

# Homology of Facial Structures in Extant Archosaurs (Birds and Crocodylians), With Special Reference to Paranasal Pneumaticity and Nasal Conchae

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**ABSTRACT** Homology of virtually all major components of facial anatomy is assessed in Archosauria in order to address the function of the antorbital cavity, an enigmatic structure that is diagnostic for the group. Proposed functions center on its being a housing for a gland, a muscle, or a paranasal air sinus. Homology is approached in the context of the Extant Phylogenetic Bracket method of reconstructing unpreserved aspects of extinct organisms. Facial anatomy and its ontogeny was studied in extant archosaurs (birds and crocodylians) to determine the osteological correlates of each soft-tissue component; resemblances between birds and crocodylians comprised the similarity test of homology. The congruence test of homology involved surveying phylogenetically relevant fossil archosaurs for these bony signatures. The facial anatomy of extant birds and crocodylians is examined in detail to provide background and to discover those apomorphic aspects that contribute to the divergent specialization of these two groups and thus obscure homologies. Birds apomorphically show enlarged eyeballs, expanded nasal vestibules, and reduced maxillae, whereas crocodylian faces are dorsoventrally flattened (due to nasal rotation) and elongated. Most facial attributes of archosaurs are demonstrably homologous and in fact characterize much more inclusive groups. Special emphasis has been placed on the nasal conchae and paranasal air sinuses. Within Amniota, the following conchal structures are homologous, and all others are neomorphs: avian caudal concha, crocodylian concha + preconcha, *Sphenodon* caudal concha, squamate concha, and probably the mammalian crista semicircularis. The avian antorbital paranasal air sinus is homologous with the crocodylian caviconchal sinus; the maxillary sinus of placental mammals is not homologous with the archosaurian paranasal sinus. With regard to the function of the antorbital cavity, archosaurs possess homologous nasal glands, dorsal pterygoideus muscles, and paranasal air sinuses, but the osteological correlates of *only* the paranasal sinus involve the antorbital fenestrae and fossae. Thus, the antorbital cavity is best interpreted as principally a pneumatic structure. © 1995 Wiley-Liss, Inc.

The age-old image of a tiny plover calmly gleaning the leeches from within the gaping mouth of a crocodile hardly suggests the notion of any kinship between these two very different vertebrates. However, among modern vertebrates, birds and crocodylians are indeed sister taxa, representing the only surviving clades of Archosauria. Although extant archosaurs, with their 10,000 species, remain the most diverse group of terrestrial

vertebrates living today, during the Mesozoic Era extinct archosaurs (i.e., nonavian dinosaurs, pterosaurs, and a variety of early forms) radiated into virtually all habitats and by all measures were the dominant terrestrial vertebrates. As a result of this radiation,

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archosaurs present an extraordinary diversity of skull morphology. The pattern of archosaur phylogeny among extinct as well as living members is beginning to be unraveled (Gauthier, '86; Sereno, '86, '91; Gauthier et al., '88a; Benton and Clark, '88; Cracraft, '88; Norell, '89; Novas, '92; Clark et al., '93; Parrish, '93), and we are now in a good position to understand the evolution of archosaur craniofacial adaptation.

An important component of the diversity in skull morphology in archosaurs pertains to the facial skeleton, in particular to an opening and space in the side of the snout

called the antorbital fenestra and cavity, respectively (Witmer, '94). The antorbital cavity (defined below) is ubiquitous in at least the basal members of all clades of archosaurs and is a synapomorphy of a slightly more inclusive group (Archosauriformes; Fig. 1; Gauthier et al., '88a; Benton and Clark, '88). In some archosaurs (e.g., some theropod dinosaurs) the antorbital cavity is very prominent, occupying somewhat more than half the total skull length, whereas in others (e.g., some ornithischian dinosaurs) it is all but lost (see Witmer, in press). Ironically, the function (and hence soft-tissue relations) of

### Abbreviations

a o cav	cavitas antorbitalis	n l du	ductus nasolacrimalis
a o fos	fossa antorbitalis	n l du ost	ostium nasale, ductus nasolacrimalis
a o sin	sinus antorbitalis	n l gl fos	fossa glandulae nasolacrimalis
a o sin ost	ostium, sinus antorbitalis	n p du	ductus nasopharyngeus
acc cav	cavitas accessorius	nar	apertura nasi ossea (= naris)
ad co	aditus conchae	nas	os nasale
antorb sin	sinus antorbitalis	nas gl	glandula nasalis
ap cavico rec	apertura recessus caviconchalis	nas gl du	ductus glandulae nasalis
ap n l du	apertura ductus nasolacrimalis	nas gl gr	groove for glandula nasalis
atr tur	atrioturbinal	nas tur	nasoturbinal
caud co	concha nasalis caudalis	neurovas	neurovasculature
caudolat rec	recessus caudolateralis	neurovas sp	neurovascular space
cav co	cavum conchae	olf bulb rec	recessus bulbus olfactorius
cavico rec	recessus caviconchalis	ophth N	n. ophthalmicus
cavico sin	sinus caviconchalis	orb	orbita
cavico sin ost	ostium, sinus caviconchalis	pal	os palatinum
cec rec	recessus caeci	pal bulge	bulge of os palatinum
ch	choana	pal pr max	processus palatinum, os maxillare
CNP	cavum nasi proprium	pal sin	sinus palatinum
CN V <sub>1</sub>	n. ophthalmicus	par c	cartilago paranasalis
co	concha nasalis	pmx	os premaxillare
cr sem	crista semicircularis	pmx div	diverticulum premaxillare
eth tur	ethmoturbinal	pn for	foramen pneumaticum
ex a o fen	fenestra antorbitalis externa	po vest rec	recessus postvestibularis
ex add	m. adductor mandibulae externus	po vest sin	sinus postvestibularis
ex co rec	recessus extraconchalis	postco	postconcha
fen nar	fenestra narina	postco cav	cavitas postconchalis
font a o	fonticulus antorbitalis	preco	preconcha
for epiph	foramen epiphaniale	preco rec	recessus preconchalis
fr	os frontale	prf	os prefrontale
in a o fen	fenestra antorbitalis interna	prf rec	recessus prefrontalis
jo	organum vomeronasale (= Jacobson's organ)	prim ch	choana prima (= primary choana)
jug	os jugale	ptc	cartilago parietotectalis
jug bar	arcus jugalis	pter	os pterygoideum
lac	os lacrimale	pter dor	m. pterygoideus, pars dorsalis
lac cav	cavitas lacrimalis	Ram lat nas	ramus lateralis nasi, n. ophthalmicus
la div	diverticulum lacrimale	Ram med nas	ramus medialis nasi, n. ophthalmicus
lam orb	lamina orbitonasalis	rec du np	recessus ducti nasopharyngei
lat Gr	laterale Grenzalte	roof nas cap	roof of cartilaginous nasal capsule
LTR	lamina transversalis rostralis	root co	root of concha
mand	mandibula	ros co	concha nasalis rostralis
mand N	n. mandibularis	scl	sclera
max	os maxillare	sec ch	choana secundaria (= secondary choana)
max N	n. maxillaris	sep	septum nasale
max sin ost	ostium sinus maxillaris	suborb fen	fenestra suborbitalis
max tur	maxilloturbinal	sep sulc	sulcus septalis
mes	os mesethmoidale	tect nas	tectum nasi
mid co	concha nasalis media	vest	vestibulum nasi
musc fos	fossa muscularis, Os palatinum	vom	vomer

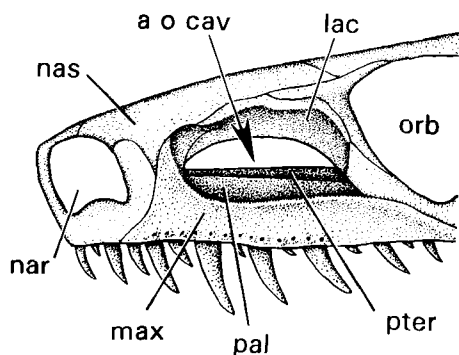


Fig. 1. *Euparkeria capensis*, a basal archosauriform from the Triassic of South Africa, in left lateral view, showing the antorbital cavity within the lateral aspect of the snout. Modified after Ewer ('65) and Witmer ('87).

the cavity is enigmatic and has been a matter of some dispute (see Walker, '61; Ewer, '65; Osmólska, '85; Witmer, '87; see Witmer, in press), the three major hypotheses being that the cavity housed 1) a gland, 2) a portion of the jaw musculature, or 3) a paranasal air sinus. The glandular hypothesis never has had many adherents, whereas the muscular hypothesis has been by far the most popular (summarized in Witmer, in press). More recently, a novel anatomical system, paranasal pneumaticity, has been implicated, and preliminary studies (Osmólska, '85; Witmer, '87) suggested that the pneumatic hypothesis is the best corroborated of the three.

To address these hypotheses, this paper probes the facial anatomy of extant archosaurs and other amniotes for homologous soft-tissue attributes that leave reliable indications of their presence on the bones (i.e., "osteological correlates") that can be assessed in fossil material. The detailed morphology and distribution of these osteological correlates in fossil archosaurs and their significance for the function of the antorbital cavity is discussed in detail elsewhere (see Witmer, in press) and summarized here in the last section. Special attention will be paid here to the patterns and homologies of paranasal air sinuses as these are the most poorly documented in the literature (Bellairs and Kamal, '81). The cartilaginous nasal conchae are important morphological landmarks in the nasal region. In the course of this study, it became apparent that the homologies of the conchae are not particularly clear, and, as a result, their homologies among amniotes also are examined.

Comparison of birds and crocodilians within the context of both amniote and archosaur phylogeny also provides the opportunity to study a striking example of divergent specialization superimposed upon a shared, inherited ground plan. Crocodilians have a "primordial" look about them and are commonly portrayed as living fossils little changed since their origin over 200 million years ago (Romer, '66). Indeed, they retain many primitive features such as the presence of teeth and most of the original complement of skull bones. However, modern crocodilians exhibit numerous apomorphies in all regions of the skull (Langston, '73) and particularly in the face, probably in association with skull flattening and formation of a long nasopharyngeal duct. On the other hand, birds, despite being highly modified for flight, show some aspects of skull morphology that are actually primitive in comparison to crocodilians. For example, although birds apomorphically have lost several skull bones in association with the evolution of cranial kinesis, they primitively retain an external antorbital fenestra. In fact, this mosaic pattern is a good illustration of why characters, not taxa, should be regarded as "primitive" or "derived" (Brooks and McLennan, '91). Specific apomorphic aspects of facial development in extant birds and crocodilians are examined in a later section so that those aspects contributing to their "divergent specialization" may be identified and accounted for when attempting to discover facial homologies.

Elucidation of facial homologies and characterization of the disparity among extant archosaurs require an appropriate phylogenetic perspective. Historically, solving these problems has been greatly hampered by typological thinking. Typology has been probably the most influential factor in, for example, the debate on the homologies of the nasal conchae and paranasal air sinuses. Numerous workers (e.g., Gegenbaur, 1873; Meek, '06, '11; Matthes, '34; Bertau, '35; Schüller, '39; May, '61; among many others) searched for features that could be homologized with named structures of mammals or, in some cases, humans, apparently working implicitly under the typological belief that all organisms will have the characteristics of the archetype. With phylogenetic thinking, however, one *expects* to discover novel attributes characterizing just a subset of a taxon.

A related problem plaguing this kind of analysis is paraphyly. Many workers (e.g.,

Romer, '66; Colbert, '80; Carroll, '88) have treated Archosauria as paraphyletic, excluding birds. Thus, extant crocodilians and many fossil archosaurs often have been compared to other "reptiles" rather than to their extant sister taxon, birds (e.g., Dollo, 1884; Meek, '11; Anderson, '36; Wettstein, '37-'54; Parsons, '59, '70; many others). Clearly, paraphyletic classification can result in exclusion from the analysis of very relevant taxa. For example, in the debate on the function of the antorbital cavity, a paraphyletic Archosauria excludes the only extant taxon actually retaining an antorbital fenestra. As a result, all comparisons and inferences made here will be within the context of an independently corroborated phylogenetic hypothesis (see Materials section).

This paper is organized in the following manner. First, the phylogenetic framework and the archosaur taxa receiving detailed study are introduced in the Materials section. The next section presents the methodological and theoretical foundation of this research, emphasizing its relationship to the Extant Phylogenetic Bracket approach for reconstructing soft tissues in extinct taxa (Witmer, '95). The following section outlines the various methods used to study the morphology and ontogeny of the anatomical systems. Next, the facial anatomy of extant archosaurs is presented system by system; the purpose here is to provide in one place (i.e., as a reference) the comparative anatomical information necessary for tackling the thornier issues of homology. Acknowledging the marked and obvious differences between birds and crocodilians, the following section identifies those facial apomorphies that strongly contribute to this disparity and obscure the homologies. The next section gets down to the business of assessing the homology of facial anatomical components—again, system by system—among archosaurs. The last section summarizes these findings and examines their impact on the debate concerning soft-tissue relations of the antorbital cavity.

#### MATERIALS

Figure 2 depicts the phylogenetic relationships of extant Tetrapoda (see Gauthier et al., '88a), and Figure 3 shows the relationships of the extant taxa examined for this study. The relationships of the major clades of archosaurs (and also nonarchosaurian archosauriforms) are provided in Figure 4. In

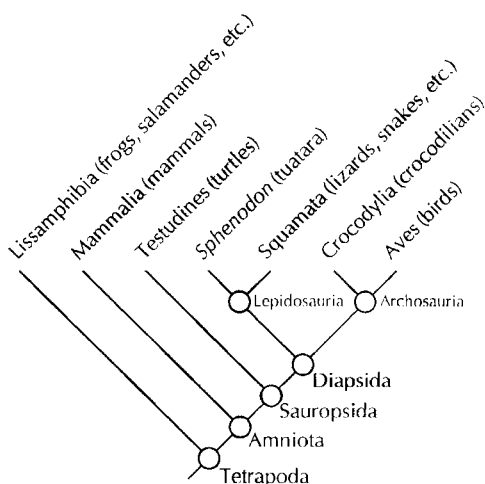


Fig. 2. Phylogenetic relationships of extant Amniota (topology after Gauthier et al., '88a).

the course of the following analysis, several extinct archosaur species will be mentioned, and these also are indicated in Figure 4.

All of the extant taxa listed below were obtained as fresh or preserved whole animals, eggs, or heads. Among the avian sample, five species received the greatest attention: commercially raised, domestic breeds of 1) White Leghorn chicken (*Gallus gallus*), 2) Peking duck (*Anas platyrhynchos*), and 3) Greylag goose (*Anser anser*), 4) commercially raised ostrich (*Struthio camelus*), and 5) wild-collected Laysan albatross embryos (*Diomedea immutabilis*). Several additional species of birds were studied for comparison, each species sample comprising fewer than three specimens: rhea (*Rhea americana*), emu (*Dromaius novaehollandiae*), ring-billed gull (*Larus delawarensis*), common crow (*Corvus brachyrhynchos*), and mourning dove (*Zenaidura macroura*). Other extant taxa (not listed) were studied from dried skulls.

Among crocodilians, three species received the greatest attention: 1) American alligator (*Alligator mississippiensis*), collected from the Rockefeller Wildlife Refuge, southwestern Louisiana, 2) saltwater crocodile (*Crocodylus porosus*), and 3) New Guinea freshwater crocodile (*C. novaeguineae*); both species of crocodiles were collected from a crocodile farm in Papua New Guinea. Additionally, juvenile specimens of common caiman (*Caiman crocodilus*) and single juvenile specimens of false gharial (*Tomistoma schlegelii*)

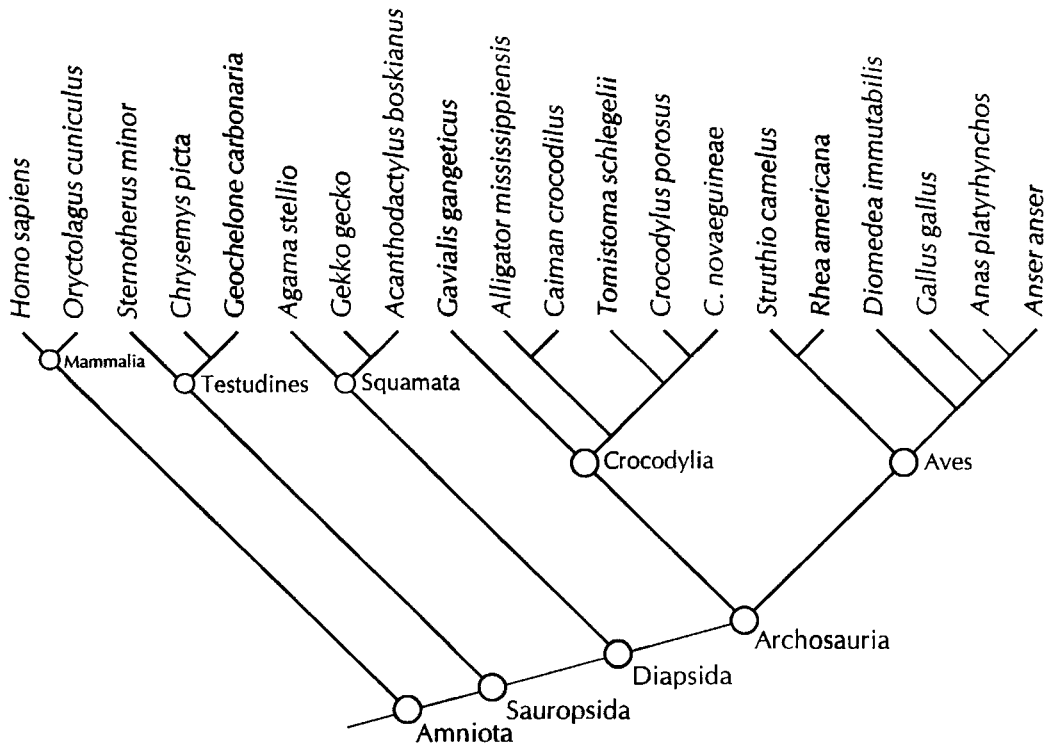


Fig. 3. Phylogenetic relationships of the extant taxa studied (topology after Gauthier et al., '88a; Gaffney and Meylan, '88; Benton and Clark, '88; Cracraft, '88).

and gharial (*Gavialis gangeticus*) were sagittally sectioned and dissected for comparison.

Species selected for detailed ontogenetic study using clearing and staining were chosen primarily based on the availability of carefully aged embryos (Table 1). Among birds, eggs of *Gallus gallus* and *Anas platyrhynchos* were obtained commercially and incubated at 37°C in a forced-draft, humidified incubator. For *Gallus*, two to six eggs (averaging about four) were removed from the incubator every day (and at about the same time of day) from day 8 of incubation up to hatching (21 days). *Gallus* embryos were weighed and staged according to the scheme of Hamburger and Hamilton ('51). Additionally, posthatching chicks aged 1 day, 7 days, and 28 days (three each) were obtained for clearing and staining. For *Anas*, two to seven eggs (averaging about four) were removed from the incubator every day from day 9 of incubation through day 17 of incubation; thereafter three to four eggs were removed every 2 days up to hatching (about 28 days). *Anas* embryos were weighed and

staged according to Koecke ('58) and Starck ('89). Although *Gallus* and *Anas* constituted the most extensive series, shorter series of *Anser anser* and *Diomedea immutabilis* also were prepared. One *Anser* embryo each from days 20 to 27 of incubation (except day 26: two embryos; 28–30 days total incubation time) and two heads of approximately 3-day-old goslings were cleared and stained. Ten *Diomedea* embryos ranging in age from day 17 to day 32 (approximately 63 days total incubation time) were selected for clearing and staining. *Anser* and *Diomedea* embryos were weighed prior to processing; no staging scheme is available for either species, and none was devised here. Additionally, a late *Rhea americana* embryo of unknown age (about 260 g) and a very young chick of *Struthio camelus* were cleared and stained.

