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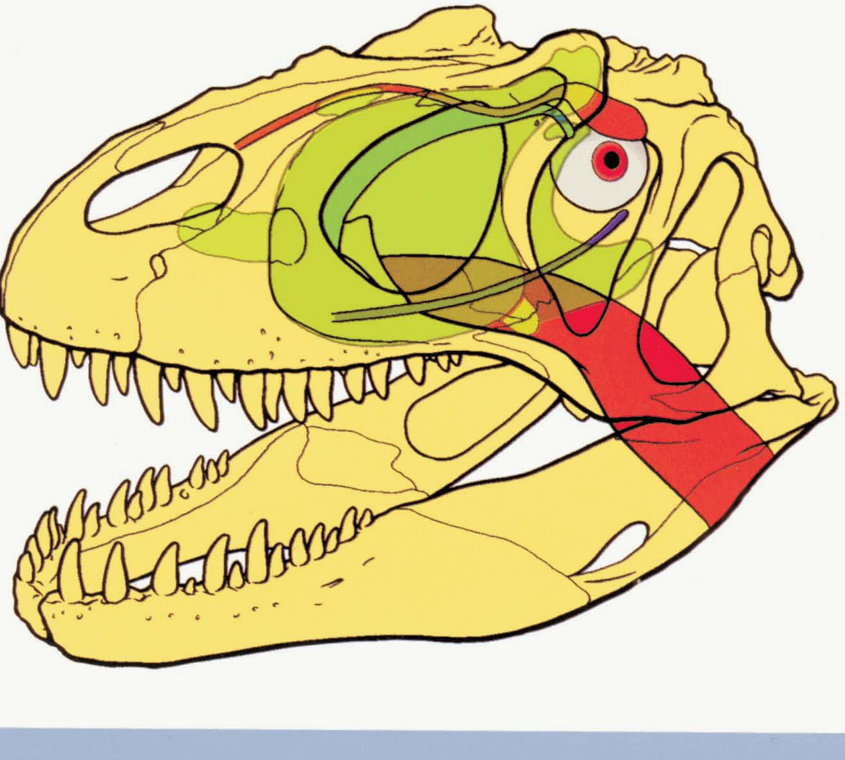
MEMOIR 3

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

Lawrence M. Witmer



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Cover Illustration:
Reconstruction of some of the cephalic soft tissues of the theropod dinosaur, *Allosaurus fragilis*.

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

LAWRENCE M. WITMER

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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

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ABSTRACT—The most commonly cited apomorphy of Archosauriformes is an opening in the snout known as the antorbital cavity. Despite the ubiquity and prominence of the antorbital cavity, its function and importance in craniofacial evolution have been problematic. Discovering the significance of the antorbital cavity is a two step process: first, establishing the function of the bony cavity (that is, its soft-tissue relations), and second, determining the biological role of the enclosed structure. The first step is the most fundamental, and hence is examined at length. Three hypotheses for the function of the antorbital cavity have been advanced, suggesting that it housed (1) a gland, (2) a muscle, or (3) a paranasal air sinus. Thus, resolution is correctly viewed as a "soft-tissue problem," and is addressed within the context of the extant phylogenetic bracket (EPB) approach for reconstructing the unpreserved features of fossil organisms. The soft-anatomical relations of the antorbital cavity (or any bony structure) are important because (1) soft tissues generally have morphogenetic primacy over bony tissues and (2) inferences about soft tissues are the foundation for a cascading suite of paleobiological inferences. The EPB approach uses the shared causal associations between soft tissues and their osteological correlates (i.e., the signatures imparted to the bones by the soft tissues) that are observed in the extant outgroups of the fossil taxon of interest to infer the soft-anatomical attributes of the fossil; based on the assessment at the outgroup node, a hierarchy characterizing the strength of the inference can be constructed. This general approach is applied to the problem of the function of the antorbital cavity, taking each hypothesized soft-tissue candidate—gland, muscle, and air sac—in turn, (1) establishing the osteological correlates of each soft-tissue system in the EPB of any fossil archosaur (i.e., extant birds and crocodilians), (2) formulating a hypothesis of homology based on similarities in these causal associations between birds and crocodilians, (3) testing this hypothesis by surveying fossil archosaurs for the specified osteological correlates, and (4) accepting or rejecting the hypothesis based on its phylogenetic congruence. Using this approach, fossil archosaurs can be reliably reconstructed with a Glandula nasalis, M. pterygoideus, pars dorsalis, and Sinus antorbitalis that are homologous with those of extant archosaurs; however, the osteological correlates of only the antorbital paranasal air sinus involve the several structures associated with the antorbital cavity. Additional evidence for the pneumatic nature of the antorbital cavity comes from the presence of numerous accessory cavities (especially in theropod dinosaurs) surrounding the main antorbital cavity. To address the origin of the antorbital cavity, the EPB approach was applied to basal archosauriforms; the data are not as robust, but nevertheless suggest that the cavity appeared as a housing for a paranasal air sinus. The second step in discovering the evolutionary significance of the antorbital cavity is to assess the function of the enclosed paranasal air sac. In fact, the function of all pneumaticity is investigated here. Rather than the enclosed volume of air (i.e., the empty space) being functionally important, better explanations result by focusing on the pneumatic epithelial diverticulum itself. It is proposed here that the function of the epithelial air sac is simply to pneumatize bone in an opportunistic manner within the constraints of a particular biomechanical loading regime. Trends in facial evolution in three clades of archosaurs (crocodylomorphs, ornithopod dinosaurs, and theropod dinosaurs) were examined in light of this new perspective. Crocodylomorphs and ornithopods both show trends for reduction and enclosure of the antorbital cavity (but for different reasons), whereas theropods show a trend for relatively poorly constrained expansion. These findings are consistent with the view of air sacs as opportunistic pneumatizing machines, with weight reduction and design optimality as secondary effects.

INTRODUCTION

With more than 10,000 species, archosaurs are the most diverse group of terrestrial vertebrates living today and have been so since almost the beginning of the Mesozoic Era when they radiated into virtually all habitats. Correlated with this high taxic diversity is a remarkable morphological diversity in skull form. A prominent aspect of skull anatomy in archosaurs is a usually large opening and space in the side of the snout called the antorbital fenestra and cavity, respectively. The antorbital cavity is such a characteristic feature of archosaurs that for many decades it has been the major diagnostic feature of the group. In fact, this feature stands as a synapomorphy of a slightly more inclusive group, Archosauriformes (Gauthier et al., 1988). Any attempt to understand the evolution of the skulls of archosaurs therefore must take the antorbital cavity into account. It is thus somewhat surprising, given both the ubiquity and prominence of the antorbital cavity, that the cavity has remained a functional enigma. This paper asks the simple question, what is the antorbital cavity for? That is, what is the function of the bony antorbital cavity? "Function" is a term with many biological meanings and has been used at many different levels of organization. In the present context, "function" relates to the fundamental mechanical and physical relationships of soft tissue to bone, and, as such, its usage conforms fairly closely to the definitions advanced by Bock and von Wahlert (1965) and Lauder (1995). Thus, to phrase it another way, this paper asks, what are the soft-tissue relations of the bony antorbital cavity? The logical next question is, what is the function (or even biological role) of the enclosed soft-tissue structure, and what does this determination tell us about facial evolution in the group?

Previous efforts to answer these questions have been hampered by treatment of Archosauria as a paraphyletic assemblage excluding birds and leaving crocodilians as the only extant archosaurs. Thus, since extant crocodilians lack an external antorbital fenestra, determination of the function of the antorbital cavity becomes problematic. Birds, however, retain an antorbital cavity and external fenestra that are directly comparable to those of fossil archosaurs (Witmer, 1987b, 1990, 1995b). This situation is thus a striking example of the insidious nature of paraphyletic taxa, because by excluding birds one ignores the only extant taxon retaining a "typical" antorbital cavity. It is tempting to wonder how the history of the debate would have progressed had birds as well as crocodilians been more explicit parts of the earlier comparisons.

Three hypotheses for the function (or soft-tissue relations) of the antorbital cavity have been proposed in the literature: (1) it housed a gland, (2) it housed a muscle, or (3) it housed an air sac. In all three cases the cavity would serve to "house" a soft-tissue structure. Thus, the function of the antorbital cavity is correctly viewed as a "soft tissue problem." It should be noted that the function and biological role of the soft tissues enclosed *within* the cavity is an issue that can be addressed only *after* the function of the antorbital cavity itself is established and is taken up in the last section. I previously provided a brief review of the three hypotheses and found the air-sac hypothesis to be best supported by what meager evidence was available then (Witmer, 1987b).

The problem is re-investigated here, making use of new studies of both extant and extinct archosaurs. It also provides the opportunity to implement (and indeed was the impetus to develop) a methodology for reconstructing soft tissues in extinct organisms. This methodology—the extant phylogenetic bracket approach—is outlined in the next section and is more fully presented elsewhere (Witmer, 1992a, 1995a). This approach is then applied specifically to the problem of the antorbital cavity of archosaurs. Since each of the major hypotheses proposes a different soft-tissue component within the antorbital cavity, these components are studied in detail in extant archosaurs to determine (or at least to hypothesize about) the causal associations of particular soft tissues and their osteological correlates. In doing so, this paper draws heavily on a companion paper on the homology of these and other facial structures among extant amniotes (Witmer, 1995b). Given these homologous causal associations and the distribution of the osteological correlates in fossil archosaurs, it is possible to infer which soft-tissue elements are associated with the antorbital cavity and which are not.

Before proceeding, the anatomy will be introduced and some terms clarified. As much as possible, the terminology will follow that codified in *Nomina Anatomica Avium* (Baumel and Witmer, 1993; see also Witmer, 1994). The most obvious facial feature is the antorbital fenestra, bounded principally by the maxilla and lacrimal with varying contributions from the jugal and nasal. The lateral surfaces of the bones surrounding the fenestra are often excavated into a depression usually termed the antorbital fossa (Fig. 1). When precision is required, the name of the bone bearing the depression will be added: e.g., maxillary antorbital fossa. Previously (Witmer, 1987b, 1990) I regarded the fenestra, depression, and adjacent cavity together as the "antorbital fossa," but here restrict fossae to actual bony structures. "Antorbital cavity" replaces my previous usage (Witmer, 1994). The antorbital cavity may be defined simply as the space rostral to the orbit, external to the cartilaginous nasal capsule, and internal to the surface of the snout (Witmer, 1995b). It is like the other named craniofacial cavities (e.g., orbit, adductor chamber, nasal cavity) in having bony limits and a variety of soft-tissue contents. It communicates with other spaces, requiring slight modification of the traditional sense of "antorbital fenestra." The lateral aperture of the cavity becomes the external antorbital fenestra (Fig. 1). When there is an antorbital fossa externally, the peripheral rim of the fossa marks the external antorbital fenestra. The bony edge internal to the antorbital fossa is the internal antorbital fenestra and roughly corresponds to the "antorbital fenestra" as traditionally conceived (Fig. 1). The internal and external antorbital fenestrae are difficult to distinguish in archosauriforms having poorly developed laminae walling the antorbital cavity. For example, in some archosaurs (such as some derived parasuchians and most pterosaurs) there really is just a single fenestra.

The rostral limits of the antorbital cavity typically are within the maxilla, although in parasuchians and some birds it may extend rostrally into the premaxilla. The bony floor of the cavity is formed by the palatine bone to a variable extent (Fig. 1). The maxilla also contributes to the floor in those taxa with at least moderate development of maxillary palatal processes. The size and caudal extent of the choana constrain maxillary and palatine involvement in the floor. Medially, the antorbital cavity tends to open broadly to the nasal cavity. In life, the lateral wall of the cartilaginous nasal capsule forms the medial wall of the cavity although there is a gap (i.e., an ostium) joining the nasal and antorbital cavities in extant archosaurs and, as argued below, extinct archosaurs as well. The medial laminae of the maxilla and/or lacrimal are so extensive in some archosaurs (many ornithischians and some crocodylomorphs) that they almost completely enclose the cavity medially such that the internal antorbital fenestra essentially becomes a foramen between nasal and antorbital cavities (Fig. 1). The antorbital cavity almost always communicates with the orbit, although the nature of this communication is seldom described in fossil taxa. This communication in the bony skull is termed the postnasal fenestra (Fig. 1; see also Witmer, 1994, 1995b). In extant archosaurs a variety of structures (e.g., nerves, vessels, musculature, pneumatic diverticula, ducts of glands) may pass through the postnasal fenestra, and the fenestra itself is partially occluded by these structures and portions of the cartilaginous nasal capsule.

SOFT-TISSUE INFERENCE AND THE EXTANT PHYLOGENETIC BRACKET

As mentioned above, each of the major hypotheses for the function of the antorbital cavity proposes that some soft-anatomical component is lodged within the cavity. How do we approach this problem when fossils hardly ever preserve such soft tissues? Furthermore, why should we even care? These questions are addressed at length elsewhere (Witmer, 1992a, 1995a) and discussed briefly in this section. The general importance of soft-tissue considerations will be examined first, followed by methodological issues.

The Significance of Soft Tissues

Accurate evolutionary and/or functional interpretations of extinct vertebrates may not be possible with information from bones alone. Soft tissues are important for two main reasons. First, in general, soft tissues often have morphogenetic primacy over skeletal tissues, such that the existence, position, maintenance, and form of bones and bony structures largely are controlled by particular soft tissues. In effect, bony structures are products of their epigenetic systems (Smith and Hall, 1990; Herring, 1993). Thus, evolutionary changes in nonskeletal aspects of anatomy are transmitted via the epigenetic machinery to the skeleton. Questions about the direction and cause of evolutionary change based on inferences from *only* the skeleton thus may be posed at the wrong hierarchical level. Moss' (1968) slogan—soft tissues evolve, bones respond—somewhat overstates the issue, but it does emphasize the notion that bones must be studied in concert with their associated soft tissues.

The second reason for the importance of soft tissues stems directly from the perspective offered by the slogan. Soft tissue considerations reside at the base of a whole host of paleobiological inferences. This point is not always appreciated and

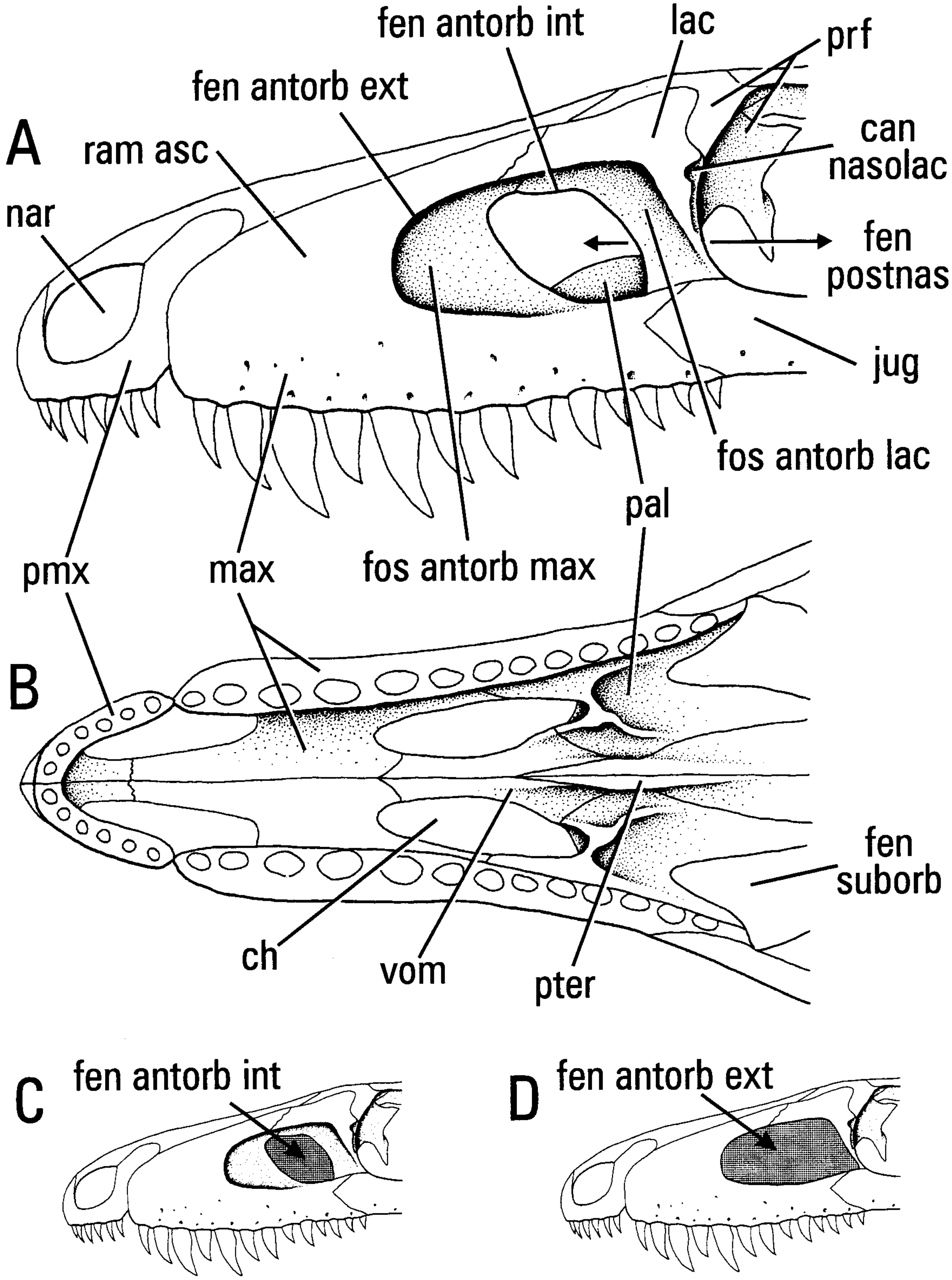

FIGURE 1. *Sphenosuchus acutus*, snout. **A**, left lateral view, showing morphology of antorbital cavity. **B**, ventral view. **C**, left lateral view with internal antorbital fenestra shaded. **D**, as **C**, but with external antorbital fenestra shaded. (Modified after Walker, 1990.)

many such inferences make assumptions—often unstated and untested—about the soft-tissue attributes of organisms. Initial mistakes in soft-tissue interpretation can be amplified up the ecological hierarchy. This notion has been graphically represented as an "inverted pyramid of inference" (Fig. 2; Witmer, 1995a), wherein higher order inferences are seen as being logically dependent on lower order inferences. Thus, errors in (or inattention to) soft-tissue reconstruction can lead to flawed analyses of functional morphology, which in turn impact on ideas about the behavior and mode of life of the organism, which lead to inaccurate assessments of paleoecological interactions with contemporaneous species, and which ultimately result in

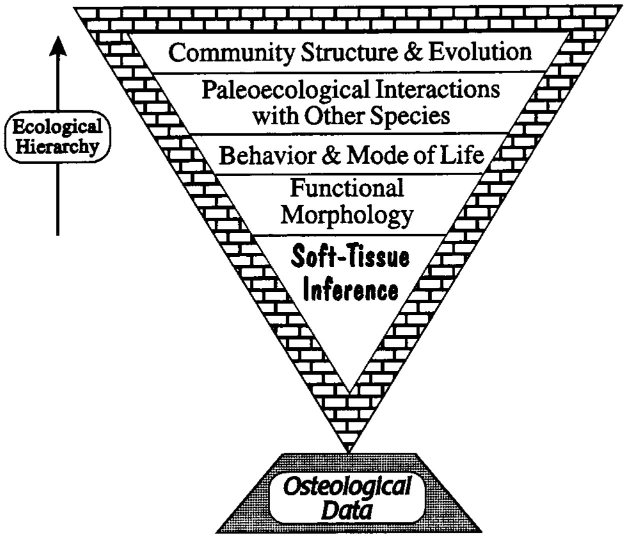

FIGURE 2. Inverted Pyramid of Inference. Inferences about the soft-tissue relations of bony structures are the foundation and justification for many paleobiological inferences. The pyramid is inverted to highlight the point that mistakes in soft-tissue inference cascade up the hierarchy, magnifying the error. (Modified from Witmer, 1992a, 1995a.)

spurious hypotheses about the structure and evolution of whole communities. As we will see, complicated paleoecological and evolutionary scenarios have been tied explicitly to particular notions about the soft-tissue relations of the antorbital cavity of archosaurs. Thus, a seemingly arcane issue can have important—and unexpected—ramifications (see Witmer, 1992a, 1995a for other examples).

The Extant Phylogenetic Bracket Approach

The next question is, how do we obtain this requisite soft-tissue information? A method is outlined here and is presented in detail elsewhere (Witmer, 1992a, 1995a; see also Bryant and Russell, 1992, for an independently-devised but generally similar approach). The approach is firmly grounded in basic phylogenetic principles, somewhat resembling two-pass systems of a posteriori character optimization (Wiley et al., 1991; Witmer, 1995a). The only source of direct information about soft tissues and their relationships to the skeleton are extant taxa, and thus they must be components of the analysis. The most relevant extant taxa are the two most–proximal living outgroups of the fossil taxon of interest (Fig. 3A). Figure 3B presents a topology in which there has been a rotation about the outgroup node such that the extant taxa now flank the fossil taxon. This rotation is simply a heuristic device that highlights a central objective of

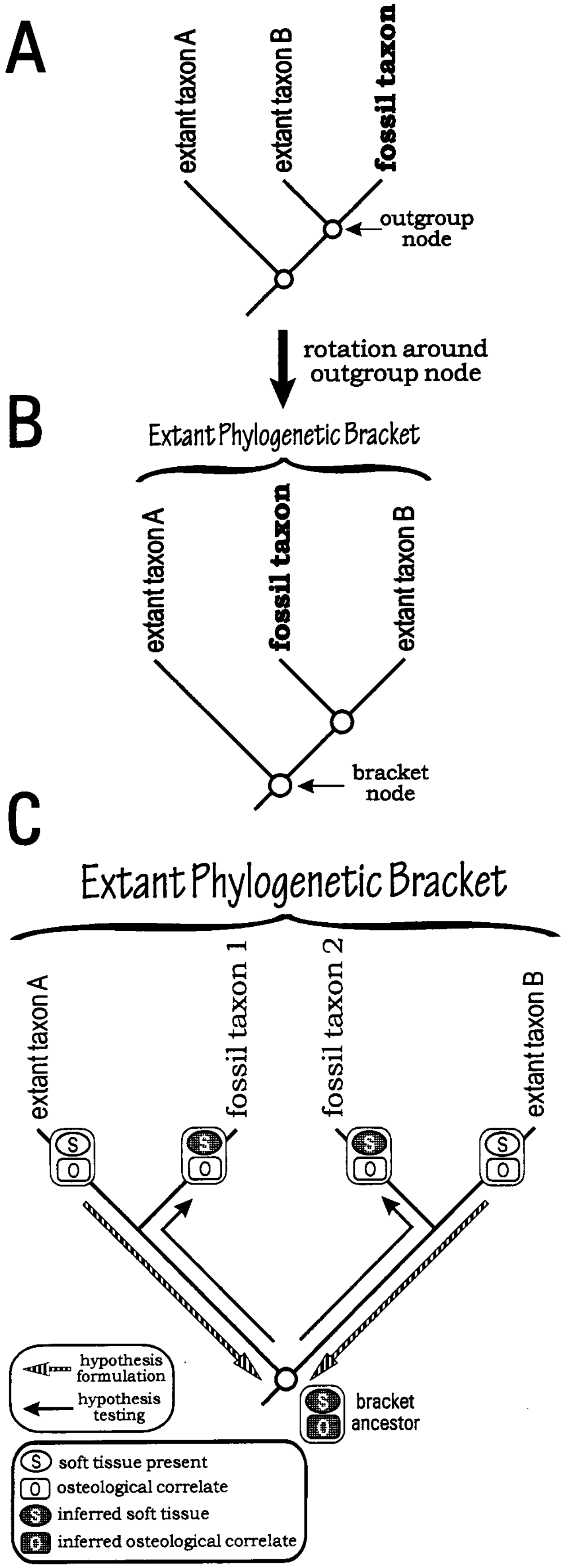

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FIGURE 3. The Extant Phylogenetic Bracket Approach. **A**, phylogenetic relationships of a fossil taxon and its first two extant sister groups. **B**, rotation about the outgroup node in **A** brings the extant taxa to the periphery, forming the Extant Phylogenetic Bracket (EPB). **C**, cladogram showing the inference of soft-tissue attributes in fossil taxa using the EPB approach. Similarities in soft tissues and osteological correlates between the extant taxa are hypothesized as having been present in their common ancestor, the bracket ancestor (hatched arrows). If the fossil taxa possess the osteological (skeletal) correlates, then the hypothesis of homology survives the congruence test. If the soft tissues and osteological correlates indeed are causally associated, then the soft tissue can be inferred in the fossil taxa with confidence. (Modified from Witmer, 1992a, 1995a.)

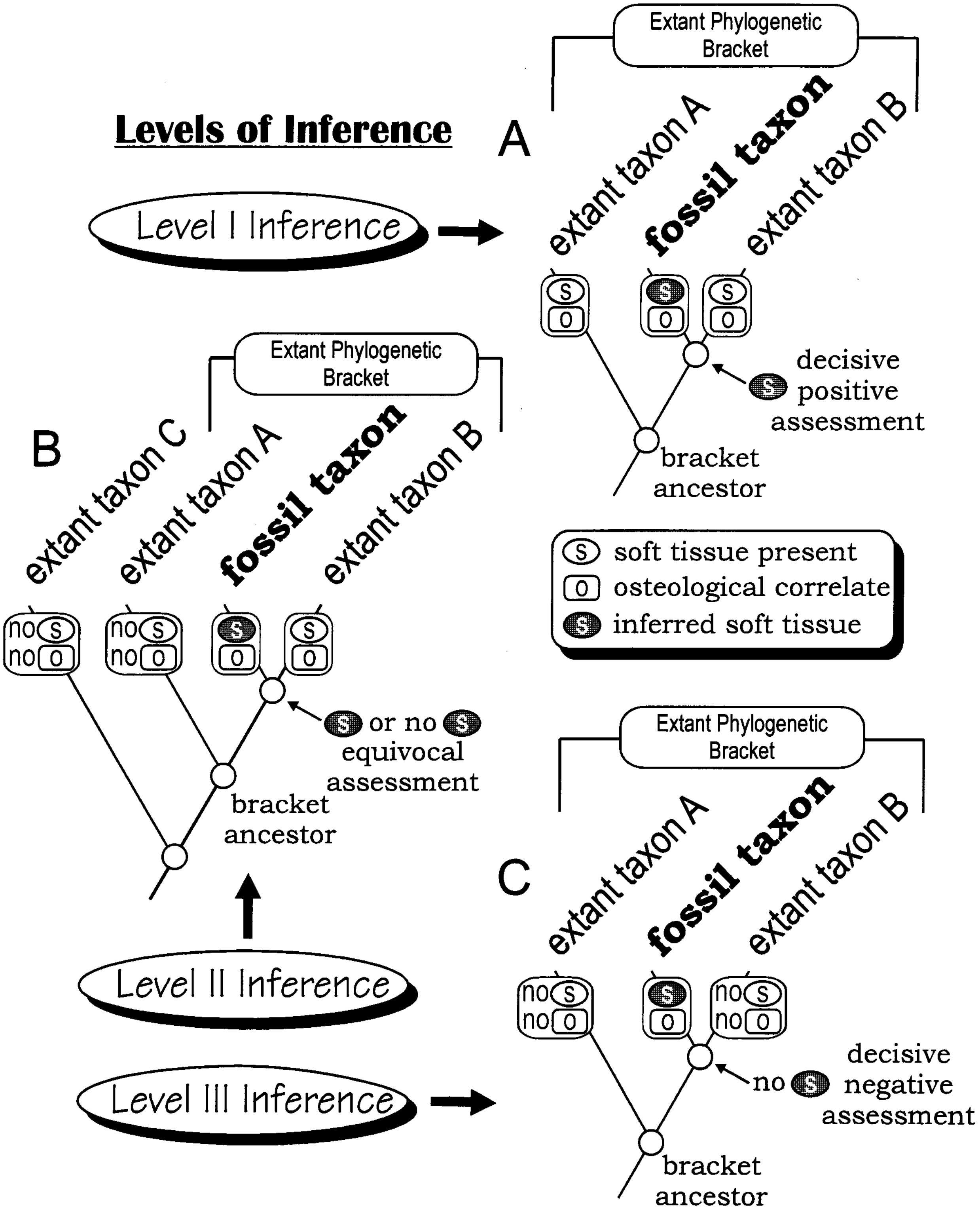

FIGURE 4. Levels of inference. The soft-tissue assessment at the outgroup node determines the level of inference and hence the relative amount of phylogenetic support such an inference draws. **A**, level I inference: as both extant members of the EPB possess the suspected soft tissue (and its causally associated osteological correlates), the assessment at the outgroup node is decisive and positive. **B**, level II inference: as only one component of the EPB has the soft-tissue attribute, the assessment is equivocal or ambiguous. **C**, level III inference: as neither component has the suspected soft tissue, the assessment is decisive and negative. Level II and level III inferences might be justifiable if a compelling morphological evidence argument can be advanced.

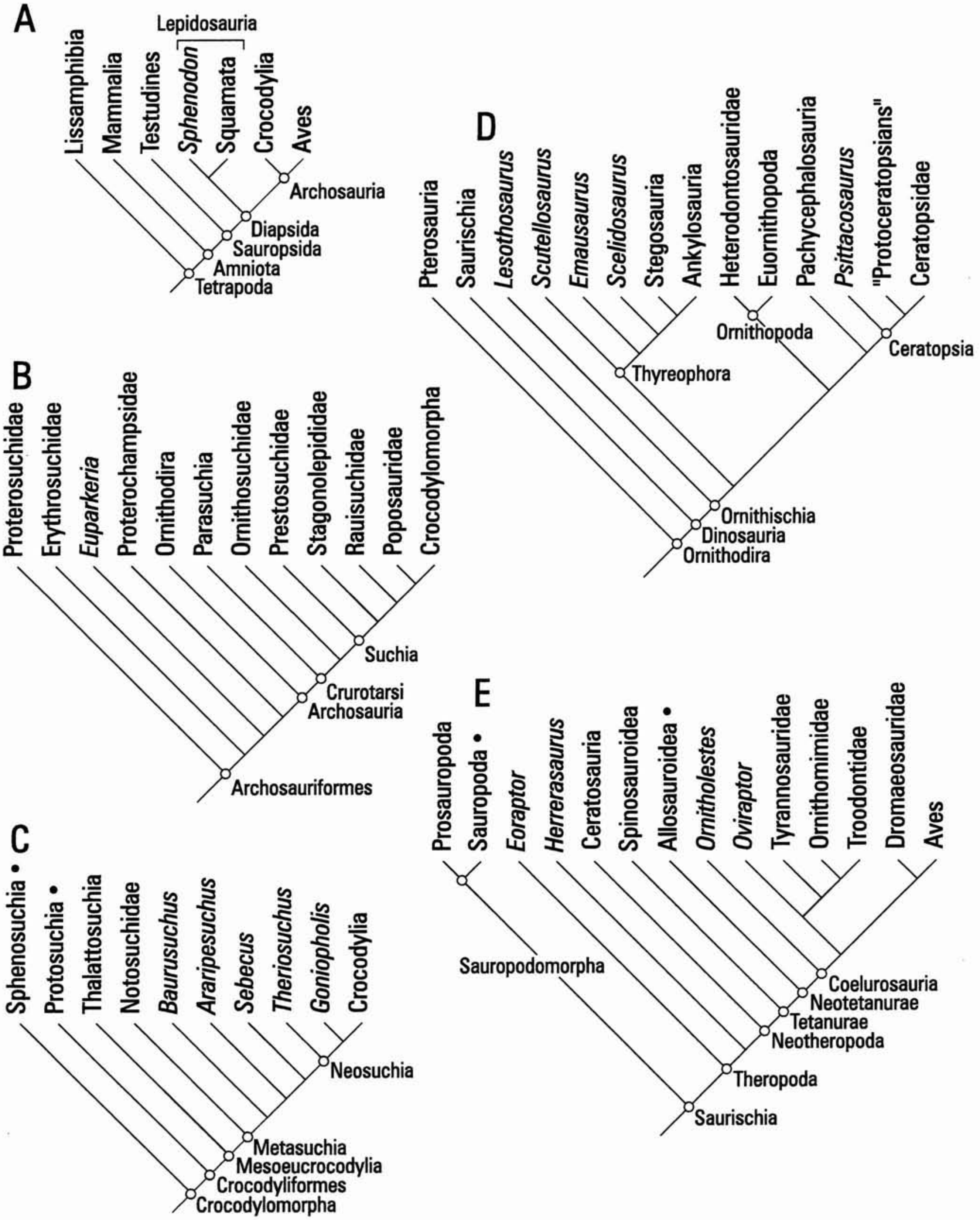

FIGURE 5. Phylogenetic framework. The intent of this figure is primarily to provide the reader with a "phylogenetic road map" of almost all of the major taxa mentioned in the text. None of the cladograms were generated by the data discussed in this paper. Phylogenetic structure within some of the terminal taxa is indicated below using parenthetical notation, usually including only those taxa mentioned in the text. Not all of the following cladograms are based on strict application of phylogenetic procedures, and some are controversial. The closed circle following the names of some taxa indicates that an alternative cladogram is presented in this caption. **A**, extant Tetrapoda (after Gauthier et al., 1988). **B**, Archosauriformes, emphasizing basal forms, and Archosauria, emphasizing Crurotarsi (after Benton and Clark, 1988; Sereno and Arcucci, 1990;

the approach, namely, that the extant taxa actually do "bracket" the fossil taxon by constraining all inferences. The extant taxa are regarded as the extant phylogenetic bracket (EPB) of the fossil taxon.

Reconstruction of soft tissues in extinct organisms involves three basic procedures (Fig. 3C). First, the morphogenetic primacy of nonskeletal over skeletal tissues leads us to expect soft tissues often to produce certain bony signatures (e.g., muscles scars, nerve foramina). These causal associations between the soft tissues and their osteological correlates are determined in the extant taxa. The causal nature of these associations sometimes is assumed rather than demonstrated, but, in almost all cases that can be envisioned, causality is a valid hypothesis amenable to testing via experimental intervention; certainly, in cases such as neurovascular or pneumatic foramina, muscle scars, and central nervous system structures the causal relationship of soft tissue to bony signature is clear (see Witmer, 1995a for specific examples). Second, similarities in these causal associations between the extant taxa are hypothesized as having been present in the bracket ancestor. Third, this hypothesis is then tested by searching for the osteological correlates in the fossil taxa. If the osteological correlates are indeed causally associated with the soft tissue (ideally, satisfying the criterion of being necessary and sufficient), then the soft tissue can be inferred with considerable certainty in the fossil taxon. In this approach, these soft-tissue/osteological-correlate causal associations are being essentially "mapped" over a more or less fixed cladogram generated from other data rather than incorporating them into a larger phylogenetic analysis. Obviously, this is an expediency that is valid only if the cladogram's nodes are sufficiently supported that they would not be altered by the incorporation of the new data. Fortunately, this is clearly the case for archosaurs.

The EPB approach is clearly and firmly based in the logic of homology determination (Patterson, 1982; Rieppel, 1988; de Pinna, 1991). Correspondences (sensu Stevens, 1984) in the causal associations between soft and bony tissues shared by the extant taxa form the similarity test of homology. Of course, it is some superficial perception of similarity that suggests homology in the first place (de Pinna, 1991), but detailed similarity remains an important and valid test (Bock, 1989). Congruence, with its foundation in parsimony, is widely regarded as the ultimate test of homology (e.g., Patterson, 1982; de Pinna, 1991; Rieppel, 1992, 1994). Surveying the fossil taxa for the osteological correlates of the soft tissue clearly corresponds to the congruence test of homology. Again, causal association of hard and soft tissues is the key to the approach in that it allows the soft-tissue attributes to be tested for congruence across both extinct and extant taxa by using the osteological correlates as proxies for the soft tissues (Witmer, 1995a).

The above discussion has assumed that *both* components of the extant phylogenetic bracket have the soft-anatomical feature suspected to occur in the fossil taxon. However, there are situations where we may suspect that a fossil taxon has a particular soft-tissue attribute that *only* its extant sister group has; furthermore, there are cases where neither component of the EPB has the suspected attribute (see Witmer, 1992a, 1995a for examples). Each of these three situations leads to a different assessment at the outgroup node, and it is this assessment that is pivotal in determining the status of the fossil. If both, one, or neither extant taxa have the soft tissue suspected to occur in an extinct taxon, then the assessment at the outgroup node is decisive and positive, equivocal, or decisive and negative, respectively. These three categories can be easily ordinated to create a hierarchy of soft-tissue inferences (Fig. 4; Witmer, 1995a): a level I inference for decisive positive assessments at the outgroup node, a level II inference when the assessment is equivocal, and a level III inference for decisive negative assessments. The greater the number, the less robust the inference, because each level draws increasingly less phylogenetic support. Level II and III inferences, however, may be justifiable if there is sufficiently compelling morphological evidence—that is, particularly persuasive osteological correlates. As will be seen in a later section, arguments of compelling morphological evidence can be very convincing, although it always must be remembered that they draw less support from phylogenetics.

The basic organization of the rest of this paper is to take each of the major hypotheses in turn, beginning with the glandular hypothesis (which has had the fewest adherents), followed by the muscular hypothesis (which always has been the most

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Sereno, 1991b; Parrish, 1993); topology within Parasuchia (after Ballew, 1989): (*Parasuchus* (*Paleorhinus* (*Angistorhinus* (*Rutiodon* (*Phytosaurus* (*Pseudopalatus, Mystriosuchus*)))))). **C**, Crocodylomorpha (after Benton and Clark, 1988; Wu, Li, and Li, 1994); topology within a paraphyletic Sphenosuchia (after Benton and Clark, 1988): (*Pseudhesperosuchus,* (*Terrestrisuchus, Saltoposuchus*)(*Dibothrosuchus, Sphenosuchus* (Kayenta sphenosuchian, Crocodyliformes))); topology within a monophyletic Sphenosuchia (after Sereno and Wild, 1992; Wu and Chatterjee, 1993): ((*Terrestrisuchus, Saltoposuchus*) (*Pseudhesperosuchus* (*Sphenosuchus, Dibothrosuchus*))); topology within a monophyletic Protosuchia (after Wu, Brinkman, and Lü, 1994): (*Orthosuchus* (*Gobiosuchus* (*Shantungosuchus* (*Hemiprotosuchus, Protosuchus,* UCMP 97638)))); topology within a paraphyletic Protosuchia (after Benton and Clark, 1988): ((*Hemiprotosuchus, Protosuchus,* UCMP 97638)(*Orthosuchus* (*Gobiosuchus,* Mesoeucrocodylia))); topology within Thalattosuchia (after Benton and Clark, 1988): (*Pelagosaurus* (*Metriorhynchus* (*Steneosaurus, Teleidosaurus*))); topology within Crocodylia (after Norell, 1989): (*Gavialis* ((*Tomistoma, Crocodylus*)(*Caiman, Alligator*))). **D**, Ornithodira, emphasizing Ornithischia (after Gauthier, 1986; Sereno, 1986; Haubold, 1990); topology within Pterosauria (after Bennett, 1991, 1994; the basal polytomy corresponds to "rhamphorhynchoids"): (*Eudimorphodon, Campylognathoides, Dimorphodon, Rhamphorhynchus* (*Pterodactylus* (*Germanodactylus* (*Pteranodon* (*Anhanguera, Santanadactylus, Tropeognathus*))))); topology of Stegosauria (after Sereno, 1986): (*Huayangosaurus* (*Chungkingosaurus, Tuojiangosaurus, Stegosaurus*)); topology of Ankylosauria (after Coombs and Maryanska, 1990; *Edmontonia* is a nodosaurid, others are ankylosaurids): (*Edmontonia* (*Pinacosaurus* (*Euoplocephalus, Ankylosaurus*))); topology of Heterodontosauridae (after Weishampel and Witmer, 1990b): (*Lanasaurus* (*Abrictosaurus, Heterodontosaurus*)); topology of Euornithopoda (after Sereno, 1986; Weishampel and Horner, 1990): (*Hypsilophodon* (*Dryosaurus* (*Camptosaurus* (*Iguanodon* (*Ouranosaurus* ((*Anatotitan, Edmontosaurus*)(*Hypacrosaurus, Corythosaurus*))))))). **E**, Saurischia, emphasizing Theropoda (after Gauthier, 1986; Sereno et al., 1993, 1994, 1996; Currie and Zhao, 1994a; Holtz, 1994); topology of Prosauropoda (after Galton, 1990; topology by Upchurch [1995] is very similar): (*Thecodontosaurus* (*Anchisaurus* (*Massospondylus, Yunnanosaurus* (*Sellosaurus* (*Coloradia* (*Lufengosaurus, Plateosaurus*)))))); alternate topology of Sauropoda (after McIntosh, 1990): (*Brachiosaurus* (*Patagosaurus* (*Euhelopus, Camarasaurus*))(*Shunosaurus* (*Omeisaurus* ((*Dicraeosaurus, Nemegtosaurus*)(*Apatosaurus, Diplodocus*))))); alternate topology of Sauropoda (after Upchurch, 1995): ((*Shunosaurus* (*Omeisaurus, Euhelopus*))((*Brachiosaurus, Camarasaurus*)(*Nemegtosaurus* (*Dicraeosaurus* (*Apatosaurus, Diplodocus*))))); topology of Ceratosauria (after Holtz, 1994): ((*Dilophosaurus* (*Coelophysis, Syntarsus*)) (*Ceratosaurus, Abelisauridae*)); alternate topology of Allosauroidea (after Sereno et al., 1996): ((*Sinraptor, Yangchuanosaurus*), *Monolophosaurus, Allosaurus* (*Giganotosaurus* (*Acrocanthosaurus, Carcharodontosaurus*))); alternate topology of Allosauroidea (after Currie and Zhao, 1994a): (*Allosaurus* (*Sinraptor, Yangchuanosaurus*)); topology of Tyrannosauridae (after Bakker et al., 1988): (*Daspletosaurus* (*Albertosaurus, Tyrannosaurus*)); topology of Aves (after Cracraft, 1988; Chiappe and Calvo, 1994): (*Archaeopteryx* (*Gobipteryx* (Hesperornithidae ((*Struthio, Rhea*)((*Gallus* (*Anser, Anas*)) (*Diomedea, Larus, Ardea*)))))).

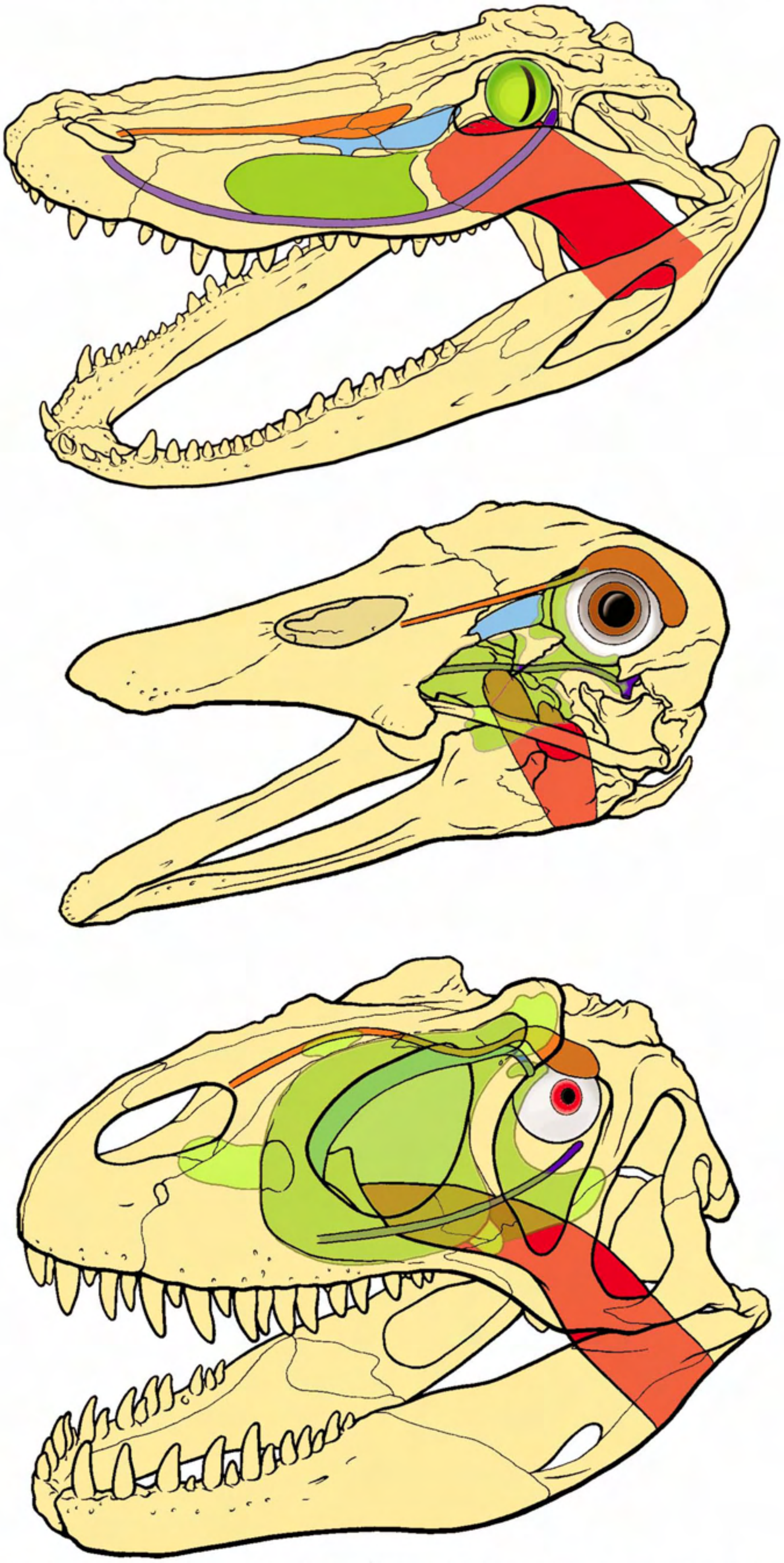

FIGURE 6. Archosaurian heads with the facial soft tissues that are of particular interest here. All are shown in oblique rostrodorsolateral views. **A**, *Alligator mississippiensis.* **B**, *Anser anser.* **C**, *Allosaurus fragilis.* Soft tissues shown include the eyeball, maxillary nerve, main paranasal air sinus (i.e., antorbital sinus [= caviconchal sinus of crocodilians]), nasal gland, nasolacrimal duct, and the dorsal pterygoideus muscle. Some bones are partially transparent. The position of the nasal gland in *Allosaurus fragilis* is defensible (see text) but is more speculative (a level II or III inference).

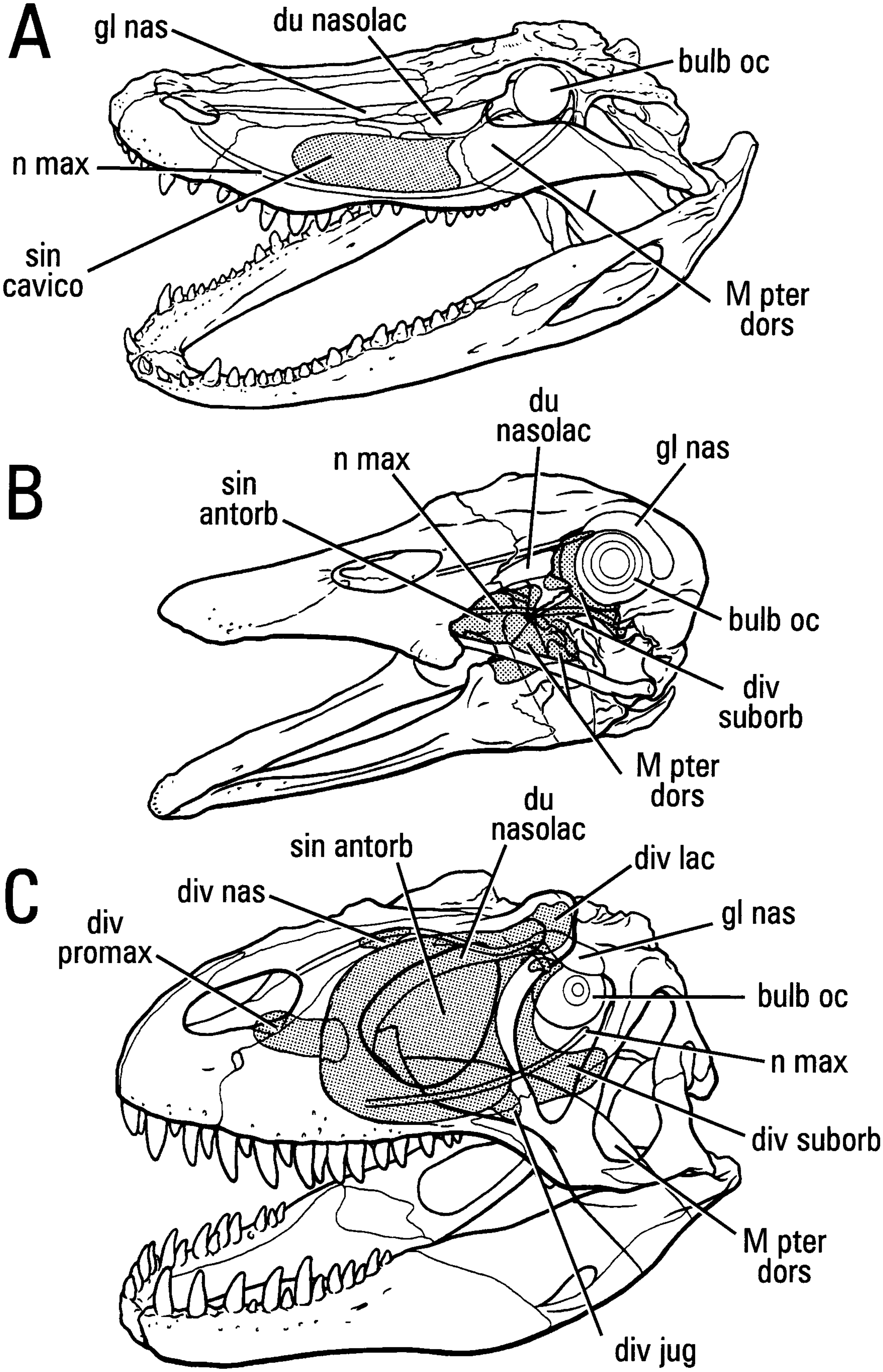

FIGURE 6. *(Continued)*

popular), and ending with the pneumatic hypothesis (which is the most recent). For each hypothesis, the soft tissues and their osteological correlates first are examined in extant birds and crocodilians (the EPB for any clade of fossil archosaurs). Detailed 1:1 correspondences in these causal associations shared by birds and crocodilians are regarded as passing the similarity test of homology. This hypothesis of homology makes certain predictions about specific attributes of the bracket ancestor. The hypothesis of homology (and hence also the hypothesis about ancestral attributes) is then tested by surveying fossil archosaur taxa for the presence of the specified osteological correlates. Finally, whether or not the hypothesis survives congruence testing is reported and the implications for the function of the antorbital cavity are discussed.

MATERIALS

The extant sample is composed principally of several species of crocodilians (e.g., *Alligator mississippiensis, Caiman crocodilus, Crocodylus porosus, C. novaeguineae, Tomistoma schlegelii,* and *Gavialis gangeticus*) and several species of birds (e.g., *Gallus gallus, Anas platyrhynchos, Anser anser, Diomedea immutabilis, Struthio camelus,* and *Rhea americana*). The extant sample was studied via dissection, serial sectioning, latex injection of various cavities, and clearing-and-staining of ontogenetic series (Witmer, 1992a, 1995b). Information from fossil archosaurs was derived from study of actual specimens, casts, and the literature. Specification of a museum catalog number indicates that the original material was studied; cast material is indicated as such. Figure 5 presents cladograms for the major clades of archosaurs and extant Amniota (see caption for specific references and discussion).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; BYU, Earth Sciences Museum, Brigham Young University, Provo; CM, Carnegie Museum of Natural History, Pittsburgh; CMN, Canadian Museum of Nature, Ottawa; FMNH, Field Museum of Natural History, Chicago; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; KUVP, Museum of Natural History, University of Kansas, Lawrence; LACM, Los Angeles County Museum, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Muséum National d'Histoire Naturelle, Paris; MOR, Museum of the Rockies, Montana State University, Bozeman; NMMNH, New Mexico Museum of Natural History, Albuquerque; PIN, Paleontological Institute, Moscow; PST, Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulan Baatar; PVSJ, Vertebrate Paleontology, San Juan Province, Argentina; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller; SAM, South African Museum, Capetown; SDSM, Geology Museum, South Dakota School of Mines, Rapid City; TTUP, The Museum, Texas Tech University, Lubbock; UC, University of Chicago; UCMP, University of California Museum of Paleontology, Berkeley; USNM, United States National Museum, Washington, D. C.; UUVP, University of Utah Museum of Natural History, Salt Lake City; YPM, Peabody Museum, Yale University, New Haven.

