**The Nature of the Antorbital Fossa of Archosaurs: Shifting the Null Hypothesis.** L.M. Witmer (Baltimore, Maryland).

The antorbital fenestra is a nearly ubiquitous feature of archosaurs and its presence remains one of the few cranial synapomorphies of the group. The antorbital fenestra is an opening in the skull situated between the orbit and external naris, communicating with the nasal cavity, and surrounded primarily by the maxilla and lacrimal with varying contributions by the nasal and jugal. The lateral surfaces of the bones surrounding the fenestra are often excavated into a basin-like depression; I will use the term "antorbital fossa" to incorporate both the fenestra and the surrounding fossa (Fig. 1). The morphology of the antorbital fossa is well known in the various groups of archosaurs. More elusive is an understanding of its general nature---that is, the function of the antorbital fossa. There have been very few studies that have investigated this problem in any depth. This paper surveys the suggested functions of the antorbital fossa. Three hypotheses have been proposed: 1) the antorbital fossa houses a gland (Broom 1913, Ewer 1965, Reig 1970, Madsen 1976); 2) the fossa is somehow associated with the pterygoideus musculature (Dollo 1884, Gregory & Adams 1915, Anderson 1936, Walker 1961, Bakker 1986); and 3) the fossa houses an air-filled diverticulum of the nasal cavity (Barsbold 1983, Osmolska 1985, Witmer 1987). The second hypothesis, association with musculature, is currently the null hypothesis. The conclusions reached here suggest that the null hypothesis should be shifted to one considering the antorbital fossa of archosaurs to be pneumatic in nature.

Figure 1. Antorbital region of *Euparkeria*. Modified from Ewer (1965).
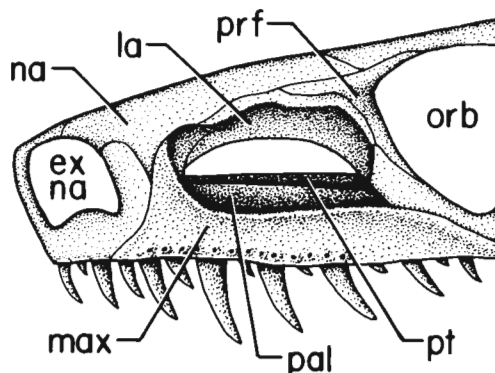
The Glandular Hypothesis

Broom (1913) is generally credited with being the first worker to suggest that the antorbital fossa housed a large gland. His discussion is limited to a single sentence noting the basin-like depression that

constituted the antorbital fossa of *Euparkeria* (Fig. 1). Ewer (1965), responding to the same antorbital morphology of *Euparkeria*, agreed with Broom that it likely housed a gland and further suggested that it was probably a nasal salt gland. Ewer considered the primitive function of the fossa to be the housing of this gland; she refuted the muscular hypothesis---but only for the earliest archosaurs, arguing that later in archosaur phylogeny the "antorbital gland" was lost as the pterygoideus musculature moved anteriorly to occupy the fossa. Thus Ewer argued for both the glandular and the muscular hypotheses. More recently, Madsen (1976) suggested that the large cavity in the body of the lacrimal of *Allosaurus* (Fig. 4C) may have housed a gland.

The only worker to offer evidence other than the general morphology of the antorbital fossa in support of the glandular hypothesis was Reig (1970). His argument is based on the assumption that archosaurs were derived from varanopsid pelycosaurs. According to Reig, because mammals are ureotelic, their precursors---the pelycosaurs---were also ureotelic; thus, because archosaurs were derived from pelycosaurs, ancestral archosaurs were also ureotelic. As archosaurs were considered primarily upland forms, Reig suggested that they required some form of extrarenal salt excretion---a salt gland in the antorbital fossa. Through this circuitous and rather tenuous chain of reasoning, Reig concluded that the archosaurian antorbital fossa functioned as a housing for a nasal salt gland.

While it is generally agreed that archosaurs are not related to pelycosaurs and instead are members of a monophyletic group, the Diapsida (invalidating Reig's basic assumption), the glandular hypothesis is a valid hypothesis that deserves discussion. Most proponents of the hypothesis have suggested that if a gland were present it was a site of extrarenal salt excretion. In extant diapsids such as squamates (Parsons 1970) and birds (Fange, et al. 1958) extrarenal salt excretion takes place via the lateral nasal gland. The question is whether or not the lateral nasal gland was housed in the antorbital fossa of fossil archosaurs. Comparisons with extant diapsids suggest that it was not. In squamates the lateral nasal gland is situated in the anterior portion of the preorbital region of the head and lies dorsal or lateral to the nasal capsule (Parson 1970). Crocodilians exhibit a similar situation with the gland lying dorsal to the nasal capsule in the vicinity of the juncture of the premaxilla, maxilla, and nasal (Parsons 1970). In birds the lateral nasal gland is generally located in the orbital region (Marples 1932).

