Witmer, L. M. 1997. Craniofacial air sinus systems. pp. 151–159 *in* The Encyclopedia of Dinosaurs, P. J. Currie and K. Padian (eds.), Academic Press, New York.

Encyclopedia of

DINOSAURS

EDITED BY

Philip J. Currie

Royal Tyrrell Museum of Palaeontology
Drumheller, Alberta, Canada

Kevin Padian

Museum of Paleontology
University of California, Berkeley

ACADEMIC PRESS
San Diego London Boston New York Sydney Tokyo Toronto

Craniofacial Air Sinus Systems

Lawrence M. Witmer
Ohio University
Athens, Ohio, USA

An unusual anatomical system pervaded the heads of dinosaurs. Insinuated among such conventional soft tissues as muscles, nerves, blood vessels, and sense organs was a complicated system of air-filled sinuses. These sinuses formed as thin-walled, epithelial outgrowths (diverticula) of other air-filled cavities, often invading and resorbing surrounding bone and producing foramina and cavities within these bones. This process is called pneumatization and the resulting state of having air-filled bones is known as pneumaticity. Many dinosaurs are highly pneumatic animals indeed, with most of the bony skull literally riddled with foramina, channels, and cavities. More technical treatments of this topic have been published by Witmer (1990, 1995, 1997) and Currie and Zhao (1993a,b) and the articles cited therein.

Pneumatic Systems in Dinosaurs

There are two well-known pneumatic systems in dinosaurs, one arising as outgrowths of the nasal cavity and the other as outgrowths of the tympanic (middle ear) cavity. Not just dinosaurs, but all archosaurs—living and extinct—have at least one main paranasal air sinus, known as the antorbital sinus, that forms as an outgrowth of the main nasal cavity (Fig. 1). The antorbital sinus produces a large cavity and opening in the side of the face known respectively as the antorbital cavity and antorbital fenestra. In many archosaurs, the antorbital sinus itself has subsidiary outgrowths that may pneumatize surrounding bones, producing so-called accessory cavities. In addition to the nearly ubiquitous antorbital sinus, a few kinds of dinosaurs have air sacs deriving from a different part of the nasal cavity, namely, the front-most portion known as the nasal vestibule. Such vestibular sinuses tend to pneumatize the bones surrounding the bony nostril (i.e., premaxilla and nasal). Humans and most other mammals have similar (but not homologous) paranasal sinuses; these are the sinuses that become congested when we have colds and that are involved in our "sinus headaches."

Paratympanic air sinuses are less common in archosaurs. In those non-dinosaurian taxa with paratympanic pneumaticity (such as crocodylomorphs and pterosaurs), the bones of the braincase are the ones that are usually invaded by air sacs. Among perhaps all archosaurs, tympanic recesses are best developed in theropod dinosaurs. As with paranasal sinuses, humans and most other mammals have a set of sinuses associated with the tympanic cavity, and particularly bad middle-ear infections may spread to our paratympanic air sinuses.

In addition to paranasal and paratympanic sinuses, there are other, more poorly known, systems pneumatizing the head skeleton. The first may simply represent diverticula from the cervical system of pulmonary air sacs that extend beyond the neck vertebrae into the occipital region of the skull. Some of the pneumatic cavities of certain theropod dinosaurs may result from these pulmonary diverticula. The second is the median pharyngeal system that forms as a midline outgrowth from the roof of the throat and invades the base of the skull in the region of the basisphenoid and basioccipital bones in many archosaurs. It is not always demonstrably of pneumatic origin in many archosaurs but is almost certainly so in theropod dinosaurs. Although the resulting "basisphenoid sinus" is often regarded as a derivative of a "median Eustachian tube," it is clearly distinct from the definitive auditory (Eustachian) tubes that, along with the tympanic cavities, have their embryological origins from the paired first pharyngeal (or branchial) pouches; whereas in some archosaurs the median system eventually connects up with the tympanic cavity, it does not always do so. Some have suggested that the median pharyngeal pneumatic system results from aeration of the embryonic hypophysial pouch (of Rathke)—a precursor of

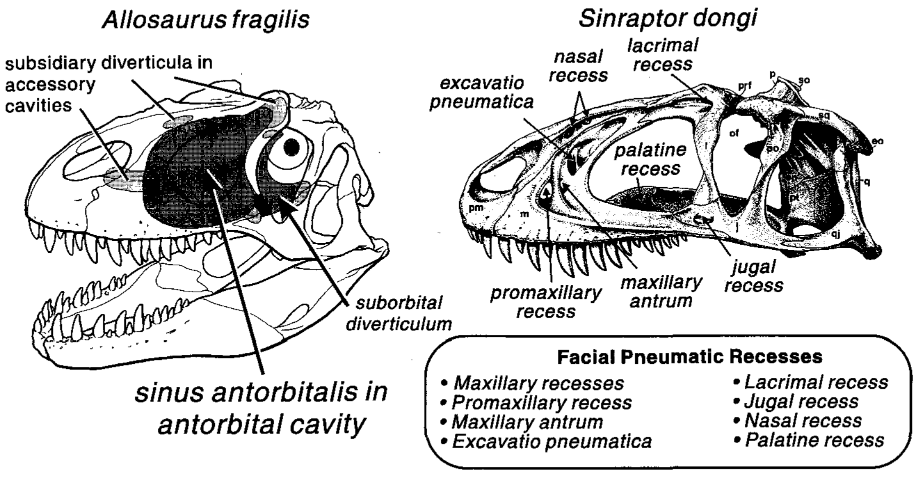


FIGURE 1 Paranasal pneumaticity in theropod dinosaurs. (Left) skull of *Allosaurus fragilis* in oblique view, showing the antorbital paranasal air sinus and some of its epithelial diverticula (modified from Witmer, 1997, with permission). (Right) skull of *Sinraptor dongi* in left lateral view with the major paranasal pneumatic accessory cavities labeled (modified from Currie and Zhao, 1994a, with permission). The accessory cavities result from pneumatization by the subsidiary diverticula of the antorbital sinus.

part of the pituitary gland—and this is an idea worthy of further investigation.

