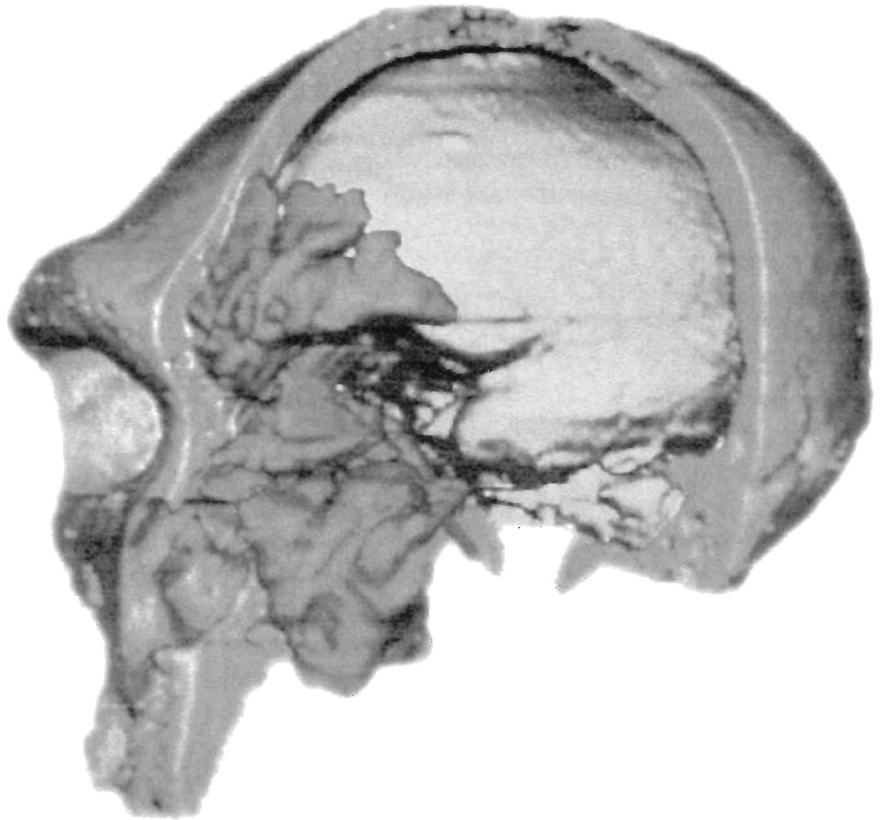


Thomas Koppe / Hiroshi Nagai / Kurt W. Alt

The Paranasal Sinuses of Higher Primates

Development, Function, and Evolution



Special Reprint

The Phylogenetic History of Paranasal Air Sinuses

Lawrence M. Witmer

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Paranasal air sinuses have long been of great interest to anatomists working on mammals in general and primates in particular; clinically oriented human anatomists probably have generated the largest proportion of the literature. Paranasal pneumaticity, however, is not restricted to mammals, and numerous other clades of vertebrates exhibit air-filled epithelial diverticula of the nasal cavity. Although paranasal sinuses in nonmammalian vertebrates often have been given the names of their presumed mammalian counterparts, the homologies of some of these sinuses have only recently been subjected to scrutiny (Witmer, 1995b).

Progress in interpreting the diversity of vertebrate sinuses historically has been hampered by typologic approaches that have sought to homologize mammalian (principally human) sinuses with those of other vertebrates under the often unstated belief that all organisms will display manifestations of the archetype. A phylogenetic perspective, however, improves prospects for successful interpretation of sinus diversity, in that it provides for a better sense of what is truly homologous, which in turn provides the appropriate framework for functional and other inferences. Furthermore, evidence from the

fossil record is often critical in bridging morphologic gaps observed in the extant realm, and a phylogenetic perspective dictates which are the most appropriate paleontologic comparisons.

Definitions

Before the distribution of pneumatic structures throughout vertebrates can be examined, a few concepts must be clarified. The first is the distinction between a soft tissue *pneumatic diverticulum* and the *bony recess* that often houses it. The term *sinus* has been applied to both, and, for many questions, the distinction is not that important. However, it often is crucial in comparisons across broad taxonomic groups. For example, an epithelial diverticulum may be present in numerous taxa, but only pneumatize bone in a subset of these taxa, an example being the suborbital diverticulum of the antorbital sinus in birds and some other archosaurs (Witmer, 1997). Likewise, very similar bony recesses may result from pneumatization via *different* pneumatic diverticula (Witmer, 1990), thus presenting problems of homology. Perhaps most fundamentally,

diverticula and bony recesses stand in morphogenetic relation to each other as cause and effect; that is, in most if not all cases, the bony recesses are actually *produced* through pneumatization via the epithelial diverticulum and its osteoclastic front (Witmer, 1995a, 1997).