Among crocodylians, *Alligator mississippiensis* eggs were retrieved from nests and incubated at the Rockefeller Wildlife Refuge (see Joanen and McNease, '77, '79). Two to three eggs were removed from the incubator every day from days 13 to 51 of incubation

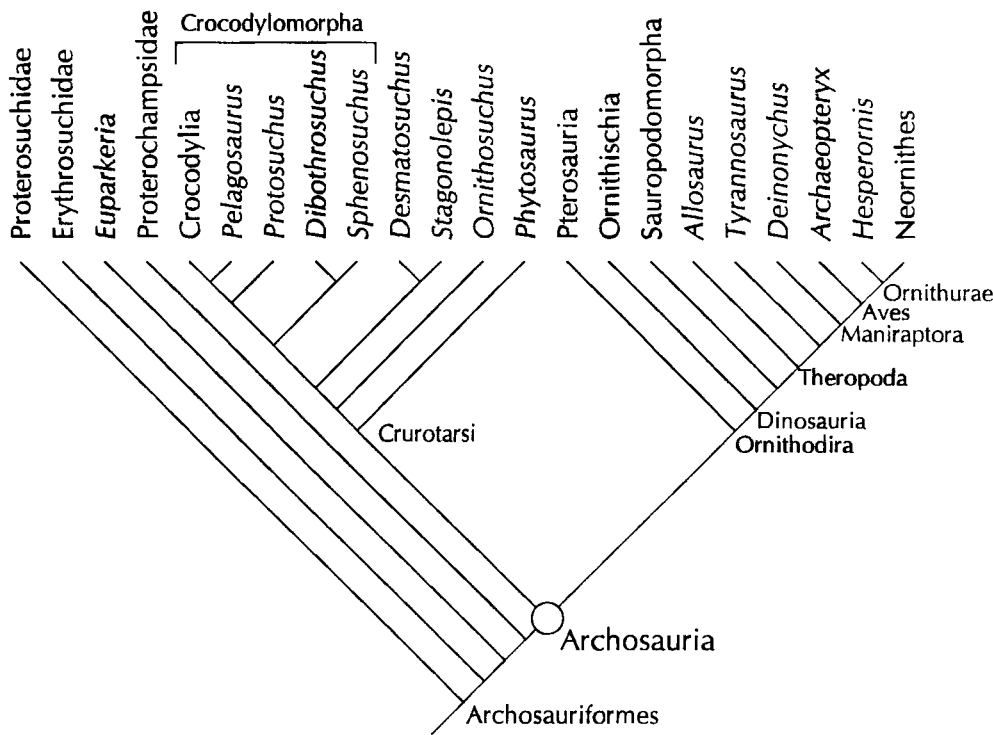


Fig. 4. Phylogenetic relationships of major clades of fossil archosauriforms, including those genera mentioned in the text (topology after Gauthier, '86; Cracraft, '86; Benton and Clark, '88; Sereno, '91; Sereno and Arcucci, '90; Sereno and Wild, '92; Wu and Chatterjee, '93).

and one or two eggs for most days thereafter until hatching (about 65 days) and fixed by injecting with 37% formaldehyde (100% formalin) until the eggshell cracked and then submerging in the same solution (see Ferguson, '81). Most embryos were weighed and measured, and all were staged according to

Ferguson's ('85) scheme. Additionally, hatchlings up to day 7 were collected (averaging five per day) and fixed in formalin. Of this sample, 45 were processed as cleared-and-stained specimens. Additionally, a *Caiman crocodilus* hatchling (187 mm SVL) also was processed in this fashion.

TABLE 1. Numbers of individuals of the major study taxa examined and their means of preparation

Taxon	Dissected	Skeletonized	Serially sectioned	Cleared and stained	Latex injected
<i>Alligator mississippiensis</i>	17	29	3 <sup>1,2</sup>	45	3 <sup>3</sup> 2 <sup>4</sup>
<i>Caiman crocodilus</i>	3	4	0	1	0
<i>Crocodylus porosus</i>	7	17	1 <sup>1</sup>	0	0
<i>C. novaeguineae</i>	2	6	1 <sup>1</sup>	0	0
<i>Struthio camelus</i>	3	4	1 <sup>1</sup>	1	1 <sup>4</sup>
<i>Diomedea immutabilis</i>	0	0	1 <sup>5</sup>	10	0
<i>Gallus gallus</i>	6	10	1 <sup>1</sup>	83	8 <sup>3</sup> 6 <sup>4</sup>
<i>Anas platyrhynchos</i>	8	10	1 <sup>5</sup>	43	6 <sup>3</sup> 4 <sup>4</sup>
<i>Anser anser</i>	7	10	2 <sup>1</sup>	11	1 <sup>3</sup> 3 <sup>4</sup>

<sup>1</sup>Serial gross sectioning.  
<sup>2</sup>Serial histological sections of numerous individuals of *Alligator mississippiensis* were studied in the laboratory of Dr. M.W.J. Ferguson, University of Manchester.  
<sup>3</sup>Cleared and stained after latex injection.  
<sup>4</sup>Prepared as corrosion cast after latex injection.  
<sup>5</sup>Serial histological sectioning.

Most information on extant nonarchosaurian amniotes was obtained from the literature. Literature reports were confirmed by sagittal section and gross dissection of the following species: 1) Squamata: *Agama stellio*, *Gekko gecko*, and *Acanthodactylus boskianus*; 2) Testudines: *Sternotherus minor*, *Chrysemys picta*, and *Geochelone carbonaria*; and 3) Mammalia: *Oryctolagus cuniculus* and *Homo sapiens*.

Fossil material of extinct archosaurs was studied in museum or university collections, scored for its morphological features, photographed, and, in a few cases, X-rayed.

#### ANALYTICAL METHODS

##### *Phylogenetics, extant taxa, and the reconstruction of soft tissues in fossils*

As alluded to at the outset, the research presented here is part of a larger project that explores the evolution of facial anatomy in archosaurs—both extinct and extant. Furthermore, it seeks to discover the function of the antorbital cavity, their most important facial apomorphy. Determining the function of the antorbital cavity clearly centers on the soft-tissue relations of the bony cavity: viz., whether it housed a gland, a muscle, a paranasal air sinus, or some other structure. As a result, this research requires an objective means of inferring soft anatomical components in the fossil remains of extinct organisms. A detailed methodology (the Extant Phylogenetic Bracket approach) is presented elsewhere (Witmer, '92, '95; see also Bryant and Russell, '92) and is briefly outlined here. As will be seen, this approach is in many ways simply a specific application of the well-understood (though still hotly debated) principles of homology determination. Thus, this study emphasizes the homologies among extant archosaurs, whereas a companion report (Witmer, in press) focuses more on fossil archosaurs. I previously have discussed (Witmer, '95) the relevance of soft-tissue considerations for accurate interpretations of bony morphology, but these issues will not be addressed here in detail.

The methodology for reconstructing soft tissues in fossils is outlined below 1) to provide the framework for the importance of extant taxa in studies of taxa known only as fossils, and 2) to highlight the kinds of data sought here from extant taxa (see Witmer, '95, for elaboration). In order to infer soft tissues in a fossil taxon, information about soft anatomy must come from extant taxa as

these are the only forms for which details of the soft tissues and their relationships to the skeleton can be observed directly. However, not all extant taxa are equally relevant. In particular, reference to (minimally) the first two extant outgroups of the fossil taxon of interest is required (Fig. 5A) because at least two outgroups are required to justify character assessments at the outgroup node (i.e., the common ancestor of the fossil and its extant sister group; see Maddison et al., '84). Reorganizing Figure 5A so that the extant taxa flank the fossil taxon provides a heuristic, graphical representation (Fig. 5B) of an important implication of this approach—that is, the extant taxa “bracket” the fossil taxon and therefore constrain any soft-tissue inferences. In fact, the extant taxa may be termed the “extant phylogenetic bracket” of the extinct taxon.

The anatomy of the extant taxa is studied with attention to the soft tissues and their relationships to the skeleton. In particular, *causal associations* of the soft tissues and bones are sought. There is mounting evidence that the form (and in many cases even existence) of bony features is largely or entirely under the morphogenetic control of nonskeletal tissues (reviewed in Witmer, '95; see also Herring, '93). That is, many soft-

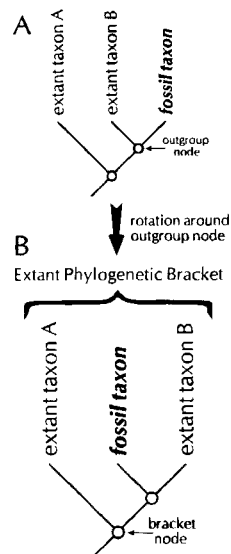


Fig. 5. **A:** Phylogenetic relationships of a fossil taxon and its first two extant sister groups. **B:** Rotation around the outgroup node in A brings the extant taxa to the periphery, forming the Extant Phylogenetic Bracket. Modified after Witmer ('95).

tissue components produce (i.e., cause) particular osteological attributes. In practice, the goal is to discover unambiguous bony signatures left on the bones by known soft anatomical components, which thus are regarded as the *osteological correlates* of that component. Of course, the causal nature of these associations are assumptions or hypotheses amenable to testing. The point (ideally) is to identify those soft-tissue attributes that are both necessary and sufficient to explain particular bony features.

However, these attributes have an evolutionary history. Once the causal associations are in hand one may return to the cladogram and pose the following hypothesis: Any similarities in the soft tissues and their osteological correlates between the extant members of the bracket were inherited from their common ancestor (located at the "bracket node"; Fig. 5B) which itself had the same causal association (Fig. 6, dashed arrow). A prediction of this hypothesis is that other descendants of the bracket ancestor also inherited the soft-tissue attribute. The hypothesis is thus tested by surveying these other descendants—i.e., the fossil taxa—for the osteological correlates (Fig. 6, solid arrow), with parsimony deciding the fate of the hypothesis. The technical paper (Witmer, '95) provides ex-

amples and examines some of the difficulties that may be encountered.

Reconstruction of ancestral (or "extinct") attributes presents no particular theoretical problems because it is based simply on the relation of biological homology. Thus, this method is basically a specific adaptation of the well-known principles for the elucidation of homologous characters. Homologies are hypotheses subject to a series of tests (Patterson, '82, '88; Stevens, '84; Rieppel, '88, '94; Bock, '89): 1) the similarity test, whereby putative homologs must share particular topographical relationships to, or 1:1 correspondences with, other structures; 2) the congruence test, whereby the homology must characterize a monophyletic group; and 3) the conjunction test, whereby putative homologs must not co-occur simultaneously in the same organism.

Clearly, the above methodology for reconstructing soft tissues in fossils is directly comparable to these tests of homology (Witmer, '95). The similarities between the living members of the extant phylogenetic bracket in both soft anatomical attributes and osteological correlates are appraised on the basis of sharing specific 1:1 correspondences, i.e., the similarity test. The hypothesis that these similarities were present in the bracket ancestor is thus a hypothesis of homology. The congruence test involves surveying other descendants of the bracket ancestor (the fossil taxa) for the osteological correlates: If the fossil taxa exhibit the specified osteological correlates, then the bony feature and its correlated soft tissue characterize the monophyletic group comprising the bracket, and the hypothesis survives the congruence test. The conjunction test is not a formal part of the methodology, but co-occurrence of putative homologs presumably is discovered in association with the similarity test. Thus, determination of homologous osteological correlates, combined with causal association of the correlates with particular soft tissues, allows the inference of the soft tissue in taxa preserving only hard parts. Bock ('89) has emphasized the importance of the similarity test, and thus this study provides detailed analysis of anatomical and ontogenetic similarities; congruence with the phylogeny of extinct and extant archosaurs is noted here but is more fully elaborated elsewhere (Witmer, in press).

The ontogeny of structures plays an important part in the discussion to follow. Although some workers (e.g., Roth, '84) have

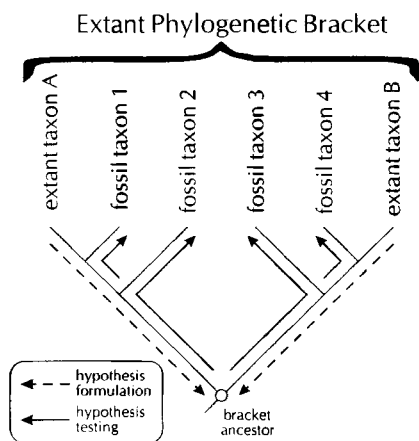


Fig. 6. Basic scheme of hypothesis formulation and testing in the Extant Phylogenetic Bracket approach. Similarities between the components of the EPB are hypothesized as being present in the bracket ancestor (broken arrows). This hypothesis is tested for its congruence with the phylogenetic pattern by surveying the fossil taxa (solid arrows). The EPB approach provides phylogenetic justification for the inference of soft tissues or other unpreserved features in fossil organisms. Modified after Witmer ('95).



argued that development is one of the clearest guides to homology, the use of ontogenetic patterns has its limitations and should not be given primacy over other evidence (see Alberch, '85; Smith and Hall, '90; Mabee, '93). Instead, ontogenetic information simply provides additional, highly detailed data on the 1:1 correspondences that go into the similarity test of homology (Remane, '52; MacPhee, '81; Stevens, '84). In some cases, the topographical relationships become so transformed during the later portions of ontogeny that 1:1 correspondences are obscured; studying the pattern of ontogenetic transformation often helps reveal these correspondences. For example, many of the air sinuses and diverticula of extant archosaurs merge and become broadly confluent in adults, whereas earlier in ontogeny they develop in relative isolation and are more easily characterized (Witmer, '90, '92; see below). Furthermore, comparison of entire ontogenies (or life cycles) is appropriate because ontogeny is continuous and cannot be divided nonarbitrarily into "stages" (de Queiroz, '85; Alberch, '85; Rieppel, '88). Even "adult" is somewhat inappropriate as a developmental stage in forms with indeterminate growth such as crocodylians. For example, the paranasal and nasopharyngeal sinuses of crocodylians (see below) continue to expand and pneumatize more of the skull long after many of the classic hallmarks of "adulthood" are reached. Therefore, whole ontogenies will be considered here when possible, and, although this goal is seldom realized, the perspective is fruitful.

#### ANATOMICAL METHODS

Four major techniques were used to study the soft tissues and their relationships to the skeletal tissues (Table 1): 1) gross dissection and skeletonization, 2) serial gross and histological sectioning, 3) clearing and staining of embryonic and young material, and 4) latex injection of various cavities (especially the paranasal air sinuses). In some cases, more than one technique was performed on the same specimen. In all cases, the goal was to understand particular aspects of the ontogeny of facial anatomy. These four techniques are discussed in turn.

##### *Gross dissection and skeletonization*

Adults and posthatching juveniles of various ages of all of the major study taxa (except *Diomedea immutabilis*) were studied through the well-known techniques of gross dissec-

tion; embryonic material of *Gallus gallus*, *Anas platyrhynchos*, *Anser anser*, *Struthio camelus*, and *Alligator mississippiensis* also was dissected (see Table 1). Some specimens for all species were frozen solid and then sagittally sectioned with a band saw prior to dissection; some crocodylian specimens were sectioned horizontally. A small, rotary, power saw was indispensable for dissecting the snouts of the crocodylians. Almost all of the dissections were extensively photographed throughout the procedure. Specimens were studied with special attention to the soft tissues of the rostral portion of the head, and in particular, their topographic relationships to each other and to the skeleton; details of the osteological correlates of the soft tissues were noted.

Some dissected specimens subsequently were fixed in 10% neutral-buffered formalin for 2–5 days and then stored in 70% ethanol. All other dissected specimens (except those destined for another technique) were skeletonized (see Witmer, '92, for details) so that the osteological correlates of the observed soft tissues could be better assessed.

##### *Serial gross and histological sectioning*

Serially sectioned specimens give detailed relational information on all tissues, and in particular are a critical complement to the cleared-and-stained specimens. For example, although cleared-and-stained specimens provide better data on the three-dimensional relationships of particular osteological correlates, serially sectioned specimens allow the soft-tissue components to be related more directly to their correlated bony (or cartilaginous) features. Adult and posthatching juvenile specimens of *Alligator mississippiensis*, *Crocodylus porosus*, *C. novaeguineae*, and *Anser anser* were serially sectioned grossly by freezing the head solid and transversely sectioning the head on a band saw, cutting sections approximately 3–12 mm thick depending on the length of the head. Heads of *Gallus gallus*, *Struthio camelus*, and small juvenile *Alligator* were sectioned transversely without freezing using a scalpel (Table 1). If not already fixed, the sectioned specimens were then fixed in 10% neutral-buffered formalin and stored in 70% ethanol. One head each of *Alligator* and *C. porosus* was sectioned as outlined above, and then these transverse sections were sectioned sagittally; one side of the head was fixed and the other side was skeletonized (see above) so that the osteological correlates of the soft tissues and

the soft tissues themselves could be compared easily.

One embryo each of *Diomedea immutabilis* (25 days of incubation, total weight 3.35 g) and *Anas platyrhynchos* (15 days of incubation, total weight 6.54 g) were subjected to routine serial histological sectioning (i.e., embedded in paraffin, serially sectioned at 10–13  $\mu\text{m}$ , and stained with hematoxylin and eosin) and studied with light microscopy (Table 1). In addition, numerous serially sectioned specimens of *Alligator mississippiensis* in the collection of Dr. M.W.J. Ferguson were studied at the University of Manchester, England, and many were photographed (see Ferguson, '81 for his techniques).

#### *Clearing and staining of embryonic or young material*

Clearing and staining is a well-known technique for visualizing bone and/or cartilage in whole-animal preparations by selectively staining bone with alizarin red S and cartilage with alcian blue, and rendering the other tissues transparent by clearing with pancreatic enzymes and a graded series of potassium hydroxide (KOH) and glycerol solutions. Special protocols for crocodilians were required, and hence a new variant of the widely used procedures of Wassersug ('76) and Dingerkus and Uhler ('77) was developed (Witmer, '92). A sketch of this method is provided below. Within an ontogenetic series, the earliest appearance of stain is a readily identifiable marker for the onset of chondrogenesis or ossification (Alberch and Alberch, '81; Hanken and Hall, '84) and was used to establish the timing of these events.

Cleared-and-stained specimens offer the advantages of 1) preserving three-dimensional relationships such that topographical relationships can be assessed from all angles, and 2) being rapid enough that large numbers of specimens can be prepared. Although the technique renders tissues other than cartilage and bone transparent, thus seemingly obscuring the desired non-bony-tissue data, the specimens retain much of the evidence for many of the soft tissues. For example, the ostia of the paranasal air sinuses are apparent in the cartilaginous nasal capsule, and foramina in the bones or nasal capsule for passage of nerves, vessels, and pneumatic diverticula also can be observed. Furthermore, muscles, ligaments, and some other connective tissues often are visible with careful lighting as "ghosts." Thus, when further compared with soft-tissue information ob-

tained from other techniques (e.g., dissection, sectioning, latex injection, etc.), cleared-and-stained specimens provided a rather detailed picture of the form and ontogeny of the facial bones and related soft anatomy.

The following procedures are extracted from Witmer ('92) which should be consulted for more details.

#### 1. Initial preparation

As a rule, specimens were skinned, enucleated, eviscerated, and debrained before fixation, although the *Alligator mississippiensis* material was fixed first with no apparent ill effects.

#### 2. Bleaching

Heavily pigmented and particularly large specimens (e.g., *Alligator* and *Anser anser* embryos, many hatchling birds) benefited from bleaching and mild maceration in a solution of about one part 3%  $\text{H}_2\text{O}_2$  to 9 parts 0.5% KOH for a period of rarely more than 1.5–2.5 hours.

#### 3. Fixation

Five different fixatives were used: a) 37% formaldehyde (100% formalin), b) 10% neutral-buffered formalin (NBF), c) 95% ethanol, d) 1% acetic acid in 95% ethanol, and e) a new fixative termed EFA (Witmer, '92), an acronym for ethanol-formalin-acid (90 parts 95% ethanol, 7 parts NBF, 3 parts acetic acid).

#### 4. Fat removal

Since fat usually fails to clear completely, diffuse fatty tissue was removed by treatment with acetone for 2–3 days.

#### 5. Cartilage staining

Specimens weighing less than 15–20 g were stained in a fresh solution of 11 mg alcian blue, 80 ml 95% ethanol, and 20 ml acetic acid. Specimens weighing more than 15–20 g (and all *Alligator* specimens) were stained in a fresh solution of 11 mg alcian blue, 77.5 ml 95% ethanol, and 22.5 ml acetic acid. Staining times were 1.5–2.0 times in hours the age of the specimen in days, up to 48 hours total.

#### 6. Dehydration

Most specimens were dehydrated by 24–48 hours in 95% ethanol, changing the solution two to four times during this period.

#### 7. Enzymatic clearing

Specimens were taken to distilled water through a graded ethanol series, and then

treated with an enzyme solution (30 ml of saturated aqueous sodium tetraborate ( $\text{Na}_2\text{B}_4\text{O}_7 \cdot 10\text{H}_2\text{O}$ ), 70 ml of distilled water, and 1 g of 4 $\times$  pancreatin) and maintained at 37°C in a water bath until much of the skeleton was visible, changing the enzyme solution every 4–5 days.

#### 8. Bone staining

The specimens were stained for bone tissue with a solution of alizarin red S in KOH (15 drops of 0.1% aqueous alizarin red S in 100 ml of 0.5% KOH), spending 1–2 days in the solution.

#### 9. Clearing

Final clearing was achieved by taking the specimens to glycerol through a graded 0.5%-KOH/glycerol series (i.e., 3:1, 1:1, 1:3, pure glycerol).

#### 10. Storage

Completed specimens were stored in clean, tightly lidded containers in fresh, pure glycerol to which some thymol crystals were added.

#### *Latex injection of sinus cavities*

In crocodilians, the paranasal air sinuses are largely enclosed in bone, such that the extent of the sinuses can be judged readily in dried skull material. In birds, however, much of the main sinus and its diverticula are situated either subcutaneously or among other soft tissues, such that it is often difficult to visualize the form and extent of the paranasal air sinus in birds. To address this problem, a technique was devised to inject a mass into the sinuses (and some other cavities) that could withstand subsequent dissection, clearing and staining, skeletonization, and total corrosion. The resulting casts allowed the detailed tabulation of the topographic relationships of the sinuses to surrounding structures. Polyester resin was attempted as an injection medium, and results were good; however, it was rather difficult to work with, and it was feared that the heat of the curing injection mass might adversely affect those specimens to be subsequently cleared and stained. Therefore, latex was selected as an injection medium. Latex offers the following advantages: 1) It is water soluble, thus allowing the viscosity to be altered easily; 2) the injection medium is reasonably stable and can be stored for some time after mixing; 3) it sets immediately under acidic conditions; 4) it is relatively safe to the user; 5) cleanup is

easy; and 6) it is inexpensive and readily available. Its major drawback is that it tends to shrink somewhat, although this can be ameliorated (see below).