Ornithischian Dinosaurs

Paratympanic air sinuses are very uncommon in ornithischians. The middle ear sac was certainly present (as evidenced by, among other things, the discovery of columellae—the slender ear bones), but apparently it did not typically send out diverticula that invaded surrounding bones. A few ornithischians, however, such as the basal thyreophoran *Scelidosaurus* and the ornithopod *Hypsilophodon*, do seem to have some excavations of portions of the braincase that are best interpreted as being of pneumatic origin. In these forms, there is a fairly extensive cavity associated with the canal for the major artery supplying the brain, the cerebral (or internal) carotid artery. This cavity is directly behind and medially undercuts a curving ridge of bone—nearly ubiquitous in archosaurs—known as the otosphenoidal crest, which runs from the basipterygoid process to the paroccipital process and segregates the orbital contents in front from the middle ear contents behind. Although such a rostral tympanic recess is, as we will see, fairly common in theropod dinosaurs (as well as in a variety of other archosaurs), it is rather rare in ornithischians.

Paranasal pneumaticity, on the other hand, is present in probably all ornithischians in that, like all other archosaurs, they possessed an antorbital sinus. This antorbital air sinus was lodged in a cavity, the antorbital cavity, located in front of the orbit and bounded by primarily the maxilla and lacrimal, and sometimes also the jugal, palatine, and nasal. In fact, this description holds for most dinosaurs (indeed, most archosaurs). Pneumatic bony accessory cavities, produced by subsidiary diverticula of the antorbital sinus, are relatively rare in ornithischians, although they are present in a few taxa, such as the intramaxillary sinuses of *Protoceratops* and its relatives and the maxillary recesses of some basal thyreophorans. Higher thyreophorans, in particular ankylosaurid ankylosaurians, deserve special mention here in that within their highly armored skulls is a maze of pneumatic sinuses. The precise pattern and arrangement of ankylosaurid paranasal sinuses remain poorly known, and it is not entirely clear if some are accessory cavities of the main antorbital sinus, novel paranasal sinuses, or even diverticula of the nasal vestibule. Pneumatic evaginations of the nasal vestibule, however, are clearly expressed in lambeosaurine hadrosaurids, such as *Corythosaurus*. In lambeosaurines, the narial region is greatly enlarged, and the bones enclosing

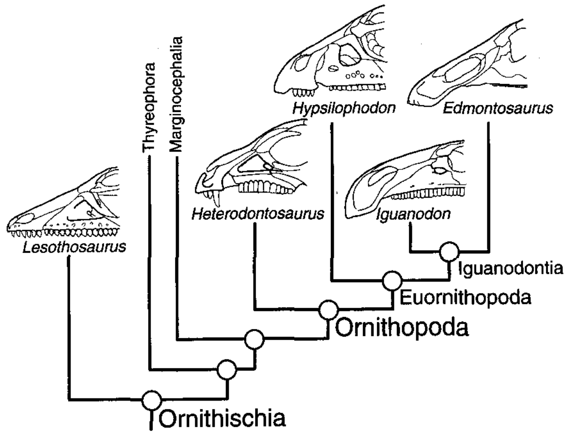


FIGURE 2 The evolving antorbital cavity of ornithischian dinosaurs, especially Ornithopoda. Most clades of ornithischians, such as Ornithopoda, show marked trends for reduction and enclosure of the antorbital cavity by laminae of the maxilla and lacrimal. Modified from Witmer (1997) and references cited therein with permission.

the nasal vestibule (the premaxilla and nasal) are folded into a complicated collection of passages and chambers, all of which are perched atop the remainder of the skull.

Perhaps the most remarkable aspect of skull pneumaticity in ornithischians is its recurrent trend for reduction. In other words, ornithischians tend to become relatively less pneumatic when comparing more advanced members of a clade with more basal members. For example (Fig. 2), the basal ornithischian *Lesothosaurus* has a more or less primitive—and hence, fairly large—antorbital cavity; it even has a small pneumatic accessory cavity associated with its palatine bone. In ornithopodan ornithischians, however, there is a general trend for reduction of the antorbital cavity and enclosure by lateral sheets of the maxilla and lacrimal bones such that the antorbital cavity becomes a relatively small and completely internalized space. The broad outlines of this trend can be viewed by making a phylogenetic march from a basal ornithopod such as *Heterodontosaurus* (which retains a relatively large antorbital cavity but also shows the beginnings of the lateral enclosure), through *Hypsilophodon* (which shows further lateral enclosure) and iguanodontians such as *Camptosaurus* and *Iguanodon* (which show further reduction and enclosure), to hadrosaurids (in which the antorbital cavity is relatively tiny and completely closed laterally). A similar phylogenetic trend can be identified in thyreophorans. These trends almost certainly relate to (especially in ornithopods) the expansion and elaboration of the feeding apparatus (in particular, the dentition and its bony supports). Thus, as the feeding apparatus expanded phylogenetically, the antorbital sinus and its bony cavity contracted.

Before concluding the discussion of ornithischian craniofacial pneumaticity, the supracranial cavities of ceratopsids such as *Triceratops* need to be considered. These cavities, formed by the folding of the frontal bones, are often referred to as "frontal sinuses" and are commonly thought to be of pneumatic origin. They are often compared to the frontal air sinuses of modern bovid mammals (cattle, sheep, etc.) because in both ceratopsids and bovids the sinuses form strutted chambers that extend up into the base of the horn cores. It is possible that the supracranial cavities of ceratopsids are indeed pneumatic, but the source of the air-filled diverticulum remains obscure. It is not yet clear how an outgrowth from either the nasal cavity or the tympanic cavity could reach the skull roof. Its mode of development is also unusual for a pneumatic recess. Thus, pending further research, the supracranial cavities of ceratopsids will remain functionally enigmatic.

Saurischian Dinosaurs

Saurischia includes neornithine birds, the most pneumatic of all known vertebrates, but not all saurischians display extensive craniofacial pneumaticity. In fact, other than the antorbital cavity itself, sauropodomorphs do not display many pneumatic features in their skulls, which is ironic because their axial skeletons are otherwise often marvels of pneumatization. Basal sauropodomorphs (i.e., prosauropods) have relatively primitive and simple antorbital cavities, although a subsidiary diverticulum of the antorbital sinus excavates a pneumatic accessory cavity in the nasal of *Plateosaurus*. The antorbital cavity of most sauropods is relatively reduced, being telescoped between the orbit behind and the greatly expanded nasal vestibule in front. As in ornithopods, the antorbital sinus appears to be, in a sense, "crowded out" by other structures. Paratympanic pneumaticity is also relatively poorly developed in sauropodomorphs. A few basal taxa, such as *Anchisaurus* and *Plateosaurus*, have, much as does *Hypsilophodon*, moderate development of a rostral tympanic recess (i.e., the cavity associated with the cerebral carotid artery and bounded by the otosphenoidal crest). Other paratympanic recesses appear to be virtually absent, although a few sauropods (e.g., *Camarasaurus*) have a deep excavation in the back surface of the quadrate bone that could be interpreted as pneumatic in nature.

