), Allosauroidea, such as *Allosaurus fragilis* (Chure and Madsen, 1996; Madsen, 1976), *Carcharodontosaurus saharicus* (Brussatte and Sereno, 2007), *Mapusaurus roseae* (Coria and Currie, 2006), *Giganotosaurus carolinii* (Coria and Currie, 2002; Coria and Salgado, 1995), *Sinraptor dongi* (Currie and Zhao, 1993a), and *Monolophosaurus jiangi* (Zhao and Currie,1993). Cranial pneumatic anatomy has also been described for numerous coelurosaurs. These include descriptions for Tyrannosauroidea, such as *Albertosaurus libratus* (Russell, 1970), *Tyrannosaurus* (Carr, 1999; Carr et al., 2005; Molnar, 1991; Brochu, 2003; Currie, 2003), *Dilong paradoxus* (Xu et al., 2004), *Stokesosaurus clevelandi* (Chure and Madsen, 1998) and *Itermius* (Kurzanov, 1976), ornithomimids, such as *Shenzhosaurus orientalis* (Ji et al., 2003), *Struthiomimus altus* and unnamed IGM 100/987 specimen (Makovicky and Norell, 1998), *Gallimimus bullatus* (Osmólska et al., 1972), *Garudimimus brevipes* (Kobayashi and Lü, 2003), and *Sinornithomimus altus* (Kobayashi and Barsbold, 2005), Oviraptorosauria, such as *Oviraptor*, underdetermined GIN A, GIN B, ZPAL MgD I/96 specimens (Osmólska et al., 2004; Maryańska and Osmólska, 1997), *Citipati osmolskae* (Clark et al., 2002), and *Conchoraptor gracilis* (Kundrát and Janáček, 2007), Troodontidae such as *Sinoventor changii* (Xu et al., 2002), *Sinornithoides youngi* (Currie and Dong, 2001), and *Troodon formosus* (Currie, 1985; Currie and Zhao, 1993b), and *Byronosaurus jaffei* (Makovicky et al., 2003), and Dromaeosauridae, such as *Deinonychus antirrhopus* (Brinkman et al., 1998; Ostrom, 1969), *Velociraptor mongoliensis* (Barsbold and Osmólska, 1999; Norell et al., 2004), *Dromaeosaurus albertensis* (Currie, 1995), and *Tsaagan mangas* (Norell et al., 2006). Several comparative studies of these cranial sinuses in an evolutionary context have been published by Witmer (1997a, 1997b).

1.3. The origin and evolution of nasal sinuses: Archosauriformes

A portion of Chapter 1.3-3.3 is from RUI TAHARA and HANS C. E. LARSSON. Cranial pneumatic anatomy of *Ornithomimus edmontonicus* (Ornithomimidae: Theropoda) and evolution of this soft tissue in Theropoda. *Journal of Vertebrate Paleontology. Submitted.*

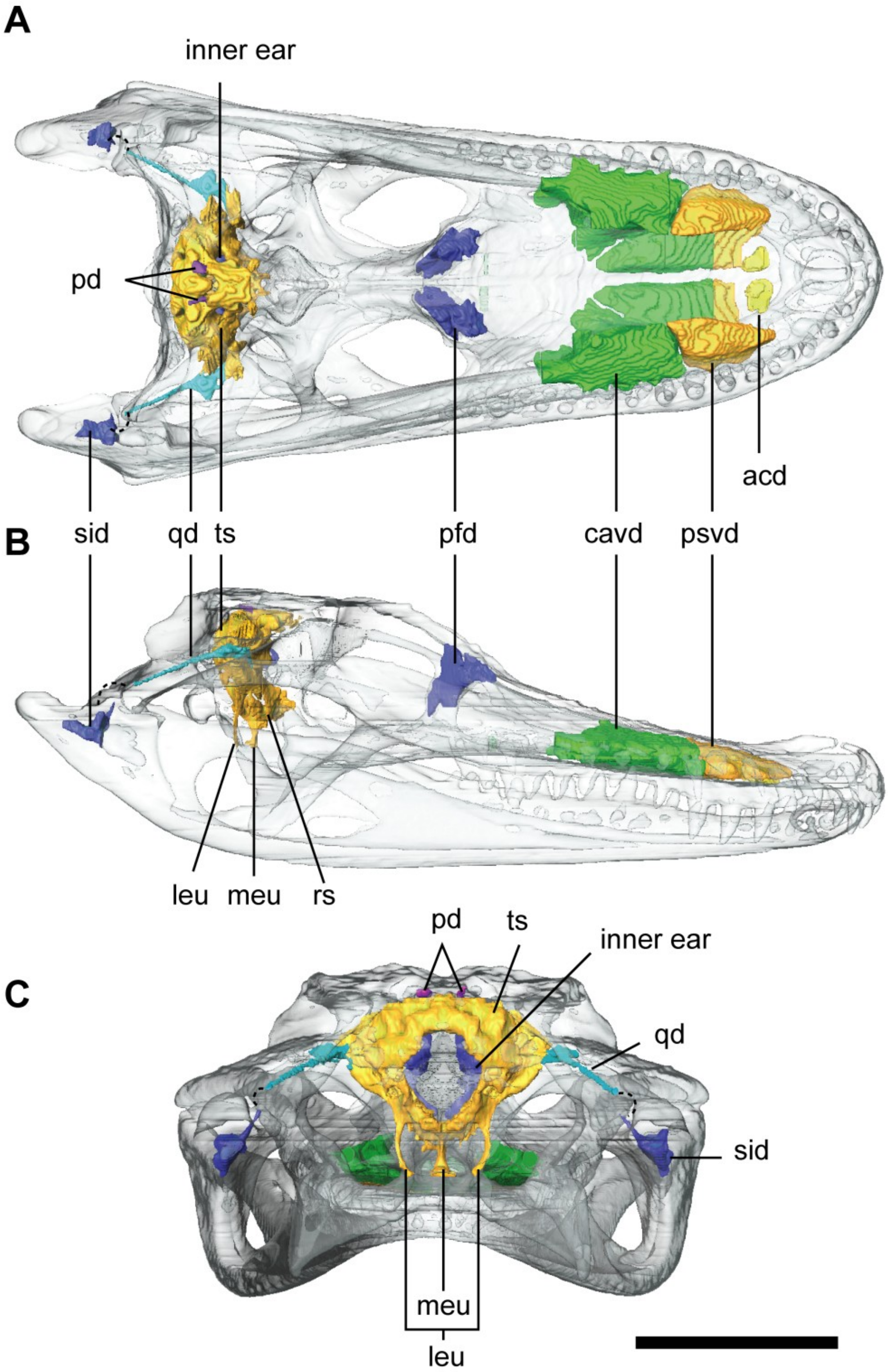
Antorbital sinus

Before detailing the cranial pneumatic anatomy of a single taxon, I present first a brief overview of this anatomy in related clades. Archosauriformes are diagnosed by the presence of an antorbital fenestra that is bounded by the maxilla, nasal, lacrimal, and / or jugal bones. This fenestra would have housed an antorbital diverticulum from the nasal sinus resulting in the formation of the antorbital cavity because the antorbital cavity of all modern archosaurs houses the same diverticulum (Witmer, 1997a). The antorbital cavity is floored by the palatine. Basal archosauriformes, such as *Euparkeria,* have no osteological correlates of pneumatic diverticula into or onto bones surrounding the antorbital sinus (Ewer, 1965).

The antorbital cavity of modern crocodiles is internalized in the snout because of a complete closure of the antorbital fenestra (Witmer, 1995). Modern crocodiles often have five pneumatic recesses within their nasal cavity proper. These are the caviconchal, postvestibular, maxillary cecal, prefrontal, and caudolateral recesses (Witmer, 1995). Associated with the nasopharyngeal duct, there are some recesses into the palatine, and pterygoid. Reconstructed cranial sinuses of *Alligator mississippiensis* (Texas Memorial Museum [TMM M-983]) presented to have the large caviconchal, postvestibular, accessory cavities in the maxilla, and prefrontal recess from the nasal cavity proper, and a palatine recess and pterygoid recess originated from the nasopharyngeal duct, and a small parietal recess (Fig. 3).

Modern birds have consistently six subsidiary diverticula from the antorbital sinus. These are the premaxillary, maxillary, lacrimal, conchal,

FIGURE 3. 3D reconstruction of cranial sinuses of *Alligator mississippiensis* (TMM M-983) based on the CT data. **A**: dorsal view, **B**: right lateral view, **C**: posterior view. Pneumatic structures not visible in the CT data are illustrated as dashed lines. **Abbreviations**: **acd**, accessory diverticulum; **cavd**, caviconchal diverticulum (=antorbital sinus); **leu**, lateral eustachian tube; **meu**, median eustachian tube; **pd**, parietal diverticulum; **pfd**, prefrontal diverticulum; **psvd**, postvestibular diverticulum; **qd**, quadrate diverticulum; **rs**, rhomboidal sinus; **sid**, siphoneal diverticulum; **ts**, tympanic sinus. Scale bar equals 5cm.


A
inner ear
pd
acd
sid
qd
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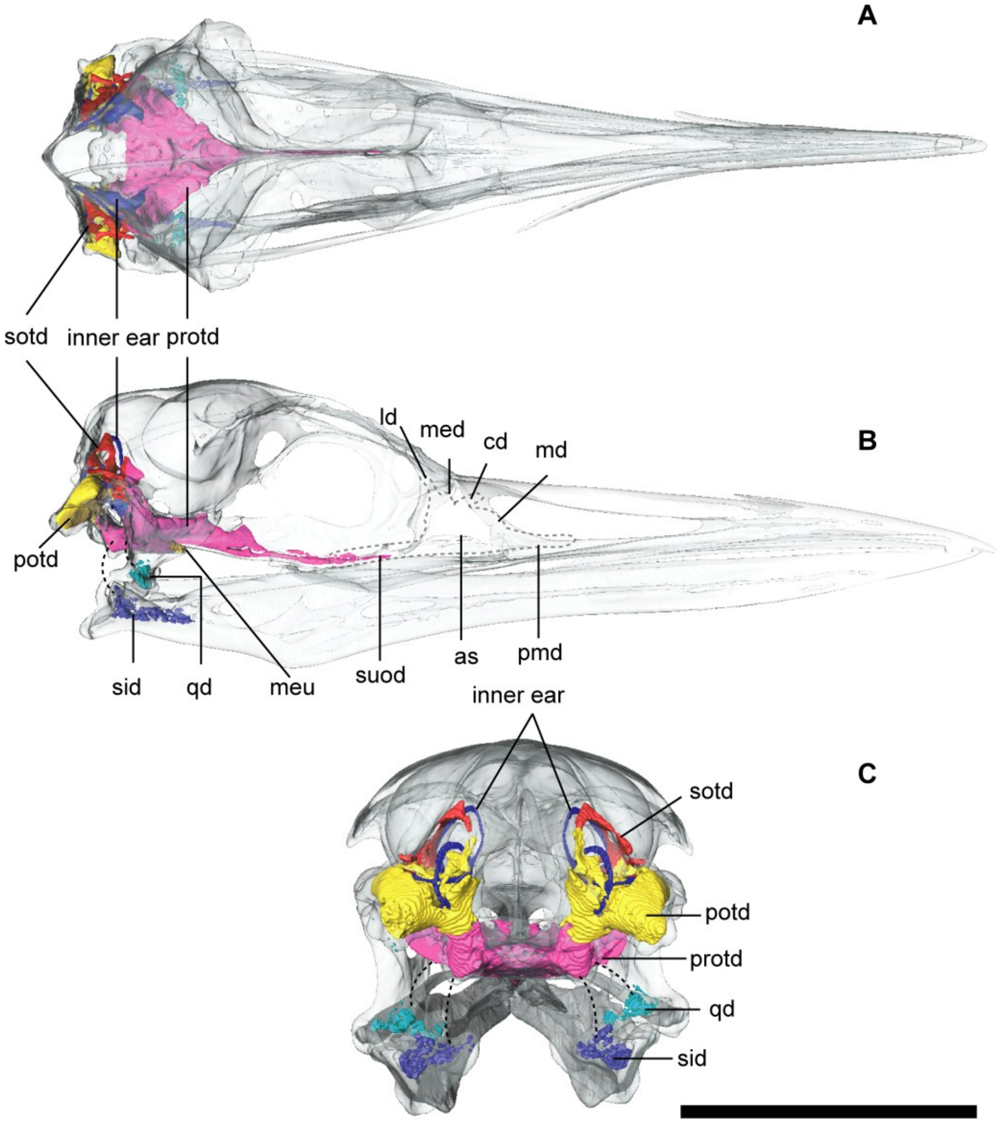
pfd
cavd
psvd
B
leu
meu
rs
C
pd
ts
inner ear
qd
sid
meu
leu

FIGURE 4. 3D reconstruction of cranial sinuses of *Gavia immer* (TCWC 13, 300) based on the CT data. **A**: dorsal view, **B**: right lateral view, **C**: posterior view. Pneumatic structures not visible in the CT data are illustrated as dashed lines. **Abbreviations**: **as**, antorbital sinus; **cd**, conchal diverticulum; **ld**, lacrimal diverticulum; **md**, maxillary diverticulum; **med**, mesethmoid diverticulum; **meu**, median eustachian tube; **pmd**, premaxillary diverticulum; **potd**, postotic diverticulum of the periotic sinus (=CTR, caudal tympanic recess); **protd**, preotic diverticulum of the periotic sinus (=ATR, anterior tympanic recess); **qd**, quadrate diverticulum; **sid**, siphoneal diverticulum; **sotd**, supraotic diverticulum of the periotic sinus (=DTR, dorsal tympanic recess); **suod**, suborbital diverticulum. Scale bar equals 5cm.