HYPOTHESIS 1: THE ANTORBITAL CAVITY HOUSES A GLAND

Historical Development

"Of the anterior process [of the lacrimal of *Euparkeria capensis*], much is below the level of the general surface of the face, suggestive of the antorbital vacuity having lodged a large gland." This quote from Robert Broom (1913: 621) represents both the extent of his advocacy of the glandular hypothesis and fairly summarizes the nature of the osteological evidence, viz. the presence of a fossa. Broom is generally credited with the glandular hypothesis, but it was suggested earlier by Smith Woodward (1896) and McGregor (1909). Ewer (1965) also supported the notion, but did not suggest a particular function for the gland. Her primary evidence was again the presence of a fossa surrounding the internal antorbital fenestra of *Euparkeria capensis* and additionally, her refutation of Walker's (1961) formulation of the muscular hypothesis. Other adherents (e.g., Price, 1959; Langston, 1973; Halstead, 1975; Nash, 1975; Madsen, 1976b; Charig, 1979; Galton and Powell, 1980; Norman, 1985) rarely have offered more than a passing remark on the subject. Reig (1970) was convinced by Ewer's treatment of the muscular hypothesis and presented the first (and still only) detailed exposition of the glandular hypothesis. Reig's direct evidence still involved only the presence of the antorbital fossa, but he offered an elaborate causal scenario that pointed to a particular function of the gland, that of salt excretion. Reig's scenario is based on his hypothesis that archosaurs were related to synapsids, and, sharing their strategy of nitrogen metabolism, would have incurred salt loads requiring extrarenal excretion (Witmer, 1987b).

Despite the flaws in Reig's scenario (not least of which is the subsequent falsification of his phylogenetic hypothesis), it is instructive as an example of how soft-tissue reconstruction of fossil taxa lies at the base of many paleobiological inferences. Reig (1970: 265) regarded the expansion of the antorbital fenestra and fossa relative to the condition in proterosuchids (which Reig regarded as primarily aquatic) as an "intensification of function of an extrarenal salt-secreting organ," marking "the early shift of the thecodonts towards the upland life to fulfill the roles of terrestrial carnivorous reptiles, a shift that triggered the radiation of the Middle and Upper Triassic pseudosuchians." If the original soft-tissue assessment of an "antorbital gland" is incorrect, then this weighty paleobiological conclusion of an ecological shift is severely compromised.

Thus, the direct evidence for the glandular hypothesis has never involved more than the presence of a "basin-like depression," that is, an antorbital fossa (Witmer, 1987b). Furthermore, the hypothesis has failed to make recourse to extant taxa, which at least constrain our inferences. The methodology for reconstructing soft anatomy in fossils will be applied here under the suspicion that the antorbital cavity may have housed a gland.

The Extant Phylogenetic Bracket

As indicated earlier, the extant phylogenetic bracket of any particular clade of fossil archosaurs comprises present-day birds and crocodilians. The initial approach is to survey the known glands of birds and crocodilians, seeking similarities in topographical relationships and noting the presence of osteological correlates. Most of the cephalic glands (e.g., lingual glands, buccal glands, Harder's gland) can be excluded because they are either far removed from the area or leave no evidence on the bones. In extant crocodilians, the epithelium of the nasolacrimal duct takes on glandular characteristics, leading Saint-Girons (1976) to refer to it as the nasolacrimal gland. Although never suggested as the "antorbital gland," it is seemingly in the perfect location because it is housed within an expanded cavity within the lacrimal bone caudally and is sheltered more rostrally by the maxilla and nasal. However, the nasolacrimal gland is unique to crocodilians among extant sauropsids (Saint-Girons, 1985, 1989). Furthermore, the osteological correlates of the nasolacrimal gland (e.g., the expanded cavity within the lacrimal) are clearly lacking in extinct archosaurian clades, including crocodylomorphs up to at least the level of Mesoeucrocodylia. Thus, the nasolacrimal gland of crocodilians also may be excluded from consideration. It may be noted here that throughout this paper nasolacrimal "duct" will be used for the epithelial tube whereas nasolacrimal "canal" or "groove" will be reserved for the bony conduit of the duct.

In contrast, Glandula nasalis is the major candidate for the "antorbital gland," being directly associated with the nasal cavity and present in all extant sauropsids. The homology of the nasal gland among sauropsids is established elsewhere (Witmer, 1995b). In general in sauropsids, the nasal gland lies within the dorsolateral portion of the snout, between the nasal capsule and dermal skull roof (Plate, 1924; Matthes, 1934; Malan, 1946; Parsons, 1959; Gabe and Saint-Girons, 1976; Witmer, 1995b).

Extant Crocodilians—In crocodilians, the nasal gland is a large, highly vascular structure running with the lateral ramus of the ophthalmic division of the trigeminal nerve. Early in ontogeny its position is lateral or dorsolateral as in other sauropsids but later assumes (concomitant with ontogenetic rotation of the nasal cavity; Witmer, 1995b) a dorsal position under the nasal bones and along the nasomaxillary suture (Fig. 6A).In older animals and adults, the nasal gland is relatively long, often extending dorsal to the postconcha and making it into the general area of the antorbital cavity. It is medial to the nasolacrimal duct except for where the latter turns ventromedially under the gland to enter the nasal cavity.

Extant Birds—The supraorbital salt gland that is so apparent in aquatic birds (Fänge et al., 1958) and has become a textbook example of extrarenal salt excretion (Welty and Baptista, 1988; Schmidt-Nielsen, 1995) would seem to have little in common with the nasal glands of other sauropsids. However, the avian nasal gland (Fig. 6B) is found in a variety of locations, ranging from being completely preorbital and within the antorbital cavity to extending far caudally over the orbit onto the frontal (Technau, 1936). The ancestral avian condition for the location of the body of the gland is very difficult to deduce by ingroup comparison. However, regardless of the position of the body of the gland, a portion of it (or certainly its ducts) follows the same general course as in other sauropsids (Witmer, 1995b). Thus, the gland and/or its ducts are outside of the nasal capsule and protected externally by the reciprocal, subnarial processes of the nasal and maxilla; in cases where the gland is caudally placed, the lacrimal, nasal, and/or frontal may cover the gland externally (Marples, 1932; Technau, 1936). As in crocodilians, the gland and its ducts are generally medial (and usually somewhat dorsal) to the nasolacrimal duct, except rostrally where they enter the nasal capsule.

Osteological Correlates—The osteological evidence for the (external) nasal gland in sauropsids is often subtle. In crocodilians, the ventral surfaces of the nasals have a shallow, elongate concavity lateral to the paramedian sulcus for the cartilaginous nasal septum and roof. In *Alligator mississippiensis,* this area of the nasal bone bears a finely striated surface texture. The longitudinal concavity crosses the nasomaxillary suture onto the maxilla. It houses not only the nasal gland but also branches of N. ophthalmicus (Ramus lateralis nasi) and accompanying blood vessels. In birds in which the nasal glands extend onto the skull roof (e.g., penguins, loons, albatrosses, gulls), there usually are very distinct fossae on the frontal bones and usually also foramina (lateral orbitonasal foramina) between the lacrimal, frontal, and/or ectethmoid for passage of the ducts (Baumel and Witmer, 1993). In other birds, especially those manifesting the preorbital position, there may be little clear evidence of the gland itself. However, in some cases, the ducts of the gland may inscribe grooves on the ventral and/or medial surface of the nasal (e.g., *Ardea herodias, Anser anser,* some *Larus* spp.), although the absence of these grooves is common. Young and embryonic specimens of *Anser anser, Anas platyrhynchos, Gallus gallus, Rhea americana,* and *Struthio camelus* reveal that the ducts pass close to or along the nasomaxillary suture (or, in the case of the ratites, adjacent to the nasomaxillary ligament).

The Hypothesis

Given these similarities between birds and crocodilians (the EPB), we may hypothesize that their common ancestor had a nasal gland that had the following characteristics: (1) it resided in the dorsal or dorsolateral portion of the snout; (2) it grooved the internal surfaces of the nasal and/or maxilla in the vicinity of their suture; and (3) it was situated generally dorsomedial (if not completely rostral) to the bony nasolacrimal canal.

Testing the Hypothesis

This hypothesis is tested by searching among fossil archosaurs for the presence of the specified osteological correlates. Specimens providing the appropriate internal views are concentrated in Suchia and Dinosauria.

Suchia—Among suchians, Crocodylomorpha is particularly well represented. For example, *Sebecus icaeorhinus* (AMNH 3160) and the thalattosuchians *Pelagosaurus typus* (BMNH 32600) and *Metriorhynchus superciliosus* (BMNH R3900; taxonomy of metriorhynchids follows Adams-Tresman, 1987) have shallow sulci running along or next to the nasomaxillary suture, although only in the last-mentioned taxon can it be traced to the naris. Deeper sulci within the ventrolateral aspect of the nasal and probably the adjacent surface of the maxilla are visible in the sphenosuchid crocodylomorphs *Sphenosuchus acutus* (Walker, 1990:fig. 5) and *Dibothrosuchus elaphros* (FMNH CUP 2081). Earlier, Walker (1972) suggested that *Sphenosuchus acutus* may have had a birdlike supraorbital nasal gland. Tarsitano and Hecht (1980) and Martin (1983a) were skeptical, and Walker (1990) later retreated from strong advocacy but maintained the possibility. Considering the morphological evidence noted above, a more typical position of the gland in *S. acutus* seems likely. The hypothesized relationships of the nasal-gland groove to the nasolacrimal canal obtain in these crocodylomorphs, although the rostral ostium of the canal was not observed conclusively in *Dibothrosuchus elaphros,* and most of the thalattosuchians examined for this study appear to lack the nasolacrimal canal.

For *Postosuchus kirkpatricki,* Chatterjee (1985: fig. 3) figured a ventromedial groove or recess running rostrally to the naris along the suture between the nasal and the maxilla and lacrimal. TTUP 9000 shows that the groove is real but has been accentuated and rendered ragged due to breakage. Walker (1961) described prominent depressions in the ventral surfaces of the nasals of *Stagonolepis robertsoni* (BMNH R8586), which extend slightly onto the prefrontals and frontals and continue rostrally to the nares as grooves; he regarded these structures as being produced by the nasal glands, and I agree. Furthermore, Parrish (1994) described for the stagonolepidid *Longosuchus meadei* a large groove extending caudally from the naris in the suture between nasal, maxilla, lacrimal, and prefrontal. The caudal portion of this groove is indeed probably a "nasolacrimal groove" (i.e., for the nasolacrimal duct) as labelled by Parrish (1994), but the rostral portion has all the features of a nasal gland groove. In extant crocodilians, the nasal gland often assumes the same general trajectory rostrally that the nasolacrimal duct has more caudally (Fig. 6A; Witmer, 1995b); such a situation in *L. meadei* would explain such a large groove extending from orbit to naris.

Dinosauria—The osteological correlates of a nasal gland are relatively clear in a few non-avian dinosaurs. For example, the right nasal of the ornithopod ornithischian *Hypsilophodon foxii* (BMNH R2477) displays a ventrolateral sulcus just medial to the lacrimal articulation; the sulcus is broad caudally near the articulation of the nasal with the frontal and prefrontal and narrows rostrally to a groove extending to the ventrolateral edge of the naris. Similarly, the prosauropod saurischian *Plateosaurus engelhardti* (AMNH 6810) exhibits a shallow medial concavity along the dorsal margin of the lacrimal bone. Unfortunately, the nasal is missing in this area, but, more rostrally, it displays a narrow but distinct groove leading from the area of the lacrimal sulcus to the margin of the naris not far from the nasomaxillary suture. In both *Hypsilophodon foxii* and *Plateosaurus engelhardti,* the grooves and sulci are clearly medial to the nasolacrimal canal.

The Cretaceous birds *Ichthyornis dispar* (YPM 1450), *Hesperornis regalis* (KUVP 71012, YPM 1206), and *Parahesperornis alexi* (KUVP 2287) clearly display the supraorbital position of the gland that is found in most extant marine birds (Marsh, 1880), as evidenced by very characteristic excavation of the frontal bone. Similarly, Gauthier (1986) suggested that the fine grooves and small foramina in the lateral edge of the frontal bone in certain non-avian maniraptoran theropods (e.g., *Troodon formosus*; see Currie, 1985:fig. 1a) were perhaps evidence for a bird-like supraorbital nasal gland. The structure is indeed suggestive, although the course of the duct is uncertain. The early troodontid *Sinornithoides youngi* apparently lacks these features (Russell and Dong, 1994). At least in *Allosaurus fragilis* (UUVP 2133, 5814; see also Madsen, 1976b) and some tyrannosaurids (RTMP 83.30.1), the lacrimal has a dorsomedial foramen caudally near the prefrontal articulation that opens into the rostrodorsal portion of the orbit; the foramen leads into a canal opening into the cavity in the body of the lacrimal. This canal could be for the duct of a supraorbital nasal gland, although the course of the duct would be a little different from that in birds, passing through the lacrimal rather than medial to it (Fig. 6C). The nasal fenestra of *Syntarsus* spp. (Raath, 1977; Rowe, 1989) was interpreted by Rowe (1989) as possibly for the nasal gland, which could point to a supraorbital position in this ceratosaurian as well. If such structure is discovered in other theropods, it is possible that the supraorbital position of the gland observed in birds may characterize a more inclusive group of theropods (Fig. 6C), perhaps at the level of Tetanurae or even Theropoda. It should be noted, however, that some taxa (e.g., *Deinonychus antirrhopus,* YPM 5232; *Dromiceiomimus brevitertius,* CMN 12228) definitely lack any of the canals or fenestrae noted above. Nevertheless, several non-avian theropods (e.g., *Dilophosaurus wetherilli,* UCMP 77270; *Allosaurus fragilis,* UUVP 3839; *Deinonychus antirrhopus,* MOR 747) show the more conventional osteological correlates specified earlier, namely, shallow internal grooves on the nasals leading to the naris.

Two workers have proposed explicit alternatives for the position of the nasal gland in some or all dinosaurs. Osmólska (1979) reconstructed the nasal gland in the rostroventral portion of the nasal vestibule (i.e., within the premaxilla) of many fossil archosaurs. Similarly, Whybrow (1981) argued that the caudal portion of the circumnarial depression in hadrosaurines and the lateral diverticula of the crests of lambeosaurines were associated with salt glands. Although these possibilities cannot be ruled out for some unknown gland, neither situation accords well with the topographical relationships observed for the glandula nasalis in extant archosaurs and other sauropsids in which the gland is situated just external to the nasal cavity proper rather than within the nasal vestibule.

Conclusions

The hypothesis posed earlier survives testing, and we may infer with confidence (i.e., a level I inference) in the common ancestor of Archosauria the presence of a nasal gland with the general topographic relationships observed in extant archosaurs. The osteological correlates of the gland were found in virtually all major clades of fossil archosaurs that were examined and thus the hypothesis is congruent with the pattern of archosaur phylogeny. It may be noted at this point that similar bony features also were observed in the non-archosaurian archosauriform *Erythrosuchus africanus* (BMNH R3592) and figured by Young (1964) for the erythrosuchid *Shansisuchus shansisuchus,* and thus they may characterize a more inclusive group.

In all cases, the inferred positions of the nasal gland and its ducts are distinct from the antorbital fenestrae and antorbital fossae. In other words, none of the osteological correlates involve the bony structures of the antorbital cavity. Although the nasal gland was indeed one of the soft-tissue contents of the antorbital cavity, the hypothesis that the antorbital cavity as a whole was associated with the nasal gland is without any positive evidence and hence is untenable. The only option left is that some unknown gland occupied the antorbital cavity, filling the antorbital fossa and causing the fenestra. Such a hypothesis would require loss of this gland in both crocodilians (which retain the antorbital cavity) and birds (which retain cavity, fenestra, and fossa). Furthermore, the hypothesis is untestable in the fossil forms since the osteological correlates of an unknown gland also must be unknown. In conclusion, there is absolutely no reason to interpret the antorbital fenestrae and cavity as having originated or been maintained to house a glandular structure.

HYPOTHESIS 2: THE ANTORBITAL CAVITY HOUSES A MUSCLE

Historical Development

The first hypothesis suggested for the function of the antorbital fenestra and fossa is that it was associated in some way with the jaw musculature (Dollo, 1884). This notion has held sway ever since (Gregory and Adams, 1915; Adams, 1919; Gregory, 1920, 1951; Camp, 1930; Janensch, 1935–36; Anderson, 1936; Walker, 1961; Molnar, 1973; Galton, 1973, 1974; Krebs, 1976; Bakker, 1986; Paul, 1987, 1988a; Bakker et al., 1988, 1992; Horner and Lessem, 1993). Briefly, the muscular hypothesis states that a portion of the jaw adductor musculature passes through the internal antorbital fenestra to attach to or "bulge" into the antorbital cavity. Ironically, there never has been much direct evidence offered in support of the muscular hypothesis. In many respects, the hypothesis stems from the elegant and attractive idea that all skull fenestration can be explained based on a single feature, i.e., the expansion of the adductor musculature (Gregory and Adams, 1915). As Gregory (1920: 125) noted, "the general resemblance of the antorbital fenestra to the lateral temporal fenestra [of the parasuchian *Mystriosuchus planirostris*], which is known to be a muscle fossa, is very evident."

However, in its original formulation (Dollo, 1884), the argument was based on indirect associations. According to Dollo, lizards are "temporalis-(M. adductor mandibulae externus-) dominant" and possess certain features (sagittal crests, coronoid processes, large dorsotemporal fossae, etc.) whereas crocodilians are "pterygoideus-dominant" and lack these features. Thus, since some dinosaurs (e.g., *Iguanodon bernissartensis* and *"Diclonius mirabilis"* [*Anatotitan copei*]) possess the attributes of "temporalis-dominant" animals and either have small antorbital fenestrae or lack them, and other dinosaurs (e.g., *Ceratosaurus nasicornis* and *Diplodocus longus*) resemble "pterygoideus-dominant" animals and have well-developed antorbital fenestrae, the antorbital fenestra must be associated with large pterygoideus musculature.

Dollo's argument received no critical treatment in subsequent presentations of the muscular hypothesis. Instead, the argument focused on two areas (Witmer, 1987b): the biomechanical "necessity" of a large muscle originating on the snout (Walker, 1961; Bakker, 1986; Paul, 1988a) and the presence of just such a muscle in crocodilians (Adams, 1919; Anderson, 1936). Again, paraphyletic treatment of archosaurs (i.e., excluding birds) has compromised the resulting interpretations.

Implications of the Muscular Hypothesis

A muscle-related antorbital fenestra and fossa is such a pervasive notion that it is worthwhile to examine its implications briefly before testing the hypothesis with the EPB approach. For example, the fact that a nasal cavity must both exist and function seems to be overlooked in some formulations of the muscular hypothesis. If a muscle completely filled the antorbital cavity and fossa of a narrow-snouted archosaur such as *Coelophysis bauri* (Bakker, 1986) or *Postosuchus kirkpatricki,* then there would be simply no room to accommodate the nasal cavity and capsular structures such as the nasal conchae. Parasuchians present a striking example. Camp (1930; see also Anderson, 1936) suggested that the median cavity within the premaxillae rostral to the nares was filled with muscle in parasuchians. If this were the case, the contralateral muscles together would have formed a sling-like sphincter, constricting the nasal capsule with each contraction—certainly an unlikely arrangement. Furthermore, in many formulations, such as Janensch's (1935–36), the muscle would have to pass over, and thus occlude, the choana.

Another problem involves the architecture of the bones forming the internal antorbital fenestrae. As mentioned, the superficial appearance sometimes resembles that of known muscular fossae such as that surrounding the laterotemporal fenestra. However, the two fossae differ in detail in that the laterotemporal fenestra has rounded, heavily buttressed edges whereas the internal antorbital fenestra often has thin, delicate, sharp edges. A muscle passing through the internal antorbital fenestra could attach to the maxillary antorbital fossa with little apparent problem, but would have to curve around the rostral border of the lacrimal and pass caudally to fill the lacrimal antorbital fossa. However, the rostral border of the lacrimal is often bladelike (e.g., *Ornithosuchus longidens,* BMNH R3143) and sometimes paper-thin (e.g., *Lesothosaurus diagnosticus,* BMNH R11956, RUB17, R8501; see Fig. 7), and does not seem competent to resist muscular stresses.

A different course for the muscle was suggested by Galton (1974) for *Hypsilophodon foxii,* passing not through the internal antorbital fenestra but rather through an opening interpreted here as a neurovascular canal (see below and Fig. 8). Galton (1974) also reconstructed a portion of the adductor musculature (the ventral pterygoideus) as passing through the suborbital fenestra to attach within the antorbital cavity, but the suborbital fenestra does not transmit muscle in this manner in any sauropsids, so this idea can be safely discounted.

Some archosaurs (e.g., some large pterodactyloid pterosaurs and some theropods) have cavities and chambers associated with their lacrimal and/or maxillary antorbital fossae. The septa within these chambers seem ill-equipped to withstand the forces of muscular contraction. In fact, the entire structure of the snout of some archosaurs seems too frail to withstand such loads. For example, Bakker (1986: 262) regarded the enormous antorbital fenestrae of *Coelophysis bauri* and the pterosaur *Dimorphodon macronyx* as filled with an equally enormous muscle. Considering the thin bars of bone of which these skulls are constructed, such a muscular system probably would not have had the opportunity to contract more than once!

As alluded to earlier, the impetus for the notion of a muscular antorbital cavity historically has come more from theory than empirics, invoking the "need" for a large muscle originating on the snout. Walker (1961) articulated this argument most clearly, and it has been summarized previously (Witmer, 1987b). Bakker (1986) and Paul (1988a) also believed a large antorbital muscle was necessary for rapid adduction of the mandible, "snapping" the jaws shut. Many of Ewer's (1965) criticisms of Walker's formulation are on target, but the point here is that even if formal biomechanical analysis predicts a large muscle, that prediction alone is insufficient to reconstruct the muscle within the antorbital fenestra and fossa.

The Extant Phylogenetic Bracket

Only a single candidate for the "antorbital muscle" has been proposed: a rostral portion of M. pterygoideus, in particular, M. pterygoideus, pars dorsalis (or simply "dorsal pterygoideus"). The muscle has had several different designations over the years (e.g., M. adductor mandibulae internus pterygoideus anterior, M. pterygoideus internus, M. pterygoideus anterior, pterygoideus D), but its homology among sauropsids is generally unquestioned (Adams, 1919; Lakjer, 1926; Lubosch, 1933; Edgeworth, 1935; Kesteven, 1945; see also Witmer, 1995b). The precise hierarchical level within Sauropsida at which division into dorsal and ventral portions of the muscle occurred is unclear, yet all workers agree that extant birds and crocodilians have a homologous dorsal pterygoideus muscle (Witmer, 1995b). As will be seen, the maxillary division of the trigeminal nerve figures into the argument, and its homology across Vertebrata also is unquestioned (Witmer, 1995b). In extant archosaurs, the size of the nerve varies greatly, being reduced in most neornithine birds in association with reduction of the maxillary bone and loss of the teeth (Witmer, 1995b) but remaining large in crocodilians. The maxillary nerve carries general somatic afferent fibers (as well as postganglionic autonomic fibers from the sphenopalatine ganglion; Bubien-Waluszewska, 1981) and is not to be confused with the pterygoideus nerves, which are motor branches of the mandibular division of the trigeminal nerve.

Extant Crocodilians—The adductor muscles of extant crocodilians have been studied extensively (Schumacher, 1973; Busbey, 1989). The rostral attachments of the muscle are briefly described below (Fig. 6A), based mostly on original dissections (for details see Witmer, 1995b). The dorsal pterygoideus is a very large muscle passing dorsally over the palatal bones, ventral to the eyeball, and through the postnasal fenestra to fill the caudolateral portion of the antorbital cavity. It attaches to or is in contact with the pterygoid, ectopterygoid, jugal, maxilla, palatine, prefrontal, lacrimal, interorbital septum, and the caudolateral surface of the postconcha (a portion of the cartilaginous nasal capsule). Rostrally, the muscle tapers to a point where it attaches to the maxilla just lateral to the ostium of the caviconchal paranasal air sinus. The maxillary nerve and accompanying vessels travel through the orbit over the dorsal surface of the muscle (Fig. 6A), passing to the muscle's rostral tip where they enter a large foramen within the maxilla just lateral to the caviconchal sinus ostium (see Witmer, 1995b). Thus, in extant crocodilians, M. pterygoideus, pars dorsalis is indeed one of the contents of the antorbital cavity and, in fact, fills the caudolateral portion of the cavity.

Extant Birds—As in crocodilians, the dorsal pterygoideus of birds is usually a large muscle, although its size varies greatly (see Witmer, 1995b and references therein for variations). In general, the muscle originates from the dorsolateral surfaces of the palatine and pterygoid bones (Fig. 6B). Since the ectopterygoid bone and transverse pterygoid flange have been lost in birds (at least above the phylogenetic level of *Archaeopteryx lithographica*; Witmer and Martin, 1987; Elzanowski and Wellnhofer, 1996), the muscle fibers extend in a relatively straight line caudoventrally to the mandible, rather than curving around the palatal bones as they do in crocodilians. The rostral attachment on the palatine often reaches the caudoventral portion of

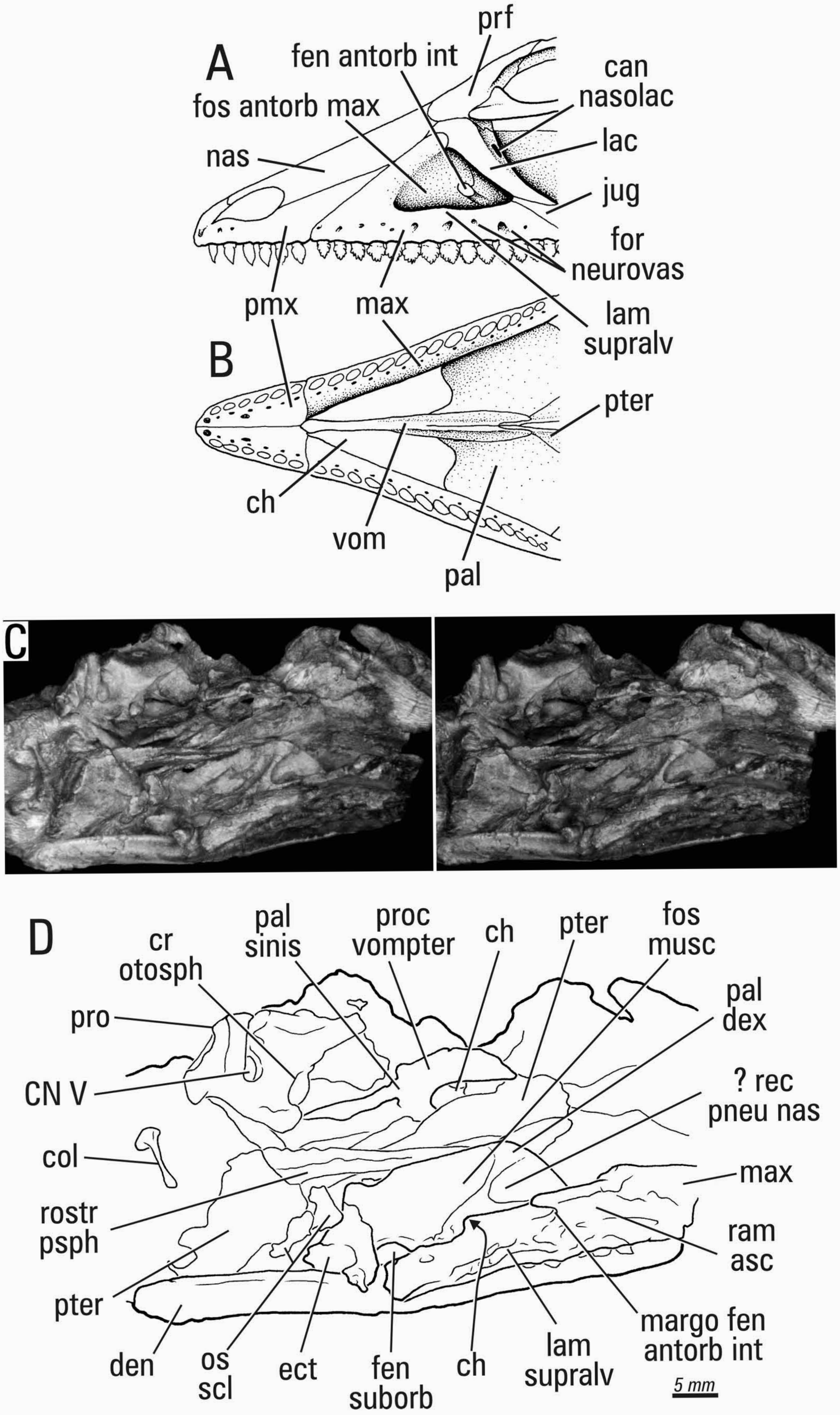

FIGURE 7. *Lesothosaurus diagnosticus,* facial skeleton. **A**, rostral part of skull in left lateral view. **B**, same in ventral view. **C**, stereophotographs of BMNH RUB 17 in right caudodorsolateral view, showing the palatal elements. **D**, interpretive drawing of **C**. (**A**,**B** modified after Sereno, 1991a.)

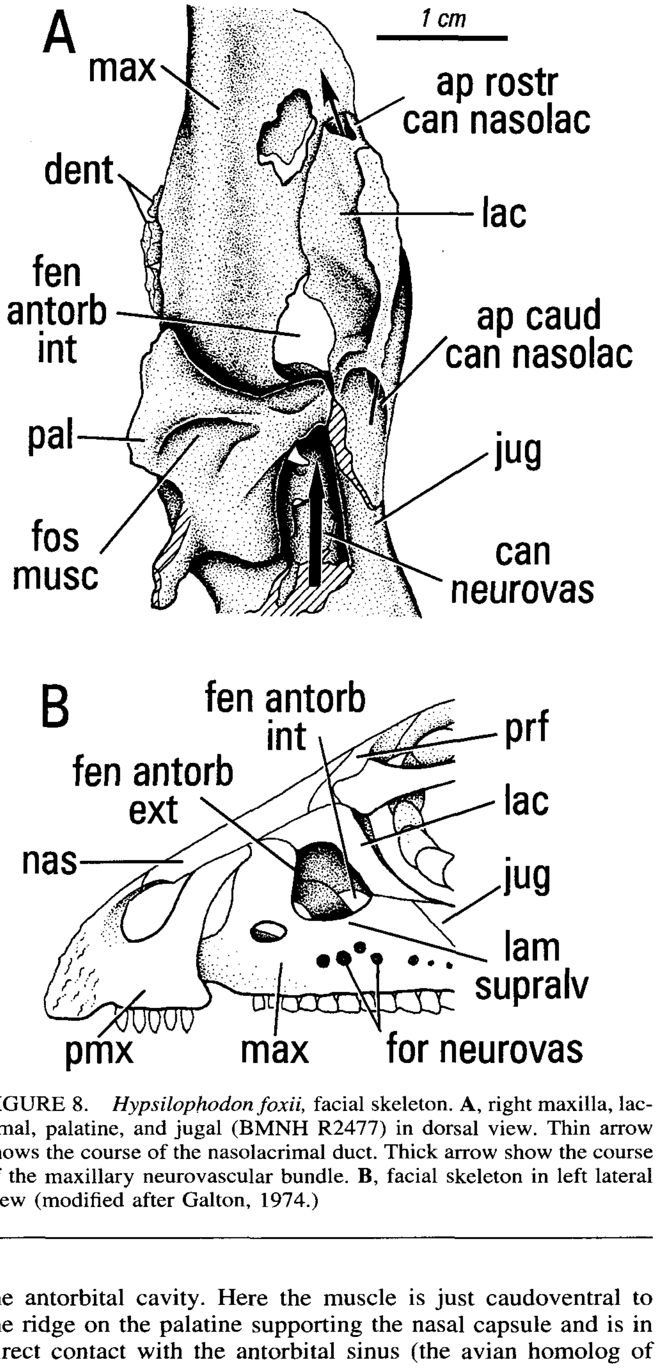

FIGURE 8. *Hypsilophodon foxii*, facial skeleton. **A**, right maxilla, lacrimal, palatine, and jugal (BMNH R2477) in dorsal view. Thin arrow shows the course of the nasolacrimal duct. Thick arrow show the course of the maxillary neurovascular bundle. **B**, facial skeleton in left lateral view (modified after Galton, 1974.)

the antorbital cavity. Here the muscle is just caudoventral to the ridge on the palatine supporting the nasal capsule and is in direct contact with the antorbital sinus (the avian homolog of the caviconchal sinus of crocodilians; see below and Witmer, 1995b). For much of its length, the muscle is just ventral to the suborbital diverticulum of the antorbital sinus (Witmer, 1990), and this air sac separates the pterygoideus from the other jaw muscles. As in crocodilians, the dorsal pterygoideus is ventral to the maxillary nerve (Fig. 6). In some cases (e.g., *Gallus gallus*), the neurovasculature closely adheres to the muscle, whereas in other cases (e.g., *Anser anser*) the nerve is dorsal to the muscle, suspended within the suborbital diverticulum by a double-walled, epithelial fold, a pneumatic "mesentery."

Dollo (1884) reported that in birds the pterygoideus muscles attach to the rostral border of the antorbital cavity, but this is not the case in the birds I have personally dissected and appears not to have been reported otherwise in the literature. In a very few birds, a tendinous slip may contact the caudoventral tip of the maxilla (Lakjer, 1926) or the palatal process of the maxilla (Hofer, 1950; Burton, 1984), but this is a rare condition. Thus the dorsal pterygoideus muscle of birds is indeed often one of the contents of the antorbital cavity, but never originates from any of the margins of the antorbital fenestrae.

Osteological Correlates—The osteological correlates of M. pterygoideus, pars dorsalis are more consistent in crocodilians than in birds. In crocodilians, the medial surfaces of the jugal and maxilla tend to have a patchy striated or punctate pattern that increases somewhat in relief rostrally. The palatine usually has a raised dorsal ridge extending near the lateral edge rostral to the prefrontal articulation; this ridge marks the boundary between postconchal cartilage medially and the dorsal pterygoideus laterally. The bones surrounding the suborbital fenestra may display a slight excavation where the muscle attaches, but this fossa is usually weak and is absent in many individuals of *Crocodylus* spp. Thus, the direct evidence in crocodilians for the presence of a dorsal pterygoideus is strongest rostrally where the muscle attaches to the maxilla, jugal, and palatine. In birds, probably because of their small size, the muscle often leaves little evidence on the bone. Unlike crocodilians, the avian dorsal pterygoideus originates only from the palatine and pterygoids, never from the jugal and almost never from the maxilla. The rostral attachment sometimes excavates a fossa on the dorsolateral surface of the palatine near the choana.

To determine if bony surfaces could be examined directly to ascertain if muscles were attached to them, bone samples from *Alligator mississippiensis* and *Anser anser* were examined by means of scanning electron microscopy. Samples came from surfaces known to be adjacent to gland, muscle, or air sac. The results indicated that bony surfaces are highly variable in these animals, and surface textures are not reliable indicators of the adjacent soft tissues (although surface features usually are). Although samples occasionally had the predicted surface-texture pattern (e.g., Sharpey-fiber bone for muscle [Jones and Boyde, 1974] or uniformly smooth bone for gland and air sac), very often a sample showed the reverse pattern.

Muscles are generally potent and well-understood functional matrices (sensu Moss, 1968, 1971). However, the ambiguity of the direct osteological correlates in both birds and crocodilians may reflect their archosaurian heritage in that their muscles are less likely to produce reliable bony evidence (i.e., scars) than those of, for example, mammals (Bryant and Seymour, 1990, and references therein). It also reflects the small sizes of virtually all the birds and many of the crocodilians in the sample. It was found that, in the more or less complete ontogenetic series available for this study (e.g., *Alligator mississippiensis, Crocodylus porosus, Struthio camelus, Anser anser, Gallus gallus*), older (and hence larger) individuals had more deeply etched muscle scars.

Nevertheless, despite these ambiguities, extant birds and crocodilians do have similarities that can be hypothesized to have been present in their common ancestor. For example, in both groups of extant archosaurs, the dorsal pterygoideus is a relatively large muscle originating from the dorsal or dorsolateral surfaces of the pterygoid and palatine. The attachment on the palatine bone extends into the caudal portion of the antorbital cavity and usually excavates a fossa. This muscular fossa on the palatine is sometimes separated by a bony ridge from a fossa for the cartilaginous nasal capsule, the muscular fossa being generally caudoventrolateral to the nasal fossa. In neither group does the muscle fill the entire antorbital cavity, but rather is restricted to the caudal portion of the cavity, behind a homologous air sac (the crocodilian caviconchal sinus and avian antorbital sinus; see below and Witmer, 1995b).

Direct information regarding the extent and position of the muscle can be obtained by making use of the fact that in both birds and crocodilians (indeed in all sauropsids) the maxillary nerve always travels dorsal to the pterygoideus musculature (Fig. 6A, B). Thus, the position of the foramen or groove for the maxillary nerve (or neurovascular bundle, since vessels accompany the nerve) provides a sensitive guide to the maximal dorsal extent of the muscle. In crocodilians, the dorsal pterygoideus fills the caudal part of the antorbital cavity, and the foramen is dorsally situated. In birds, the dorsal pterygoideus is restricted to the palatine bone at the caudoventral corner of the antorbital cavity, and the maxillary nerve traverses a foramen or gap between maxilla and palatine. Despite the difference in size and apparent position of the muscle, the position of the maxillary neurovascular foramen faithfully indicates the muscle's general location.

The Hypothesis

Given these correspondences between the components of the extant phylogenetic bracket, we may hypothesize that the common ancestor of Archosauria had a large M. pterygoideus, pars dorsalis that had the following characteristics: (1) it originated from the palatine and pterygoid and probably excavated a fossa on the palatine, and (2) it was situated ventral to the maxillary neurovascular foramen and/or grooves, indicating that the muscle was restricted to the caudoventral portion of the antorbital cavity. This hypothesis is tested by searching for the osteological correlates in the other, extinct descendants of the common ancestor.

Testing the Hypothesis

There is abundant evidence in most major clades of fossil archosaurs for the presence and general position of a dorsal pterygoideus muscle. As will become apparent, most fossil archosaurs resemble extant birds more than crocodilians. As a result, crocodylomorphs deserve special attention.

Crocodylomorpha—In many fossil crocodylomorphs, the prefrontal bone has a transversely broad flange that projects far ventrally into the postnasal fenestra (Fig. 1) diverting any musculature ventrally and creating a cavity rostral to it within the nasoantorbital cavity. This prefrontal flange is found in *Dibothrosuchus elaphros* (IVPP V 7907; Wu and Chatterjee, 1993), *Sphenosuchus acutus* (Walker, 1990), *Protosuchus richardsoni* (UCMP 130860; Clark, 1986), all thalattosuchians examined for this study, and *Theriosuchus pusillus* (BMNH 48330), among others, and is probably primitive for Crocodylomorpha if not a more inclusive group (it is somewhat developed in the stagonolepidids *Desmatosuchus haplocerus* [TTUP 9023] and *Stagonolepis robertsoni* [Walker, 1961], but apparently not in *Postosuchus kirkpatricki* [TTUP 9000, 9002]). In many of these (e.g., *Protosuchus richardsoni, Pelagosaurus typus* [BMNH 32599], *Metriorhynchus superciliosus* [BMNH R3900], *Theriosuchus pusillus*), the prefrontal flange is a delicate, thin plate that appears too fragile to serve as area for adductor muscle attachment; rather, it probably supported the nasal capsule. Thus, the muscle was probably displaced ventrally relative to extant crocodilians.

The suborbital fenestra also provides some measure of the rostral extent of the muscle. In basal crocodylomorphs (sphenosuchians and protosuchians), the suborbital fenestra, at most, barely reaches into the antorbital cavity. In *Sphenosuchus acutus,* there is a distinct muscular fossa on the dorsal surface of the palatine, just rostral to the suborbital fenestra (Walker, 1990: fig. 3b); the area rostral to this crest is probably associated with the nasal cavity in some way. In most mesoeucrocodilians, however, the suborbital fenestra—and presumably the dorsal pterygoideus—is carried farther into the antorbital cavity. In some thalattosuchians (e.g., *Metriorhynchus superciliosus,* BMNH R2048), there is a tapering fossa or groove on the dorsal surface of the palatine rostral to the suborbital fenestra, whereas in others (e.g., *Pelagosaurus typus*) there is little direct evidence of the muscle.

With regard to the maxillary neurovasculature, Walker (1990) described and figured for *Sphenosuchus acutus* a large medial foramen and groove in the body of the maxilla just internal to the antorbital fenestra and dorsal to the palatine, suggesting that, as in birds, the muscle was restricted to the caudoventral aspect of the antorbital cavity. Similarly, in the protosuchian *Shantungosuchus hangjinensis* (Wu, Brinkman, and Lü, 1994) and the thalattosuchians *Pelagosaurus typus* (BMNH 32599, 32607) and *Metriorhynchus superciliosus* (BMNH R3900), the maxillary neurovascular foramina enter the medial surface of the bone ventral to the antorbital fenestra. In *Sebecus icaeorhinus* (AMNH 3160), the neurovascular foramina also enter the maxilla internally just dorsal to the teeth, suggesting limited dorsal extent of the dorsal pterygoideus, which is in agreement with Colbert's (1946a) reconstruction of that muscle.

Thus, basally in crocodylomorphs, there is good evidence that the dorsal pterygoideus did not extend beyond the caudoventral portion of the antorbital cavity. Although this study has not sought to determine at which level in Crocodylomorpha the modern condition appeared, it may coincide with loss or transformation of the descending transverse flange of the prefrontal. Alternatively, it may coincide with the appearance of the morphogenetic rotation of the nasal cavity (Witmer, 1995b) that, in extant crocodilians, brings the neurovasculature to a dorsal position in the snout relative to its primitive, more ventral position.

Other Crurotarsi—There appear to be two types of putative muscular fossae on the dorsal surfaces of the palatine bones in other crurotarsan archosaurs. In the first type (found also in the crocodylomorph *Sphenosuchus acutus* [Walker, 1990]), there is a well defined fossa just rostral to and clearly associated with the suborbital fenestra. *Stagonolepis robertsoni* has this type of fossa, clearly possessing (BMNH R8582) a dorsal excavation of the palatine rostral to the suborbital fenestra that strongly undercuts the rostral portion of the palatine and curves onto the pterygoid and maxilla (Fig. 9C). The rostral portion of the palatine also has a fossa that must be associated with the nasal cavity in some way. It floors the antorbital cavity caudal to the choana in *S. robertsoni,* but in *Desmatosuchus haplocerus* (TTUP 9023) this rostral portion of the palatine appears to extend rostrally lateral to the choana to attach to the ascending ramus of the maxilla, forming a partial rostromedial wall to the antorbital cavity. Furthermore, in *Longosuchus meadei,* processes from the lacrimal and prefrontal essentially close the postnasal fenestra, preventing any substantial muscular incursion into the antorbital cavity (Parrish, 1994). Thus, stagonolepidids would seem to have had a caudoventrally restricted dorsal pterygoideus.

In the second type of muscular fossa on the palatine, the fossa appears to extend rostrally all the way up to the choana, resembling the situation in birds. This condition characterizes many groups of archosaurs and may well be the primitive condition although the situation in many nonarchosaurian archosauriforms is unknown and is equivocal for many archosaurs. *Ornithosuchus longidens* (BMNH R3143; see also Walker, 1964) has this type of fossa, displaying a large excavation on the dorsal surfaces of the palatine and pterygoid bones extending rostrally up to and undercutting a strong, elevated ridge or strut bordering the choana (Fig. 10C). This postchoanal strut itself is grooved, presumably for attachment of the cartilaginous nasal capsule. Parasuchians also show this condition, usually with the maxilla also contributing to the floor of the antorbital cavity. In most parasuchians (e.g., *Pseudopalatus pristinus,* AMNH 7222; well figured by Case [1929: fig. 16] and Camp [1930: fig. 33]), the palatine and vomer are drawn up dorsally behind the choana into a spout-like structure directed toward the naris. The conjoined transverse postchoanal crests of the vomer and palatine often trend caudolaterally, delimiting a fos-

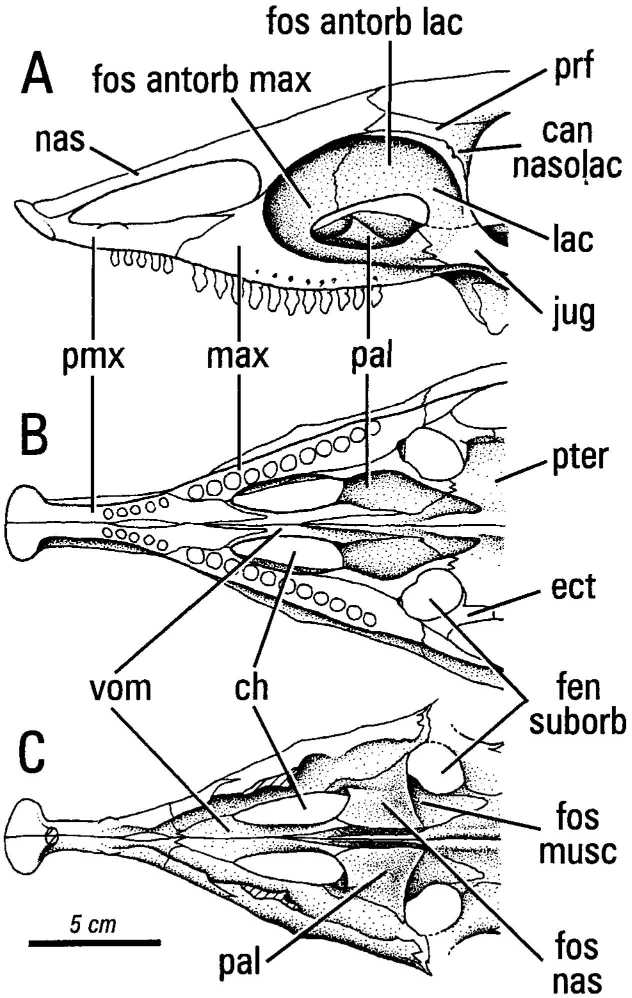

FIGURE 9. *Stagonolepis robertsoni,* facial skeleton. **A**, left lateral view. **B**, ventral view. **C**, dorsal view of the palate. (Modified from Walker [1961] and specimens).

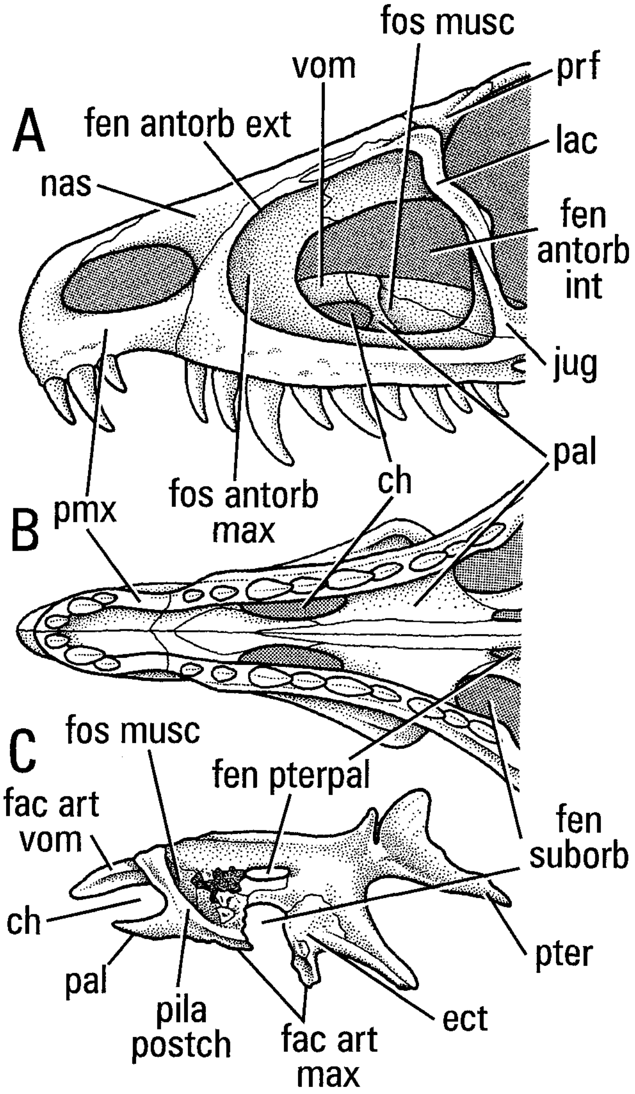

FIGURE 10. *Ornithosuchus longidens,* facial skeleton. **A**, left lateral view. **B**, ventral view. **C**, dorsolateral view of right side of palate (BMNH R3143). (Modified from Walker [1964] and specimens.)

sa, here interpreted as a muscular fossa. A final non-dinosaurian example is the poorly known "*Pallisteria angustimentum*" (BMNH unnumbered; still a nomen nudum, regarded as "Thecodontia incertae sedis" by Carroll [1988]). "*P. angustimentum*" has a large dorsal fossa on the palatine and pterygoid that extends up to the choana under almost the entire antorbital cavity, suggesting an extensive (or at least long) muscle.

Thus, in this latter group, it might seem that because an extensive dorsal pterygoideus was present in much of the antorbital cavity, perhaps it may have even extended beyond the floor and onto the adjacent fossa surrounding the antorbital fenestra. However, the morphological details in these taxa make this unlikely. In *Ornithosuchus longidens,* for example, the strong postchoanal strut on the palatine extends caudolaterally along its contact with the maxilla, overhanging and providing a rostrolateral border to the muscular fossa (Fig. 10C). Similarly, in "*Pallisteria angustimentum,*" the maxilla projects dorsomedially along its palatine contact, overhanging the muscular fossa. Thus, in these taxa, the muscular fossa was in a topological domain within the antorbital cavity that was separate from the fenestral region.