Another distinction must be made between intracapsular and extracapsular recesses. *Intracapsular recesses* are those internal to the cartilaginous nasal capsule, and, although their names sometimes sound like pneumatic recesses (eg, Mihalkovics' [1898] identification of a "sinus maxillaris" in the lizard *Lacerta*), it appears that only epithelial diverticula that have escaped the bounds of the cartilaginous capsule (that is, *extracapsular sinuses*) are competent to pneumatize bone (Witmer, 1995b). In many clades of vertebrates, the nasal capsule is not a complete cartilaginous box, but rather has various openings (in addition to the nares and choanae) that may transmit evaginations of nasal epithelium, allowing, in effect, intracapsular epithelium to become extracapsular. As discussed later in this chapter, some of these outpocketings bear some histologic resemblance to pneumatic diverticula, but only a few actually pneumatize bone.

A final point of clarification relates to the site of origination within the nasal cavity of the pneumatic diverticulum. Parsons' (1970) division of the nasal cavity is useful in this regard. He divided the nasal cavity into the *vestibule* rostrally, the *nasal cavity proper* (cavum nasi proprium) in the middle, and the *nasopharyngeal duct* caudally. In primates, as in apparently all mammals (Paulli, 1900a, 1900b, 1900c; Moore, 1981), all of the various paranasal sinuses originate as diverticula of the

nasal cavity proper. However, in those nonmammalian vertebrates exhibiting paranasal pneumaticity, diverticula arise not only from the nasal cavity proper, but also from the other portions of the *cavitas nasalis*. Thus, although mammals generally have extensive paranasal sinuses, the morphogenetic diversity of sinuses in mammals is less than in some other vertebrate clades.

Phylogenetic Distribution of Paranasal Sinuses

The literature on the phylogenetic distribution of sinuses is widely scattered among the primary literature. Summary information can be found in comparative anatomic texts, especially older ones, such as Dieulafé (1905a, 1905b, 1905c, 1905d), Plate (1924), and Matthes (1934), among others. Nemours (1930a, 1930b) published two rather naive and very typologic reviews on the status of the paranasal sinuses of modern amphibians, reptiles, and birds. Negus (1958) published an extensive comparative treatise that provides excellent information on mammals but only superficial coverage of nonmammalian vertebrates. The closest thing to a modern review is Witmer's (1995b) study of facial anatomy of archosaurs, which reviews much of the previous literature on other extant amniotes. This chapter is intended only as an overview, and there are a number of areas that require much more in-depth study. In the following survey, vertebrate taxa will be taken in turn, roughly following the pectinate cladogram topology of Fig 2-1.

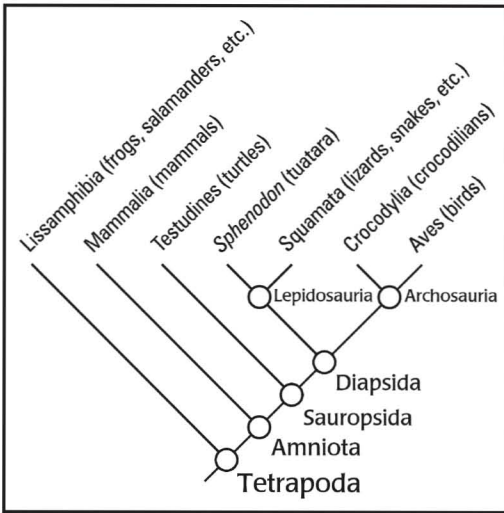


Fig 2-1 Phylogenetic relationships of extant tetrapods. (Topology after Gauthier et al., 1988.)

Nonamniote vertebrates

To my knowledge, bony pneumatic recesses have not been reported in any extinct or extant nonamniote vertebrate (i.e., fishes and amphibians), a finding that is perhaps not too surprising, given the aquatic habits of most of these animals. However, the potential for pneumatization of bone would seem to be present in some modern amphibians, in that extracapsular epithelial diverticula have been described and/or illustrated for various salamanders and especially frogs by Mihalkovics (1898), Plate (1924), Nemours (1930a), Matthes (1934), and Jurgens (1971), among others.

These diverticula appear in section (Fig 2-2A), to be generally similar to the diverticula that pneumatize bone in amniotes, but they do not do so, raising the question

of why some paranasal diverticula pneumatize bone and others do not. Given this situation, it would be of interest to survey fossil material of the large-skulled “reptiliomorph” nonamniote anthracosaurs to seek evidence of paranasal sinuses.

Amniota

Despite any prospects for the discovery of paranasal air sinuses in nonamniote vertebrates, it remains that paranasal pneumaticity is still known only in amniotes. However, as discussed in detail elsewhere (Witmer, 1995b), it appears that the presence of paranasal sinuses is not a synapomorphy of Amniota. Rather, pneumaticity evolved independently at least twice—in Mammalia and Archosauria—and, in each case, numerous different paranasal sinuses evolved. The following will be a very brief survey of the major clades of amniotes (see Fig 2-1), examining their various epithelial diverticula and bony pneumatic recesses, when present.