In contrast to sauropodomorphs, theropod dinosaurs display the most extensive craniofacial pneumaticity of all archosaurs with perhaps the exception of some pterosaurs. Not only are the paranasal and paratympanic systems well developed in theropods but also the median pharyngeal system—for the first time in dinosaurs—takes on clearly pneumatic attributes. In virtually all theropods, the antorbital cavity is huge, occupying in some cases more than half of the total skull length; thus, the enclosed antorbital paranasal air sinus must have been very voluminous (Fig. 1). As in other archosaurs, the maxilla and lacrimal were the major bones housing the air sac, although the nasal, jugal, and palatine were also commonly involved. With the exception of the bizarre oviraptorosaurs, which have dramatically complicated pneumatic skulls, there is no evidence that the facial skeleton of theropods was pneumatized by any air sacs other than the antorbital sinus.

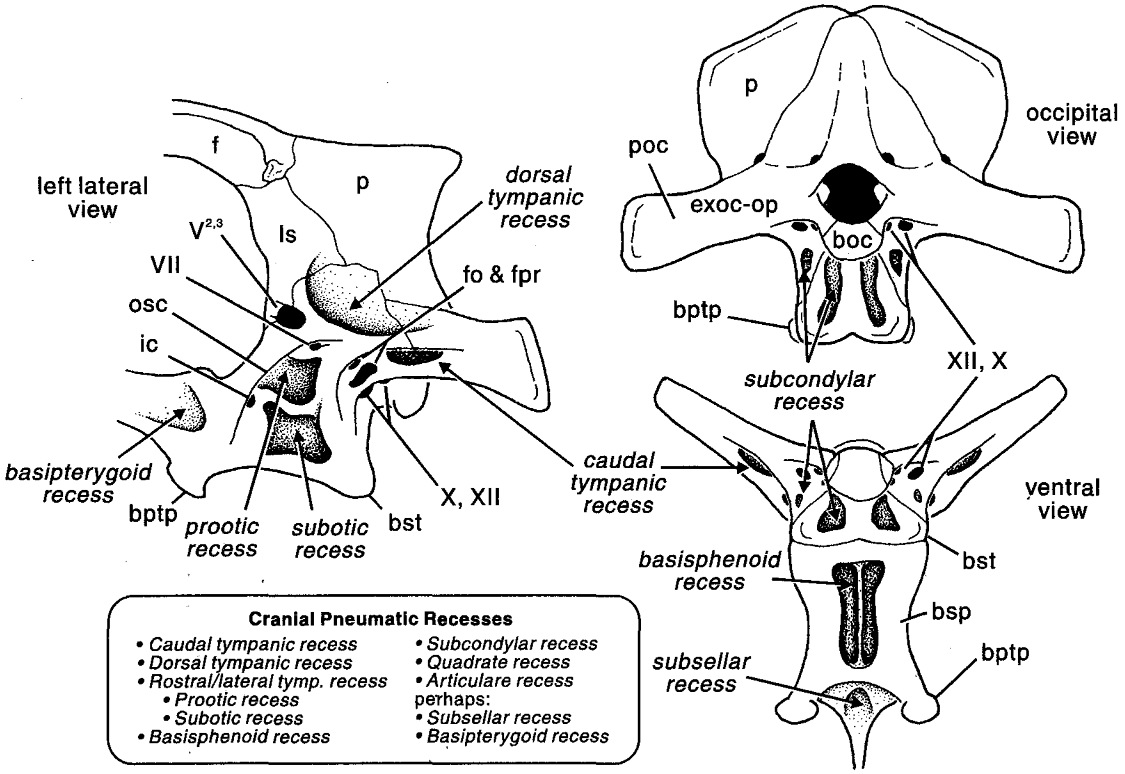
Nevertheless, one of the remarkable aspects of paranasal pneumaticity in theropods was the tendency for the antorbital sinus to send out subsidiary diverticula that penetrated into the adjacent facial bones, often producing large pneumatic accessory cavities (Fig. 1). Although many other archosaurs have more or less shallow pneumatic depressions on various facial bones, it is theropods alone that routinely exhibit a facial skeleton that is produced into an open series of hollowed struts and chambers. The most commonly observed accessory cavities are those in the maxilla, with the two most consistent maxillary sinuses being the promaxillary recess and the maxillary antrum. Both these accessory cavities are widely (but not universally) distributed among neotetanurans, and many (but again not all) ceratosaurians have a single maxillary sinus, which is probably homologous to the promaxillary recess of higher theropods. The lacrimal bone is also commonly pneumatized by a subsidiary diverticulum of the antorbital sinus. It is this lacrimal sinus that invades and hollows out the "horns" of theropods such as *Allosaurus* and *Ceratosaurus*. The nasal, jugal, and palatine bones are less frequently pneumatized, but in some cases these recesses can result in spectacular structures, such as the inflated nasal crest of *Monolophosaurus* or the puffed-up palatine bones of *Tyrannosaurus*.

The phylogenetic distribution of these paranasal pneumatic accessory cavities can be rather confusing. Some groups, such as tyrannosaurids, tend to be fairly consistent. Other groups, however, can be more variable. For example, among dromaeosaurids, *Deinonychus* has all the accessory cavities noted previously, but the closely-related form, *Velociraptor*, has only a few of them. Moreover, a few taxa, such as the basal tetanuran *Torvosaurus* and the aberrant maniraptoran *Erlikosaurus*, lack many or even all of the accessory cavities that phylogenetics indicates they "should" have. Nevertheless, despite these problems, one point that emerges is that the facial skeleton of theropods, as a group, is highly pneumatic; in fact, pneumaticity has been recorded in every bone of the facial skeleton except two (the prefrontal and vomer).

A final aspect of the paranasal air sinus system of theropods involves a diverticulum of the antorbital sinus that only very rarely pneumatizes bone. This air sac, the suborbital diverticulum, is almost always present in modern theropods (i.e., birds). It forms as an outgrowth of the back wall of the antorbital sinus and expands into the orbit where it often encircles the eyeball and interleaves with the jaw musculature. In at least a few nonavian theropods, there are good reasons to believe that a bird-like suborbital diverticulum was present (Fig. 1). The significance of this suborbital sac is that it provides a mechanism for actively ventilating the antorbital sinus (i.e., pumping air in and out). Movements of the lower jaw—such as in closing and opening the mouth—will set up positive and negative pressures in the suborbital sac because of its intimate relationship to the jaw muscles. These pressure changes are transferred to the antorbital sinus and, thus, like a bellows pump, air passes to and fro between the nasal cavity and antorbital sinus. This situation is unique: In other animals with paranasal sinuses, such as crocodilians and mammals, the sinuses are never actively ventilated but rather are stagnant, dead-air spaces. What role such a paranasal bellows pump plays in the physiology of birds and probably other theropods is still unknown.