The course of the maxillary neurovasculature is apparent in many of the above forms. In *Stagonolepis robertsoni* (BMNH R4787), there is a broad groove on the dorsal surface of the body of the maxilla medial to the lacrimal and jugal articulations that narrows rostrally as it leads into a foramen located at the mid-length of the internal antorbital fenestra. Farther rostrally, there is another, larger foramen within a fossa in the base of the caudal surface of the ascending process (also visible in BMNH R8582). The poposaurid (or rauisuchid; see Galton, 1985a; Benton, 1986; Parrish, 1993) *Teratosaurus suevicus* (BMNH 38646) exhibits a large medial foramen in the maxilla within a depression below the antorbital fenestra and dorsal to the palatine contact. Sill (1974) reported and figured for the prestosuchid *Saurosuchus galilei* a similar medial foramen in the body of the maxilla, as did Dutuit (1979) for an unnamed Moroccan form. For *Prestosuchus chiniquensis,* Azevedo (1995) did not discuss the specific skeletal features of interest here but reconstructed the dorsal pterygoideus as being restricted to the caudoventral portion of the antorbital cavity, well away from the internal antorbital fenestra. Among parasuchians, specimens referred to *Phytosaurus cylindricodon* (BMNH 38039, 38040) and *Rutiodon carolinensis* (AMNH 4) exhibit medial foramina leading into large canals running within the maxillae just ventral to the antorbital fenestra and probably ex-

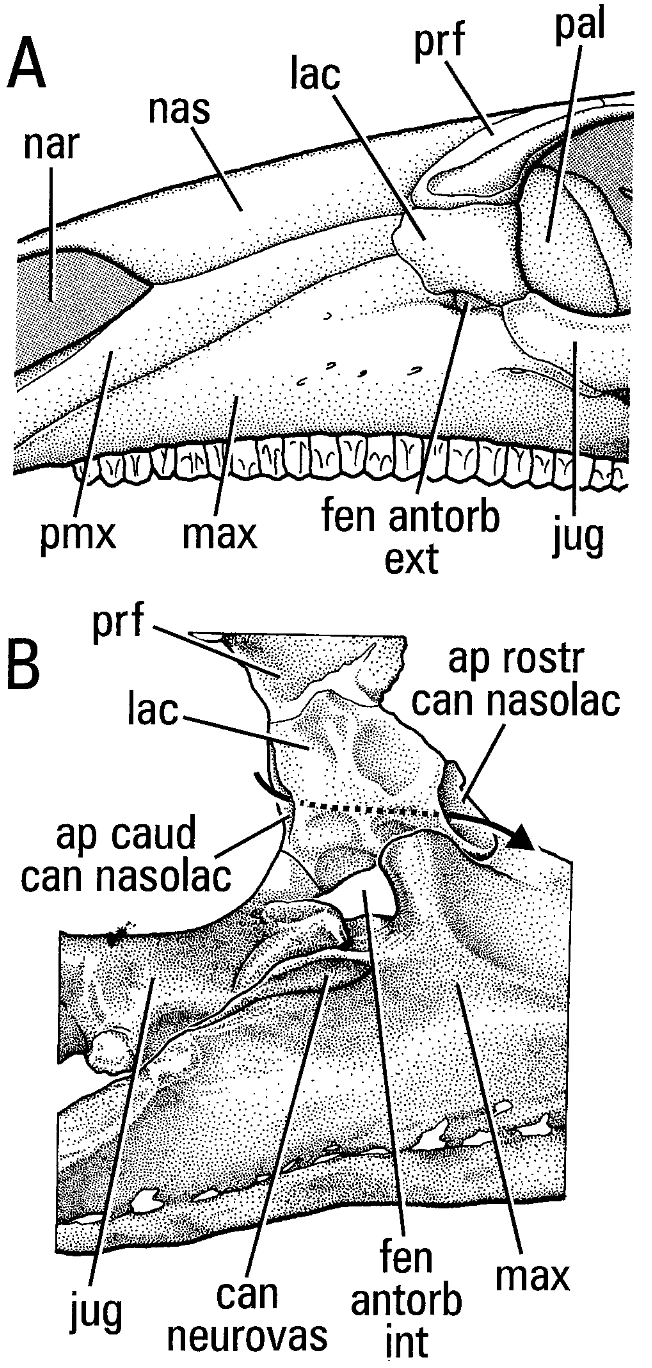

FIGURE 11. *Iguanodon atherfieldensis,* facial skeleton. **A**, Snout in left lateral view (modified from Norman,1986). **B**, left maxilla, jugal, lacrimal, and prefrontal of BMNH R5764 in medial view. Arrow shows the course of the nasolacrimal duct.

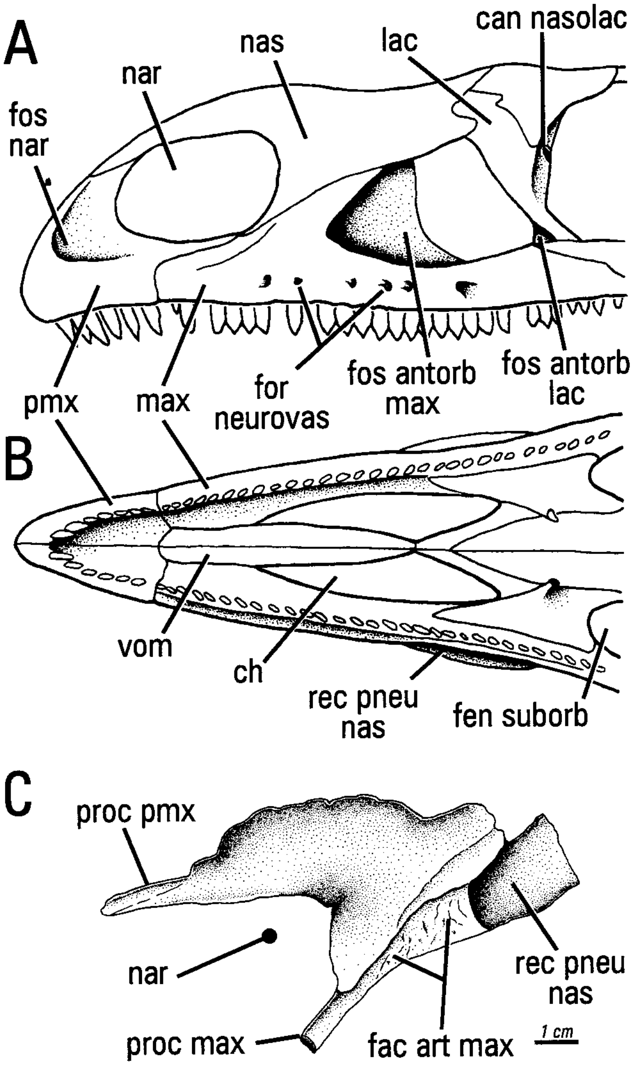

FIGURE 12. *Plateosaurus engelhardti,* facial skeleton. **A**, reconstruction of snout in left lateral view. **B**, same in ventral view. **C**, right nasal of AMNH 6810 in ventromedial view. **D**, stereophotographs and interpretive drawing of right maxilla, lacrimal, and palatine of AMNH 6810 in dorsal and somewhat medial view. The nasal recess shown in **C** caps the hiatus in **D**. **A,B** modified after Galton (1990).

tending into the premaxillae as well. These foramina and canals likely conveyed branches of the maxillary nerve and accompanying vessels. Their positions dorsal or dorsolateral to the putative muscular fossa on the palatine are consistent with the dorsal pterygoideus muscle being restricted to the floor of the antorbital cavity.

Dinosauria—Among Ornithodira, comparable data are abundant for dinosaurs, but less so for other taxa. Good material is available for the basal members of many of the major clades of Ornithischia (Sereno, 1986). The basal ornithischian *Lesothosaurus diagnosticus* (Weishampel and Witmer, 1990a; Sereno, 1991a) provides information on both the existence and position of a dorsal pterygoideus and the course of the maxillary neurovasculature. The dorsal surface of the palatine (BMNH R8501, RUB17) has a well developed excavation extending rostrally up to the lateral aspect of the choana (Fig. 7C, D). This excavation is here interpreted as a muscular fossa and is bounded rostrally by a strong ridge that extends from the maxillary contact (where it borders the choana) rostrodorsomedially to the contact with the vomer. The palatine (BMNH RUB17) has an additional deep fossa rostral to this ridge and dorsomedial to the choana and directly opposite the internal antorbital fenestra that must be associated with either the nasal or antorbital cavity. The muscular fossa is restricted to the caudoventral portion of the antorbital cavity. The proximity of the ridge bordering the fossa to the medial edge of the lacrimoprefrontal wall (BMNH R8501) suggests that the postnasal fenestra was narrow in this area and would make rostral passage of a muscular slip unlikely. The course of the maxillary neurovas-

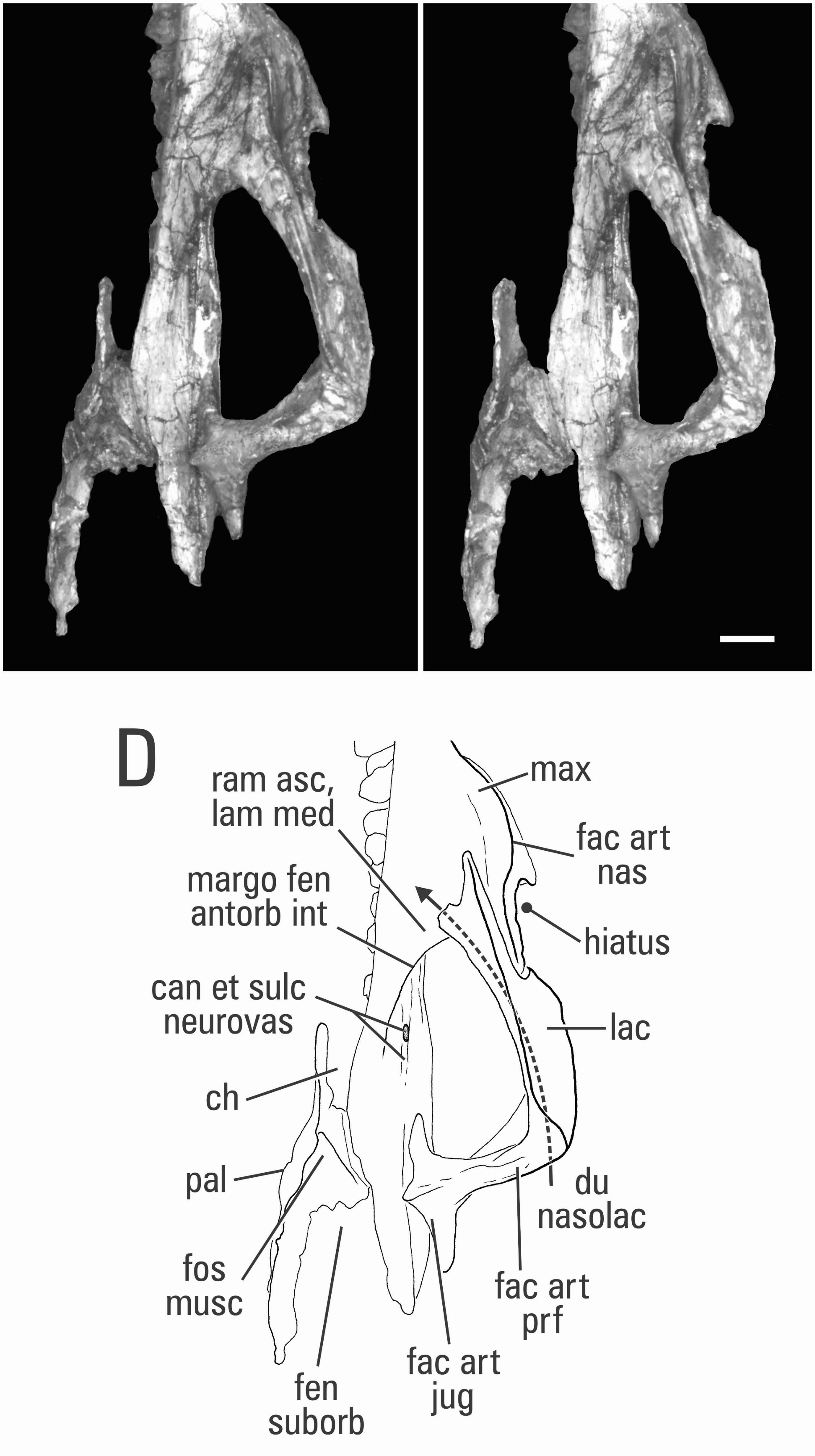

FIGURE 12. *(Continued)*

culature is very clear (BMNH R11956, R8501, RUB17), passing through a canal formed by maxilla, lacrimal, jugal, and perhaps palatine. The maxilla and lacrimal (BMNH R11956) are both strongly grooved for the neurovascular bundle. In fact, the dorsal groove on the maxilla extends rostrally within the floor of the antorbital cavity, ending at a slit-like foramen directed ventrally into the bone and opposite the internal antorbital fenestra (BMNH R11956). This slit almost certainly conducted the maxillary neurovasculature because all of the external neurovascular foramina are directed toward it (Fig. 7A).

Among Ornithopoda, as in *Lesothosaurus diagnosticus, Heterodontosaurus tucki* (BMNH R8179 [cast of SAM 337]) probably had a neurovascular canal between maxilla, lacrimal, and jugal. However, more similar to *Hypsilophodon foxii* (discussed below), the neurovascular branches exited more or less separately from the antorbital cavity rather than from a single foramen. Better data are available for *Hypsilophodon foxii* (BMNH R197, R192, R5862, R2477). The dorsal surface of the palatine (BMNH R2477) has a clear fossa extending rostrally up to the choana (Fig. 8A). Unlike *Lesothosaurus diagnosticus,* there is no nasal fossa rostral to it, but the postchoanal strut is grooved dorsally for the nasal capsule. As in *L. diagnosticus,* however, there is a very clear neurovascular canal formed by maxilla, jugal, lacrimal, and a dorsal, laterally arching process of the palatine (Fig. 8A). The portion of the maxilla forming the ventral rim of the external antorbital fenestra (supralveolar lamina) is drawn up dorsally such that the nerves and vessels would be lodged in a deep groove. As alluded to above, the neurovasculature exited the antorbital cavity ventrolaterally via several large foramina (Fig. 8B).

Whereas these more basal ornithopods retain the basic craniofacial architecture of other archosaurs, the facial and palatal skeleton in iguanodontian ornithopods becomes highly transformed, with reduction of the antorbital cavity and development of larger dentitions (Weishampel, 1984; see section on trends below). Probably above the level of *Iguanodon* spp. within Iguanodontia, the palatine assumes a much more vertical orientation (Fig. 11A; Lambe, 1920; Heaton, 1972; Norman, 1980; Norman and Weishampel, 1990; Weishampel and Horner, 1990), largely occluding the postnasal fenestra and restricting the rostral advance of any pterygoideus musculature. The more basal iguanodontians retaining an antorbital cavity, such as *Camptosaurus dispar* (UUVP 5946), *C. prestwichii* (Galton and Powell, 1980), and *Iguanodon atherfieldensis* (BMNH R5764, R11521), nevertheless resemble more basal ornithischians with regard to the relationship of the neurovasculature. There is a deep groove in the dorsal surface of the maxilla which is formed into a canal by the addition of the jugal and palatine (the jugal excludes the lacrimal from the canal in at least *Iguanodon atherfieldensis*; Fig. 11B). This groove extends in the floor of the small antorbital cavity before entering the neurovascular foramen located opposite the antorbital fenestra (as in *Lesothosaurus diagnosticus*; see Fig. 11B for *Iguanodon atherfieldensis*). Hadrosaurs have a completely closed external antorbital fenestra (Weishampel and Horner, 1990), yet retain a shallow fossa on the palatine and the same basic structure of the neurovascular canal (e.g., *Edmontosaurus regalis,* CMN 2289; *Corythosaurus casuarius,* AMNH 5338; *Hypacrosaurus* sp., MOR-609–88–91)

The evidence provided by the basal thyreophoran *Scelidosaurus harrisonii* (BMNH R1111) is particularly important because many higher thyreophorans are so derived that direct correspondences are difficult to identify. *S. harrisonii* resembles *Hypsilophodon foxii* in that the caudodorsal surface of the palatine is excavated into a fossa extending up to the choana and the postchoanal strut is grooved for the nasal cartilages. Likewise, very similar to the other ornithischians discussed here, there is a neurovascular canal formed by maxilla, lacrimal, jugal, and palatine that is carried rostrally as a groove in the floor of the antorbital cavity, entering the body of the maxilla at a foramen opposite the antorbital fenestra. *Emausaurus ernsti* (Haubold, 1990) is an even more basal thyreophoran, retaining a much larger antorbital cavity. Although the existence of a muscular fossa on the palate is unknown, the course of the maxillary neurovasculature in *E. ernsti* closely resembles that in *Scelidosaurus harrisonii* and other ornithischians.

The basal ceratopsian *Psittacosaurus mongoliensis* (AMNH 6535; see Sereno, 1987) holds similar importance as a more basal member of a very specialized group. It also has a shallow fossa on the dorsolateral surfaces of the palatine and pterygoid extending rostrally to the choanal margin and a neurovascular canal surrounded by maxilla, palatine, and jugal. The neurovascular canal is large and leads to a series of ventral foramina opening into the buccal cavity.

Saurischians differ in that the maxillary neurovasculature is not typically enclosed in a canal formed by several bones; a canal is presumably an ornithischian apomorphy associated with the tendency to wall in the antorbital cavity (see section on trends below). Otherwise, some saurischians, such as *Plateosaurus engelhardti,* resemble such ornithischians as *Lesothosaurus diagnosticus* and *Hypsilophodon foxii* in the osteological correlates of the dorsal pterygoideus and maxillary neurovasculature. Most basal prosauropods (e.g., *Thecodontosaurus antiquus,* Kermack, 1984; *Anchisaurus polyzelus,* Galton, 1976) are poorly known with regard to the relevant features and the following discussion focuses mostly on *Plateosaurus engelhardti* (principally AMNH 6810; see also Galton, 1984, 1985c, 1990). The dorsolateral surface of the palatine of *P. engelhardti* has a postchoanal strut that is strong laterally and weakens rostrodorsally, delimiting a caudal (muscular) fossa from a flatter, rostral, nasal area (Fig. 12D). Although Galton (1985c) did not list the palatine as an attachment site for the dorsal pterygoideus in *P. engelhardti,* the fossa compares well with the presumptive muscular fossa of other archosaurs.

As in ornithischians, there is, within the antorbital cavity, a dorsal groove on the maxilla that passes rostrally until it enters a ventral, slit-like foramen opposite the rostral margin of the internal antorbital fenestra (Fig. 12D); as in *Lesothosaurus diagnosticus,* the external neurovascular foramina are all directed toward this slit (Fig. 12A). The dorsal groove and foramen apparently are present in *Sellosaurus gracilis* (Galton, 1985b), and almost identical relationships of the external neurovascular foramina also are seen in that taxon and *Massospondylus carinatus* (Gow et al., 1990). Caudally in *Plateosaurus engelhardti,* processes of the lacrimal and palatine approach each other in the vicinity of their junction with the maxilla and jugal (Fig. 12D), but do not form the complete bony canal observed in the ornithischians (although it was probably completed with soft tissue).

As a whole, sauropods are poorly known with regard to these features. The palatines and pterygoids of *Camarasaurus lentus* (CM 11338; see also Madsen et al., 1995) and *Diplodocus longus* (CM 11161) are more or less vertically oriented in the vicinity of the antorbital cavity, with perhaps a slight concavity to their caudodorsolateral surfaces (Fig. 13A). The palatine of *Euhelopus zdanskyi* has a stronger dorsolateral fossa, undercutting the postchoanal portion of the bone (Mateer and McIntosh, 1985). Zhang's (1988) reconstruction of the adductor musculature attaching to this portion of the palate in *Shunosaurus lii* seems reasonable, although he carried the muscle rostrally onto the vomer which is unlikely. Janensch (1935–36) reconstructed the pterygoideus musculature of *Brachiosaurus brancai* as extending over the entire dorsal surface of the palatine to attach to the antorbital fenestra; however, the palatine of this form resembles that of *Camarasaurus lentus* (McIntosh, 1990; Mad-

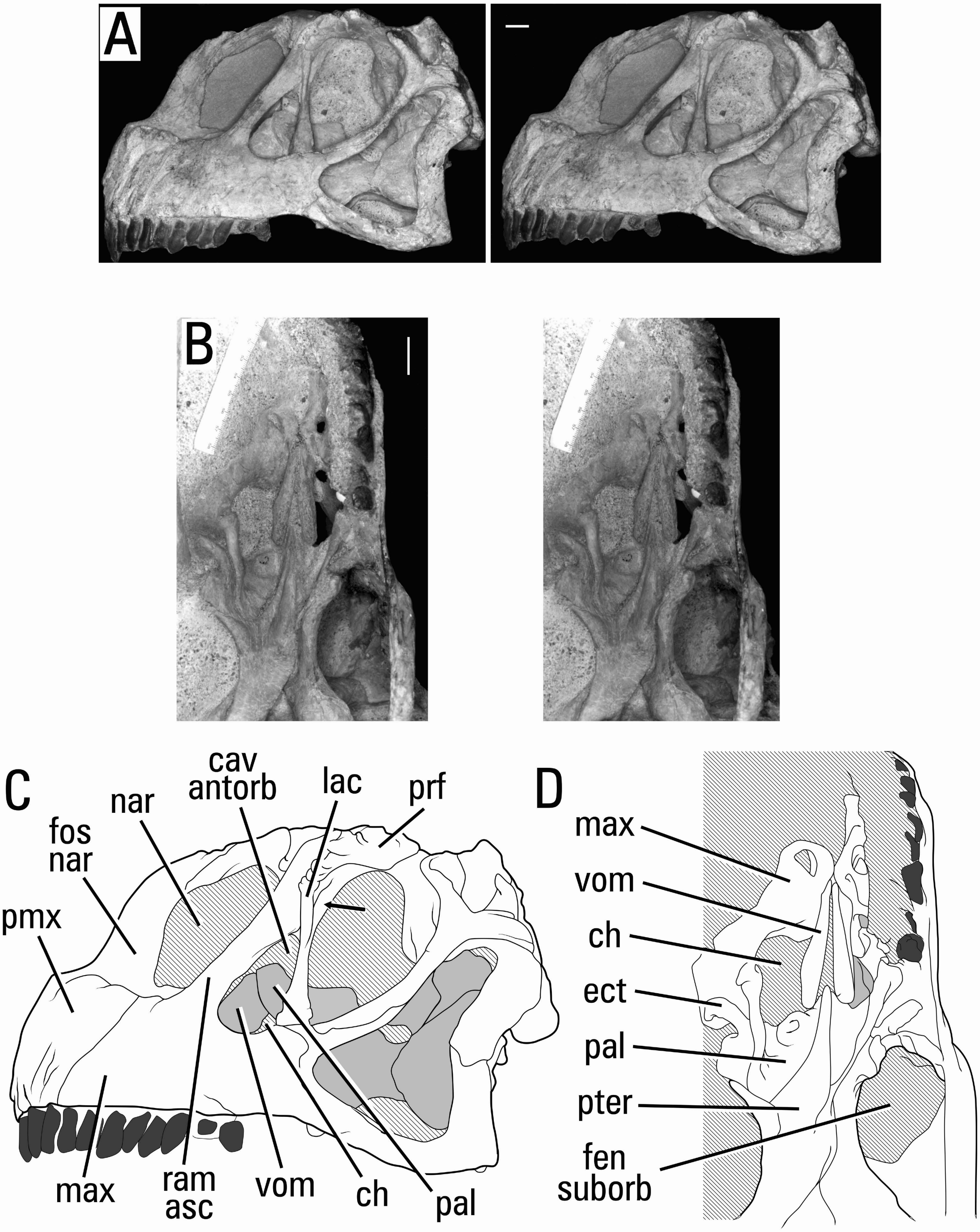

FIGURE 13. *Camarasaurus lentus.* **A**, stereophotographs of skull of CM 11338 in left lateral view. **B**, same in ventral view. **C**, interpretive drawing of **A**. **D**, interpretive drawing of **B**.

sen, et al., 1995) in having a caudolaterally facing postchoanal surface that probably marks the rostral limit of the muscle.

The inferred position of the neurovasculature is clearest for *Camarasaurus lentus* in which one or more medial foramina are present in the maxilla just ventral to the antorbital fenestra. The number of foramina appears to be a size-related feature, which is consistent with their interpretation as neurovascular structures. For example, in small specimens of *C. lentus* (CM 11338, 41694, 21702) there is a single foramen in the rostral apex of the internal antorbital fossa whereas in larger individuals there are additional foramina (three in CM 113) equally spaced along the dorsomedial margin; in specimens with foramina within the narial fossa (CM 21702, 113), these foramina probably communicate with those within the antorbital cavity. Janensch (1935–36:173) described similar foramina (his "innere Mündung des Foramen infraorbitale") for *Brachiosaurus brancai.*

Among non-avian theropods, the osteological correlates of the dorsal pterygoideus are clear and indicate that the muscle often extended far into the antorbital cavity. The basal theropod *Herrerasaurus ischigualastensis* (PVSJ 407; see also Sereno and Novas, 1994) displays a fossa on the dorsal surfaces of the palatine and pterygoid well within the antorbital cavity and extending rostrally up to the choana. Similar to *Ornithosuchus longidens,* the rostrolateral margin of the palatine forms a strong postchoanal strut that is continued caudolaterally along its contact with the maxilla. The palatines and maxillae are slightly disarticulated revealing that, again as in *O. longidens,* the lateral margin of the palatine curves dorsomedially somewhat, indicating that the muscular fossa is topologically separate from the region of the antorbital fenestra and fossa. The arrangement of the palatal bones is very similar in the ceratosaurians *Coelophysis bauri* (CM 31374, 31375) and *Ceratosaurus nasicornis* (USNM 4735). In these forms, the dorsolateral surface of the palatine exhibits a strong, rounded ridge passing from the maxillary contact just in front of the suborbital fenestra rostrodorsomedially toward the vomeropterygoid contact (Fig. 14). This ridge clearly delimits a deeply etched fossa caudal to it on the palatine and pterygoid. As in *Ceratosaurus nasicornis,* the area rostral to this muscular fossa (presumably supporting the nasal cavity) is flat or only gently concave. The palatine of *Allosaurus fragilis* (UUVP 5427) has a more prominent dorsolateral fossa associated with the suborbital fenestra; as in "*Pallisteria angustimentum,*" *Ornithosuchus longidens, Herrerasaurus ischigualastensis,* and other taxa, the lateral rim of the muscular fossa is drawn up dorsally, separating the muscular fossa from the fenestral region. Dromaeosaurids, such as *Deinonychus antirrhopus* (YPM 5210, 5232; Ostrom, 1969) and *Velociraptor mongoliensis* (Osmólska, 1985), and *Archaeopteryx* sp. (cast of Solenhofer Aktien-Verein specimen; see also Elzanowski and Wellnhofer, 1996) have a well marked fossa on the palatine caudal to a rounded ridge similar to that of ceratosaurs. Dromaeosaurids and *Archaeopteryx* sp. have another deep fossa rostral to the muscular fossa and just medial to the maxillary contact that is clearly associated with the antorbital cavity (see section on accessory cavities below). Tyrannosaurids, however, such as *Daspletosaurus torosus* (CMN 8506) and *Albertosaurus* cf. *A. sarcophagus* (RTMP 81.10.1), do not exhibit prominent muscular fossae.

The maxillae of theropods are very consistent with regard to the course of the maxillary neurovasculature. Usually there are a series of foramina in the dorsal surface of the body of the maxilla, just medial to the internal antorbital fenestra. These have been observed in, for example, *Dilophosaurus wetherilli* (UCMP 37303, 77270), the abelisaurid *Indosuchus raptorius* (AMNH 1955), *Megalosaurus hesperis* (BMNH R332), *Allosaurus fragilis* (UUVP 5427), *Albertosaurus libratus* (RTMP 83.35.100), and *Dromaeosaurus albertensis* (AMNH 5356), among others. In some cases (e.g., large tyrannosaurids such as *Tyrannosaurus rex,* UCMP 118742), some of these foramina are enlarged and probably transmitted pneumatic diverticula as well as neurovasculature (see below).

Conclusions

The hypothesis about the soft-tissue attributes of the common ancestor of extant archosaurs survives testing and indeed indicates (requiring little or no speculation—a level I inference) the presence of M. pterygoideus, pars dorsalis in the vicinity of the antorbital cavity. Numerous fossil archosaurs—or at least basal members of all major clades—have demonstrable excavations on the palatine bones that, in extant birds and crocodilians, are associated with the muscle. Although in some clades (e.g., Ornithischia, perhaps Prosauropoda) the muscle appears to be all but excluded from the antorbital cavity, the osteological correlates in many other archosaurs suggest that the muscle was extensive, reaching far rostrally on the floor or ventromedial wall of the cavity. However, in no case was there any direct evidence implicating the antorbital fenestrae or fossae in muscular attachment, and, in fact, in some cases there is good morphological evidence that the muscular and fenestral regions were restricted to separate topological domains.

Considerable emphasis has been placed on the inferred course of the maxillary neurovasculature in fossil taxa because in all modern sauropsids the nerve always travels dorsal to the pterygoideus musculature (Witmer, 1995b). In all fossil archosaurs that could be sampled for this feature, the neurovascular foramina were dorsal (or, in cases where the muscular fossa was medially disposed, dorsolateral) to the inferred position of the dorsal pterygoideus. Under the muscular hypothesis, however, the maxillary nerve would have to take a course—unique among Sauropsida—ventral to at least part of the pterygoideus muscle. This fundamental relationship between muscle and nerve in sauropsids may well be an intrinsic property of neuromuscular ontogeny, that is, a morphogenetic constraint. As a result, the attachment of pterygoideus musculature to the antorbital fenestra and fossa may be in fact a morphology denied by this constraint. Thus, not only is there little or no direct evidence for the muscular hypothesis, but there even may be a reason (a morphogenetic constraint) why it never could be true.

Despite the impressive list of adherents tallied at the outset, there appears to be no reason to sustain the notion of a large muscle lodged within the antorbital fenestra and fossa of archosaurs. As seen earlier, many of the morphological and functional implications of the muscular hypothesis are unrealistic. The failure of the muscular hypothesis has important paleobiological implications, again highlighting the fundamental nature of soft-tissue inferences. Under the muscular hypothesis, many archosaurs would have had a huge dorsal pterygoideus muscle whereas others would have had a very small one. In some cases (e.g., *Coelophysis bauri*), such a muscle probably would have been larger than all of the other adductors combined. The adductor musculature is obviously an intrinsic component of the feeding apparatus, and inferences about it are fundamental to any complete analysis of craniofacial functional morphology (e.g., interpretation of loading regimes, kinesis, utilization of the trophic structures). These biomechanical studies, in turn, influence inferences about the dietary preferences and behavior of the organism, habitat preference, paleoecological interactions with other species in the community, and so forth up the ecological hierarchy. Thus, although the analysis presented here falsifies the muscular hypothesis, it provides data on the size, extent, and attachments of the dorsal pterygoideus muscle in fossil archosaurs that are critical to these paleobiological inferences. Galton and Powell (1980:413) argued that

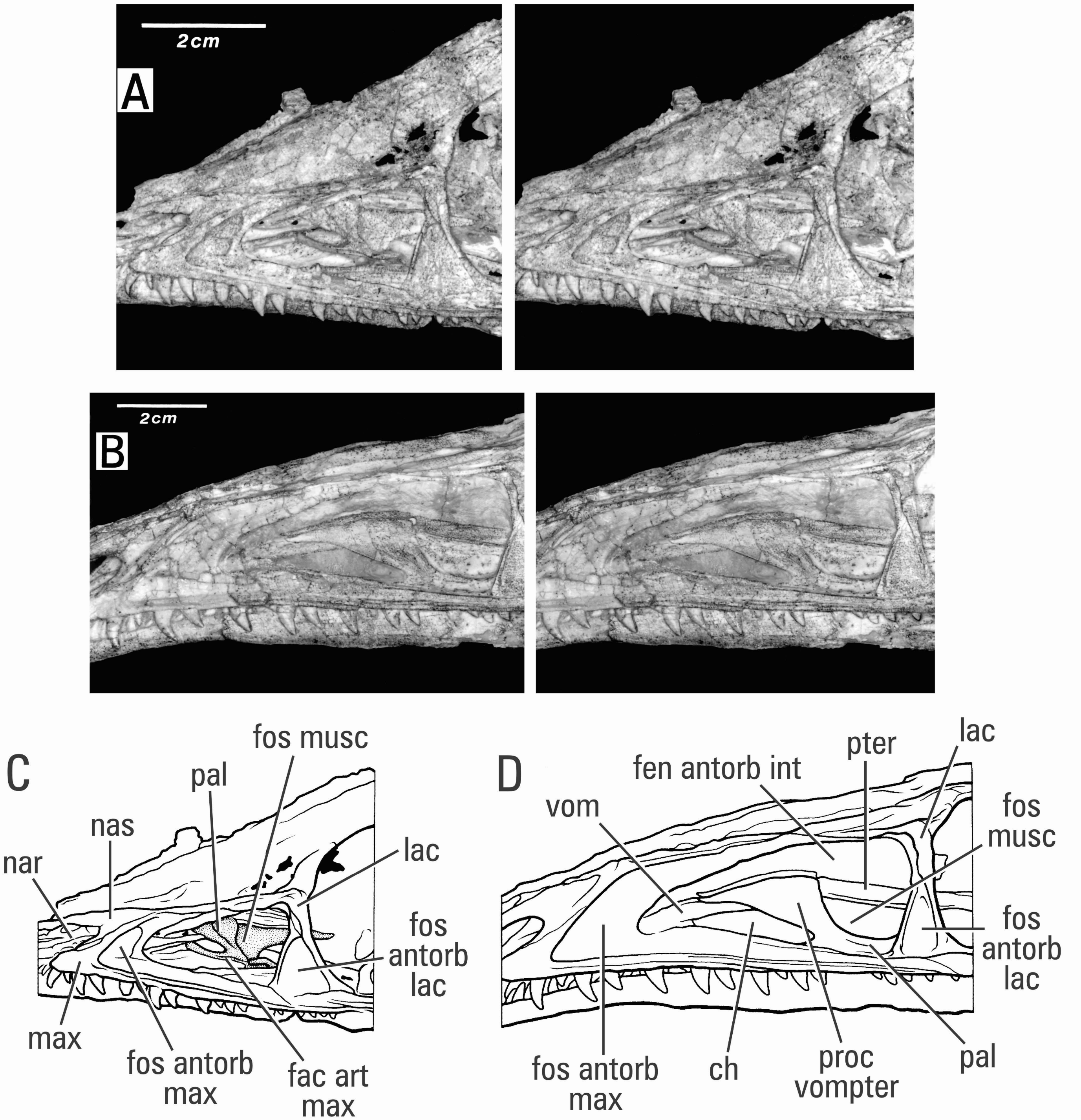

FIGURE 14. *Coelophysis bauri.* **A**, stereophotographs of antorbital region of CM 31375 in left lateral view. **B**, same for CM 31374. **C**, interpretive drawing of **A**. The left palatine (somewhat disarticulated) is stippled and shows the fossa for the dorsal pterygoideus. **D**, interpretive drawing of **B**.

since the antorbital cavity of *Camptosaurus prestwichii* was too small to house a muscle, "the only structure which could have occupied such a cavity is a gland." With the failure of both glandular and muscular hypotheses, yet another explanation must be sought for the principal function of the antorbital cavity.

HYPOTHESIS 3: THE ANTORBITAL CAVITY HOUSES AN AIR SAC

Historical Development

The last, and most recently proposed, hypothesis for the function of the archosaurian antorbital cavity is that it housed an air-filled epithelial diverticulum of the nasal cavity. Although a number of earlier workers regarded some of the various cavities surrounding the antorbital fenestra, principally in theropods, as being pneumatic (e.g., Gilmore, 1920; Stovall and Langston, 1950; Osmólska, 1976; Barsbold, 1983; Molnar, 1973, 1985), Osmólska (1985) was the first to suggest that the antorbital cavity of probably all archosaurs was associated with the nasal cavity in general and perhaps a paranasal air sac in particular. While investigating the early evolution of avian craniofacial pneumaticity (Witmer, 1990), I independently came to similar conclusions (Witmer, 1987b). Osmólska's (1985) formulation was intimately involved with the biological role of the air sac itself and the ecology and physiology of fossil archosaurs; as indicated earlier, these matters are secondary to elucidating the function (i.e., soft-tissue relations) of the cavity, but, of course, are necessary for interpreting its paleobiological significance.

In some respects, the concept of a pneumatic antorbital cavity is frustrating in that the function of craniofacial air sacs in general are obscure (e.g., Negus, 1958; Blanton and Biggs, 1969; Blaney, 1990; see below). However, in other respects, this is an advantage in that determination of the function of the bony cavity does not become muddled with the perceived "utility" of the enclosed structure, which has been a failing of both the glandular and muscular hypotheses. Issues relating to the function of an antorbital air sac are addressed in a later section.

The Extant Phylogenetic Bracket

Because air sacs are unusual organ systems, their basic properties will be briefly outlined here (see also Witmer, 1990, 1995b, and references therein). Paranasal air sinuses in general are air-filled epithelial outgrowths or diverticula of the nasal cavity that evaginate beyond the cartilaginous nasal capsule, always maintaining communication with the external environment via the naris. They should not be confused with the various intracapsular recesses or cavities, as only the extracapsular air sacs are competent to pneumatize bone (Witmer, 1995b). Not all air sacs pneumatize bone; some insinuate themselves among other soft tissues or even reach a subcutaneous position (Bignon, 1889; Witmer, 1990).

Birds and crocodilians have highly pneumatic skulls. Birds have only one major diverticulum of the nasal cavity proper, the antorbital sinus (Witmer, 1990), whereas crocodilians have five types of diverticula of the nasal cavity proper and several more diverticula of the nasopharyngeal duct (Wegner, 1958; Witmer, 1987b, 1995b). Based on a variety of criteria derived from study of extant amniotes, there exists strong evidence that one of the crocodilian paranasal sinuses, the caviconchal sinus, is homologous to the antorbital sinus of birds. Detailed comparison of all the diverticula and the justification for the homology is presented elsewhere (Witmer, 1995b).

Extant Birds—The avian antorbital sinus evaginates the nasal cavity toward the caudoventral margin of the cartilaginous nasal capsule, directly opposite the lacrimal bone and near the caudal margin of the choana. The proximal portion of the sinus diverticulum is closely associated with the major branch of the maxillary nerve in this region (i.e., the nasopalatine nerve), and the air sac tends to partially surround the nerve. The sinus expands into the area lateral to the nasal capsule, filling the available space within the antorbital cavity (Fig. 6B). Within the antorbital cavity, the sinus lies directly adjacent to the maxilla, lacrimal, palatine, and usually also the jugal and nasal. In most cases, diverticula of the antorbital sinus pneumatize many of these bones, producing characteristic pneumatic foramina or fossae collectively termed "accessory cavities" (Witmer, 1994). Extant birds are variable with respect to these features, but what remains constant is the presence of a large air sac within the antorbital cavity lodged principally in the caudal portion of the maxilla and rostral to the lacrimal. In addition to the diverticula into the facial bones, the antorbital sinus has another diverticulum, the suborbital diverticulum (Witmer, 1990; Fig. 6B). This diverticulum extends often far caudally beyond the postnasal fenestra, interleaving between the pterygoideus and external adductor muscles, curving ventrally around the eyeball, and often reaching the region of the trigeminal foramen (see Bignon, 1889).

Laterally, the antorbital sinus extends to the margins of the external antorbital fenestra (except dorsally where the nasolacrimal duct passes) and, in many cases, excavates an antorbital fossa, especially on the maxilla (Fig. 15A). The presence of antorbital fossae appears to be a size- and age-related attribute, with larger and older individuals tending to have more deeply excavated fossae. The external antorbital fenestra and antorbital sinus are covered with skin laterally. The nasolacrimal duct passes lateral to (or, in most ratites, partially through) the lacrimal bone and then through the dorsal portion of the internal antorbital fenestra, after which it turns sharply ventromedially to open into the nasal cavity proper toward the rostral end of the choana (Figs. 6B, 15A). Thus, the nasolacrimal duct passes dorsomedial to the antorbital sinus and is among the contents of the antorbital cavity. As mentioned in the previous section, the dorsal pterygoideus commonly reaches into the caudoventral portion of the antorbital cavity where it comes into direct contact with the antorbital sinus.

Extant Crocodilians—The crocodilian caviconchal sinus, the homolog of the avian antorbital sinus, evaginates the nasal capsule directly opposite the primary choana (the primary choana is the rostral [nasal] end of the nasopharyngeal duct and is homologous to the choana of birds and other archosaurs; Witmer, 1995b), passing dorsally over the palatine to enter the antorbital cavity. The sinus expands early in ontogeny into the area of the fontanelle between maxilla, lacrimal, nasal, and prefrontal (fonticulus antorbitalis; Witmer, 1995b), but later is housed almost completely within the bony caviconchal recess of the maxilla (Fig. 15B). The maxilla usually is extensively pneumatized by the sinus.

The maxillary nerve is closely associated with the diverticulum and travels within the bony recess (most alligatorids) or within a bony canal adjacent to the recess (most crocodylids). In adult crocodilians, the nasolacrimal duct makes only a glancing contact with the caviconchal sinus, passing dorsomedially over the diverticulum before the latter enters the aperture of the caviconchal recess (Figs. 6A, 15B), although earlier in ontogeny the duct and sinus contact each other more broadly. As indicated earlier, the caudal portion of the antorbital cavity in crocodilians is dominated by the large dorsal pterygoideus muscle, restricting the sinus to the rostral, largely intramaxillary portion of the cavity; in other words, the suborbital diverticulum observed in birds is absent in crocodilians.

Osteological Correlates—The osteological correlates of paranasal pneumaticity in each clade of extant archosaurs are very clear. In both clades, the paranasal air sac leaves the nasal capsule and passes through a bony aperture (corresponding to the internal antorbital fenestra) situated directly lateral to the primary choana, passing laterally dorsal to the palatine bone and expanding to occupy a large, recessed cavity within the caudal portion of the maxilla (Fig. 15). In both clades, the paranasal sinus pneumatizes the maxilla via additional diverticula, resulting in pneumatic foramina and bony accessory cavities opening into the main sinus chamber. The nasolacrimal duct passes dorsomedially around the sinus, producing canals and/or grooves in the adjacent bones; in adult crocodilians, the duct is partly enclosed in bone such that it makes only slight contact with the diverticulum, whereas, in birds, the duct generally broadly contacts the sinus.

In birds, the sinus fills the antorbital cavity and extends to

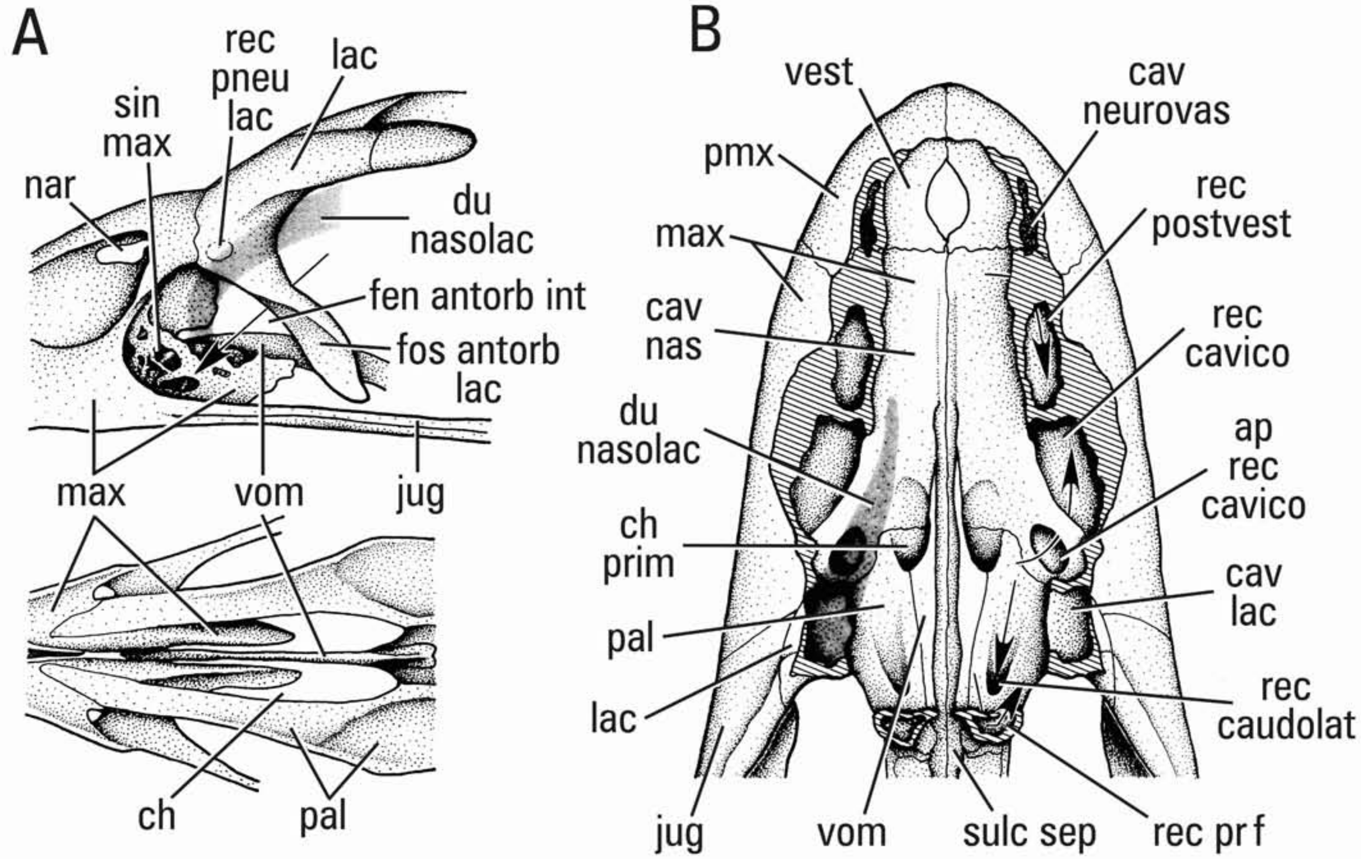

FIGURE 15. Osteological correlates of paranasal pneumaticity. **A**, *Aquila chrysaetos* (golden eagle), skull in left lateral (top) and ventral (bottom) views. **B**, *Alligator mississippiensis,* horizontally sectioned skull in dorsal view. Arrows show the course or position of pneumatic diverticula. Shaded structure shows the position of the nasolacrimal duct. (**B** modified from Witmer, 1995b.)

the margin of the external antorbital fenestra, often excavating a fossa on the maxilla and lacrimal (Figs. 6B, 15A). A few avian clades (e.g., owls) have extensive contact between the maxilla and lacrimal, obliterating the external fenestra (except the dorsal passage for the nasolacrimal duct) and enclosing the antorbital sinus. In adult crocodilians, there is no external antorbital fenestra and hence no comparable fossa. In birds, the external antorbital fenestra forms morphogenetically as a fontanelle that never closes (rather than as a hole that opens up during ontogeny; Witmer, 1995b). The fontanelle of embryonic crocodilians likewise is associated with the air sac and may be homologized with the external antorbital fenestra, although I hesitate to apply the latter term as the fontanelle never has the finished edges of a true fenestra.

With regard to the internal antorbital fenestra, birds have an irregular and variable opening. Some birds (e.g., *Anser anser*) have such a large maxillary contribution that much of the medial wall of the antorbital cavity is bony, but, in many other birds, the maxilla is small and most of the internal antorbital fenestra is closed by the cartilage of the nasal capsule. In crocodilians, the maxillary contribution to the medial wall of the cavity is virtually complete in the comparable (i.e., prechoanal) region (Fig. 15). Thus, in crocodilians, the internal antorbital fenestra is small and represented by at least part of the aperture within the maxilla leading to the caviconchal recess and by the tip of the lacrimal. In both clades of extant archosaurs, the only structure that passes through the internal antorbital fenestra is the pneumatic diverticulum, and, because the internal fenestra is partially occluded by the nasal cartilages, it is larger in area than the sinus ostium itself.

The Hypothesis

Based on the correspondences in soft and hard anatomical attributes in the EPB, we may hypothesize that the bracket ancestor had a large paranasal air sac with the following characteristics: (1) it passed laterally from the nasal cavity through the internal antorbital fenestra to occupy a bony cavity bounded by primarily the lacrimal, palatine, and especially maxilla; (2) it excavated fossae within the maxilla; (3) the opening to the air sac (i.e., the internal antorbital fenestra) was located directly opposite the primary choana (Osmólska, 1985); (4) the nasolacrimal canal passed dorsomedially over the air sac; and (5) the air sac is associated with the external antorbital fenestra (based on the presence of the latter in birds and the fonticulus antorbitalis in embryonic crocodilians).

Testing the Hypothesis

Testing will begin with fossil birds, progressing down the cladogram toward the root and then up again toward crocodilians.

Dinosauria: Theropoda—Previous studies of the early evolution of facial pneumaticity in birds suggested that the osteological correlates of the antorbital sinus were present in the Mesozoic birds *Archaeopteryx lithographica, Hesperornis regalis, Parahesperornis alexi,* and *Gobipteryx minuta* (Witmer and Martin, 1987; Witmer, 1990). The antorbital cavity of hesperornithids is remarkably modern, and there is good evidence for maxillary and lacrimal diverticula of the antorbital sinus (KUVP 71012, 2287, YPM 1206, LACM 128317; Fig. 16A; see Witmer, 1990 for details). The choana was directly opposite

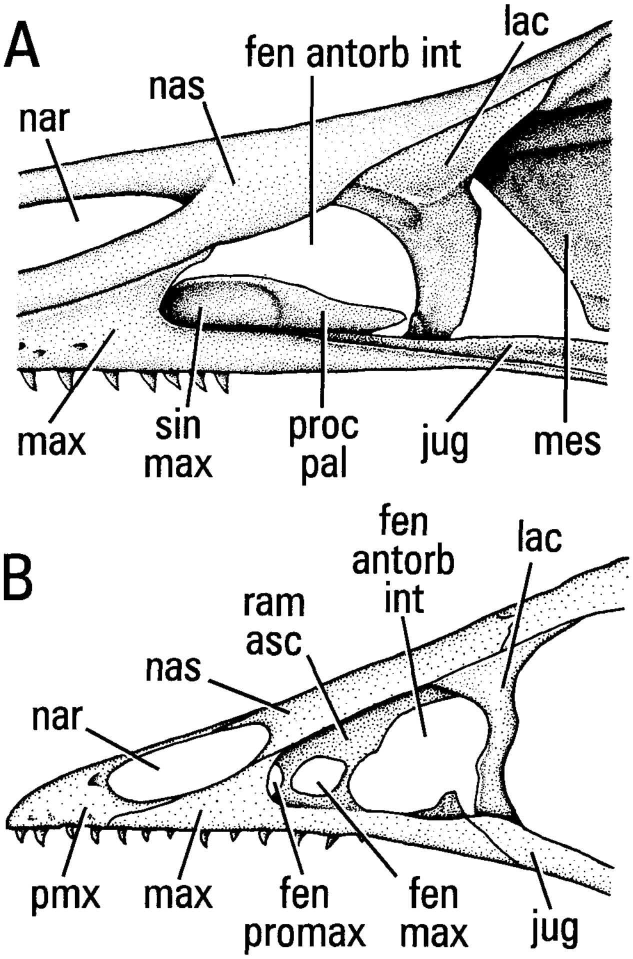

FIGURE 16. Antorbital cavities in left lateral view of **A**, *Hesperornis regalis* and **B**, *Archaeopteryx lithographica.* (Modified from Witmer, 1990.)

the caudal portion of the internal antorbital fenestra. As in most other ornithurine birds, the nasolacrimal duct of hesperornithids grooved the lateral surface of the lacrimal on its way through the external antorbital fenestra.

Archaeopteryx lithographica has a more primitive antorbital cavity than perhaps any known bird (Fig. 16B) and provides an important transitional link to more basal forms. In particular, it retains (unique among birds) the dorsal portion of the nasal process of the maxilla (Cracraft, 1986; Witmer, 1990). In *A. lithographica,* this portion of the maxilla (the "ascending ramus" of other archosaurs) is recessed and fenestrated as in many other theropods, enclosing a large portion of the antorbital cavity. Because part of the maxilla is recessed, the external antorbital fenestra is formed by the maxilla, lacrimal, and nasal. The rostral margin of the internal antorbital fenestra is formed by the medial lamina of the ascending ramus. There is probably not much of an antorbital fossa on the lacrimal except perhaps ventrally (BMNH 37001), but the recessed part of the ascending ramus of the maxilla forms a broad antorbital fossa. As mentioned, the ascending ramus has two fenestrae (Wellnhofer, 1974), the rostral one (i.e., the promaxillary fenestra) apparently being associated with a small chamber within the maxilla opening caudally into the antorbital cavity (Witmer, 1990). The fenestrae are the "subsidiary antorbital" or "maxillary" fenestrae of other authors and are widely distributed among theropod dinosaurs. They cannot be studied adequately in the crushed material referable to *A. lithographica,* but are given more attention in the discussion of accessory cavities below.

New discoveries of palatal elements of *Archaeopteryx* sp. (cast of Solenhofer Aktien-Verein specimen; see also Elzanowski and Wellnhofer, 1996; Paul, 1996) confirm that the choanae were directly opposite the internal antorbital fenestra (Witmer and Martin, 1987). The vertical shaft of the lacrimal (BMNH 37001) is pierced by a foramen that almost certainly is an opening for the nasolacrimal duct, suggesting that the duct passed through the dorsal portion of the antorbital cavity over the air sac without otherwise being enclosed in a bony canal.