Mammalia

Paulli's (1900a, 1900b, 1900c) masterful work on mammalian paranasal pneumaticity remains the primary reference and was the basis for most of the recent reviews (Moore, 1981; Novacek, 1993), although Negus (1958) also provided some novel observations. According to these sources, monotremes and marsupials (with perhaps a single exception) lack paranasal sinuses of any kind. Furthermore, among eutherians (i.e., placental mammals), only the maxillary sinus is a nearly ubiquitous feature. (It is absent in a few small bats [Novacek, 1993] and most

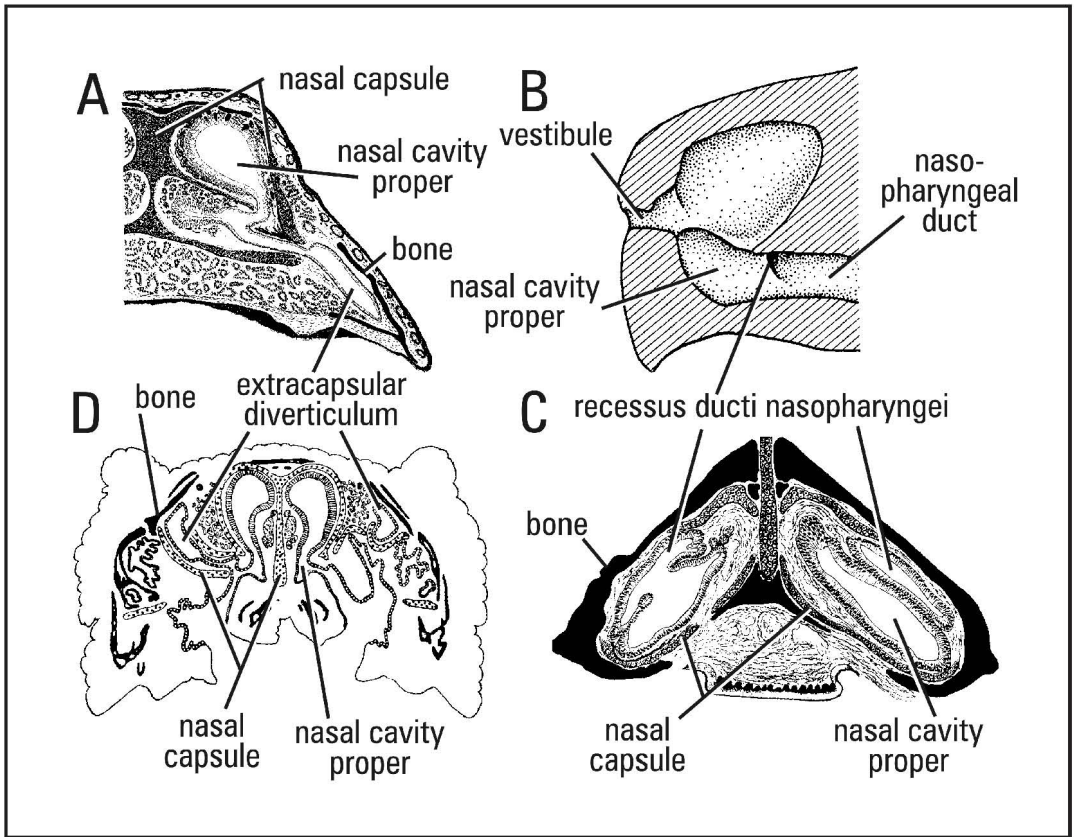


Fig 2-2 Extracapsular epithelial diverticula without pneumatization of bone in (A) the anuran amphibian, *Hyla arborea* (transverse section); (B) the turtle, *Testudo graeca* (sagittal section); (C) the turtle, *Emys europaea* (transverse section); and (D) the squamate lepidosaur, *Varanus niloticus* (transverse section). Pneumatization of bone requires the evagination of a thin-walled epithelial diverticulum beyond the bounds of the cartilaginous nasal capsule. The taxa shown have such a diverticulum, but it fails to pneumatize bone. In *Varanus*, the diverticulum has been named the *recessus extracapsularis* (Malan, 1946), whereas in turtles it is known as the *recessus ducti nasopharyngei*. (A) Modified from Mihalkovics (1898). (B) Modified from Parsons (1970) and Witmer (1995b). (C) Modified from Mihalkovics (1898). (D) Modified from Malan (1946).

marine mammals [Moore, 1981]). It appears that all of the eutherian maxillary sinuses are homologous, although a rigorous test of this hypothesis has not been published.

Whereas the maxillary sinus derives from the respiratory portion of the nasal cavity, some eutherians have another system of sinuses that derives more or less

from the olfactory region of the nasal cavity. This system may be best termed the *ethmoidal sinus system*, although the terms *frontal* and *sphenoidal* have also been applied. Sinuses derived from the ethmoidal system have evolved in a number of eutherian clades, and the homologies of many of the sinuses are far from clear; it seems certain that many of the

described “frontal” and “sphenoidal” sinuses have appeared independently. In humans, it is this ethmoidal system that produces the frontal and sphenoidal sinuses, as well as the definitive ethmoidal air cells.