As with the paranasal system, the paratympanic air sinuses are generally very diverse and extensive in theropods. Most of the sinuses invade the bones of the braincase and otic (ear) region, such as the prootic, opisthotic, basisphenoid, and basioccipital. Some of these recesses are obviously associated with the middle ear sac, but others, as mentioned previously, seem to result from median pneumatic outgrowths of the roof of the pharynx and perhaps even from extensions from the pulmonary air sacs in the neck. The pneumatic sinuses of the braincase will be briefly discussed using a hypothetical form (Fig. 3) because no known species has all the air cavities.

There are three fairly consistent pneumatic cavities that clearly derive from diverticula of the middle ear sac, and they all aptly bear the name "tympanic recess." Perhaps the most commonly encountered tympanic recess is the rostral or lateral tympanic recess noted previously in some other dinosaurs. This recess is located just behind the otosphenoidal crest in the area of the cerebral carotid artery foramen. In some theropods, such as *Syntarsus* or *Dilophosaurus*, this recess resembles that of other archosaurs in being a more or less simple but expanded cavity, whereas in others, such as some coelurosaurs, it becomes complicated and multichambered. For example, taxa such as *Deinonychus* and *Struthiomimus* have a discrete prootic recess within the rostral tympanic recess just ventral to the facial nerve foramen, and a varied group of tetanurans have a more ventral cavity, the subotic recess, that excavates the basal tubera. In some forms, such as ornithomimids, troodontids, and birds, the



Cranial Pneumatic Recesses

- *Caudal tympanic recess*
- *Dorsal tympanic recess*
- *Rostral/lateral tymp. recess*
    - *Prootic recess*
    - *Subotic recess*
- *Basisphenoid recess*
- *Subcondylar recess*
- *Quadrate recess*
- *Articulare recess*

perhaps:

- *Subsellar recess*
- *Basipterygoid recess*

FIGURE 3 Braincase of a hypothetical theropod dinosaur showing the diversity of pneumatic recesses. Pneumatization from the middle ear sac produces the dorsal, caudal, and rostral tympanic recesses and the recesses within the quadrate and articular bones (not shown). The subcondylar recesses derive from either the middle ear sac or extensions from the pulmonary air sacs. Pneumatization from a median pharyngeal system produces the basisphenoid recess. The basipterygoid and subsellar recesses are not clearly pneumatic structures, and the source of the diverticulum, if present, is also uncertain. fo, fenestra ovalis (or vestibularis) [note: not foramen ovale, which is the maxillary n. foramen in mammals); fpr, fenestra pseudorotundum (or cochlearis); osc, otosphenoidal crest.

rostral tympanic recess and part of the main middle ear sac are covered laterally by a thin sheet of bone, the parasphenoid. The caudal tympanic recess is typically found in Coelurosauria (*Troodon* being an important exception) and involves a large air space within the paroccipital process that opens into the tympanic cavity via an oval foramen on the front of the base of the paroccipital process. The dorsal tympanic recess, a moderate to very deep depression on the dorsolateral surface of primarily the prootic bone, has a very patchy distribution but is found in ornithomimids, velociraptorine dromaeosaurids, and all known birds.

In a few groups of nonavian theropods, such as birds, tyrannosaurids, and at least some ornithomimids and troodontids, the quadrate and/or articular bones are also invaded by outgrowths of the middle ear sac. In some respects, such pneumaticity makes good sense in that the quadrate and articular bones have their embryological origins as parts of the first pharyngeal (= mandibular) arch; recall that the middle ear sac itself derives from the same pharyngeal arch. In fact, it is a mystery as to why more groups of theropods—especially bird-like forms such as *Deinonychus* that have extensive braincase pneumaticity—lack mandibular arch pneumaticity. Interestingly, crocodyliforms, many pterosaurs, and some other non-dinosaurian archosaurs have pneumatic quadrates and articulars.

The median pharyngeal system, a rudimentary blind pit or small foramen between the basioccipital and basisphenoid in other archosaurs, takes on the unmistakable appearance of an invasive air-filled cavity in theropod dinosaurs, in which it is usually referred to as a "basisphenoid sinus" (Fig. 3). Typically, the sinus is roughly pyramidal or conical, with its base being a large opening in the midline of the basicranium between the paired basal tubera and basipterygoid processes and its apex being directed dorsally toward the pituitary fossa. Even in basal forms such as *Coelophysis* and *Dilophosaurus*, the basisphenoid sinus is already somewhat expanded. However, in most tetanurans the basisphenoid sinus becomes a large expansive cavity, invading back into the basioccipital bone, sometimes even into the occipital condyle. Sometimes a median septum is preserved within the sinus, partially dividing it into left and right sides.

Paired openings on the occipital surface of the cranial base below the occipital condyle, known as the subcondylar recesses (Fig. 3), are not widely distributed in theropods but are well developed in tyrannosaurids and ornithomimids. These cavities are obviously of pneumatic origin in that they expand within the bone and are multichambered. What is uncertain is the source of the air-filled diverticulum. The diverticulum could indeed derive from the middle ear sac—that is, it is another tympanic recess. Certainly, the subcondylar recess is close enough to the tympanic cavity that it would not be a "far reach." Another idea, however, cannot be ruled out: The subcondylar recesses derive from diverticula of the cervical division of the lung air-sac system. The cervical air sacs pneumatize the backbone up to the second cervical vertebra in tyrannosaurids and ornithomimids and thus are very close to the occiput. Furthermore, they presumably interleaved with neck muscles that attached to the occiput in the vicinity of the subcondylar recesses. Choosing between a tympanic or pulmonary source is currently very difficult.

A couple of other cavities may be of pneumatic origin but are much more uncertain (Fig. 3). The basipterygoid recess is a depression within the lateral surface of the basipterygoid process within the orbit of theropods such as *Allosaurus*. If it is pneumatic, the source of the diverticulum is unclear. Instead, it may be a site of muscular attachment, perhaps for a palatal protractor (if indeed such muscles were present in nonavian theropods). The subsellar recess is a median ventral cavity located just in front of the basisphenoid recess at the base of the parasphenoid rostrum. As its name implies, it resembles the basisphenoid recess in being directed toward the pituitary fossa, but obviously both recesses could not result from a diverticulum tracking along the single embryonic hypophysial stalk (if in fact either did). Clearly, both the basipterygoid and subsellar recesses are structures that need a good deal more research.