Among non-avian theropods, many of the correlates are clear (Fig. 14) and require little discussion. For example, the choana is always directly opposite the internal antorbital fenestra. Similarly, the internal antorbital fenestra opens medially into the nasal cavity and laterally into a space excavated into the surrounding bones. In fact, the antorbital fossa in most non-avian theropods occupies most of the snout and, in some forms, much of the skull (about 45–55% of total skull length in *Coelophysis bauri* and *Proceratosaurus bradleyi* [BMNH R4860]). The maxillae of all theropods (except *Herrerasaurus ischigualastensis* and some abelisaurids) have extensive antorbital fossae on their lateral surfaces. In most cases, the fossa extends far ventrally below the margin of the internal antorbital fenestra, occasionally approaching the labial edge of the bone (e.g., *Ceratosaurus nasicornis,* USNM 4735; *Dilophosaurus wetherilli,* UCMP 37303, 77270; *Coelophysis bauri,* many specimens, Fig. 14; *Allosaurus fragilis,* UUVP 5427, BYU 5126, USNM 4734; *Ornitholestes hermanni,* AMNH 619; *Proceratosaurus bradleyi,* BMNH R4860; many others). In other clades, however, the fossa extends only slightly below the internal fenestra (e.g., some tyrannosaurids) or essentially not at all (e.g., abelisaurids [Bonaparte et al., 1990; Bonaparte, 1991a], *Carcharodontosaurus saharicus* [SGM-Din 1; see Sereno et al., 1996], troodontids [*Saurornithoides mongoliensis,* AMNH 6516, *Troodon formosus,* CMN 12392; see also Osmólska and Barsbold, 1990]). In virtually all non-avian theropods, the maxillary antorbital fossa extends onto the ascending ramus (Fig. 14). Most theropods also have portions of the antorbital fossa extending onto the lacrimal bone, with a common pattern being ventrolateral and dorsolateral fossae separated by a sculptured (subcutaneous) area (e.g., *Coelophysis bauri,* CM 31374, Fig. 14; *Ceratosaurus nasicornis,* USNM 4735; *Allosaurus fragilis,* UUVP 2133; most tyrannosaurids). Often the ventrolateral lacrimal fossa extends onto the jugal, such that there is a prominent recess caudoventrolateral to the internal antorbital fenestra. Whereas in most theropods the lacrimal and maxillae exclude the nasal from the antorbital fossa, the nasal bone enters into the fossa in a few taxa (e.g., *Monolophosaurus jiangi* [Zhao and Currie, 1994] and Allosauroidea [see Currie and Zhao, 1994a; Sereno et al., 1996]). Associated with the antorbital fossae in many non-avian theropods are various foramina and accessory cavities within the facial bones (see below).

The course of the nasolacrimal duct is another landmark for the main paranasal sinus of extant archosaurs, in which it passes dorsally over the major part of the sinus, then becoming medial to the sinus as it approaches the choana. In non-avian theropods, the bony nasolacrimal canal passes wholly within the lacrimal bone. Its orbital aperture is usually (if not always) single, but there is considerable variation in the subsequent course of the duct. For example, in *Dromiceiomimus brevitertius* (CMN 12228) and *Troodon formosus* (RTMP 82.19.23; Currie, 1985), the nasolacrimal canal is long and runs for some distance within the rostral ramus of the lacrimal; its rostral (nasal) aperture opens medially. In *Allosaurus fragilis* (UUVP 2133) and *Deinonychus antirrhopus* (MOR 747; see Witmer and Maxwell, 1996), the short canal opens into the lacrimal recess and the epithelial duct must have continued rostrally through the internal antorbital fenestra. In *Tyrannosaurus rex* (CM 9401; see also Molnar, 1991), the canal apparently traverses only the short distance through the vertical jugal ramus between orbit and antorbital cavity. Other variants could be cited, but, despite this variation, it is clear that non-avian theropods exhibit the same general relations as observed in extant archosaurs. As in present-day birds, the duct ran through the most dorsal portion of the internal antorbital fenestra.

Dinosauria: Sauropodomorpha—In virtually all sauropodomorphs, the internal antorbital fenestra opens into the nasal cavity opposite the choana. Laterally, the antorbital cavity is bounded principally by the lacrimal and maxilla, with varying contributions from the nasal (some prosauropods) or from the jugal (some sauropods). The relationship of fenestra with choana can be observed in *Plateosaurus engelhardti* (AMNH 6810; Fig. 12), probably *Thecodontosaurus antiquus* (Kermack, 1984), *Massospondylus* spp. (Attridge et al., 1985; Gow et al., 1990), *Lufengosaurus huenei* (Young, 1941), *Brachiosaurus brancai* (Janensch, 1935–36), *Euhelopus zdanskyi* (Mateer and McIntosh, 1985), *Camarasaurus lentus* (CM 11338; Fig. 13), *Shunosaurus lii* (Zhang, 1988), *Omeisaurus tianfuensis* (He et al., 1988), and *Diplodocus longus* (CM 11161, 3452).

Few if any sauropodomorphs have the large external antorbital fossae that are so commonly observed in more basal archosaurs. Rather, there seems to be a trend to enclose the antorbital cavity in prosauropods, and distinguishing between internal and external antorbital fenestrae is often necessary. In most prosauropods, the supralveolar lamina of the maxilla is present and encloses a portion of the antorbital cavity medial to it. This lamina is unknown for *Thecodontosaurus antiquus* (Kermack, 1984) and is virtually absent in *Anchisaurus polyzelus* (YPM 1883; see also Galton, 1976: fig. 13); it is well-developed in *Plateosaurus engelhardti* (AMNH 6810; Fig. 12A), *Massospondylus carinatus* (Gow et al., 1990), and *Lufengosaurus huenei* (Young, 1941), but very low and of limited caudal extent in *Sellosaurus gracilis* (Galton, 1985b). Similarly, the ascending ramus of the maxilla tends to send lateral and medial laminae caudally. The short lateral lamina is continuous with the supralveolar lamina, and the two together form the sharp margin of the external antorbital fenestra. Sauropodomorphs synapomorphically reduce the medial lamina of the ascending ramus (Sereno, 1989). In prosauropods, the medial lamina is variably developed, ranging from being very short in *Anchisaurus polyzelus* (YPM 1883), short to moderately developed in *Massospondylus carinatus* (Gow et al., 1990), *Coloradisaurus brevis* (Bonaparte, 1978), *Sellosaurus gracilis* (Galton, 1985b), and *Lufengosaurus huenei* (Young, 1941), to very extensive in *Plateosaurus engelhardti* (AMNH 6810; Fig. 12). The caudal extent of the medial lamina largely determines the size of the internal antorbital fenestra. All these laminae enclose the maxillary antorbital fossa.

The lacrimal of prosauropods has a ventrolateral antorbital fossa resembling many theropods (e.g., *Thecodontosaurus antiquus,* Kermack, 1984; *Massospondylus carinatus,* Gow, et al., 1990; *Sellosaurus gracilis,* Galton, 1985b; *Lufengosaurus huenei,* Young, 1941; *Plateosaurus engelhardti,* AMNH 6810, Fig. 12A). The bone usually twists somewhat along its length such that the fossa is carried dorsomedially where, in at least *Plateosaurus engelhardti* (AMNH 6810; Fig. 12) and apparently also *Sellosaurus gracilis* (Galton, 1985b), there is an expansive cavity—part of the antorbital cavity. The maxilla and lacrimal contact each other above the antorbital cavity in probably all prosauropods (Galton, 1990). Furthermore, in *Plateosaurus engelhardti* (AMNH 6810), possibly in *Sellosaurus gracilis* (Galton, 1985b), and in *Massospondylus carinatus* (Gow et al., 1990), the nasal bone overhangs the antorbital cavity and may house a small accessory cavity (Fig. 12C; see section on accessory cavities below). Thus, the antorbital cavity in prosauropods is clearly associated with well-marked excavations of the maxilla, lacrimal, and, at least sometimes, nasal, which, in some derived forms, enclose substantial portions of the cavity.

The antorbital cavities of sauropods generally are relatively small (Fig. 13). In most forms, retraction of the naris has displaced the cavity ventrally, and the dorsal portion of the antorbital fenestra often has a pinched appearance (McIntosh, 1990). Most sauropods have well-developed supralveolar laminae giving a sharp ventral edge to their antorbital fenestrae (e.g., *Brachiosaurus brancai,* Janensch, 1935–36; *Patagosaurus fariasi,* Bonaparte, 1986; *Euhelopus zdanskyi,* Mateer and McIntosh, 1985; *Camarasaurus lentus,* CM 11338, 11969, 41694, 21702, 113; adult *Shunosaurus lii,* Zhang, 1988; *Omeisaurus tianfuensis,* Dong et al., 1983; *Apatosaurus louisae,* CM 11162; *Diplodocus longus,* CM 11161, 11255, 3452; *Nemegtosaurus mongoliensis,* Nowinski, 1971). The supralveolar lamina thus partly encloses the antorbital cavity so that the aforementioned taxa have a prominent antorbital fossa on the medial surface of the maxilla (unknown for *Apatosaurus louisae* and not readily comparable in *Diplodocus longus*). The ascending ramus of the maxilla is a thin process in most sauropods (Fig. 13A) and does not develop the medial and lateral lamina seen in higher prosauropods. Retraction of the naris and expansion of the nasal vestibule has carried the ascending ramus caudodorsally, presumably tracking the maxillary (subnarial) process of the nasal with which it articulates (except in *Nemegtosaurus mongoliensis*; Nowinski, 1971). Probably as a result, the rostral ramus of the lacrimal is almost absent, and the lacrimal is usually a simple pillar, with little or no development of an antorbital fossa. Thus, the antorbital cavities of most sauropods are relatively simple.

However, *Diplodocus longus* and presumably also its more poorly known relatives have a relatively complex snout (Fig. 17). The most obvious features are the relatively long antorbital fenestra and the preantorbital fenestra rostral to it, the two being separated by an interfenestral bridge (CM 11161, 11255, 3452). The preantorbital fenestra is reminiscent of the maxillary fenestra of theropods, but unlike the latter it is not recessed within a single large fossa. Rather, the interfenestral bridge is at the same level as the surrounding surface. The preantorbital fenestra itself, however, is clearly set in a distinct fossa rostroventral to the fenestra; the fossa is somewhat better developed in a juvenile skull of *D. longus* (CM 11255; Fig. 17A, B). There is also a shallower, triangular fossa extending caudally ventral to the interfenestral bridge. The preantorbital fenestra and fossa open medially into a space continuous with the antorbital cavity. Thus, the antorbital cavity extends rostrally medial to the interfenestral bridge and dorsally over a strong medial shelf formed by the palatal process of the maxilla and palatine and buttressed by the ectopterygoid and pterygoid wing (Holland, 1924; McIntosh and Berman, 1975) to open laterally again via the preantorbital fenestra (Fig. 17C).

A likely explanation for the unique facial structure of *Diplodocus longus* is not the apomorphic appearance of the preantorbital fenestra, but rather the interfenestral bridge. In other words, the long lateral aperture of the antorbital cavity becomes subdivided by the bridge. The bridge probably served to buttress the long, low snout; it is significant in this regard that the medial shelf complex is situated at the ventral end of the bridge. Whether or not other diplodocids exhibit this system is not clear. A preantorbital fenestra may be present in *Apatosaurus louisae* (CM 11162; Berman and McIntosh, 1978). *Dicraeosaurus hansemanni* (Janensch, 1935–36) shows no sign of either fenestra in the fragmentary maxillary material, although the preserved lacrimal suggests that an antorbital fenestra was present. *Nemegtosaurus mongoliensis* (Nowinski, 1971) also

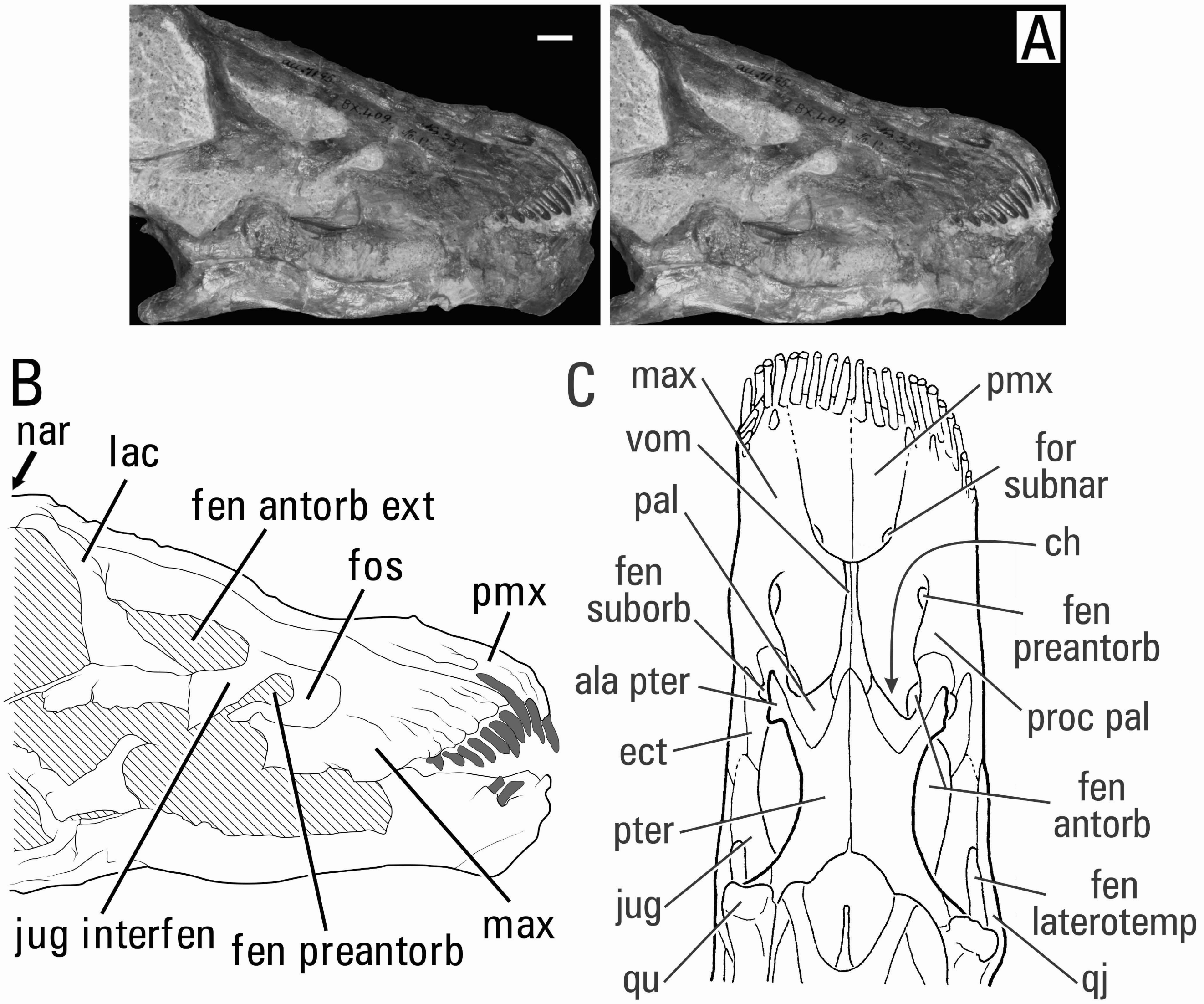

FIGURE 17. *Diplodocus longus*. **A**, stereophotographs of the facial portion of a juvenile skull (CM 11255) in right lateral view. **B**, interpretive drawing of **A**. **C**, drawing of palatal skeleton in ventral view. (C modified after Holland [1924], McIntosh and Berman [1975], and specimens.)

lacks a preantorbital fenestra although there are two small, elongate openings in this region.

The course of the nasolacrimal duct is known in a few sauropodomorphs. In *Plateosaurus engelhardti* (AMNH 6810), the nasolacrimal canal enters the lacrimal via a single orbital opening, passes dorsomedially through the lamina overhanging the antorbital cavity, and exits through the rostral end of the bone medial to the medial lamina of the ascending ramus of the maxilla (Fig. 12A, D). The orbital end of the canal is in a similar position in *Thecodontosaurus antiquus* (Kermack, 1984), *Massospondylus* spp. (MCZ 8893; Attridge et al., 1985; Gow et al., 1990), *Mussaurus patagonicus* (Bonaparte and Vince, 1979), *Yunnanosaurus huangi* (Young, 1942), *Sellosaurus gracilis* (Galton, 1985b), and *Lufengosaurus huenei* (Young, 1941). In sauropods, with the virtual absence of the rostral process, the nasolacrimal canal is simply an oval foramen in the lacrimal pillar (e.g., *Brachiosaurus brancai*, Janensch, 1935–36; *Euhelopus zdanskyi*, Mateer and McIntosh, 1985; *Camarasaurus lentus*, CM 11338, Gilmore, 1925; *Dicraeosaurus hansemanni*, Janensch, 1935–36). Thus the duct in most sauropods passed through the dorsomedial portion of the internal antorbital cavity, either through the dorsal region of the antorbital fenestra (as in theropods) or just medial to it.

Dinosauria: *Lesothosaurus* and Ornithopoda—There is a trend in most clades of Ornithischia toward enclosure and reduction of the antorbital cavity (Osmólska, 1985; Sereno, 1986; see section on facial trends below). Therefore, the following discussion focuses on the basal members of the major clades to establish the basic pattern. The basal ornithischian *Lesothosaurus diagnosticus* and the basal ornithopods *Abrictosaurus consors, Heterodontosaurus tucki,* and *Hypsilophodon foxii* are similar in facial structure and are treated together (see Crompton and Charig, 1962; Galton, 1974; Thulborn, 1974; Charig and Crompton, 1974; Weishampel and Witmer, 1990 a, b; Sues and Norman, 1990; Sereno, 1991a). In all except *Abrictosaurus consors* (BMNH RUB54) and perhaps *Heterodontosaurus tucki* it can be shown that the internal antorbital fenestra was directly opposite the choana and opened medially into the nasal cavity (Figs. 7, 8). In fact, in *Hypsilophodon foxii* (BMNH R2477), the postchoanal strut of the palatine extends laterally to contact the caudal margin of the internal antorbital fenestra (Fig. 8A). The antorbital cavity itself is partially enclosed medially by the extensive medial lamina of the maxillary ascending ramus and a similar medial lamina from the lacrimal bone such that there is an extensive antorbital fossa (Figs. 7, 8). These thin medial laminae are well preserved in *Lesothosaurus diagnosticus* (BMNH RUB23, R11956, RUB17, R8501), *Heterodontosaurus tucki* (BMNH R8179 [cast of SAM 337]), and *Hypsilophodon foxii* (BMNH R197, R2477) and constrict the size of the internal antorbital fenestra to a foramen. The maxillary medial lamina of *Hypsilophodon foxii* (BMNH R2477) and also *Heterodontosaurus tucki* (but not that of the basal heterodontosaurid *Lanasaurus scalpridens*; Gow, 1975) has an additional opening between the antorbital and nasal cavities.

The antorbital cavity is enclosed laterally to a variable degree. In all the aforementioned taxa, there is a well-developed supralveolar lamina projecting dorsally, giving the ventral margin of the external antorbital fenestra a sharp edge. In *Lesothosaurus diagnosticus* there is no significant development of a lateral lamina of the maxillary ascending ramus; the rim around the extensive antorbital fossa is sometimes distinct (BMNH R11956) and sometimes not (BMNH RUB17). In *Heterodontosaurus tucki* and probably *Abrictosaurus consors,* but not in *Lanasaurus scalpridens,* the rostral rim of the antorbital fossa more strongly overhangs the cavity. In *Hypsilophodon foxii,* the lateral lamina of the ascending ramus is extensive and greatly restricts the size of the external antorbital fenestra (Fig. 8B). In all taxa, the lacrimal also develops a lateral lamina that overhangs and further encloses the cavity (Figs. 7, 8).

The course of the nasolacrimal duct is known in *Lesothosaurus diagnosticus* (BMNH R8501) and *Hypsilophodon foxii* (BMNH R2477). In the latter (Fig. 8A), the canal passes through the lacrimal from the orbit, through the rostral ramus, emerging at the rostral end medial to the medial lamina of the maxilla as observed in *Plateosaurus engelhardti* (Fig. 12D). In *Lesothosaurus diagnosticus,* only the orbital opening of the canal is visible but the canal clearly does not open rostrolaterally and therefore probably had a course similar to that in *Hypsilophodon foxii.* Thus, in both cases, the nasolacrimal duct passed dorsomedially around the antorbital cavity.

Finally, *Lesothosaurus diagnosticus* has an additional fossa on the palatine medial to the choana (mentioned above in the discussion of the muscular hypothesis; Fig. 7C, D). This fossa perhaps supported the nasal capsule, but it is more likely that it is an accessory recess associated with the antorbital cavity (see section on accessory cavities below).

In higher ornithopods, many of the aforementioned trends are carried further. In *Tenontosaurus tilletti* (MOR 682), *Dryosaurus altus* (CM 3392; see also Galton, 1983), and *Camptosaurus dispar* (UUVP 5946) the antorbital cavity is further reduced in size, and lateral laminae from the maxilla and lacrimal (and jugal in *D. altus*) constrict the external antorbital fenestra to a relatively small aperture. The same relationships of antorbital cavity to choana that were observed in more basal ornithopods and *Lesothosaurus diagnosticus* are present in the iguanodontians *Iguanodon atherfieldensis* (BMNH R5764, 11521; Norman, 1986; Fig. 11), probably *I. lakotaensis* (SDSM 8656 [cast]; Weishampel and Bjork, 1989), and *Ouranosaurus nigeriensis* (MNHN GDF 300 [cast]; Taquet, 1976), but here the antorbital cavity is very small, does not deeply excavate the maxilla or lacrimal, and is enclosed laterally by only the lacrimal such that a faint fossa extends a short distance rostrally on the maxilla. Where known, the nasolacrimal canal passes dorsomedially around the antorbital cavity (Fig. 11B). Hadrosaurids present an interesting case in that they have a completely closed external antorbital fenestra, which is walled in not only by the massive maxilla, but also by the lacrimal, premaxilla, and a large rostral process of the jugal (Weishampel and Horner, 1990). The antorbital cavity, however, is retained medially as a small cavity bounded mostly by maxilla, lacrimal, and palatine; it is open caudally and floored ventrally with foramina for passage of neurovasculature. The cavity is directly opposite the choana. It should be noted that Heaton (1972) positioned the choana much too far caudally, behind the vomer; instead, the choana of hadrosaurids is lateral to the vomer, bounded caudally by palatine and laterally by maxilla as in other ornithopods.

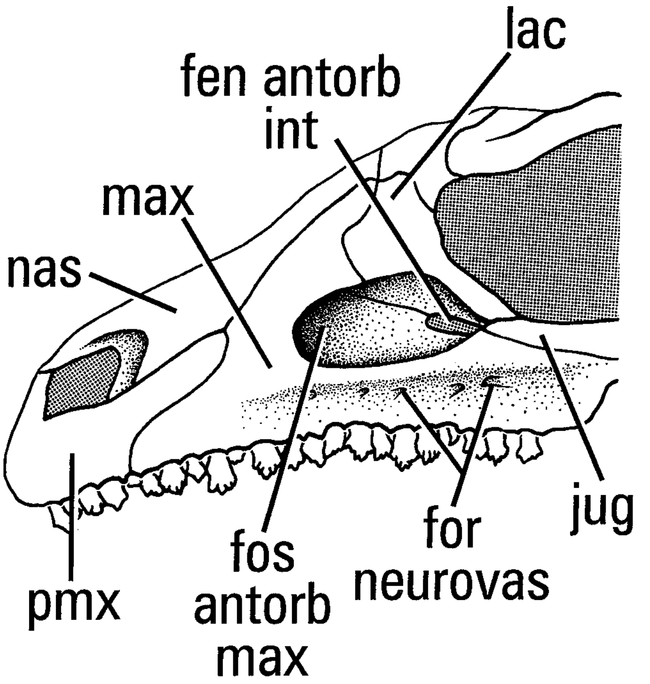

FIGURE 18. *Emausaurus ernsti,* facial skeleton in left lateral view. (Modified after Haubold, 1990.)

Dinosauria: Thyreophora—Thyreophoran ornithischians also tend to reduce the antorbital cavity and close the external antorbital fenestra. Unfortunately, little relevant data are available in the published material of the basal thyreophoran *Scutellosaurus lawleri* (Colbert, 1981). The slightly more derived thyreophoran, *Emausaurus ernsti* (Haubold, 1990), provides critical data. In this taxon, a well-developed antorbital cavity is formed within the maxilla and lacrimal (Fig. 18). As in *Lesothosaurus diagnosticus* and other forms, the maxilla and lacrimal have broad medial laminae constricting the internal antorbital fenestra to a relatively small opening. Although the palatal elements are not known, the medial surface of the maxilla shows the palatine articular surface, thus fixing the position of the choana as directly opposite the internal antorbital fenestra. There is a low supralveolar lamina (Haubold, 1990), and the maxilla and lacrimal both have lateral laminae constricting the size of the external antorbital fenestra. Significantly, Haubold (1990) described a deep cavity entering the maxilla from the antorbital cavity. The nasolacrimal canal passes through the lacrimal bone, dorsomedial to the antorbital cavity.

Scelidosaurus harrisonii, the next higher thyreophoran, is generally similar but shows greater closure of the cavity. In *S. harrisonii* (BMNH R1111), the internal antorbital fenestra is not only directly opposite the choana, but the postchoanal strut of the palatine contributes to the caudal margin of the fenestra. The massive maxilla is so transversely thick that there is actually a short canal passing laterally from the internal fenestra to the main cavity. The antorbital cavity is enclosed by the maxilla, lacrimal, and probably jugal. There is a distinct antorbital fossa well excavated into the external surface of the maxilla; presumably this entire portion of the maxilla is the homolog of the medial lamina of other ornithischians. In the rostral apex of the antorbital fossa is a moderately large foramen directed rostrally into the bone. It is unknown if the foramen expands into an accessory cavity comparable to the cavity described for *Emausaurus ernsti.* As in the latter taxon, the nasolacrimal duct passes dorsomedially around the antorbital cavity through the lacrimal bone.

Among stegosaurs, the basal taxon *Huayangosaurus taibaii* exhibits a small but distinct external antorbital fenestra within the maxilla, lacrimal, and jugal (see Sereno and Dong, 1992). The internal antorbital fenestra is caudally situated within the antorbital cavity and is probably opposite the choana. A well-developed medial lamina of the maxilla walls the cavity internally, forming an antorbital fossa that undercuts the dorsal margin of the external antorbital fenestra. The cavity is partially walled-in laterally by a prominent supralveolar lamina and a lateral lamina of the lacrimal. The external antorbital fenestra is absent in *Chungkingosaurus jiangbeiensis* (Dong et al., 1983) and *Tuojiangosaurus multispinus* (Dong et al., 1983). It is present, however, in *Stegosaurus stenops,* in which the antorbital cavity is similar to *Huayangosaurus taibaii* but smaller and shallower (Sereno and Dong, 1992).

The Ankylosauria are a highly apomorphic group: they lack an external antorbital fenestra, most of the skull sutures have been obliterated by overlying dermal ossifications, and their snouts enclose a complicated pattern of cavities (Coombs, 1971, 1978; Maryanska, 1977; Coombs and Maryanska, 1990). As a result, the specified osteological correlates are difficult to assess. There clearly is a cavity within the maxillae of probably all ankylosaurids that may be homologous with the antorbital cavity (e.g., *Euoplocephalus tutus,* AMNH 5843, Fig. 19A; *Ankylosaurus magniventris,* AMNH 5894; see also Maryanska, 1977; Coombs, 1971, 1978; Tumanova, 1987; Coombs and Maryanska, 1990). This cavity—the "maxillary sinus" of the aforementioned authors—communicates rostrally with the narial region via a foramen in the premaxilla ventral or lateral to the true naris (e.g., *Pinacosaurus grangeri,* AMNH 6523; *Euoplocephalus tutus,* AMNH 5843; *Ankylosaurus magniventris,* AMNH 5214, 5895; see Maryanska, 1977). Maryanska (1977) suggested that the maxillary sinus lodged the glandula nasalis, which is not unreasonable since the cavity opens into the caudal part of the naris; furthermore, such a communication between the antorbital cavity and naris would be unique. However, the cavity seems inordinately large for a gland, and it communicates with other paranasal cavities (e.g., in *Ankylosaurus magniventris,* AMNH 5895). Moreover, Maryanska (1977) described a vertical septum within this cavity in *Pinacosaurus grangeri* and noted that both parts of the cavity open into the nasal cavity proper. Perhaps strictly the caudal portion of the cavity is the homolog of the antorbital cavity. Unfortunately, the communications of the various sinuses with each other and with the nasal cavity proper are poorly known (Coombs and Maryanska, 1990).

Although similar paranasal cavities have not been reported for nodosaurid ankylosaurs, it is not clear if sufficient material providing the necessary views is available to regard this as a positive absence. The frequently figured cross-section of *Edmontonia longiceps* (AMNH 3076; Coombs, 1971, 1978; Norman, 1985; Coombs and Maryanska, 1990) indeed shows a single, large cavity on each side within the snout (Fig. 19B). However, this cavity is partially subdivided by a dorsally projecting maxillary ridge that housed the tooth roots (Coombs, 1971). Since the cross-section (produced by a natural break) passes through that portion of the snout in which the antorbital cavity is lodged in other ornithischians, the possibility remains that the maxillary ridge is a septum between nasal cavity proper and antorbital cavity, the snout having broken transversely at the position of the ostium (which would be dorsal to the septum). The point is that nodosaurids may indeed have paranasal cavities similar to, although simpler than, those in ankylosaurids.

Dinosauria: Ceratopsia—There are three major groups of ceratopsian ornithischians, all presenting different conformations of the snout. In the basal ceratopsian *Psittacosaurus* spp. (Sereno, 1986), the external antorbital fenestra is probably absent. Earlier reports of the presence of a homologue of the maxillary antorbital fossa (Sereno, 1987; Sereno and Chao, 1988; Sereno et al., 1988) were later corrected (Sereno, 1990). Most specimens of *Psittacosaurus* spp. have an unossified gap between the lacrimal and premaxilla opening into a cavity in which the nasolacrimal canal opens (Sereno, 1987, 1990; Sereno et al., 1988). It is possible that this gap represents the remnants of an external antorbital fenestra, with the expansive caudodorsal lamina of the premaxilla restricting the size of the opening as it overlaps the lacrimal. The course of the nasolacrimal duct (Sereno, 1987; Sereno et al., 1988) tends to support this assessment. In juveniles of *Psittacosaurus mongoliensis* (AMNH 6535, 6536; see also Coombs, 1982; Sereno, 1987), this gap (perhaps best viewed as a fontanelle) is somewhat larger, although preservational artifact may increase its apparent size. Arguing against this notion is the observation of a specimen of this species in which the gap is fully within the lacrimal bone (Sereno, 1987), which would be unlike an external antorbital fenestra. Thus, it is probably judicious to follow Sereno (1990) in regarding the external antorbital fenestra as absent.

The snouts of basal neoceratopsians ("protoceratopsians") are well known from many specimens (Brown and Schlaikjer, 1940; Maryanska and Osmólska, 1975; Osmólska, 1986). In *Protoceratops andrewsi* (many AMNH specimens), *Bagaceratops rozhdestvenskyi* (Maryanska and Osmólska, 1975), and *Leptoceratops gracilis* (Sternberg, 1951), there is a small internal antorbital fenestra between the maxilla, lacrimal, and usually the jugal (Fig. 20A, B). The internal fenestra is relatively larger in young individuals (e.g., *Protoceratops andrewsi,* AMNH 6421). This aperture clearly communicates solely with the nasal cavity directly opposite the caudal portion of the choana (Osmólska, 1986). In most specimens, there is a well-marked antorbital fossa excavated into the maxilla, lacrimal, jugal, and, in *Bagaceratops rozhdestvenskyi,* the nasal. In most specimens of *Protoceratops andrewsi,* the antorbital cavity undercuts the margins of the external antorbital fenestra so that there are shallow lacrimal and jugal recesses and much deeper maxillary recesses; in many larger skulls (AMNH 6433, 6429, 6414, 6466) the rostral portion of the fossa is not deeply excavated into the surface (Fig. 20A, B). In *B. rozhdestvenskyi* and *P. andrewsi,* an accessory cavity is present within the body of the maxilla (Maryanska and Osmólska, 1975; Osmólska, 1986; see below).

The course of the nasolacrimal duct is unknown, and in fact, despite excellent material of *Protoceratops andrewsi* (AMNH 6429), no evidence of the nasolacrimal canal could be discovered. Sternberg (1951) also could not locate a canal in *Leptoceratops gracilis.* It should be noted that *Bagaceratops rozhdestvenskyi* has an additional opening in the snout rostral to the antorbital cavity, between maxilla and premaxilla (Maryanska and Osmólska, 1975); this structure remains poorly understood, but it appears to have little to do with the antorbital cavity.

In Ceratopsidae, the specified osteological correlates are easily interpreted, although the antorbital cavity is apparently very small. The internal antorbital fenestra is usually little more than an oval foramen situated between maxilla and lacrimal with varying contribution from the nasal and jugal (Dodson and Currie, 1990). It opens medially into the nasal cavity opposite the caudal portion of the choana; the palatine sends a lateral process to form the caudomedial border of the internal fenestra (Hatcher et al., 1907). Although there is sometimes a small maxillary

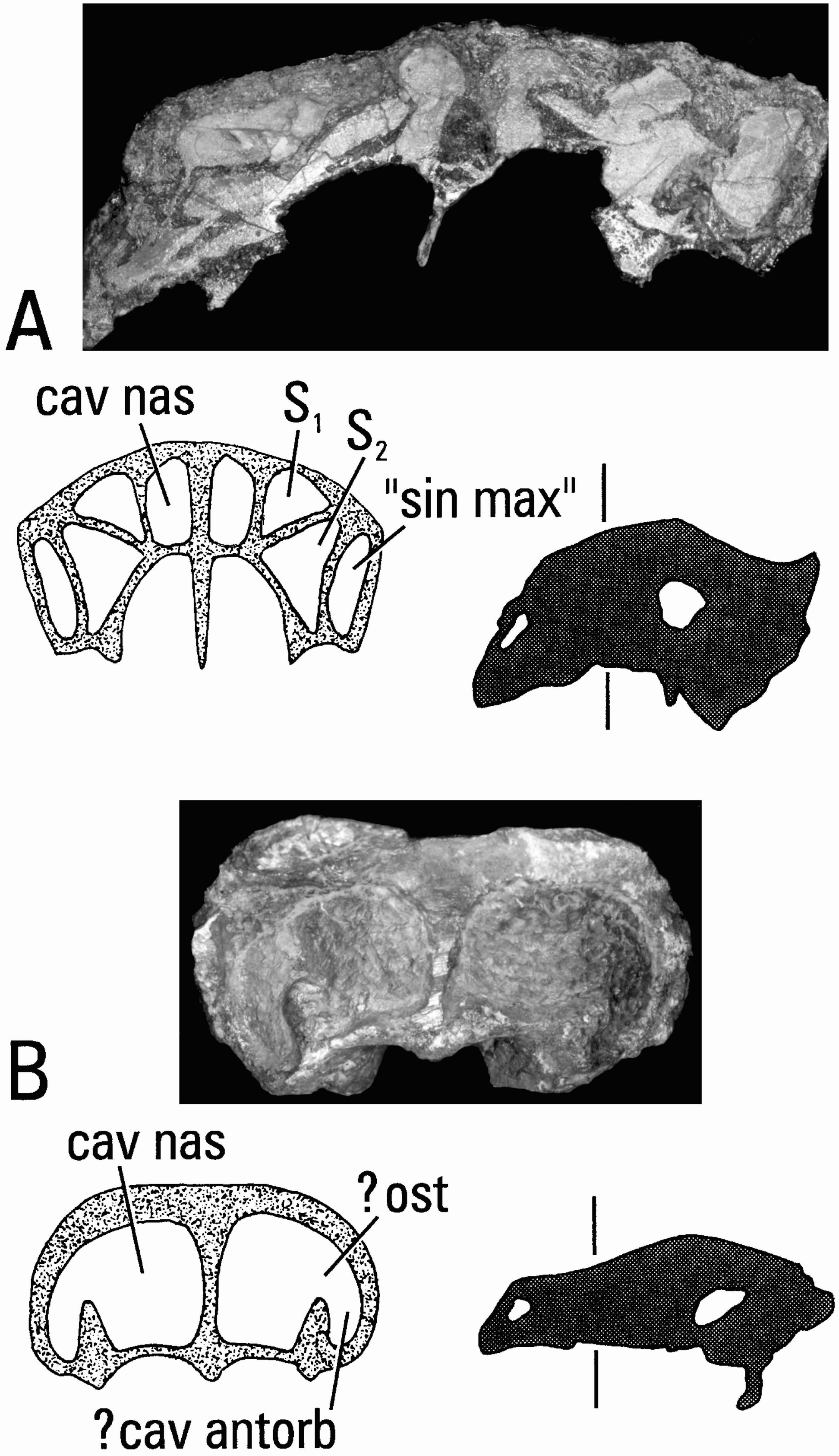

FIGURE 19. Transverse sections of snouts of Ankylosauria. **A**, *Euoplocephalus tutus* (AMNH 5403), rostral view of caudal part of skull. **B**, *Edmontonia longiceps* (AMNH 3076), caudal view of rostral part of skull. (Drawings after Coombs, 1978.)

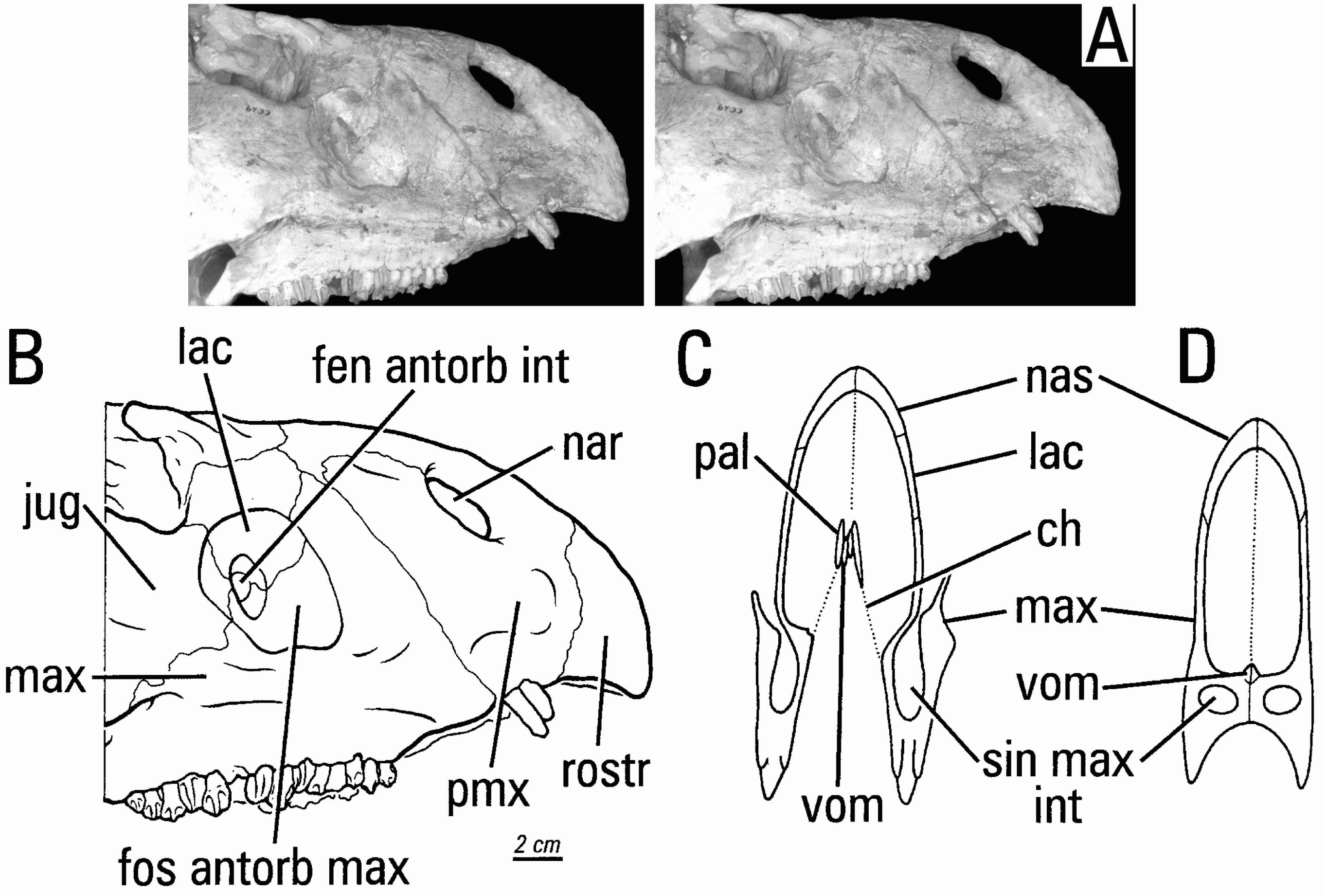

FIGURE 20. Protoceratopsians. **A**, stereophotographs of snout of *Protoceratops andrewsi* (AMNH 6433) in right lateral view. **B**, interpretive drawing of **A**. **C**, schematic transverse section of the snout of *Bagaceratops rozhdestvenskyi* showing the intramaxillary sinus. Left side of figure depicts a more rostral section than the right side which is more caudal. **D**, more rostral transverse section of the same species. (**C,D** modified after Osmólska, 1986).

antorbital fossa, the external antorbital fenestra is not usually well marked, and the fenestra is sometimes completely closed. Internally, the antorbital cavity passes into a cavity formed between maxilla and palatine and through which passed the maxillary neurovasculature (well displayed in a disarticulated skull referable to *Chasmosaurus belli,* BMNH R4948). The jugal walls this cavity caudolaterally (Lehman, 1989), such that the whole area, although highly transformed, exhibits the same topographic relations as in more basal ornithischians. The course—indeed, even the presence—of the nasolacrimal canal is not discernible in many specimens. Lehman (1989) described one for *Chasmosaurus mariscalensis,* but it is noted as absent in *Triceratops horridus* by Forster (1990) and Centrosaurinae by Sampson (1993).

Dinosauria: Pachycephalosauria—Most of the relevant data on Pachycephalosauria come from Maryanska and Osmólska's (1974) study of *Prenocephale prenes. P. prenes* is the only known pachycephalosaur that retains an external antorbital fenestra, which forms a small opening between maxilla and lacrimal; there is no external fossa surrounding the fenestra. The external fenestra leads internally into a large antorbital cavity (the "intramaxillary sinus" of Maryanska and Osmólska, 1974) that extends within the length of the maxilla and is bounded caudally by lateral and medial laminae of the lacrimal. The cavity opens medially into the nasal cavity directly opposite the choana. The nasolacrimal canal pierces the lacrimal, passing dorsomedially through the antorbital cavity. Furthermore, the maxillary neurovasculature enters the cavity caudoventrally. Thus, this structure displays the specified osteological correlates. Although no other known pachycephalosaurs retain an external antorbital fenestra, Maryanska and Osmólska (1974) noted that the cavity was found in other members of the clade. Based on the pattern of crushing, Sues and Galton (1987) suggested that the sinus was present also in *Stegoceras validum.* These other forms, therefore, carry to its extreme the ornithischian trend of enclosure of the antorbital cavity (see below).

Pterosauria—All pterosaurs retain an antorbital cavity (Fig. 21), but apparently in all Pterodactyloidea (Bennett, 1994) the ascending ramus of the maxilla has been lost and the reciprocal, maxillary (subnarial) process of the nasal has been reduced so that the naris and antorbital cavity have become confluent, forming the nasoantorbital fenestra. Among "rhamphorhynchoids" (generally assumed to be a paraphyletic grouping; see Padian, 1985), there is usually little or no development of an antorbital fossa so that the internal and external antorbital fenestrae have the same borders (e.g., *Campylognathoides liasicus,* CM 11424; *Rhamphorhynchus longiceps,* CM 11428; *Rhamphorhynchus muensteri,* CM 11431; see also Wellnhofer, 1978; Wild, 1978). The borders of the fenestra vary but usually include the maxilla, lacrimal, jugal, and sometimes nasal. In probably all pterodactyloids (Bennett, 1991, in press), rostroventrally directed processes from each nasal fuse, forming a

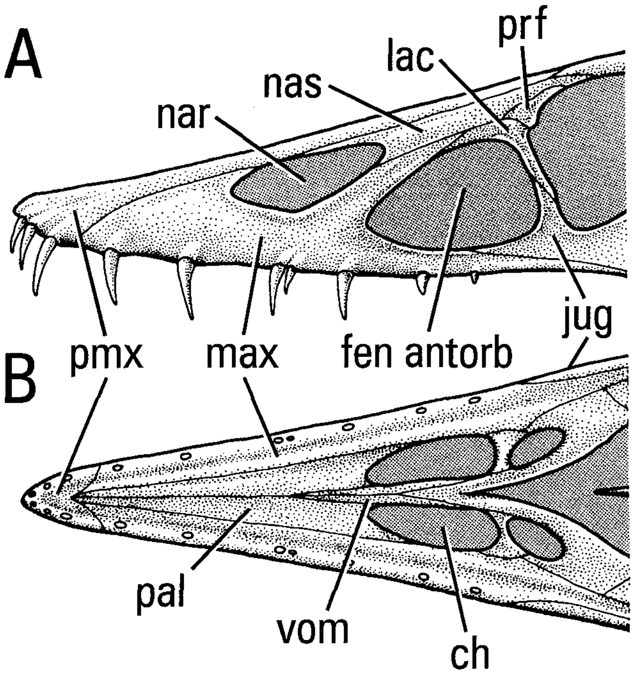

FIGURE 21. *Scaphognathus crassirostris.* Drawings of rostral part of skull in **A**, left lateral and **B**, ventral views. (Modified after Wellnhofer, 1991b.)

single median "nasal process" (e.g., *Pterodactylus kochi,* Wellnhofer, 1968; *Germanodactylus cristatus,* Wellnhofer, 1978; *Anhanguera santanae,* Wellnhofer, 1987; *Pteranodon longiceps,* Bennett, 1991). This structure probably marks the boundary between the narial and antorbital cavities.

The only "rhamphorhynchoid" in which the antorbital cavity excavates any significant antorbital fossa is *Eudimorphodon ranzii* (Wild, 1978), in which the jugal ("lacrimal" of Wild, 1978) bears a shallow rostral fossa. Jugal antorbital fossae are present in the pterodactyloids *Pteranodon longiceps* (KUVP 976, USNM 13868; see also Witmer, 1987b; Bennett, 1991, in press) and perhaps *Santanadactylus araripensis* (Wellnhofer, 1985). Lacrimal antorbital fossae are present in *Pteranodon longiceps* (KUVP 976, USNM 13868; Witmer, 1987b; Bennett, 1991, in press), *Anhanguera santanae* (AMNH 25555), and probably *Tapejara wellnhoferi* (Wellnhofer and Kellner, 1991) and *Tropeognathus mesembrinus* (Wellnhofer, 1987). Despite extensive transformation of palatal conformation (Wellnhofer, 1978), the antorbital cavity in all Pterosauria opens medially into the nasal cavity, directly opposite the choana (Fig. 21). The course of the nasolacrimal canal is rarely discernible, although Wellnhofer (1985) described an orbital aperture of the canal in *Araripesaurus santanae,* which, by its position, indicates a probable course dorsomedial to the antorbital cavity. Accessory cavities are developed in many, if not all, of the large pterodactyloids (see below).

Crurotarsi: Parasuchia—The taxonomic allocation of individual parasuchian specimens remains in a state of flux, as do the phylogenetic relationships of the taxa (see Doyle and Sues, 1995). This paper primarily uses the names employed by Ballew (1989) and/or the holding museums, with the attributions made in Long and Murry's (1995) important monograph, when different, indicated in brackets; not all taxa are demonstrably monophyletic. In general in parasuchians, the antorbital cavity is within the maxilla and lacrimal with varying contributions from the jugal and nasal (Fig. 22D). In basal parasuchians (Ballew, 1989), such as *Parasuchus hislopi* [*Paleorhinus* sp.] (Chatterjee, 1978a), *Paleorhinus bransoni* (FMNH UC 632), *Paleorhinus scurriensis* [*Paleorhinus bransoni*] (TTUP 8090), and *Angistorhinus grandis* (FMNH UC 631), there is a well-developed antorbital fossa rimming the caudal, dorsal, and rostral margins of the internal antorbital fenestra, extending onto the jugal, lacrimal, nasal, and maxilla; the ventral edge of the external fenestra, however, is formed by the sharp edge of the supralveolar lamina of the maxilla. In most higher parasuchians there is usually little or no external antorbital fossa (e.g., *Rutiodon lithodendrorum* [*Leptosuchus crosbiensis*], UCMP 27181, Fig. 22D; *Rutiodon* [*Leptosuchus*] *adamanensis,* UCMP 26699; *Pseudopalatus pristinus,* AMNH 7222, UCMP 34249, 27281, NMMNH P-4256; *Mystriosuchus planirostris,* AMNH 10644). In all known parasuchians, the antorbital cavity opens medially into the nasal cavity just opposite the choana where it is floored by the palatine and usually the maxilla. In *Phytosaurus* sp. (BMNH 38037) and *Pseudopalatus pristinus* (NMMNH P-4256), the nasolacrimal canal passes between the lacrimal and prefrontal; to reach the choana, the duct would have had to pass dorsomedially over the antorbital cavity (it should be noted that Camp [1930] placed the canal within the lacrimal bone, but this could not be confirmed on the specimens cited by him). Parasuchians thus display the specified osteological correlates.

Crurotarsi: Ornithosuchidae—Ornithosuchidae have a large internal antorbital fenestra bounded by the maxilla, lacrimal, and jugal (Fig. 10). In both *Ornithosuchus longidens* (BMNH R2409, R3143; see also Walker, 1964) and *Riojasuchus tenuisceps* (Bonaparte, 1972) the internal fenestra communicates medially with the nasal cavity and its rostral third is directly opposite the choana. The antorbital cavity is partly floored medially by the palatine, as mentioned earlier. Laterally, the antorbital cavity excavates an extensive antorbital fossa on the maxilla, lacrimal, and jugal around the entire margin of the internal fenestra, except for a small section caudally where the lacrimal overhangs the cavity (Fig. 10A). The antorbital fossa is more extensive in *R. tenuisceps* (Bonaparte, 1972) than in *O. longidens.* There are two alternative courses for the nasolacrimal canal in *O. longidens* (the canal is unknown or undescribed in *R. tenuisceps*). In the first alternative, the canal would pass through the lacrimal bone such that the duct would open laterally into the region of the lacrimal antorbital fossa (much as in theropods). Walker (1964) cited as evidence an apparent caudal foramen within an isolated lacrimal of *O. longidens* (BMNH R3143, a cast from a natural mold), which he interpreted as the orbital aperture of the canal. However, in an actual bony specimen (BMNH R3142), this putative foramen is clearly absent. In the second alternative, the nasolacrimal duct would pass between the lacrimal and prefrontal bones. The orbital aperture of the nasolacrimal canal appears to be represented by a notch between the lacrimal and prefrontal (BMNH R3142, R3143); the canal then passed rostrally as a rostrally widening groove within the suture (BMNH R3143; Walker, 1964: fig. 3b). The latter alternative is probably more likely, but in either case, the nasolacrimal duct would assume a course dorsomedial to the antorbital cavity. In the latter interpretation, the deep caudodorsal lacrimal fossa could well be an "incipient pneumatic cavity" as described by Walker (1964:104). Ornithosuchids thus display all the osteological correlates of a pneumatic antorbital cavity.