Although the presence of a maxillary sinus would seem to be an apomorphy of Eutheria (given its absence in marsupials and monotremes), this assessment may be premature, in that a number of non-mammalian cynodonts (i.e., mammal-like reptiles) have been described as possessing maxillary sinuses (Witmer, 1995b). Thus, although the skulls of many modern mammals are extensively pneumatized by the nasal cavity, there is still a great deal about the pattern of evolution of these sinuses that remains to be elucidated.

Testudines

With the possible exception of a single fossil taxon, no turtles have been described as having any bony pneumatic recesses associated with the nasal cavity. However, turtles do possess an extracapsular epithelial diverticulum, arising not from the nasal cavity proper, but rather from the nasopharyngeal duct (Parsons, 1970). This recessus ducti nasopharyngei evaginates laterally from the rostralmost end of the nasopharyngeal duct, but does not pneumatize bone in any known taxa (see Fig 2-2B, C; Witmer, 1995b). Mihalkovics (1898) and Nemours (1930b) referred to the recessus as the “maxillary sinus,” but it clearly is not homologous to the mammalian structure (Witmer, 1995b).

The only candidate for a bony pneumatic recess in turtles is the Pleistocene

horned turtle *Meiolania* (Gaffney, 1983), which has an intraosseous cavity associated with the naris; should this prove to be truly pneumatic, it would likely represent a diverticulum of the nasal vestibule rather than of the nasal cavity proper.

Lepidosauria

Lepidosaurians (i.e., lizards, snakes, amphisbaenians, and *Sphenodon*) can be regarded as lacking any paranasal pneumaticity. Certainly no evidence of bony recesses has been reported. In some lizards, an intracapsular space, known as the *extraconchal recess*, becomes exposed laterally by a gap in the wall of the cartilaginous capsule. This recess bears some resemblance to a paranasal diverticulum, again leading Mihalkovics (1898) and Nemours (1930b) to regard some lizards as possessing “maxillary sinuses.”

In *Varanus*, the extraconchal recess is especially extensive (see Fig 2-2D), taking a fully extracapsular course to lie adjacent to the bones of the snout (Malan, 1946); although this recess never pneumatizes these bones, this is probably the nearest approach to a paranasal sinus among lepidosaurs.

Archosauria

Archosaurs (crocodilians, birds, nonavian dinosaurs, pterosaurs, etc.) present probably the greatest known diversity of paranasal air sinuses and bony pneumatic structures (Witmer, 1997), which is not too surprising, given that Archosauria is today the most speciose group of terrestrial vertebrates and has been so for probably the past 200 million years. The pneumatic diverticula of archosaurs are best

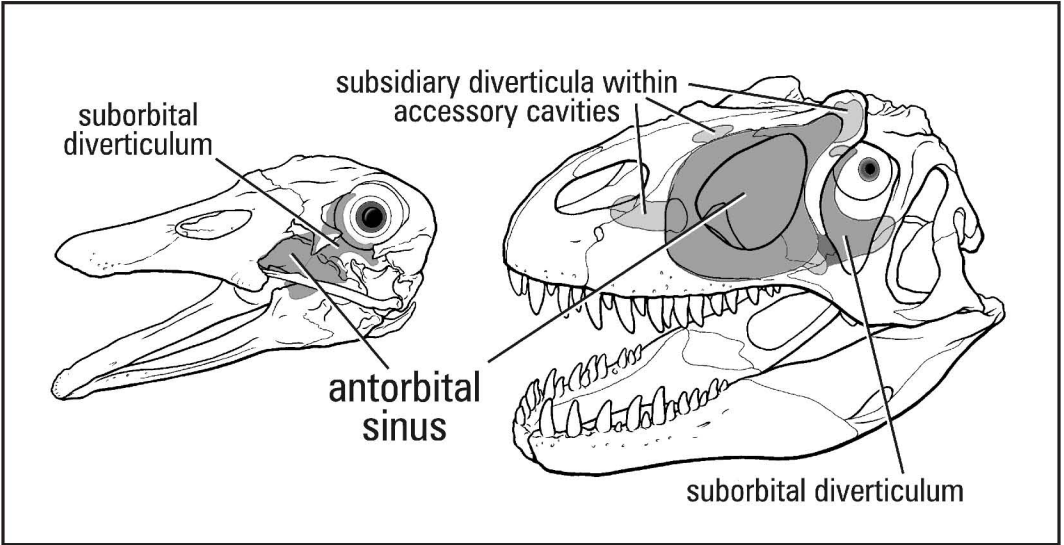


Fig 2-3 Antorbital paranasal air sinus of archosaurs in a goose, *Anser anser* (left), and a nonavian theropod dinosaur, *Allosaurus fragilis* (right). The archosaurian antorbital sinus is often only partially enclosed in bone (as shown) and is almost always covered only with skin laterally. The antorbital sinus often has a number of subsidiary diverticula that may pneumatize surrounding bones, resulting in accessory cavities (shown in *Allosaurus*). One such subsidiary diverticulum, the suborbital diverticulum, interleaves with jaw musculature, providing a mechanism for actively ventilating the paranasal sinus system. (Modified from Witmer, 1997.)

discussed on the basis of their site of origin, in the nasal cavity proper, the nasopharyngeal duct, or the vestibule.