Thus, although fossil archosaurs may have had lateral nasal glands, they almost certainly did not reside in the antorbital fossa. Osmolska (1979) likewise rejected the antorbital fossa as a site of the lateral nasal gland and suggested that the gland in some dinosaurs may have had a more primitive position in the vicinity of the external naris. The possibility will always remain that some glandular structure not known in modern organisms may have been housed in the antorbital fossa. But such an assertion will never be supported by much evidence and is not testable. Indeed, the morphology that originally led Broom to suggest the glandular hypothesis---the basin-like morphology of the antorbital fossa---obtains in a group of archosaurs that show demonstrable pneumatic features in their antorbital fossae; many theropods show very similar depressions in the maxilla and lacrimal (Fig. 2C). As is argued below, one of the best cases for a pneumatic antorbital fossa can be made for theropod dinosaurs.

The Muscular Hypothesis

The most widely accepted hypothesis is that the antorbital fossa of archosaurs is closely associated with the pterygoideus musculature and I consider this the current "null hypothesis." In a sense, the fossa has been considered to be in the same general class as the temporal fenestrae (Gregory & Adams 1915); that is, *M. pterygoideus anterior* originated from or bulged into the antorbital fossa. Evidence supporting this hypothesis does not come from direct observation of the morphology of antorbital fossae. Rather, evidence derives from two sources: 1) biomechanical considerations "demanding" a large *M. pterygoideus anterior*, and 2) that extant crocodilians have a large *M. pterygoideus anterior* originating from the maxilla in the region of the skull where the antorbital fossa exists in other archosaurs.

Walker's (1961) treatment of the jaw mechanics of early archosaurs represents the most cogent argument for the muscular hypothesis. His biomechanical discussions are largely theoretical. Walker (1961) noted that in carnivorous archosaurs like *Ornithosuchus* and theropods the gape must have been very large. Because the temporal muscles are the most powerful adductors when the jaws are almost closed (Anderson 1936), Walker (1961) suggested that a large *M. pterygoideus anterior* must have been present to act when the gape was wide. In his view, the large *M. pterygoideus anterior* originated from the antorbital fossa. This powerful adductor occupying much of the preorbital region would have

provided "an exceedingly rapid 'snap'" (Walker 1961). For the same functional reasons, Bakker (1986) postulated a huge *M. pterygoideus anterior* within the antorbital fossae of *Coelophysis* and *Dimorphodon*.
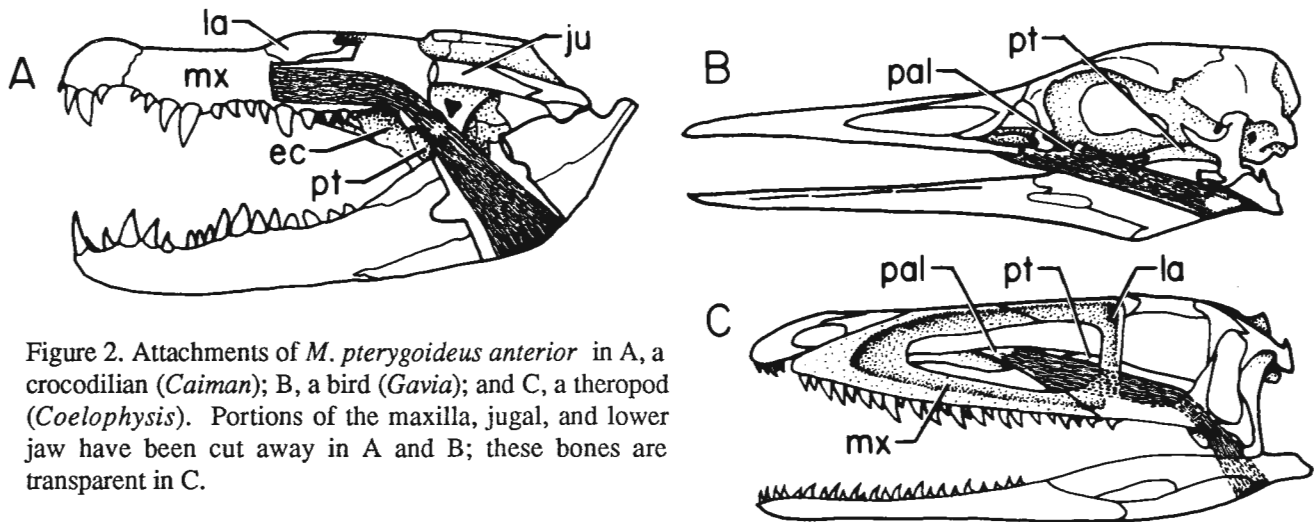