A
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sid

mesethmoid, and suborbital diverticula (Witmer, 1995). Due to the less or absence of pneumatization of surrounding bones (discussed in Chapter 3 in detail), only the maxillary diverticula indicate the clear trace of the osteological recesses in modern birds. However, the maxillary recess could not be identified from the CT data. Thus, the nasal diverticula of *Gavia immer* (Texas Cooperative Wildlife Collection [TCWC 13,300]) are putatively reconstructed by estimated extensions based on Witmer (1990) and Witmer and Ridgely (2008) (Fig. 4). In addition to the maxillary recess, the lacrimal indicates the osteological signature of the diverticula consistently in Mesozoic birds (Witmer, 1990).

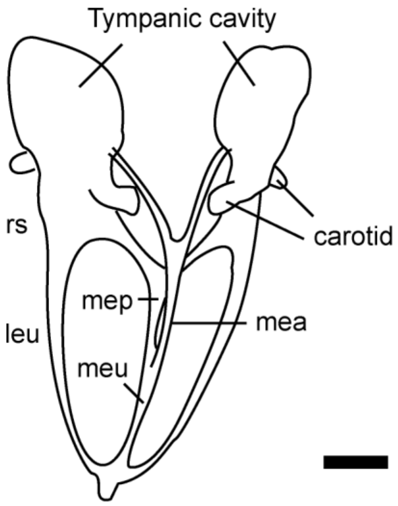
Of these nasal sinuses, the crocodylian caviconchal sinus is likely homologous to the avian antorbital sinus (Witmer, 1995). The other nasal diverticula of crocodiles and birds are less easily comparable to each other because crocodylian diverticula have extensive osteological correlates while many diverticula in modern birds lie on the surface of the bones. Thus, osteological correlates of these diverticula occur independently within each extant stem lineage.

Eustachian system

A pneumatic tympanic recess is common to many tetrapods and is always supplied by Eustachian tubes spanning between the tympanic cavity and the pharynx. This supply is more elaborate in crocodiles and birds with the presence of a third, median Eustachian tube that pierces the ventral basioccipital-basisphenoid suture. The Eustachian system and its associated structure (rhomboidal sinus) were first examined by Owen (1850) and illustrated in *Crocodilus acutus* by Colbert (1946)(Fig. 5). The median Eustachian tube is divided into an anterior portion that runs to the basisphenoid (basisphenoid recess) and runs into posterior to the basioccipital (basioccipital recess) in crocodylians.

This median Eustachian tube is absent in basal pseudosuchians and

FIGURE 5. Tympanic cavities and eustachian tubes of *Crocodilus acutus* in an antero-oblique view. Modified from Colbert (1946) and Walker (1990). **Abbreviations**: **leu**, lateral eustachian tube; **meu**, median eustachian tube; **mea**, anterior branch of median eustachian tube; **mep**, posterior branch of median eustachian tube; **rs**, rhomboidal sinus. Scale bar equals 1cm.


Tympanic cavity
rs
carotid
mep
mea
leu
meu

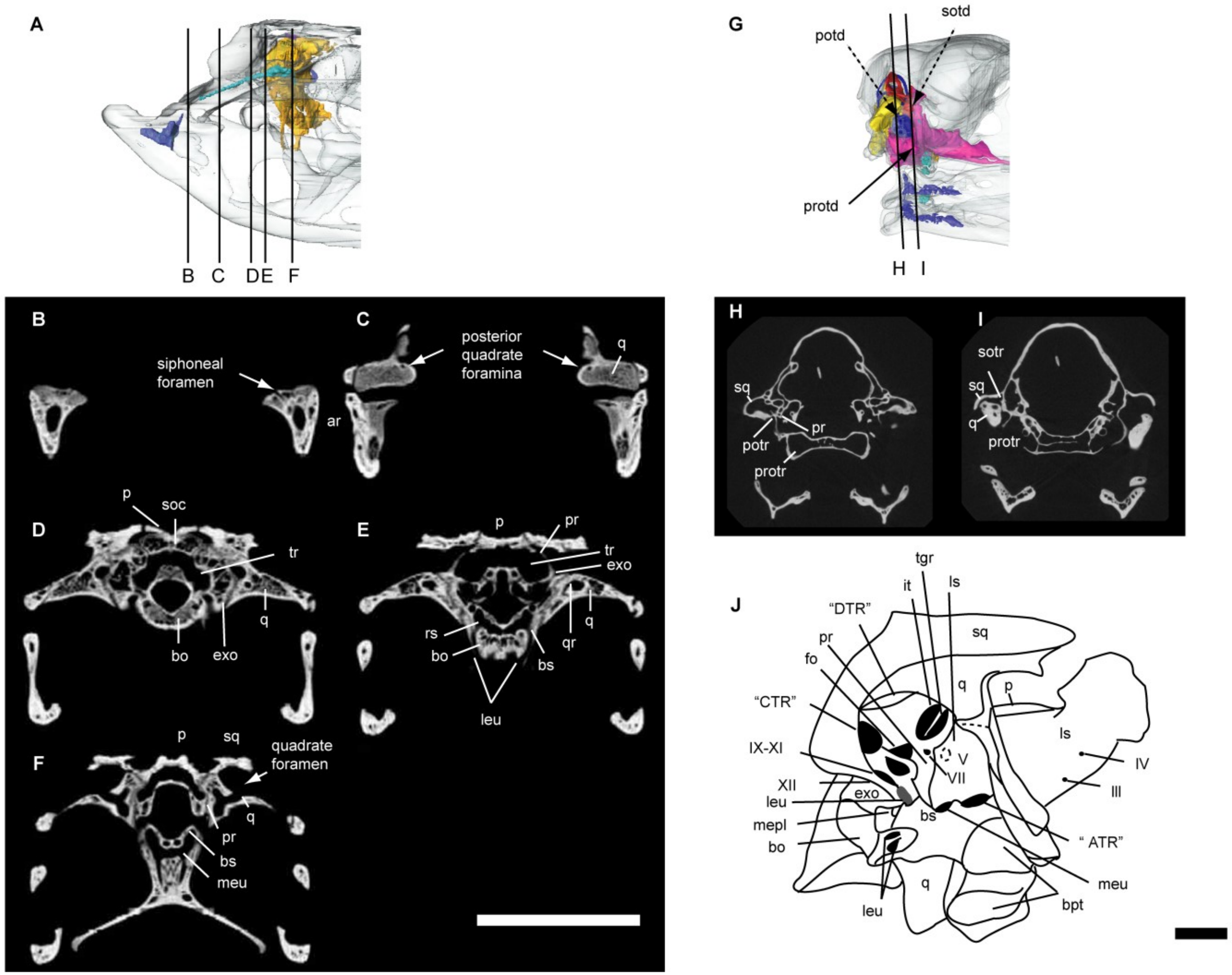
ornithodirans indicating an independent origin of this structure in crocodiles and birds. The origin of the median Eustachian system in crocodiles appears within basal crocodylomorphs. Some sphenosuchians, such as *Hesperosuchus*, have no clear trace of a median Eustachian recess or tube (Colbert, 1952). However, *Sphenosuchus* exhibits deep recesses in the ventral basioccipital–basisphenoid suture and suggests the presence of a median Eustachian recess that has not fully extended into the braincase and middle ear (Walker, 1990). Other sphenosuchians, such as *Dibothrosuchus*, have a fully elaborated median Eustachian system that would have penetrated the braincase and communicated with the middle ear (Wu and Chatterjee, 1993)(Fig. 6J). Protosuchians, such as *Eopneumatosuchus colberti* and *Protosuchus haughtoni* have extremely elaborated periotic sinuses associated with a lateral and median Eustachian system (Busbey and Gow, 1984; Crompton and Smith, 1980).

The origin of the avian medial Eustachian system appears to be within theropod dinosaurs. Larsson (1996) first identified this structure within the basioccipital-basisphenoid suture of *Carcharodontosaurus*, a large allosauroid. A number of other theropods appear to have this structure such as Torvosauroidea and Troodontidae. But the distribution of the structure within theropod phylogeny indicates that it may be more associated with large body size rather than have any straightforward phylogenetic pattern (Larsson, unpublished data). The tympanic sinus of modern crocodiles and birds can be divided into two main pneumatic systems. One extends ventrolaterally into the quadrate and articular while the other extends medially over and into the braincase.

Tympanic sinus: *branchial pneumatic system*

To simplify the discussion, a new term to refer to the quadrate and articular pneumatic diverticula as the *branchial pneumatic system* is introduced here. This name reflects the association of these diverticula with

FIGURE 6. Comparisons of tympanic pneumaticities among *Alligator mississippiensis* (TMM M-983), **A**-**F**, *Gavia immer* (TCWC 13, 300), **G**-**I**, and early crocodylomorph, *Dibothrosuchus,* **J**. Coronal CT data of *Alligator* ndicating tympanic pneumaticity. CT slices of B-F are correspondent to the alphabets indicated in the reconstructed skull of A. Coronal CT data of *Gavia* indicating the entries of periotic recesses. CT slices of H-I are correspondent to the alphabets indicated in the reconstructed skull of G. Tympanic recesses of *Dibothrosuchus* in right lateral view, J, (Modified from Wu and Chantterjee (1993)). All CT-sections are seen in anterior view, so that the right hand side of the figures corresponds to the left side of the specimen. Quotation marks indicate non-homology of the recess. **Abbreviations**: **III**, opening for oculomotor nerve; **IV**, opening for trochler nerve; **V**, opening for trigeminal nerve; **VII**, opening for facial nerve; **IX-XI**, openings for glossopharyngeal, vagus, and accessory nerves; **XII**, opening for hypoglossal nerve; **ar**, articular; **bo**, basioccipital; **bs**, basisphenoid; **bpt**, basipterygoid process; **exo**, exoccipital; **fo**, fenestra ovalis; **it**, intertympanic recess; **leu**, lateral Eustachian tube; **ls**, laterosphenoid; **mepl**, posterior branch of median eustachian tube; **meu**, median eustachian tube; **p**, parietal; **potd**, postotic diverticulum of the periotic sinus (=CTR, caudal tympanic recess); **pr**, prootic; **protd**, preotic diverticulum of the periotic sinus (=ATR, anterior tympanic recess); **q**, quadrate; **qr**, quadrate recess; **soc**, supraoccipital; **sotd**, supraotic diverticulum of the periotic sinus (=DTR, dorsal tympanic recess); **sq**, squamosal; **tr**, tympanic recess. Scale bar equals 5cm in A-I and 1cm in J.


A
B
C
DE
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B
siphoneal foramen
ar
C
posterior quadrate foramina
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D
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soc
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tr
exo
q
qr
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the palatoquadrate and Meckel's cartilages. In modern crocodiles, the branchial diverticula pass into the quadrate through a complex arrangement of multiple entries on the antero-, dorso-, and posteromedial surfaces of that bone. This anatomy has not yet been well described. A single pneumatic duct exits the quadrate near the medial mandibular hemicondyle, bridges the mandibular joint, and enters the articular (Figs. 3, 6B, C). This duct is called the siphoneum.

The branchial pneumatic system is also present in modern birds with two main diverticula that pneumatize the quadrate and articular independently (Witmer, 1990) (Fig. 4).