Nasal cavity proper

Based on studies of extant and extinct archosaurs (Witmer, 1995b, 1997), a single epithelial diverticulum of the nasal cavity proper can be inferred to be present in all archosaurs. This air sac, known as the antorbital sinus (equivalent to the caviconchal sinus of crocodilians), is lodged in a bony cavity (the antorbital cavity) formed primarily by the maxillary and lacrimal bone, with varying contributions from the nasal and/or jugal bones (Fig 2-3).

The antorbital sinus itself often has a

variety of subsidiary diverticula that pneumatize bone, producing so-called accessory cavities within the surrounding bones. These subsidiary diverticula are best developed in the theropod dinosaurs (including birds), producing accessory cavities in the maxillary, lacrimal, nasal, jugal, and/or palatine bones. In some theropods, the entire facial skeleton is intensely pneumatized by these diverticula, reducing the facial skeleton to a series of struts between large, air-filled spaces. Subsidiary diverticula of the antorbital sinus are not limited to theropods, and accessory cavities are found also in various taxa of prosauropod and ornithischian dinosaurs, pterosaurs, and a few basal archosaurs (Witmer, 1997).

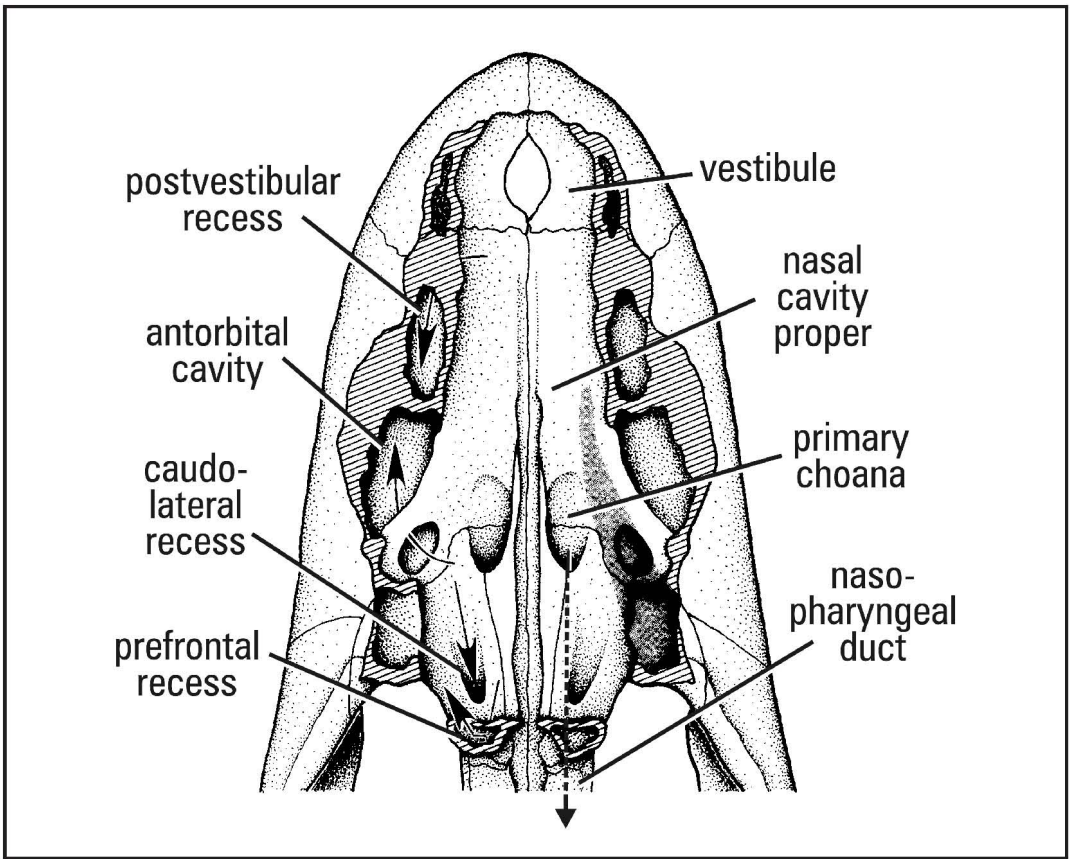


Fig 2-4 Snout of *Alligator mississippiensis* in dorsal view (horizontally sectioned with roof removed). Parts of the nasal cavity are labeled at right; the broken arrow shows the course of the nasopharyngeal duct. Paranasal sinuses that derive from the nasal cavity proper are labeled at left (*solid arrows*). (Modified from Witmer, 1995b.)