Figure 2. Attachments of *M. pterygoideus anterior* in A, a crocodilian (*Caiman*); B, a bird (*Gavia*); and C, a theropod (*Coelophysis*). Portions of the maxilla, jugal, and lower jaw have been cut away in A and B; these bones are transparent in C.

Support for this view was found in extant crocodilians which have a wide gape and a large *M. pterygoideus anterior*. In modern crocodilians *M. pterygoideus anterior* does indeed originate from the maxilla (in addition to other bones; Schumacher 1973). The muscle passes over the dorsal surface of the palate and inserts on the medial surface of the articulare and angular and also on the "intermuscular tendon" (Fig. 2A; Anderson 1936, Schumacher 1973). The paradox of using extant crocodilians as evidence for the muscular hypothesis is that, despite the massive development of *M. pterygoideus anterior*, eusuchian crocodilians lack the antorbital fossa. Ewer (1965) and Osmolska (1985) recognized this paradox and Osmolska considered the muscular hypothesis untenable.

The other group of extant archosaurs, the birds, retain the antorbital fossa and also have a large anterior division of *M. pterygoideus* (*M. pterygoideus lateralis* or *M. pterygoideus dorsalis* of avian anatomy; this portion of *M. pterygoideus* is certainly homologous to *M. pterygoideus anterior* of crocodilians). In birds, however, the pterygoideus musculature, although often the largest adductor, never arises from the bones forming the antorbital fossa. Instead, the muscle originates from the dorsolateral surface of the palatine bone medial to the antorbital fossa (Fig. 2B). Thus, birds are like crocodilians in having a large anterior division of *M. pterygoideus*; but in birds the muscle neither originates from the antorbital fossa nor "bulges" into the fossa. Postulation of a large *M. pterygoideus anterior* on biomechanical grounds is insufficient evidence to support the association of this muscle with the antorbital fossa.

But the functional arguments of Anderson (1936) and Walker (1961) suggesting a large *M. pterygoideus anterior* in fossil archosaurs are persuasive. I suggest, however, that the origin of this muscle was not the antorbital fossa itself but rather the bones medial to the fossa---the pterygoid and palatine. In many fossil archosaurs the pterygoids and especially the palatines were more or less vertically-oriented plates at their anterior extremities. It seems likely that in most fossil archosaurs, as in birds, *M. pterygoideus anterior* originated from the palatine and pterygoid and not the bones forming the antorbital fossa (Fig. 2C).

The Pneumatic Hypothesis

In the course of my studies of the cranial air sac system of fossil and recent birds (Witmer 1987) it became apparent that the null hypothesis of a muscular antorbital fossa had to be rejected for birds. In birds the antorbital fossa houses a large air-filled diverticulum of the nasal cavity---the antorbital sinus (Fig. 3). There are several subsidiary diverticula of the antorbital sinus that may pneumatize the maxilla, lacrimal, premaxilla, palatine, and other bones (Witmer 1987). Osmolska (1985) in a necessarily brief but highly insightful paper suggested that the antorbital fossae of some fossil archosaurs were also associated in some way with the airway.

Figure 3. Antorbital sinus in a golden eagle (*Aquila chrysaetos*). Only the premaxillary and lacrimal diverticula are figured.
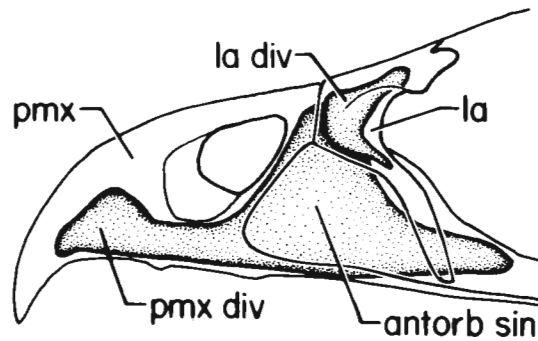
Birds are not alone among archosaurs in exhibiting pneumatic features in the antorbital region. Although eusuchian crocodilians lack antorbital fenestrae, they nonetheless resemble birds in possessing air-filled diverticula of the nasal cavity. But whereas birds have only a single diverticulum, the antorbital sinus, crocodilians have four (Parsons 1970); which of these, if any, are homologous to the avian antorbital sinus is presently under study. These diverticula produce vast pneumatic cavities in the maxillae and palatines of crocodilians (Fig. 4A; Wegner 1957).