The basic constituents of the injection medium were 1) about 65 g of latex, 2) 10 ml of distilled water (to decrease the viscosity), 3) 3.5 g of a finely particulate filler composed of amorphous fumed silica (to reduce shrinkage; brand: Aerosil 200), and 4) 150 drops of colored latex-based drafting-pen ink (to add some contrasting color to the off-white latex). The relative proportions can be altered. The injection apparatus consisted simply of a standard 3-ml or 5-ml disposable syringe mounted with a modified 18- to 25-gauge needle. The needle was modified by bending the distal 10 mm into about a 45° angle, being careful not to crimp the lumen; then, under a microscope, the point of the needle was ground down with a whetstone or rotary grinding wheel until the aperture was completely terminal and no burrs remained. This modified blunt needle thus could be directed into various subcavities within the sinuses without undue concern for puncturing the epithelial walls of the sinus.

Fresh material was more suitable than preserved (fixed) material because the fresh tissues were more supple and natural. Fresh or thawed heads of several bird species were injected (Table 1). If various skull bones were suspected to be aerated and in communication with the chamber to be directly injected, small pressure-release holes were drilled through the outer table of the bone. In a few cases, the nasolacrimal duct and nasal cavity also were injected with contrasting colors. A small hole was incised in the lateral aspect of the antorbital sinus in the region of the external antorbital fenestra. The latex medium was injected into the aperture and directed in various directions known or suspected to be locations of diverticula. When injection was completed, the mandible was propped maximally abducted with modeling clay and the incision was closed by swabbing it with 10% acetic acid which immediately sealed the incision on contact. When both sides were injected, the head was submerged in 10% acetic acid and refrigerated for a couple of hours to allow the latex to solidify; if the volume of injected latex was high (e.g., in adult *Anser anser*), the specimen was removed from the acid and stored overnight in a refrigerator.

The specimen usually was dissected at this point. If a partial corrosion cast (i.e., preserv-

ing the skeleton) was desired, then the specimen was skeletonized using routine procedures (Witmer, '92). In a few cases, complete corrosion casts were obtained by immersing the entire head in 88% formic acid, yielding a sinus cast free of any other tissues in 2–4 days. The casts faithfully reproduced the form of the sinuses, preserving the tunnels and grooves through which nerves, vessels, and ligaments passed and even the striations of the adjacent muscles.

Injecting embryonic material for subsequent clearing and staining employed the same basic technique but required a great deal more care, most of the procedure taking place under the dissecting microscope. Fresh material again gave the best results. It was imperative that injection preceded enucleation in that removal of the eyeball could have damaged the antorbital sinus or its sub-orbital diverticulum. After injection was complete, the embryo was submerged in 10% acetic acid for 30–60 minutes, followed by enucleation, evisceration, debraining, fixing, etc. (see above).

#### FACIAL ANATOMY IN BIRDS AND CROCODYLIANS

The following description of adult facial anatomy in extant archosaurs is intended to provide background for discussion of facial homologies but not to comprehensively depict the complexity of this anatomy or its taxonomic diversity. More detailed anatomical reviews are relatively plentiful for birds, although strongly biased toward domestic species (see Stresemann, '27–'34; Getty, '75; Nickel et al., '77; Baumel et al., '79, '93; King and McLelland, '84; Zusi, '93), but few such works are available for crocodylians (see Wettstein, '37–'54). The descriptions here are based primarily on original dissections of the major study taxa (Table 1) and focus on anatomy rostral to the orbit (with some exceptions). Avian (and, as much as possible, crocodylian) osteological terminology follows Baumel and Witmer ('93) and Witmer ('94), and other terminology follows Baumel et al. ('93). It is assumed (but not rigorously tested) that the descriptions apply to the common ancestor of each most-inclusive, monophyletic, extant clade (i.e., Neornithes and Crocodylia).

#### *Birds*

##### Bones

The facial skeleton (including the rostral portion of the palate) of most birds includes

seven bones (Fig. 7): premaxilla, nasal, maxilla, lacrimal, jugal, palatine, and vomer. The frontal and mesethmoid (an ossification of the interorbital septum) also encroach on the region. The naris is caudally situated (due to the large premaxilla) and is surrounded by premaxilla and nasal and floored partially by the maxillary bone. The osseous portion of the nasal cavity is roofed by the premaxilla, nasal, and dorsal lamina of the mesethmoid. Its lateral wall is largely open in dried skulls, but has partial walls formed rostrally by reciprocal (subnarial) processes of the maxilla and nasal and the palatal process of the maxilla (maxillopalatine) and caudally by the lacrimal. The nasal cavity is partially floored by the palatine, vomer, premaxilla, and palatal process of the maxilla. The choana is bounded by the vomer medially, palatine caudally and laterally, and maxilla rostrally and sometimes medially; it opens caudally from the nasal cavity into the oral cavity via a very short nasopharyngeal duct.

The antorbital cavity is defined simply as the space rostral to the orbit, external to the cartilaginous nasal capsule, and internal to the outer surface of the snout. Although rarely recognized as such, the antorbital cavity is an important cephalic compartment comparable to other compartments (e.g., the orbit, adductor chamber, etc.) in having bony boundaries and a variety of contents. In birds, it is an irregular space bounded principally by the maxilla rostrally, lacrimal and ectethmoid (when ossified) caudally, nasal dorsally, jugal arch ventrolaterally, and usually palatine ventromedially. Among the contents of the antorbital cavity are the antorbital paranasal air sinus, the nasolacrimal duct, sometimes part of the jaw musculature, and the nasal gland and/or its ducts (see below). Several of the bones surrounding the antorbital cavity often are pneumatized by the antorbital sinus: the palatal process and body of the maxilla, lacrimal, and less commonly the palatine (Fig. 7). The lateral aperture of the antorbital cavity, the external antorbital fenestra, is closed by skin and is bounded by the reciprocal processes of the maxilla and nasal, lacrimal, and jugal arch. The medial aperture of the antorbital cavity, the internal antorbital fenestra, opens into the nasal cavity and is bounded by the palatal process of the maxilla and sometimes the rostral edge of the lacrimal (although its osseous borders are usually difficult to define). The antorbital cavity opens caudally into the orbit via the

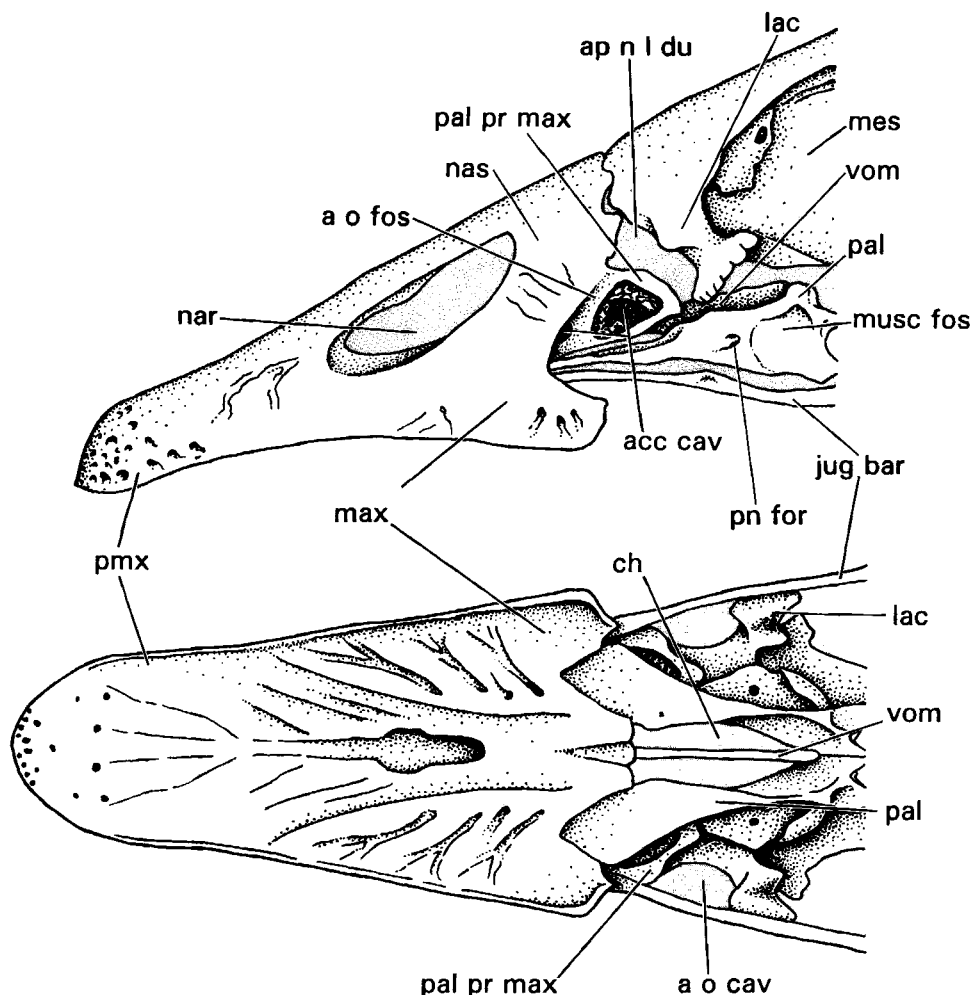


Fig. 7. *Anser anser*. Rostral portion of the skull in left lateral view (top) and ventral view (bottom). Modified after Komárek ('79) and specimens.

postnasal fenestra (Witmer, '94, in press), which is bounded by the lacrimal laterally, mesethmoid medially, palatine ventromedially, and ectethmoid dorsally (when ossified). The postnasal fenestra should not be confused with the orbitonasal fissure and foramen which are openings generally dorsomedial to the ectethmoid (or cartilago lamina orbitonasalis) for passage of nerves and the nasal gland duct(s) (Crompton, '53; Baumel and Witmer, '93).

#### Nasolacrimal duct

The form and course of the nasolacrimal duct is very consistent in birds (Fig. 8). It is a thin-walled, spacious tube running from the

orbit, where it opens via dual puncta, to the nasal cavity. It passes just lateral to the lacrimal, which is usually faintly grooved for the duct. The duct itself passes rostradorsally through the external antorbital fenestra, crossing dorsally over the antorbital air sinus and aditus conchae and then turning ventrally medial to the sinus, perforating the capsule to open into the choanal region of the nasal cavity just ventral to the middle nasal concha and caudal to the crista nasalis (the "Schwelle" of the older literature). Bremer ('40) regarded the avian nasolacrimal duct as an air sac, comparable to the antorbital sinus (his "subocular sac"), but the only basis for this assertion is the large volume of the duct.

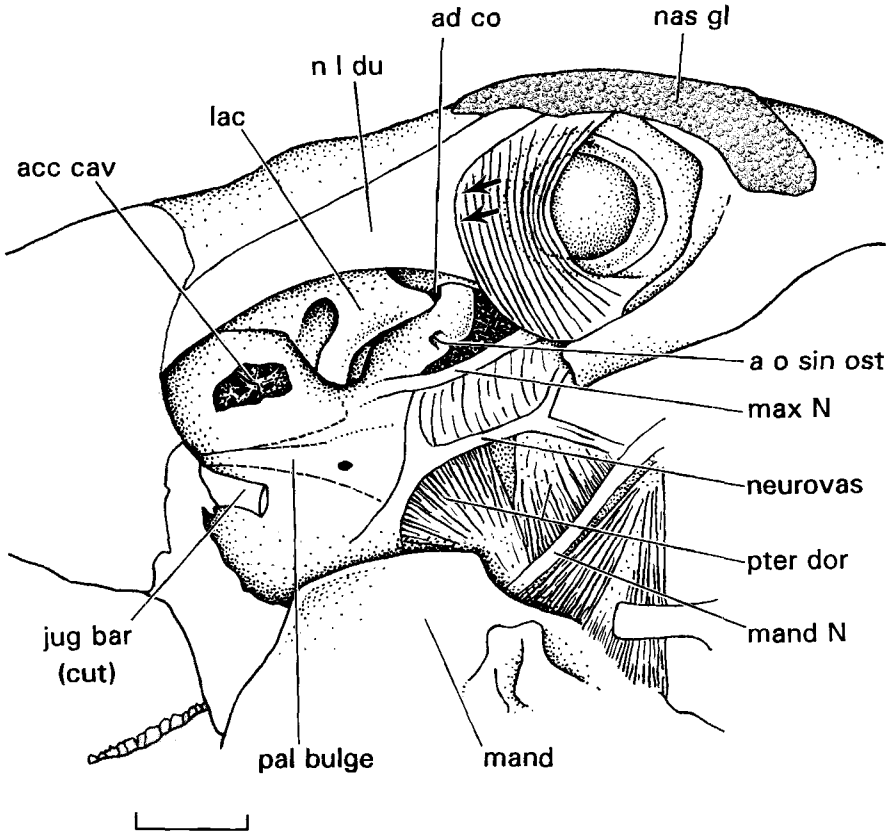


Fig. 8. *Anser anser*. Dissection of the antorbital cavity and adjacent regions in left lateral view. The antorbital sinus (i.e., the epithelial air sac) is opened to view the internal structures. The external adductor muscles

have been removed from the coronoid process of the mandible. The jugal bar has been cut and the middle section removed. Arrows indicate the openings into the nasolacrimal duct. Scale bar = 1 cm.

As in other amniotes, it develops as a solid epithelial cord that later cavitates, rather than as an epithelial evagination of the nasal cavity, the latter being a characteristic of pneumatic diverticula.

#### Nasal gland

Glandula nasalis occupies a number of positions in birds (see Technau, '36), ranging from being located completely preorbitally (as in some gruiforms and pelecaniforms) to extending far caudally in a supraorbital position (many marine birds; see also Fig. 8). The usually paired ducts always open into the caudal portion of the nasal vestibule (Bang, '71). When the gland is located preorbitally, the body of the gland is situated dorsally within the antorbital cavity, just ventral to the mesethmoid and nasal, medial to the lacrimal, lateral to the nasal capsule, dorso-

medial to the nasolacrimal duct, and caudo-dorsal to the antorbital air sinus; it may project a short distance into the antorbital sinus (e.g., *Fregata magnificens*; Bang, '71) or even into the cavum conchae (*Gallus gallus* and *Rhea americana*; see also Sandoval, '63; Müller, '61). If it has a more caudal position, the ducts pass into the antorbital cavity along with ramus lateralis nasi of the ophthalmic nerve via the lateral orbitonasal foramen. In all cases, the ducts travel along with ramus lateralis nasi in the caudal portion of the antorbital cavity, then pass rostro-ventrally medial to (and sometimes grooving) the reciprocal subnasal processes of the nasal and maxilla and lateral to the capsular wall; the lateral duct enters the vestibule directly, whereas the medial duct passes transversely through the crista nasalis to open medially into the vestibule adjacent to

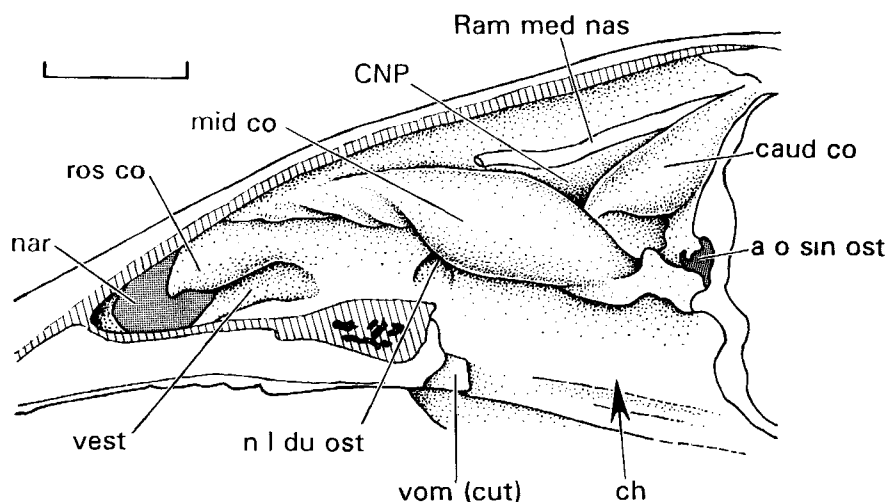


Fig. 9. *Anas platyrhynchos*. Rostral half of the right side of a sagittally sectioned head in medial view, showing the parts of the nasal cavity, the nasal conchae, and the antorbital sinus ostium. Hatching denotes cut bone surfaces. Scale bar = 1 cm.

the nasal septum (Marples, '32; Bang, '71; Vorster, '89).

### Nerves

The nerves innervating the face are very consistent (Figs. 8–10) and are composed primarily of sensory branches of the trigeminal nerve (autonomics will not be discussed; see Webb, '57; Buben-Waluszewska, '81). The ophthalmic division of the trigeminal nerve (CN V<sub>1</sub>) passes through the orbit between the interorbital septum and eyeball and divides into two major branches upon reaching the nasal capsule. The larger, medial branch, ramus medialis nasi, is mostly intracapsular, entering the nasal capsule through the medial orbitonasal foramen; it tends to run along the septum, usually dividing rostrally into dorsal and ventral premaxillary nerves. The smaller, lateral branch, ramus lateralis nasi, is entirely extracapsular, entering the antorbital cavity through the lateral orbitonasal foramen along with the nasal gland ducts and rarely (e.g., *Passer domesticus* and *Melospittacus undulatus*; Lang, '55) passing through a small foramen epiphaniale within the cartilaginous capsule; it always passes just lateral or dorsal to the aditus conchae as it hugs the capsular wall. The maxillary division of the trigeminal nerve (CN V<sub>2</sub>) is relatively smaller than in most vertebrates, almost certainly owing to reduction of the maxilla and loss of the teeth. Its supraorbital branch will be ignored here. The main branch

of the maxillary nerve travels through the ventrolateral portion of the orbit ventral to both the eyeball and the suborbital diverticulum of the antorbital sinus and dorsal to m. pterygoideus, pars dorsalis (Fig. 8). The nasopalatine branch of the maxillary nerve carries fibers from the nasal capsule, palate, and maxillary bone.

### Muscles

As is true of all sauropsids, birds lack any muscles attaching superficially to the facial skeleton (their "facial musculature" being restricted only to those innervated by the seventh cranial nerve, viz. m. depressor mandibulae and m. columellae). However, one of the jaw adductors, m. pterygoideus, pars dorsalis, has been involved in the debate on the function of the antorbital cavity. Although most avian anatomists (e.g., Hofer, '50; Sims, '55; Fisher and Goodman, '55; Goodman and Fisher, '62; Merz, '63; George and Berger, '66; Owre, '67; Richards and Bock, '73; Bhattacharyya, '82, '89) have found m. pterygoideus divided into pars dorsalis and pars ventralis, in some cases the lateral portions of pars dorsalis and pars ventralis are fused, suggesting mediolateral rather than dorsoventral division of the pterygoideus mass (Zusi, '62; Zusi and Storer, '69; Burton, '74; Elzanowski, '87). In a few taxa the dorsal pterygoideus is reduced or even absent (Webb, '57; Bhattacharyya, '82, '89; Elzanowski, '87). In most birds, however, the dorsal pterygoi-

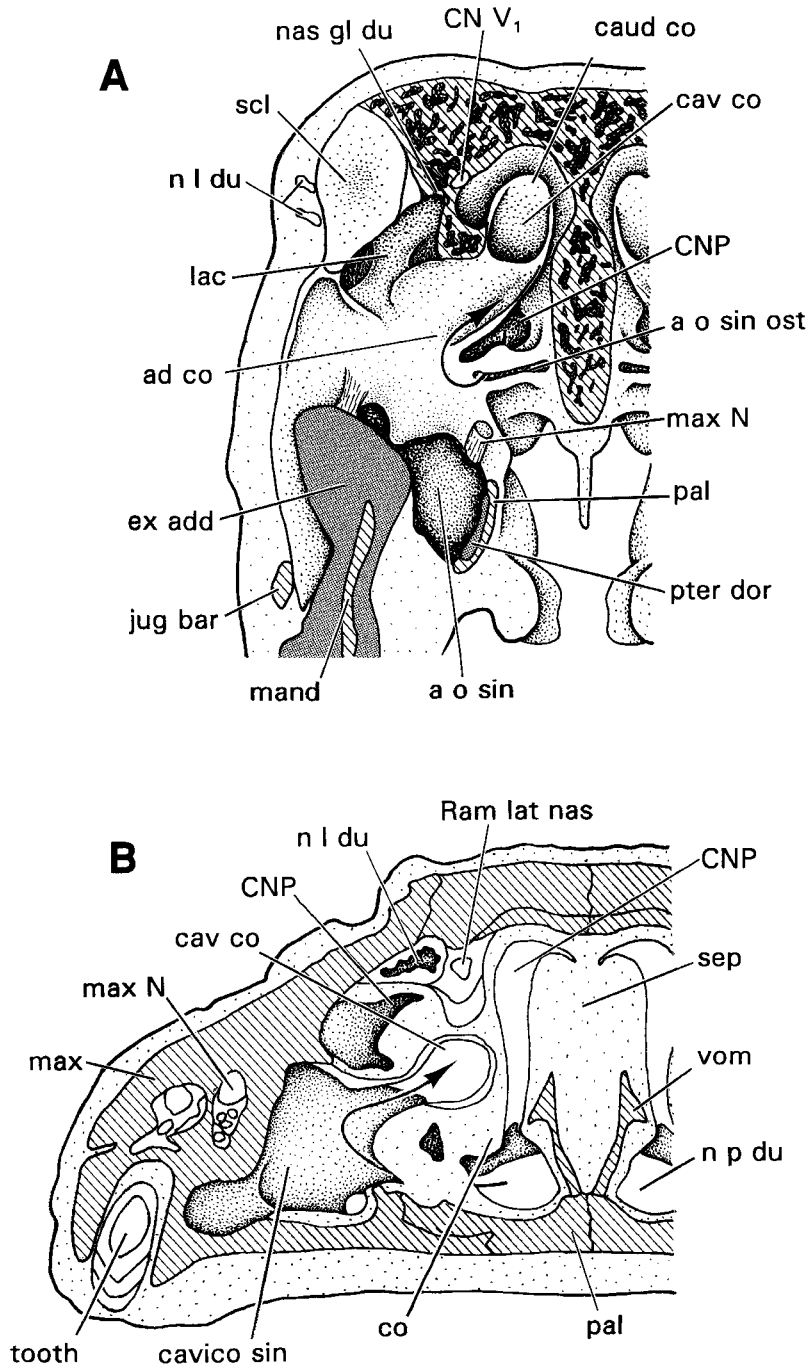


Fig. 10. **A:** *Anser anser* (in caudal view). **B:** *Crocodylus porosus* (in rostral view). Transverse sections of adult heads at the level of the aditus and cavum conchae. In A (and B), arrow passes from nasal cavity proper, through

antorbital (caviconchal) sinus ostium into antorbital (caviconchal) sinus, and into aditus and cavum conchae. Hatching denotes cut bone surfaces.



deus originates from the dorsolateral surface of the palatine and pterygoid and extends caudoventrally as a broad sheet to insert on the mandible (Figs. 8, 10A). The muscle often reaches into the caudoventral portion of the antorbital cavity where it contacts the antorbital sinus. Within the orbit, the muscle is always just ventral to the maxillary nerve and the suborbital diverticulum of the antorbital sinus (Figs. 8, 10A).