A remarkable difference between the antorbital sinus of archosaurs and the paranasal sinuses of mammals is that, whereas the mammalian sinuses are generally fully enclosed in bone (except for the ostium), the archosaurian antorbital sinus is in most cases only partially enclosed in bone and is covered with skin laterally (see Fig 2-3). Furthermore, in some taxa, such as birds and probably at least some nonavian theropod dinosaurs,

one of the subsidiary diverticula, the sub-orbital diverticulum, extends caudally into the orbit beneath the eyeball to interleave with the adductor musculature (see Fig 2-3). Thus, as the mandible is abducted and adducted, negative and positive pressures, respectively, are set up within the suborbital diverticulum and hence the whole antorbital sinus system. These pressure changes allow the sinus system to be actively ventilated, with mandibular

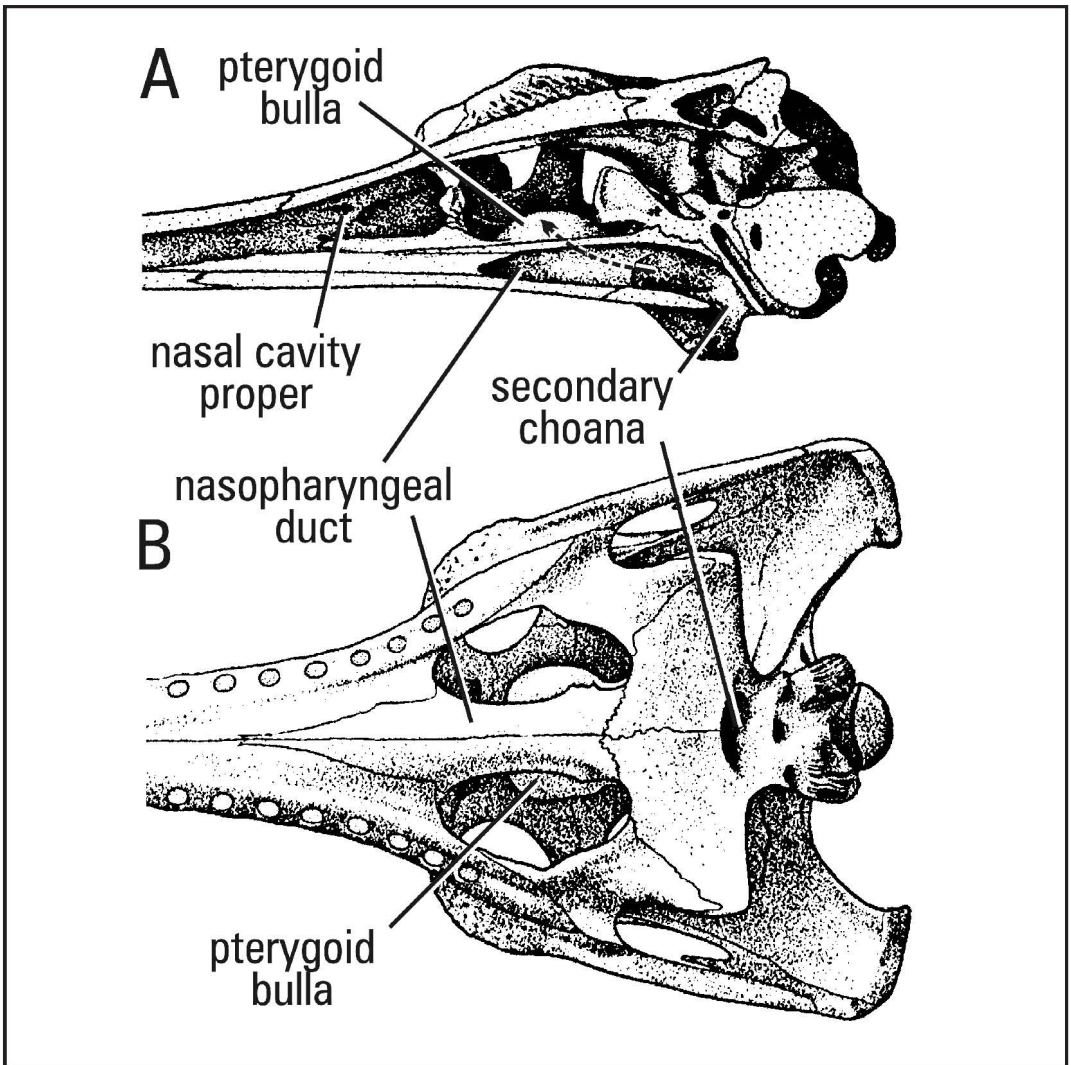
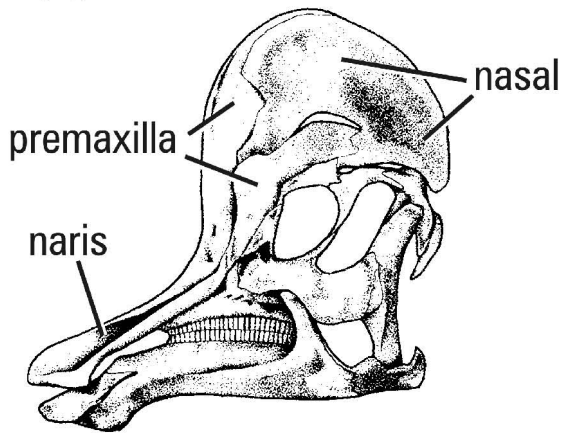
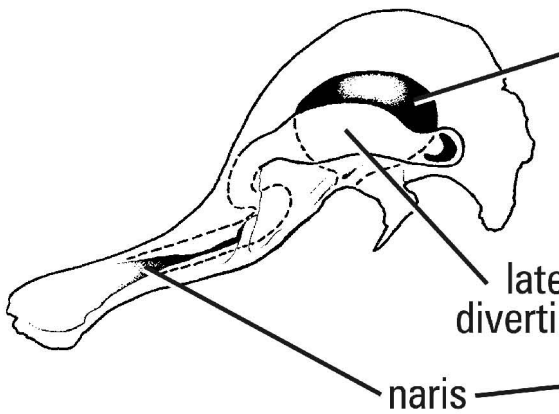
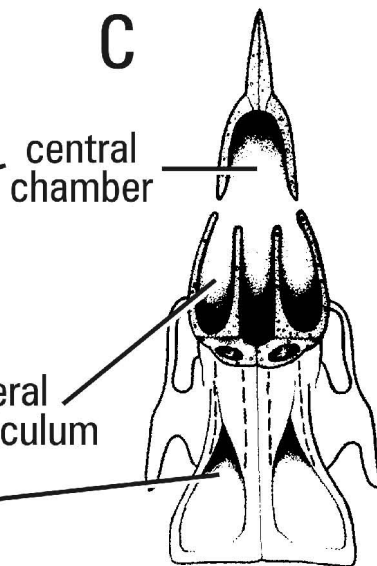