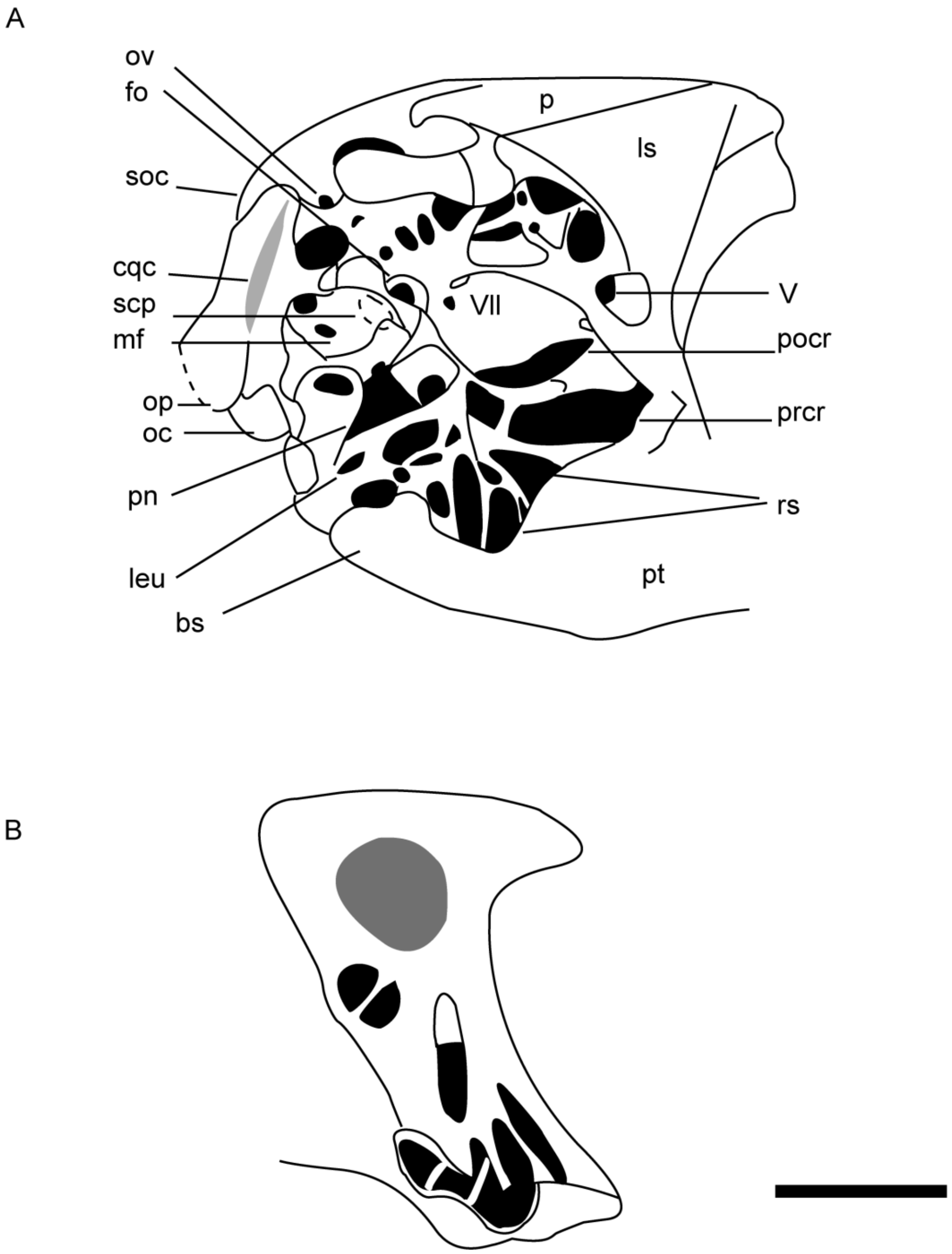
Contrary to the multiple complex diverticula in crocodylians, a single quadrate diverticulum is present in birds and enters the quadrate through a single medial or anteromedial foramen. Unlike crocodylians, there is no opening near the mandibular joint spanning between the quadrate and articular recess and the siphoneal diverticulum invades the articular independently without penetrating the quadrate. Many modern diving birds lack a pneumatized quadrate and have been attributed to a general decrease in pneumaticity associated with pachyostosis (O'Connor 2004). However, the quadrate of a modern adult *Gavia* (Texas Cooperative Wildlife Collection [TCWC 13,300]) was found to have internal spaces and a dorsomedial duct reminiscent of the typical avian quadrate diverticulum, but lacking an external opening (pers. obs.). Similarly, this specimen exhibits no external opening for the siphoneal diverticulum in the articular although a large chamber is present inside this bone. I suggest that this taxon may have had developed quadrate and siphoneal diverticula in early ontogeny, but the pachyostotic development of the quadrate and articular pinched off the diverticulum leaving a vestige of it within their body. Thus, adult avian apneumatic quadrates and articulars may be the result of the pachyostotic condition obscuring an early developing quadrate and siphoneal diverticula rather than a complete absence of the diverticula during early ontogeny.

In spite of the presence of the branchial diverticula both in crocodylians and aves, this system also appears to be derived independently within the two extant archosaur lineages. Basal archosaurs have no trace of this system. It appears first in the crocodylian lineage in the sphenosuchians *Sphenosuchus* and *Dibothrosuchus* (Walker, 1990; Wu and Chatterjee, 1993). The siphoneal duct appears to have traveled over the posterior surface of the quadrate, rather than within it, before entering the articular. Protosuchians frequently would have had a well elaborated pneumatic siphoneal and quadrate system within their quadrates (Busbey and Gow, 1984) that becomes simplified to the general extant crocodylian condition within all Mesoeucrocodylia (Figs. 6B, C, 7B). The reduction in branchial diverticular anatomy in the quadrate throughout the development of modern crocodylians (Dufeau and Witmer, 2007) may be reminiscent of this evolutionary reduction.

The origin of the avian branchial pneumatic system does not appear until within theropod dinosaurs although the occurrence of the branchial pneumatic system in Mesozoic are infrequent. However, apneumatic quadrate of some Mesozoic birds such as *Archaeopteryx*, *Baptornis*, *Parahesperonis, Hesperornis* (Witmer, 1990) may have resulted from the pachyostotic condition as in *Gavia*. The absence of siphoneal diverticulum in Mesozoic birds may have been the same reason. This area needs to be studied to interpret the presence of the branchial pneumatic system in phylogeny but as far as the presence of the structure is reported, the branchial pneumatic system is discussed in Chapter 3 in detail.

An osteological trace of the quadrate diverticulum is commonly found as fossa or shallow depression on the posterior, anterolateral, or medial surface of the quadrate or less commonly as an internal recess of the quadrate in theropods. A siphoneal diverticulum appears to be present only in tyrannosaurids and an ornithomimid, *Sinornithomimus dongi* (Currie and Zhao, 1993b; Kobayashi and Lü, 2003; Xu et al., 2004). *Aerosteon*, an allosauroid, exhibits a rare condition of a hypertrophied quadrate diverticulum that exited

FIGURE 7. Complex osteological recesses of the pneumaticity of *Protosuchus hanghotoni* in lateral view of braincase, **A**, and posterior oblique aspect of dorsal surface, **B**. Modified from Busbey and Gow (1984). Abbreviations: **V**, opening for trigeminal nerve; **VII**, opening for facial nerve; **bs**, basisphenoid; **cqc**, cranioquadrate canal; **fo**, fenestra ovalis; **leu**, lateral eustachian tube; **ls**, laterosphenoid; **mf**, metotoic fissure; **oc**, occipital; **op**, opisthotic; **ov**, occipital vein; **p**, parietal; **pn**, pneumatic; **pocr**, postcarotid recess; **prcr**, precarotid recess; **pt**, pterygoid; **rs**, rhomboidal sinus; **soc**, supraoccipital; **scp**, subcapsular process. Scale bar equals 1cm.


A
ov
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pt
B

the quadrate via a large foramen over the medial articular condyle (Sereno et al. 2008). This diverticulum may have entered the articular or joined with a siphoneal diverticulum, but no articular is known for this taxon yet. This morphology is compared in Chapter 3 along the theropod phylogeny.

Tympanic sinus: periotic pneumatic system

The tympanic system associated with the braincase pneumatized the surface and/or internal regions of the braincase. To separate this set of diverticula from the branchial pneumatic system, this will be referred as the *periotic pneumatic system* to reflect its association with the otic region of the braincase.

The earliest archosauriformes, such as *Euparkeria*, have no indication of the periotic diverticula (Ewer, 1965). These diverticula do appear to originate within the crocodile stem lineage, in sphenosuchians, such as *Sphenosuchus* and *Dibothrosuchus* (Walker, 1990; Wu and Chatterjee, 1993). These taxa, protosuchians, and most other crocodyliforms (including modern taxa) would have had a complex pattern of pneumatization into much of the braincase. These complex pneumatic structures are superficially similar to those in modern birds (Fig. 6A-J). Several authors suggested that the similarities between crocodylian and avian tympanic recesses are in fact homologies and erroneously led to a hypothesis of a common origin of these structures, and an origin of birds from a crocodylomorph clade (e. g., Walker, 1990). However, as warned by Wu and Chatterjee (1993), if the definition of the recesses should be based on the bones which surround them, the locations of the tympanic pneumaticities of crocodylians appears to be non-homologues to those of Aves and have developed independently (Fig. 6A-I).

Before beginning a comparison of the periotic tympanic anatomy of modern archosaurs, I will need to outlinethe anatomy of modern birds, the best described modern archosaur. Modern birds typically have three main diverticula branching from their tympanic sinus into and onto their braincase bones. The anterior diverticulum has been called the Anterior Tympanic Recess (ATR) and enters the basisphenoid, prootic, laterosphenoid, and particularly alaparasphenoid. The dorsal diverticulum has been called the Dorsal Tympanic Recess (DTR) and enters between the squamosal and prootic bones. The caudal diverticulum has been called the Caudal Tympanic Recess (CTR) and generally occupies most of the internal portion of the paroccipital processes (see details in Discussions).

The earliest indication of periotic diverticula surrounding the braincase in the avian stem lineage appears within theropod dinosaurs. Simplified morphologies are probably already present in Coelophysoidea, *Syntarsus* (Raath, 1985; Tykoski, 1998) and become complex with the three major avian recesses in Coelurosauria. These are clearly present in basal Aves, *Archaeopterynx* (Walker, 1985).

Terminology of the ATR, DTR, and CTR has been generally used to describe the similar pneumatic structures of birds in crocodyliformes. The pneumatic regions that have been called the ATR are in fact pneumatized by the Eustachian system in crocodylians and occupy the basioccipital and basisphenoid (Fig 6E, F). This recess is reduced in modern crocodiles while that of early crocodyliformes such as *Sphenosuchus*, *Dibothrosuchus*, and *Protosuchus* is extensively developed by the Eustachian system (Figs. 6A, J, 7A). The median Eustachian tube has extended into the precarotid and postcarotid recess and the lateral Eustachian tube is expanded as a rhomboidal sinus (Figs. 6J, 7A). The recess identified as the CTR is absent in modern crocodiles, however, it is developed in some fossil crocodyliforms between the prootic and paroccipital process (Wu and Chatterjee, 1993) (Figs. 6A, G, H, J, 7A). The location of a dorsal pneumatic extension is variable among crocodyliformes but mostly situated involving the prootic. This recess has been called the DTR and the intertympanic recess (Fig. 6E- J). It is likely that the location of the avian postotic and supraotic recesses are similar to that of the expanded “DTR” in crocodylians, however, the details of these comparisons need to be addressed. All these patterns of the osteological recesses of the pneumaticity are poorly described in modern crocodiles and its early evolution has not yet been described. What is clear, though, is that the origin of the elaborated tympanic diverticula is independent from that of birds and different terminologies should be applied to avoid confusions of homology.The terminology for birds is also confusing for a number of reasons. Anterior and caudal directional descriptions use two different systems of anatomical nomenclature; the classical Romerian nomenclature common in paleontological descriptions and the Nomina Anatomica, Nomina Anatomica Veterinaria, and Nomina Anatomia Avium nomenclature common in modern veterinary and human anatomy (Wilson, 2006). Furthermore, recesses generally refer to excavated structures, such as fossae and chambers within bone. Pneumatic diverticula are extensions of the pneumatic sinuses. I suggest the osteological and pneumatic structures commonly referred to as the ATR, DTR, and CTR be renamed the preotic, supraotic, and postotic respectively, recesses for bony anatomy and diverticula for soft tissue pneumatic anatomy. This terminology uses a common anatomical nomenclature for direction and does not overlap with bone element nomenclature in this region.

Institutional Abbreviations--RTMP, Royal Tyrrell Museum of Palaeonotlogy; **TCWC**, Texas Cooperative Wildlife Collection; **TMM**, Texas Memorial Museum.

CHAPTER 2. 3D RECONSTRUCTION OF CRANIAL PNEUMATICITY OF *ORNITHOMIMUS EDMONTONICUS*

2.1. Materials and Methods

Materials

A well-preserved skeleton of *Ornithomimus edmontonicus* (RTMP 95.110.1) (Fig. 8) was recovered from the Dinosaur Park Formation (Campanian ~74 Ma) in Dinosaur Provincial Park in Alberta, Canada. The skull and anterior cervicals were removed from the rest of the skeleton and prepared with the exception of the antorbital, orbital, and occipital regions. 420 consecutive coronal CT slices of this specimen (0.63 mm thickness) were generated with a GE LightSpeed Plus CT scanner.

CT scan data of *Alligator mississippiensis* (TMM M-983) and *Gavia immer* (TCWC 13, 300) were obtained from the DigiMorph database. The cranial pneumaticity of these two taxa was reconstructed as representatives of extant archosaurs in order to compare to that of non-avian theropods. Those specimens were scanned at the High-Resolution X-ray CT Facility in University of Texas at Austin. The horizontal CT data of the *Alligator* specimen consist of 146 slices with a thickness of 0.25 mm and the coronal CT data of the *Gavia* specimen consist of 1455 slices with a thickness of 0.1092mm.

Methods

Three dimensional reconstructions of the skull, braincase, and sinuses were created using a 3D computer program, Avizo software (Mercury Computer Systems, Version 5.0 & 5.1).