Crurotarsi: Non-crocodylomorph Suchia—In most non-crocodylomorph suchians, the internal antorbital fenestra is moderately large (very large in *Gracilisuchus stipanicicorum*; Romer, 1972), invariably opening toward the nasal cavity directly opposite the choana, usually in the rostral half of the fenestra (see Figs. 9, 23). The fenestra is bordered by the maxilla, lacrimal, and sometimes part of the jugal. In most cases, the palatine partly floors the medial portion of the antorbital cavity. The internal fenestra is surrounded, usually on all sides,

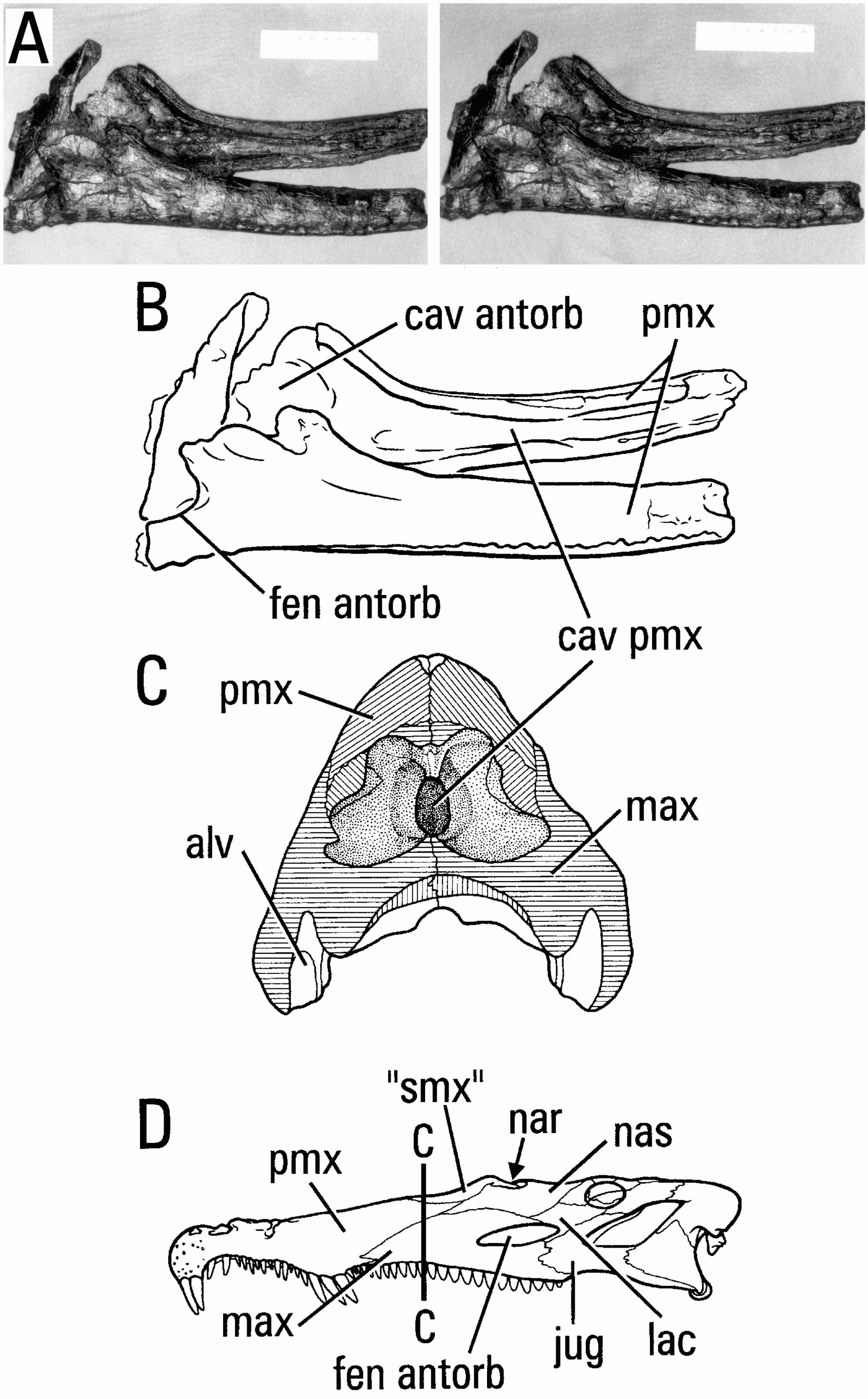

FIGURE 22. Parasuchians. **A**, stereophotographs of partially disarticulated snout of *Rutiodon carolinensis* (AMNH 4). The left side of the skull is displaced dorsally relative to the right side, such that the right side is viewed laterally and the left side medially. **B**, interpretive drawing of **A**. **C**, transverse section through the snout of *Rutiodon* [*Leptosuchus*] *adamanensis* (UCMP 26699) at the level shown in **D**, showing the large premaxillary cavity that communicates with the antorbital cavity. **D**, skull of same in left lateral view. (**C**,**D** redrawn from Camp, 1930.)

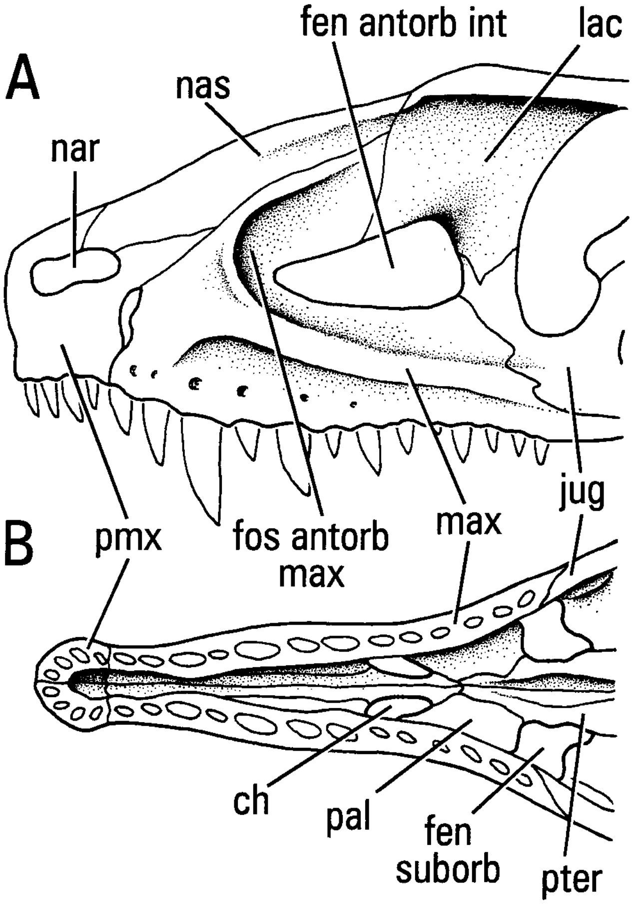

FIGURE 23. *Postosuchus kirkpatricki*, facial skeleton. **A**, left lateral view. **B**, ventral view. (Redrawn from Chatterjee, 1985.)

by an extensive, well-marked antorbital fossa (Fig. 23). In *G. stipanicicorum*, however, there is no fossa on the lateral surface of the jugal ramus of the lacrimal or ventrally on the body of the maxilla. *Desmatosuchus haplocerus* (TTUP 9023; see also Case, 1922) is also an exception in that the fossa does not extend ventrally onto the maxilla.

The course of the nasolacrimal canal is known in the stagonolepidids *D. haplocerus* (TTUP 9023) and *Stagonolepis robertsoni* (Fig. 9A,B; Walker, 1961) where it clearly opens orbitally between the lacrimal and prefrontal. The rostral course of the duct is a little less clear. It probably did not extend to the naris as suggested by Walker (1961) but rather opened into the choanal recess medial to the ascending ramus of the maxilla (e.g., *S. robertsoni,* BMNH R4787), passing dorsomedially around the antorbital cavity. The nasolacrimal canal is present in *Postosuchus kirkpatricki* (TTUP 9000; Chatterjee, 1985), extending from orbit to antorbital cavity, but it is not clear if it runs within the lacrimal or in the lacrimoprefrontal suture.

Crurotarsi: Crocodylomorpha—The general conformation of the facial bones in basal crocodylomorphs does not differ substantially from that observed in most other archosaurs, although the trend for reduction and enclosure of the antorbital cavity is already evident (see section on facial trends below). The basal sphenosuchians *Terrestrisuchus gracilis* (Crush, 1984), *Saltoposuchus connectens* (Huene, 1921; Sereno and Wild, 1992), and *Pseudhesperosuchus jachaleri* (Bonaparte, 1972) retain a relatively large antorbital cavity that excavates a deep antorbital fossa on the extensive medial laminae of the maxilla and lacrimal. Thus, the internal antorbital fenestra, bordered by the lacrimal and maxilla, is relatively long and low and is much smaller than the external fenestra. A well-developed supralveolar lamina provides a sharp ventral border to the fenestra, and the palatine partially floors the antorbital cavity. The internal antorbital fenestra opens directly opposite the choana within the nasal cavity, as in all sphenosuchians (Figs. 1, 24).

The course of the nasolacrimal canal is known best in *Sphenosuchus acutus* where it passes dorsomedially over the antorbital cavity completely within the lacrimal, just internal to the antorbital fossa, to open medially above the dorsal portion of the internal antorbital fenestra; the duct presumably continued to the choana along a low ridge on the medial surface of the ascending ramus of the maxilla (Walker, 1990). The position of the orbital aperture of the canal in *Terrestrisuchus gracilis* (Crush, 1984), *Saltoposuchus connectens* (Sereno and Wild, 1992), and *Dibothrosuchus elaphros* (IVPP V7907; Fig. 24) implies a similar course in these animals.

Basal crocodyliforms (protosuchians) continue the trend of reduction of the antorbital cavity and external antorbital fenestra. In the forms for which data are available, the internal antorbital fenestra is a relatively small opening bounded by the lacrimal and maxilla (Fig. 25A). It clearly opens medially into the nasal cavity, and it can be seen to be opposite the choana in *Protosuchus richardsoni* (MCZ 6727, UCMP 130860, AMNH 3024; Crompton and Smith, 1980; Clark, 1986), an unnamed protosuchid (UCMP 97638; Clark, 1986), *Orthosuchus stormbergi* (Nash, 1975), *Gobiosuchus kielanae* (Osmólska, 1972; Fig. 25B,C), and *Hoplosuchus kayi* (CM 11361). The antorbital cavity is floored medially by the palatine in at least *Gobiosuchus kielanae* (Osmólska, 1972; Fig. 25B,C). The antorbital fossa is not extensive in any of these taxa, but tends to excavate the lacrimal and maxilla caudally, dorsally, and rostrally. It is not clear if the apparently prominent maxillary fossa of *Hemiprotosuchus leali* (Bonaparte, 1972) or the "accessory antorbital depression" of *Platyognathus hsui* (Wu and Sues, 1996) are associated with the antorbital cavity. The course of the nasolacrimal canal has been described only for *Protosuchus richardsoni,* where it extends within the lacrimal from the orbit, dorsomedially over the antorbital cavity, to open into the caudodorsal margin of the internal antorbital fenestra (Clark, 1986).

Further reduction of the antorbital cavity and closure of the external antorbital fenestra occurs more than once in Mesoeucrocodylia, how many times depending on the cladogram adopted (see below). Before surveying this taxon, one of the osteological correlates, the position of the choana, requires clarification. The most obvious synapomorphy of Mesoeucrocodylia involves the formation of a bony nasopharyngeal duct such that the opening of the airway is diverted caudally (Huxley, 1875; Langston, 1973; Benton and Clark, 1988; Clark, 1994; Busbey, 1995). This opening usually is referred to as the "choana." However, as mentioned above for extant crocodilians, the rostral end of the nasopharyngeal duct is the primary choana, homologous to the choana of other archosaurs (Witmer, 1995b), and the caudal end of the duct is a mesoeucrocodilian neomorph, the secondary choana. Thus, in the following discussion, explicit reference will be to only the primary choana.

The basal mesoeucrocodilian clade (Buffetaut, 1982; Benton and Clark, 1988; Wu, Li, and Li, 1994), Thalattosuchia, represents the earliest instance of extensive reduction of the antorbital cavity. The basal thalattosuchian *Pelagosaurus typus* (Fig. 26; BMNH 32599) resembles teleosaurids such as *Steneosaurus* spp. (FMNH UC 402, CM 360, MCZ 1063, many BMNH specimens) in having a very small, slitlike external antorbital fenestra between the maxilla and lacrimal with very little to no development of an antorbital fossa (Fig. 26A); in some specimens the fenestra may even be absent (see Westphal,

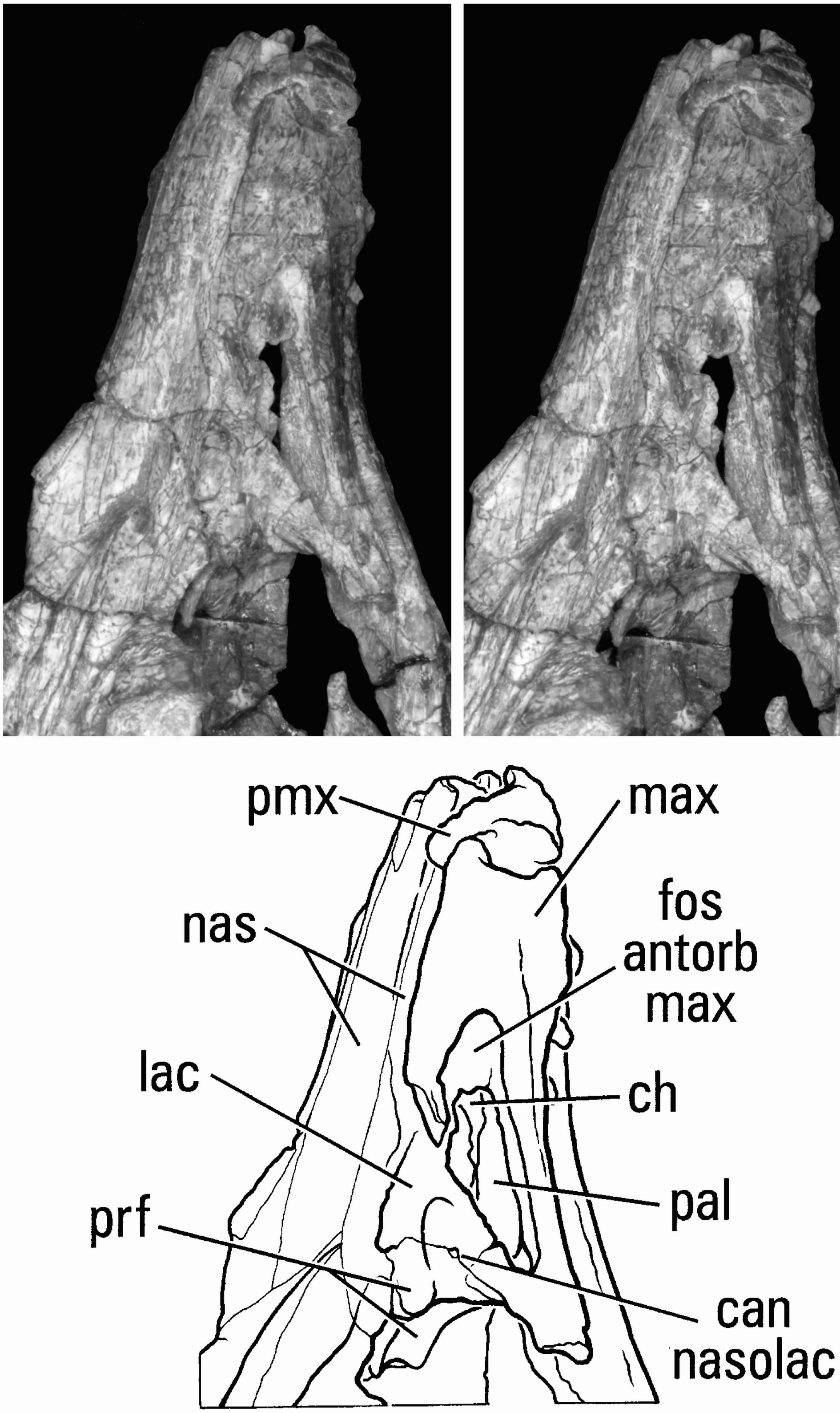

FIGURE 24. *Dibothrosuchus elaphros.* Stereophotographs of the snout of IVPP V7907 in right dorsolateral view, with interpretive drawing below.

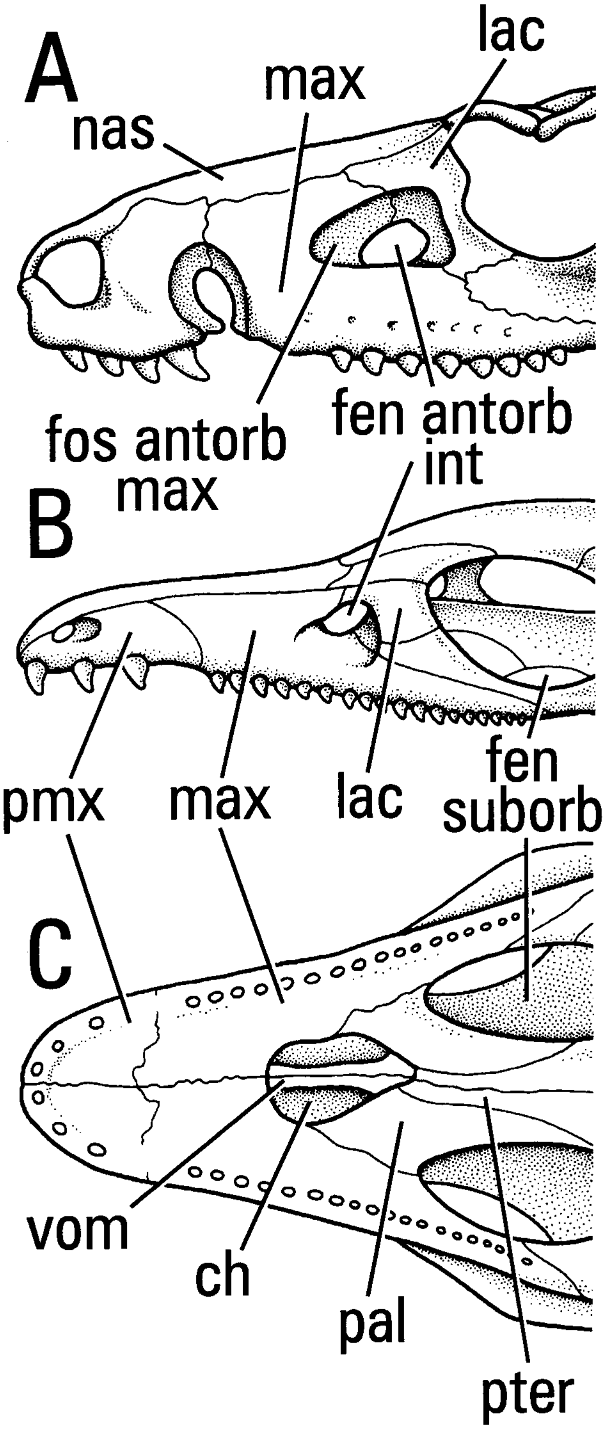

FIGURE 25. Protosuchian crocodylomorphs. **A**, *Protosuchus richardsoni*, snout of MCZ 6727 (with some details modified from Crompton and Smith [1980] and Sues et al. [1994]) in left lateral view. **B**,**C**, *Gobiosuchus kielanae*, snout in (**B**) left lateral and (**C**) ventral views. (**B**,**C** modified after Osmólska, 1972.)

1962). Metriorhynchids have a small internal antorbital fenestra, bounded by the maxilla and lacrimal and often the nasal, but usually have a much more extensive antorbital fossa (Fig. 27). Whereas the external antorbital fenestra is often continued rostrally as a narrow groove in *P. typus* and some teleosaurids (Fig. 26A), there is always a broad antorbital fossa in metriorhynchids (bounded by the maxilla and lacrimal and usually also the nasal and jugal), excavated into the side of the snout rostral to the fenestra and continued rostrally as a tapering groove on the maxilla (Fig. 27; Wenz, 1968; Gasparini and Chong Díaz, 1977; Buffetaut, 1982). There is considerable intraspecific variation in the form of the fossa and groove. For example, in *Metriorhynchus superciliosus*, the boundary between fossa and groove may be relatively subtle (BMNH R3014, R3900, R4762), or the fossa may be very deeply excavated and extensive with the rostral groove being distinct from (although continuous with) the rostral edge of the fossa (BMNH R3899). Also in this species and in *Teleidosaurus gaudryi* (BMNH R3353), the antorbital fossa clearly extends caudally onto the lacrimal (BMNH R3900, R4762; see Fig. 27).

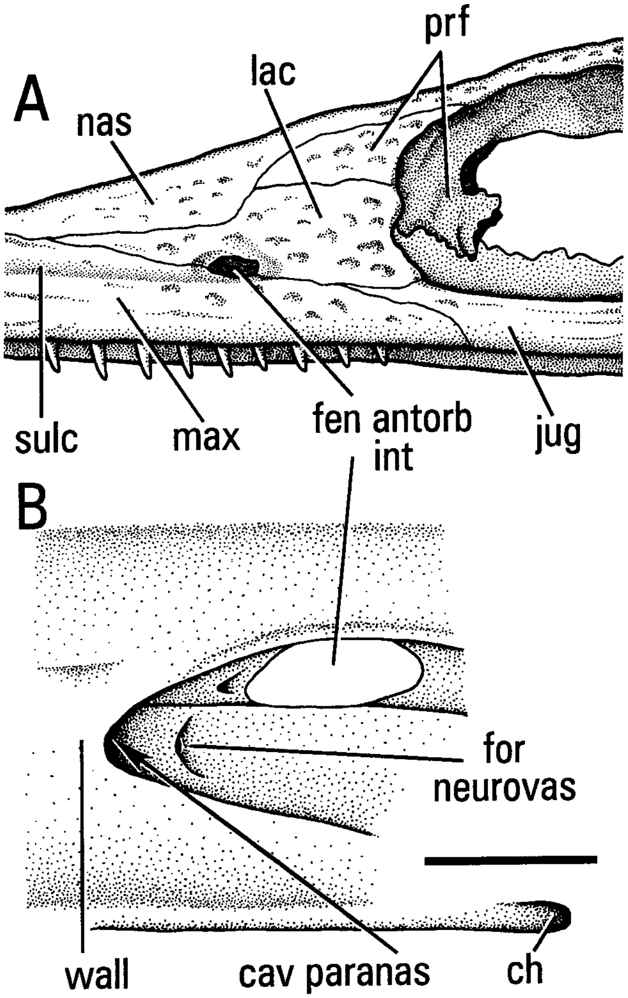

FIGURE 26. *Pelagosaurus typus*. **A**, drawing of antorbital region of BMNH 32599 in left lateral view. **B**, schematic drawing of a medial view of the right antorbital region of the same specimen (observed through the orbit directly and with dental mirror).

The relationship between the primary choana and internal antorbital fenestra is known in *P. typus* (BMNH R32599) and *M. superciliosus* (BMNH R2048; see also Wenz, 1968) where the fenestra clearly opens medially into the nasal cavity and is directly opposite the primary choana. An unequivocal nasolacrimal canal could not be located in even the well-preserved material of *P. typus*, *Steneosaurus* spp., and *M. superciliosus*; the only possible candidate is a matrix-filled pit within the orbital margin of the lacrimal in *Teleidosaurus gaudryi* (BMNH

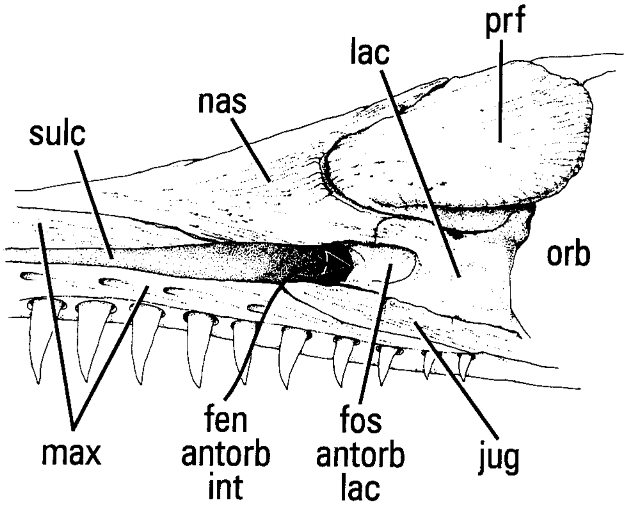

FIGURE 27. *Metriorhynchus superciliosus.* Reconstruction of antorbital region in left lateral view based on BMNH R3900, R4762, and R3899.

R3353). Thus, although requiring further confirmation, it is possible that absence of the nasolacrimal canal (and presumably the duct, as well) may characterize this already distinctive group.

In extant crocodilians, the antorbital cavity is located completely internally. *Pelagosaurus typus* also appears to have "internalized" its antorbital cavity. In *P. typus* (BMNH 32599, 32607), a conical paranasal chamber within the maxilla is separated from the nasal cavity proper by a thin, caudally emarginate septum (Fig. 26B). This chamber is immediately rostral to the external antorbital fenestra and clearly associated with the antorbital cavity in that the dorsolateral attachment of the septum runs caudodorsally over the fenestra, thus forming its dorsal margin. The maxillary neurovasculature also traversed the paranasal chamber, as indicated by foramina in the lateral wall of the chamber, but the chamber appears too large solely for vessels and nerves. The caudal aperture of this paranasal chamber closely resembles the aperture leading into the caviconchal sinus in modern crocodilians. Thus, the caudal margin of the septum is probably equivalent to the internal antorbital fenestra of other archosaurs, which implies that the chamber is the antorbital cavity.

Metriorhynchus superciliosus (BMNH R3900, R2048) clearly lacks such an internal paranasal chamber but retains a moderately large external antorbital fossa. Thus, it seems likely that, in *Pelagosaurus typus,* the formerly external cavity has been enclosed laterally and internalized, constricting the external fenestra to a slit. In both *P. typus* and metriorhynchids, a groove extends rostrally from the external fenestra, which is consistent with this assessment. Antunes (1967) suggested that this groove conducted neurovasculature, which is a reasonable interpretation. If the situation in *P. typus* is interpreted correctly here, its internalization of the antorbital cavity would represent an acquisition independent of that observed in extant crocodilians, because several higher mesoeucrocodilians display the primitive condition (i.e., a relatively large external antorbital fenestra, well developed external antorbital fossa).

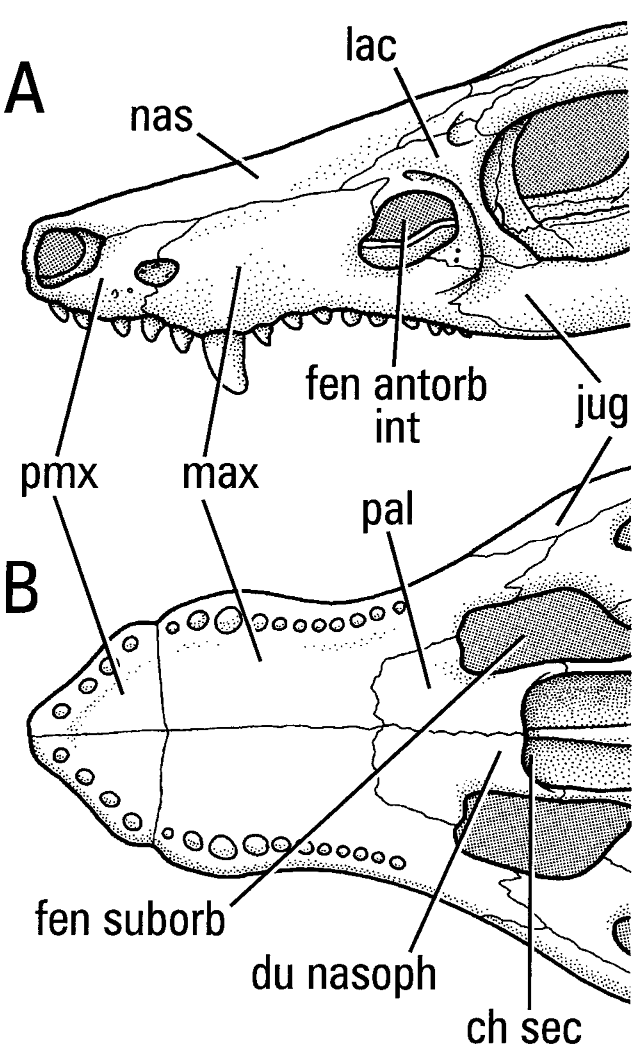

FIGURE 28. *Araripesuchus gomesii.* **A**, Drawing of snout in left lateral view (modified after Hecht, 1991). **B**, same in ventral view (modified after Gasparini, 1971).

Higher mesoeucrocodilians (i.e., Metasuchia; Benton and Clark, 1988; Wu, Li, and Li, 1994) include a series of forms that exhibit aspects of facial morphology more similar to basal crocodylomorphs than to thalattosuchians. These include *Hsisosuchus chungkingensis* (Li et al., 1994; although its precise phylogenetic position is somewhat uncertain: see Wu, Li, and Li, 1994), *Notosuchus terrestris* (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991b), a notosuchid from Malawi (Clark et al., 1989), *Uruguaysuchus aznarezi* (Rusconi, 1932; Gasparini, 1971), and *Araripesuchus gomesii* (AMNH 24450; Price, 1959; Gasparini, 1971; Hecht, 1991; Fig. 28). All have a small internal antorbital fenestra between the maxilla and lacrimal that leads medially into the nasal cavity (the position of the primary choana has not been described). Similarly, all these forms exhibit a well-developed antorbital cavity excavating a fossa on the maxilla and lacrimal. In at least *Notosuchus terrestris* and *Uruguaysuchus aznarezi,* the antorbital cavity extends deeply rostroventrally into the maxilla beyond the margin of the external antorbital fenestra (Rusconi, 1932; Gasparini, 1971; Bonaparte, 1991b), perhaps forming an accessory cavity. According to Gasparini (1971), the nasolacrimal canal in *N. terrestris, U. aznarezi,* and *A. gomesii* passes through the lacrimal to open within the caudodorsal portion of the antorbital cavity; from here the duct presumably passed medially through the internal antorbital fenestra (as in theropods) to reach the primary choana. Thus, the specified osteological correlates are present and in fact quite similar to more basal crocodylomorphs.

Araripesuchus gomesii (Fig. 28) is very closely related to the clade of higher metasuchians called Neosuchia (Benton and

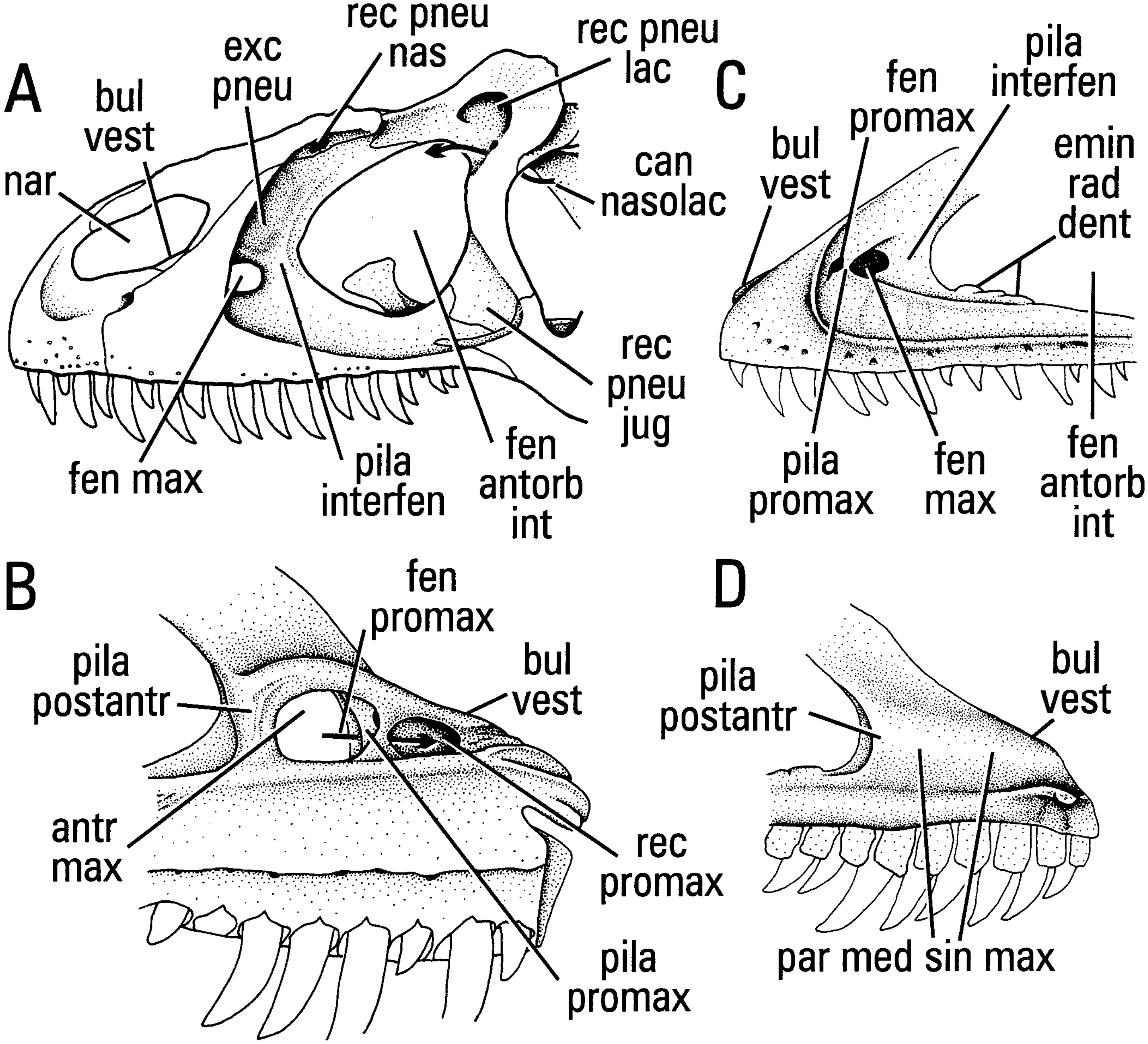

FIGURE 29. The accessory cavities in the maxilla, lacrimal, and/or nasal of two theropods. **A**, *Allosaurus fragilis,* antorbital region in left lateral view. **B**, left maxilla of same in medial view. **C**, *Marshosaurus bicentesimus,* left maxilla in lateral view. **D**, same in medial view. (**A,B** modified after Madsen [1976b] and specimens; **C,D** reconstructed from UUVP 1846 and UUVP 4695.)

Clark, 1988). This is significant because some metasuchians more basal than *A. gomesii* have closed the external antorbital fenestra. Among these are *Baurusuchus pachecoi* (Price, 1945), *Sebecus icaeorhinus,* and probably *Libycosuchus brevirostris* (Stromer, 1914; Buffetaut, 1982). Benton and Clark (1988) regarded this reduction as a synapomorphy of these taxa and neosuchians, with the condition in *A. gomesii* being a reversal. However, Gasparini et al. (1991) placed *A. gomesii* more basally and considered closure of the fenestra a synapomorphy of *B. pachecoi* and *S. icaeorhinus.* Clearly this segment of crocodylomorph phylogeny needs additional work, as noted by Benton and Clark (1988).

As its name implies, Neosuchia includes crocodylomorphs of genuinely modern aspect. This modern appearance results from the characteristic pattern of skull flattening in which structures, such as the lacrimal, that were laterally placed in more basal forms are now located dorsally on the roof of the snout. Thus, it is possible that the morphogenetic mechanism producing this pattern in extant crocodilians—i.e., rotation of the nasal cavity (Witmer, 1995b)—arose in the common ancestor of Neosuchia. Most non-crocodilian neosuchians were not examined in great detail for this study, but comments will be made on a few of them.

Retention of an (external) antorbital fenestra was regarded by Norell and Clark (1990) as a plesiomorphy of Atoposauridae, the basal clade of neosuchians, although Clark (1986) and Buscalioni and Sanz (1988) noted its absence in some atoposaurids. The atoposaurid *Theriosuchus pusillus* almost certainly has a small opening between the maxilla and lacrimal and even appears to have a thalattosuchian-like groove on the maxilla leading rostrally from it (BMNH 48330, 48260). The maxillary groove in *T. pusillus* may signal, as in *Pelagosaurus typus*, the

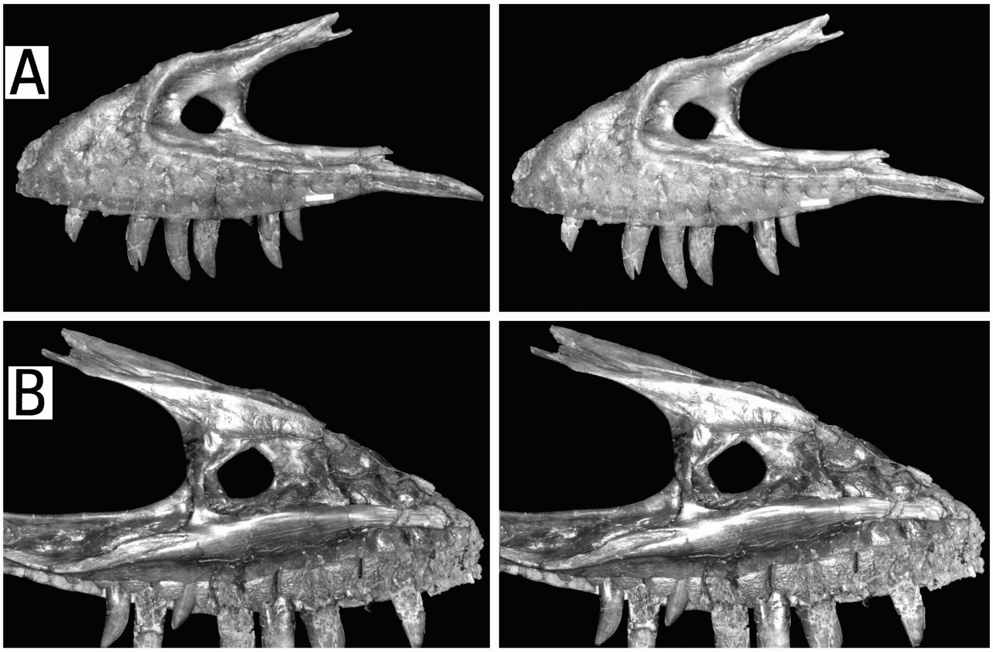

FIGURE 30. *Albertosaurus libratus*. **A**, stereophotographs of left maxilla of RTMP 83.35.100 in lateral view. **B**, same in medial view. **C**, Interpretive drawing of **A**. Arrow points to the promaxillary fenestra concealed behind the ascending ramus. **D**, interpretive drawing of **B**. Arrow passes through the caudal fenestra in the maxillary antrum, between the postantral and interfenestral struts. **E**, drawing of the same specimen in oblique rostrodorsomedial view. Arrow at right passes from the antorbital cavity through the promaxillary fenestra into the promaxillary recess. Arrow at left passes through the caudal fenestra in the maxillary antrum. Curved arrows point into the interalveolar pneumatic recesses.

internalization of the antorbital cavity. An isolated maxilla of *T. pusillus* (BMNH 48260) has ample space for an internalized antorbital cavity between the lateral wall of the nasal cavity and the tooth-bearing portion. A maxillary groove was not observed in any more derived neosuchians, and its absence may correlate with complete closure of the external antorbital fenestra.

Goniopholidids have an unusual feature aptly termed the "maxillary depression" by Buffetaut (1982, 1986). In *Goniopholis simus* (BMNH 41098), this depression is completely within the maxilla, just dorsal to the tooth row, and, although somewhat subdivided by two low septae, does not open medially. Buffetaut (1982) identified a small foramen between the lacrimal and maxilla in this specimen and in *Eutretauranosuchus delfsi* that he regarded as the antorbital fenestra. Although he suggested that the foramen was associated with the maxillary depression, I could not confirm the presence of this foramen in BMNH 41098, and it is not clear how such a foramen would relate to the depression. In any case, the maxillary depression is an unusual feature of problematic function.

All higher neosuchians (i.e., Dyrosauridae, *Bernissartia fagesii,* Eusuchia) have completely closed the external antorbital fenestra (Norell and Clark, 1990). Given their similarity to extant eusuchians, the extinct higher neosuchians presumably internalized the antorbital cavity in a similar manner, although appropriate material was not available to confirm this for all taxa.

Conclusions

Having examined in detail all of the major clades of archosaurs, it is possible to infer the presence of an epithelial air sac within the antorbital cavities of all Archosauria with very little speculation (a level I inference). Whereas previous hypotheses failed to implicate the antorbital fenestrae and fossa in housing a gland or jaw muscle, these bony structures are, in fact, intimately (almost certainly causally) related to the presence of an epithelial air sac. In other words, all of the osteological correlates of the air sinus that were observed in extant birds and crocodilians (the extant phylogenetic bracket) were observed in virtually all clades of extinct archosaurs. For example, the internal antorbital fenestra is the bony aperture through which the epithelial diverticulum passes. The antorbital fossae are pneumatic fossae excavated by the air sac. The external antorbital fenestra develops as a fontanelle around the paranasal air sac. Thus the original hypothesis survives the congruence test, and the avian antorbital sinus is indeed homologous to the caviconchal sinus of crocodilians. Therefore, given that the osteological correlates are indeed causally associated with the air sac, all extinct archosaurs possessed a homologous paranasal air sinus, unless it was apomorphically lost. The term developed for birds for the epithelial diverticulum—the antorbital sinus (Witmer, 1987b, 1990)—may be applied to all archosaurs, reserving the designation "antorbital cavity" for the bony space (Witmer, 1994).

Given the above conclusions, closure of the external antorbital fenestra is a derived condition. Although a large antorbital cavity and a prominent external fenestra remain important features of Archosauria as a whole, the external antorbital fenestra independently closes in at least ten different clades: a number of crocodylomorphs clades, a few birds (e.g., some owls), Stegosauridae, Ankylosauria, Hadrosauridae, most Pachycephalosauria, Psittacosauridae, some Ceratopsidae. In almost all of these taxa, there is evidence that the antorbital cavity is still present, just internalized.

ACCESSORY CAVITIES AS COMPELLING MORPHOLOGICAL EVIDENCE FOR PARANASAL PNEUMATICITY

Accessory cavities are recesses located in the bones surrounding the antorbital cavity (e.g., lacrimal, maxilla, nasal,

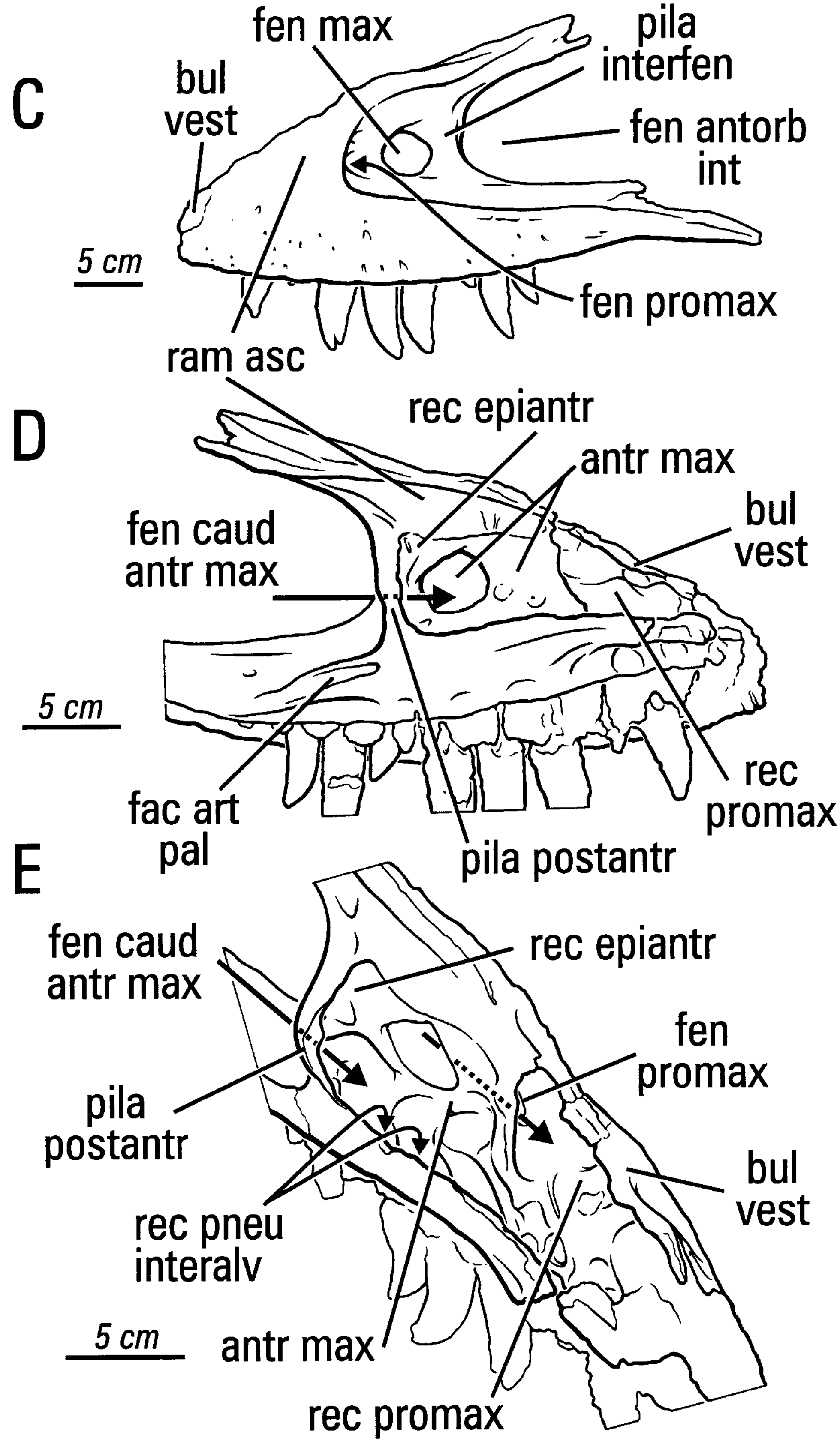

FIGURE 30. *(Continued)*

palatine). In extant forms, they are produced by pneumatization and house subsidiary epithelial diverticula of the antorbital paranasal air sinus (Witmer, 1994, 1995b). Therefore, accessory cavities are the osteological correlates of the subsidiary diverticula. In most cases, the cavities are smooth-walled, strutted recesses and may be multi-chambered. Sometimes they communicate with the antorbital cavity via a relatively small pneumatic foramen, other times through a very broad aperture (Wegner, 1958; Witmer, 1990, 1995b). Although both clades of extant archosaurs (birds and crocodilians) have such subsidiary diverticula and accessory cavities, none could be hypothesized to be homologous (i.e., they failed the both the similarity and congruence tests). Thus, the presence of accessory cavities was not posited as an ancestral feature of Archosauria, and was not listed among the osteological correlates of paranasal pneumaticity in the previous section. Indeed, few accessory cavities characterize more than a small clade. Nevertheless, such spaces are present in many fossil archosaurs, and, making use of an argument for "compelling morphological evidence" (see discussion of the EPB approach above and in Witmer, 1995a), strongly corroborate the pneumatic nature of the antorbital cavity although requiring a level II or level III inference. These accessory cavities are discussed in detail below, following roughly the same systematic order as above.

The Diversity of Accessory Cavities

Theropoda—The greatest diversity of accessory cavities occurs within Theropoda. As a result, these are given a fairly thorough (but not exhaustive) treatment. The complicated morphology of these bony sinuses requires the creation of a number of new anatomical terms (Witmer, 1994 and in preparation). The following discussion is intended as an initial characterization of the anatomical diversity. Further study will likely expand the known variation, and the interpretation of the accessory cavities may require revision, especially as theropod phylogeny becomes better resolved.

The *maxillary recesses* (or sinuses) are among the most common accessory cavities in theropods below the level of ornithurine birds. They (Fig. 29) tend to be separable into three named cavities: (1) a promaxillary recess rostrally, (2) a maxillary antrum caudally, and (3) an excavatio pneumatica within the ascending ramus of the maxilla. All three systems communicate laterally with the space associated with the maxillary antorbital fossa: the promaxillary recess via the promaxillary fenestra, the maxillary antrum via the maxillary fenestra, and the excavatio pneumatica via a usually broad fossa. The promaxillary and maxillary fenestrae are the "accessory" or "subsidiary antorbital fenestrae" of previous authors (e.g., Osborn, 1912; Ostrom, 1969). The plan of this section is first to discuss the three named cavities in taxa (in general, neotetanurans) for which their identification is less problematic. More basal theropods (i.e., Ceratosauria, including abelisauroids) will be taken up after this basic pattern is established, because they present a problem in that they have just a single fenestra or no fenestra at all. The problem rests on the identification of the single fenestra in ceratosaurians: Is it a maxillary fenestra or a promaxillary fenestra?

The promaxillary fenestra (Carpenter, 1992) is located just rostral to the maxillary fenestra, the two being separated by the pila promaxillaris. In lateral view, the promaxillary fenestra usually forms a slit-like aperture just caudal to the rim of the external antorbital fenestra within the antorbital fossa. Examples of this pattern are common, including *Ornitholestes hermanni* (AMNH 619), *Marshosaurus bicentesimus* (Fig. 29C; UUVP 4695, 1846; referral of these specimens to this taxon is uncertain but will be employed for purposes of discussion), *Deinonychus antirrhopus* (YPM 5232, MCZ 8791), *Velociraptor mongoliensis* (AMNH 6515, cast of PIN 3143/8), *Archaeopteryx lithographica* (cast of Eichstätt specimen; Fig. 16B), *Sinornithoides youngi* (Russell and Dong, 1994), and *Saurornithoides junior* (Barsbold, 1974). Ornithomimosaurs also probably fall in this class, but here the promaxillary fenestra is situated somewhat more ventrally (e.g., *Struthiomimus altus,* ROM 1790; *Dromiceiomimus samueli,* ROM 841; Parks, 1928; Barsbold and Osmólska, 1990). Although the promaxillary fenestra is usually smaller than the maxillary fenestra, the reverse seems to be the case in the sinraptorids *Yangchuanosaurus* spp. (Dong et al., 1983) and *Sinraptor dongi* (Currie and Zhao, 1994a). My interpretation of the situation in the latter conflicts somewhat with that of Currie and Zhao (1994a: fig. 4). According to my scheme, their "maxillary fenestra" is actually the large promaxillary fenestra and their "pneumatic opening 8" is the small maxillary fenestra. *Dromaeosaurus albertensis* (AMNH 5356; see also Currie, 1995) also appears to have a relatively large, round promaxillary fenestra, but its size relative to the maxillary fenestra is unknown.

In some taxa, the promaxillary fenestra is not visible in lateral view, but rather is tucked up rostromedially, concealed by the lamina lateralis of the ascending ramus of the maxilla; in these cases, the presence of the promaxillary fenestra is easily overlooked (e.g., Paul [1988b] regarded it as absent in *Proceratosaurus bradleyi*). Examples of this concealed promaxillary fenestra are *P. bradleyi* (BMNH R4860), *Allosaurus fragilis* (UUVP 5427; Fig. 29A, B), *Tyrannosaurus rex* (UCMP 118742), *Albertosaurus libratus* (RTMP 83.35.100, AMNH 5664; Carr, 1996; Fig. 30), *Troodon formosus* (CMN 12392; see also Currie, 1985), and perhaps *Afrovenator abakensis* (UC OBA 1; see also Sereno et al., 1994). A concealed promaxillary fenestra may well characterize other taxa but remains unrecognized or even unprepared.