### Nasal cavity

The nasal cavity and cartilaginous nasal capsule of birds is very complex and variable (see Bang, '71) but usually has the same basic elements. The nasal cavity may be divided into the three major compartments described by Parsons ('59, '70) for "reptiles" (Fig. 9): 1) the vestibule rostrally, 2) nasal cavity proper (= *cavum nasi proprium*) caudally, and 3) the nasopharyngeal duct caudoventral to the nasal cavity proper. The boundary between the first two is usually taken to be the region into which the nasal gland ducts open (Müller, '61; Bang and Wenzel, '85) and which corresponds roughly to the position of the crista nasalis. The vestibule is expanded in birds, probably in association with development of a large rostral concha (see below), and is enclosed within the narial region of the skull, principally the premaxilla, nasal, maxilla, and in some birds (e.g., ratites) the vomer. The nasal cavity proper is sometimes subdivided into a rostral respiratory or main cavity and a caudal olfactory cavity (Matthes, '34; Bang, '71; Bang and Wenzel, '85). The nasal cavity proper extends to the orbit, and the capsule is supported by the maxilla, nasal, palatine, vomer, lacrimal, and mesethmoid. As mentioned earlier, the nasopharyngeal duct is usually very short in birds, although in some birds (e.g., *Diomedea immutabilis*) caudoventral expansion of the crista ventralis of the palatine, forming a choanal fossa, has the effect of elongating the duct somewhat (Baumel and Witmer, '93).

The nasal capsules in most clades of birds have the seven major cartilaginous elements noted by Macke ('69), most of which are aptly named: septum nasi (nasal septum, dividing the left and right nasal cavities), tectum nasi (nasal roof), paries nasi (nasal side wall), lamina orbitonasalis (=planum antorbitale, forming the caudal wall of the nasal cavity), and three conchae or "turbinals"—caudal, middle, and rostral concha—projecting into the nasal cavity. Most birds have a very poorly developed solum nasi (nasal floor; Müller,

'61). Some of these elements develop from somewhat independent anlage, which will be discussed further later. The tectum nasi and paries nasi together form a ventrally open box, with the box closed caudally by the more or less transversely situated lamina orbitonasalis; sometimes there is a rostral cupola closing the box rostrally. The paries nasi occludes much of the internal antorbital fenestra and forms part of the medial wall of the antorbital cavity. The nasal conchae project medially from the paries nasi or tectum (Fig. 9). The rostral concha is located in the vestibule, whereas the middle and caudal conchae are located in the respiratory and olfactory portions of the nasal cavity proper, respectively. The rostral and middle conchae range from simple lamellar projections to highly branched structures, with the most common morphology being simple scrolls (see Bang, '71). The caudal concha is usually a hollow, bubble-shaped hillock in medial view, and is pneumatized by a diverticulum of the antorbital sinus. The cavity within the caudal concha is called the *cavum conchae*, and the lateral entrance to the *cavum* is the *aditus conchae* (Figs. 8, 10). The caudal concha tends to be caudodorsal to the middle concha, such that the latter extends caudally ventral to the former to also reach the lamina orbitonasalis. The caudal concha has been lost, apparently independently, in a few clades of small birds (e.g., swifts, some small passeriforms; Engelbrecht, '58; Bang, '71). The nasal cartilages only occasionally ossify in birds (see Baumel and Witmer, '93), with the nasal septum and lamina orbitonasalis (ectethmoid) ossifying more commonly than the other elements.

### Air sacs

Birds have a single major air-filled, epithelial diverticulum of the nasal cavity, the antorbital sinus (Fig. 11), which itself has several subsidiary diverticula (Witmer, '90, and references therein). The antorbital air sac exits the nasal cavity via a small ostium in the caudal portion of the nasal capsule just ventral or caudoventral to the caudal concha and just rostral to the lamina orbitonasalis (Fig. 9). The ostium is directly opposite and usually close to the caudal part of the choana, and in the vicinity of the entrance of the maxillary nerve to the antorbital cavity (Fig. 10A). The antorbital sinus fills most of the antorbital cavity ventral to the nasolacrimal duct and is directly in contact with the skin covering the external antorbital fenestra. The

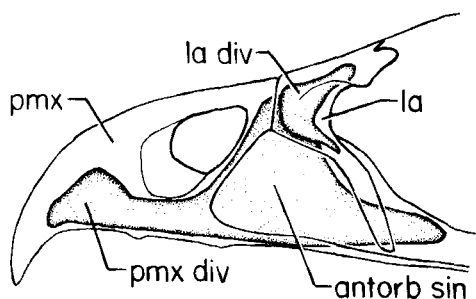


Fig. 11. *Aquila chrysaetos*. Schematic drawing of the antorbital sinus and its lacrimal, premaxillary, and suborbital diverticula in left lateral view. Modified after Witmer ('87).

antorbital sinus has several subsidiary diverticula that typically pneumatize the bones surrounding the antorbital cavity: the palatal process of the maxilla, the body of the maxilla (often leading rostrally into large pneumatic cells within the premaxilla), the lacrimal, and less commonly the palatine and mesethmoid (Fig. 7; see Witmer, '90). As mentioned above, the sinus also sends a diverticulum into the cavum of the caudal concha, entering via the aditus conchae. A final diverticulum, only very rarely pneumatizing bone, is the suborbital diverticulum which exits the antorbital cavity caudally via the postnasal fenestra and expands into the often most voluminous of the cephalic air sacs, situated rostral and especially ventral to the eyeball (Fig. 11; see Bignon, 1889). The suborbital diverticulum commonly interleaves between the dorsal pterygoideus and external adductor muscles, sometimes even reaching the region of the trigeminal foramen.

### *Crocodylians*

#### Bones and nasal cavity

The facial skeleton of extant crocodylians is composed of nine bony elements: premaxilla, nasal, frontal, prefrontal, lacrimal, maxilla, jugal, palatine, and vomer (Fig. 12). The snouts of crocodylians are remarkable for being both long and dorsoventrally flattened. Since the nasal cavity is largely enclosed in bone in crocodylians, the general organization of the cavity will be introduced here rather than with the description of the cartilaginous nasal structures, as was done for birds. Parson's ('70) tripartite division of the nasal cavity works well for crocodylians.

The vestibule is small and restricted to the narial region, forming a short vertical tube leading ventrally from the nostril. The naris

itself is dorsally situated at the rostral end of the snout, and is enclosed mostly by the premaxilla and, to a variable extent, the nasal. Both maxilla and premaxilla have well-developed palatal processes forming a secondary palate (Fig. 12). The nasal cavity proper is very long, extending from the rostralmost tip of the skull to the orbit. As in birds, the ostium of the nasal gland ducts (see below) is regarded as the boundary between vestibule and nasal cavity proper. The rostral half to one-quarter of the nasal cavity proper (or more, depending on the extent of elongation of the snout) is a tube surrounded by the premaxilla and maxilla ventrally and laterally and the nasal dorsally. More caudally, the nasal cavity opens caudolaterally into the orbit via the postnasal fenestra; in this region, the nasal cavity otherwise is surrounded by the vomer and palatine ventrally, maxilla laterally, lacrimal, prefrontal, and frontal dorsally, and the prefrontal pillar caudally.

Crocodylians are characterized by a very long nasopharyngeal duct enclosed by ventral laminae of the palatine and pterygoid, which divert the opening of the airway far caudally. The terminology for the nasal and pharyngeal openings of the duct has had a long, confusing, and often contradictory history, using terms such as "primitive," "primary," "secondary," and "tertiary" choanae (e.g., Born, 1879; Voeltzkow, 1899; Fuchs, '08; Plate, '24; Wettstein, '37-'54; Müller, '67). The rostral end of the nasopharyngeal duct opens in the middle to caudal quarter of the nasal cavity and is regarded here as the primary choana, whereas the caudal opening is the secondary choana (Fig. 12B,C). The primary choana is bounded by the vomer medially and caudally, palatine caudally and laterally, and maxilla laterally and rostrally; the secondary choana is completely within the pterygoids.

The term "antorbital cavity" is applied here to crocodylians based on the strictly morphological definition given above for birds, viz. the space between the orbit, nasal capsule, and surface of the snout. The antorbital cavity is usually relatively small in extant crocodylians, although it is sometimes moderately large in *Alligator*. The antorbital cavity is largely within the maxillary bone, with the rostral portion of the lacrimal forming its roof caudally and the palatine part of its floor. There is no external antorbital fenestra. Most of the cavity is occupied by the caviconchal sinus, an epithelial paranasal air sac (see below). The bony caviconchal recess

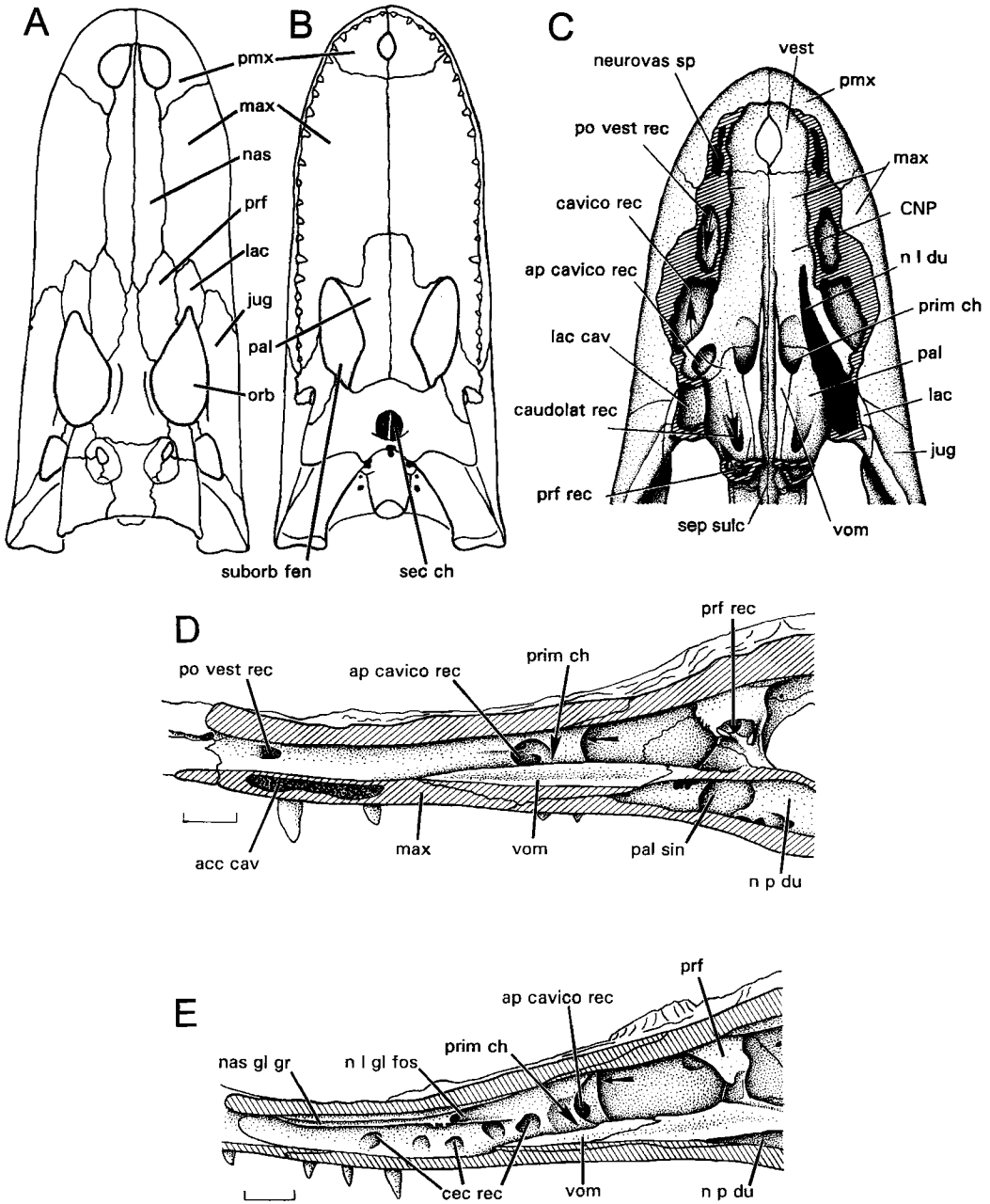


Fig. 12. **A:** *Alligator mississippiensis* skull in dorsal view. **B:** Same in ventral view. **C:** Same, horizontally sectioned snout with roof removed in dorsal view. **D:** same, sagittally sectioned and in medial view (rostral to left).

**E:** *Crocodylus porosus* skull, sagittally sectioned and in medial view (rostral to left). Hatching denotes cut bone surfaces. Scale bars in D and E = 2 cm and 1 cm, respectively. A and B after Wettstein ('37-'54) and specimens.

opens caudomedially into the antorbital cavity via a large aperture in the maxilla that is bordered dorsally by the rostral tip of the lacrimal and ventrally by the palatine (Fig.

12C-E). This caviconchal aperture is always directly opposite the primary choana and caudal to the rostral opening of the nasolacrimal duct. The bony caviconchal recess often has

been referred to as the "maxillary sinus" (Gegenbaur, 1873; Meek, '06; Nemours, '30; Wegner, '58; Ferguson, '81; among others), but this term has been applied also to a separate, rostral cavity in *Alligator mississippiensis* (Bertau, '35; Parsons, '70); it seems best to avoid confusion by abandoning the term "maxillary sinus" altogether for crocodilians. The space within the antorbital cavity caudomedial to the caviconchal aperture is small but important because several structures (e.g., the nasolacrimal duct, sometimes the nasal gland) pass through it (see below). There are usually various pneumatic cells ("accessory cavities") associated with the caviconchal recess of the antorbital cavity, the most consistent one being an extensive medial recess within the palatal process of the maxilla (Fig. 12D).

In addition to the caviconchal recess, there usually are other openings leading from the nasal cavity into pneumatic cavities within the facial bones. In fact, crocodilians as a whole exhibit a greater diversity of such cavities than perhaps any other group except perhaps mammals (see Paulli, 1900; Dieulaufé, '05). Wegner ('58) provided a detailed description of most of these; his terminology, however, is generally too cumbersome, as he applied names to many structures that have extreme intraspecific variability. There are five major recesses associated with the nasal cavity proper, although no species has all of them: 1) the caviconchal recess (discussed above), 2) the postvestibular recess, 3) maxillary cecal recesses, 4) the caudolateral recess of the palatine, and 5) the prefrontal recess. As "maxillary sinus" is unacceptable for the reasons noted above, the term "postvestibular recess and sinus" has been proposed for the bony cavity and epithelial diverticulum, respectively (Witmer, '94, in press). The postvestibular recess is a very common feature in *Alligator*, being a relatively small cavity completely within the maxilla lateral to the nasal cavity proper and rostral to the caviconchal recess, and opening into the nasal cavity via a medial foramen opposite the second or third maxillary tooth (Fig. 12C,D). In some large alligators, the postvestibular and caviconchal recesses broadly communicate, but usually they are separated by a transverse bony septum opposite the largest (fourth) maxillary tooth. *Crocodylus* spp. often has numerous, similar lateral evaginations of the nasal cavity into the maxilla, but usually they are very short and end blindly—hence their name, maxillary cecal recesses

(Wegner, '58). Another bony cavity associated with the nasal cavity proper is the "caudolateral recess" (Bertau, '35) within the palatine bone just lateral to the nasopharyngeal duct and ventral to the postconcha (Fig. 12C). The caudolateral recess varies from being a discrete foramen that opens into a chamber (e.g., *Melanosuchus niger* [Wegner, '58], some *Alligator mississippiensis*) to one or more deeply excavated fossae (e.g., some *Alligator* and *Caiman crocodilus*). This recess was absent in my material of *Crocodylus*, but Wegner ('58) figured an apparent caudolateral recess in a large individual of *C. niloticus*. Finally, the prefrontal sinus is apparently restricted to *Alligator*, where it forms a large cavity within the prefrontal communicating with the nasal cavity proper via a medial foramen within the prefrontal pillar just adjacent to the nasal septum and caudal to the postconcha (Fig. 12C,D). Wegner ('58) described for several species a "premaxillary sinus;" however, this is almost certainly the cavity for the enlarged premaxillary vascular space (associated with the narial cavernous tissue; Bellairs and Shute, '53) and not a pneumatic feature at all. Similarly, Iordansky ('73) labeled as "accessory air cavity" the non-pneumatic neurovascular foramen at the premaxillomaxillary suture.

There are also six consistent major recesses associated with the nasopharyngeal duct: 1) the vomerine bulla, 2) the palatine sinus, 3) the pterygopalatine sinus, 4) the palatine bulla, 5) the pterygoid bulla, and 6) the pterygoid sinus. Vomerine recesses or bullae occur apparently only in *Melanosuchus niger* (Howes, 1891; Wegner, '58) and *Alligator mississippiensis*; they are of fundamentally different construction in the two taxa (and of questionable homology), the former being rostral to the primary choana and the latter being caudal to it. The palatine sinus is an often large cavity within the palatine bone opening medially into the nasopharyngeal duct just rostral or ventral to the prefrontal pillar (Fig. 12D). Although in a few large *Alligator* skulls a communication between palatine sinus and caudolateral recess could be demonstrated, they were usually separated by a thin lamina; unfortunately, Wegner ('58) rarely differentiated between the two cavities within the palatine and applied the same name to them. Within the orbit of many crocodilians, there is a marked inflation of the nasopharyngeal duct (both pterygoid and palatine) called the pterygopalatine bulla (Mertens, '43; Wegner, '58).

In *A. sinensis* only the palatine is involved, forming a bulbous palatine bulla, whereas in *Gavialis gangeticus* only the pterygoid is involved, forming an often enormous pterygoid bulla (Mertens, '43; Wegner, '58; Martin and Bellairs, '77). Finally, best-developed in *Alligator* spp. (Wegner, '58; Norell, '89), the pterygoid sinus is an often multichambered cavity dorsal to the nasopharyngeal duct, ventral to the basisphenoid, and communicating with the airway in the vicinity of the secondary choana.