When the two dimensional data was imported, the physical dimensions of the images were inputted as a voxel size. The physical dimensions of the voxels of the CT slice of *O. edmontonicus* are 0.488mm, 0.488mm, and 0.63mm, for the x, y, and z axes, respectively. The first two

FIGURE 8. *Ornithomimus edmontonicus* (RTMP 95.110.1) in right lateral view. Scale bar equals 5cm.

values were calculated by the data size divided by the pixel size (250mm/512pixel), while z was a defined value when the specimen was scanned. The physical dimensions of the voxels of *Alligator* are 0.25mm, 0.25mm, and 0.48mm, for the x, y, and z axes respectively. The physical dimensions of the voxels of *Gavia* are 0.05mm, 0.05mm, and 0.1mm, for the x, y, and z axes, respectively.

After the dimensions were inputted, the CT data of each specimen were automatically aligned and combined into a single 3D set based on the consecutive slice numbers.

Initially, a rough segmentation of *O. edmontonicus* was made on the 3D set using a semi-automatic segmentation tool that extracts bone regions based on thresholds. The braincase and mandible were segmented separately from the skull to aid in visualization of the pneumatic anatomy. If the sutures were not identified, the boundaries were reconstructed based on literature and pictures of the specimen.

The skull and the cranial sinuses of *Alligator* and *Gavia* were reconstructed using both semi-automatic and manual reconstruction. Locations of the cranial pneumaticity of *Alligator* and *Gavia* were used as a guide to aid identify pneumatic spaces in *O. edmontonicus*. Segmented areas in the CT slices were examined in multiple planes: xy, yz, and xz.

The smoothing function was applied to the data to smooth the sharp edges from each set of volume data. The 3D images of these segmented areas were then visualized as transparent and solid volume to best present the data.

Assessing the reliability of cranial sinus reconstructions

The reliability of reconstructions of pneumatic diverticula is an important issue to consider because soft tissue is rarely preserved in fossil taxa and diverticula do not always leave osteological recesses within and/or on bones. Nasal diverticula of modern birds are an example of the latter condition since many extend through soft connective and muscle tissues. To assess the reliability of the presence of cranial sinuses of *O. edmontonicus*, a crocodile (*Alligator mississippiensis* [TMM M-983]) and bird (*Gavia immer* [TCWC 13, 300]) were selected as representatives of extant archosaurs. Cranial sinuses and associated diverticula in both taxa were reconstructed based on CT data (Figs. 3, 4) and compared to published pneumatic anatomy of modern archosaurs (e.g., Witmer and Ridgely, 2008). The comparisons confirmed that much of the primary cranial pneumatic morphology of modern taxa have osteological signatures and can be identified using CT data. These reconstructions were used as a guide to aid the identification of putative pneumatic spaces in *O. edmontonicus.* Some diverticula, such as many of the modern avian nasal sinus diverticula, cannot be reconstructed from CT data of prepared skulls alone and the absence of some of these in fossil taxa should not be taken as evidence for absence, but rather absence of evidence.

2. 2. Description of cranial pneumaticity of *O. edmontonicus*

The CT data revealed clear distinctions between bone and matrix with submillimeter resolution but not enough to determine many of the bone sutures. The left squamosal and left quadrate are partially crushed. The crushed surfaces are reconstructed to match the opposite side but the internal spaces of these crushed bones were not considered in this study.

As expected, the two cranial sinuses common to archosaurs are identified in this specimen. The nasal sinus would have invaded the maxilla, lacrimal, jugal, ectopterygoid, and palatine bones and the tympanic sinus would have been present in or on the squamosal, parasphenoid-basisphenoid, prootic, basioccipital, exoccipital, supraoccipital, quadrate, and articular bones (Fig. 9A-F). The source of the pneumatization of the ectopterygoid, squamosal, and some recesses of the basisphenoid (subsellar and subcondylar recess) is unknown, however, I infer these spaces to have been supplied by the nasal and tympanic sinus.

Nasal sinuses

Maxilla--The anterior margin of the antorbital fenestra is delineated as an antorbital fossa. This fossa is located on the body of the maxilla. A relatively large promaxillary fenestra is found within the anterodorsal margin of the antorbital fossa (Fig. 9 A). A maxillary fenestra is not clearly identified from the CT data but appears to be present from direct observation of the specimen.

Lacrimal--The body of the lacrimal is hollowed with communication to the antorbital sinus through an opening at the posterodorsal corner of the antorbital fenestra (Figs. 9A, 10B). This anatomy suggests the presence of a lacrimal diverticulum in life.

FIGURE 9. Reconstructed cranial sinuses in *Ornithomimus edmontonicus* (RTMP 95.110.1). Skull is oriented with the horizontal semicircular canal in the horizontal plane. Entire skull in right lateral, **A**, and ventral, **B**, views. Reconstructed tympanic sinuses in *O. edmontonicus* (RTMP 95.110.1) in left lateral, **C**, right lateral, **D**, and posterior, **E**, and ventral, **F**, views. Estimated extensions of the antorbital and tympanic sinuses and quadrate and siphoneal diverticula are indicated by transparent colors. Scale bar equals 5cm. **Abbreviations**: **as**, antorbital sinus; **bod**, basioccipital diverticulum; **bsd**, basisphenoid diverticulum; **com**, communication; **ecd**, ectopterygoid diverticulum; **ld**, lacrimal diverticulum; **prmf**, promaxillary fenestra; **meu**, median eustachian tube; **osas**, osteological correlates of the antorbital sinus; **pld**, palatine diverticulum; **potd**, postotic diverticulum of the periotic sinus (=CTR, caudal tympanic recess); **prd**, prootic diverticulum; **psd**, parasphenoid diverticulum; **qd**, quadratediverticulum; **scd**, subcondylar diverticulum; **sid**, siphoneal diverticulum; **socd**, supraoccipital diverticulum; **sotd**, supraotic diverticulum of the periotic sinus (=DTR, dorsal tympanic recess); **sqd**, squamosal diverticulum; **suod**, suborbital diverticulum; **ts**, tympanic sinus. Scale bar equals 5cm.

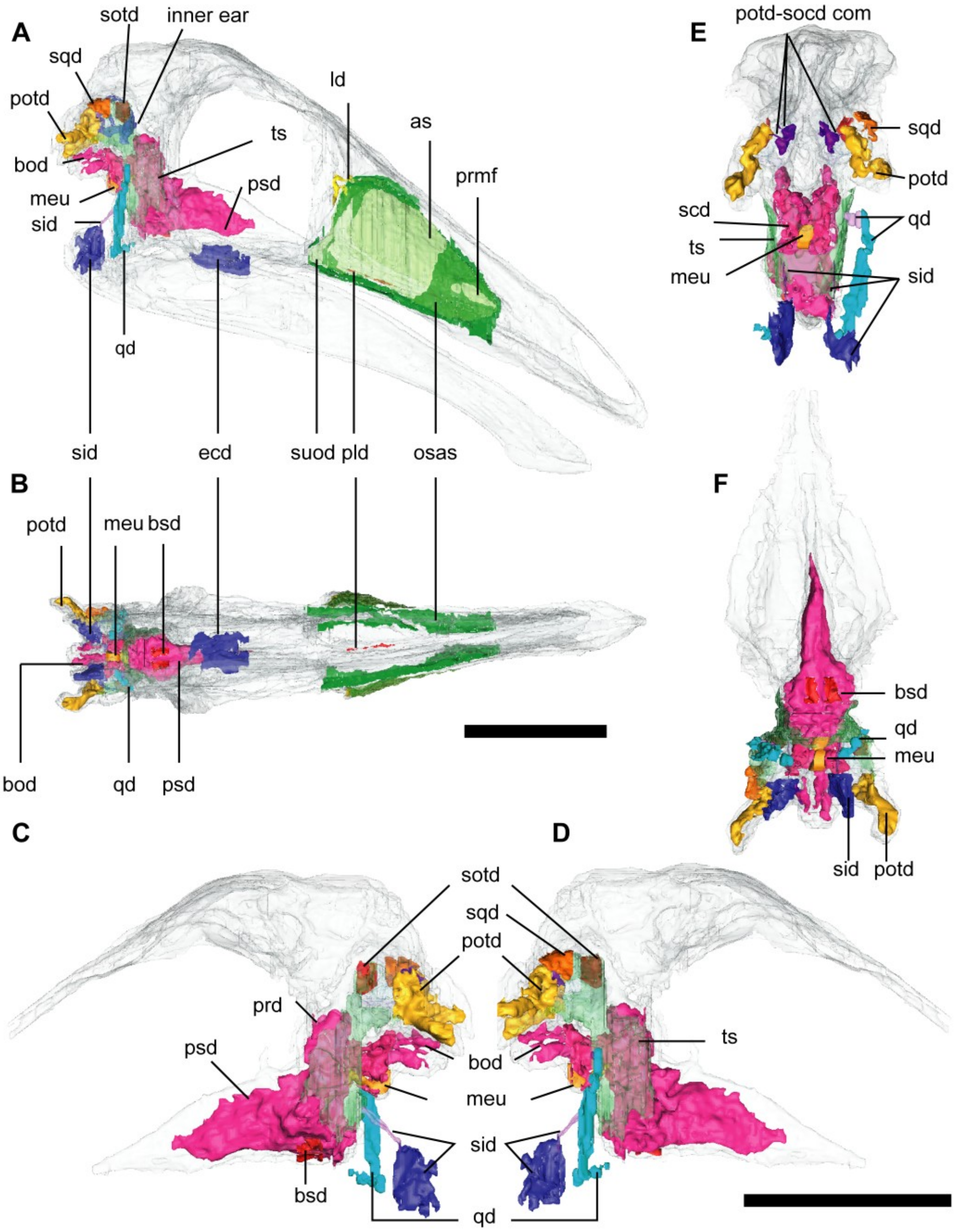
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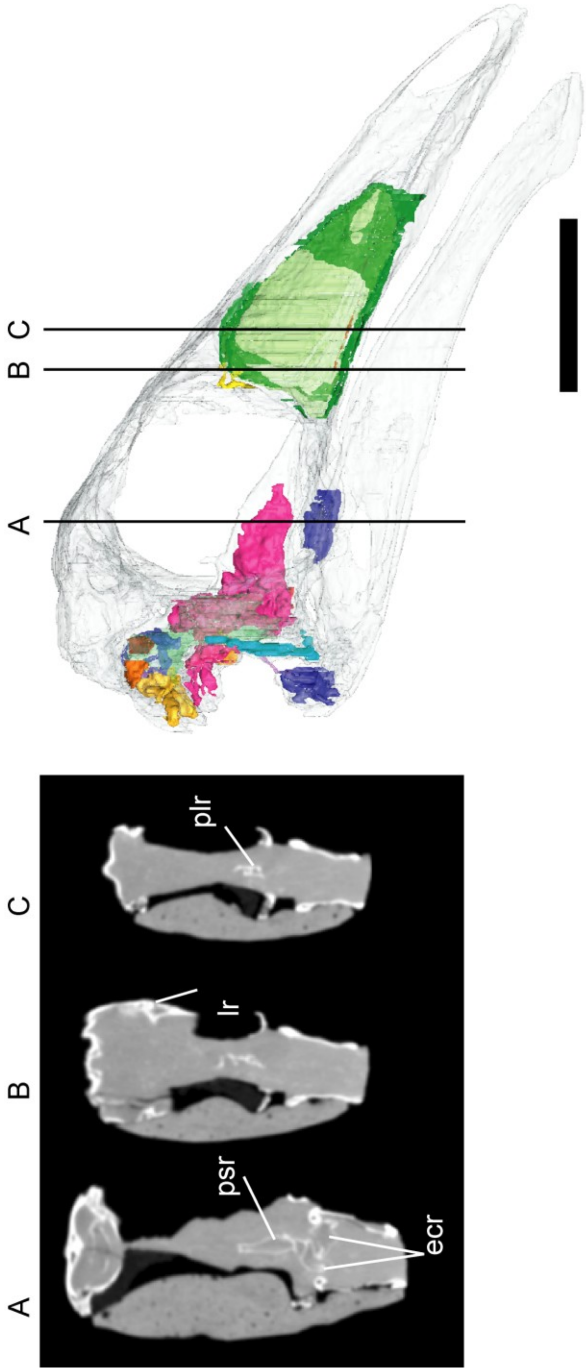
FIGURE 10. Coronal CT data of *Ornithomimus edmontonics* (RTMP 95.110.1) showing the nasal sinuses. CT slices of A-C are correspondent to the alphabets indicated in the reconstructed skull. All CT-sections are seen in anterior view, so that the right hand side of the figures corresponds to the left side of the specimen. **Abbreviations**: **ecr**, ectopterygoid recess; **lr**, lacrimal recess; **plr**, palatine recess; **psr**, parasphenoid recess. Scale bar equals 5cm.


A
B
C
A
B
C
psr
ecr
lr
plr

Jugal--Although the jugal is completely solid, a shallow fossa within the posteroventral corner of the antorbital fossa extends onto this bone suggesting the presence of a suborbital diverticulum of birds (see Discussion) (Fig. 9A).

Ectopterygoid--The body of the ectopterygoid is greatly inflated. A coronal CT cross-section through this region (Figs. 9A, B, 10A) indicates that this chamber is similar in size to a large parasphenoid diverticulum. The ectopterygoid chamber opens posteroventrally and the recess does not appear to be bounded anterolaterally. These indicate that the diverticula may have been extended from the cavity to the dorsal surface of the ectopterygoid.