Owing to their delicate construction, the internal structure of any of the accessory cavities is known for very few species (see Madsen [1976b] for *Allosaurus fragilis*). Where known, the promaxillary fenestra leads into a single or, more often, a series of interconnected cavities within the ascending ramus of the maxilla (Figs. 29, 30; see Molnar [1991] for tyrannosaurids). In some cases, it can be shown that the rostralmost cavity of the promaxillary fenestra inflates that portion of the maxilla flooring the naris, forming a sort of thin-walled bulla within the nasal vestibule. A bulla vestibularis can be observed in, for example, *Proceratosaurus bradleyi* (BMNH R4860), *A. fragilis* (UUVP 5427, BYU 5126, YPM-PU 14554, Fig. 29), probably *Sinraptor dongi* (Currie and Zhao, 1994a), *Albertosaurus libratus* (RTMP 83.35.100, Fig. 30), *Marshosaurus bicentesimus* (UUVP 1846, Fig. 29), *Deinonychus antirrhopus* (YPM 5232), cf. *Velociraptor mongoliensis* (IGM 100/972), and *Troodon formosus* (CMN 12392). The vestibular bulla does not open into the naris (with perhaps one or two equivocal exceptions). The promaxillary recesses and vestibular bullae of *Afrovenator abakensis* (UC OBA 1), *M. bicentesimus* (UUVP 4695, 1846; Fig. 29C, D), as well as probably *D. antirrhopus* (YPM 5232) and *Ornitholestes hermanni* (AMNH 619) lack dorsal or medial openings, but such openings are present in *A. fragilis* (Fig. 29B), apparently *Sinraptor dongi* (Currie and Zhao, 1994a), and at least some tyrannosaurids. It should be reiterated, however, that the presence or absence of such openings is often problematical given that the delicate bone of the maxillary recesses is often damaged.

The maxillary fenestra (Gauthier, 1986) is much more consistent in morphology than the promaxillary fenestra, usually being a large, more-or-less round opening in the lamina medialis of the maxillary ascending ramus. Again, it appears to be relatively small in sinraptorids and also *Afrovenator abakensis* (UC OBA 1; Sereno et al., 1994). It is separated from the promaxillary fenestra by the promaxillary strut (pila promaxillaris) and from the internal antorbital fenestra by the interfenestral strut (pila interfenestralis). In troodontids (e.g., *Saurornithoides mongoliensis,* AMNH 6516) and ornithomimosaurs (including apparently the basal form *Pelecanimimus polyodon,* Pérez-Moreno et al., 1994), the maxillary fenestra is apomorphically relatively long and low. In a number of taxa (e.g., *A. abakensis,* UC OBA 1, Sereno et al., 1994; *Albertosaurus libratus,* RTMP 83.35.100, Fig. 30; *Marshosaurus bicentesimus,* UUVP 4695, 1846, Fig. 29C,D; *Deinonychus antirrhopus,* YPM 5232, MCZ 8791; *Velociraptor mongoliensis,* AMNH 6515, cast of PIN 3143/8), the maxillary fenestra is recessed within a shallow, caudally or caudodorsally open fossa, which is itself located within the maxillary antorbital fossa; this is also the case in sinraptorids (Dong et al., 1983; Currie and Zhao, 1994a), supporting the reinterpretation offered above.

The maxillary antrum is an often large cavity within the lamina medialis of the ascending ramus of the maxilla. It has variable communications with other spaces, the only constant being the maxillary fenestra. The rostral wall of the antrum usually has an aperture, the fenestra communicans, into the promaxillary recess (e.g., *Allosaurus fragilis,* UUVP 5427, Fig. 29B; *Albertosaurus libratus,* RTMP 83.35.100, Fig. 30E; *Deinonychus antirrhopus,* YPM 5232), but such a fenestra communicans is apparently absent in at least *Ornitholestes hermanni* (AMNH 619) and *Marshosaurus bicentesimus* (UUVP 4695, 1846; see also Madsen, 1976a). Tooth roots bulge into the antrum in several taxa, and, reciprocally, there are deep evaginations of the antrum (recessus pneumatici interalveolares) ventrally into the alveolar process, especially in tyrannosaurids (e.g., *Tyrannosaurus rex,* UCMP 118742; *Albertosaurus libratus,* RTMP 83.35.100, MOR 395, ROM 1247, Fig. 30E). The caudal wall of the antrum is medially reinforced in many taxa by a postantral strut that arches from the medial aspect of the pila interfenestralis to the torus maxillaris of the palatal process. In at least tyrannosaurids, this pila postantralis is fenestrated, allowing communication of the antrum with the main antorbital cavity. In *O. hermanni* (AMNH 619), most individuals of *A. fragilis* (e.g., UUVP 5427), *M. bicentesimus* (UUVP 4695, 1846), and apparently *D. antirrhopus* (YPM 5232), however, there is no caudal antral fenestra, although the pila postantralis bears a deep caudal fossa. In *A. fragilis* and tyrannosaurids, the antrum opens dorsally. In *A. fragilis,* a suprantral strut reinforces the antrum dorsomedially, so that the dorsal wall actually is fenestrated (see also Madsen, 1976b). Tyrannosaurids have a more-or-less distinct cavity, the epiantral recess, excavating the medial surface of the dorsal end of the interfenestral strut at its junction with the pila postantralis (Figs. 30D, E). The medial wall of the antrum is variable: It is complete (i.e., with no aperture at all) in *Afrovenator abakensis, O. hermanni, M. bicentesimus* (Fig. 29D; see also Madsen, 1976a), and probably *D. antirrhopus* (in YPM 5232, the paper-thin medial wall is broken open and all edges are broken), exhibiting a medial antral fenestra in most individuals of *A. fragilis,* or being almost absent in tyrannosaurids. Whether or not the dorsal or medial openings were open to the nasal cavity in life or occluded by the nasal cartilages is uncertain. In at least some tyrannosaurids (e.g., *Tyrannosaurus rex,* UCMP 118742; *Albertosaurus libratus,* RTMP 83.35.100, MOR 395, Fig. 30D,E), there is a medial, horizontal, rugose ridge just dorsal to the maxillary fenestra that may be for attachment of a portion of the nasal capsule, and hence may be evidence that the antrum had a cartilaginous roof.

The pneumatic excavation in the ascending ramus of the maxilla has received little attention in the literature. Hay (1908: 362) first noted its presence in *Ceratosaurus nasicornis* (USNM 4735) and called it the "maxillary vacuity." This name never caught on and is rather vague, so a new, more descriptive name—excavatio pneumatica rami ascendenti, or simply excavatio pneumatica—is coined here. It is an often large, teardrop-shaped fossa within the medial lamina of the maxillary ascending ramus directly above the pila interfenestralis. It is best developed in the sinraptorids *Yangchuanosaurus* spp., *Sinraptor hepingensis,* and *S. dongi,* and, at least in *S. dongi,* it communicates with the other maxillary recesses rostroventrally (Dong et al., 1983; Gao, 1992; Currie and Zhao, 1994a). As Hay (1908) and Gilmore (1920) correctly noted, an excavatio pneumatica is also found in *C. nasicornis* (USNM 4735 and especially a newly discovered specimen under study by J. H. Madsen, Jr. and S. P. Welles), where it is remarkably similar to that of sinraptorids. *Allosaurus fragilis* (e.g., UUVP 5427, YPM-PU 14554; Fig. 29A) also exhibits an excavatio pneumatica, but it is much more shallow. In all cases (except *C. nasicornis*), the excavatio pneumatica continues the course of the fossa (noted above) surrounding the maxillary fenestra, lending additional support to the interpretation of fenestration in sinraptorid maxillae. In *A. fragilis* (UUVP 5427, YPM-PU 14554) and sinraptorids (Dong et al., 1983; Gao, 1992; Currie and Zhao, 1994a), the excavatio pneumatica is adjacent to and clearly associated with the pneumatic foramina in the nasal bone.

Deinonychus antirrhopus (YPM 5232, MCZ 8791) represents an interesting case in that the maxillary fenestra is much more dorsally placed than in other coelurosaurs, and, in fact, is in the position of an excavatio pneumatica; the recess is even associated with the nasal pneumatic foramina. The situation becomes even more curious in that *Sinraptor hepingensis* (Gao, 1992) has apparently lost the maxillary fenestra (already small in other sinraptorids) so that its maxilla looks very much like that of *D. antirrhopus.* There are at least two additional explanations for this situation: (1) *D. antirrhopus* has an excavatio pneumatica and not a maxillary fenestra; and (2) the excavatio pneumatica in general is simply the maxillary fenestra, only displaced dorsally. The first is refuted by reference to *Velociraptor mongoliensis* in which the maxillary fenestra is very similar to *D. antirrhopus* but located in a much more typical, almost certainly plesiomorphic, more ventral position; thus, the latter taxon is simply derived in the more dorsal position of its maxillary fenestra. The second idea, homology of the maxillary fenestra and excavatio pneumatica, is refuted by reference to other sinraptorids and to *Allosaurus fragilis* which possess both structures; thus, the hypothesis of homology fails the conjunction test of Patterson (1982).

Having established the broader, more consistent patterns of maxillary sinus configuration in more derived theropods, we will now turn to basal theropods. As mentioned earlier, ceratosaurians and basal tetanurans (i.e., the problematic nexus of "megalosaurs" or "spinosauroids") tend to have fewer accessory cavities in their maxillae. Although Molnar and Carpenter (1989) figured a small fenestra within the rostral apex of the antorbital fossa of *Coelophysis bauri,* I cannot confirm this opening or any other maxillary accessory cavities in the specimen they note (AMNH 7224) or any other specimens of this taxon (Fig. 14). Similarly, maxillary sinuses are apparently absent in the coelophysid *Syntarsus* spp. (Raath, 1977; Rowe, 1989). Among ceratosaurians, the presence of a single fenestra within the maxilla is known in the coelophysoid *Dilophosaurus wetherilli* (UCMP 77270, 37303, Fig. 31) and the abelisauroids *Abelisaurus comahuensis* (Bonaparte and Novas, 1985) and *Carnotaurus sastrei* (Bonaparte et al., 1990); Chatterjee (1978b) reported, and I confirmed, the presence in *Indosuchus raptorius* (AMNH 1955) of foramina in the rostroventral corner of the antorbital cavity that seem to communicate with cavities within the ascending ramus.

The question again is: Is this single aperture of ceratosaurians homologous to the promaxillary or to the maxillary fenestra of higher theropods? The question is not easily resolved. Most previous authors have called the aperture the maxillary fenestra

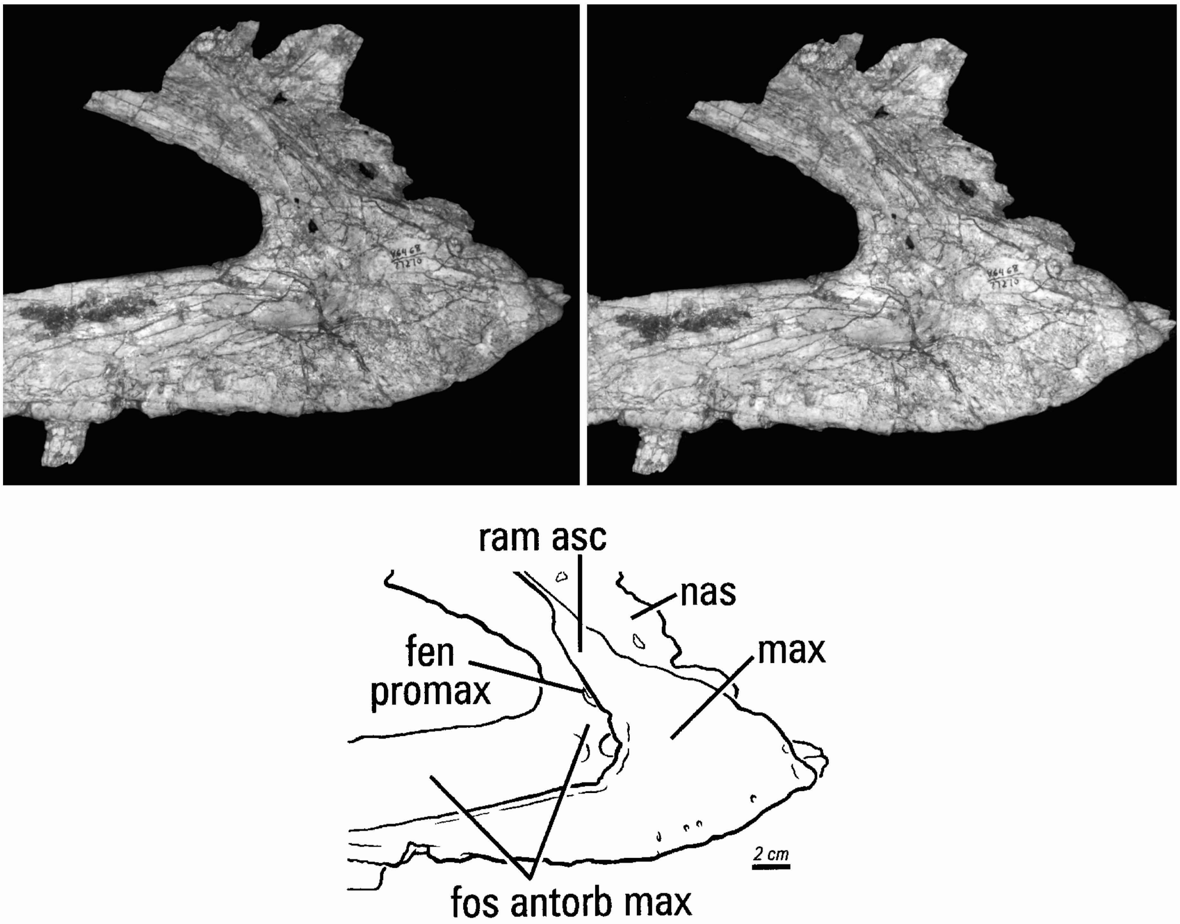

FIGURE 31. *Dilophosaurus wetherilli.* Stereophotographs of right antorbital region of UCMP 77270 in lateral view, with interpretive drawing.

(e.g., Gauthier, 1986; Bonaparte et al., 1990), but even the presence (not to mention the broad distribution) of the promaxillary fenestra has not been widely recognized. In the ceratosaurians mentioned above, the aperture is relatively small, located just caudomedial to the rim of the external antorbital fenestra within the maxillary antorbital fossa, and faces more caudally than laterally; its shape is more-or-less slitlike, being taller than long. In at least *Dilophosaurus wetherilli* (UCMP 77270, Fig. 31; see also Welles, 1984), the aperture leads into a single cavity within the ascending ramus of the maxilla. This structure is precisely that of the promaxillary fenestra and recess of neotetanurans. I suggest here that the presence of a promaxillary fenestra probably characterizes neotheropods, with the maxillary fenestra being a synapomorphy of a less inclusive clade, perhaps Tetanurae or Neotetanurae.

The situation in basal tetanurans remains unclear. *Megalosaurus hesperis* (BMNH R332; Waldman, 1974) has only a single, moderately large fenestra visible, although it is not clear from available material if a concealed promaxillary fenestra was present. Likewise, Zhao and Currie (1994) identified only a single, fairly large opening within the rostral apex of the antorbital cavity of *Monolophosaurus jiangi.* Although in both cases these openings have been called maxillary fenestrae, they occupy the position of promaxillary fenestrae. Further complicating matters, Sereno et al. (1996) scored *M. jiangi* as having both a promaxillary recess and a maxillary fenestra. Again, resolution is difficult. It is possible that one fenestra (and accessory cavity) or the other could be lost, perhaps even incorporated into the other (like the joining of soap bubbles), by breakdown of the promaxillary strut. Certainly they can be lost in that the peculiar maniraptoran *Erlikosaurus andrewsi* (PST 100/111; Clark et al., 1994) apparently lacks both promaxillary and maxillary fenestrae. The situation gets worse when taxa such as *Torvosaurus tanneri* (Jensen, 1985; Britt, 1991) and *Ceratosaurus nasicornis* (USNM 4735) are considered; in both, there are no distinct fenestrae at all, despite having a deep recess in the area. Absence of maxillary accessory cavities (i.e., sinuses) of any kind in coelophysids (see above) and some other forms (such as the abelisauroid *Noasaurus leali*; Bonaparte, 1991a) are further evidence of homoplasy in the system.

To summarize this discussion of theropod maxillary recesses, three relatively discrete systems are found in at least higher theropods. The promaxillary recess and maxillary antrum are widely distributed among neotetanurans, but the excavatio pneumatica presently is known only in some allosauroids and *Ceratosaurus nasicornis.* Fenestration of the maxilla has been an important character in theropod classification (Gauthier, 1986; Holtz, 1994; Sereno et al., 1994, 1996), but needs revision and clarification. The basal theropods *Eoraptor lunensis* (PVSJ 512; Sereno et al., 1993) and *Herrerasaurus ischigualastensis* (PVSJ 407; Sereno and Novas, 1994) plesiomorphically appear to lack maxillary recesses of any kind, and thus the appearance of such sinuses is a neotheropodan synapomorphy. The issue is which recess appeared at the level of Neotheropoda. Available evidence would suggest that the promaxillary recess and fenestra appeared first, and that the maxillary antrum and fenestra are innovations of Tetanurae or Neotetanurae, but new discoveries could easily change this conclusion. Clearly there has been a fair amount of homoplasy, especially among the earlier lineages; this variation becomes, in effect, sorted out in Coelurosauria in which the maxillary recesses are fairly consistent. Despite the phylogenetic ambiguities, the point emerging from this discussion is that the complicated and variable nature of the maxillary recesses of theropods are indeed compelling morphological evidence for the presence of paranasal air sinuses.

Paul's (1988a) compromise solution to the function of the antorbital cavity is pertinent at this point. He suggested that the dorsal pterygoideus muscle attached to the margin of the internal antorbital fenestra and that the surrounding antorbital fossa lodged paranasal air sinuses; the epithelial diverticulum would have traversed the maxillary fenestra to pass from the nasal cavity to the antorbital cavity. Notwithstanding the problems detailed earlier regarding the muscular hypothesis, Paul's hypothesis fails in that it cannot apply to all archosaurs or even to all theropods because maxillary fenestrae are limited perhaps to just a single clade, thus leaving the fossae of other archosaurs unexplained. Furthermore, with regard to theropods, it reverses the direction of pneumatization. Although the maxillary sinuses of some theropods (e.g., *Allosaurus fragilis*) have medial apertures, the following taxa can be shown to have no internal fenestrae, demonstrating that the subsidiary diverticula must have entered the accessory cavities (passing through the promaxillary and/or maxillary fenestrae) from the external side of the maxilla, not the internal side: *Piatnitzkysaurus floresi* (Bonaparte, 1986), *Megalosaurus hesperis* (BMNH R332), *Afrovenator abakensis* (UC OBA 1), *Ornitholestes hermanni* (AMNH 619), *Marshosaurus bicentesimus* (UUVP 4695, 1846), and perhaps *Deinonychus antirrhopus* (YPM 5232). Thus, Paul's (1988a) compromise is not applicable even for these theropods.

The *lacrimal recess* is another accessory cavity associated with the antorbital cavity. In many theropods (especially large forms), the lacrimal has a large recess expanding within the caudodorsal portion (body) of the bone that opens rostrolaterally into the antorbital cavity (Fig. 29A). In most cases, the opening of the cavity is a single, rather broad aperture located in the rostroventrolateral surface of the body of the bone, and is continuous with the smooth surfaces of the lacrimal antorbital fossa. Examples include *Ceratosaurus nasicornis* (USNM 4735), *Afrovenator abakensis* (UC OBA 1; Sereno et al., 1994), *Allosaurus fragilis* (UUVP 2133, YPM-PU 14554, Fig. 29A), and *Yangchuanosaurus shangyuensis* (Dong et al., 1983), among others. In *Tyrannosaurus rex* (AMNH 5027, CM 9401, others), this single aperture is restricted to a relatively small, more discrete foramen. In a number of taxa, additional openings may be present rostral to the main aperture: e.g., *Acrocanthosaurus atokensis* (Stovall and Langston, 1950), *Giganotosaurus carolinii* (Coria and Salgado, 1995), some individuals of *Allosaurus fragilis* (e.g., UUVP 5814, BYU 5125), *Sinraptor dongi* (Currie and Zhao, 1994a), and *Daspletosaurus torosus* (CMN 8506). A number of taxa lack any lateral apertures into the body of the lacrimal bone, although they may retain moderately deep lacrimal antorbital fossae; examples include *Coelophysis bauri* (CM 31374; Fig. 14), *Dilophosaurus wetherilli* (UCMP 77270), abelisaurids (Novas, 1992), *Torvosaurus tanneri* (Britt, 1991), *Monolophosaurus jiangi* (Zhao and Currie, 1994), *Troodon formosus* (RTMP 82.19.23; Currie, 1985; Witmer, 1990), *Dromiceiomimus brevitertius* (CMN 12228), *Utahraptor ostrommaysi* (Kirkland et al., 1993), *Archaeopteryx lithographica* (BMNH 37001; Fig. 16B), and *Erlikosaurus andrewsi* (PST 100/111; see also Clark et al., 1994). Given the absence of such openings in most small maniraptorans it is probably significant that *Deinonychus antirrhopus* (YPM 5232; MOR 747; see also Witmer and Maxwell, 1996) shows the more-or-less typical condition of more basal tetanurans, a moderately large aperture; furthermore, as in some of the other theropods noted above, there is an additional, smaller foramen just rostral to the main opening. Sereno et al. (1994, 1996) listed "lacrimal pneumatic excavation" as a synapomorphy of their Tetanurae, and this seems reasonable although the lacrimal recess of *Ceratosaurus nasicornis* is well within tetanuran variation (Witmer, 1995c). Holtz's (1994) analysis definitely showed a lot of homoplasy in this feature, and, in fact, he probably significantly underestimated the amount of homoplasy (e.g., the discovery of lacrimal pneumatic recesses in *D. antirrhopus* noted above; see also Witmer, 1995c).

These lacrimal pneumatic apertures lead into cavities of variable size, such that the body and cornual process (if present, as in *Ceratosaurus nasicornis* and *Allosaurus fragilis*) is hollow. The internal architecture of the lacrimal recess can be assessed for only a few taxa. For example, in one specimen of *A. fragilis* (UUVP 2133), the lacrimal recess has three cavities partly subdivided by internal ridges; the recess does not extend far into either the rostral or ventral rami. Molnar (1991) also identified three cavities within the lacrimal of *Tyrannosaurus rex*, and the recess extends far into the rostral ramus in one specimen (CM 9401). In *Albertosaurus sarcophagus* (CMN 5601, RTMP 86.114.1; see also Carr, 1996), the cavity within the rostral ramus opens laterally within the antorbital cavity via a foramen. The ventral ramus of the lacrimal usually has no evident cavities, although it appears to be hollow in one tyrannosaurid specimen (RTMP 83.30.1).

Jugal recesses are found in a number of theropods, and, in most cases, take the form of a slit-like or occasionally round foramen at the caudoventral apex of the jugal antorbital fossa. Such a foramen is found in all tyrannosaurids and has been regarded as a synapomorphy of that group (Bakker et al., 1988; Molnar et al., 1990; Molnar, 1991). The distribution of this feature, however, is more complicated. It is fairly certain that ceratosaurians and at least some basal tetanurans (Bakker et al., 1992) lack jugal recesses. Sereno et al. (1994, 1996) regarded a "jugal pneumatic excavation" as a synapomorphy of Tetanurae, and deep jugal antorbital fossae with pneumatic foramina similar to tyrannosaurids are found in *Monolophosaurus jiangi* (Zhao and Currie, 1994), *Afrovenator abakensis* (UC OBA 1; Sereno et al., 1994), *Sinraptor dongi* (Currie and Zhao, 1994a), some individuals of *Allosaurus fragilis* (Currie and Zhao, 1994a), *Acrocanthosaurus atokensis* (Stovall and Langston, 1950), and *Carcharodontosaurus saharicus* (Sereno et al., 1996). Most coelurosaurs (other than tyrannosaurids), however, appear to lack jugal recesses; this seems to be the case for *Ornitholestes hermanni* (AMNH 619), oviraptorosaurs, troodontids, and ornithomimosaurs, although additional preparation (and the proper search image) could change this assessment. For example, further preparation of specimens of *Deinonychus antirrhopus* (YPM 5210, 5232; MOR 747; Maxwell and Witmer, 1996) reveals a well developed jugal pneumatic recess. The internal structure of the jugal recess is known for few taxa, but, in *Sinraptor dongi* (Currie and Zhao, 1994a) and *Tyrannosaurus rex* (Molnar, 1973, 1991), the pneumatic foramen leads into a series of cavities within the maxillary and postorbital rami of the jugal.

Nasal recesses, foramina, and cavities within the nasal bones associated with the nasal antorbital fossa, are not common. They are absent in ceratosaurians, although Gilmore (1920:82) identified "a number of pneumatic cavities" in the nasal of *Ceratosaurus nasicornis. Allosaurus fragilis* (UUVP 3839, BYU 5124, USNM 4734, YPM-PU 14554; Fig. 29A), *Sinraptor dongi* (Currie and Zhao, 1994a), *Yangchuanosaurus shangyouensis* (Dong et al., 1983), and *Carcharodontosaurus saharicus* (Sereno et al., 1996) exhibit one to three foramina leading into chambers within the nasal bone. As noted previously, these nasal recesses appear to be associated with the excavatio pneumatica in the maxillary ascending ramus. Currie and Zhao (1994a) noted that the two cavities of *S. dongi* are extensive but do not communicate. *Monolophosaurus jiangi* (Zhao and Currie, 1994) deserves special mention in that its nasal bones form a large hollow crest with two large apertures caudally that actually pass from one side to the other, establishing a contralateral communication between the antorbital cavities, as well as invading the body of the nasal; furthermore, two additional, more rostral, foramina pneumatize the nasal bone and then continue rostrally to pneumatize the premaxillae. Nasal pneumatic recesses have not been described for other theropods (except for oviraptorosaurs; see below), and they can be shown to be positively absent in Tyrannosauridae, Ornithomimosauria, Troodontidae, *Erlikosaurus andrewsi* (PST 100/111; Clark et al., 1994), and *Archaeopteryx lithographica* (cast of Eichstätt specimen). As with the lacrimal and jugal recesses, nasal recesses are described in *Deinonychus antirrhopus* (YPM 5210, 5232; MOR 747) here for the first time (see also Witmer, 1995c; Witmer and Maxwell, 1996). Ostrom (1969:19) described a "groove with three moderate-sized, oval foramina" within the nasal of *D. antirrhopus* but had "no explanation for this pattern." Comparison with other theropods (as well as further preparation) reveal that Ostrom's groove is the nasal antorbital fossa and the "oval foramina" are pneumatic foramina leading into small cavities.

Palatine recesses are found in some theropods and typically are cavities or foramina in the dorsal surface of the palatine bone that are clearly associated with the antorbital cavity. These are absent in Ceratosauria and some large tetanurans such as *Allosaurus fragilis.* Where present, they invariably are caudal or caudolateral to the choana, just medial to the contact with the maxilla, and rostrolateral to the presumed pterygoideus fossa, if present. In *Archaeopteryx* sp. (cast of Solenhofer Aktien-Verein specimen; see also Elzanowski and Wellnhofer, 1996), the dromaeosaurids *Deinonychus antirrhopus* (YPM 5210, 5232; Fig. 32) and *Velociraptor mongoliensis* (cast of PIN 3143/8; Osmólska, 1985), and the troodontid *Saurornithoides mongoliensis* (AMNH 6516), there is a well-developed fossa in this position, and, in at least *D. antirrhopus,* this fossa leads into a small cavity. In *Sinraptor dongi,* the fossa surrounds a moderately large foramen that leads into a cavity within the choanal process (Currie and Zhao, 1994a). Tyrannosaurids have often large foramina in the dorsal surface of the palatine that lead into a strutted cavity with the bone (Molnar, 1991; Carr, 1996). There may be just a single large foramen leading into the bone (e.g., *Daspletosaurus torosus,* CMN 8506; *Tyrannosaurus rex,* AMNH 5027) or sometimes two or more (e.g., *Nanotyrannus lancensis,* Gilmore, 1946; *Albertosaurus sarcophagus,* CMN 5601; *Tarbosaurus bataar,* Maleev, 1974). Few theropod taxa can be scored for palatine recesses, and thus the phylogenetic distribution of these features is problematic. If it were not for the clear presence of palatine recesses in *Sinraptor dongi,* it might have been possible to regard them as a synapomorphy of at least Maniraptora (assuming Holtz's [1994] placement of Tyrannosauridae is correct) if not Coelurosauria.

A discussion of the facial structure of theropods would not be complete without special mention of the peculiar Mongolian oviraptorosaurs (Barsbold et al., 1990). *Oviraptor philoceratops* and its relatives clearly manifest the osteological correlates permitting the inference of an antorbital air sac. Furthermore, their facial skeletons have been described as being extensively pneumatic by virtually all recent workers (Osmólska, 1976; Barsbold, 1983; Barsbold et al., 1990). In fact, the facial bones in some species are developed into a tall, cassowary-like crest formed by a fine lattice of bony trabeculae (Barsbold et al., 1990). Oviraptorosaurs were not discussed much in the above analysis of theropod accessory cavities because their skulls are so transformed that it is not always easy to identify homologous pneumatic structures. Virtually all of the facial elements have complex cavities within them. The ones in the maxilla, lacrimal, and nasal are associated with the antorbital cavity (Osmólska, 1976), whereas the cavities within the premaxilla and others in the nasal and even the frontal bone are apparently connected with the nasal vestibule (Barsbold et al., 1990).

Coelophysis bauri also merits further discussion in that it lacks all of the cavities and chambers in the facial bones, thus strongly resembling many non-dinosaurian archosaurs; yet it is regarded as a derived member of its clade, Ceratosauria (Rowe and Gauthier, 1990; Holtz, 1994). Since more basal ceratosaurians such as *Ceratosaurus nasicornis* and *Dilophosaurus wetherilli* are large-skulled forms manifesting some of these cavities (and, presumably, pneumatic diverticula of an antorbital air sac), it is reasonable to suggest that *C. bauri* also possessed a large paranasal air sinus, but, by virtue of small skull size, did not develop pneumatic diverticula into its facial bones. Therefore, some aspects of facial pneumaticity may have a size-related (i.e., allometric) component.

Sauropodomorpha—In the prosauropod *Plateosaurus engelhardti* (AMNH 6810), the nasal bone sends a lamina lateral to the maxillolacrimal contact that broadly overhangs the antorbital cavity (Fig. 12A). In fact, there is large, dorsal, C-shaped (laterally open) hiatus framed by the laminae of the maxilla and lacrimal that the nasal caps (Fig. 12D). That portion of the nasal roofing the aperture has a deeply excavated recess (Fig. 12C), and may be the closest approach among sauropodomorphs to a theropod-like bony accessory cavity. It is not known how widely this nasal recess is distributed among prosauropods, but since the nasal overhangs the antorbital cavity in *Sellosaurus gracilis* (Galton, 1985b) and perhaps *Massospondylus carinatus* (Gow et al., 1990), the recess also may be present in these forms.

Ornithischia—The palatine of *Lesothosaurus diagnosticus* has two well-marked fossae on its dorsolateral surface. The caudal fossa was interpreted earlier as a muscular fossa. The rostral fossa (Fig. 7C, D), however, appears to be associated with the antorbital cavity and may well be a pneumatic fossa. It resembles in some respects the palatine fossa noted above for the small theropods *Deinonychus antirrhopus* (Fig. 32) and *Velociraptor mongoliensis.*

Haubold (1990) described a deep rostral extension of the antorbital cavity within the maxilla of the basal thyreophoran *Emausaurus ernsti* (Fig. 18), which could be an accessory cavity. Similarly, in another basal thyreophoran, *Scelidosaurus harrisonii,* there is a moderately large foramen at the rostral apex of the maxillary antorbital fossa that could lead to an accessory cavity, but it is unknown whether it expands into a chamber within the bone.

Clearer evidence of accessory cavities is available for protoceratopsians (Fig. 20C, D). In at least *Bagaceratops rozhdestvenskyi* and *Protoceratops andrewsi,* an accessory cavity is associated with the maxillary antorbital fossa (Maryanska and Osmólska, 1975; Osmólska, 1986). This "intramaxillary sinus" enters the bone via a slit or cleft (sometimes two slits as in AMNH 6466) within the floor of the maxillary recess. It subsequently expands, forming a cavity running the length of the maxilla dorsal to the tooth roots (Osmólska, 1986; Fig. 20C, D). It is not known whether it occurs in other protoceratopsians, but Sternberg (1951:232) regarded the antorbital fossa (his "maxillary sinus") as being "much deeper" in *Leptoceratops gracilis* than in *P. andrewsi,* perhaps suggesting the presence of an accessory sinus in this form as well.

Pterosauria—Many large pterodactyloids have spaces that can be interpreted as accessory cavities. For example, in *Pteranodon longiceps* (KUVP 976, USNM 13868), there is a clear

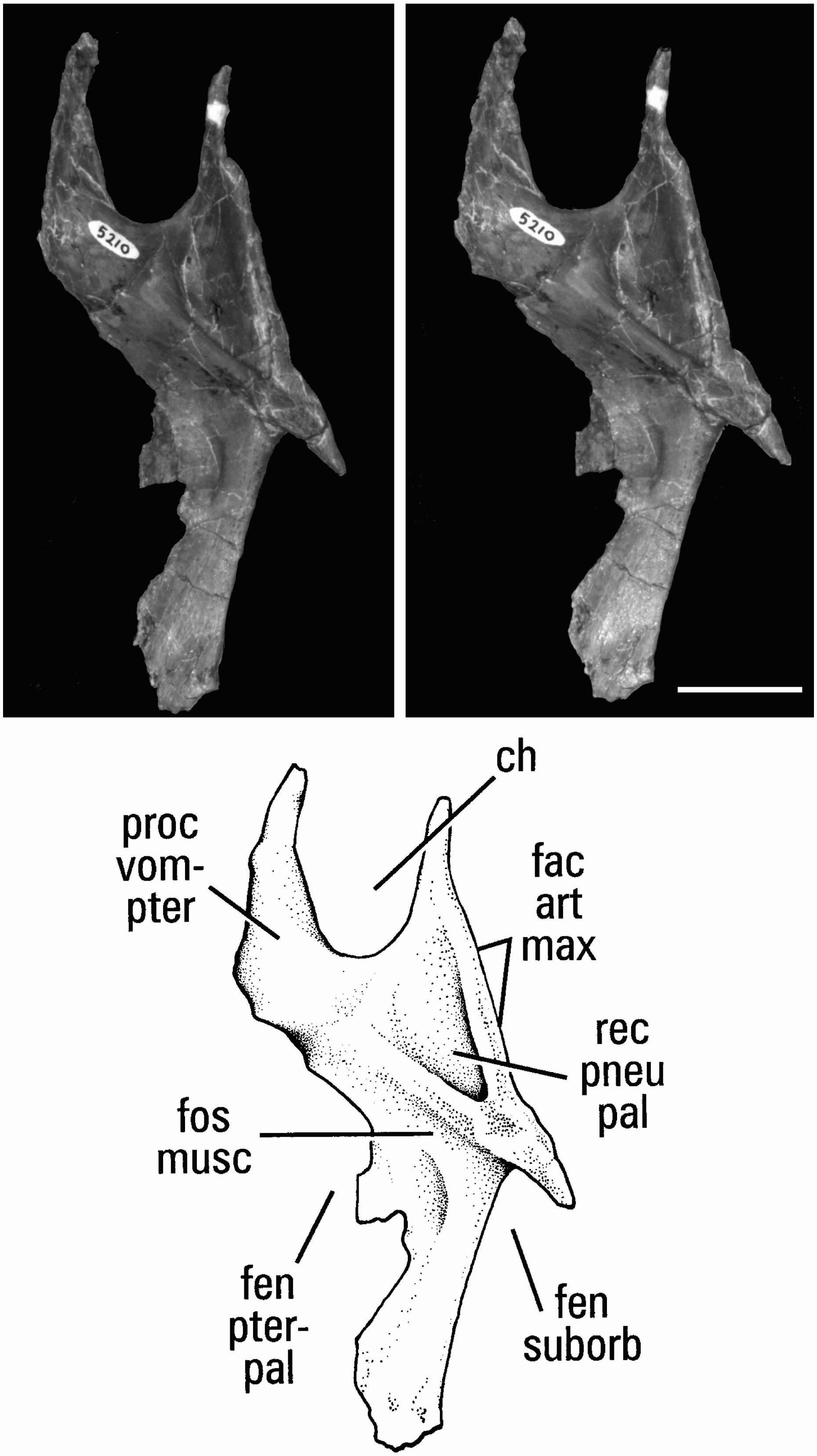

FIGURE 32. *Deinonychus antirrhopus.* Right palatine of YPM 5210 in dorsal view, with interpretive drawing.

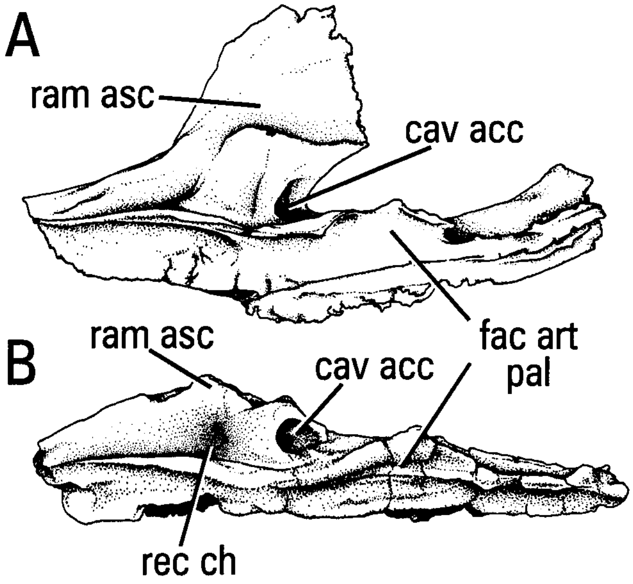

FIGURE 33. Maxillary accessory cavities in stagonolepidids. **A**, *Stagonolepis robertsoni,* right maxilla (BMNH R4787) in medial view. **B**, *Desmatosuchus haplocerus,* left maxilla (UCMP 78698; reversed for comparison) in medial view.

foramen within the lacrimal in the caudodorsal corner of the antorbital fossa, apparently leading into chambers within the supracranial crest (Witmer, 1987b; Bennett, 1991 and in press). Other pterodactyloids also exhibit lacrimal bones with patterns of fenestration consistent with a pneumatic interpretation (e.g., *Anhanguera santanae,* AMNH 25555, see also Wellnhofer, 1991a; *Araripesaurus santanae,* Wellnhofer, 1985; *Tropeognathus mesembrinus,* Wellnhofer, 1987; *Tapejara wellnhoferi,* Wellnhofer and Kellner, 1991). Bennett (1991, and in press) described a large pneumatic space dorsal to the nasoantorbital cavity within the nasal bones, perhaps with a rostral diverticulum in *Pteranodon longiceps.* The foramina within the nasal process of *Araripesaurus santanae* (Wellnhofer, 1985) may be pneumatic foramina associated with a similar cavity. Furthermore, the upper bill rostral to the nasoantorbital opening is a thin shell with a large cavity internally (e.g., *A. santanae,* AMNH 25555; *P. longiceps,* Bennett, 1991, in press); assuming for the moment that the beak cavity was pneumatic, it is uncertain if it is pneumatized by a diverticulum of the antorbital sinus, as in large-billed birds, or from a novel narial diverticulum.

Parasuchia—In parasuchians, there is a median cavity extending into the premaxillary rostrum—the one rejected earlier as a site of muscle attachment—that is here regarded as an accessory cavity of the antorbital cavity. This premaxillary cavity is completely continuous with the antorbital cavities on each side, so that the smooth inner walls narrow and converge rostrally in front of the nasal cavity proper, forming a long hollow tube (Fig. 22). This tubular cavity is visible on many specimens (e.g., *Rutiodon tenuis* [*Arribasuchus buceros*], UCMP 27149; *Rutiodon tenuis* [*Pseudopalatus pristinus*], UCMP 34228; *Rutiodon carolinensis,* AMNH 4, Fig. 22A,B; *Mystriosuchus planirostris,* AMNH 10644; *Phytosaurus* sp., BMNH 38040, 38039). In some forms (e.g., *R. carolinensis,* AMNH 1), the cavity continues to the rostral end of the premaxilla. Although the median cavity almost certainly carried a neurovascular bundle, it is usually too large, especially caudally, for vessels and nerves to be the only contents. Alternatively, given the supposition of an antorbital air sinus, it is possible that a diverticulum of this sinus evaginated rostrally, merged with its fellow in front of the nasal capsule, and pneumatized the premaxilla, following the heterogeneity provided by the neurovasculature. Thus, the snout is produced into a relatively low-mass, torsion-resisting tube (Fig. 22C).

Non-crocodylomorph Suchia—The presence of accessory cavities in basal suchians is best documented in stagonolepidids. In *Stagonolepis robertsoni* (BMNH R4787, R8582; Fig. 33A), a large fossa and foramen enter the caudal surface of the base of the ascending ramus of the maxilla that is reminiscent of the promaxillary fenestra of theropods. These specimens are casts of natural molds, so the precise nature of the cavity is unknown. In *Desmatosuchus haplocerus* (e.g., UCMP 78698; Fig. 33B), however, there is an even larger, round, caudomedial aperture within the base of the ascending ramus that leads into an expanded, smooth-walled chamber. Evidence for accessory cavities in other basal suchians is a bit more equivocal. The maxillary antorbital fossa in the rauisuchids *Saurosuchus galilei* (Sill, 1974) and *Fasolasuchus tenax* (Bonaparte, 1981) is very deep rostrally, sharply undercutting the margin of the external fenestra, but accessory cavities within the ascending ramus have not been described. *Postosuchus kirkpatricki* (TTUP 9000; Chatterjee, 1985) and *Teratosaurus suevicus* (BMNH 38646; Galton, 1985a) have medial fossae within the ascending ramus which in the latter may be associated with a foramen, but they are too poorly preserved to point unequivocally to pneumaticity.

Crocodylomorpha—Some sphenosuchians may have accessory cavities, but, again, the assessment is somewhat problematic. Walker (1990), in opposition to his earlier support of the muscular hypothesis, regarded the internal antorbital fenestra and antorbital fossa of *Sphenosuchus acutus* as pneumatic features. Furthermore, he identified a number of other cavities as having a pneumatic origin. Walker (1990) suggested that a cavity within the rostral portion of the maxillary secondary palate might be pneumatic. This cavity apparently communicates medially with the nasal cavity and broadly with the palate via openings between the premaxilla and maxilla. It is not clear how such a cavity would relate to an antorbital air sac, and it is conceivable that it could represent a separate epithelial diverticulum (as occurs in some extant crocodilians). This palatal aperture is unusual and does not occur in *Dibothrosuchus elaphros* (IVPP V7907) or apparently *Terrestrisuchus gracilis* (Crush, 1984).

Walker (1990) identified three features that he thought might be evidence for a bird-like suborbital diverticulum of the antorbital air sinus. The first feature, a dorsal channel within the lateral aspect of the maxilla and jugal, probably is associated with branches of the maxillary neurovasculature instead of an air-filled diverticulum. The second and third features, ventral recesses within the ectopterygoid and pterygoid bones, indeed are suggestive, but would require passage of the air sac ventral to the dorsal pterygoideus muscle through the suborbital fenestra (the avian suborbital diverticulum passes dorsal to the pterygoideus musculature; Witmer, 1990, 1995b). This matter is discussed further below.

Pseudhesperosuchus jachaleri has two openings within its snout in addition to the antorbital cavity, one rostrally within the maxilla and another dorsally within the nasal bone (Bonaparte, 1972). Clark (1986) suggested that the opening within the nasal might be an artifact. It is not clear from the published description if either opening communicates with the antorbital or nasal cavities, although the opening within the nasal bone probably would have to communicate with one or the other. These could be pneumatic features but clearly require further study. In an unnamed sphenosuchian from the Kayenta Formation of Arizona (UCMP 131830), there is a large, rostrally directed foramen in the rostral corner of the maxillary antorbital fossa, which is again somewhat reminiscent of the promaxillary fenestra of some theropods. There is not much room for it to expand into a chamber, but a pneumatic interpretation is perhaps as, if not more, likely than a neurovascular one.

In the protosuchian *Platyognathus hsui,* Wu and Sues (1996) identified pneumatic cavities in the maxillary, jugal, and ectopterygoid. Unfortunately, no foramina (i.e., entrances to the cavities) are preserved, so a pneumatic interpretation of the cavities, while valid, may be somwhat difficult to distinguish from a neurovascular or even a marrow-cavity interpretation. Early in the ontogeny of extant crocodilians, a large vascular space is developed within the jugal with an often enormous foramen; this vascular space and foramen become greatly reduced in relative size thoughout ontogeny. The jugal cavity of *P. hsui* could represent such a vascular space. The maxillary cavity, however, seems to bear the best chances of being of pneumatic origin if only because the maxilla is the most commonly pneumatized element in archosaurs generally.

Finally, in the mesoeucrocodilian *Notosuchus terrestris,* the maxillary antorbital fossa has a deep rostroventral extension (Bonaparte, 1991b) that may lead into an accessory cavity.

Summary—Numerous clades of archosaurs have additional, accessory cavities extending beyond the bounds of the antorbital fossa but maintaining communication with the antorbital cavity. Many of the cavities are obviously pneumatic: the several accessory cavities of theropods (e.g., promaxillary recess, maxillary antrum, and the recesses with the lacrimal, nasal, jugal, and palatine), the intramaxillary sinus of protoceratopsians, the lacrimal and rostrum cavities in many pterodactyloids, and the cavity within the base of the maxillary ascending ramus of *Stagonolepis robertsoni* and *Desmatosuchus haplocerus.* Some accessory cavities are a little less clear but still are best explained as having a pneumatic origin: the nasal recess of some prosauropods, the rostral fossa on the palatine of *Lesothosaurus diagnosticus,* the rostral cavity within the maxillae of *Emausaurus ernsti* and perhaps *Scelidosaurus harrisonii,* the cavity within the premaxillary rostrum of many parasuchians, the ectopterygoid and pterygoid cavities of *Sphenosuchus acutus,* the maxillary cavity of *Platyognathus hsui,* and the rostral maxillary cavity of *Notosuchus terrestris.* Taken together, the independent evolution of so many different varieties of accessory cavities is compelling morphological evidence for the pneumatic nature of the antorbital cavity and furthermore is a good indication of the tendency of air-filled diverticula to evaginate into and pneumatize surrounding bone (see below).

Presence of a Bird-like Suborbital Air Sac in Fossil Archosaurs

This tendency for epithelial air sacs to expand and evaginate is manifested in birds by the development of the suborbital diverticulum of the antorbital sinus (mentioned earlier), which passes caudally out of the antorbital cavity, through an ostium in the ventral portion of the postnasal fenestra, to expand within the orbit (Fig. 6B). Although such a diverticulum is ubiquitous in modern birds (Bignon, 1889; Witmer, 1990, 1995b), its absence in extant crocodilians prevented its being hypothesized unequivocally as present in the bracket ancestor. In birds, this diverticulum is often much more voluminous than the antorbital sinus itself, passing between the jaw muscles and in rare cases pneumatizing bone (the dorsal surface of the pterygoid in some individuals of *Casuarius casuarius*).

Again using a "compelling morphological evidence" argument, is there any evidence for such a diverticulum in extinct archosaurs? This question is raised here for two reasons. First, some workers have suggested that some attributes of certain postfacial bones suggest pneumaticity, and it is possible that a suborbital air sac could explain these attributes. For example, Molnar (1985, 1991; see also Molnar et al., 1990), Currie and Zhao (1994a), Sereno et al. (1994, 1996), and Currie (1995) suggested that cavities in the ectopterygoids of many theropods were pneumatic in nature. Furthermore, Molnar (1991) noted that the squamosals of some tyrannosaurids are hollow. Walker's (1990) suggestion of pneumatic palatal elements in *Sphenosuchus acutus* was mentioned earlier. Second, the avian suborbital diverticulum has interesting functional properties (see below), and thus the phylogenetic history of the structure is critical to its correct functional interpretation.

Squamosal Recess—Squamosal cavities have been observed in the tyrannosaurids *Tyrannosaurus rex* (Molnar, 1991), *Albertosaurus libratus* (FMNH PR 308), and *Daspletosaurus torosus* (CMN 8506; Fig. 34C), and also in the ornithomimid *Dromiceiomimus brevitertius* (CMN 12228; Fig. 34A,B). A very large ventral foramen, rostral to the cotyle for the quadrate, leads into the cavity (Fig. 34). Molnar (1991) reported that the cavity has a caudal opening in *T. rex,* but none was observed in *A. libratus, Daspletosaurus torosus,* or *Dromiceiomimus brevitertius.* The cavity has the appearance of being pneumatic: it is smooth-walled and expansive, undercutting the edges of a rounded foramen. Assuming that the squamosal cavity is indeed pneumatic, it is possible that a bird-like suborbital diverticulum passed between the jaw muscles into the adductor chamber to reach the squamosal. Alternatively, a diverticulum from the middle ear sac could have produced the squamosal recess, because the squamosal in birds is pneumatized by a tympanic diverticulum (Witmer, 1990), and tyrannosaurids have many characteristics associated with paratympanic pneumaticity (Molnar, 1985, 1991; Bakker et al., 1988; Witmer, 1990, 1995c). With the available evidence, it is difficult to choose between the paranasal or paratympanic options, but, given the presence of a large aperture leading into a cavity, a pneumatic explanation for the squamosal recess remains most likely.