#### Nasolacrimal duct

The nasolacrimal duct in crocodilians passes through the lacrimal bone from the

orbit to the nasal cavity. After exiting the lacrimal rostrally, the duct passes dorsomedially through the antorbital cavity where it lies against the caviconchal sinus ventrolaterally and nasal capsule ventromedially; in the more rostral portion, the nasal gland is interposed between the capsule and duct (Fig. 13). The duct opens medially into the nasal cavity just ventral to the preconcha, usually extending rostrally a short distance beyond its nasal ostium as the "Saccus nasolacrimalis" of earlier authors (e.g., Rathke, 1866; Shiino, '14; Bertau, '35). Unlike other vertebrates, the epithelium of the nasolacrimal duct of extant crocodilians is greatly hypertrophied and formed into tubular crypts such that the

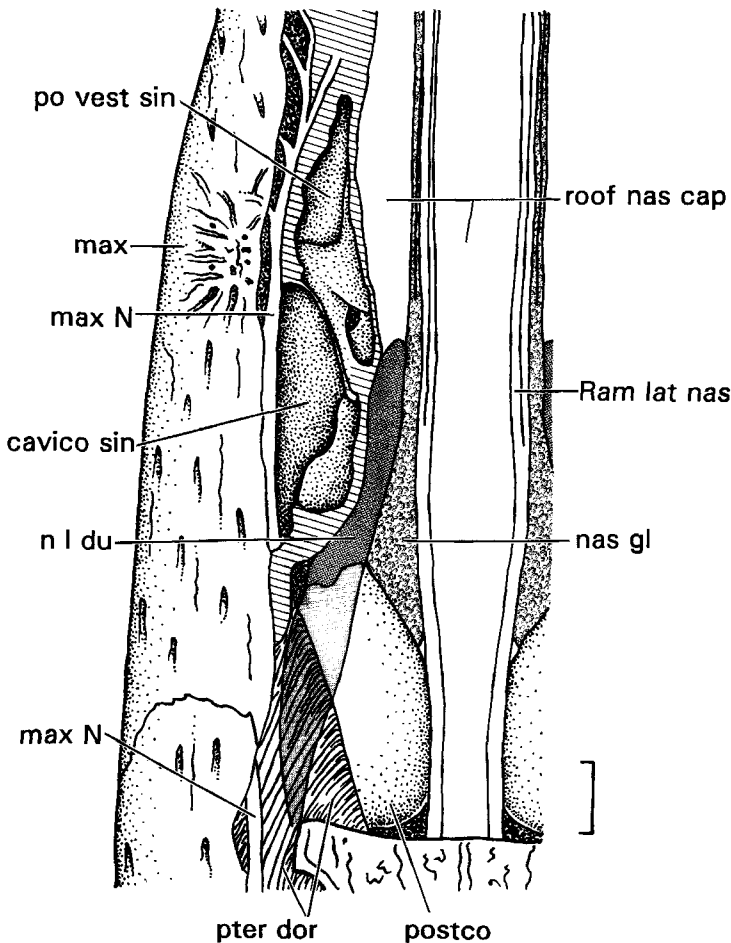


Fig. 13. *Alligator mississippiensis*. Horizontally sectioned head in dorsal view, showing the paranasal air sinuses, nasolacrimal duct, nasal gland, parts of the nasal capsule, the attachment of the dorsal pterygoideus onto

the postconcha, and the course of some branches of the trigeminal nerve (CN V). Hatching denotes cut bone surfaces. Scale bar = 1 cm.

whole structure may be termed the nasolacrimal gland (Saint-Girons, '76); the duct runs through the middle of the gland and the crypts open into the duct (Fig. 17B). The nasolacrimal gland contacts the maxilla rostrally, and in *Crocodylus* spp. (but not *Alligator mississippiensis*, *Caiman crocodilus* or the examined juvenile *Tomistoma schlegelii* and *Gavialis gangeticus*) the gland (in particular, the saccus) is lodged within a deep medial cavity within the maxilla.

### Nasal gland

The nasal gland of crocodilians extends for much of the length of the snout. In adults, the gland is a generally large, vascularized structure running from the region dorsal to the postconcha (in at least *Alligator mississippiensis*) rostrally up to the caudal margin of the narial region (i.e., the nasal vestibule) where its ducts empty (Fig. 13). Although Röse (1893), Reese ('24), Plate ('24), and Bertau ('35) reported that the gland has limited caudal extent (e.g., to about the level of the preconcha; see also Parsons, '70), they studied only embryonic or young animals, and in adults the caudal portion of the gland usually just reaches the antorbital cavity. The nasal gland is situated medial to the nasolacrimal gland (and duct) and dorsal to the nasal capsule (Figs. 13, 17B). Ramus lateralis nasi of the ophthalmic nerve passes through the substance of the gland (Bellairs and Shute, '53). The gland generally runs along the nasomaxillary suture and may faintly groove the nasal (see Fig. 12E and Witmer, in press).

### Nerves

The basic organization of the nerves closely resembles that of birds (Figs. 10B, 13, 14, 17B). The ophthalmic nerve (CN V<sub>1</sub>) passes through the orbit between the eyeball and septum and then medial to the prefrontal to enter the facial region where it splits into medial and lateral branches. Ramus medialis nasi enters the cartilaginous nasal capsule and travels between the nasal septum and adjacent mucosa. Ramus lateralis nasi remains extracapsular, in *Alligator mississippiensis* and *Caiman crocodilus* passing through a foramen epiphaniale (Fig. 15A) just dorsal to the aditus conchae (see also Bertau, '35; Bellairs and Shute, '53; Klembara, '91); rostral to the epiphaniale foramen it travels with the nasal gland between the nasal capsule and nasal bone (Figs. 10A, 13, 17B). The

maxillary nerve (CN V<sub>2</sub>) is larger, passing dorsally over the dorsal pterygoideus muscle on its way through the orbit (Figs. 10A, 13, 14), and giving off here n. alveolaris dorsalis caudalis (Poglayen-Neuwall, '53), which passes through a foramen within the maxilla (erroneously labeled as a pneumatic foramen by Iordansky, '73, Fig. 14). The rostral dorsal alveolar branch of the maxillary nerve continues rostrally into the antorbital cavity, entering a neurovascular foramen just lateral or dorsolateral to the aperture of the caviconchal recess (arrows in Fig. 12D,E). In *Alligator* and *Caiman*, the nerve and accompanying vessels (the internal maxillary vessels; Hochstetter, '06) pass through the caviconchal recess of the antorbital cavity lateral and adjacent to the caviconchal air sinus, entering a bony canal that courses dorsolateral to the postvestibular recess on its way to the premaxillary vascular space; in *Crocodylus* spp., the neurovasculature runs entirely within a bony canal.

### Muscles

As in birds, the dorsal portion of the pterygoideus muscle is the only muscle encroaching on the facial region (the narial muscles may be ignored here; see Bellairs and Shute, '53). Busbey ('89) noted that in *Alligator mississippiensis* the dorsal pterygoideus is the longest and third largest (by volume) of all the jaw muscles. Only the rostral attachments of the muscle are described (see Schumacher, '73, for the caudal attachments). The dorsal pterygoideus is a large mass passing dorsally over the pterygoid and ectopterygoid bones and suborbital fenestra, ventral to the eyeball, and through the postnasal fenestra to terminate in the caudolateral portion of the antorbital cavity (Figs. 13, 14). Within the orbit, it attaches to or is in contact with the internal surfaces of the pterygoid, ectopterygoid, jugal, maxilla, prefrontal pillar, the laminae of the pterygoid and palatine bones roofing the nasopharyngeal duct, and the interorbital septum. Rostral to the postnasal fenestra, the snout becomes flattened and the muscle fills the caudolateral part of the antorbital cavity. Again, throughout its course, the maxillary nerve is just dorsal to the muscle. Within the antorbital cavity, the muscle attaches broadly to the caudolateral surface of the bubble-shaped postconcha and to the palatine bone lateral to the dorsal ridge or crest that supports the postconcha. Dorsally, the muscle attaches to the lacrimal bone lateral to an oblique ridge (the postcon-

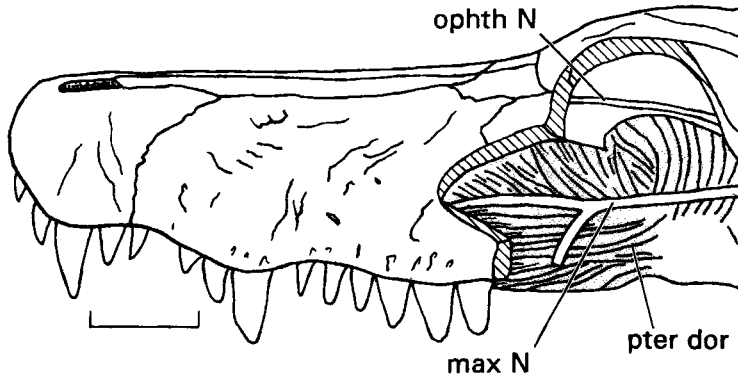


Fig. 14. *Alligator mississippiensis*. Snout with portions resected to show the position of the dorsal pterygoideus muscle and the course of branches of the trigeminal nerve (CN V). Modified after Schumacher ('73) and specimens. Hatching denotes cut bone surfaces. Scale bar = 10 cm.

cha is medial to the ridge) and also to the maxilla and jugal. Rostrally, the muscle tapers to a point where it attaches to the maxilla just lateral to the ostium of the caviconchal air sinus. In crocodylids and *Gavialis gangeticus*, the muscle stops at the maxillary neurovascular foramen, whereas in *Alligator* and *Caiman crocodilus* the muscle enters the ventral part of the foramen and passes rostrally a short distance. In the latter case, the muscle is directly adjacent to the epithelial air sac of the caviconchal sinus.

#### Nasal capsule

Crocodylians have eight major components in their cartilaginous nasal capsule, bearing, with the exception of the conchae, the same general names and relationships as those described previously for birds: septum nasi, tectum nasi, paries nasi, solum nasi, lamina orbitonasalis, postconcha, concha, and pre-concha. These elements form an extensive capsule (Fig. 15) with major apertures 1) rostrolaterally, the fenestra narina, 2) caudoventrally, the fenestra basalis (through which pass the nasopharyngeal duct, caviconchal sinus, and the palatine ramus of the facial nerve), and 3) caudodorsally, the fenestra cribrosa (through which pass the olfactory nerves [CN I], ramus medialis nasi, and vasculature: Meek, '11; Shiino, '14; Klembara, '91). The palatal process and medial lamina of the ascending ramus of the maxilla are adjacent to the solum nasi and much of the paries nasi, respectively. The paries nasi partially occludes the aperture of the caviconchal recess. The caudal portion of the paries nasi (i.e., the external surface of the postcon-

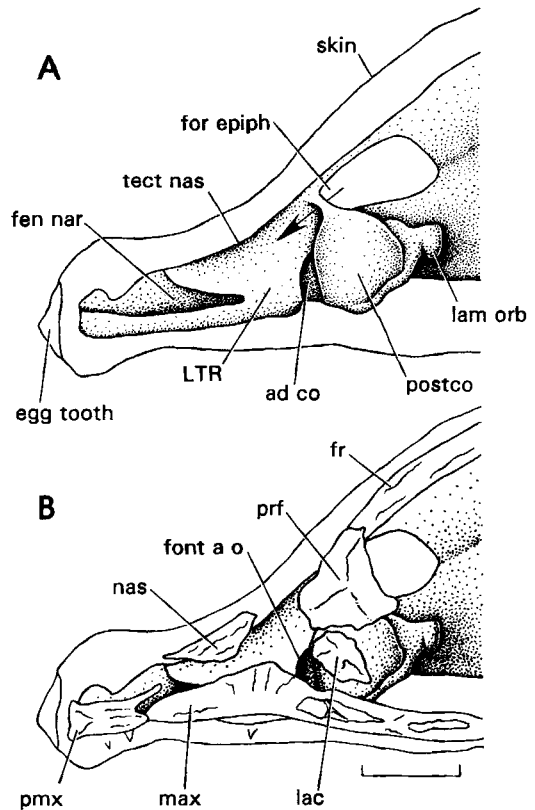


Fig. 15. *Alligator mississippiensis*. A: Rostral part of the chondrocranium of a 34-day embryo in left lateral view. B: Same with bones in place, showing the fonticulus antorbitalis. The arrow in A passes through the foramen epiphaniale. Drawn with camera lucida from a cleared-and-stained specimen. Scale bar = 2 mm.

cha) fills most of the postnasal fenestra and is part of the origin of the dorsal pterygoideus muscle (see above and Fig. 13). The tectum nasi is adjacent to the nasal, frontal, prefrontal, and lacrimal. The nasal septum is lodged ventrally in a median sulcus between the premaxillae, maxillae, vomers, and pterygoids (Fig. 12C). The fenestra basalis is largely coextensive with the primary choana.

The nasal conchae project medially from the paries nasi and tectum (Fig. 16). The preconcha is a low swelling with its greatest dimension caudally and diminishing rostrally. The nasal gland, saccus nasolacrimalis, ramus lateralis nasi, and accompanying vessels partially fill the preconcha, and the nasolacrimal duct opens just ventral to its caudal portion. The concha is a large, somewhat scrolled structure projecting freely into the cavity and attaching ventrolaterally to the paries nasi via rostromedial and caudolateral limbs in the vicinity of the primary choana; there is usually a fossa in the concha ventrally between the limbs. In *Gavialis gangeticus* and *Crocodylus* spp., the concha is hollow, with a large cavum conchae filled with a diverticulum from the caviconchal air sinus (hence the name of the latter), entering the cavum via the aditus conchae; in *Alligator mississippiensis* and *Caiman crocodilus*

(and the young *Tomistoma schlegelii* specimen), the cavum conchae is much smaller and not pneumatic in adults (Figs. 16, 17). The nasolacrimal gland (and duct) passes just lateral to the concha (Fig. 17B). The postconcha is a large, egg-shaped structure located well caudal to the primary choana and supported by the palatine ventrally, prefrontal pillar caudally and dorsally, and lacrimal dorsally; as mentioned, it bulges caudolaterally through the postnasal fenestra (Figs. 13, 15–17). The postconcha is hollow, communicating rostrally with the nasal cavity proper via a cartilaginous tube ventrolaterally within the postconcha (the post-turbinal sinus of Meek [11] and later authors). There are four, consistent, named, intracapsular spaces (i.e., preconchal recess, extraconchal recess, postconchal sinus, and post-turbinal sinus; Fig. 16), but these do not merit further discussion here (see Parsons, '70, and references therein).

#### Air sacs

The epithelial diverticula of the nasal cavity were introduced earlier in the osteological description because there usually is close correspondence between the air sac and the bony cavity. Their relationships to capsular structures are outlined below. The ostium of the

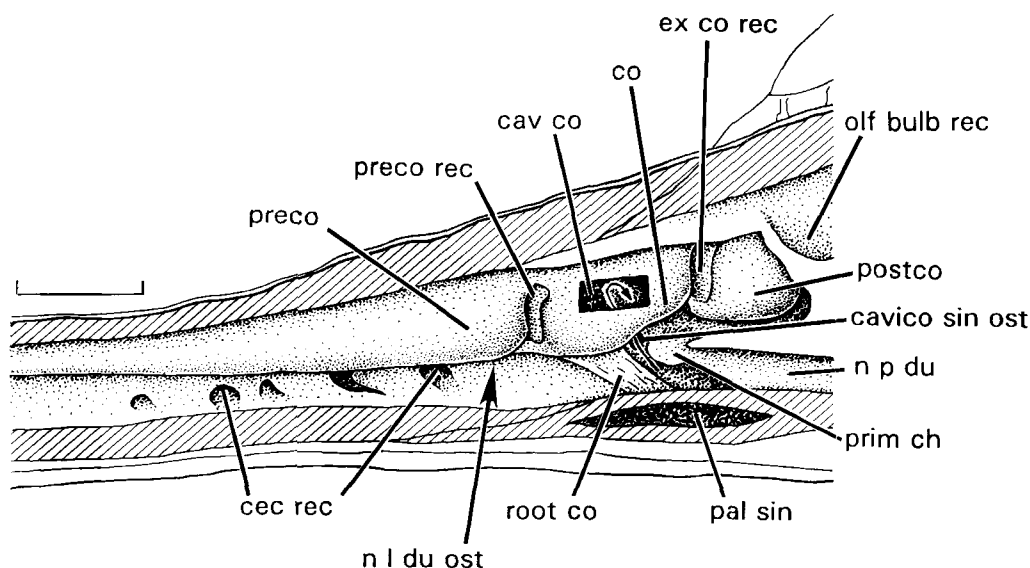


Fig. 16. *Crocodylus novaeguineae*. Right side of sagittally sectioned snout in medial view, showing nasal conchae, intracapsular recesses, cecal recesses, and nasopharyngeal duct. A window is cut into the concha, revealing

the cavum conchae; the arrow passes through the ostium of the caviconchal sinus into the cavum. The vomer is removed. Hatching denotes cut bone surfaces. Scale bar = 1 cm.



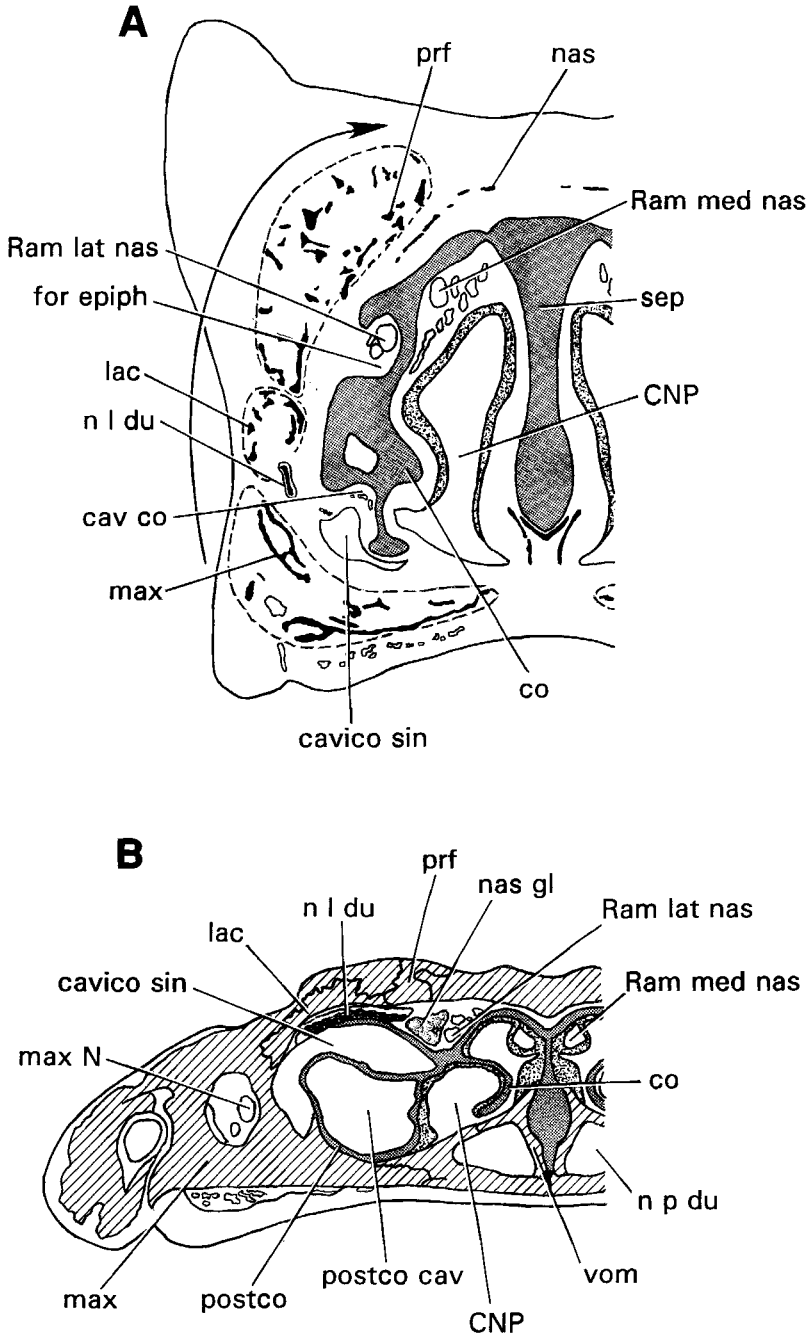


Fig. 17. *Alligator mississippiensis*. Transverse sections at the level of the concha of **A**) a 36-day embryo and **B**) an adult. Arrow shows direction of nasal rotation. Structures that are lateral early in ontogeny rotate into a

dorsal position. Note, in particular, the rotation of the ascending ramus of the maxilla, the lacrimal bone, nasolacrimal duct, cavicochal sinus, and concha. Hatching denotes cut bone surfaces.

caviconchal sinus is located immediately ventral or slightly caudoventral to the root of the concha just lateral to the primary choana (Figs. 12C–E, 16, 17). In fact, the fibrocartilage band that anchors the concha to the bony skull attaches within the primary choana in at least *Alligator mississippiensis* and forms the rostral margin of the ostium. External to the ostium, the sinus enters the antorbital cavity where it passes ventral to the nasolacrimal gland (and duct) before traversing the aperture of the caviconchal recess (Fig. 13); the ostium is always much smaller than the aperture. As mentioned, the caviconchal sinus fills the bony recess in *Gavialis gangeticus* and *Crocodylus* spp., whereas in *Alligator* and *Caiman crocodilus* the maxillary neurovasculature and the tip of the dorsal pterygoideus muscle are also (minor) contents of the recess. The postvestibular sinus (perhaps *Alligator* only) evaginates the lateral wall of the nasal cavity proper immediately caudal to the vestibule and expands within the maxillary bone (Figs. 12C, D, 13). The maxillary cecal recesses of *Crocodylus* have the appearance of “aborted” pneumatic recesses, being very variable in number and position. They often form a row that starts rostral to the nasal ostium of the nasolacrimal duct and extends rostrally for most of the length of the maxilla (Figs. 12E, 16). The caudolateral sinus evaginates the floor of the nasal cavity proper ventral to the postconcha, producing an extremely variable pattern of pneumatic recesses and/or foramina within the palatine. The prefrontal sinus is a constant feature of adult *Alligator*, evaginating the nasal cavity proper at its caudomedial corner, precisely at the angle where the prefrontal bone contacts the nasal septum; the cavity expands within the bone, eventually pneumatizing both the pillar and the dorsal lamina (Fig. 12C,D).