Palatine--Thin spaces with several lateral apertures are present in the palatine. These appear to be pneumatic structures because all the apertures open into the nasal cavity (Figs. 9A, B, 10C).

Tympanic sinuses

Eustachian system--A foramen that would have housed a median Eustachian tube is present at the ventral basioccipital-basisphenoid suture. The foramen opens into a chamber which would have been confluent posteriorly with a pneumatic chamber within the ventral portion of the basioccipital invading the basioccipital posteriorly (Fig. 9A, B, E, F). A small bony sagittal septum is present immediately anterior to the median Eustachian tube foramen and indicates the divisions of the carotid artery associated with the pneumatic diverticula as in other theropods (e.g., Coria and Currie, 2002).

Squamosal--Although the specimen exhibits a cavity in the right squamosal (Figs. 9A, D, E, 11B), this space should be interpreted with caution.

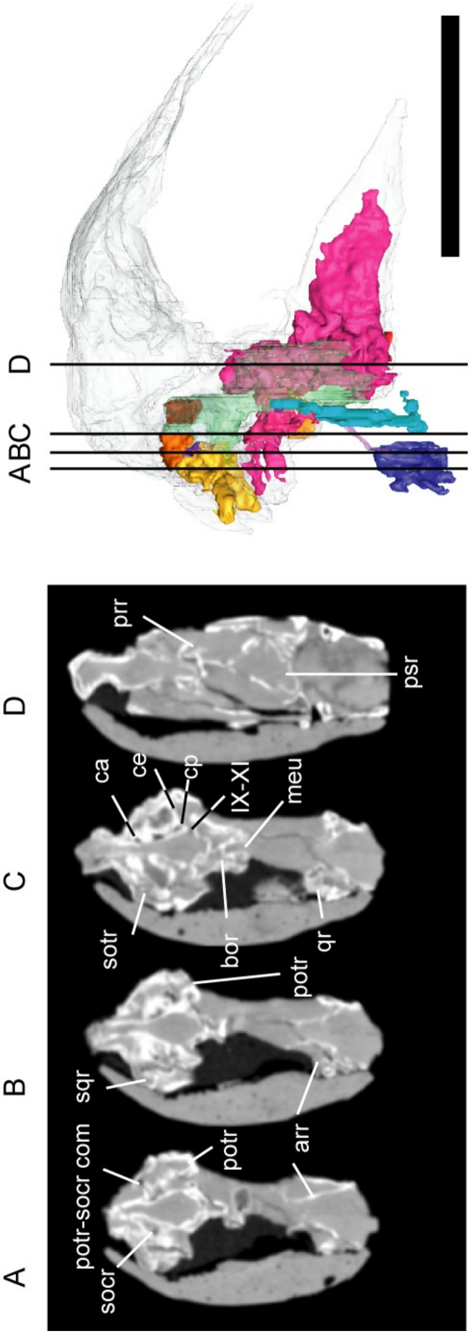
This region is also the presumed site of attachment for the musculus adductor mandibulae externus as in modern birds. This space is treated as only a potential pneumatic squamosal recess.

Parasphenoid-basisphenoid--A large subotic recess (sensu Witmer 1997b) is present on the lateral basioccipital-basisphenoid suture ventral to the tympanic recess. The subotic recess marks the proximal extent of the preotic recess (=ATR) in birds and is inferred to be present in *O. edmontonicus* as well. Preotic diverticulum appear to have penetrated into the parasphenoid anteriorly and basisphenoid posteroventrally (Figs. 9C-F, 11C). The diverticula also would have invaded the prootic dorsally and basioccipital posterodorsally.

Prootic--A small depression is present on the lateral surface of the prootic anteroventral to the exit of cranial nerve VII. This depression is separated from the opening of the subotic recess and is regarded as the prootic recess (sensu Witmer 1997b) (Figs. 9C, D, 11D). The smooth surface of the lateral wall of the braincase, probably primarily on the prootic, indicates the presence of a supraotic recess (=DTR)(Figs. 9C, D, 11C). The supraotic recess is adjacent to the squamosal recess and may indicate that at least part of the squamosal may have been pneumatized via a posterior extension from the supraotic diverticulum.

Basioccipital--Diverticula extending posteriorly from the subotic recess would have penetrated within the basioccipital and communicated with the subcondylar recesses (sensu Witmer, 1997b) on the posterior surface of the basal tubera (Figs. 9E, 11C). One sagittal and a pair of lateral small sinuses would have been present in the occipital condyle all derived from the preotic diverticula. The ventral sinus would have connected with the left lateral sinus clearly but no connection with right lateral sinus was identifiable.

FIGURE 11. Coronal CT slices of *Ornithomimus edmontonicus* (RTMP 95.110.1) showing the tympanic sinuses. CT slices of A-D are correspondent to the alphabets indicated in the reconstructed braincase. All CT-sections are seen in anterior view, so that the right hand side of the figures corresponds to the left side of the specimen. **Abbreviations**: **IX-XI**, foramina for glossopharyngeal, vagus, and accessory nerves; **ac**, anterior canal; **bor**, basioccipital recess; **com**, communication; **lc**, lateral canal; **meu**, median eustachian tube; **pc**, posterior canal; **potr**, postotic recess of the periotic recesses (=CTR, bony caudal tympanic recess); **prr**, prootic recess; **psr**, parasphenoid recess; **qr**, quadrate recess; **socr**, supraoccipital recess; **sotr**, supraotic recess of the periotic recess (=DTR, bony dorsal tympanic recess); **sqr**, squamosal recess. Scale bar equals 5cm.


A
B
C
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socr
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ca
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cp
IX-XI
meu
prr
psr
ABC
D

Exoccipital--The proximal portion of the exoccipital has a large foramen on its anterolateral surface. This probably indicates the proximal portion of the postotic recess (=CTR). This diverticulum would have invaded the bodies of both paroccipital processes (Figs. 9C-F, 11A). The supraotic recess and the proximal portions of the postotic recess are superficial to the braincase bones but are only adjacent to each other. There are no osteological signatures to indicate if these recesses communicated with each other.

Supraoccipital--The supraoccipital is hollowed above the foramen magnum. Two small tube-like extensions from this midline chamber communicating with the postotic recess near the base of the exoccipital and supraoccipital recess are observed on the left side but not on the right having only one communication bridges between them (Figs. 9E, 11A).

Quadrate-- A relatively large foramen is located on the medial surface of the quadrate and opens into the mostly hollow quadrate (Fig. 11C). This foramen projects toward the tympanic recess and would have housed a quadrate diverticulum similar to that of modern birds (Fig. 9A, C-E).

Articular--The articular has large, deep chambers on its dorsal surface immediately behind the mandibular cotyles (Fig.11A, B). These chambers extend posteriorly into the retroarticular process where they are covered dorsally by the articular. Their size and position suggest they would have been pneumatic, indicating the presence of a siphoneal diverticulum that would have bypassed the quadrate (Fig. 9A, C-E).

CHAPTER 3. DISCUSSION

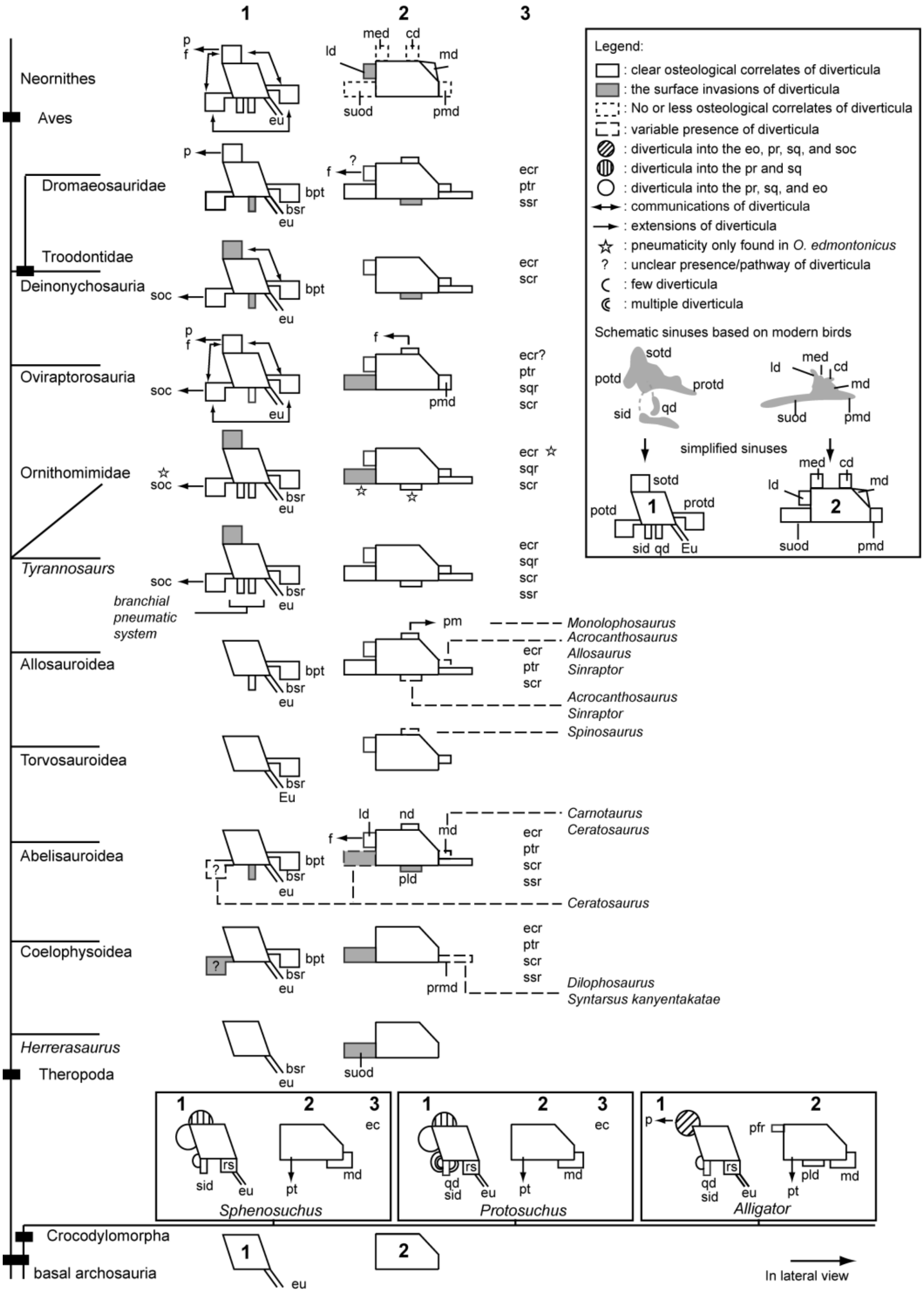
Evolution of the cranial pneumatic systems of theropods can now be reassessed with greater resolution. I used all available published data for non-avian theropods. These include taxa from basal theropods, *Herrerasaurus*, *Eoraptor*, Coelophysoidea, Abelisauroidea, Torvosauroidea, Allosauroidea, Tyrannosauroidea, Ornithomimosauria, Oviraptorosauria, Troodontidae, and Dromaeosauridae. To aid discussion of this complex anatomy, all cranial pneumatic diverticula are presented schematically in Figure 12. The schematized format is meant to clarify the discussion. However, a basipterygoid recess is not discussed in detail because descriptions of it are few and the scattered occurrence of this recess in phylogeny is proposed to be reflected by ontogenetic variation (Chure and Madsen, 1996). Cranial pneumatic systems are compared first within Ornithomimosauria and then interpreted in an evolutionary context within Theropoda.

3.1. Antorbital sinus

Ornithomimosauria--As described above, *O. edmontonicus* has a maxillary fenestra, promaxillary recess, internal lacrimal recess, shallow fossa on the lacrimal-jugal contact at the antorbital fenestral margin, and internal palatine recess. The ectopterygoid recess may have also been pneumatized by the nasal sinus. A maxillary fenestra is common to all other known ornithomimosaurs. There is no clear indication of a promaxillary fenestra in *Shenzhousaurus orientalis* but is present in *O. edmontonicus*, *Garudimimus brevipes*, *Sinornithomimus dongi*, *Struthiomimus altus*, possibly *Gallimimus bullatus*, and *Harpymimus oklandnikovi* (Ji et al., 2003; Kobayashi and Barsbold, 2005a, b; Kobayashi and Lü, 2003; Makovicky et al., 2004; Osmólska et al., 1972). A lacrimal recess with an anterior opening is present in *O. edmontonicus* and *Garudimimus*. However, instead of a fully developed recess, a deep fossa is present in *Dromiceiomimus* (Witmer, 1997a). The jugal of *O. edmontonicus* is well-preserved among ornnithomimids and appears to have a shallow fossa at the lacrimal-jugal contact. Palatine diverticula invading the palatine have not been described in other ornithomimid dinosaurs although a dorsal palatine fossa is noted in *Shenzhousaurus* and *Garudimimus*. An ectopterygoid recess is currently present only in *Garudimimus* and *O. edmontonicus.* A squamosal recess is present in *Dromiceiomimus*, *Sinornithomimus*, *Gallimimus*, and probably in *O. edmontonicus*.