Ectopterygoid Recess—As noted by Ostrom (1969), the ectopterygoid cavity ("carnosaur pocket") once was thought to be strictly a "carnosaurian" feature, but such a fossa in fact may characterize much of Theropoda (Gauthier, 1986; Sereno et al., 1994, 1996). Walker (1990) and Wu and Sues (1996) identified ectopterygoid cavities in *Sphenosuchus acutus* and *Platyognathus hsui,* respectively (see above), and Case (1929) and Doyle and Sues (1995) did the same in the parasuchian skulls they studied, but otherwise such cavities clearly are not widely distributed outside of theropod dinosaurs. Among theropods, ceratosaurians may well have a shallow, ventral fossa on the ectopterygoids (*Coelophysis bauri,* CM 31375; *Syntarsus rhodesiensis,* Raath, 1977; Fig. 35B), but it is not clear how widely an ectopterygoid recess obtains in the clade; Molnar (1991) reported its absence in *Ceratosaurus nasicornis.* However, a large, invasive cavity within the ventral portion of the pterygoid process of the ectopterygoid, opening caudomedially in most cases, is indeed an apomorphy of at least Neotetanurae (Sereno et al., 1994, 1996), although this feature remains poorly known for certain coelurosaurian taxa. In some coelurosaurians (e.g., *Deinonychus antirrhopus* and *Saurornitholestes langstoni*), the dorsal surface of the pterygoid process also has a cavity (Sues, 1978), such that in these taxa one must distinguish between dorsal and ventral ectopterygoid recesses. The ectopterygoid of *Archaeopteryx* spp. probably has a recess, but it is not clear if it is dorsal or ventral in the seventh specimen (Elzanowski and Wellnhofer, 1996); Paul (1988a, 1996) earlier had identified a dorsal recess from the Eichstätt specimen. In most theropod taxa, the (ventral) recess is a simple, smooth-walled cavity, as in *Allosaurus fragilis* (UUVP 5871), *D. antirrhopus* (YPM 5210, MOR 747), *Dromaeosaurus albertensis* (AMNH 5356; Fig. 35A), and others (see Barsbold [1983] for the ornithomimosaur *Garudimimus brevipes* and the troodontid *Saurornithoides junior*). In tyrannosaurids, however, the cavity is

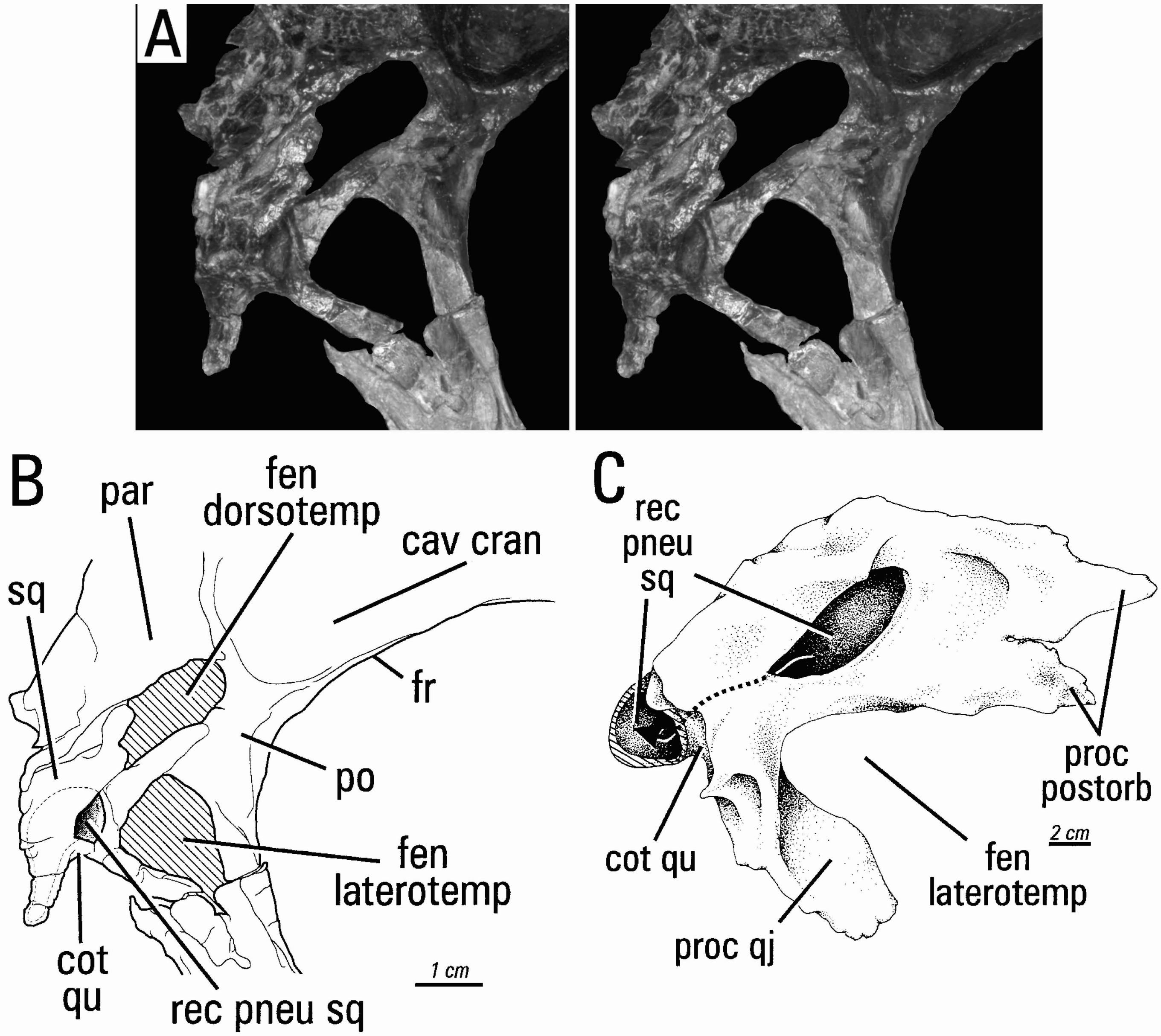

FIGURE 34. Squamosal recesses. **A**, *Dromiceiomimus brevitertius*, stereophotographs of caudal portion of skull (CMN 12228) in medial view showing the large accessory cavity in the squamosal bone. **B**, interpretive drawing of **A**. Broken line around squamosal recess depicts extent of recess as currently prepared. **C**, *Daspletosaurus torosus*, left squamosal (CMN 8506) in medial view. Arrow shows the communication of the large foramen with the cavity in the postquadratic process (broken open).

multi-chambered and strutted (e.g., *Tyrannosaurus rex*, LACM 23844; Molnar, 1991), and the external opening may be septate (e.g., *Daspletosaurus torosus*, CMN 8506; see also Carr, 1996). In the above taxa, the (ventral) recess is blind, but, in *Sinraptor dongi*, the recess is reported to extend well into the jugal process and emerge through a ventrolateral foramen (Currie and Zhao, 1994a). The dorsal ectopterygoid recess of *D. antirrhopus* (YPM 5210, 5232, MOR 747; Witmer and Maxwell, 1996) is highly variable in extent, ranging from being virtually absent to perhaps exceeding the ventral recess in volume; in all cases, the dorsal aperture is situated within a fossa that opens broadly medially toward the pterygoid bone. Sues (1978) reported a communication between the dorsal and ventral recesses in *Saurornitholestes langstoni*, but removal of all matrix from the recesses of three preserved ectopterygoids of *D. antirrhopus* showed that the recesses do not communicate in this species.

Although not strictly within the ectopterygoid, it is appropriate to mention here an adjacent cavity within the pterygoid of *Syntarsus rhodesiensis* (Raath, 1977; Fig. 35B) and *Sinraptor dongi* (Currie and Zhao, 1994a). In these taxa, the (ventral) ectopterygoid recess continues medially onto the ventral surface of the pterygoid such that the two bones together house a single large cavity (Fig. 35B). It is obvious that the pterygoid and ectopterygoid recesses were produced by the same agent and have a unitary function.

The general function of ectopterygoid recesses has been a matter of some discussion. Unfortunately, no recourse can be made to extant taxa because crocodilians (and other non-avian

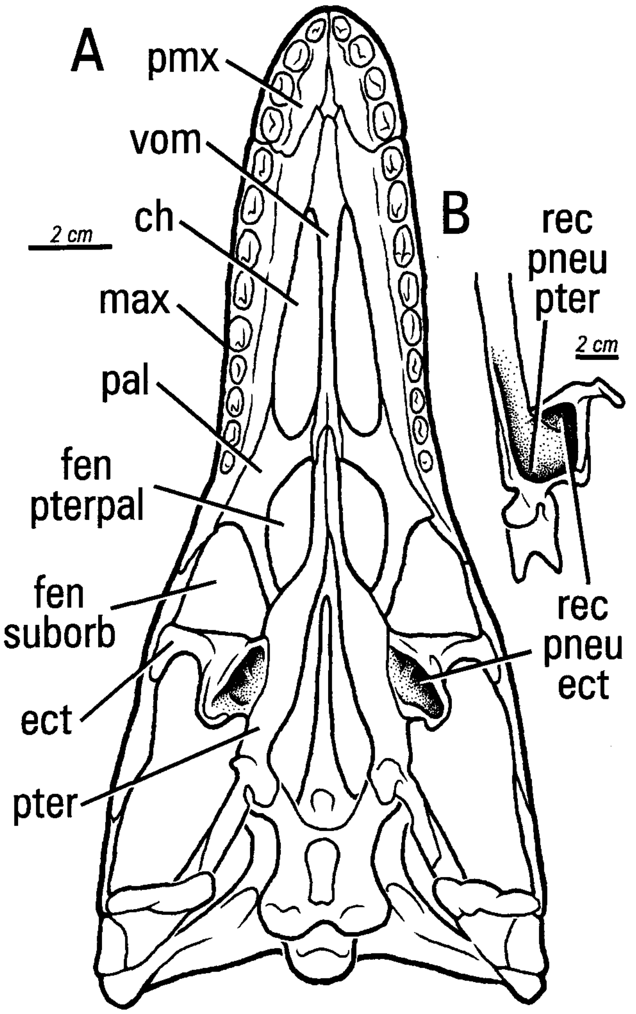

FIGURE 35. Ectopterygoid recesses. **A**, *Dromaeosaurus albertensis*, drawing of ventral view of the skull with the ectopterygoid cavity stippled (modified after Currie [1995] and specimen.) **B**, *Syntarsus rhodesiensis*, drawing of articulated pterygoid and ectopterygoid showing confluent ectopterygoid and pterygoid recesses (modified after Raath, 1977.)

amniotes) lack ectopterygoid recesses, and birds at least above the level of Ornithurae (Witmer and Martin, 1987) lack ectopterygoid bones altogether. Although more recent authors have favored a pneumatic interpretation for the recesses of theropods, Raath (1977) argued that those of *Syntarsus rhodesiensis* housed jaw musculature. Indeed, the simple (ventral) ectopterygoid recesses of, say, *Allosaurus fragilis* or *Dromaeosaurus albertensis* (Fig. 35) seem well disposed to accommodate a discrete portion of M. pterygoideus, pars ventralis, perhaps being analogous to the masseteric canal of macropodine marsupials (Ride, 1959). The strutted, multi-chambered cavities of tyrannosaurids, however, seem inconsistent with a muscular interpretation. Similarly, Ostrom (1969:27) suggested that the dorsal recesses of *Deinonychus antirrhopus* might "be related to the origin of the M. pterygoideus dorsalis," but again the depth and variability of the recess argues against a muscle. In fact, as noted by Currie (1985), high variability and asymmetry are properties of pneumatic systems.

If the cavities are pneumatic, as they indeed seem to be (see also Molnar, 1985, 1991), then the question again arises whether the diverticulum originates from the nasal cavity, tympanic cavity, or some other space. Another question is whether the dorsal and ventral ectopterygoid recesses of *Deinonychus antirrhopus* and *Saurornitholestes langstoni* necessarily were pneumatized by diverticula from the same air-filled space. The ventral recess will be considered first, and three hypotheses briefly will be examined. First, Currie and Zhao (1994a:2051; see also Currie, 1995) sided with the diverticulum being "linked to the antorbital pneumatic system" in *Sinraptor dongi*, and this is a reasonable possibility for all relevant taxa. The problem is: How would such a diverticulum reach the (ventral) ectopterygoid recess? For a bird-like suborbital diverticulum to reach the recess, it somehow would have to wind its way among the jaw musculature to either (a) curve caudally around the ala pterygoidea (the "flange" formed by pterygoid and ectopterygoid) or (b) take a shorter, rostral route through the suborbital fenestra. The recess opens caudoventromedially and not at all rostrally, effectively ruling out a course (b above) through the suborbital fenestra. A course around the ala pterygoidea (a above) remains possible but seems so circuitous as to strain plausibility. A second alternative is for the ectopterygoid to be pneumatized by a diverticulum from the middle ear sac. The tympanic cavity is reasonably close to the (ventral) ectopterygoid recess, and a rostral diverticulum conceivably could have reached this area. A third alternative is that neither paranasal nor paratympanic pneumaticity is involved, but rather that some novel diverticulum of the oropharynx produced the (ventral) ectopterygoid recess. This idea may be what Molnar (1991:149) had in mind when describing the recesses of *Tyrannosaurus rex* as opening caudoventrally, "presumably into the oral cavity."

Considering that the dorsal and ventral ectopterygoid recesses of at least *Deinonychus antirrhopus* do not communicate, it is justifiable to suggest that they were pneumatized from different sources rather than being separate apertures of the same sinus. The dorsal ectopterygoid recesses of velociraptorines (or at least *D. antirrhopus* and *Saurornitholestes langstoni*) have a much higher likelihood of having been pneumatized by a bird-like suborbital diverticulum of the antorbital sinus than did the ventral recesses. In fact, it may be the only possibility in that both the tympanic cavity and oropharynx are effectively closed off from this region. Furthermore, the avian suborbital diverticulum passes dorsal to the palatal elements (Fig. 6B), and thus, the dorsal position of the recess in velociraptorines is consistent with pneumatization by a similar diverticulum. The recess opens medially and is directed laterally within the jugal process. Thus, the dorsal pterygoideus muscle must have been displaced medially, with the suborbital diverticulum (if present) passing dorsolateral to it as in extant birds.

Orbital Recess within Lacrimal Bone—One virtually constant feature of the suborbital diverticulum of extant birds (Fig. 6B) is the presence of a portion of the diverticulum that extends dorsally, just caudal and directly adjacent to the lacrimal bone and just rostral to the eyeball (with the main portion of the diverticulum passing ventral to the eyeball). At least one specimen of *Allosaurus fragilis* (UUVP 2133) shows that such an air sac was present outside of birds. In this specimen, the caudal (orbital) surface of the lacrimal bone is grooved, leading dorsally to a recess just medial to the tuberositas lig. suborbitalis (Fig. 6C); within the recess is located the orbital end of the nasolacrimal canal. Such a structure is commonly observed in theropods. What is unusual about UUVP 2133 is that, ventral to the nasolacrimal foramen, a larger foramen leads into a blind cavity that extends rostrally within the body of the lacrimal bone ventral to the lacrimal recess. This blind cavity, termed here the orbital recess, is almost certainly pneumatic and is best explained as being produced by the dorsal portion of a birdlike suborbital diverticulum (Fig. 6C). Such orbital recesses have not been observed elsewhere, but a lacrimal of the ornithomimid *Dromiceiomimus brevitertius* (CMN 12228) shows evidence of a perhaps similar situation. Here the caudal surface of the ventral ramus bears a marked oval depression that extends dorsally up to the orbital aperture of the nasolacrimal canal. This depression is probably a pneumatic fossa, although a fossa for the gland of the nictitating membrane (of Harder) cannot be completely ruled out.

Summary—Reconstruction of a bird-like suborbital diverticulum of the antorbital sinus in fossil archosaurs requires an argument of "compelling morphological evidence" (Witmer, 1995b). Certain structures of theropod dinosaurs were advanced above as potentially indicative of a suborbital diverticulum: (1) the squamosal recess of tyrannosaurids and *Dromiceiomimus brevitertius,* (2) the (ventral) ectopterygoid recess of many theropods (as well as the pterygoid recess of a couple of taxa), (3) the dorsal pterygoid recess of *Deinonychus antirrhopus* and *Saurornitholestes langstoni,* and (4) the orbital recess within the lacrimal bone of *Allosaurus fragilis.* All of the above recesses are almost certainly pneumatic in origin. The question is the source the diverticula. The evidence is scant that the first two recesses are products of pneumatization via a suborbital diverticulum of the antorbital sinus, and other explanations (e.g., tympanic pneumaticity) cannot be ruled out. The last two recesses, however, are best explained as having been produced by a suborbital diverticulum (Fig. 6C). The problem here is that these features do not appear to have a wide distribution. Nevertheless, it is worth reiterating that this diverticulum only very rarely has osteological correlates in extant birds, and thus the scarcity of such correlates in fossil taxa perhaps is not unexpected. Although the evidence is somewhat equivocal, it is my opinion that at least some theropods had a suborbital diverticulum of the antorbital sinus that extended caudally through the postnasal fenestra, interleaved with the jaw musculature, and, as in present-day birds, only occasionally pneumatized bone (Fig. 6C).

In birds, the significance of the suborbital diverticulum of the antorbital sinus is that it is directly adjacent to the jaw musculature and interleaves with the various muscles. Therefore, adduction and abduction of the mandible sets up positive and negative pressures within the air sac. As a result, the antorbital sinus and its diverticula are ventilated like a bellows pump (Witmer, 1992a). Among extant vertebrates, birds are unique in actively ventilating their paranasal air sinuses, because the sinuses in mammals and crocodilians are bone-enclosed dead spaces in which air flows solely by diffusion. The physiological importance of active ventilation remains obscure and is under study. Thus the discovery of this system in non-avian archosaurs is a significant finding in that it provides a historical constraint on any functional interpretation of the avian system—in other words, it shows that it did not evolve as a flight-related adaptation.

Summary

There is very strong evidence that the presence of paranasal air sinuses characterizes Archosauria. The extant phylogenetic bracket approach demonstrated not only that archosaurs possess a homologous paranasal air sac, but also that the osteological correlates of this air sac specifically involve the antorbital cavity, fenestrae, and fossae. This inference requires very little speculation (level I inference). Furthermore, this section documents that there is compelling morphological evidence from several clades of archosaurs (especially theropod dinosaurs) that this air sac sometimes pneumatized the bones surrounding the antorbital cavity, forming accessory cavities. Since homologous accessory cavities could not be discovered in the EPB, interpretation of the accessory cavities as pneumatic requires somewhat more speculation (i.e., a level II or III inference). Finally, cavities in some of the postfacial bones of various fossil archosaurs are very suggestive of pneumaticity, and at least a couple of them probably provide adequate evidence of the presence of a bird-like suborbital diverticulum of the antorbital sinus.

ORIGIN OF THE ANTORBITAL CAVITY: BASAL ARCHOSAURIFORMS

Application of the Extant Phylogenetic Bracket Approach

Archosauria is not the most inclusive clade of sauropsids manifesting an antorbital fenestra. As mentioned earlier, the presence of an antorbital fenestra and cavity is a synapomorphy of Archosauriformes (see Fig. 5B). What are the soft-tissue relations of the antorbital cavity in basal archosauriforms? The approach for inferring soft tissues within the antorbital cavity in these taxa proceeds as for Archosauria. Following the analysis of Gauthier et al. (1988), the extant phylogenetic bracket of any clade of basal archosauriforms is Archosauria (Aves plus Crocodylia) and Lepidosauria (*Sphenodon* plus Squamata). However, extant lepidosaurs lack antorbital fenestrae and cavities and paranasal air sinuses, and it is uncertain even if a dorsal pterygoideus muscle can be deduced as an ancestral feature of Lepidosauria (Witmer, 1995b). Thus, many relevant soft tissues cannot be hypothesized to be present unequivocally in the common ancestor of archosaurs and lepidosaurs (i.e., Diapsida). Therefore, the fallback approach, despite requiring level II inferences (Witmer, 1995a), must involve searching for compelling morphological evidence for particular soft-anatomical attributes in basal archosauriforms. Each hypothesis again will be considered in turn, but in much briefer form.

Glandular Hypothesis—Lepidosaurs have the homolog of the archosaurian nasal gland (Witmer, 1995b). It was noted earlier that at least one basal archosauriform clade (Erythrosuchidae) has clear osteological correlates of a nasal gland, suggesting a position like that in archosaurs far removed from the antorbital fenestrae or fossae.

Muscular Hypothesis—The specified osteological correlates of the dorsal pterygoideus (e.g., a dorsal fossa on the palatine, neurovascular grooves or foramina) are poorly known or undescribed for most basal archosauriforms. The dorsal view of the palate figured by Broom (1903) for *Proterosuchus fergusi* shows nothing resembling a muscular fossa. If Young's (1964) figures of the palatines of the erythrosuchid *Shansisuchus shansisuchus* are interpreted correctly, there may be a dorsal fossa similar to that in "*Pallisteria angustimentum*" or *Ornithosuchus longidens.* Evidence for the course for the maxillary neurovasculature comes from *Erythrosuchus africanus* (BMNH R3592), *S. shansisuchus* (Young, 1964), and *Euparkeria capensis* (Ewer, 1965), in which, as in most archosaurs, there is a large foramen or two on the dorsal surface of the body of the maxilla, just internal to the ventral margin of the antorbital fenestra. Thus published data are probably too poor to assess adequately the muscular hypothesis for basal archosauriforms, although the available evidence (especially the neurovascular foramina) suggests that the dorsal pterygoideus muscles in these forms, if present at all, were no more extensive than in Archosauria.

Pneumatic Hypothesis—Somewhat better data are available for assessing the pneumatic hypothesis. In all basal archosauriforms, the antorbital fenestra is usually large (except in proterochampsids) and always opens medially into the nasal cavity directly opposite the choana (Ewer, 1965; Sill, 1967; Gow, 1970; Romer, 1971; Cruickshank, 1972; Fig. 36). In proterochampsids, the antorbital cavity appears to be apomorphically reduced and caudally situated; it is tempting to believe that, as in crocodyliforms, this trend is associated with the caudal retreat of the choana behind the extensive maxillary secondary palate. The course of the nasolacrimal duct is unknown or undescribed for basal archosauriforms. There is no external an-

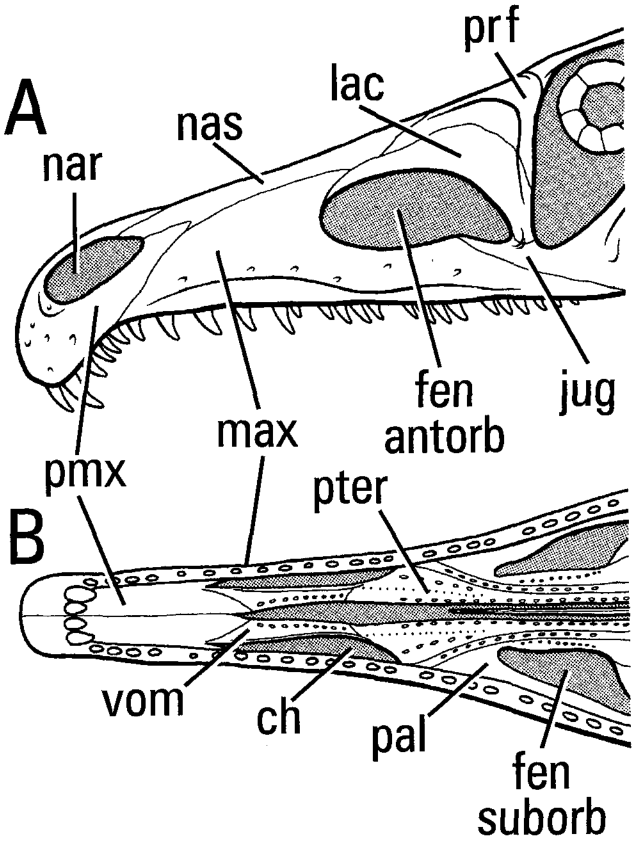

FIGURE 36. *Chasmatosaurus vanhoepeni.* **A**, drawing of snout in left lateral view. **B**, same in ventral view. (Modified from Cruickshank, 1972.)

torbital fossa in proterosuchids and basal erythrosuchids, but a well-developed fossa excavates a cavity within usually both the maxilla and lacrimal in more derived erythrosuchids (Parrish, 1992), *Euparkeria capensis* (Ewer, 1965), and the proterochampsids *Chanaresuchus bonapartei* (MCZ 4309), *Gualosuchus reigi* (Romer, 1971), and *Cerritosaurus binsfeldi* (Price, 1946) (Sereno and Arcucci, 1990; Sereno, 1991b). In fact, the general structure of the antorbital cavity differs very little between these basal archosauriforms and many archosaurs. Thus, the morphological evidence is probably sufficiently "compelling" to infer the presence of an antorbital air sinus in basal archosauriforms, although again this inference (a level II inference) requires more speculation than that for Archosauria (a level I inference).

The Origin of the Antorbital Fenestra and Cavity

Given the assumption of an antorbital air sac in basal archosauriforms, what is the impact of the pneumatic hypothesis on the origin of the antorbital fenestra and cavity? Based on the discussion above, it is almost certain that the function of the bony antorbital cavity at its inception was to house an epithelial paranasal air sinus. If the ontogeny of birds is a reliable guide (Witmer, 1995b), the external antorbital fenestra of the ancestral archosauriform species formed as an embryonic fontanelle that did not close, not a hole that opened within contiguous bones during ontogeny. The air sac may have been (and remains today) an important functional matrix controlling structure in this region of the face, physically intervening between the growing facial bones and preventing their apposition (see Moss and Young [1960] for air sinuses as functional matrices). The bones comprising the antorbital cavity and external fenestra thus formed around this pneumatic functional matrix (Witmer, 1995b). In extant archosaurs, accessory pneumatic cavities within the facial bones develop subsequent to hatching (i.e., after the air sac becomes aerated) via pneumatically induced processes of resorption (Witmer, 1995b). Thus, if air sinuses are indeed functional matrices, we have a causal basis for explaining the origin of the antorbital fenestra, fossa, and cavity of archosauriforms. In other words, the focus shifts from skeletal to soft-tissue concerns.

The origin of the epithelial diverticulum itself (i.e., the antorbital sinus) remains problematic and is perhaps intractable. Relative to their outgroups (e.g., Prolacertiformes, *Trilophosaurus,* Choristodera, Rhynchosauria; Gauthier et al., 1988; Evans, 1988; Benton and Clark, 1988), archosauriforms are not drastically divergent in facial structure, and thus their evolution of a paranasal sinus is not easily comprehensible. At least two possibilities exist for the origin of the antorbital air sac. First, perhaps a novel genetic program for evaginating air sacs evolved. This scenario may suggest an initial adaptive value to the air sac, but not necessarily so. Second, perhaps archosauriforms evolved some unique conformation of the cartilaginous nasal capsule, choana, and neurovasculature that *permitted* evagination of an epithelial diverticulum. Such an evolutionary change could have originated simply as a heterochronic modification of the pattern of tissue interactions. For example, Brylski and Hall (1988) showed that the novel evolution of external, fur-lined cheek pouches in geomyoid rodents results from a simple change in developmental timing of the interaction between oral and dermal tissues. Thus, according to the second scenario the air sac may be selectively neutral, being a by-product of other (perhaps adaptive, perhaps not) aspects of facial conformation (i.e., it is a non-aptation sensu Gould and Vrba [1982]). The mysterious function of paranasal pneumaticity perhaps offers some support to this notion, such that the antorbital sinus may have originated for "no particular reason" and was subsequently co-opted for specific roles (e.g., its pneumatizing capabilities, a flotation device; see the next section).

THE FUNCTION OF PNEUMATIC SINUSES: A NEW PERSPECTIVE AND ITS IMPACT ON ANALYSIS OF SOME TRENDS IN FACIAL EVOLUTION

It has been emphasized throughout this study that elucidation of the function of the antorbital cavity must precede discussion of the function of the structure enclosed within the cavity. The previous sections have focused on the former issue, concluding that the antorbital cavity housed a paranasal air sinus. We now are in a position to ask the question, what is the function of this antorbital air sac? As will be seen, the functions and biological roles of any of the pneumatic systems of amniotes—not just the paranasal system but also the paratympanic, and pulmonary systems—remain controversial. This section explores some of the general issues surrounding the functions of pneumatic diverticula, examining previously published ideas, and then presenting a novel alternative hypothesis. Predictions of this new hypothesis are tested by analyzing the transformation of the antorbital cavity in the course of morphological trends in facial structure in selected clades.

The Enigmatic Biological Role of Pneumaticity

Of all of the pneumatic systems, the paranasal system has received the most attention, probably because the high incidence of sinusitis and "sinus headache" in humans has made the system clinically very important. Despite this attention and interest, the basic function of paranasal pneumaticity continues to be obscure. The topic has been reviewed on various occa-

Table 1. Functions proposed for the paranasal, paratympanic, and pulmonary air sinuses of pneumatic amniotes. Abbreviations: b, birds; c, crocodilians; cet, cetaceans; h, humans; m, mammals; p, pterosaurs; t, non-avian theropods; *, cited from Blanton and Briggs (1969).

Function	Reference
Paranasal Pneumaticity	
1. Equipoise (i.e., balancing head on neck)	Galen* (2nd century CE)
2. Vocal resonators	Bignon, 1889 (b); O'Malley, 1924 (h); Eckert-Möbius, 1933 (m); Wegner, 1958 (c); Dyce et al., 1987 (m)
3. Humidification and warming of inspired air (i.e., respiratory function)	O'Malley, 1924 (m); Eckert-Möbius, 1933 (m)
4. Increase area of olfactory epithelium	Negus, 1957, 1958 (m)
5. Absorb shocks to protect brain	Riu et al., 1960 (h); Geist, 1971 (m); Schaffer and Reed, 1972 (m); Dyce et al., 1987 (m)
6. Flotation devices	Bignon, 1889 (b); Proetz, 1953 (c, m); Wegner, 1958 (c)
7. Thermal insulation of CNS and sense organs	Bignon, 1889 (b); Bremer, 1940a (b); Proetz, 1953 (h); Verheyen, 1953 (b); Dyce et al., 1987 (c)
8. Role of facial ontogeny, actively increasing facial dimensions	Moss and Young, 1960 (h); Enlow, 1968 (h); Blaney, 1990 (h); Moore and Persaud, 1993 (h)
9. Functionless: evolutionary remnants of structures with actual functions (e.g., olfaction)	Negus 1957, 1958 (m); Hargett, 1972 (h); Shea, 1977 (h)
10. Functionless: occupy spaces between biomechanically important pillars	Weidenreich, 1924, 1941 (m, h); Sicher, 1952 (h); Enlow, 1968 (h); Moore, 1981 (m); DuBrul, 1988(h)
11. Allow functional decoupling of inner and outer tables by occupying intervening space	Paulli, 1900 (m); Weidenreich, 1924, 1941 (m, h); Proetz, 1953 (h); Möller, 1969 (b); Bühler, 1970, 1972, 1992 (b)
12. Facial architecture: provide maximal strength with minimal materials	O'Malley, 1924 (b, m); Badoux, 1966 (m); Enlow, 1968 (h); Bühler, 1972, 1986 (b)
13. Weight reduction (removal of mass)	Paulli, 1900 (m); Möller, 1969 (b); Schummer et al., 1979 (m); Bühler, 1986 (b, m); Winkler, 1985 (b)
Paratympanic Pneumaticity	
a. Lower impedance of middle ear, increasing sensitivity to low frequency sounds	Webster, 1962, (m); Henson, 1974 (c, b, m); Funnell, 1974 (h); Whetstone and Martin, 1979 (c, b); Kuhne and Lewis, 1985 (b); Chatterjee, 1991 (b); Currie and Zhao, 1994b (b, t)
b. Localization of sounds	Rosowski and Saunders, 1980 (b); Witmer, 1987a, 1988 (b, c, t); Chatterjee, 1991 (b); Currie and Zhao, 1994b (t)
c. Acoustic isolation of auditory apparatus from self-generated sounds	Tumarkin, 1959 (h); Fraser and Purves, 1960 (cet); Norris, 1968 (cet); Fordyce and Barnes, 1994 (cet)
d. Equalization of pressure on either side of tympanum (or between ears in crocodilians)	Tumarkin, 1959 (h); Colbert, 1946b (c)
e. Absorb shocks to protect brain	Verheyen, 1953 (b); Bühler, 1986 (b)
f. Thermal insulation of CNS	Verheyen, 1953 (b); Stork, 1972 (b); Warncke and Stork, 1977 (b); Bühler, 1986 (b)
g. Allow functional decoupling of inner and outer tables by occupying intervening space	Bühler, 1970, 1972, 1992 (b); Winkler, 1979, 1985 (b)
h. Cranial architecture: provide maximal strength with minimal materials	Bühler, 1972, 1986, 1992 (b)
i. Weight reduction (removal of mass)	Winkler, 1985 (b); Bühler, 1986, 1992 (b)
Pulmonary Pneumaticity	
i. Weight reduction (removal of mass)	Strasser, 1877 (b); Stresemann, 1927–1934 (b); Currey and Alexander, 1985 (b, p); Norberg, 1985 (b, p); Bühler, 1986, 1992 (b); Vogel, 1988 (b)
ii. Biomechanics: increase stiffness and bending strength with minimal mass by increasing second moment of area and decreasing wall thickness	Hunter, 1774 (b); Strasser, 1877 (b); Stresemann, 1927–1934 (b); Bellairs and Jenkin, 1960 (b, p); King and King, 1979 (b); Currey and Alexander, 1985 (b, p); Wellnhofer, 1991b (p)
iii. Thermoregulation	Martin, 1983b (b); Wellnhofer, 1991b (p)

sions (e.g., Skillern, 1920; O'Malley, 1924; Proetz, 1953; Negus, 1957; Riu et al., 1960; Blanton and Biggs, 1969; Moore, 1981; Blaney, 1990), usually with a significant bias toward humans and other mammals. The standard approach adopted by most reviews in refuting suggested functions was to present counter examples in which a taxon could not have the stated function. The most important review is that of Blanton and Biggs (1969) who concluded that none of the hypotheses that had been proposed was satisfactory. Their paper effectively closed off further debate, and authors of recent texts (e.g., Schummer et al., 1979; Williams et al., 1989; Hellquist, 1990; Lee, 1991) tend simply to express pessimism about resolution of the functional question and move on to other topics. The other pneumatic systems have not been subjected to the same level of functional debate, but, as Table 1 shows, numerous ideas have been proposed for paratympanic and pulmonary pneumaticity as well.

The archosaurian antorbital sinus is, of course, a paranasal sinus, but paratympanic pneumaticity (arising from diverticula of the middle ear sac) and pulmonary pneumaticity (arising from the lung air sacs) will also be considered. In other words, the function of pneumaticity *in general* is reviewed here. The justification for expanding the scope is the worry that we are "too close" to the problem. Perhaps further scrutiny of the nose and face will *not* reveal the significance of paranasal air sinuses. Perhaps stepping back and looking for the common properties of pneumatic systems will provide the long-sought insight.

The next section will briefly examine some of the ideas that have been advanced on the functions of the various pneumatic systems. Table 1 lists most of the previously proposed ideas for paranasal, paratympanic, and pulmonary pneumaticity. I have not attempted to go into the details of or refute each argument, and interested readers should examine the references in Table 1 and the reviews cited above. As noted above, most discussions have distinctly mammalian, if not human, biases, and I often could cite counter examples from archosaurs to provide additional evidence refuting the generality of a particular functional explanation. However, I have usually refrained from doing so, rather than devoting space to whipping a dead horse.

Paranasal Pneumaticity—(1) The earliest idea, that human paranasal sinuses exist to *improve the balance of the head on the neck,* has been attributed to the second-century Greek physician Galen (Blanton and Biggs, 1969). The obvious problem with this "equipoise" idea is that it applies only to humans (and perhaps owls), because the head in virtually all other amniotes is not positioned over the neck but rather is cantilevered. Although Braune and Clasen (1877) noted that filling the human paranasal sinuses with cancellous bone would increase the weight of the skull by only about one percent, the idea persisted, leading Biggs and Blanton (1970) to attempt to deal it a final crushing blow. Although this hypothesis should be of little more than historical interest, it is still cited occasionally by clinicians.

(2) The idea of sinuses acting as *vocal resonators* has been popular but never has been regarded as a primary function of the paranasal sinuses. Although most workers have accepted that sinuses should be able to act as resonating chambers (often citing the altered voices of people with head colds), a more general hypothesis was effectively refuted by Proetz (1953), Negus (1957), and Blanton and Biggs (1969). A favorite counter example are giraffes, which have enormous paranasal sinuses but virtually never vocalize.

(3) A respiratory function, namely, the *humidification and warming of inspired air* also is still often voiced by clinicians. This idea has been repeatedly refuted in the literature by the observation that the sinus epithelium is almost aglandular in virtually all pneumatic amniotes and furthermore that the sinus ostia tend to reside out of the path of respiratory currents. The stated function is performed not by sinuses but rather by nasal conchae (see Hillenius, [1992] for the importance of nasal conchae for endothermic vertebrates).

(4) The notion that sinuses serve to *increase the area of the olfactory epithelium* is usually attributed to Negus (1957, 1958) who suggested that the ancestral function of the sinus spaces was to house olfactory conchae (as is characteristic of macrosmatic mammals) and that taxa with empty sinuses represent a reduction or retreat of conchal structures (see [9] below). This idea never attracted many adherents, and extant archosaurs offer no support for it (Witmer, 1995b). Riu et al. (1960) are probably correct in their assertion that the sinuses are primitively empty and that macrosmatic mammals have apomorphically expanded their olfactory conchae into the sinus cavities.

(5) A function in *shock absorption* has been advanced principally for the expanded frontal sinuses of ungulates such as bovids, although Riu et al. (1960) suggested something similar for humans. The idea is that sinuses are interposed between the cite of impact loading (as occurs during intraspecific combat) and the brain and/or sense organs. Schaffer and Reed (1972) suggested that the bony septa within the sinuses help dissipate the stresses of impact, perhaps by acting as springs. Recently, Jaslow and Biewener (1995) experimentally investigated impact loading in goats, finding instead that sutures were effective in absorbing shock; unfortunately, they did not address the potential role of pneumatic sinuses in shock absorption. Even if shock absorption is a function of bovid frontal sinuses (which is far from established), it does not appear to apply widely among pneumatic amniotes—in fact, as noted by Negus (1957), it does not apply even to other "horned" ungulates in that cervids have very small frontal sinuses that are not situated between the antlers and the braincase.

(6) It has been suggested from time to time that paranasal sinuses could serve as *flotation devices.* Obviously this could not be a function of wide applicability.

(7) A number of workers have noted that the sinuses could function as *thermal insulators* of the central nervous system and/or sense organs. As air is a poor conductor, a "jacket" of air-filled sinuses indeed could function to mitigate the effects of environmental temperature fluctuations on sensitive neural structures. Most formulations have focused on insulation against endogenously produced heat loss, and Bignon (1889) specifically envisioned the diverticula of the antorbital air sinus as insulating birds against the cold during high-altitude flights. Proetz (1953) was fairly enthusiastic about this hypothesis, and Blanton and Biggs (1969) did not come out strongly against it. Negus (1957), however, was not convinced, arguing that it does not apply widely enough in mammals to explain paranasal sinuses generally. This hypothesis obviously applies best to endotherms (such as extant birds and mammals) that maintain physiological temperatures within narrow limits, but many archosaurs (certainly crocodilians and probably most extinct clades) are or were ectotherms.

(8) An active role in *facial ontogeny* has been suggested from time to time. It is mentioned commonly in textbooks on human anatomy that facial growth lags behind cranial growth, catching up later with expansion of the paranasal sinuses and eruption of the teeth. The idea is that "sinuses . . . expand given areas of bone in conjunction with regional adaptations of morphological structure" (Enlow, 1968:193). Moss (e.g., Moss and Young, 1960) regarded sinuses as taking an even more fundamental role by acting as functional matrices; the archosaurian antorbital sinus was mentioned earlier as having some properties of a capsular functional matrix. That air sacs can directly affect bone growth has been controversial, and debate has continued as to whether sinuses are invasive and competent to displace bone (or bony cortices) or whether they are morphogenetically "inert" structures that are passively "sucked" into retreating bones during ontogeny (Proetz, 1953). This issue will be discussed further later.

(9) Some have suggested that sinuses are *functionless evolutionary remnants* of once functional structures. Hargett's (1972) notion that human paranasal sinuses are vestiges of "nasal gills" can be safely ignored, but the suggestion by Negus (1957) that sinuses are "unwanted" spaces left over after the reduction of once more extensive olfactory nasal conchae has had some adherents (e.g., Shea, 1977). In fact, although they were not swayed by the particulars of the Negus argument, Blanton and Biggs (1969:143) suggested that "perhaps this theory of a non-functional nature of these spaces is the most acceptable, leaving the burden of proof that [they] do perform a significant function with those investigators taking a different view."

(10) A related hypothesis is that sinuses represent *functionless "spaces between the braces"* (DuBrul, 1988:49) in that they occupy the area between biomechanically important bony pillars. Most clearly articulated by Sicher (1952; see also Moore, 1981), this hypothesis suggests that biomechanically unstressed bone is removed and replaced not by marrow but by an air-filled diverticulum. Thus the sinus spaces play no particular role, although they do reduce the weight of the structures somewhat.

(11) Several workers have suggested that sinuses allow a *functional decoupling of inner and outer bony tables* by occupying the intervening space. The external and internal surfaces of a bone may have different functional requirements (e.g., the outer table for muscle attachment and the inner table for housing a sense organ or the brain). Bühler (1970) dramatically demonstrated this point by showing that the braincases of nightjars (*Caprimulgus ruficollis*) are twice as wide as their endocranial cavities (the greater external breadth enhancing gape in association with capturing flying insects); pneumatic bone fills the space between the two lamellae. It is not always clear if those discussing this idea believe that the epithelial air sacs

actively separate the bony tables (i.e., providing a mechanism to "inflate" the bone) or that the sinus simply enters the space between the diverging lamellae (i.e., similar to hypothesis [10]).

(12) An architectural function, namely, *providing maximal strength with minimal materials,* has not been as popular as one might suppose given that this is a central axiom of vertebrate biomechanics. This lack of popularity can probably be attributed again to the bias toward humans in the debate, in that, as noted in hypothesis (1), the savings in materials in humans is probably negligible. Nevertheless, O'Malley (1924:63) suggested that the "primary reason of their existence" is, "on the hollow girder principle . . . [to] give the necessary bulk and strength to the framework of the face, without adding to the weight." Similar arguments on the "economy of materials" have been made forcefully by Bühler (1972, 1986, 1992). Again, whether the sinus is viewed as invasive (i.e., actively hollowing out the girder) or passively drawn in is not always clear in the literature.

(13) A few workers, mostly ornithologists, have suggested that *weight reduction* (i.e., the active removal of bone mass) is the primary function of paranasal air sinuses. Presumably, supporters of this hypothesis would actually ascribe to hypothesis (12), although some ornithologists clearly regard flight as providing such a strong selection pressure that weight reduction is most important.

It is clear from the above brief review that no consensus on the function of paranasal sinuses is imminent. The last four hypotheses (10–13) are obviously quite similar in that all relate in some way to facial architecture or biomechanics.

Paratympanic Pneumaticity—(a) *Increasing sensitivity to low-frequency sounds* is probably the most common functional explanation for paratympanic air spaces. Middle ears act as transformers, converting sound pressure at the tympanic membrane into displacement at the fenestra vestibuli. Pneumatization of the bones surrounding the tympanic cavity by the middle ear sac thus increases the total volume of the middle ear. This expansion decreases the impedance of the middle ear, especially at lower frequencies, and enhances sensitivity to lower-frequency sounds (Henson, 1974; Kuhne and Lewis, 1985; Lombard and Hetherington, 1993). This hypothesis is very attractive because it is based on simple biophysical principles. Furthermore, the hypothesis has survived some experimental testing in that cochlear microphonics of kangaroo rats (Webster, 1962) and crocodilians (Wever and Vernon, 1957) and behavioral studies of birds (Dooling, 1980) have shown that enlarged middle ear cavities are coupled to enhanced audition at the lower registers. As a result, this function has been suggested at one time or another for all groups of pneumatic amniotes—including some clades of fossil archosaurs (see Table 1). However, elegant as this notion is, it does not explain all aspects of paratympanic pneumaticity. For example, the pneumatic cavities within the quadrates and articulares of a few clades of archosaurs (e.g., birds, crocodilians, some non-avian theropods) usually are connected to the tympanic cavity via only narrow, often collapsed, tubes, and thus could contribute very little to any auditory function (Witmer, 1987a).

(b) In some taxa, paratympanic sinuses may contribute to *localization of sounds* in space. This idea was originally suggested (e.g., Rosowski and Saunders, 1980) for birds, which, because of their generally small head size and lack of pinnae, are not usually able to derive directional information from interaural differences in phase, arrival time, or attenuation of incoming sounds. Sound localization in birds instead often results through acoustic coupling of the two ear drums via the "interaural pathway," a pneumatic channel formed by contralateral communication of the two rostral tympanic recesses (see Kuhne and Lewis [1985], Witmer [1987a], and references therein for details of the mechanism). Witmer (1988) suggested that a variety of non-avian archosaurs also may have had such an interaural pathway. As with hypothesis (a), however, this hypothesis is not applicable to all amniotes with pneumatic features or even to all of the paratympanic systems of archosaurs.

(c) Another proposed function of limited distribution is *acoustic isolation of the auditory apparatus from self-generated sounds.* This idea has been advanced principally for cetaceans (see Table 1), although Tumarkin (1959) suggested something similar for humans. In cetaceans, the petrosal bone is surrounded by a tympanic diverticulum, the "peribullary sinus." This peribullary sinus tends to reflect sounds generated by the animal away from its auditory apparatus, and furthermore provides a mechanism to aid in the localization of sounds. It also may be noted that many cetaceans (especially delphinids) have very extensive paratympanic air sacs that are filled with an air/oil/mucus emulsion (see Fraser and Purves, 1960).

(d) A few workers have suggested that paratympanic sinuses function in *pressure equalization.* Colbert (1946b) made the reasonable supposition that, as the complicated paratympanic pneumatic recesses of crocodilians communicate with the auditory (Eustachian) tubes, they may have something to do with equalizing the pressure on either side of the tympanum or between the two ears. However, several workers (e.g., Wever and Vernon, 1957) noted that a single large tube would accomplish this function in a much simpler fashion.

(e) A role in *shock absorption* was suggested for the paratympanic recesses of birds by Verheyen (1953) and Bühler (1986). Whereas a pneumatic skull roof in mammals derives from paranasal pneumaticity (usually the frontal sinus), the skull roof in birds is usually pneumatized by paratympanic diverticula (Witmer, 1990 and references therein). The same basic argument obtains, but the pneumatic skull roof in birds usually takes on a much more ordered, "multistoried" (Bühler, 1986, 1992) appearance.

(f) A *thermal–insulation* function of the pneumatic skull roof of birds has been proposed by a number of authors (Table 1). As in hypothesis (5), the multistoried skull roof in this model acts to insulate the brain from external temperature fluctuations in much the same way as double- or triple-pane windows insulate a house. Warncke and Stork (1977) showed experimentally that finches with an apneumatic skull roof fluffed up their feathers at higher temperatures than did finches with a pneumatic skull roof; similarly, they showed that the rate of pneumatization was four times higher in birds kept at lower temperatures than in birds kept at higher temperatures. These findings suggest a thermoregulatory function. However, this model does not work as well for other components of the avian paratympanic pneumatic system or for other pneumatic amniotes.

(g) A *functional decoupling of the inner and outer tables* has been suggested for the paratympanic pneumatic system as well as for the paranasal system (see hypothesis [11] for discussion).

(h) As in hypothesis [12], the argument of *maximal strength with minimal materials* has been seldom advanced. Similarly, the active removal of bone mass for *weight reduction* (i) has not received much attention. In both cases, Bühler (1972, 1986, 1992) has been the major advocate.

As with paranasal pneumaticity, there is not much of a consensus on the function of paratympanic recesses. The closest approach (hypothesis [a]) is some relation to enhancement of auditory sensitivity to low-frequency sounds. Interestingly, the recurrent architectural or biomechanical hypotheses in the discussion of paranasal pneumaticity were seldom proposed for the paratympanic system. Similarly, the discussion of the paranasal system was biased toward mammals whereas that of the paratympanic pneumaticity was biased toward birds and other archosaurs. This situation probably results for at least two reasons. First, as mentioned, the paranasal system has considerably greater clinical importance than does the paratympanic pneumatic system, and there simply are a vast number of researchers interested in clinically relevant issues. Second, there is a rough taxonomic difference in the relative development of the two systems: in mammals, the paranasal system is generally extensive and the paratympanic system is relatively inconspicuous, whereas in birds the opposite (more or less) is true.

Pulmonary Pneumaticity—There is a considerable literature on the lung air sac system of birds (see McLelland, 1989 and references therein). Most of this literature focuses more on the air sacs that are situated among the body cavities than the aerated bones. As result, functional studies are skewed toward the former, and the significance of pneumatic bones is often treated in passing. It may be noted here that pterosaurs also have pneumatic foramina within many of their postcranial bones.

(i) Pneumatic postcranial bones are widely seen as functioning in *weight reduction* by actively removing the mass of the skeleton. Winkler (1985:475) voiced a common sentiment, suggesting that "it is obvious that pneumatization primarily serves to save weight and so enhance flying ability." Although the mass saved by hollowing out the bones might not be great, a general feeling pervades the literature that natural selection acts very strongly on flying organisms and their wing loadings. Furthermore, Currey and Alexander (1985) argued forcefully that mass reductions of even 10 percent can lead to significant savings in the energetic costs of locomotion. On the other hand, many flightless birds retain postcranial skeletal pneumaticity, and perhaps no Mesozoic birds (including those with more or less "advanced" flight apparatus) had pneumatic appendicular skeletons (Martin, 1983b).

(ii) A biomechanical function, namely, pneumatic bones exhibiting *increased stiffness and bending strength with minimal mass,* has also been quite popular (and is certainly an old notion, dating back to Hunter [1774]). The idea is that pneumatization provides a mechanism to increase the second moment of area and decrease the wall thickness of a bone, thus providing a least mass solution for bony structures that are both sufficiently stiff and strong in bending (Currey and Alexander, 1985). Bones are subject to a number of often conflicting constraints, such that there is considerable variation in the actual thicknesses of the walls of pneumatic bones. For example, the bones of the pterosaur *Pteranodon longiceps* are extraordinarily thin (showing that saving mass is critical), whereas those of many birds are a bit thicker, in accordance with "the fairly rough-and-tumble lives that most birds lead" (Currey and Alexander, 1985:464).

(iii) A *thermoregulatory function* has been suggested for both birds (Martin, 1983b) and pterosaurs (Wellnhofer, 1991b). The idea here is that pneumatizing a bone places a relatively cool air pocket at the core of the heat-generating muscle mass. It is not clear, however, how the minimal air circulation in most pneumatic bones would allow the hypothesized heat transfer to occur to any significant extent, air being, of course, a better insulator than conductor (see hypotheses [7] and [f] above). Nevertheless, this hypothesis has not been subjected to any experimental testing to my knowledge, and it is worthy of further investigation.

A New Perspective

Having surveyed most of the functions that have been proposed for the diverse pneumatic sinuses of amniotes, we are in a position to ask if there is a common thread running among the hypotheses. None of the hypotheses that are specific to a particular system (e.g., vocal resonance for the paranasal system or enhanced low frequency audition for the paratympanic system) are completely satisfying, and each has enough counter examples to be of less than universal applicability—hence the pessimism of so many authors. The closest approach to a unifying function is some relation to skeletal architecture and biomechanics, but even here the connection is vague and no clear explanation emerges.

Empty Space is a Red Herring—There is, however, one element that is shared by almost all of the hypotheses, namely, they attempt to explain the *empty space* within the bony sinus. In other words, it is the empty space that is supposed to have the function. For example, the empty space of the paranasal sinus functions as perhaps a resonating chamber, a shock absorber, a float, an insulator, a useless void between important pillars or the skull tables, etc. The empty space of the paratympanic recesses functions as perhaps a chamber for lowering impedance, a channel for localizing sounds, a cavity for isolating the inner ear, a pressure equalizer, etc. The empty space of the pneumatic postcranial bones functions as perhaps a useless void between the thin but strong tubular bony cortices, a heat exchanger at the core of a muscle mass, etc. Since "weight reduction" has been suggested for all systems, the empty spaces might be simply light areas not occupied by relatively heavy bone. Perhaps viewing the bony sinuses and cavities as empty space—and then searching for a function for this empty space—has led us down the wrong path for so long. Perhaps the empty space is indeed a red herring.

The Epithelial Hypothesis for Pneumatic Function—Pneumatic sinuses, of course, are not truly empty, but rather they always have a thin lining of epithelium. The epithelium, not the enclosed volume of air, may be the key. This is the new perspective promised in the section header. Perhaps the function of air sacs (i.e., the pneumatic epithelium) is simply to expand and to promote pneumatization—and no more. Air sacs simply may be pneumatizing as much bone as they can within the limits imposed by a certain biomechanical loading regime, perhaps in a completely opportunistic manner. The air sacs remain in contact with the resulting pneumatic cavities, and thus are well disposed to adjust dynamically the balance of osseous deposition and resorption as loading regimes change throughout the ontogeny of the organism. This hypothesis thus suggests that there are two competing forces at work: (1) the tendency for air sacs to expand, and (2) the tendency for bone to be deposited to maintain sufficiently strong structures. As long as adequate cross-sectional area of bone is maintained in a region, the sinus epithelium is free to expand until constrained elsewhere. The resulting bony structure is thus a compromise between these two tendencies, producing the familiar pattern of strutted chambers. An interesting corollary to this hypothesis is that natural selection need *not* act directly to produce "optimal" structures (i.e., maximal strength with a minimum of materials). Rather, they result *incidentally* from the interplay between the tendency to pneumatize and the tendency to lay down bone, with local loading patterns determining the locations of the struts and cavities. In other words, "optimal design" is, in a sense, an automatic, secondary by-product of this system.

What, then, is the function of paranasal (or paratympanic or pulmonary) pneumatic sinuses? Probably they have no function at all. Epithelial evaginations of air-filled chambers may simply occur (for morphogenetic reasons that may remain forever obscure). It might be argued that air sacs evolved as adaptations to produce this sensitive and dynamic system for controlling skull architecture. Although this may in fact be the case, the point is that *adaptation or natural selection does need to be invoked to explain the data.* Strong but light structures result from the intrinsic properties of the tissues involved. The advantage of this hypothesis is that it works for all pneumatic systems and all taxa with pneumaticity. Since it does not require the sinuses of particular taxa to have a particular function, no special pleading is required to explain embarrassing counter examples.

At the same time, however, the hypothesis does not deny that sinuses could have a real, positive function in some cases. The issue here relates to Gould and Vrba's (1982) discussion of current utility and historical genesis. A distinction must be made between what a structure does for an organism today versus its ancestral function. For example, an ornithologist unfamiliar with the situation in fossil archosaurs may readily accept the idea that the antorbital sinus is just another "adaptation for reducing the weight of the skull for flight" (King and McLelland, 1984:46). However, a homologous sinus was present before any archosaurs took to the air, and thus the historical genesis of the sinus was not as a flight adaptation. Similarly, Wegner (1958) suggested that the extensive paranasal air sinuses of extant crocodilians are adaptations to allow the head to float at the surface of the water, yet homologous sinuses are known to occur in the terrestrial outgroups of extant crocodilians. These examples are not intended to diminish the notion that paranasal air sinuses might have current functional utility for flying birds and floating crocodilians. In the terminology of Gould and Vrba (1982), these features may be exaptations for their current function, which then may be honed by natural selection as secondary adaptations.