A couple of errors in Parsons ('70) influential treatment should be noted: 1) He illustrates (his Fig. 30) the caviconchal sinus ostium as rostral to the concha when it should be ventral or caudal to it, and 2) he labels (his Fig. 30) the cavity within the palatal process of the maxilla as communicating with the postvestibular sinus (his “maxillary sinus”) when it is instead a diverticulum of the caviconchal sinus.

#### MAJOR INFLUENCES ON FACIAL MORPHOLOGY IN EXTANT ARCHOSAURS

Having just completed a survey of the facial anatomy of birds and crocodilians, I will

briefly examine some of the morphogenetic factors potentially impacting on the apomorphic aspects of their respective facial morphologies and contributing to their divergent specialization. The point is to introduce these factors and bear them in mind when later trying to tease apart disparity and unity. Reference to extant amniote outgroups (e.g., for birds: *Crocodylia*, *Lepidosauria*, *Testudines*, *Mammalia*) confirms that the following features are apomorphic.

#### Birds

Three factors that play a significant role in avian facial conformation are 1) the large size of the eye, 2) the prominence of the nasal vestibule, and 3) the reduction of the maxilla. The extent to which the last two are correlated is unknown. The morphogenetic importance of the eyeball is well documented for a number of vertebrate groups, and it is clearly often a potent functional matrix (Taylor, '39; Malan, '46; Coulombre and Crelin, '58; Belairs and Kamal, '81; Hanken, '83). Since birds have inordinately large eyes, even as adults (Walls, '42; Pumphrey, '61; Gans, '88), and the eyes appear very early in ontogeny (Romanoff, '60), it is not surprising that these structures strongly constrain the development of adjacent areas, such as the caudal components of the face. For example, the bulging eyeball encroaches on the antorbital cavity, displacing the vertical, orbital process of the lacrimal bone rostrally such that more medial portions of the nasal capsule project caudally beyond it (in other diapsids, the capsule and lacrimal have a similar caudal extent). The effects of the eye are not always consistent, however. For example, the lamina orbitonasalis, which is directly adjacent to the orbital contents, is normally (probably plesiomorphically) transversely oriented, but due to compression from the eyeball may be either more sagittally oriented (e.g., *Ardea cinerea*, *Struthio camelus*) or more horizontal (e.g., *Rhea americana*, *Nyctisyrigmus pectoralis*); in *Rhea*, the lamina is initially vertical and transverse, and later in ontogeny becomes more horizontal and somewhat compressed laterally (Frank, '54; Müller, '61). Similarly, in *Struthio* the eyeballs are truly enormous and encroach on the nasal region to such an extent that the caudal part of the capsule is basically interorbital, having the effect of rotating the caudal concha so that its cavum conchae is directed rostrally (rather than more laterally) and diverting the ostium of the antorbital sinus ventrally (Frank, '54;

Lang, '55, '56). The caudal concha is absent in some small bird species, and these species typically have the lowest olfactory ratios (a rough measure of olfactory capability; Bang, '71), perhaps leading one to the suspicion that those birds with a decreased sense of smell have lost the caudal concha. However, it seems possible that the relatively very large eye size in these small birds in effect "crowds out" the caudal concha, such that absence of the latter is not really an adaptation for decreased olfaction but rather only a consequence of large eye size. A similar "telescoping" of the caudal portion of the nasal capsule by the eye has been implicated in loss of the concha in chamaeleonid squamates (Bellairs and Kamal, '81).

Relative to most other sauropsids, the vestibular portion of the nasal cavity is large and complicated in birds (Fig. 9), although the vestibules of many squamates also are complex (see Parsons, '70, and references therein). In birds, the rostral concha is a prominent structure and only rarely is absent (e.g., Sulidae; Bang, '71). Since the naris is somewhat caudally placed (Fig. 7), the vestibule by necessity encroaches on the nasal cavity proper. Thus, in many birds, the enlarged vestibule has the effect of, again, telescoping the nasal cavity and compressing more caudal structures (Engelbrecht, '58). This relationship is paralleled in some lepidosaurs, where elaboration of vestibular structures is correlated with shortening of the nasal capsule (Malan, '46).

Finally, birds generally have relatively small maxillary bones, having lost the dorsal ramus of the nasal process of the maxilla (i.e., the ascending ramus of other archosaurs) at the phylogenetic level above *Archaeopteryx lithographica*, as well as teeth at the level of Neornithes (Cracraft, '86; Witmer, '90). In *Gallus gallus*, for instance, the body of the maxilla is not much more than the intersection of its various processes. Although *Gallus* is extreme, in many birds, the maxilla offers little support to structures in the facial region, and its neurovasculature is greatly reduced relative to other amniotes.

### *Crocodylians*

The most obvious aspect of crocodilian facial morphology is the great length and, especially, flattening of the snout. Ontogenetically, the effects of elongation are easily comprehended. Flattening, however, does not occur morphogenetically simply by dorsoventral compression or differential lateral

growth, but rather by a complex mechanism referred to here as nasal rotation: The nasal capsule and surrounding structures rotate internally such that lateral structures become dorsal (Fig. 17). This phenomenon was first noted in a brief statement by Meek ('11), but its significance has not been appreciated.

Nasal rotation appears to be unique to crocodylians. It effects virtually all systems, so transforming facial anatomy during ontogeny that, although 1:1 correspondences are preserved for the most part, relational terms such as "lateral" and "dorsal" cannot be applied to the entire ontogeny of many structures. Perhaps the most obvious example is the nares which are initially situated laterally and later "wander" (Wettstein, '37-'54) into their dorsal positions, eventually becoming a single opening within the dried skulls of many crocodylians. Other conspicuous examples are the lacrimal bone and nasolacrimal duct, which initially are lateral and eventually rotate dorsally onto the skull roof (Fig. 17). Additional, more subtle, examples will be encountered in the next section.

Nasal rotation seems to occur at somewhat different rates in different parts of the snout. Rotation of the naris in *Alligator mississippiensis*, for instance, is virtually complete by about day 42 of incubation, a time at which the ascending ramus of the maxilla is only beginning to turn dorsomedially and the limbs of the concha are only starting to assume their adult positions; the lacrimal and nasolacrimal duct do not rotate into their final dorsal positions until between hatching and the first several weeks posthatching. Thus, to a first approximation, it seems that nasal rotation begins rostrally, and more caudal regions lag behind. Interestingly, the bony nasopharyngeal duct undergoes relative growth in an opposite direction (i.e., the lateral edges of the palatine and pterygoid grow ventromedially), suggesting that growth patterns are very complex in crocodylians. It is probably worth noting that nasal rotation apparently does not characterize all extinct crocodylomorphs, because some forms (e.g., *Pelagosaurus typus* among many others) retain primitive positions for most facial features (e.g., laterally situated lacrimals, etc.), although otherwise resembling extant crocodylians in many ways. Thus, nasal rotation may appear at or near the phylogenetic level of Neosuchia (Witmer, in press).

Another uniquely derived feature observed in extant crocodylians is that the nasal cavity

proper extends far caudally beyond the rostral aperture of the nasopharyngeal duct (primary choana), rather than terminating directly dorsal to this aperture as in other sauropsids. This caudal extension of the nasal cavity proper houses the postconcha (Fig. 16).

#### HOMOLOGIES

As the facial anatomy of extant birds and crocodilians and their respective facial apomorphies have been examined in some detail, it remains to determine which anatomical attributes are homologous. Of special interest here are those attributes that figure prominently in the debate on the soft-tissue relations of the antorbital cavity—i.e., the nasal glands, the dorsal pterygoideus muscles, and the paranasal air sinuses. Other aspects of facial anatomy will be used as topographic landmarks in assessing the homologies of these structures. Obviously, these landmarks also must be homologous and, as elaborated below, most of these are uncontroversial and receive only brief treatment, the exception being the nasal conchae. The circularity seemingly imposed by using putative homologs to assess other putative homologs is addressed by assuming homology rather than homoplasy at the outset (according to the Hennig's ['66] auxiliary principle) and testing their congruence with phylogeny under the expectation that homologies will tend to covary with other homologies (Brooks and McLennan, '91). Since homologies are hypotheses, the stepwise process of reciprocal illumination should reveal those putative homologies that in fact are homoplasies (Hennig, '66; Wiley, '81). Fortunately, in the present case, the homologies of most of the topographical landmarks can be assessed with little or no reference to the other features under consideration. For example, the homology of the nasolacrimal duct can be assessed without using evidence from, say, the nasal gland.

The basic plan is as outlined above with respect to Patterson's ('82) three tests of homology: 1) similarity or 1:1 correspondence, 2) conjunction, and 3) congruence. Congruence is tested first using the phylogeny of extant amniotes (see Fig. 2; Gauthier et al., '88a); mammals will not be explicitly treated if lepidosaurs and turtles provide a decisive assessment. Congruence with archosaur phylogeny (i.e., including fossils) is also tested here, drawing mostly on the more extensive treatment provided elsewhere (see Witmer, in press). No attempt is made to

determine the most inclusive phylogenetic level at which the features first appear; clearly many of the features characterize vertebrate taxa at high levels and are symplesiomorphies of archosaurs.

#### Bones

Most of the facial bones of extant archosaurs appeared much earlier in vertebrate phylogeny and have very consistent relationships with each other and surrounding structures (see de Beer, '37; Romer and Parsons, '86). Thus, the homology of the premaxilla, maxilla, jugal, nasal, palatine, and vomer in birds and crocodilians has never been in dispute.

Whereas crocodilians have both prefrontal and lacrimal bones, birds have only a single "preorbital" bone that has been regarded as either a prefrontal or a lacrimal (see Tables 2 and 3 in Müller, '63). Determination of the homology of this element in birds has involved three major issues (see Gaupp, '10; Gregory, '20; Müller, '63; and references therein) which will be discussed in turn: 1) the fact that numerous groups of extant amniotes have lost either the prefrontal or the lacrimal, and it has not always been clear which bone has been lost; 2) the topographic relationships of the bones to the nasolacrimal duct; and 3) the phylogenetic history of the bones.

Among extant amniotes, only some squamates and crocodilians have both lacrimals and prefrontals. The single element in extant mammals has always been called a lacrimal, and in extant turtles, *Sphenodon punctatus*, and many squamates it has been called a prefrontal (see Camp, '23; Wettstein, '31-'37; Bellairs and Boyd, '50; Gaffney, '79; Estes et al., '88). Based on the distribution in extant amniotes and disregarding the traditional names, one would be forced by adherence to a parsimony criterion to regard the ancestral amniote condition as having only one bone, with two bones (i.e., the addition of a bone) being a homoplasy of crocodilians and some squamates. This is clearly not the traditional interpretation, and more information and other criteria are required (see below). [It should be noted here that Erdmann ('40) identified two ossification centers in his material of *Gallus gallus* that he identified as lacrimal and prefrontal. However, Jollie ('57), May ('61), and Müller ('63) were not convinced by these observations, and more than one ossification center was not observed

in my material of *Gallus* or any of the other avian species studied here. Extant birds indeed have a single preorbital bone.]

The topographic relationships of the prefrontal and/or lacrimal to the nasolacrimal duct have figured prominently in previous arguments (Gaupp, '10; Gregory, '20; de Beer, '37; Jollie, '57; Webb, '57; Müller, '63; Macke, '69). In those squamates with both bones, the nasolacrimal duct passes between the lacrimal and prefrontal (Bellairs and Boyd, '50), and in crocodilians it passes through the lacrimal bone (and hence lateral to the prefrontal). Thus, it is reasoned that because, as described above, in most extant neornithine birds the duct passes lateral to the preorbital element (Figs. 7, 8), the element must be the prefrontal (Jollie, '57). In ratites, however, most or all of the duct is enclosed within the bone (Pycraft, 1900), which is more characteristic of mammalian and crocodilian lacrimals. Müller ('63) offered a compromise based on his study of the ontogeny of the skull of the ratite *Rhea*. He suggested that the medial portion of the bone could be homologous to the prefrontal and that the ventrolateral portion enclosing the duct could be homologous to the lacrimal (despite there being only one ossification center); in the majority of other birds, there thus would be no lacrimal component. Curiously, although Müller ('63) and Macke ('69) regarded the bone as mostly or completely homologous to the prefrontal, they referred to it as lacrimal.

The question then becomes, how trustworthy is this topographic relationship? In other words, is it an invariant attribute? Already in birds, we have seen that the nasolacrimal duct may pass through or lateral to the bone. In *Sphenodon punctatus*, the duct passes more ventral to the prefrontal bone than lateral to it (Wettstein, '31-'37; Gabe and Saint-Girons, '76; Bellairs and Kamal, '81). Squamates are variable, in some cases (e.g., *Varanus*) piercing the lacrimal bone and in other cases (e.g., the amphisbaenian *Monopeltis*; *Vipera* and possibly all other snakes) piercing the prefrontal (Bellairs and Boyd, '50). The point here is that the course of the nasolacrimal duct in extant amniotes does not provide unequivocal evidence for the homology of the avian preorbital bone.

The ingredient missing from the previous two paragraphs is adequate information about the phylogenetic history of the structures involved. Because many extinct (often more basal) members of amniote clades have

both lacrimals and prefrontals, the inclusion of fossil taxa provides a more complete data set for assessing the congruence of these hypotheses of homology within the context of amniote phylogeny. For example, consideration of synapsid phylogeny reveals that mammals lack the prefrontal and retain the lacrimal, loss of the prefrontal actually having occurred at a more inclusive level than Mammalia (i.e., Rowe, '88; Gauthier et al., '88a; Hopson, '91). Similarly, the basal turtle *Proganochelys quenstedti* retains both elements and indicates that higher turtles have lost the lacrimal (Gaffney, '90). Finally, the basal rhynchocephalian *Gephyrosaurus bridensis* retains a tiny lacrimal along with its large prefrontal, confirming that the single element of sphenodontids is indeed a prefrontal (Gauthier et al., '88b; Evans, '88; Fraser and Benton, '89).

Turning to the clade that includes birds, Dinosauria also plesiomorphically retains both lacrimal and prefrontal, and it appears that birds are the only dinosaurs (indeed the only archosaurs) to have definitely lost one of these bones. In general in archosauriforms, the lacrimal is much larger than the prefrontal and forms a strong vertical strut between the orbit and antorbital cavity, contacting ventrally the maxilla and/or jugal in the region of their suture; the prefrontal is a smaller element (except in some crocodylomorphs), and braces the lacrimal medially (Fig. 1). In Theropoda, the lacrimal apomorphically is enlarged further and is exposed dorsally on the skull roof (Gauthier, '86), such that the prefrontal becomes a relatively small element that is wedged in the rostradorsal portion of the orbit and that sends an often slender ventral process medial to the lacrimal. Furthermore, in maniraptoran theropods (the clade of theropods including birds) the prefrontal is further reduced and perhaps even absent in some taxa (Gauthier, '86). Wellnhofer ('74) identified a small prefrontal in the basal bird *Archaeopteryx lithographica*, but most later workers have regarded the putative lacrimoprefrontal suture as equivocal (Gauthier, '86; Witmer, '90; Martin, '91). Thus, based on the phylogenetic history of the lacrimal and prefrontal in the clade leading to birds, there is little doubt that the avian preorbital bone is homologous to the lacrimal of extant crocodilians and other amniotes (indeed probably all Choroata) and that the prefrontal bone has been lost.

### *Nasolacrimal duct*

The ontogeny, morphology, course, and topographic relationships of the nasolacrimal duct are very similar not only in extant birds and crocodilians but also in all other Tetrapoda. In all amniotes in which its development has been described, the duct arises as a solid epithelial cord lateral to the cartilaginous nasal capsule, running in the furrow between the lateral nasal and maxillary processes of the early embryo; it later develops its lumen through canalization and gains communication rostrally with the nasal cavity (Born, 1879; Peter, '06; Matthes, '34; Bellairs and Boyd, '50; Romanoff, '60; Ferguson, '85).

The position of the nasal ostium is somewhat variable. In Lissamphibia and Mammalia, the duct enters the nasal cavity in the region of the fenestra narina, rostral to a cartilaginous band called the *zona annularis* or *lamina transversalis rostralis* (de Beer, '37; Zeller, '89), although many mammals (including humans) have a second, late-appearing ostium and subsequently close the rostral ostium (Matthes, '34; Starck, '67). Extant turtles lack nasolacrimal ducts (Mikhailovics, 1898). In living diapsids, the ostium of the duct enters the nasal cavity caudal to the *lamina transversalis rostralis* in the region of the (primary) choana (Fuchs, '08; de Beer, '37; Bellairs and Boyd, '50). The intimate association of the nasolacrimal duct with the vomeronasal organ is a derived feature of squamates (Bellairs and Boyd, '50; Gauthier et al., '88b). In birds and crocodilians, the duct opens directly into the rostral portion of the (primary) choana via an ostium just ventral to the middle concha and preconcha, respectively (Figs. 9, 16). Crocodilians are unique in their elaboration of the nasolacrimal epithelium into a glandular structure (Saint-Girons, '89) and in the dorsal position of most of the duct in adults (associated with nasal rotation; see Fig. 17B). In summary, on the basis of ontogenetic and topographical similarities and the phylogenetic distribution of these similarities within extant amniotes, there is no doubt on the homology of the nasolacrimal duct.

Under the empirical "checking and re-checking" (Hennig, '66) associated with the principle of reciprocal illumination, the homologies of the lacrimal bone and nasolacrimal duct of birds with those of other amniotes confirm that in birds either the course of the duct has changed relative to the lacrimal

bone or vice versa. In other words, no recourse can be made to a "new" duct in birds to explain its unusual topographic relationships to the bone. As mentioned above, although ratites have the duct partly enclosed within the lacrimal, this is almost never the case in other neornithine birds. Furthermore, in the next outgroup for which we have data, the Cretaceous hesperornithid birds, the duct passes lateral to the lacrimal in a groove as in most non-ratite neornithines (Witmer, '90). In *Archaeopteryx lithographica*, the lacrimal appears to be pierced by the nasolacrimal duct (see Witmer, in press). In fact, this situation is found in virtually all dinosaurs (see Witmer, in press). Thus, relative to *Archaeopteryx* and nonavian dinosaurs, the condition in hesperornithids and non-ratite neornithines is derived. Whether ratites represent a reversal or hesperornithids represent a convergent acquisition of the non-ratite neornithine condition is not entirely clear. Given that in ratites the lacrimal usually does not completely surround the duct but is instead open laterally (often completed by connective tissue; Webb, '57), it is possible that the ratite condition involves a secondary "re-evolution" of the portion of the lacrimal lateral to the duct.

The basal bird *Archaeopteryx lithographica* and nonavian dinosaurs resemble extant crocodilians in having the nasolacrimal duct pierce the lacrimal bone, suggesting that this soft/hard-tissue association is the ancestral archosaurian condition. However, reference to *Crurotarsi*, the archosaur clade that includes crocodilians (Sereno and Arcucci, '90; Sereno, '91; Parrish, '93), indicates that this condition arose within the crocodylomorph clade. In the following successively more basal crurotarsans, the duct passes between the lacrimal and prefrontal bones (Witmer, in press): the basal crocodylomorph *Dibothrosuchus elaphros* (Wu and Chatterjee, '93), the stagonolepidids *Desmotosuchus haplocerus* and *Stagonolepis robertsoni* (Walker, '61), probably *Ornithosuchus longidens*, and the parasuchian *Phytosaurus* sp. The course of the nasolacrimal canal is not known in basal Ornithodira (i.e., pterosaurs and basal dinosauromorphs). Thus, despite passing the similarity test (i.e., the lacrimal transmits the duct), the condition in extant crocodilians and dinosaurs is judged as nonhomologous on the basis of the congruence test.

To summarize, it is difficult to postulate homologous causal associations between the

nasolacrimal duct and its osteological correlates in extant birds and crocodilians, because both taxa exhibit such apomorphic associations that little is left in common. Again, in probably all birds higher than *Archaeopteryx lithographica*, the duct passes lateral to the lacrimal, and at the most, grooves the lateral aspect of the bone (except in ratites). In crocodilians, the duct passes through the lacrimal, the nasolacrimal canal is greatly enlarged to accommodate glandular tissue, and both duct and bone assume a dorsal position due to nasal rotation. Interestingly, although the duct and its course from orbit to choana are homologous in extant archosaurs (see above), there are no homologous osteological correlates. Fortunately, regardless of whether the duct pierces the lacrimal (as in dinosaurs and crocodilians) or passes between the lacrimal and prefrontal (most crurotarsans), this homologous course is indicated in fossil archosaurs and suggests that the ancestral archosaurian condition is to have the duct passing through the dorsomedial portion of the antorbital cavity as in extant archosaurs (see Witmer, in press).