Putative homology of a jugal recess and suborbital diverticulum--The antorbital fossa extension onto the lacrimal-jugal contact at the posteroventral corner of the antorbital fenestra deserves some attention. As will be discussed below, this region is generally pneumatized in theropods as either a broad, shallow fossa or as a large ovate foramen opening into the jugal body. This feature has generally been referred to as the jugal recess (e.g., Witmer, 1997a; Witmer and Ridgely, 2008) and has no obvious homolog in modern birds in which the jugal has been modified to a thin, elongate rod. In

FIGURE 12. Schematic diagram of the evolution of theropod cranial sinuses. Selected taxa are illustrated with schematized tympanic sinus, **1**, and antorbital sinus, **2**, morphology. Pneumatic regions with uncertain relationships to these two sinuses are listed beside each, **3**. A box legend describes each of the symbols used in the figure and an illustration of the anatomical to schematic translation of the pneumatic morphology of a generalized bird. Schematic figures are not to scale. **Abbreviations**: **bsr**, basisphenoid recess; **bpt**, basipterygoid recess; **cd**, conchal diverticulum; **ec**, ectopterygoid; **eo**, exoccipital; **eu**, eustachian tube system; **f**, frontal; **md**, maxillary diverticulum; **med**, mesethmoid diverticulum; **nd**, nasal diverticulum; **p**, parietal; **pld**, palatine diverticulum; **pfr**, prefrontal recess; **pmd**, premaxilla diverticulum; **pmd**, premaxillay diverticulum; **potr**, postotic recess of the periotic recesses (=CTR, bony caudal tympanic recess); **pr**, prootic; **prmd**, promaxillary diverticulum; **protr**, preotic recess of the periotic recess (=ATR, bony anterior tympanic recess); **pt**, pterygoid; **qr**, quadrate recess; **rs**, rhomboidal sinus; **scr**, subcondylar recess; **sid**, siphoneal diverticulum; **soc**, supraoccipital; **sotr**, supraotic recess of the periotic recess (=DTR, bony dorsal tympanic recess); **sq**, squamosal; **sqr**, squamosal; **ssr**, subsellar recess; **suod**, suborbital diverticulum.


1
2
3
Legend:
: clear osteological correlates of diverticula
: the surface invasions of diverticula
: No or less osteological correlates of diverticula
: variable presence of diverticula
: diverticula into the eo, pr, sq, and soc
: diverticula into the pr and sq
: diverticula into the pr, sq, and eo
: communications of diverticula
: extensions of diverticula
☆ : pneumaticity only found in O. edmontonicus
? : unclear presence/pathway of diverticula
: few diverticula
: multiple diverticula
Schematic sinuses based on modern birds
sotd
potd
protd
sid
qd
ld
med
cd
md
suod
pmd
simplified sinuses
Eu
Neornithes
Aves
p
f
eu
Dromaeosauridae
bpt
bsr
ecr
ptr
ssr
Troodontidae
Deinonychosauria
soc
scr
Oviraptorosauria
ecr?
sqr
Ornithomimidae
Tyrannosaurs
branchial pneumatic system
Allosauroidea
pm
Monolophosaurus
Acrocanthosaurus
Allosaurus
Sinraptor
Acrocanthosaurus
Sinraptor
Torvosauroidea
Spinosaurus
Abelisauroidea
nd
pld
Carnotaurus
Ceratosaurus
Ceratosaurus
Coelophysoidea
prmd
Dilophosaurus
Syntarsus kanyentakatae
Herrerasaurus
Theropoda
suod
ec
rs
pt
Sphenosuchus
Protosuchus
pfr
Alligator
Crocodylomorpha
basal archosauria
In lateral view

modern birds, similar regions are occupied by a suborbital diverticulum extended from the posteroventral margin of the antorbital sinus. The suborbital diverticulum fills a large space anterior and ventral to the orbit. Most of this space is bounded by soft tissue and has no osteological signature. The antorbital sinus extends to a preocular sac that lies in the orbital margin of the lacrimal. Connections often exist between the preocular sac and lacrimal diverticulum (Witmer and Ridgely, 2008). Witmer and colleagues have suggested the presence of a suborbital diverticulum and preocular sac in many theropods ranging from *Majungasaurus, Allosaurus,* and *Tyrannosaurus* with possible connections to the lacrimal diverticulum via thin canals within the lacrimal but admitted that their evidence is weak and based on the interpretation of a shallow depression on the orbital margin of the lacrimal. The principal extension of the suborbital diverticulum from the antorbital sinus in birds is from the posteroventral corner of the sinus (Witmer, 1990). The shared anatomical position of the jugal diverticulum of non-avian theropods and the base of the suborbital diverticulum of birds suggests these pneumatic diverticula are homologous. The avian suborbital diverticulum is extensive throughout the orbital region but the diverticulum of non-avian theropods is restricted to posteroventral corner of the antorbital fossa and has little to no osteological signatures of being present within the orbit. I propose that non-avian theropods may lack a preocular sac because of the limited extent of the suborbital diverticulum. The sac may be supplied by small ducts from the lacrimal diverticulum or via ducts with no osteological signature, but these alternatives are not testable with the available fossil data. The small canals sometimes present in the lacrimal could also represent nasolacrimal ducts or vascular canals (Sampson and Witmer, 2007; Witmer, 1997a).

Basal theropoda--As discussed above, the evolution of antorbital pneumatic diverticula along the avian stem lineage appears first within theropod dinosaurs. Basalmost taxa, such as *Eoraptor* and *Herrerasaurus* have no trace of antorbital diverticula beyond their antorbital fenestra with the exception of a large superficial fossa extending onto the jugal and lacrimal at the posteroventral corner of the antorbital fenestra (Sereno and Novas, 1993; Sereno et al., 1993).

Coelophysoidea--Ceratosauria are recently considered to be paraphyletic and divided into a basal clade, Coelophysoidea, and a clade more closely related to all other theropods, Abelisauroidea (Carrano and Sampson, 1999; Carrano et al., 2002). Coelophysoids, such as *Coelophysis* and *Syntarsus kayentakatae* express the large superficial fossa at the posteroventral corner of the antorbital fenestra (Rowe, 1989; Tykoski, 1998; Tykoski and Rowe, 2004). *Coelophysis* does not appear to have had any other antorbital diverticula while *Dilophosaurus* and *S. kayentakatae* appear to have had diverticula within their maxilla (Welles, 1984). *S. kayentakatae* and *S. rhodesiensis* appear to have had ventral pneumatic extensions from the nasal sinus into the ectopterygoid and the latter taxon also seems to have had lateral extensions of these diverticula within the ectopterygoid toward the adjacent pterygoid (Tykoski, 1998; Witmer, 1997a).

Abelisauroidea--Many abelisauroids do have extensive osteological evidence for antorbital diverticula. The cranial pneumatic anatomy of *Majungasaurus* is the most thoroughly described for the clade. Sampson and Witmer (2007) identified the presence of a large number of antorbital diverticula in this taxon. These include nasal diverticula that may be autoapomorphic to this abelisauroid (Sampson and Witmer, 2007), and evidence of pneumatic diverticula within a promaxillary fenestra, internal lacrimal recess, large frontal chamber, lateral depression on the palatine, ventromedial pterygoid recess, and ventral ectopterygoid recess. A pneumatic frontal chamber is postulated in *Majungasaurus* and *Ceratosaurus*, however, it’s presence may be variable among *Majungasaurus* specimens (Sampson and

Witmer, 2007). Most postulated pneumatic diverticula of *Majungasaurus* appear to have been extensively derived in this taxon because other abelisauroids, such as *Carnotaurus* and *Abelisaurus* have a reduced antorbital fossa and would have had limited diverticular invasions into the maxilla (Bonaparte and Novas, 1985; Bonaparte et al., 1990). No maxillary fenestra was identified in *Majungasaurus* but is common to other abelisauroids, such as *Carnotaurus* and *Ceratosaurus* (Madsen and Welles, 2000). Witmer (1997) urged care in assessing putative homologies for this region in non-coelurosaurian taxa because of its state of large anatomical variation. The presence of a secondary fenestra (maxillary fenestra) of *Carnotaurus* was hypothesized to be an automorphy by Sampson and Witmer (2007). *Ceratosaurus* has a particular pneumatic excavation (sensu Witmer, 1997a) along the maxillary fossa similar to some allosauroids. No jugal fossa or recess is present in *Majungasaurus* and no obvious pneumatic anatomy in the jugal appears in abelisauroids with the exception of a shallow fossa at the lacrimal-jugal contact in *Ceratosaurus.* This pneumatic invasion is supported by the presence of the putative pneumatic extension along the middle part of the ventral ramus of the lacrimal separate from the more typical lacrimal recess. An ectopterygoid recess is also present in *Ceratosaurus* but only as a shallow fossa and sometimes associated with a pneumatic pterygoid fossa (Sampson and Witmer, 2007).

Torvosauroidea--Torvosauroids had minimal pneumatic invasion into the antorbital bones. The antorbital fossa is typically narrow or absent in these taxa and a single pneumatic feature is present within the anterior region of this fossa. *Torvosaurus* has a large pneumatic opening there while taxa such as *Irritator* and *Suchomimus* have a smaller conical foramen (Britt 1991; Sereno et al. 1998; Sues et al. 2002). This foramen entered a maxillary antrum in *Irritator* and the morphology was probably shared among other torvosauroids. This foramen is probably homologous to the maxillary fenestra of other theropods. A depression with a foramen is present at the posterodorsal corner of the lacrimal in *Baryonyx* and *Irritator* and may indicate the presence of a lacrimal diverticulum into the body of the lacrimal (Charig and Milner, 1997). The jugal is excluded from the posteroventral part of the antorbital fenestra in these taxa by the lacrimal with no depression in the region. Nasal air chambers have not been reported in these taxa except for a putative pneumatic concavity in a fragmentary nasal crest of *Spinosaurus* (Sasso et al., 2005). The ectopterygoid is unknown in Torvosauroidea and a palatine is known only from *Irritator* but it is not possible to identify any evidence of a palatine diverticulum.

Allosauroidea--Allosauroids would have had numerous nasal invasions into the antorbital bones and relatively large antorbital fossae compared to more basal theropods. Nasal diverticula commonly would have invaded the nasal, maxilla, and lacrimal in *Allosaurs fragilis*, S*inraptor dongi*, *Monolophosaurus jiangi*, *Mapusaurus roseae*, *Carcharodontosaurus saharicus*, probably *Acrocathosaurus atokensis*, and *Giganotosaurus carolinii* (Brusatte and Sereno, 2007; Coria and Currie, 2006; Coria and Salgado, 1995; Currie and Carpenter, 2000; Currie and Zhao, 1993a; Eddy, 2008; Madsen, 1976; Sereno et al., 1996; Zhao and Currie, 1993). *Monolophosaurus* does not appear to have a typical lacrimal recess, however, the nasal crest would have been filled by large diverticula within the premaxilla, nasal, and lacrimal. *Allosaurus*, *Acrocanthosaurus*, and possibly *Mapusaurus* have the small promaxillary and large maxillary fenestrae whereas *Sinraptor* have reversed the relative size of these two fenestrae (Eddy, 2008). In *Allosaurus*, diverticula in the maxilla would have extended anteriorly into a promaxillary recess and maxillary antrum, and these recesses contact their counterparts. In contrast, *Monolophosaurus*, *Giganotosaurus*, and *Carcarodontosaurus* have only a single fenestra in this region. However, at least in the latter taxon diverticula through a single fenestra would have extended anteriorly and excavated the anterior part of the maxilla in a position comparable to a promaxillary recess (Brusatte and Sereno, 2007). These morphological variations suggest that diverticula in the maxillary body may have been derived from a single diverticulum that divided anteriorly before or after entering the maxilla. An accessory caudal maxillary fenestra and pneumatic depressions dorsal to the maxillary fenestra are found only in *Sinraptor* (Currie and Zhao, 1993a). Pneumatization of the jugal, however, is variable. *Allosaurus* has only a depression on its jugal at the posteroventral corner of the antorbital fenestra and most other allosauroids, such as *Acrocanthosaurus*, *Sinraptor*, *Monolophosaurus*, *Mapusaurus*, *Carcarodontosaurus*, and some specimens of *Allosaurus* have an internal jugal recess in a similar position (Currie and Carpenter, 2000; Harris, 1998; Madsen, 1976; Sereno et al., 1996). Witmer (1997a) treated the clear presence of the palatine recess in *Sinraptor* as problematic when interpreted phylogenetically. The palatine fossa is commonly present in Coelurosauria but the presence of a pneumatic palatine is variable in non-coelurosaurian theropods. A lateral palatine pneumatic fossa is present in *Sinraptor* and *Acrocanthosaurus* (Currie and Carpenter, 2000; Harris, 1998). A ventral ectopterygoid recess is present in *Allosaurus*, *Acrocanthosaurus*, and *Sinraptor* and lies adjacent to pneumatic excavations in the ectopterygoid and pterygoid (Eddy, 2008; Harris, 1998).