Fig 2-5 Pterygoid bulla of the crocodilian, *Gavialis gangeticus*, in (A) medial view (sagittally sectioned skull) and (B) ventral view. The pterygoid bulla is an inflated paranasal air sinus derived from the nasopharyngeal duct. (Modified from Kälén, 1955.)

Fig 2-6 Narial crest of the lambeosaurine hadrosaurid dinosaur, *Corythosaurus casuarius*. (A) Left lateral view of skull. (B) Left lateral view of passages and chambers within the narial crest. (C) Rostral view of skull with narial crest transversely sectioned to reveal cavities. The nasal vestibule is greatly hypertrophied, as are the bones that surround it (the premaxilla and nasal bones), and the whole apparatus is mounted above the rest of the skull. The lateral diverticula may be viewed as examples of paranasal sinuses derived from the nasal vestibule. (Modified from Weishampel, 1981.)

A**B****C**

movements acting as a bellows pump (Witmer, 1997).

Such a powered ventilation system is unique in vertebrates. Mammalian sinuses are dead-air spaces, with air exchange occurring only very slowly through diffusion. Interestingly, modern crocodilians have lost the open construction of the antorbital cavity and lack a suborbital diverticulum (Fig 2-4) (Witmer, 1995b, 1997); as a result, they have converged with the mammalian system and lack active ventilation.

The antorbital sinus system is clearly the most important of the pneumatic systems of archosaurs because it is found in all known archosaurian taxa and truly dominates the facial morphology of some of them. For example, in some archosaurs, the bony antorbital cavity and its accessory cavities exceed the combined volumes of the brain and all cephalic sense organs. The antorbital sinus, however, is not the only sinus system known in archosaurs. Extant crocodilians, for example, have as many as four additional diverticula of the nasal cavity proper, although no single species has them all (Witmer, 1995b, and references therein). These are best developed in alligatorines (see Fig 2-4) and pneumatize the maxillary, palatine, and prefrontal bones.

Nasopharyngeal duct

Crocodilians also show pneumaticity associated with the nasopharyngeal duct. In fact, six different pneumatic recesses derived from the nasopharyngeal duct can be recognized (Witmer, 1995b), involving the pneumatization of the vomer, palatine, and pterygoid bones. In many cases, large, inflated bullae are produced, such

as the vomerine bulla of alligatorines, the pterygopalatine bulla within the orbit of many crocodilians, and, most dramatically, the enormous and bulbous pterygoid bulla of the gharial, *Gavialis gangeticus* (Fig 2-5). Finally, the pterygoid sinus of alligators is a remarkable, invasive pneumatic recess with many communicating chambers that extends dorsally from the nasopharyngeal duct in the vicinity of the secondary choana.

Vestibule

The third and final division of the nasal cavity, the vestibule, also is a source of pneumatic diverticula and bony recesses in a few archosaur taxa. Best known are the cavities within the narial crests of lambeosaurine hadrosaurid dinosaurs (Weishampel, 1981; Weishampel and Horner, 1990). In lambeosaurines, the nasal vestibule is greatly enlarged, and the premaxillary and nasal bones are expanded and folded into a series of tubes and chambers mounted above the rest of the skull (Fig 2-6). Hadrosaurids retain the antorbital sinus and its bony cavity, but it is smaller and internalized as a result of expansion of the nasal vestibule and its recesses as well as expansion of the dentition and its supporting structures (Witmer, 1997).