Theropod dinosaurs also exhibit unequivocal pneumatic features in the bones surrounding the antorbital fossa. The most striking example is *Oviraptor* (Osmolska 1976, Barsbold 1983) in which all of the bones surrounding the fossa are produced into a lattice of pneumatic foramina that in some individuals result in an air-filled bony crest (Fig. 4B). Less extravagant manifestations are found in other theropods. The most common pneumatic features are the distinctive chambering of the maxilla and lacrimal (Fig. 4C) in all but the more primitive ceratosaurians (*Coelophysis* and *Syntarsus*). The nasal bones of *Allosaurus* (Fig. 4C) and *Ceratosaurus* also are pierced by pneumatic foramina communicating with chambers inside the bone. Additionally, some carnosaurs exhibit pneumatic formamina into the jugal bone. The muscular hypothesis cannot accomodate these observations as it is very unlikely that muscle fibers would enter bones such as the lacrimal, nasal, and jugal through small foramina and then expand within the body of the bone. Likewise, the thin struts of bone forming the maxillary sinuses (Madsen 1976) are too fragile to serve as area of muscle attachment.
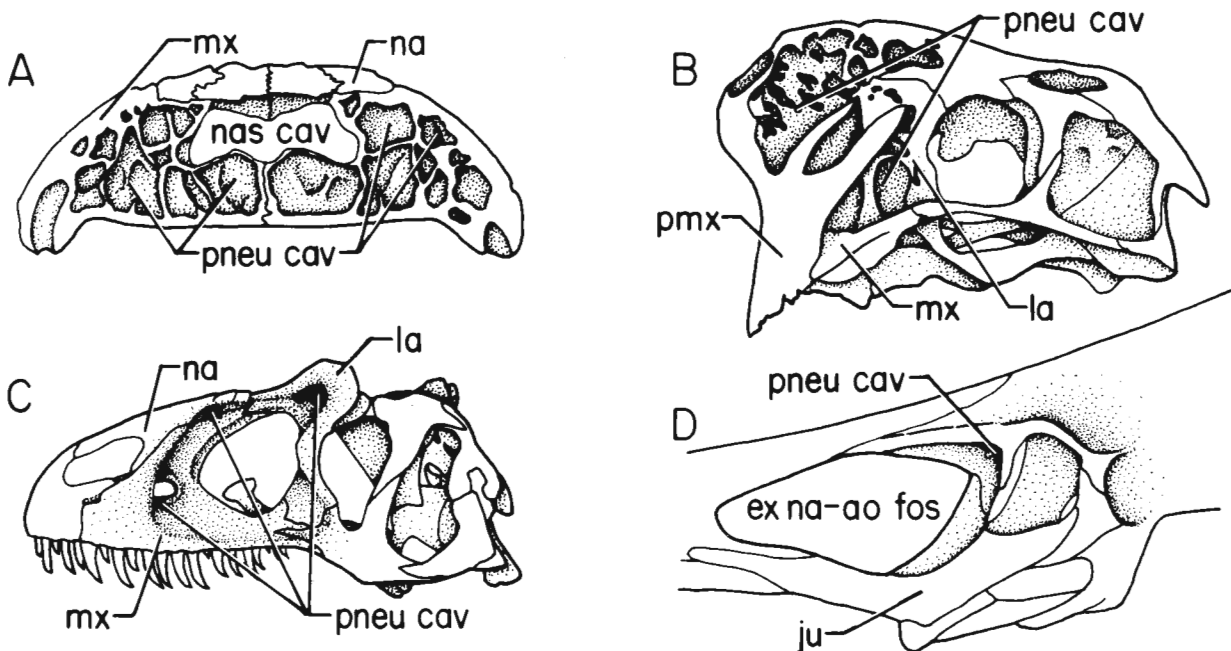

Figure 4. Pneumatic cavities in skulls of A, *Caiman* (cross section; after Wegner 1957); B, *Oviraptor* (after Barsbold 1983); C, *Allosaurus* (after Madsen 1976); and D, *Pteranodon* (partly after Wellnhofer 1978).