It may be noticed that function 10 in Table 1 is fairly close to the hypothesis proposed here. Indeed, in researching this hypothesis, it was discovered that especially Sicher (1952) and Moore (1981) entertained some similar notions. The difference is that these authors still focused on the empty spaces (rather than the epithelium) as being important, they restricted their attention to the paranasal system of mammals, and, at least Sicher (1952) tied the process into adaptation more strongly.

Supporting Evidence—The previous section sought to lay down the epithelial hypothesis and its implications in an abbreviated, "data-free" form. This section provides the supporting evidence for some of the claims made therein. For example, the hypothesis requires that the epithelial air sacs are morphogenetically competent to pneumatize bone; in fact, this statement itself is a hypothesis amenable to testing. The process of pneumatization and its control remain somewhat obscure at the tissue or cellular level, but are sufficiently well known for the present purpose. Although some authors (e.g., van Gilse, 1935) speak of the "pneumatizing function or capacity" of the air sacs, this is just a shorthand form. The epithelium itself, of course, does *not* have the capacity to resorb bone, but rather resorption is accomplished by the blood-borne, multinucleated osteoclasts (van Limborgh, 1970) that form as a "front" around the air sac. Bremer (1940b) showed that pneumatization of the humerus in *Gallus gallus* proceeded by an air sac penetrating the bony cortex, following a blood vessel, with accompanying osteoclastic resorption of bone. Stork (1972) described similar phenomena for the pneumatization of the skull roof of pigeons. The air sacs are sometimes highly vascularized and sometimes poorly vascularized (Fraser and Purves, 1960; Bang, 1971), and it is unknown whether the vascularization of the air sacs changes throughout ontogeny. In other words, perhaps the epithelial diverticula become more vascularized during times of active pneumatization; certainly, as Grevers and Kastenbauer (1996) have shown, nasal muscosa in general has special properties resulting from its unusual angioarchitecture. To my knowledge, both the signaling mechanism of epithelium to osteoclasts and the control of activation/cessation of pneumatization are unknown, although the latter may be mediated by parathyroid hormone in some cases (Bremer, 1940b; Miller et al., 1984). Despite these uncertainties, the epithelial/osteoclastic complex is clearly the pneumatizing agent.

The new perspective proposed here also requires that the epithelial air sacs have an intrinsic tendency to expand in an invasive and opportunistic manner. This hypothesis has been fairly controversial. As mentioned earlier, some authors have argued that the sinus epithelium is a passive structure that is simply "sucked" into the voids created by the bones as they grow away from each other. Proetz (1953) was the strongest advocate of this view, and, although this idea was based primarily on study of skulls of a single species (humans), it gained some supporters (Shea, 1977; Ranly, 1988). The other idea is that air-filled epithelial diverticula are active, expansive, and invasive structures. This notion has had more supporters (e.g., Coffin, 1905; van Gilse, 1935; Bremer, 1940b; Sicher, 1952; Fraser and Purves, 1960; Moss and Young, 1960; DuBrul, 1988; among others), and explains the observed data better, leading Koppe et al. (1996:39; see also Libersa et al., 1981; Koppe et al., 1994; Koppe and Nagai, 1995) to note that "it has been demonstrated that the sinuses possess a developmental potential of their own." Three examples corroborating this hypothesis will be given here. (1) In species with determinate growth, the process of pneumatization does not stop but rather continues after the bones have ceased further growth. For example, in elderly humans, the maxillary sinus may continue to expand, even crossing sutural boundaries to pneumatize the palatine bone and/or jugal (zygomatic) bone; this observation (and numerous similar ones for birds) cannot be accounted for by passive air sacs being drawn into retreating bones, but only by an active, invasive process. (2) More striking examples are provided by the numerous "inflated bullae" that are found scattered throughout pneumatic amniotes: the auditory bullae of desert rodents (Webster, 1962), the numerous bullae associated with the nasopharyngeal duct of extant crocodilians (see Witmer, 1995b and references therein; see also the remarkable pterygoid bulla of gharials [Martin and Bellairs, 1977]), the parasphenoid capsules of troodontids, ornithomimosaurs, and many birds (Osmólska and Barsbold, 1990; Barsbold and Osmólska, 1990), the vestibular bullae of theropods described above, among many others. These bullar structures clearly document both the competency of air sacs to inflate and displace bone and also the expansive nature of the sacs. (3) A dramatic demonstration of the potential expansion of epithelial air sacs is seen in cases of compensatory sinus hypertrophy with cerebral hemiatrophy, a clinical condition that generated considerable interest 40 to 50 years ago (Ross, 1941; Noetzel, 1949), but is relevant in the present context. In these cases, the cerebral hemisphere on one side either degenerates or does not develop properly (for any number of reasons), and, in the absence of cranial contents offering resistance, some or all available pneumatic sinuses (e.g., frontal, ethmoid, mastoid, petrous) greatly expand to more or less fill the void, carrying the endocranial bony cortices with them. While this situation could be interpreted in a Proetzian way (i.e., the drop in intracranial pressure sucks the sinuses in), there are faster and easier mechanisms (e.g., CSF or vascular effusion) to restore intracranial pressure, and in fact most students of the phenomenon have regarded the sinuses as actively invading the unoccupied space (Ross, 1941). Although epithelial air sacs indeed have these invasive capabilities, the mechanism is again obscure. Coffin (1905), van Gilse (1935), and others have written about air sacs exerting "pneumatic pressure," but the source of this pressure is unclear. Air pressure would seem the most likely alternative, but many of the epithelial diverticula evaginate the main cavity (nasal, tympanic, pulmonary) prior to birth (or hatching), i.e., prior to aeration of the diverticula. Therefore, although the mechanism is somewhat mysterious, the expansive and invasive capabilities of epithelial air sacs are well documented.

The epithelial hypothesis also requires that bone be responsive to its mechanical milieu. In other words, local biomechanical loading regimes should dictate bone remodeling. There is ample evidence, both experimental and theoretical, that remodeling is controlled to a very large extent by the strain environment experienced by the bone matrix (see Currey, 1984; Lanyon et al., 1982; Lanyon, 1987; Thomason, 1995; and references therein). Once again, the transduction mechanism by which functional strains are converted into adaptive remodeling is enigmatic, but the phenomenon is real.

The final corollary of the epithelial hypothesis is that there is a "struggle" between the conflicting tendencies of pneumatization and bone deposition. Five quite different examples will be presented here to support this claim. (1) The mere fact that pneumatic cavities are usually supported by bony struts and buttresses tends to support this notion of a compromise between pneumatization and biomechanical demands. Furthermore, the position of the struts are non-random and often correspond to the locations of high stress. For example, in *Alligator mississippiensis,* the caviconchal and postvestibular sinuses pneumatize most of the snout (see Witmer, 1995b), but the two sinuses usually remain separated by a bony strut (Fig. 15B) that is situated directly opposite the largest maxillary tooth, which is presumably a site of high bite loads. (2) An interesting example of these conflicting tendencies may be seen in cases where an epithelial air sac is closed off from the main air-filled chamber. For example, chronic otitis media in humans leading to obstruction of the auditory tube results in the paratympanic air sacs losing communication with the pharynx; in the absence of a patent sinus ostium, new bone formation increases and fills the cavity (Tos et al., 1984). The same findings (i.e., new bone filling in a pneumatic cavity upon closure of its ostium) result from experimental studies of auditory tubal occlusion in rats (Kuijpers et al, 1979) and pneumatic foramen closure in chicken humeri (Ojala, 1957). Likewise, clinical studies of humans (e.g., Proctor and Naclerio, 1996; Batsakis and El-Naggar, 1996) have repeatedly shown that a normally functioning mucosa and patent sinus ostium are necessary for normal sinus growth. Although these situations represent pathological cases, they show that nonpathological epithelial air sacs are competent to maintain the cavity and keep new bone formation at bay. (3) As discussed above, the skull roofs of most birds are pneumatized by paratympanic diverticula and produced into a multistoried lattice. Chapin (1949:691) noted, however, that the skull roof of woodpeckers (Picidae) "is composed of a single layer of bone, thicker and stiffer than that" of most other birds. He attributed this (p. 691) to "direct adaptation to their hammering and the use of the beak as a chisel." This reasoning seems sound. In a sense, the mechanical rigors of repeated axial loading of the skull have apomorphically tipped the balance toward bone deposition and away from pneumatization (nonpicid piciforms retain the pneumatic skull roofs). (4) In another avian example, Strasser (1877), Müller (1908), and subsequent authors noted that the position of the pneumatic foramina on avian postcranial long bones is non-random, and the pulmonary diverticula pneumatize the bones only at locations under relatively little biomechanical stress. (5) Finally, Sicher (1952) and DuBrul (1988) noted that in elderly humans that have lost their teeth, the paranasal sinuses greatly expand, crossing sutural boundaries into adjacent bones, and reducing the facial bones to thin shells. Having lost their teeth, the skulls of these individuals are no longer subjected to the repetitive masticatory stresses that require substantial cross-sectional area of bone. As a result, the sinuses expand in a relatively unconstrained manner.

In summary, the epithelial hypothesis for pneumatic function is supported by a considerable amount of data, and can explain quite disparate findings. It is a testable hypothesis, as are all of its corollary hypotheses. Questions remain about the details of the mechanisms of pneumatization and bone strain transduction, but these do not compromise the applicability of the hypothesis or falsify it.

Trends in the Evolution of the Facial Skeleton

What does this "new perspective" on the function of pneumaticity tell us about archosaurs? Can it provide any insight into the observed patterns of morphological evolution? What role, if any, does this antorbital air sac play in the evolution of the facial skeleton in various clades of archosaurs? This section will briefly examine trends in three groups of archosaurs—crocodylomorphs, ornithopod ornithischian dinosaurs, and theropod saurischian dinosaurs. These three clades were selected because they each show fairly clear evolutionary trends in the anatomy of the antorbital cavity: namely, a reduction in the size of the cavity and a tendency for closure of the external antorbital fenestra in crocodylomorphs and ornithopods; and expansion of the cavity with the development of pneumatic accessory cavities in theropods (Witmer, 1992b). In some cases, there are concurrent trends in other anatomical systems that impact on the interpretation of the antorbital cavity. The intent is to document the broad phylogenetic changes in the antorbital cavity in each clade, compare these changes with modifications in other anatomical systems, and evaluate these data in light of the epithelial hypothesis for pneumatic function. Thus, examination of these trends is a sort of test of the epithelial hypothesis, albeit one of plausibility and consistency.

It is understood that "evolutionary trend" is a term and concept loaded with considerable (and formidable) intellectual baggage (Nitecki, 1988; Gould, 1988, 1990). Actually, the causal basis of the trends is not the focus here (although it is occasionally too difficult to resist the temptation of causal explanation). Rather, the patterns themselves are of interest for these allow an evaluation of the functional question with fewer assumptions about the action (or non-action) of natural selection. Strictly speaking, the trends examined here are not of the conventional "change-through-time" variety that dominate the literature (e.g., papers in McNamara, 1990). They are phylogenetic trends. The goal simply is have a sense of the historical pattern of acquisition of the features of interest. Detailed resolution is not sought here, and only a handful of taxa will serve to illustrate each trend. The broad outlines of the trends will be sufficient to examine the role of the antorbital cavity and air sinus in facial evolution.

Crocodylomorpha—The primitive archosaurian condition for the antorbital cavity, as described earlier, is to have a relatively large cavity excavating an antorbital fossa on the maxilla and lacrimal, no pneumatic accessory cavities, and large internal and external antorbital fenestrae. Extant crocodilians, of course, have closed their external antorbital fenestrae, and thus have markedly diverged from the primitive condition. At the risk of constructing an arbitrary "anagenetic highway" (Gould, 1990:7), the basic outline of the trend is as follows (Fig. 37). Basal crocodylomorphs such as the basal sphenosuchians *Terrestrisuchus gracilis, Saltoposuchus connectens,* and *Pseudhesperosuchus jachaleri* can be scored as having essentially the primitive condition. In derived sphenosuchians such as *Dibothrosuchus elaphros, Sphenosuchus acutus,* and the Kayenta sphenosuchian, the antorbital cavity is smaller, the fossa occupies less of the maxilla, and the internal fenestra is more caudally placed. Protosuchians (basal crocodyliforms) show a similar reduction in the antorbital cavity and the external antorbital fenestra. Ignoring thalattosuchians for the moment, basal metasuchians such as *Uruguaysuchus aznarezi* and *Araripesuchus gomesii* continue the reduction and enclosure of the cavity, but to a relatively minor extent. At the level of Neosuchia (e.g., *Theriosuchus pusillus* and *Alligator mississippiensis*), the external antorbital fenestra is closed or extremely small and the antorbital cavity is completely internalized. Thus, the trend is for the antorbital cavity to become reduced and restricted to the caudal portion of the snout and the external antorbital fenestra

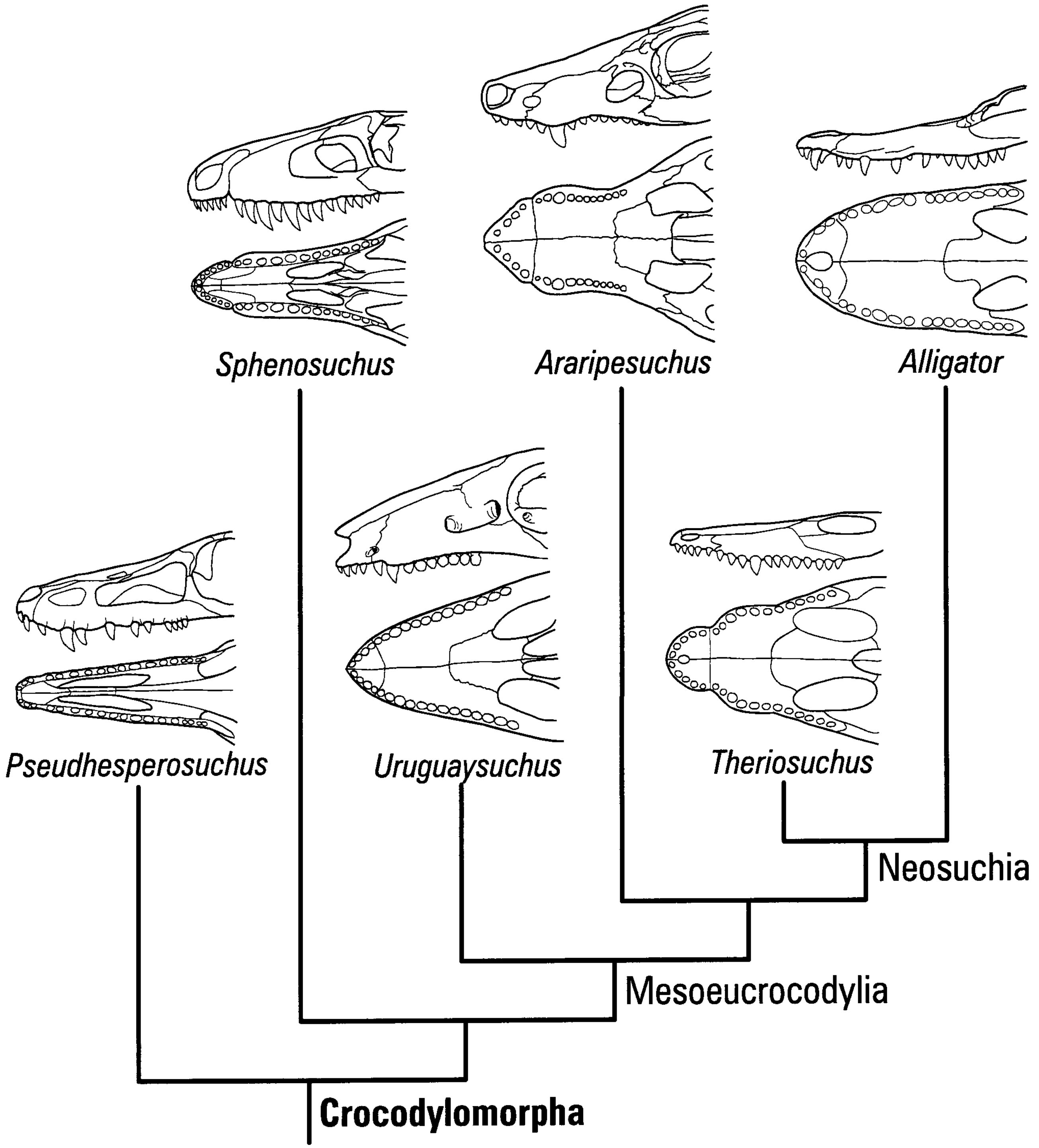

FIGURE 37. Facial trends in Crocodylomorpha. In the course of crocodylomorph evolution, the external antorbital fenestra becomes reduced and eventually closed, and the antorbital cavity likewise becomes reduced and eventually completely internalized. These trends are associated with restriction of the main paranasal air sinus in connection with the development of maxillary palatal processes and dorsoventral flattening of the snout. Skull drawings modified from Owen (1878), Rusconi (1932), Kälin (1955), Bonaparte (1972), Gasparini (1971), Buffetaut (1982), Walker (1990), and Hecht (1991).

to become smaller, eventually closing such that the antorbital cavity is completely internalized within the snout.

There are a couple of concurrent trends that also need to be considered here: first, the formation of a so-called "secondary palate," and second, dorsoventral flattening of the skull. The first of these itself subsumes two probably separate phenomena: (1) formation of palatal processes of the maxilla and (2) formation of a bony nasopharyngeal duct. Of these last two, the formation of more extensive palatal processes of the maxilla is, in fact, correlated with the initial reduction of the antorbital cavity. Expansion of the maxillary palatal processes (e.g., in *Sphenosuchus acutus* or *Protosuchus richardsoni* relative to

Pseudhesperosuchus jachaleri) diverted the primary choana caudally. Because of the fundamental morphogenetic relationship between the primary choana and antorbital sinus (discussed above; see also Witmer, 1995b), the entire system shifted caudally where, encroaching on the orbit and its contents, there simply was less space available for the antorbital cavity; in other words, it was constrained by "packing" phenomena. It turns out, however, that formation of a nasopharyngeal duct in mesoeucrocodilians seems to have had virtually no effect on the subsequent reduction or enclosure of the antorbital cavity, because forms such as *Notosuchus terrestris, Uruguaysuchus aznarezi,* and *Araripesuchus gomesii* retain an antorbital cavity similar to that of protosuchians. This situation probably results because the development of a nasopharyngeal duct involves the presence and position of the secondary choana, not the primary choana (Witmer, 1995b); the primary choana (i.e., the rostral end of the duct) had not moved relative to the antorbital cavity. In fact, all this is further evidence affirming the causal relationship of primary choana and antorbital sinus.

So, if the initial reduction of the antorbital cavity perhaps has its causal basis in the evolution of palatal processes of the maxilla, what factors are involved in the ultimate reduction of the cavity? As discussed earlier, extreme reduction and closure of the external antorbital fenestra occurs multiple times in Crocodylomorpha: once or twice in Thalattosuchia, at least once or twice among basal metasuchians, and at least once or twice in Neosuchia. Concomitant internalization of the antorbital cavity occurred clearly at least twice: at least once in Thalattosuchia and at least once in Neosuchia. In most of these cases, closure of the external fenestra can be shown to be associated with apomorphic flattening of the snout. Skull flattening, the other important concurrent trend mentioned above, has been well documented by Langston (1973) and especially Busbey (1995).

The biomechanical consequences of dorsoventral flattening are considerable. Flattening the snout (Fig. 38B) moves it away from the design optimum of a cylinder (Fig. 38A), potentially making it less competent to resist sagittal bending and torsional loads (Witmer, 1992b). Busbey's (1995) elegant functional analysis of the trend from oreinirostral (tall-snouted) sphenosuchians and protosuchians to platyrostral (flat-snouted) neosuchians confirmed these mechanical sequelae and suggested mechanisms to resist these stresses. In particular, Busbey (1995) noted that platyrostral taxa show increased cross-sectional area of bone through (1) thickening of the bones and (2) the development of a secondary palate (interestingly, even an incomplete secondary palate has biomechanical benefits). Furthermore, Busbey (1995) was correct in noting that platyrostral skulls loaded in sagittal bending exhibit stress concentrations at the caudal end of the snout, just in front of the orbits. These stress concentrations are in precisely the position of the external antorbital fenestrae. Therefore, an external fenestra severely decreases the ability of the snout to resist these torsional and especially sagittal loads, because such a gap or discontinuity would produce a so-called "open section" (Fig. 38B). In fact, it would result in the coincidence of an open section and a stress concentration—a potentially catastrophic design. Therefore, I would suggest (see also Witmer, 1992b) that the ultimate closure of the external fenestra is causally linked to platyrostry as another mechanism to increase cross-sectional area of bone.

Thus, in light of the epithelial hypothesis for the function of pneumaticity, the evolutionary trends in the snouts of crocodylomorphs support the claim of a "struggle" between the conflicting tendencies of pneumatization and maintenance of adequate strength. The caudal shift of the primary choana resulting from the development of maxillary palatal processes pushed the whole pneumatic system caudally and constricted it as it competed for space with the orbital contents. Nevertheless, the cavity remained tolerably large in the oreinirostral metasuchians such as *Araripesuchus gomesii.* However, the flattening of the snout produced a biomechanical weak spot at exactly the location of the external antorbital fenestra. Thus closure of the external fenestra and internalization of the paranasal air sac was a biomechanical solution to the problem (and nasal rotation was probably the morphogenetic mechanism accomplishing this closure; Witmer, 1995b). It would seem that in crocodylomorphs, the paranasal air sinus "loses" in the metaphorical struggle, and this is probably a fair conclusion. But, interestingly, in the broad- but flat-snouted alligatorines, pneumaticity has rebounded, and the snout is a multi-chambered maze with stout bony struts at biomechanically predictable locations.

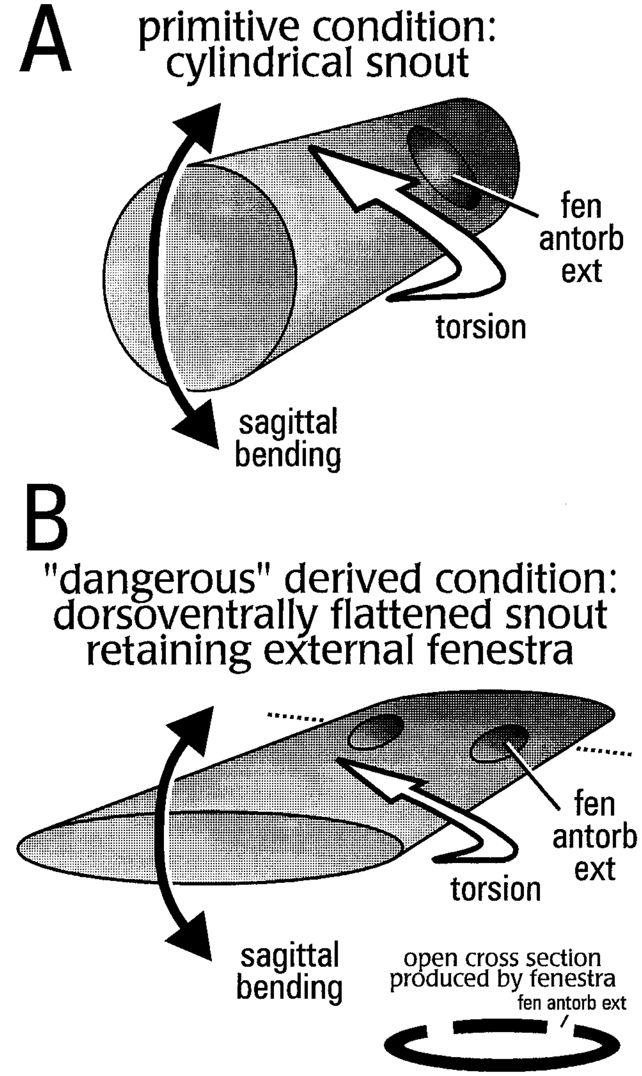

FIGURE 38. Biomechanical implications of platyrostry (flattening of the snout). **A**, the primitive condition (manifested by sphenosuchians, protosuchians, many basal metasuchians) is to have a much taller, more cylindrical snout. **B**, the dorsoventral flattening observed in some clades (most notably neosuchians) makes the snout particularly susceptible to failure under sagittal bending and/or torsion. Furthermore, the stress concentrations resulting from platyrostry are in precisely the locations of the external antorbital fenestra, which would produce an open cross section further weakening the snout. Ultimate closure of the external antorbital fenestra and internalization of the antorbital cavity was probably largely a biomechanical consequence of platyrostry.

Ornithopoda—Turning to ornithischian dinosaurs, the focus will be Ornithopoda, but most major clades of ornithischians

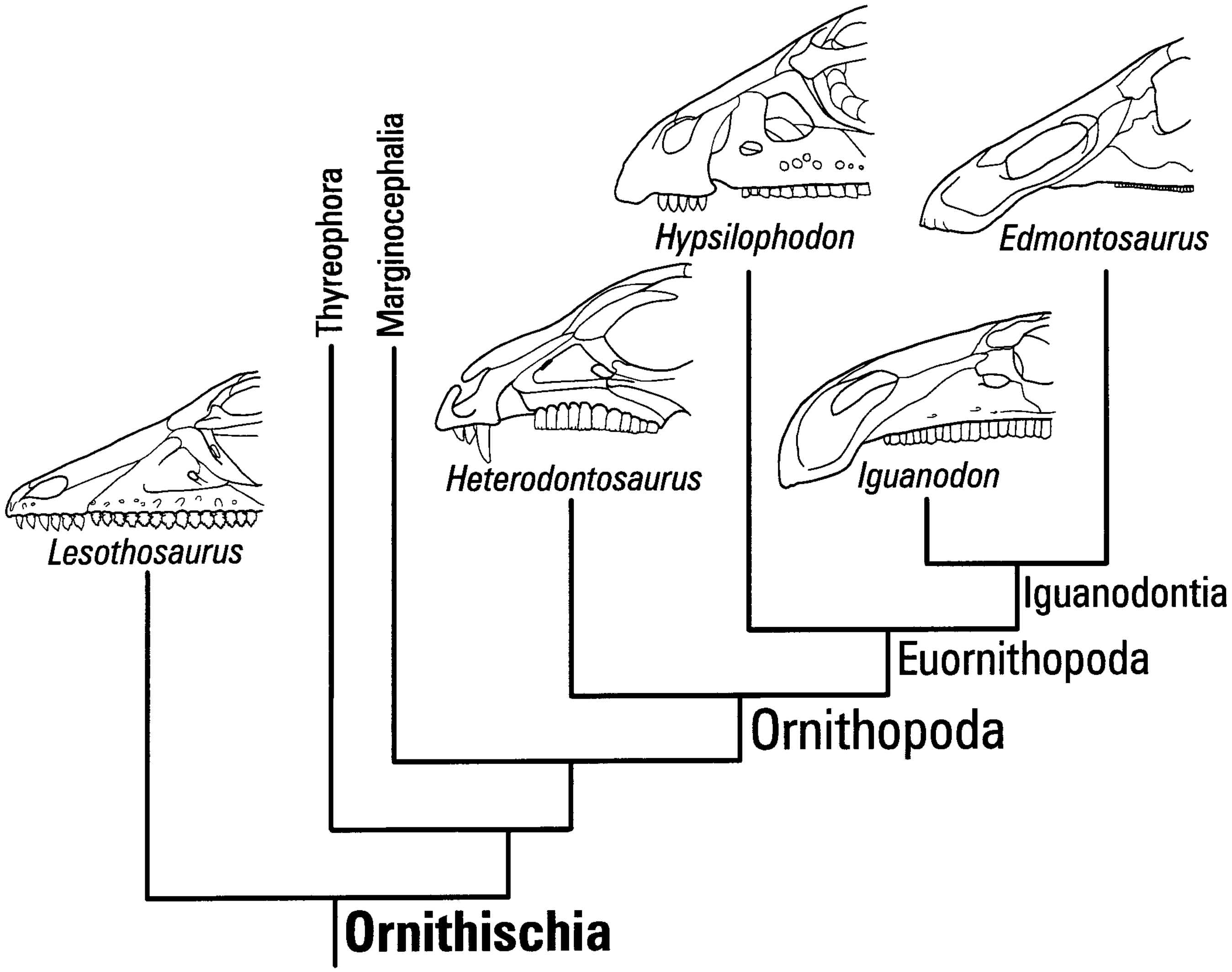

FIGURE 39. Facial trends in Ornithopoda. In the course of ornithopod evolution, the external antorbital fenestra becomes reduced and eventually closed at the level of Hadrosauridae. The antorbital cavity also becomes reduced and eventually completely internalized, as in crocodylomorphs. These trends are associated with restriction of the main paranasal air sinus in connection with the elaboration of the masticatory apparatus and enlargement of the nasal vestibule. Skull drawings modified from Galton (1974), Norman (1986), Weishampel and Horner (1990), Weishampel and Witmer (1990b), and Sereno (1991a).

independently show the same basic trends, namely, like crocodylomorphs, reduction of the antorbital cavity and closure of the external antorbital fenestra (Fig. 39). The primitive ornithischian condition, manifested by *Lesothosaurus diagnosticus,* is to have a small internal antorbital fenestra (essentially the ostium of the antorbital paranasal air sinus) and a relatively large external antorbital fenestra. Basal ornithopods, such as *Heterodontosaurus tucki,* display the first signs of the trend in that lateral laminae from the maxilla and lacrimal constrict the external antorbital fenestra. These laminae are even more extensive in hypsilophodontids, and the external antorbital fenestra is relatively small. In basal iguanodontians, the antorbital cavity and external fenestra are further reduced and displaced caudally. Finally, in hadrosaurids, the external fenestra is completely closed (sometimes partly covered by the jugal), and the antorbital cavity is internalized and relatively small.

An important concurrent trend here is the expansion of the feeding apparatus, in particular, the dentition and its bony buttresses (see Weishampel, 1984, 1993 and references therein). Ornithopods show functional innovations indicative of extensive oral processing in association with herbivory, such as a transverse power stroke (achieved independently through different mechanisms in heterodontosaurids and euornithopods). Aspects of this masticatory trend are increases in the number of teeth (but a decrease in the relative size of each tooth), their packing in the jaws, and the relative size of the maxilla, culminating in the characteristic dental batteries of hadrosaurids. Another trend worth noting takes place in Iguanodontia, and this relates to expansion of the nasal vestibule with enlargement of the naris and resultant caudal displacement of the antorbital cavity. (There is also a marked trend for size increase, but such allometric effects are too complex to merit laboring the discussion here.)

Therefore, the relationship between the trends in the antorbital cavity (and its enclosed sinus) and in other anatomical systems is relatively straightforward. As the relative volume of the dentition and its buttresses increases, the relative volume of the antorbital paranasal air sinus and its bony cavity decreases; and, in iguanodontians, as the nasal vestibule expands, the antorbital cavity becomes further reduced. As in crocodylo-

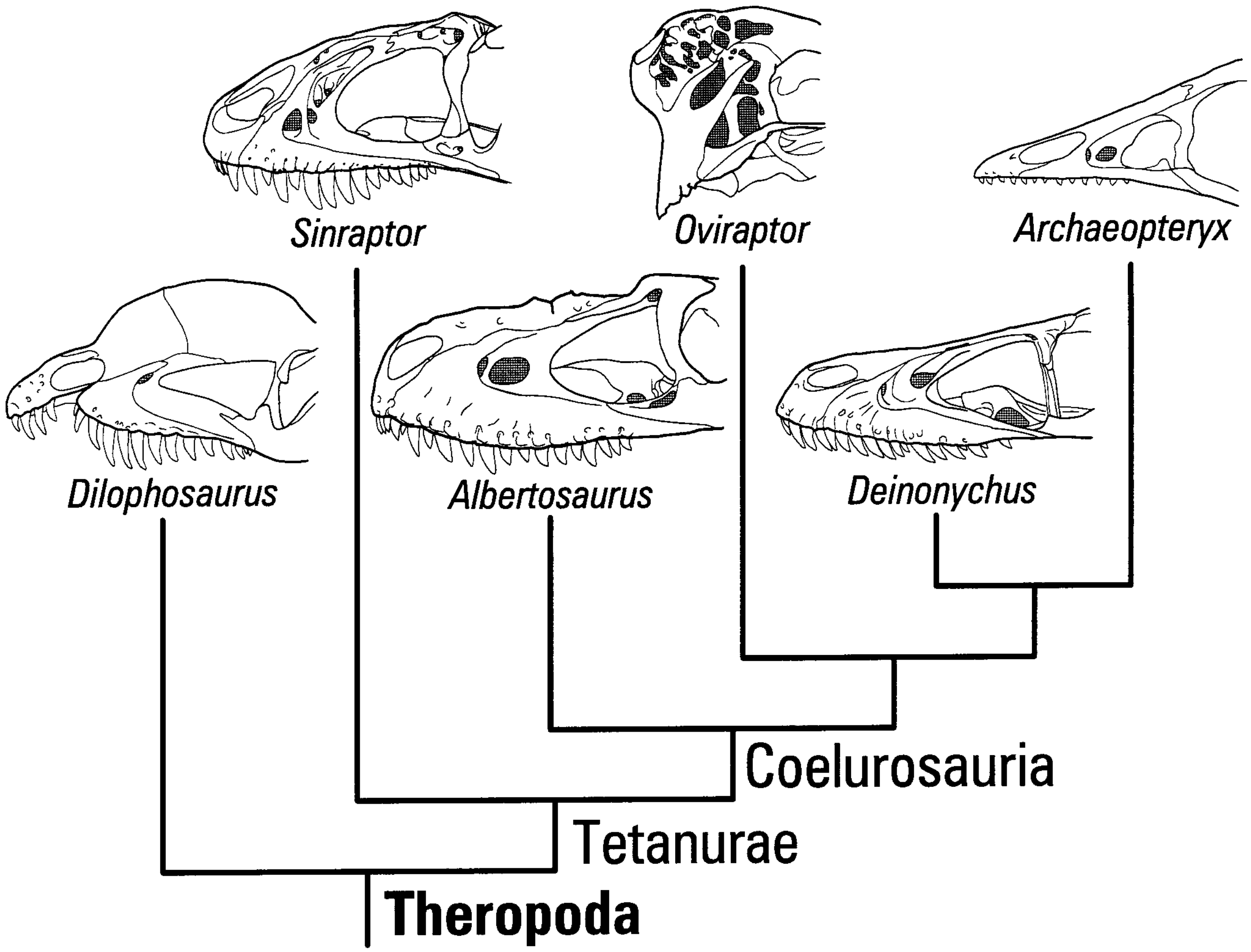

FIGURE 40. Facial trends in Theropoda. In the course of theropod evolution, the antorbital cavity expands with the development of diverse bony accessory cavities (shaded areas) to house the subsidiary diverticula. The bewildering array of pneumatic accessory cavities in neotetanurans is good evidence for the expansive nature of pneumatic diverticula. Skull drawings modified from Russell (1970), Barsbold (1983), Welles (1984), Paul (1988a,b), Witmer (1990), and Currie and Zhao (1994a).

morphs, ornithopods present another example in which the biomechanical requirements for adequate cross-sectional area of bone (in this instance coupled to the rigors of repetitive masticatory bite loadings) apparently prevail over the tendency for pneumatic expansion.

Theropoda—Whereas crocodylomorphs and ornithopods both manifest trends for reduction of the antorbital cavity, theropod dinosaurs show the opposite trend: expansion of the antorbital paranasal air sinus and formation of bony accessory cavities to house these subsidiary diverticula. At its earliest appearance, the antorbital cavity of theropods was very extensive and almost always is the most conspicuous aspect of facial structure. The accessory cavities of theropods received fairly extensive treatment in a previous section, so detailed discussion is not required here. The trend is quite simple (Fig. 40): in basal theropods such as *Eoraptor lunensis, Herrerasaurus ischigualastensis, Dilophosaurus wetherilli,* or *Coelophysis bauri,* there are very few or no pneumatic accessory cavities, whereas there is both a much greater diversity and frequency of pneumatic recesses in more derived theropods (certainly at and above the level of Neotheropoda). The trend is carried to its extreme in *Oviraptor philoceratops* in which virtually all of the facial elements are highly pneumatic. It is difficult to identify specific concurrent trends in other anatomical systems in theropods. In fact, it is even difficult to present an orderly pattern of acquisition of the accessory cavities (Witmer, 1995c). Consider, for example, the pneumatic recesses in the nasal bone: They are present in *Sinraptor dongi* and *Allosaurus fragilis,* but not in any tyrannosaurid. *Oviraptor philoceratops* has them, but ornithomimosaurs lack them; they are present in *Deinonychus antirrhopus,* but *Velociraptor mongoliensis* lacks them, etc. Although the example seems whimsical, other similar patternless instances could be cited.

In fact, this almost haphazard pattern of highly homoplastic pneumatic characters is compelling evidence for the epithelial hypothesis of pneumatic function in that these subsidiary diverticula of the antorbital sinus appear to be expanding in a very invasive and opportunistic manner. Numerous examples of "swollen" or "inflated" pneumatic bones can be cited, such as the palatines of large tyrannosaurids and the lacrimals and vestibular bullae of many theropods. Given the phylogenetic distribution of these recesses, pneumaticity seems to be a fairly poorly constrained system in theropods. Nevertheless, the main structural members (e.g., the ventral ramus of the lacrimal, the ascending ramus of the maxilla, etc.) never appear to be compromised. In fact, in *Tyrannosaurus rex,* an apomorphically massive form capable of generating enormous bite forces, many of the pneumatic apertures have become apomorphically reduced in relative size (increasing the cross-sectional area of cortical bone), yet the pneumatic recesses within are extensive, yielding—probably incidentally and automatically—"optimally designed" tubular bars.

Summary

The discovery of the function of the bony antorbital cavity of archosaurs allowed the asking of the next logical question: What is the function of the enclosed structure? In other words, what is the role of the antorbital paranasal air sinus? A survey of paranasal sinus function in pneumatic amniotes shows that no clear, widely applicable function presents itself. Widening the search to include paratympanic and pulmonary pneumaticity reveals the same situation: a diversity of suggestions but no consensus. The position is advanced here that the wrong perspective has hindered our understanding of pneumatic function. Rather than attempting to ascribe function to the empty space enclosed within the bony sinuses, focusing on the pneumatic epithelium (i.e., the air sac itself) might be more rewarding. Under this new perspective, pneumatic diverticula are viewed simply as opportunistic pneumatizing machines, resorbing as much bone as possible within the constraints imposed by local biomechanical loading regimes. Thus, this "struggle" between the tendency to pneumatize and the tendency to deposit bone *secondarily* provides a dynamic mechanism for controlling skull architecture, producing "optimal" structures without necessarily requiring the action of natural selection.

In light of this hypothesis, crocodylomorphs and ornithopods both show trends toward reduction and enclosure of the antorbital cavity not because they share any particular paleobiological attributes, but rather because both clades independently (and for different reasons) show an apomorphic change in skull biomechanics dictating deposition of bone rather than pneumatically induced resorption of bone. In theropods, the opposite trend occurs, and in some cases it seems as if the expansion of the air sacs is simply opportunistic, and is, in a sense, biomechanically "tolerated" or "unchecked."

SUMMARY

Complete understanding of the structure of extinct organisms cannot be gained by recourse to bones alone; soft tissues matter. In fact, soft-tissue components often direct the ontogenetic development, structure, and arrangement of bony elements, such that evolutionary studies involving only bones may not have the appropriate focus, especially if elucidating process (e.g., adaptation, selection regimes) is a goal. Soft-tissue relations often are the foundation of accurate paleobiological inference, and hypotheses regarding adaptation or the action of natural selection may require soft-tissue information if the hypotheses are to be tested adequately. Initial mistakes in soft-tissue assessments are compounded up the ecological hierarchy. Speculation in inferring soft tissues in fossils can be identified and minimized by approaching the problem phylogenetically, basing inferences on the osteological correlates of the soft tissues observed in the extant outgroups of a fossil taxon. A major result of this study is that a surprisingly large amount of sophisticated soft-tissue information can be teased out of fossil specimens. Many, if not most, soft tissues have predictable relationships with osteological structures, which is not unexpected given the integration of anatomical systems. Even if a soft-tissue component lacks reliable osteological correlates, information about its size, position, and conformation can often be recovered by reference to those surrounding soft tissues with known bony signatures, which, in effect, limit the realm of possible structures of the unknown component.

Careful application of this extant phylogenetic bracket approach has resolved the status of the antorbital cavity of Archosauria, and, in the process, allowed reconstruction of much of the facial structure of many taxa within diverse clades. For virtually all archosaurs, the inference of an air-filled diverticulum of the nasal cavity housed within the antorbital cavity requires almost no speculation (a level I inference sensu Witmer, 1995a). Such a paranasal air sinus is found in the extant phylogenetic bracket (i.e., both birds and crocodilians) of any clade of fossil archosaurs, and the osteological correlates of this sinus are ubiquitous in the extinct taxa. Alternative soft-tissue explanations for observed osteological features also must be sought. In the present example, the EPB approach demonstrated that there is good evidence that both the nasal gland and the dorsal pterygoideus muscle were among the contents of the antorbital cavity. However, the osteological correlates of these anatomical systems indicate that neither is associated with the antorbital fenestrae or fossae.

It is tempting to believe that much of the controversy stems historically from the traditional treatment of archosaurs as a paraphyletic group. If at the outset the antorbital cavity of extinct archosaurs had been recognized as homologous to that of birds, perhaps the glandular and muscular hypotheses would have never been proposed. Both the glandular and muscular hypotheses fail the tests provided by this method and accepting them requires excessive homoplasy. The pneumatic hypothesis, arguing that the antorbital fenestra and cavity of virtually all archosaurs housed a paranasal air sac, survives the tests, requires little or no speculation, and is applicable to all archosaurs. In cases where the soft-tissue assessment is equivocal because an extant outgroup lacks relevant attributes, compelling morphological evidence still may point to a particular aspect of soft anatomy, although this necessarily requires more speculation. Such is the case with the accessory cavities in the bones surrounding the antorbital cavity of many archosaurs, in that these bony cavities strongly support the notion of paranasal pneumaticity. Such is also the case with basal archosauriforms, where it seems likely that, like Archosauria, the antorbital cavity lodged an air sac. If in the latter case one regards the level of inference as acceptable, then it becomes likely that the origin of the antorbital fenestra and cavity is causally linked to the origin of the epithelial air sinus. Given this soft-tissue inference, more accurate reconstructions of archosaurian craniofacial structure provide a firmer foundation for interpreting the evolving lifestyles of extinct archosaurs.

Finally, with a firm idea of the function of the bony antorbital cavity in hand, it then becomes possible to investigate the function of the structure housed within the cavity. The function of paranasal pneumaticity—in fact, of any of the air-filled sinuses—has long been a mystery. This problem stems primarily from viewing it from what is probably the wrong perspective. Traditionally, functional explanations have been sought for the empty spaces (i.e., the enclosed volume of air) within the bony sinuses. However, a new perspective, focusing instead on the epithelial lining of the recesses, is much more promising. Under this hypothesis, pneumatic sinuses are seen as essentially without a positive function (unless natural selection secondarily co-opts a sinus for some novel role). Rather, sinuses result from the intrinsic capacity of the air sacs to expand and pneumatize bone in an invasive and opportunistic fashion until constrained by the biomechanical requirements for maintaining sufficiently strong structures. Thus, a "struggle" may be envisioned between the conflicting tendencies for expansive pneumatization on the one hand and mechanically mediated bone deposition on the other. This struggle secondarily and automatically provides a mechanism for producing "optimally designed" structures of maximal strength and requiring minimal materials without the necessity of invoking active natural selection for these attributes.

This new hypothesis is borne out in the evolution of the facial skeleton in several clades of archosaurs. In crocodylomorphs, a trend occurs for reduction and enclosure of the main antorbital paranasal air sinus and its bony cavity in conjunction with the increased biomechanical requirements that resulted from the evolution of a maxillary secondary palate and a dorsoventrally flattened snout. In ornithopods, a similar trend can be observed in the antorbital sinus and cavity, but here the biomechanical requirements relate more to the expanding masticatory apparatus and specialized nasal vestibule. Theropods show the opposite trend, with the highly unpredictable and homoplastic evolution of expansive pneumatic accessory cavities to house subsidiary diverticula of the antorbital sinus.

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ABBREVIATIONS

ala pter	ala pterygoidea	pterygoid wing (flange)
alv	alveolus dentalis	dental alveolus
antr max	antrum maxillaris	maxillary antrum
ap caud	apertura caudalis (orbitalis)	caudal (orbital) aperture
ap rec cavico	apertura recessus caviconchalis	aperture of caviconchal recess
ap rostr	apertura rostralis (nasalis)	rostral (nasal) aperture
bul vest	bulla vestibularis	vestibular bulla
bulb oc	bulbus oculi	eyeball
can nasolac	canalis nasolacrimalis	nasolacrimal canal
can neurovas	canalis neurovascularis	neurovascular canal
cav acc	cavites pneumatici accessoria	pneumatic accessory cavities
cav antorb	cavitas antorbitalis	antorbital cavity
cav cran	cavitas cranialis	cranial cavity
cav lac	cavitas lacrimalis	lacrimal cavity
cav nas	cavitas nasalis (= cavum nasi proprium)	nasal cavity proper
cav neurovas	cavitas neurovascularis	neurovascular cavity
cav paranas	cavitas paranasalis	paranasal cavity
cav pmx	cavitas premaxillaris	premaxillary cavity
ch	choana	choana
ch prim	choana (prima)	primary choana
ch sec	choana secundaria	secondary choana
CN V	N. trigeminus	foramen for trigeminal n.
col	columella	columella (= stapes)
cot qu	cotyla quadratica	quadrate cotyla
cr otosph	crista otosphenoidalis	otosphenoidal crest
den	os dentale	dentary bone
dent	dentes	teeth
div jug	diverticulum jugale	jugal diverticulum
div lac	diverticulum lacrimale	lacrimal diverticulum
div nas	diverticulum nasale	nasal diverticulum
div promax	diverticulum promaxillare	promaxillary diverticulum
div suborb	diverticulum suborbitale	suborbital diverticulum
du nasolac	ductus nasolacrimalis	nasolacrimal duct
du nasoph	ductus nasopharyngeus	nasopharyngeal duct
ect	os ectopterygoideum	ectopterygoid bone
emin rad dent	eminentia radicis dentis	tooth root bulge
exc pneu	excavatio pneumatica rami ascendenti	pneumatic excavation in ascending ramus
fac art jug	facies articularis jugalis	articular surface for jugal bone
fac art max	facies articularis maxillaris	articular surface for maxillary bone
fac art nas	facies articularis nasalis	articular surface for nasal bone
fac art pal	facies articularis palatina	articular surface for palatine bone
fac art prf	facies articularis prefrontalis	articular surface for prefrontal bone
fac art vom	facies articularis vomeralis	articular surface for vomer
fen antorb	fenestra antorbitalis	antorbital fenestra
fen antorb ext	fenestra antorbitalis externa	external antorbital fenestra
fen antorb int	fenestra antorbitalis interna	internal antorbital fenestra
fen caud antr max	fenestra caudalis antri maxillaris	caudal fenestra of maxillary antrum
fen dorsotemp	fenestra dorsotemporalis	dorsotemporal fenestra
fen laterotemp	fenestra laterotemporalis	laterotemporal fenestra
fen max	fenestra maxillaris	maxillary fenestra
fen postnas	fenestra postnasalis	postnasal fenestra
fen preantorb	fenestra preantorbitalis	preantorbital fenestra
fen promax	fenestra promaxillaris	promaxillary fenestra
fen pterpal	fenestra pterygopalatina	pterygopalatine fenestra
fen suborb	fenestra suborbitalis	suborbital fenestra
for neurovas	foramina neurovasculares	neurovascular foramina
for subnar	foramen subnarialis	subnarial foramen
fos antorb lac	fossa antorbitalis lacrimalis	lacrimal antorbital fossa
fos antorb max	fossa antorbitalis maxillaris	maxillary antorbital fossa
fos musc	fossa muscularis	muscular fossa
fos nar	fossa narialis	narial fossa
fos nas	fossa nasalis	nasal fossa
fr	os frontale	frontal bone
gl nas	glandula nasalis	nasal gland
jug interfen	jugum interfenestrale	interfenestral bridge
jug	os jugale	jugal bone
lac	os lacrimale	lacrimal bone
lam med	lamina medialis	medial lamina of ascending ramus
lam supralv	lamina supralveolaris	supralveolar lamina
M pter dors	Musculus pterygoideus, pars dorsalis	dorsal pterygoideus muscle
margo fen antorb int	margo fenestrae antorbitalis internae	margin of internal antorbital fenestra
max	os maxillare	maxillary bone
n max	n. maxillaris (CN V^2)	maxillary nerve
nar	naris	naris (nostril)
nas	os nasale	nasal bone
os scl	ossa sclerae	scleral bones
ost	ostium	ostium

pal dex	os palatinum, dexter	right palatine bone
pal sinis	os palatinum, sinister	left palatine bone
pal	os palatinum	palatine bone
par	os parietale	parietal bone
par med sin max	paries medialis sinus maxillares	medial wall of maxillary sinuses
pila interfen	pila interfenestralis	interfenestral strut
pila postantr	pila postantralis	postantral strut
pila postch	pila postchoanalis	postchoanal strut
pila promax	pila promaxillaris	promaxillary strut
pmx	os premaxillare	premaxillary bone
po	os postorbitale	postorbital bone
prf	os prefrontale	prefrontal bone
pro	os prooticum	prootic bone
proc max	processus maxillaris	maxillary process
proc pal	processus palatinus	palatine process
proc pmx	processus premaxillaris	premaxillary process
proc postorb	processus postorbitalis	postorbital process
proc qj	processus quadratojugalis	quadratojugal process
proc vompter	processus vomeropterygoidea	vomeropterygoid process
pter	os pterygoideum	pterygoid bone
qj	os quadratojugale	quadratojugal bone
qu	os quadratum	quadrate bone
ram asc	ramus ascendens, os maxillare	ascending ramus of maxillary bone
rec caudolat	recessus pneumaticus caudolateralis	caudolateral pneumatic recess
rec cavico	recessus caviconchalis	caviconchal recess
rec ch	recessus choanalis	choanal recess
rec epiantr	recessus epiantralis	epiantral recess
rec pneu ect	recessus pneumaticus ectopterygoideus	ectopterygoid pneumatic recess
rec pneu interalv	recessus pneumaticus interalveolaris	interalveolar pneumatic recess
rec pneu jug	recessus pneumaticus jugalis	jugal pneumatic recess
rec pneu lac	recessus pneumaticus lacrimalis	lacrimal pneumatic recess
rec pneu nas	recessus pneumaticus nasalis	nasal pneumatic recess
rec pneu pal	recessus pneumaticus palatinus	palatine pneumatic recess
rec pneu pter	recessus pneumaticus pterygoideus	pterygoid pneumatic recess
rec pneu sq	recessus pneumaticus squamosalis	squamosal pneumatic recess
rec postvest	recessus pneumaticus postvestibularis	postvestibular pneumatic recess
rec prf	recessus pneumaticus prefrontalis	prefrontal pneumatic recess
rec promax	recessus promaxillaris	promaxillary recess
rostr	os rostrale	rostral bone
rostr psph	rostrum parasphenoidale	parasphenoid rostrum
S_1, S_2	sinus paranasales 1, 2	paranasal sinuses 1, 2
sin antorb	sinus antorbitalis	antorbital sinus
sin cavico	sinus caviconchalis	caviconchal sinus
sin max	sinus maxillaris	maxillary sinus
sin max int	sinus maxillaris interna	internal maxillary sinus
"smx"	os "septomaxillare"	"septomaxilla"
sq	os squamosum	squamosal bone
sulc	sulcus	groove
sulc neurovas	sulcus neurovascularis	neurovascular groove
sulc sep	sulcus septalis	septal sulcus
vest	vestibulum nasi	nasal vestibule
vom	vomer	vomer