Two more "problem sinuses" need to be considered. Large cavities within both the ectopterygoid and squamosal bones are clearly pneumatic. The source of the diverticula, however, remains unclear. The ectopterygoid recess is an almost ubiquitous feature of theropods. It usually takes the form of a simple, smooth-walled ventromedial "pocket" in the bone, although in some tyrannosaurids it becomes a multichambered affair. However, did the diverticulum come from the middle ear sac, the antorbital sinus, or from some unknown source (perhaps yet another pharyngeal outgrowth!)? All these ideas are possible but have problems. Likewise, the large recess within the squamosal bones of tyrannosaurids and ornithomimids could have been produced by subsidiary diverticula of either the antorbital sinus or the middle ear sac, and we currently have little strong evidence that allows us to make a reasoned choice.

In summary, theropod dinosaurs obviously exhibit an extraordinary—often bewildering—diversity of air-filled sinuses. Without question, pneumaticity is the single most important anatomical system shaping theropod skull morphology. Interestingly, however, it seems fraught with high levels of homoplasy (the evolutionary loss and/or convergent acquisition of a feature). Certainly, there are some very consistent, phylogenetically informative pneumatic characters, such as the presence of the two main maxillary sinuses in neotetanurans or the caudal tympanic recess in coelurosaurs. However, many of the pneumatic characters seem to have been evolved or been lost repeatedly—often yielding a morphology so similar that the only hint of homoplasy comes through phylogenetic analysis. The dorsal tympanic recess of coelurosaurs is a good, but by no means the only, example. This recess is found in Mesozoic birds, such as *Hesperornis* and *Archaeopteryx*, as well as the dromaeosaurids *Deinonychus* and *Velociraptor*. So far, so good, but it is absent in the dromaeosaurid *Dromaeosaurus*. It is also absent in the bullatosaur *Troodon* but is clearly present in the bullatosaur *Struthiomimus*. The addition of other taxa only complicates the picture further.

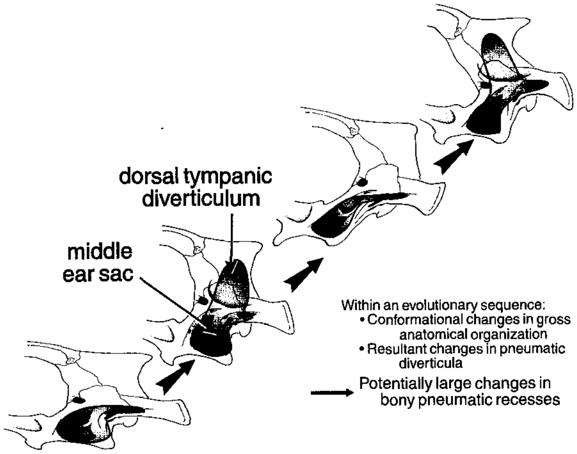


FIGURE 4 A transgression–regression model for homoplasy in pneumatic systems. Hypothetical evolutionary transformation series of theropod braincases depicting the changing status of a dorsal tympanic diverticulum of the middle ear sac and, hence, the variable presence or absence of the bony recess. As the anatomical conformation of the whole region changes, the possibility for a diverticulum to evaginate changes. Thus, the mechanism for pneumatic homoplasy is easily envisioned, with an apt analogy being the fluctuating sea levels associated with transgression and regression.

When the workings of pneumatic systems—that is, the soft tissue systems that literally produces the bony recesses—are understood, morphogenetic mechanisms for phylogenetic reversal and convergence become rather easy to envision. For example, in the diagram in (Fig. 4) showing a hypothetical ancestor–descendant sequence of species, the ancestral form has a relatively simple middle ear sac with no dorsal tympanic diverticulum. A descendant species might evolve some anatomical change in the conformation of the general region (in this case, a higher and shorter braincase) that, for some reason, permits evagination of a diverticulum, and this diverticulum excavates a pneumatic cavity on the prootic. A further conformational change might prevent evagination of this diverticulum or cause it to shift its position, which would appear to us as a reversal. Subsequent changes could permit the diverticulum to evaginate once again, perhaps resulting in a bony recess that is identical to the second species, which then would represent convergence. The point is that these epithelial air sacs are highly labile structures, the position (or even the presence) of which is easily affected by surrounding anatomical structures. Thus, given this almost capricious ebb and flow of pneumatic diverticula, perhaps it is unreasonable even to expect these bony cavities to fall out neatly on a cladogram.

Functions of Sinuses

It is somewhat ironic that, despite air-filled sinuses being very prominent components of head anatomy in not just birds and other dinosaurs but also in mammals, the function of pneumaticity has remained obscure. Numerous ideas have been proposed over the years, including sinuses acting as shock absorbers, flotation devices, vocal resonators, thermal insulators, weight-reducing air bubbles, and the list goes on. Many of these ideas at first may seem absurd but still may apply to some animals in some cases. For example, the sinuses within the crests of lambeosaurine hadrosaurids are thought to have functioned as resonating chambers. However, these functions obviously cannot apply broadly across all animals that possess the sinus. In fact, because almost all the ideas that have been proposed fail because of limited applicability, the problem of the general function of pneumatic sinuses has been regarded as one of the great mysteries of craniofacial functional morphology.

It is significant that virtually all the suggestions hinge on the empty space within the sinuses being that which provides the suggested functional benefits. With regard to the lambeosaurine example discussed previously, the empty space would provide the chamber in which sound resonates. It now seems that it is this focus on the enclosed volume of air that has led us astray. Sinuses are not truly "empty," but rather they contain the air sac itself—that is, the thin epithelial balloon that lines the bony recess. It turns out that the epithelium—not the empty space—may be the key. Pneumatic epithelium (and its associated tissues) appear to have the intrinsic capacity to expand and to pneumatize bone. Therefore, these air sacs may simply be opportunistic pneumatizing machines, expanding as much as possible—but within certain limits. These limits are provided by the local biomechanical loading regimes (i.e., the stresses and strains within the bone substance). Bone is sensitive to and responsive to its local stress environment, such as the forces involved in chewing or biting or laying down new bone to maintain sufficiently strong and stiff structures. Thus, there are two competing tendencies, one involving expanding air sacs and the other involving mechanically mediated bone deposition. A compromise is struck ensuring that pneumatization does not actually jeopardize the strength of the whole structure. An interesting consequence of this "battle" is that mechanically "optimal" structures will result as a secondary and completely incidental by-product—in other words, there is no reason to invoke natural selection to act directly to produce structures of maximal strength but minimal materials. Put simply, architecturally "elegant" structures are automatic outcomes of these two intrinsic, but opposite, processes.