Other dinosaurs, such as ankylosaurids, may also have paranasal sinuses that derive from vestibular diverticula. Certainly, ankylosaurids have a variety of paranasal sinuses, and at least one of them appears to communicate with the nasal vestibule (Coombs and Maryanska, 1990; Witmer, 1997).

Discussion

Paranasal air sinuses, although common in the more conspicuous terrestrial vertebrates such as birds and mammals, do not have a universal—or even a wide—distribution among Vertebrata. In fact, the only extant clades that definitely can be said to have true paranasal pneumaticity are eutherian mammals and archosaurs. It seems almost certain that at least some synapsids more basal than Eutheria had some form of paranasal pneumaticity, but the published distribution is difficult to interpret and homologies are very unclear; a review of the evolution of paranasal pneumaticity in Synapsida is in order.

Reconstruction of the phylogenetic history of paranasal pneumaticity in archosaurs has been a major focus of my research for some time, and patterns are beginning to emerge (Witmer, 1995b, 1997). Virtually all known taxa of Archosauria, extinct as well as extant, manifest at least some evidence of the presence of the antorbital air sinus. Moreover, it seems likely that this paranasal air sac characterizes a slightly more inclusive group, a group known as *Archosauriformes* that includes a variety of basal forms (“thecodonts” such as *Euparkeria*) as well as Archosauria itself.

All mammalian paranasal pneumaticity derives from diverticula from the nasal cavity proper. These diverticula can be divided roughly into two systems. The first system derives from the respiratory portion of the nasal cavity proper and involves the maxillary sinus; this sinus may well be common to all Eutheria, with the exception of a few taxa that apparently have lost it. The second system derives essentially

from the olfactory portion of the nasal cavity proper and involves the ethmoidal system and its derivatives (e.g., frontal, ethmoidal, and sphenoidal sinuses); ethmoidal pneumaticity has a scattered distribution among eutherians but may be present in some nonmammalian synapsids (Luo Z., personal communication, 1996).

Whereas mammalian paranasal pneumaticity is restricted to diverticula arising from the nasal cavity proper, archosaurs show examples of diverticula arising from all portions of the nasal cavity. The antorbital sinus is the major (and usually only) paranasal air sinus arising from the nasal cavity proper, although this sinus often has a number of subsidiary diverticula that may pneumatize surrounding bones. Crocodylians are remarkably pneumatic animals and exhibit additional diverticula of the nasal cavity proper and an even greater diversity of diverticula of the nasopharyngeal duct. Sinuses arising as diverticula of the nasal vestibule are very rare, but the cavities within the narial crest of lambeosaurine dinosaurs may be classified as such.

The status of paranasal sinuses in taxa other than mammals and archosaurs is a little more problematic. Certainly, there are no known unequivocal examples of bony paranasal pneumatic recesses in fishes, amphibians, turtles, or lepidosaurs. Nevertheless, thin-walled, epithelial, extracapsular diverticula of the nasal cavity have been described in a number of these taxa (see Fig 2-2), and in mammals and archosaurs it is just such diverticula that are involved in pneumatization of osseous tissue.

What, then, is special about mammals and archosaurs that allows their diverticu-

la to play a role in pneumatization? The answer is not at all clear. It might seem at first that physiologic considerations, such as endothermy, may explain why mammals and birds are so pneumatic, but crocodilians are ectothermic and are, by some measures, the most pneumatic of all vertebrates. The fact is that very little is known about the processes of pneumatization at the cellular and tissue levels, and even less is known about how pneumatization is controlled. In any event, one conclusion emerging from this situation is that the distinction between epithelial diverticulum and bony recess discussed at the outset of the chapter is more than a semantic issue but rather is integral to understanding the nature of pneumaticity.

Conclusion

The phylogenetic history of paranasal air sinuses suggests that pneumaticity is a fairly poorly constrained system (Witmer, 1997). Sinuses appear repeatedly and independently, and they are lost just as frequently. In other words, the anatomic system is characterized by a high level of homoplasy. The directions of future research are clear. New paleontologic and comparative anatomic studies of particular clades of vertebrates—such as extant mammals, nonmammalian cynodonts, and nonamniote antracosaurs—are needed, not only to establish the presence or absence of paranasal air sinuses but also to acquire sufficient anatomic resolution to shed light on the issue of homology. Furthermore, microanatomic and ontogenetic studies of extant taxa,

including those that have extracapsular diverticula but lack bony recesses, are essential for elucidating gross aspects of the process of pneumatization.

Perhaps most interesting would be mechanistic studies of how the process of pneumatization is *controlled*. What factors effect initiation of evagination of an epithelial diverticulum? What controls its subsequent growth? What determines whether or not such a diverticulum actually pneumatizes bone? What is the relationship of the pneumatic epithelium to the front of osteoclasts that are actually involved in the business of pneumatization? Once these and other similar questions have satisfactory answers, then new ideas on the function of pneumatic sinuses (e.g., Witmer, 1997) will have appropriate tests, and the interpretation of the phylogenetic history of paranasal sinuses will be on a better footing.

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