#### *Nasal gland*

The homology of the nasal glands of tetrapods was discussed by Parsons ('59) and to a lesser extent by Gaupp (1888), Peter ('06), and Plate ('24), all of whom concluded that these named glands were probably homologous in all Tetrapoda based on their innervation and association with the nasal vestibule. This homology may well be true, but there is a fundamental dichotomy in that the gland is intracapsular in Lissamphibia and Mammalia and extracapsular in Sauropsida. Although this dichotomy may reflect no more than the acquisition of an apomorphic position in sauropsids (as argued by Gauthier et al., '88a), I choose to make explicit reference only to Sauropsida where the homology of the gland is more certain.

In all sauropsids that have been surveyed for this structure, the nasal gland 1) arises early in ontogeny as an evagination of the nasal epithelium near the caudal margin of the nasal vestibule, 2) grows caudally, assuming a position lateral to the cartilaginous nasal capsule, and 3) is innervated by autonomics traveling with the ramus lateralis nasi of the ophthalmic nerve (Born, 1883; Gaupp, 1888; Röse, 1893; Marples, '32; Hoppe, '34; Bertau, '35; Technau, '36; Parsons, '59). It should be noted that this gland is often called the "external" or "lateral"

nasal gland, but in extant birds and crocodilians (and squamates as well) there is no medial nasal gland, so the term requires no modifiers; some turtles and *Sphenodon punctatus* have medial nasal glands (Saint-Girons, '89). As described above, extant crocodilians and most birds have apomorphic positions of the gland. In crocodilians, it rotates ontogenetically into a dorsal position, whereas in many birds the body of the gland is located within the orbit.

The osteological correlates of the nasal gland are very subtle in extant sauropsids (with the exception of the supraorbital fossa in marine birds). In crocodilians there is usually a faint, often striated depression on the internal surface of the nasal bone lateral to the sulcus for the nasal septum and near and often within the nasomaxillary suture; this groove, which mostly lodges the gland but also ramus lateralis nasi and accompanying vessels, is broader caudally and narrows as it approaches the vestibular region. In birds, the nasal gland ducts run on the medial surface of the bones in the vicinity of the nasomaxillary suture, and in some cases (e.g., *Anser anser*, *Ardea herodias*) groove the bones. In those squamates in which the nasal gland is lodged within the cavum conchae (Gabe and Saint-Girons, '76), there are no osteological correlates and perhaps only a faint groove otherwise. Some turtles (e.g., *Chrysemys picta*) show a groove associated with the gland, although here it is along the prefrontomaxillary suture (extant turtles other than chelids lack nasal bones; Gaffney, '79). Thus, based on the distribution of these bony features in extant sauropsids, a hypothesis may be formulated that the ancestral archosaurian condition is to have the nasal gland situated caudodorsolaterally within the snout and possibly grooving the adjacent bones in the vicinity of the nasomaxillary suture. The few fossil archosaurs that can be sampled for these features corroborate this hypothesis (see Witmer, in press) and hence support the homology of both the nasal gland and its osteological correlates in extant birds and crocodilians.

#### *Nerves*

The homology among vertebrates of the divisions of the trigeminal nerve and their major branches is virtually certain (de Beer, '37; Romer and Parsons, '86), and requires no further justification here. In fact, their highly conserved topographic relationships

have long been used as landmarks in studies such as this one.

The general course of the nerves described above for birds and crocodilians pertains to other amniotes as well (Gaupp, 1888; Wettstein, '31-'37; Lakjer, '26; Oelrich, '56; Getty, '75). The ophthalmic nerve travels through the dorsomedial portion of the orbit before dividing rostrally into medial and lateral nasal rami near the juncture of the nasal and orbital cavities. The maxillary nerve travels ventrally or ventrolaterally through the floor of the orbit dorsal to the pterygoideus musculature (or its presumed partial mammalian homolog, m. tensor veli palatini; Adams, '19; Lakjer, '26; Barghusen, '86) before entering the maxillary bone. The only consistent osteological correlates of the ophthalmic nerve in extant archosaurs are foramina within the premaxilla transmitting nerves carrying sensory information from the integument; it could not be determined for other amniotes if this territory was covered consistently by the ophthalmic nerve or the maxillary nerve.

The maxillary nerve itself has almost constant osteological correlates among extant amniotes in the form of foramina and canals within the maxilla (and often jugal, as well) innervating dental and integumentary structures. These foramina provide important clues to the course of the homologous nerve in all amniotes, both fossil and extant.

### Muscles

As described earlier, in both extant birds and crocodilians one of the adductor muscles reaches into the facial region. In both cases it has been referred to as m. pterygoideus, pars dorsalis (although it has had a variety of synonyms: m. adductor mandibulae internus pterygoideus anterior, m. pterygoideus internus, m. pterygoideus anterior, pterygoideus D, etc.). The homology of the various jaw muscles among sauropsids and other vertebrates has been the subject of numerous monographic treatments, and the evidence does not need to be reviewed again here (see Adams, '19; Lakjer, '26; Lubosch, '33; Edgeworth, '35; Kesteven, '45). These workers all agreed that the dorsal pterygoideus of extant birds and crocodilians is homologous, citing evidence primarily from the ontogeny, topographic relationships, and/or pattern of innervation of the muscles.

There is disagreement, however, as to the extent to which the pterygoideus mass is subdivided in other sauropsids. For example,

for turtles, Adams ('19) and Lakjer ('26) discuss only a single pterygoideus muscle that occasionally reaches rostrally onto the dorsal surface of the palatal bones; Schumacher ('73) regarded this portion as a separate pars dorsalis. The muscle in *Sphenodon punctatus* is generally similar, extending onto the dorsal surface of the palate under the eyeball for a short distance, but most workers have not regarded the muscle as having separate parts (Adams, '19; Lakjer, '26; Wettstein, '31-'37; Lubosch, '33). The pterygoideus muscle in Squamata is usually described as undivided or only occasionally divided into superficial and deep portions. Thus, only in extant birds and crocodilians is there a well-demarcated division into a pars dorsalis and pars ventralis (Lakjer, '26; Lubosch, '33). In fact, Lubosch ('33) argued that the pars dorsalis in birds and crocodilians is actually a portion of the m. pseudotemporalis (another portion of m. adductor mandibulae internus) that has become separated from the main mass and that this separation is absent in other sauropsids. Whether or not Lubosch's ('33) idea is correct, it is clear that the presence of a more or less separate pars dorsalis and pars ventralis is a synapomorphy of extant archosaurs.

As just demonstrated, the dorsal pterygoideus muscle of extant birds and crocodilians passes both the similarity test and the test of congruence among extant sauropsids. However, unlike the situation with structures such as the nasolacrimal duct and nasal gland that characterize extant vertebrate taxa at much higher levels, the dorsal pterygoideus is restricted to Archosauria. As a result, rigorous testing for congruence with archosaur phylogeny becomes more important. The osteological correlates of the dorsal pterygoideus are relatively few because of the divergent specialization of extant birds and crocodilians, but an excavation on the dorso-lateral surface of the palatine near or within the caudoventral portion of the antorbital cavity remains as a reliable indicator of the presence of the muscle. As elaborated elsewhere (Witmer, in press), in at least the basal members of all major clades of archosaurs there is a well-developed palatine excavation extending well within the ventral portion of the antorbital cavity. Given the causal association of the bony excavation with the dorsal pterygoideus in extant archosaurs, the similar structure in the fossil taxa is almost certainly a muscular fossa. Thus, the hypothesis



of homology is congruent not only with extant amniote phylogeny but also archosaur phylogeny, and the homology of m. pterygoideus, pars dorsalis in extant archosaurs is well founded.

*Parts of the nasal cavity and the choana*

In accordance with Parsons' ('59, '70) revision of the earlier (often confusing) terminology of the parts of the nasal cavity, three major components have been recognized here: vestibule, nasal cavity proper, and nasopharyngeal duct. The boundaries between these regions are sometimes more definitional and arbitrary than discrete, but the terms are used so commonly that they are discussed briefly here. The vestibule in virtually all extant sauropsids is rostral to the apertures of the nasal gland ducts (Parsons, '59; Müller, '61). In turtles, *Sphenodon punctatus*, many squamates, and crocodilians the vestibule is a small cavity within the nasal capsule, but in some squamates (Pratt, '48; Bellairs and Kamal, '81) and birds it is apomorphically enlarged. In most cases, it is generally restricted to the narial region of the skull, but in many avian species a ventral recess extends caudally back to the crista nasalis (where the nasal gland ducts enter), undercutting somewhat the nasal cavity proper (see also Bang, '71).

In tetrapods, the nasal cavity proper is fairly consistent, occupying the cartilaginous nasal capsule from the vestibule to the primary choana and having respiratory as well as olfactory epithelium (Plate, '24; Matthes, '34; de Beer, '37; Parsons, '71). The capsule extends all the way back to the rostral margin of the orbit, in extant amniotes usually attaching to the lacrimal and/or prefrontal. The homology of both the vestibule and nasal cavity proper in extant amniotes has never been contested.

As its name implies, the nasopharyngeal duct runs from the nasal cavity proper to the pharynx. To my knowledge, it is not lined by the cartilage of the nasal capsule in any vertebrates but rather is lined by respiratory or perhaps partly oral or pharyngeal epithelium. As a result, its rostral end (the choana or primary choana; see below) is roughly coextensive with the fenestra basalis of the chondrocranium. It is variably developed in extant amniotes. Most mammals have a well-developed nasopharyngeal duct, as do many turtles, some squamates, all crocodilians, and a few birds; it is essentially absent in *Sphenodon punctatus*, most squamates, and most

birds (Plate, '24; Matthes, '34; Bellairs and Boyd, '50; Parsons, '59). No one has suggested that the nasopharyngeal ducts of amniotes are homologous, and, given both the phylogenetic distribution and topographic relationships of the structure, homology is indeed unlikely. Instead, its repeated development probably reflects a tendency among many clades to divert the airway caudally, usually associated with the evolution of a bony "secondary" palate (Fuchs, '08; Rieppel, '93).

The complicated nature of the issues surrounding the terminology of the choana of amniotes was only hinted at above in the description of crocodilian facial anatomy. It gets even worse when more basal vertebrates are considered (see papers on the origin of tetrapods in Schultze and Trueb, '91). For the matter at hand, the question centers on the homology (and name) of the opening located at the juncture of the nasal cavity proper and nasopharyngeal duct, particularly in crocodilians. In forms such as *Sphenodon*, most squamates, and the vast majority of birds, in which the nasopharyngeal duct is poorly developed or absent, the issue is simple and the opening is the choana. Again, it more or less coincides with the borders of the cartilaginous fenestra basalis (this fenestra is not really identifiable in most birds because they usually lack a solum nasi).

Osteologically, in those turtles lacking an extensive nasopharyngeal duct, in most extant lepidosaurs, and in birds, the choana is surrounded by the vomer medially, palatine caudally and laterally, and maxilla laterally and/or rostrally; the rostral border of the choana is variable, being either the maxilla or premaxilla depending on the presence and extent of palatal processes of the maxilla (Romer, '56; Gaffney, '79; Witmer and Martin, '87). In crocodilians, the aperture termed earlier the primary choana has precisely the same topographic relationships: vomer medially, palatine caudolaterally, and maxilla rostrolaterally (Fig. 12C). Thus, given this similarity and its congruence with the phylogeny of extant sauropsids, the homology of the crocodilian primary choana with that of other sauropsids is well founded. Moreover, virtually all fossil archosaurs (as well as extinct, more basal members of other amniote clades) exhibit this same morphology. In fact, only *within* the phylogeny of Crocodylomorpha does the formation of a bony nasopharyngeal duct (and hence a secondary choana) obscure

the primary choana from ventral view. Thus, the hypothesis of homology of the (primary) choanae of extant archosaurs is also congruent with archosaur phylogeny.

### *Nasal conchae*

#### Historical background

The outgrowths of the lateral wall of the nasal cavity (conchae, turbinals, etc.) vary tremendously in morphology among extant vertebrates, and as a result, there is an extensive literature addressing their homologies (see Table 2). Although it is far beyond the scope of this paper to adequately review the various arguments, the following discussion focuses on a few of the more influential treatments, in particular those studies representing alternative approaches to the problem. The next subsection presents the results of my research, drawing evidence from the mode of development of the structures, their topographic relationships, and the congruence of this information with phylogeny.

Before proceeding, however, it is necessary to introduce the named structures found in the higher taxa of amniotes. As described above, birds have rostral, middle, and caudal conchae, and crocodilians have a preconcha, concha, and postconcha (Figs. 9, 16). Squamates have a single concha (Fig. 18A; although it is absent occasionally). *Sphenodon punctatus* has rostral and caudal conchae (Fig. 18B). Turtles have no named conchae, but the Muschelwulst and laterale Grenzsfalte have been compared to the squamate concha (Fig. 18C; Gegenbaur, 1873; Parsons, '59). Mammals have a very complex and variable nasal cavity with a large variety of named turbinals (see Starck, '67); of these, the maxilloturbinal, ethmoturbinal, nasoturbinal, atrioturbinal, and the crista semicircularis have figured most prominently in the debate on conchal homologies (Fig. 18D). For morphological details of these structures in nonarchosaurian amniotes, see de Beer ('37), Parsons ('59, '70), Starck ('67), and Moore ('81) and references therein. Although de Beer ('37, p. 180) identified an "exceedingly rudimentary concha nasalis" in the urodele *Ambystoma* sp., conchae are usually regarded as being restricted to amniotes and absent from Lissamphibia (Dieulafé, '05; Peter, '06; Plate, '24; Matthes, '34; Parsons, '59; Jurgens, '71; Gauthier et al., '88a).

Without a doubt, the most influential paper on the homologies of the nasal conchae is that by Gegenbaur (1873), whose proposed homologies have been followed for the most

part in most of the succeeding important reviews (e.g., Dieulafé, '05; Peter, '06; Matthes, '34; Parsons, '59, '70; Starck, '67; Gauthier et al., '88a; Zeller, '89). Gegenbaur's (1873) evidence comes almost exclusively from a very strict, typological definition of his conception of a "Nasenmuschel": a simple, more or less independent lamella projecting inward from the capsular wall and supported by a cartilaginous or bony skeleton. Thus, he homologized the lamellar structures seen in mammals (maxilloturbinal), squamates (concha), crocodilians (concha), and birds (middle concha). Following his strict definition, Gegenbaur eliminated the avian caudal concha and crocodilian postconcha from consideration because they are not lamellar projections but rather invaginations and evaginations of the nasal cavity, respectively; thus, he regarded both structures as independent neomorphs. Most later workers (e.g., those cited in the first sentence of this paragraph) who otherwise followed Gegenbaur argued that the avian caudal concha and crocodilian postconcha are in fact homologous. I will refer to this scheme as the Gegenbaur/Matthes scheme to recognize Gegenbaur's initial formulation and Matthes' ('34) subsequent influential review.

Gegenbaur's (1873) selection of *Alligator mississippiensis* as his crocodilian sample rather than, say, a species of *Crocodylus* had a profound impact on his results. *Alligator* has a poorly developed cavum conchae, and hence its concha is indeed somewhat lamellar, thus conforming to his definition of a Nasenmuschel (Fig. 17B). *Crocodylus*, on the other hand, has a well-developed cavum such that its concha more closely resembles an avian caudal concha and thus would not adhere to his strict definition (Fig. 10B). Thus, it is tempting to wonder what both his results and the subsequent history of the debate would have been had he simply chosen *Crocodylus* rather than *Alligator*.

Although Solger (1876) found merit in Gegenbaur's (1873) strict definition, Born (1879) and virtually all later workers found it too restrictive and called any kind of projection into the cavity a Muschel or concha. In fact, rather than simply applying a definition, some workers sought alternative criteria on which to homologize the conchae. For example, Hoppe ('34) and Bertau ('35) used an approach advocated by Beecker ('03) whereby the various intracapsular spaces and recesses (Hohlräume) of the nasal cavity were used as

TABLE 2. Summary of proposed homologies for the nasal conchae of Amniota<sup>1</sup>

Reference	Avian rostral concha	Avian middle concha	Avian caudal concha	Other
Gegenbaur (1873)	<i>Neomorph</i>	Crocodylian concha; squamate concha; mammalian maxilloturbinal	<i>Neomorph</i>	<i>Neomorph</i> : crocodylian postconcha
Mihalkovics (1898)	—	Mammalian maxilloturbinal	Squamate concha; mammalian ethmoturbinal	—
Dieulafé ('05)	<i>Neomorph</i>	Crocodylian concha; squamate concha; mammalian maxilloturbinal	Crocodylian postconcha; mammalian ethmoturbinal	—
Peter ('06)	<i>Neomorph</i>	Squamate concha; mammalian maxilloturbinal	Crocodylian postconcha; mammalian nasoturbinal	—
Nemours ('30)	—	Mammalian maxilloturbinal	Crocodylian concha; squamate concha	—
Hoppe ('34)	—	<i>Sphenodon</i> rostral concha; squamate Lippe am Choanengang	<i>Sphenodon</i> caudal concha; squamate concha	—
Matthes ('34)	<i>Neomorph</i>	Crocodylian concha; squamate concha; <i>Sphenodon</i> caudal concha; mammalian maxilloturbinal	Crocodylian postconcha; mammalian nasoturbinal	—
de Beer and Barrington ('34)	—	Crocodylian preconcha (in part)	Crocodylian concha; squamate concha; mammalian crista semicircularis	Crocodylian postconcha = mammalian ethmoturbinal?
Bertau ('35)	<i>Neomorph</i>	Crocodylian concha + preconcha; <i>Sphenodon</i> rostral concha; squamate Lippe am Choanengang; mammalian maxilloturbinal	Crocodylian postconcha; <i>Sphenodon</i> caudal concha; squamate concha; mammalian nasoturbinal	—
de Beer ('37)	Crocodylian preconcha; mammalian atrioturbinal	Crocodylian preconcha (in part); mammalian maxilloturbinal	Crocodylian concha; squamate concha; mammalian crista semicircularis; urodele concha	<i>Neomorph</i> : crocodylian postconcha
Lang ('55)	<i>Neomorph</i>	Crocodylian concha; squamate concha; mammalian maxilloturbinal	Mammalian ethmoturbinal or maxilloturbinal	—
Parsons ('59, '70)	<i>Neomorph</i>	Crocodylian concha + preconcha; <i>Sphenodon</i> caudal concha; squamate concha; mammalian maxilloturbinal	Crocodylian postconcha	—
Müller ('61)	<i>Neomorph</i>	mammalian maxilloturbinal; crocodylian concha; squamate concha	Crocodylian concha; squamate concha	—
Starck ('67)	—	Crocodylian concha; squamate concha; mammalian maxilloturbinal	Crocodylian postconcha; mammalian nasoturbinal	<i>Neomorphs</i> : mammalian frontoturbinal & ethmoturbinal
Gardiner ('82)	—	Crocodylian concha; mammalian maxilloturbinal	—	—
Gauthier et al. ('88a)	<i>Neomorph</i>	Crocodylian concha + preconcha; <i>Sphenodon</i> caudal concha; squamate concha; ? turtle laterale Grenzfalte; mammalian maxilloturbinal	Crocodylian postconcha	—
This study	<i>Neomorph</i>	<i>Neomorph</i>	Crocodylian concha + preconcha; <i>Sphenodon</i> caudal concha; squamate concha; ? mammalian crista semicircularis	<i>Neomorphs</i> : crocodylian postconcha; <i>Sphenodon</i> rostral concha; ? turtle laterale Grenzfalte; mammalian ethmoturbinal, nasoturbinal, maxilloturbinal

<sup>1</sup>Birds are selected arbitrarily here as the reference to which other amniotes are compared.