Thus, what is the function of the antorbital sinus or the diverticula of the middle ear sac? The answer is probably, at its base, no particular function whatsoever. That is not to say that any of these air sacs could not be secondarily pressed into service for some positive function, subsequently honed by natural selection. Such is likely the case for the resonating chambers of hadrosaurs and, additionally, aspects of the expanded tympanic cavities of theropod dinosaurs, which enhance hearing due to certain acoustic properties. However, at the same time, positive functions need not be sought for every pneumatic recess in every species that has them. Again, they are simply intrinsic properties of pneumatic systems.

This new view on the function of pneumaticity helps explain certain trends in various dinosaur groups. For example, the reduction of the antorbital cavity in ornithopod ornithischians that was discussed previously (Fig. 2) clearly reflects a situation in which bone deposition "won out" over pneumatically-induced resorption of bone. The evolution and refinement of chewing in ornithopods required extensive bony buttressing and reinforcement, and so expansion of the antorbital sinus was severely limited. On the other hand, skull pneumatization in theropods appears to have progressed with few constraints and was clearly opportunistic. Although carnivory may involve fairly large bite stresses (force per unit area), the stresses and strains that a theropod skull as a whole underwent were minimal in comparison with the repetitive masticatory forces to which chewing animals such as ornithopods were subject. Thus, in theropods, sinuses were generally free to expand. It is significant, however, that the remaining bony struts in theropod skulls are positioned in mechanically advantageous locations, giving the appearance of exquisite design. It is also worth mentioning that *Tyrannosaurus rex*, a theropod that secondarily became adapted for particularly hard biting, increased the dimensions of some bony buttresses and bars to resist the stresses, yet it maintained pneumaticity—and even expanded some sinuses—by pneumatizing the bones internally, yielding a skull composed of a series of hollow, often truly tubular bars and plates.

See also the following related entries:

Braincase Anatomy • Postcranial Pneumaticity • Skull, Comparative Anatomy

References

Currie, P. J., and Zhao, X.-J. (1993a). A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Can. J. Earth Sci.* **30,** 2037–2081.

Currie, P. J., and Zhao, X.-J. (1994b). A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Can. J. Earth Sci.* **30,** 2231–2247.

Witmer, L. M. (1990). The craniofacial air sac system of Mesozoic birds (Aves). *Zool. J. Linnean Soc.* **100,** 327–378.

Witmer, L. M. (1995). Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *J. Morphol.* **225,** 269–327.

Witmer, L. M. (1997). The evolution of the antorbital cavity of archosaurs: A study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Mem. Soc. Vertebr. Paleontol (J. Vertebr. Paleontol.)* **17**(Suppl.), 1–75.

Crests

see ORNAMENTATION

Cretaceous Extinction

see EXTINCTION, CRETACEOUS

Cretaceous Period

EVA B. KOPPELHUS
Geological Survey of Denmark and Greenland
Copenhagen, Denmark

The Cretaceous is the last period of the Mesozoic. It lasted for approximately 80 million years, ending 65 million years ago. The name is derived from the Latin word "*creta*," which means "chalk," and refers to the thick beds of Cretaceous chalk that are characteristic of parts of Europe.

Once divided into three epochs, the Cretaceous of Europe is now divided into the Early and Late Cretaceous, which are further subdivided into 12 stages. These were all defined on the basis of strata in the Anglo–Paris–Belgian area. In North America, the period is also divided into Early (Comanchean) and Late (Gulfian) Cretaceous.

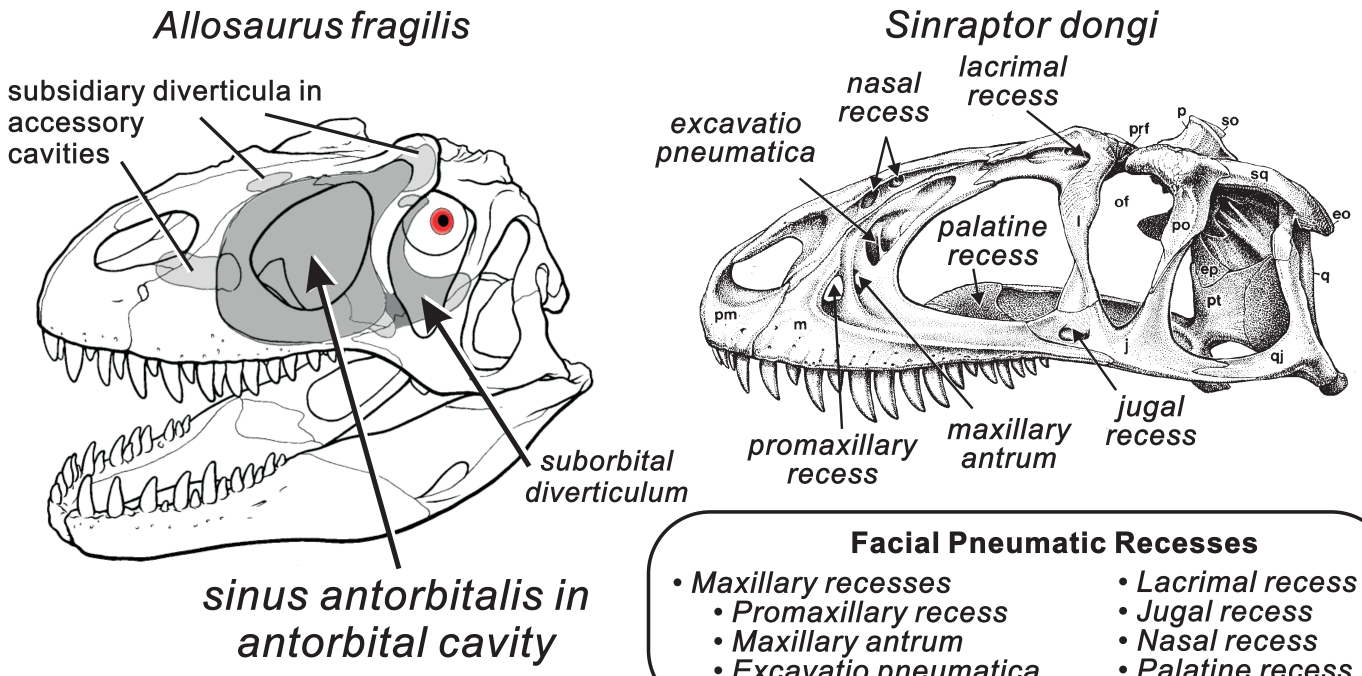
The earth's climate was generally warm in the Cretaceous. Early in the period, conditions were becoming more humid and seasonal, which favored explosive diversification of the floras and the animals that fed on them. By the end of the Cretaceous, global cooling led to a drop in diversity of plants and animals in the higher latitudes.