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Ornithischian dinosaurs tend to close the external wall of the antorbital fossa and form a cavity within the maxilla (Osmolska 1985). Ankylosaurids have large pneumatic cavities in their maxillae formed by diverticula of the nasal cavity (Maryanska 1977). Thus, some ornithischians are like crocodilians in having closed the antorbital fenestra yet retaining pneumaticity in the region.

Pterosaurs are another group in which diverticula of an antorbital air space can be inferred. Not having examined rhamphorhynchoids, I can only comment on pterydactyloids and in particular *Pteranodon*. In large pterydactyloids the external naris and antorbital fossa become confluent suggesting a relationship between the fossa and the nasal cavity. Furthermore, specimens of *Pteranodon* exhibit a large pneumatic foramen at the posterodorsal corner of the antorbital fossa in the same position as the pneumatic foramen of theropods and birds (Fig. 4D); this foramen does not communicate with the orbit and cannot be for the nasolacrimal duct.

Thus, in recent and many fossil archosaurs the antorbital fossa shows many features indicative of pneumaticity, and even if the fossa is closed externally, pneumaticity is retained. It should be noted that while the function of the fossa was to house an air sac, the function of the air sac itself is a separate matter and is not considered here.

Discussion

A relevant test of the hypothesized function of a structure is the observation of the situation when the structure is absent. Two different hypotheses have been proposed for the loss of the antorbital fossa. Dollo (1884) noted that in dinosaurs that grind plant food, the temporal fossae are enlarged and the antorbital fossa is reduced; he correlated this reduction of the antorbital fossa with reduction of the pterygoideus musculature. Walker (1961), following Dollo, suggested that in herbivores the "speedy closure of the jaws" provided by *M. pterygoideus anterior* was "no longer essential." This correlation is real but the argument fails on consideration of modern crocodilians which have prominent pterygoideus muscles but lack the fossa.

Osmolska (1985) advanced a perceptive alternative hypothesis. Osmolska noted the "coincidence" between the positions of the antorbital fossa and the choana (that is, they are in the same coronal plane) and cited this as evidence that the fossa was somehow associated with the nasal passage. Forms with large fossae retain this coincidence, but taxa that exhibit modifications of the nasal passage (ankylosaurids, hadrosaurids, ceratopsids) show reduction or loss of the antorbital fossa (Osmolska 1985). An additional example are crocodilians. Primitive crocodilians retain the coincidence of fossa and choana, but with the modification of the nasal passage associated with their extensive secondary palates, derived crocodilians lost the antorbital fossa. Thus, despite their perceived biomechanical "need" of an antorbital fossa, crocodilians are like some ornithischians in loss of the fossa---not due to changes in muscle attachment but due to changes in the nasal cavity.

A final consideration is whether or not the antorbital fossa *originated* in response to a diverticulum of the nasal cavity. Unfortunately, this question may never have a satisfactory answer. It seems likely that the antorbital fossae of "thecodonts" such as ornithosuchids, rauisuchids, stagonolepidids, phytosaurs, and proterochampsids housed an air-filled diverticulum; indeed, the antorbital morphology of some of these taxa is strikingly similar to that of ceratosaurian theropods such as *Coelophysis*. The point is whether or not this diverticulum could have produced the fenestration. By way of analogy it may be noted that some mammals (many cervids, some fossil equids, lagomorphs) exhibit fenestrate preorbital regions due to the agency of air-filled diverticula; the morphology of the lagomorph *Ochotona*, in fact, is remarkably similar to the antorbital fossa of many archosaurs.

In conclusion it may be stated that the pneumatic hypothesis for the archosaurian antorbital fossa is the most strongly supported by evidence. It involves direct comparisons with living forms, direct observation of morphology, explains all relevant data, and makes no recourse to the perceived "needs" of extinct organisms. As such, the pneumatic hypothesis should replace the muscular hypothesis as the "null hypothesis" for the nature of the antorbital fossa of archosaurs.

Acknowledgements

Abbreviations

antorb sin, antorbital sinus; ec, ectopterygoid; ex na, external naris; ex na - ao fos, confluent external naris and antorbital fossa; ju, jugal; la, lacrimal; la div, lacrimal diverticulum; mx, maxilla; na, nasal; nas cav, nasal cavity; orb, orbit; pal, palatine; pmx, premaxilla; pmx div, premaxillary diverticulum; pneu cav, pneumatic cavity; prf, prefrontal; pt, pterygoid.

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