Tyrannosauroidea--*Tyrannosaurus rex* has osteological signatures of all the nasal diverticula of *O. edmontonicus* (Brochu, 2003; Molnar, 1991; Witmer, 1997a; Witmer and Ridgely, 2008). These include the maxillary and slit-like promaxillary fenestrae for maxillary and promaxillary diverticula, internal lacrimal recess for a lacrimal diverticulum, a deep jugal recess for a suborbital diverticulum, and deep lateral palatine cavities for a palatine diverticulum. *Tyrannosaurus* also has a ventral ectopterygoid recess similar to that of *O. edmontonicus*. The extensions of diverticula into the maxilla of *Tyrannosaurus* would have been elaborated with some accessory recesses such as cavities into the alveolar process, a caudal antromaxillary fenestra, maxillary antrum, epiantral recess, and depressions on the dorsal margin of the maxilla (Brochu, 2003; Molnar, 1991; Witmer, 1997a). *Dilong paradoxus*, a basal tyrannosaurid, had somewhat different with two large pneumatic recesses dorsolateral of the maxilla above the antorbital fenestra (Xu et al., 2004).

Oviraptorosauria--Oviraptorid skulls are divergent from the general morphology of theropod cranial anatomy and elaborated with extensive pneumatic cavities. Elaborated nasal diverticula would have pneumatized the premaxilla, maxilla, nasal, lacrimal, and pterygoid (Clark et al., 2002; Kundrát and Janáček, 2007). A single maxillary fenestra is common to oviraptorids with several pneumatic cavities extending anteroventral from the maxillary fenestra. A small accessory fenestra is present posterior to the maxillary fenestra only in the basal oviraptorosaur, *Incisivosaurus* (Xu et al., 2002a). The jugal at the antorbital fenestra is rod-like, but the distal portion of the lacrimal is transversely broad in oviraptorids and has a shallow anterolaterally facing fossa (Clark et al., 2002), suggesting the presence of a reduced suborbital diverticulum. A similar fossa is present at the lacrimal-jugal contact in *Incisivosaurus*. The ectopteryoid is broad without the hook-like jugal contact common to most theropods and lacks a ventral recess. However, a ventral concavity may indicate that a reduced ectopterygoid diverticulum was present. A palatine recess has not yet been reported.

Troodontidae--Troodontids commonly have a large maxillary fenestra. A pneumatic passage from the antorbital fenestra to a common maxillary fenestra and maxillary antrum are present in *Byronosaurus jaffei* (Makovicky et al., 2003). A promaxillary fenestra is not common in troodontids but is present in *Sinovenator changii* and *Sinornithoides youngi* (Currie and Dong, 2001; Xu et al., 2002b). A medial palatine fossa and ventral ectopterygoid recess are found in *Saurornithoides mongoliensis* (Osborn, 1924; Witmer, 1997a). The jugal is only partially preserved in available fossils making any determination of a jugal fossa or recess problematic.

Dromaeosauridae--The maxilla of dromaeosaurids would have been extensively invaded by diverticula from the nasal sinus. These include the maxillary and promaxillary fenestrae, caudal fenestra of the maxillary antrum, a maxillary antrum, evaginations within this antrum (recessus pneumatici interalveolares), a promaxillary recess, an epiantral recess, and sometimes pneumatic excavations on the dorsal rim of the antorbital fossa (Barsbold and Osmólska, 1999; Burnham, 2004; Currie and Varricchio, 2004; Norell et al., 2004, 2006; Norell and Makovicky, 2004). A nasal recess is present in *Deinonychus* and *Velociraptor* (Ostrom, 1969; Norell and Makovicky, 2004; Witmer, 1997a). A typical cup-like excavation at the lacrimal-jugal contact, pneumatic dorsal palatine fossa, and ventral ectopterygoid recess are commonly present in dromaeosaurids (Barsbold and Osmólska, 1999; Currie, 1995; Norell et al, 2006; Witmer, 1997a; Xu and Wu, 2001). A dorsal ectopterygoid recess is uncommon but described in *Saurornitholestes langstoni* and *Deinonychus antirrhopus* (Ostrom, 1969; Sues, 1978). Sues (1978) reported communications between the dorsal and ventral ectoperygoid recesses in *Saurornitholestes* via a foramen but repreparation of *Deinonychus* revealed no communications (Witmer, 1997a). The presence of a lacrimal diverticulum is evinced by an internal lacrimal recess, such as in *Velociraptor mongolienis,* or by a deep fossa on the surface of the lacrimal, such as in *Deinonychus* (Barsbold and Osmólska, 1999; Witmer and Maxwell, 1996). A putative pneumatic diverticulum into a frontal recess and extensions of diverticula within the ectopterygoid toward the pterygoid has only been reported for *Tsaagan mangas* (Norell et al, 2006).

Evolution of nasal pneumatic anatomy in Extant Aves--Soft tissue preparations of modern birds reveal an extensive system of nasal diverticula (Witmer and Ridgely, 2008). Osteological correlates of these pneumatic structures are less obvious and some, such as the palatine diverticulum, leave no osteological trace. The maxilla is consistently pneumatic with cup-shaped recesses on the caudal palatine process in neognaths and a recess within the anterior maxillary palatine process in palaeognaths representing the presence of a maxillary diverticulum (Witmer, 1990). A lacrimal diverticulum lies against the medial surface of the lacrimal body and a suborbital diverticulum extends along the surface of the pterygoid in many birds. These diverticula probably serve important ventilatory functions with associated muscles and leave little to no obvious osteological signatures (Witmer, 1990, 1999; Witmer and Ridgely, 2008). Maxillary, lacrimal, and suborbital diverticula are consistently present in Abelisauroidea and Tetanurae and diagnose this unnamed clade with only some Abelisauroidea, Torvosauroidea, and Troodontidae lacking osteological signatures for this diverticulum.

Other avian nasal diverticula have less or no osteological signatures making evolutionary interpretations of those soft tissue structures difficult. The mesethmoid diverticulum of modern birds cannot even be assessed in most non-avian theropods due to the absence of this bone in many of these taxa. However, premaxillary diverticulum of modern birds occupies the avian bill and putative homologies can be made with similar pneumatic chambers within the premaxilla of beaked non-avian theropods, such as Oviraptorosauria. The premaxillary diverticulum is probably equivalent to the promaxillary diverticulum because of their shared location and no theropod indicates the presence of both diverticula. The conchal diverticulum of birds is located in the caudal nasal concha that is similar in location to the nasal diverticulum of non-avian theropods, however, the evolution of this diverticula appears to be homoplastic in this clade (Fig. 12).

Although the antorbital sinus of birds has no osteological signature on the palatine, the ventrally located palatine diverticulum is likely homologous to the pneumatic invasion on the dorsal surface of the palatine in non-avian theropods such as *Tyrannosaurus* and *Ornithomimus* (Brochu, 2003; Molnar, 1991). Some abelisauroids and allosauroids, such as *Majungasaurus*, *Acrocanthosaurus*, and *Sinraptor* (Currie and Zhao, 1993a; Eddy, 2008; Harris, 1998; Sampson and Witmer, 2007) possess a lateral depression or recess on the palatine. Most non-avian coelurosaurs have deep fossae in the dorsal palatine surface and a few, such as *Deinonychus*, has a shallow palatine depression indicating the presence of a palatine diverticulum (Ostrom, 1969:fig.14; Witmer, 1997a). The smaller body size of most paravians may be associated with the reduced osteological signatures of this diverticulum on the palatine.

3.2. Tympanic sinus

Ornithomimosauria--Most tympanic pneumatic features of *O. edmontonicus* have been reported for other ornithomimd dinosaurs (Makovicky and Norell, 1998; Makovicky et al., 2004). *O. edmontonicus* adds a supraocciptal recess and a connection between it and the postotic recess to the range of ornithomimid pneumatic anatomy.

Basal theropoda--Tympanic pneumatic morphology of the basalmost theropods, such as *Herrerasaurus* (Sereno and Novas, 1993), exhibits the general tetrapod condition with no diverticula extending from the tympanic sinus. As far as can be observed, a shallow depression is present in the ventral basisphenoid suggesting the presence of a basisphenoid recess.

Coelophysoidea--Coelophysoids, such as *Dilophosaurus* had a superficially pneumatized basisphenoid evinced by the basisphenoid, subcondylar, and subsellar recesses (Welles, 1984). Other coelophysoids, such as *Syntarsus rhodesiensis* and *Syntarsus kayentakatae* appear to have had anterior extensions of the tympanic sinus within the braincase and a ventral basisphenoid recess (Raath, 1985; Tykoski, 1998). The position of the anterior extensions suggests homologies to the preotic diverticulum of the periotic sinus. The preotic diverticulum would have imprinted the shallow recess on the surface of a basipterygoid process (basipterygoid recess). A depression with a foramen is present at the base of the paroccipital process in both *Syntarsus* which is interpreted as the presence of superficially pneumatization (Currie and Zhao, 1993b; Raath, 1985; Tykoski, 1998). A depression on the posterior surface of the exoccipital and basioccipital, paracondylar recess, is present in *S. kayentakatae* and *Dilophosaurus*. According to Rauhut (2004), a paracondylar recess is probably homologous to the elaboration of a subcondylar recess.

Abelisauroidea--The posterior extension does not appear in *Majungasaurus* would have had only an anterior tympanic extension housed within the basisphenoid and prootic (Simpson and Witmer, 2007; Witmer and Ridgely, 2008) while both tympanic diverticular extensions appear to have been present within a braincase in *Ceratosaurus* (Sanders and Smith, 2005). But pneumatic spaces in the paroccipital process in *Ceratosaurus* are unclear from CT data and the presence of the postotic recess appears questionable. A basisphenoid recess and subsellar recess are present in *Majungasaurus* and *Ceratosaurus* with the basipterygoid and subcondylar recesses also present in the latter taxon (Madsen and Welles, 2000; Sampson and Witmer, 2007). A quadrate diverticulum appears to have been present within a relatively large fossa on the medial surface on the pterygoid's quadrate ramus in *Majungasaurus*, but no evidence for a siphoneal diverticulum is present in the quadrate or articular.

Torvosauroidea--The braincase of *Irritator* is one of the best preserved and described within Torvosauroidea (Sues et al., 2002). Pneumatic diverticula appear to have been present anterior to the otosphenoidal crest and ventral basisphenoid, which are topologically equivalent to the preotic and basisphenoid recesses. A basisphenoid recess is also present in *Baryonyx* (Charig and Milner, 1997). No osteological signature of a quadrate and siphoneal diverticulum is present.

Allosauroidea--Tympanic sinus extensions appear to be limited in Allosauroidea. A deep basisphenoid recess and basipterygoid recess is commonly present in allosauroids (Brusatte and Sereno, 2007; pers. obs.) and were probably pneumatized by the preotic diverticulum (Chure and Madsen, 1996). An elaborated subcondylar recess also appears to be present in *Carcharodontosaurus* and *Giganotosaurs* (Coria and Currie, 2002; pers. obs.).

However, the supraotic and postotic diverticula have not yet been found in allosauroids. A quadrate recess is present on the posteromedial surface of the quadrate in *Mapusaurus*, *Acrocanthosaurus*, and possibly *Giganotosaurus* (Coria and Currie, 2006; Eddy, 2008; Eddy and Clark, 2008) indicated the presence of a quadrate diverticulum. *Aerosteon* may reflect an exception. It has been putatively assigned to a phylogenetic position within Allosauroidea (Sereno et al., 2008). This taxon has a unique quadrate with anatomy suggesting the presence of an avian-like quadrate diverticulum that may have pneumatized the articular. However, no trace of a siphoneal diverticulum has been reported in any allosauroid.

Tyrannosauroidea--*Tyrannosaurus rex* would have had extensions of three diverticula (Brochu, 2003). The preotic diverticula would have invaded the basisphenoid, prootic, basioccipital, and parasphenoid. A subcondylar recess would have communicated with three sets of air spaces within the basioccipital that merged with a prootic recess anteriorly (Brochu, 2003). The ventral and anteroventral portions of the basisphenoid are also pneumatized and imprinted as the basisphenoid and subsellar recesses. A basipterygoid recess is not found in *Tyrannosaurs* but present in some other tyrannosauroids, such as *Gorgosaurus libratus*, *Albertosaurus sarcophagus*, *Stokesosaurus clevelandi*, and *Itermirus medullaris* (Chure and Madsen, 1998; Currie, 2003; Kurzanov, 1976). The postotic diverticulum would have been housed within the exoccipital and often invaded the opisthotic and supraoccipital (Brochu, 2003). A superficial depression at the ventral prootic-laterosphenoid suture suggests the presence of the supraotic diverticulum (Brochu, 2003). A squamosal recess is present adjacent to the supraotic recess in *Tyrannosaurus* and is similar to the possible squamosal recess of *O. edmontonicus*. Two pneumatic features of the quadrate are present. A large medial fossa on the pterygoid ramus and a deep cavity at the base of the pterygoid ramus junction to the quadrate body (Brochu, 2003; Currie, 2003; Molnar, 1991) suggests the presence of a quadrate diverticulum. A siphoneal diverticulum would have entered the articular through a single foramen near the posteromedial corner of the mandibular cotyle (Molnar, 1991; pers. obs.). This diverticulum seems to have left no trace on the posterior surface of the quadrate in tyrannosaurs, with the exception of a small posterior fossa in the basal tyrannosauroid, *Dilong* (Xu et al., 2004). The siphoneal diverticulum is assumed to have had a course similar to that of modern birds in all other tyrannosaurs.