Throughout the Cretaceous, the continents drifted apart to approach their current positions. The Atlantic Ocean opened up, India reached Asia, and extensive inland seas subdivided the continental masses.

Cretaceous rocks are widely distributed and exposed, and it is not surprising that almost half of the known dinosaurs have been found at this level. Hadrosaurs and ceratopsians in particular are common in the Late Cretaceous of the Northern Hemisphere. It was a time of great diversification, and dinosaurs shared their world with many other vertebrate groups that have changed little since the Cretaceous. Placental mammals, birds, snakes, and many other animals established the bauplans that are familiar to us today. Insects and other invertebrates were taking on a more modern appearance. It was a time when the terrestrial floras changed from being entirely dominated by pteridophytes and gymnosperms in the early part of the Cretaceous to angiosperms in the Late Cretaceous. The floral assemblages from the Late Jurassic persisted into the Early Cretaceous in the lower latitudes, whereas angiosperms became more prominent in the higher latitudes. By the early Late Cretaceous, there was a dramatic change into assemblages dominated by angiosperms. Four floral provinces based on pollen have been recognized in the Cenomanian: northern Laurasia, southern Laurasia, northern Gondwana, and southern Gondwana (Brenner, 1976). By Santonian–Campanian times, angiosperm pollen assemblages have been used to divide Laurasia into a southern *Normapolles* province and a northern *Aquilapollenites* province (Batten, 1984). The Cretaceous is a most interesting period from an evolutionary point of view.

Toward the end of the period, however, things

Witmer, L. M. 1997. Craniofacial air sinus systems. pp. 151-159 in The Encyclopedia of Dinosaurs, P. J. Currie and K. Padian (eds.), Academic Press, New York.



Facial Pneumatic Recesses

- *Maxillary recesses*
  - *Promaxillary recess*
  - *Maxillary antrum*
  - *Excavatio pneumatica*
- *Lacrimal recess*
- *Jugal recess*
- *Nasal recess*
- *Palatine recess*

Figure 1

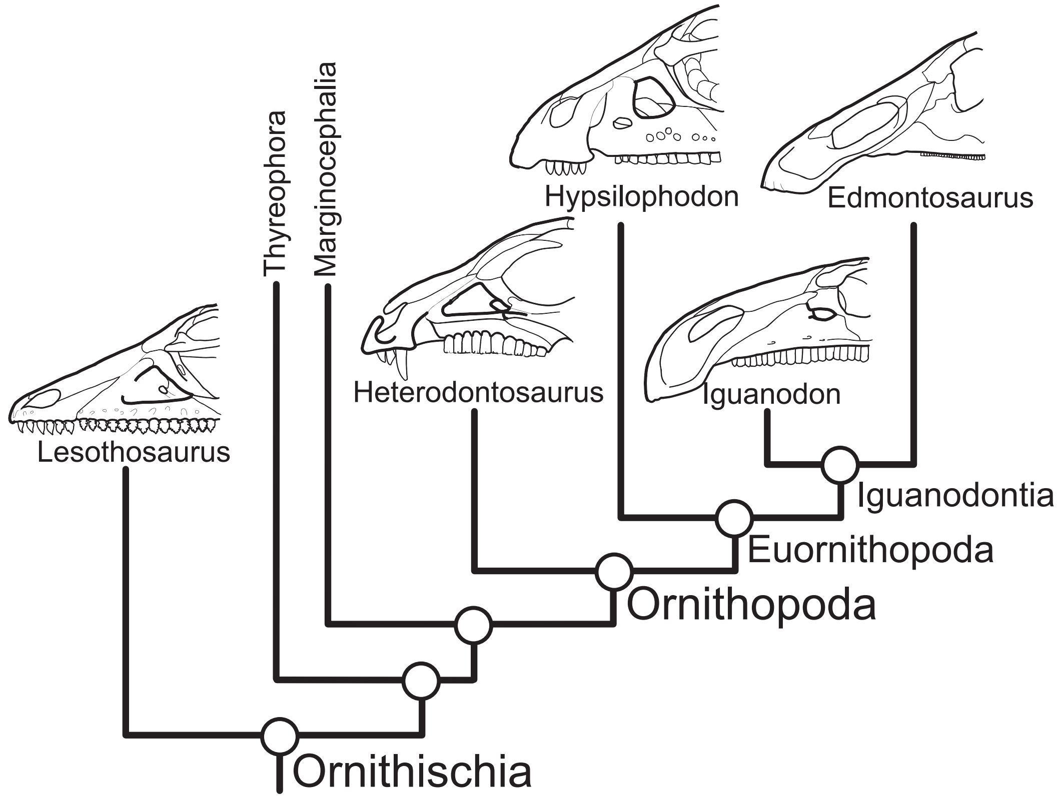


Figure 2

Witmer, L. M. 1997. Craniofacial air sinus systems. pp. 151-159 in The Encyclopedia of Dinosaurs, P. J. Currie and K. Padian (eds.), Academic Press, New York.

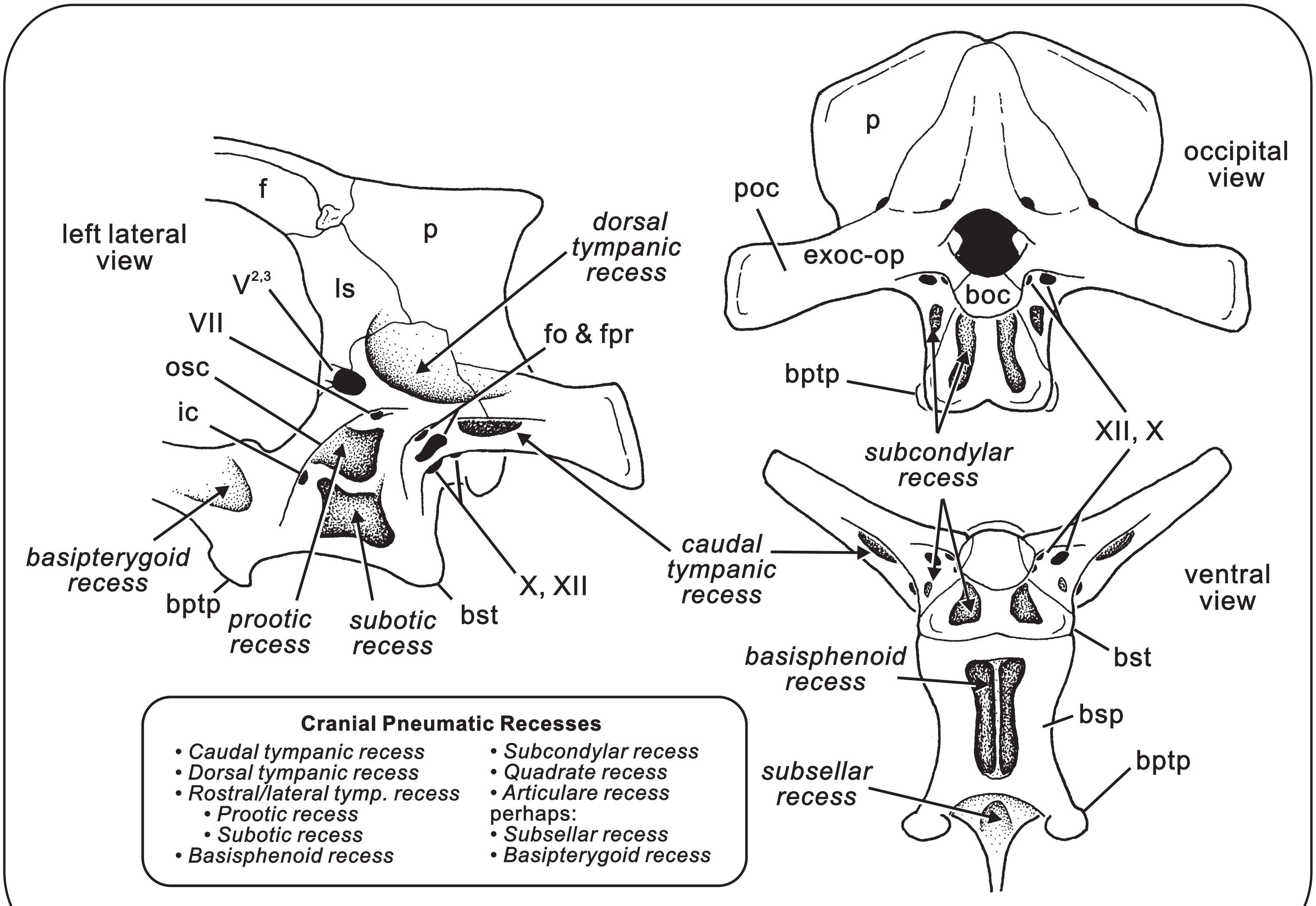


Figure 3

Witmer, L. M. 1997. Craniofacial air sinus systems. pp. 151-159 in The Encyclopedia of Dinosaurs, P. J. Currie and K. Padian (eds.), Academic Press, New York.

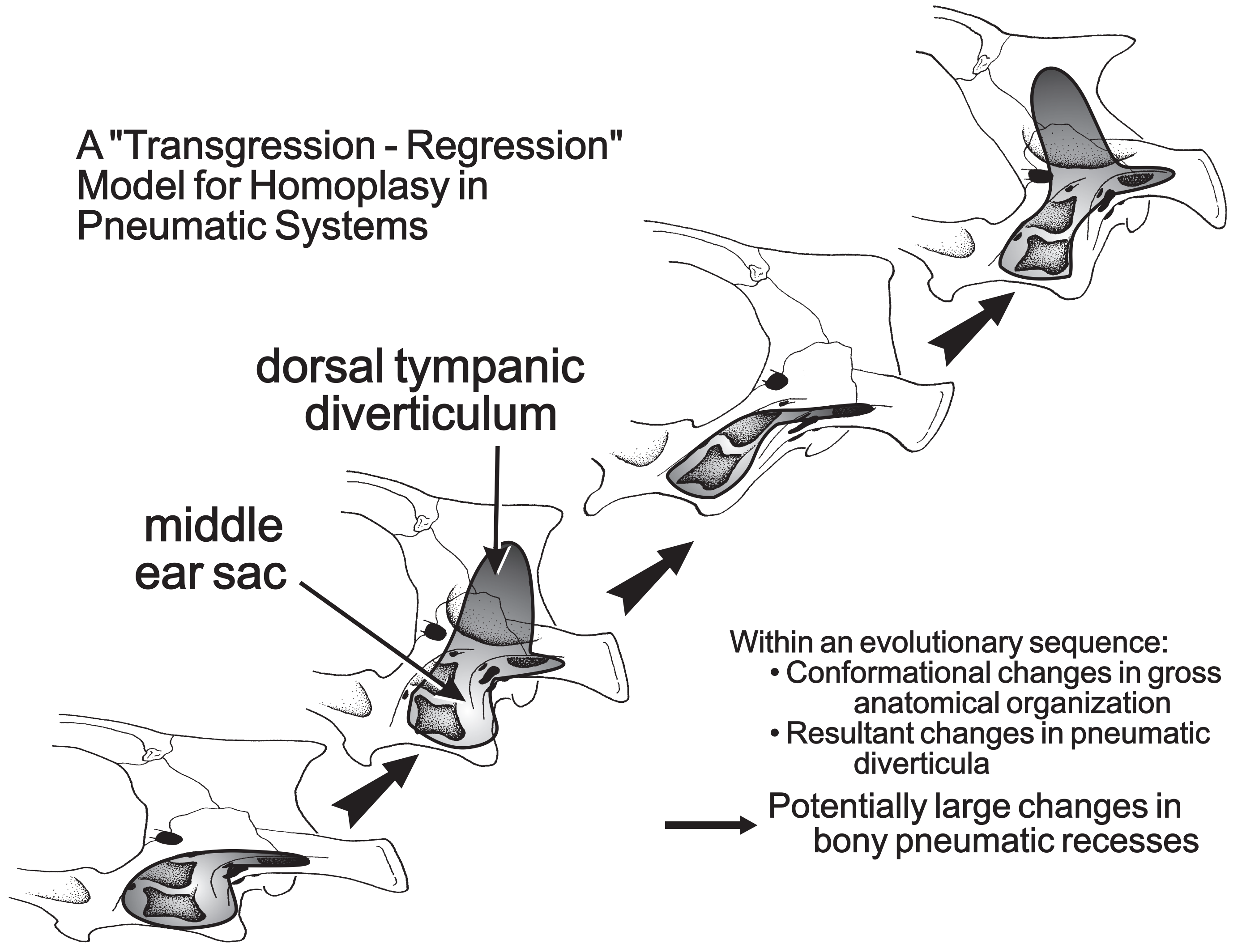


Figure 4