Oviraptorosauria--Oviraptorosaurus would have had the three primary tympanic diverticula with extensive intertympanic pneumatic communications (Clark et al., 2002; Kundrát and Janáček, 2007). A reconstruction of the pneumatic anatomy of *Conchoraptor gracilis* revealed that the preotic diverticulum would have occupied the subotic and prootic recesses and would have expanded within the laterosphenoid, prootic, basioccipital, basisphenoid, and parasphenoid (Kundrát and Janáček, 2007). A lateral braincase of *Chirostenotes* (Sues, 1997) has a lateral depression and a large pneumatic foramen into the basioccipital similar to *Troodon* (Currie, 1985; Currie and Zhao, 1993b). A typical ventral basisphenoid recess is present in the basal oviraptorosaur, *Incisivosaurus* (Xu et al., 2002a) whereas a pair of pneumatic openings on the posteroventral to the surface of the basioccipital is present in derived taxa such as *Citipati* and *Chirostenotes* (Clark et al., 2002). The supraotic diverticulum would have invaded large portions of the parietal and frontal (Clark et al., 2002). Reconstructions of *Conchoraptor* revealed that the pneumatic extensions into the frontal would have communicated with the nasal sinus (Kundrát and Janáček, 2007). The postotic recess and associated pneumatic opening is housed largely within the exoccipital communicating with a supraoccipital recess via the opisthotic in *Conchoraptor*. A subcondylar recess and squamosal recess are also present and the latter probably communicates with the quadrate recess. The quadrate diverticula were complex, multichambered, and would have filled much of the quadrate body in oviraptorids (Maryańska and Osmólska, 1997), with the exception of only a pneumatic fossa on the caudal surface in *Incisivosaurus*. A large proximomedial foramen in the quadrate body seems to have been the entry for the diverticulum into the bone. Contrary to the extensive anatomy of the quadrate diverticulum, the surface of the articular is smooth and appears to have lacked a siphoneal diverticulum (Currie et al., 1993).

Troodontidae--Troodontids would have also had the three primary tympanic diverticula. Most troodontids feature a large lateral depression surrounding the otic region with exceptions only in an unnamed taxon and *Sinovenator* (Barsbold et al., 1987; Xu et al., 2002b). The elaborate expansions of the preotic diverticula would have exited the depression via several variable pneumatic foramina in the basioccipital and basisphenoid in *Troodon formosus* (Currie, 1985; Currie and Zhao, 1993b). Those diverticula would have extensively invaded the parasphenoid and laterosphenoid anteriorly. A subotic recess is present in *Byronosaurus*,*Troodon*, and probably *Saurornithoides junitor* (Barbold, 1974; Makovicky et al., 2003). Diverticula in the subotic recess would have extended into the paroccipital process in *Troodon* without passing through foramina into a postotic recess whereas a small pit is present in the more typical postotic recess in *Byronosaurus* (Currie and Zhao, 1993b; Makovicky et al., 2003). The supraoccipital is hollow and was pneumatized by part of the supraotic diverticulum in *Troodon*, however, whether the diverticulum passed through the paroccipital process is unclear. A possibly pneumatic depression has been described on the surface of the ventral process of the squamosal for *Saurornithoides junitor* and may be associated with the postotic diverticulum (Barsbold, 1974; Makovicky and Norell, 2004). The basisphenoid recess common to most theropods is absent in troodontids (Makovicky et al., 2003) except for the presence of superficial basipterygoid and parabasisphenoid recesses in the basal troodontid *Sinovenator*. A depression similar to the paracondylar recess of *Dilophosaurus* is present in

Stenonychosaurus inequalis (Currie, 1985). A small supraotic diverticulum would have imprinted a shallow depression on the prootic and appears to have communicated with the preotic diverticula through a pit on the laterosphenoid (Currie and Zhao, 1993b). A pneumatic depression on the caudal surface of the quadrate is present in *Troodon*, *Sinovenator*, and an unnamed taxon (Barsbold et al., 1987; Varricchio, 1997). A foramen is present in the quadrate depression in the latter taxon and may have provided an entry for the diverticulum into the quadrate. No evidence for a siphoneal diverticulum has been found (Currie and Zhao, 1993b).

Dromaeosauridae--Dromaeosaurids would have also had three tympanic diverticula (Barsbold and Osmólska, 1999; Norell et al., 2004, 2006). A prootic diverticulum would have been present only in *Velociraptor mongoliensis* within the trigeminal foramen and other branches of the preotic diverticula would have been housed in the basioccipital, basisphenoid, and prootic (Norell et al., 2004). A small parasphenoid recess is present dorsal to a basipterygoid recess in *Tsaagan* and is probably also pneumatized by the preotic diverticulum (Norell et al., 2006). The basipterygoid recess is also present in *Bambiraptor* and at least one specimen of *Velociraptor* (GIN 100/24) but appears to be absent in other *Velociraptor* specimens (Barsbold and Osmólska, 1999; Bunham, 2004; Norell et al., 2004). A basisphenoid recess is commonly present in dromaeosaurids (Barsbold and Osmólska, 1999; Currie, 1995; Norell et al., 2004, 2006). The supraotic recess is large in *Velociraptor* and *Deinonychus* and invades the parietal through the epiotic in *Tsaagan* (Barsbold and Osmólska, 1999; Brinkman et al., 1998). *Dromaeosaurus* is an exception with a reduced or absent supraotic recess (Norell et al., 2004, 2006). Extensions of the postotic recess are variable in dromaeosaurids. The postotic recess of *Tsaagan* has only a small entry without extensions into the exoccipital, that of *Velociraptor* has a foramen invading the base of the paroccipital process, and that of *Dromaeosaurus* fills the proximal half of the paroccipital process (Currie, 1995; Norell et al., 2004). There is no evidence for a discrete foramen for entry of the postotic recess into the parocciptial in *Dromaeosaurus* and *Deinonychus* although pneumatic spaces are present in both taxa (Brinkman et al., 1998; Norell et al., 2004). This condition is similar to the loss of the postotic recess foramen in *Troodon*. A subsellar recess is present in *Velociraptor* (Barsbold and Osmólska, 1999; Norell et al., 2004). A pneumatic depression on the quadrate is only present in *Tsaagan* and is located on the posterior surface of the bone. No articular recess has not been found and it appears a siphoneal diverticulum would have been absent in dromaeosaurids (Witmer, 1997b).

Evolution of tympanic pneumatic anatomy in Extant Aves--Modern birds have three major tympanic diverticula associated with the braincase (Norberg, 1978; Starck, 1995; Witmer, 1990). The preotic recess of modern birds lies within or anterior to the facial nerve exit. It is housed typically in the prootic, basisphenoid, laterosphenoid, and parasphenoid. The preotic recess of theropods is most consistently present in similar regions although its entry is often multichambered with the presence of the subotic recess in ornithomimids, oviraptosaurids, and troodontids (Witmer, 1997b). The diverticula of the latter two taxa would have expanded into the laterosphenoid similar to extent seen with the avian preotic diverticula. These theropods also shared the communications between the preotic and supraotic diverticula present in birds.

The postotic diverticula enter the braincase posterodorsal to the fenestral ovalis and fenestra pseudorotundum which themselves have dorsal and posteroventral subsidiary diverticula within the paroccipital process and anterior subsidiary diverticula within the metotic strut. Dorsal subsidary diverticula invade the opisthotic and communicate with the supraotic diverticulum within the paroccipital process and pneumatize the epiotic and squamosal. Each postotic diverticulum often communicates with its counterpart within the epiotic and supraoccipital in many neornithine birds. Communications between the postotic and supraotic diverticula via the opisthotic and prootic were present in oviraptosaurs suggesting the presence of pneumatic anatomy similar to the avian dorsal subsidiary diverticula. This anatomy is absent in deinonychosaurs and may be convergent with modern birds. The posteroventral subsidary diverticula invade into the basioccipital and exoccipital. Diverticula in the paroccipital process appear to have been present in coelophysoids although it was likely only superficial. However, the pneumatized paroccipital process appears to have been absent in most abelisauroids (except *Ceratosaurus*), torovosauroids, and allosauroids. The internally pneumatized paroccipital process appears to be established at Coelurosauria. Diverticula in the paroccipital process would have often extended within the supraoccipital in Coelurosauria as in modern birds. These communications between the postotic and supraoccipital diverticula may also be a synapomorphy of Coelurosauria.

The supraotic diverticulum of modern birds enters between the squamosal and prootic pneumatizing both of the bones. The diverticulum also extends into the parietal and frontal with frequent communications with the supraotic and postotic diverticula via the epiotic, opisthotic, and supraoccipital. The supraotic recesses appear clearly at Coelurosauria. An invasive supraotic diverticulum into the braincase was present in oviraptosaurids and dromaeosaurids (except *Dromaeosaurus*) similar to the location to the avian supraotic diverticulum while that diverticulum of other coelurosaurians is represented by a depression mainly on the surface of the prootic.

The branchial pneumatic system of modern birds includes two diverticula that enter the quadrate and articular independently. A similar branchial pneumatic anatomy is reconstructed only in tyrannosauroids, such as *Tyrannosaurus*, and *Dilong,* and *Ornithomimus edmontonicus* among non-avian theropods. The phylogenetically restricted occurance of this anatomy should be interpreted with caution because absence of osteological signatures of these diverticula may be the result of pachyostotic development, such as that observed in *Gavia*.

3.3. Conclusions

The first reconstruction of the cranial sinuses of *Ornithomimus edmontonicus* reveals an extensive and complex set of pneumatic diverticula similar to those of birds (Fig. 12). A survey of all available reports of theropod cranial pneumatic morphology adds new information on the origin and evolution of this soft tissue anatomy in theropod dinosaurs.

The reconstruction of *Ornithomimus* fills a phylogenetic gap near the base of Coelurosauria and establishes a suite of cranial pneumatic synapomorphies for this clade. Coelurosauria is diagnosed by dramatic elaborations of the tympanic sinus system and likely represents the origin of most tympanic pneumatic diverticula present in modern Aves. Much of the avian nasal sinus system appears to have originated at Neotetanurae. These phylogenetic changes reinforce a prevalent trend of increasing pneumatic complexity within theropods toward node Aves. Among theropods, the cranial pneumatic features in *O. edmontonicus* are most similar to tyrannosaurs. Tyrannosaurs and *O. edmontonicus* share the presence of an invasive palatine diverticulum and a branchial pneumatic system similar to modern birds. They also share communications between the supraoccipital and postotic diverticula. The cranial pneumatic similarities in these closely related taxa may indicate a high degree of phylogenetic information in this anatomy and are probably synapomorphies of Coelurosauria (Fig. 12).

Reexamination of nasal and tympanic pneumatic anatomy throughout non-avian theropods also revealed a novel interpretation of the jugal fossa. A jugal fossa or recess is present in nearly all of non-avian theropods is topologically similar to a suborbital diverticulum of modern birds. The shared topology suggests that these two morphologies are homologous. The data also establishes a stepwise origin of the avian nasal and tympanic sinuses at Neotetanurae, and Coelurosauria, respectively.

The timing of occurrence of an avian-like elaborated nasal sinus at Neotetanurae may be associated with large body size and thermoregulatory requirement. Sereno and colleagues (2008) recently suggested that the origin of extensive postcranial pneumaticity at Neotetanurae may be derived from thermoregulatory requirements of these large-bodied theropods. While Torvosauridae also have a large body sizes, they also have elongated neural spines that would have supported a large "sail" thought to be used for thermoregulation. Allosauroids generally have massive skulls and the origin of the avian-like nasal sinus system may be associated with this increase in skull size. The elaboration of the tympanic sinuses at Coelurosauria may be associated with increased thermoregulatory requirements of their enlarged brain size. The initiation of the trend toward an avian-like large brain appears at Coelurosauria (Larsson, 2001). The brain has a poor tolerance for high heat and requires stringent control at high temperatures (Rogers, 1999).

Many endothermic animals have physiological adaptations to selectively cool their brains during periods of excessively high body temperatures (Caputa, 2004). For example, the brain of goats can be maintained at 41.3 C while their body temperatures reach 43 C (Taylor and Lyman, 1972). This selective brain cooling system in mammals is largely driven by evaporative cooling in the narial chamber to cool venous blood before is passes into a complex network around the carotid rete. The cooled carotid arterial blood then supplies the brain. The elaborated tympanic sinuses of birds may also function as part of this selective brain cooling physiology but no research has yet confirmed this possibility. A selective brain cooling function may also explain the association between the evolution of elaborated tympanic spaces (Kellner, 1997) and increased brain size (Witmer, et al., 2003) of pterosaurs. Evolutionary origin of the avian-like cranial sinuses of non-avian theropods may be associated with functions involved with the evolution of physiological thermoregulation. If so, this complex morphology may offer novel insights into the evolution of theropod physiology.

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