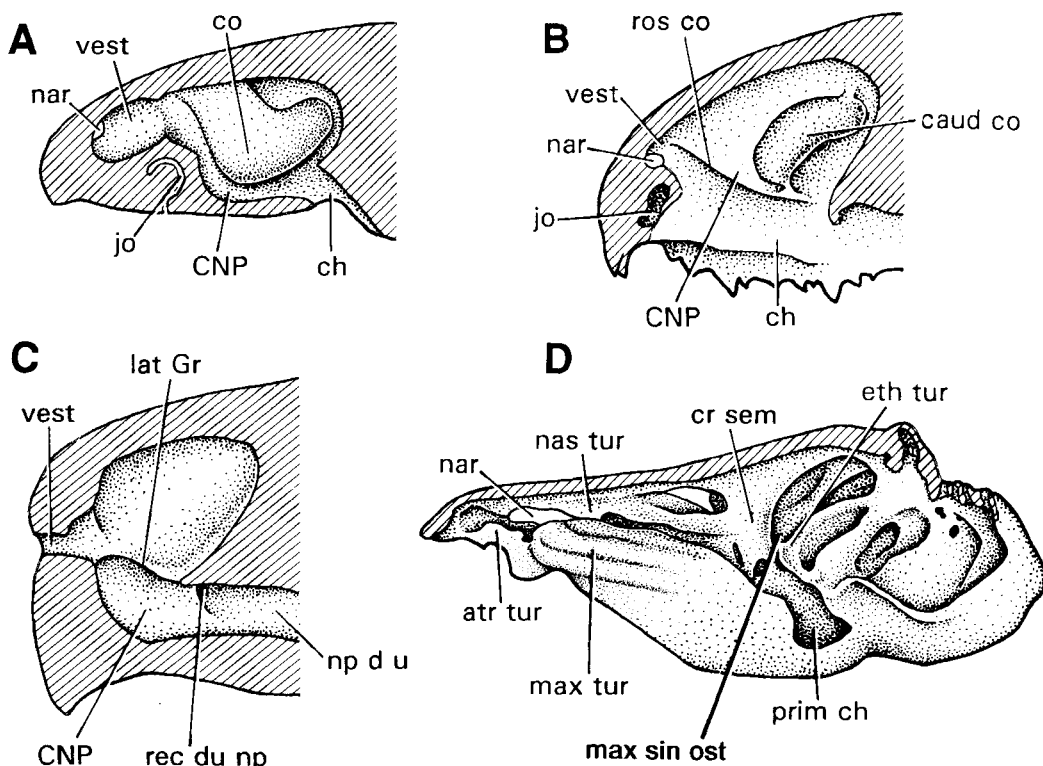


Fig. 18. **A)** *Lacerta viridis*, **B)** *Sphenodon punctatus*, **C)** *Testudo graeca*, and **D)** *Oryctolagus cuniculus* (late fetus). Right sides of sagittally sectioned snouts in medial view, showing the parts of the nasal cavity and the conchal and turbinal structures. A–C modified after Parsons ('70), B also after Hoppe ('34), and D after Starck ('67). Hatching denotes cut surfaces.

primary evidence to homologize the conchae rather than the epithelial or cartilaginous structures themselves. Hoppe ('34) homologized the structures of *Sphenodon punctatus* to those of squamates and birds, and Bertau ('35) accommodated crocodilians and mammals into this system. According to their scheme, the following two homologies pertain (Table 2): 1) the caudal concha of *Sphenodon* with the squamate concha, the crocodilian postconcha, the avian caudal concha, and the mammalian nasoturbinal; and 2) the rostral concha of *Sphenodon* with the squamate Lippe am Choanengang, the crocodilian concha and preconcha together, the avian middle concha, and the mammalian maxilloturbinal.

The Hoppe/Bertau scheme bears some resemblances to the Gegenbaur/Matthes scheme. In both schemes, the avian caudal concha, crocodilian postconcha, and mammalian nasoturbinal are homologous (for the purpose of the immediate discussion, I will

call this group A), as are the avian middle concha, crocodilian concha, and mammalian maxilloturbinal (group B). They differ primarily in the status of the structures in lepidosaurs. In the Hoppe/Bertau scheme, the caudal concha of *Sphenodon punctatus* and the squamate concha are in group A, whereas they are in group B according to the Gegenbaur/Matthes scheme. Likewise, the rostral concha of *Sphenodon* and the squamate Lippe am Choanengang are in group B in the Hoppe/Bertau scheme and group A in the Gegenbaur/Matthes scheme (the Lippe am Choanengang was not discussed by either Gegenbaur or Matthes). There is no easy way to reconcile these differences, particularly since squamates were always the standard of comparison (again reflecting a typological tradition). The Hoppe/Bertau scheme has had no lasting impact on notions of conchal homologies among amniotes, and their "Hohlräume approach" received no further atten-

tion. The Gegenbaur/Matthes scheme has held sway to the present.

The Gegenbaur/Matthes scheme, however, has not gone uncontested. De Beer ('37; see also especially de Beer and Barrington, '34) offered an alternative approach to the problem, this time making use of the form and ontogeny of the components of the cartilaginous nasal capsule and their relationships to surrounding structures. It should be noted, however, that de Beer ('37) had his own typological definitions, in some respects the opposite of Gegenbaur's (1873): He regarded a "true concha" as a structure enclosing a cavity, whereas "turbinals" are lamellar structures. De Beer offered the following homologies (Table 2): 1) avian caudal concha, crocodilian concha, squamate concha, and mammalian crista semicircularis; 2) avian middle concha, ventral edge of the preconchal recess of crocodilians, and mammalian maxilloturbinal; 3) avian rostral concha, crocodilian preconcha, and mammalian atrioturbinal; and 4) crocodilian postconcha and possibly the mammalian ethmoturbinal. De Beer ('37) reported conchae as absent in turtles and *Sphenodon punctatus*. The only homology shared by all three schemes is the avian middle concha with the mammalian maxilloturbinal. The Hoppe/Bertau scheme and de Beer's scheme additionally share the homology of the avian caudal concha and squamate concha. There are no other similarities between the Gegenbaur/Matthes scheme and de Beer's scheme.

In summary, despite approaching the problem from three different perspectives, the homologies proposed by the above workers do not converge on a single answer for all, or even most, amniotes. Of the three approaches, de Beer's is probably the most enlightening because it takes into account a great deal of morphological and ontogenetic detail—i.e., it is an effective similarity test. Likewise, the Hohlräume approach of Hoppe and Bertau involves detailed topographic correspondences, but unfortunately in this case, the things being compared are hopelessly complex and highly variable, even within a major taxon. Gegenbaur's approach appears to be the least justified in that it entails a typological, class-based definition of a structure as a basis for homology. It therefore is ironic that Gegenbaur's homologies, supplemented by later workers, have been the most popular. What all of these studies lack is input from the phylogenetic relationships of amniotes. Must all of these structures be present in

some way in each group, or do some features characterize particular groups? Which similarities truly indicate homology? Is the absence of clear conchae in turtles primitive or derived, and how does it impact on hypotheses of homology in other amniotes? These and other questions can be addressed only when the detailed morphological information arising from similarity testing is examined for its congruence with phylogeny. The questions may still not be answered, but the issues will be in better focus and will highlight areas of future research.

#### A reanalysis of conchal homologies

The following discussion begins with an analysis of the ontogeny of the cartilaginous anlage of the nasal capsule, their timing of development, and their topographic relationships. Birds will be used to introduce both the structures and the issues involved, and then successively more basal groups of extant amniotes will be analyzed in these terms. Similarities in these features will be summarized, and finally, the congruence of the similarities with amniote phylogeny will be tested.

*Birds.* The various regions of the adult nasal capsule in extant archosaurs (described above) have their developmental origins in various somewhat independent anlage, either as mesenchymatous condensations or as chondrification centers. Although there is considerable variation within birds as to the precise details of the associations of these anlage, it is clear that the major structures of the nasal capsule (e.g., the conchae) are formed by various combinations of 1) the parietotectal cartilage, 2) paranasal cartilage, and 3) lamina orbitonasalis (= planum antorbitale) (Fig. 19). Generally in birds, the nasal septum derives from the trabecula communis, the tectum nasi from the septum and parietotectal cartilage, and the paries nasi from the parietotectal and paranasal cartilages; the rostral and middle conchae arise from the parietotectal cartilage, and the caudal concha from the paranasal and parietotectal cartilages (see also de Beer and Barrington, '34; Müller, '61; Macke, '69). Given the remarkable conservation of the basic form and organization of the chondrocranium over vertebrates (de Beer, '37; Thorogood, '88), there is the prospect that these components of the nasal capsule will provide reliable guides to the homology of the conchae.

It is not quite this simple, however, because there has been considerable debate as

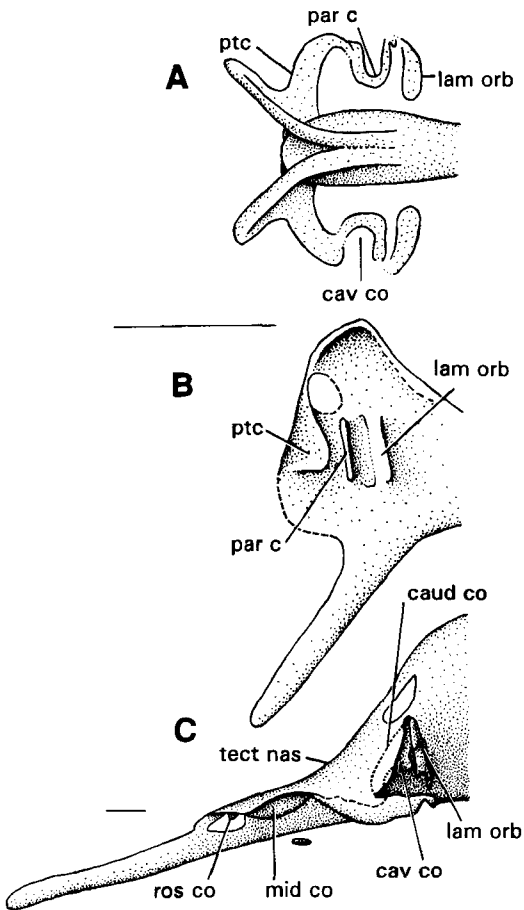


Fig. 19. *Anas platyrhynchos*. A) Dorsal and B) left lateral view of rostral part of chondrocranium of 8.5-day embryo, showing the origin of the parietotectal cartilage, paranasal cartilage, and lamina orbitonasalis. C: Rostral part of chondrocranium of 15-day embryo of same species in left lateral view, showing further development of these structures, including the nasal conchae. A and B modified after de Beer and Barrington ('34); C is camera lucida drawing of cleared-and-stained specimen. Scale bars = 1 mm.

to the independence of these anlage and the significance of independence (de Kock, '87). In fact, it has become almost mandatory in the primary literature to report whether or not the anlage appear as independent entities. For birds, de Beer and Barrington ('34), Slabý ('52), Macke ('69), and Goldschmid ('72) described the lamina orbitonasalis and paranasal cartilage as appearing in isolation, and Frank ('54), May ('61), and Toerien ('71) reported that at least the paranasal cartilage is independent. On the other hand, Cromp-

ton ('53), Engelbrecht ('58), and Vorster ('89) reported that virtually none of the elements have true independence. Resolution of this conflicting evidence is difficult. Because the nasal capsule forms relatively rapidly in birds (Vorster, '89), it is conceivable that denser ontogenetic series would reveal independent anlage in all taxa. Perhaps more importantly, the "independence" issue is probably peripheral to the question of conchal homologies. It may not be particularly important whether anlage appear in isolation or as outgrowths of other structures. Instead, independence may have to do more with the patterning provided by other tissues (e.g., the developing nasal epithelium, etc.) such that shifts in epithelial folding or even in the timing of neural crest migration may alter epitheliomesenchymal interactions enough to affect the "independence" of an anlage. What clearly is important is whether the various components are present or absent and what their form is. For example, although Frank ('54) could identify a separate paranasal cartilage in *Struthio camelus* whereas Müller ('61) could not in *Rhea americana*, the form of the caudal concha is very similar in these birds. Similarly, the absence of both the paranasal cartilage and caudal concha in *Euplectes orix* (Engelbrecht, '58) and *Melopsittacus undulatus* (de Kock, '87) is clearly a significant association. Thus, regardless of their status as "independent," the contributions of the anlage to the nasal conchae are important data.

As indicated above, in most birds the caudal concha forms at or very near the junction of the paranasal and parietotectal cartilages, later reaching caudally to the lamina orbitonasalis. The concha is formed mostly by the paranasal cartilage, which projects medially into the nasal cavity proper as a cup-shaped, hemispherical swelling. The caudal concha is concave laterally and encloses an extracapsular cavity, the cavum conchae (Figs. 8, 10A, 19). The aditus conchae leads into the cavum and is usually near the paranasal-parietotectal juncture, although in *Struthio camelus* it is apparently completely within the paranasal cartilage (Frank, '54); whether the aditus faces laterally or more rostrally is probably a function of the size of the eye (see above). The avian middle concha is a derivative of the dorsolateral edge of the parietotectal cartilage, projecting ventromedially and exhibiting a variable amount of scrolling. Although Slabý ('51) and Müller ('61) regarded the middle concha as taking its origin from the

juncture of the parietotectal and paranasal cartilages, Toerien ('71) clearly showed that this association of the middle concha with the paranasal cartilage is a secondary phenomenon, appearing late in ontogeny. In fact, in many birds the middle concha eventually extends caudally, ventral to the caudal concha, to reach the region of the lamina orbitonasalis (Figs. 9, 19; Frank, '54; Fourie, '55; May, '61). The rostral concha is formed in probably all birds by the parietotectal cartilage (Müller, '61).

The pattern of the timing of development of the nasal cartilages and conchae is available for a number of avian species. This pattern is reasonably consistent, although because nasal development is so rapid and age-sampling is rarely complete, often more than one structure seems to appear simultaneously (of course, simultaneous appearance may well occur in some cases). The order of development is derived from original study of *Anas platyrhynchos* and *Gallus gallus* and information gleaned from the following studies: de Beer and Barrington ('34), Brock ('37), Crompton ('53), Frank ('54), Engelbrecht ('58), Müller ('61), Macke ('69), Toerien ('71), and Goldschmid ('72). The nasal septum is always the first to form. The next structure to form is variable in the birds studied but usually is one or more of the following: lamina orbitonasalis, paranasal cartilage, parietotectal cartilage (most workers included the caudal concha with the paranasal cartilage). The middle concha always formed after these, and the rostral concha was always the last to appear.

The topographic relationships of these structures are very consistent in birds. The caudal concha from the beginning is located at the caudal portion of the nasal cavity proper, just dorsal to the caudal portion of the choana. Ramus lateralis nasi takes a similar course and in a very few birds (see de Beer, '37) passes through a foramen epiphaniale just dorsal to the aditus conchae. The caudal concha is always attached or next to the lacrimal bone. The middle concha extends for much of the length of the choana. The nasolacrimal duct opens into the choana just ventral to the middle concha.

*Crocodylians.* Fewer data are available for extant crocodylians, and the following discussion draws heavily on original study of ontogenetic series of *Alligator mississippiensis* and also the work of Meek ('11), Shiino ('14), Bertau ('35), and Klembara ('91). Despite the

transformation that takes place during ontogeny, the same basic components of the nasal capsule observed in birds are also present in crocodylians. The tectum nasi is formed by the nasal septum and parietotectal cartilage, and the paries nasi by the parietotectal and paranasal cartilages. Unlike most birds, there is a solum nasi rostral to the fenestra basalis, formed by the septum, lamina transversalis rostralis, and paraseptal cartilage (Klembara, '91).

The concha initially is formed at the juncture of the paranasal and parietotectal cartilages, and eventually the lamina transversalis rostralis also contributes to the concha (i.e., its rostromedial limb; see above). At first, it projects caudodorsomedially into the nasal cavity proper but later rotates into its adult position. The concha encloses an extracapsular cavity (cavum conchae) laterally (at least in embryos or young animals), and the aditus conchae is elongate (Fig. 15). The preconcha is clearly a rostral portion of the concha that has become somewhat separated by the formation of the preconchal sinus (probably in association with snout elongation) and is not a separate derivative of one of the main cartilages (Shiino, '14). As a result, Bertau ('35) was correct in arguing that the concha and preconcha must be considered together as a unit when discussing conchal homologies, and hereafter "crocodylian concha" will include the preconcha. The postconcha forms mostly from the paranasal cartilage, with the lamina orbitonasalis contributing to it caudally. Development of the postconcha is complex. Originally it is a cartilaginous shell (concave laterally) that thickens and then, according to Shiino ('14), begins to form an internal cavity via resorption; later, an intracapsular epithelial diverticulum (the post-turbinal sinus) penetrates the postconcha, inflating it into an air-filled, cartilaginous bubble that is concave both medially and laterally.

The order of appearance of the various capsular structures is derived from my studies of *Alligator mississippiensis*. As in birds, the nasal septum is the first structure to appear. The paranasal cartilage, parietotectal cartilage, and lamina transversalis rostralis arise together very close in time, the first two forming the vast majority of the concha and the third also contributing later in ontogeny. The lamina orbitonasalis appears next, forming a separate chondrification. The beginnings of the postconcha develop next, fol-

lowed by segmentation of the concha into preconcha and the definitive concha.

The topographical relationships (Fig. 16) become extensively transformed during ontogeny owing to elongation of the snout and nasal rotation (see above). The postconcha is located completely behind the primary choana and attaches to the prefrontal, lacrimal, and palatine. The concha forms directly opposite the primary choana, and although it often extends caudomedially far beyond the choana in adults (especially in *Alligator mississippiensis*), the limbs of the "root" of the concha (see above) retain their embryonic association with the primary choana. In *Alligator* but not *Crocodylus* spp. (Bertau, '35), ramus lateralis nasi passes through a foramen epiphaniale located dorsolaterally, just dorsal to the aditus conchae (Fig. 15). The nasolacrimal duct opens into the nasal cavity proper just ventral to the preconcha. The ascending ramus of the maxilla develops rostral to the aditus and cavum conchae in association with that portion of the lamina transversalis rostralis contributing to the concha (Fig. 15). Early in ontogeny the lacrimal bone is attached laterally to the concha just caudal to the aditus conchae (Fig. 15; see also Shiino, '14; Klembara, '91), but later, with rostral expansion of the postconcha and nasal rotation, the lacrimal attains a more dorsomedial position such that only the rostral tip reaches the conchal region.

*Squamates.* The situation in squamates is relatively simple because they have only a single concha or none at all. Parsons ('59) effectively refuted the homology proposed by Hoppe ('34) of the "Lippe am Choanengang" of squamates with the rostral concha of *Sphenodon punctatus*, suggesting, in effect, that it fails the similarity test of homology. Squamates in general have the same components and basic organization of the nasal capsule as in archosaurs (e.g., parietotectal cartilage, paranasal cartilage, lamina orbitonasalis, lamina transversalis rostralis, etc.), although occasionally the paranasal cartilage is absent (e.g., Agamidae, possibly all snakes; Malan, '46; Bellairs and Kamal, '81). These components all arise within a short span of time, except for the nasal septum which precedes them (Kamal and Abdeen, '72). According to Kamal and Abdeen ('72; see also Zada, '81; Bellairs and Kamal, '81), the concha is formed primarily by the paranasal and parietotectal cartilages, with the lamina transversalis rostralis also contributing (as in *Alligator missis-*

*sippiensis*, see above). The concha projects medially into the nasal cavity and in general is directly dorsal to the choana or choanal tube (Fig. 18A; see Malan, '46; Bellairs and Boyd, '50). Laterally, there is almost always a well-developed aditus and extracapsular cavum conchae. A foramen epiphaniale transmitting the ramus lateralis nasi is normally present just dorsal to the aditus conchae. The lacrimal is reduced or absent in many squamates, and any particular association of this bone with the concha could not be discovered. As already indicated, the nasolacrimal duct opens apomorphically in squamates in association with the vomeronasal organ.

*Sphenodon.* *Sphenodon punctatus* appears to have the same basic components of the nasal capsule as in other extant diapsids (Bellairs and Kamal, '81). Although Fuchs ('08) and Pratt ('48) identified only a single concha, Hoppe ('34) reported the presence of two conchae. The precise ontogeny of these conchae is unclear in the literature, particularly with regard to the cartilaginous components discussed above. Bellairs and Kamal ('81) labeled the cartilage forming both conchae as the paranasal cartilage and suggested that the two structures together may represent a single concha. The caudal concha is the larger of the two and is located more caudally, opposite the caudal portion of the choana, whereas the rostral concha is a more horizontal ridge reaching almost to the vestibule (Fig. 18B; Hoppe, '34). Neither concha has a laterally open cavum conchae. According to Malan ('46), there is a foramen epiphaniale in the region of the caudal concha.

*Turtles.* The ontogeny of the nasal capsules is poorly known in turtles. De Beer ('37) identified all the familiar components of the capsule (e.g., paranasal cartilage, parietotectal cartilage, etc.), but these identifications were based on the study of a "fully formed" chondrocranium in which the various components are completely continuous. Shaner ('26) identified two isolated nasal cartilages that appear after the septum, a "paranasal cartilage" (which is clearly a paraseptal, not paranasal, cartilage) and a "lateral nasal cartilage" (which could be either parietotectal or paranasal or both). Turtles lack any named concha. The laterale Grenzfalte (Fig. 18C) has occasionally been suggested to be a rudimentary concha (e.g., Gegenbaur, 1873), and Bellairs and Kamal ('81) refer to it as a "conchal ridge." In general, it runs for most of the length of the nasal cavity proper



(Parsons, '70). Possibly only in *Testudo graeca* does the laterale Grenzsfalte project far into the nasal cavity and have any resemblance to a concha; it is a poorly developed structure in most turtles (Parsons, '70). De Beer ('37) and Bellairs and Kamal ('81) report a foramen epiphaniale in turtles.

**Mammals.** The nasal capsules of mammals are extraordinarily complex, with a large number of named turbinals (Fig. 18D; Paulli, 1900; Peter, '06; Plate, '24; Matthes, '34; de Beer, '37; Negus, '58; Starck, '67; Moore, '81; Novacek, '93). As in other amniotes, the nasal capsule of mammals is reported to develop from the same basic components (e.g., paranasal cartilage, parietotectal cartilage, lamina orbitonasalis, lamina transversalis rostralis, etc.; see de Beer, '37; Starck, '67; and Moore, '81). The ontogeny of the turbinals and crista semicircularis is as follows (Fig. 18D; see de Beer, '37; Starck, '67): 1) The crista semicircularis forms at the junction of the paranasal and parietotectal cartilages; 2) the ethmoturbinal (i.e., "first" ethmoturbinal) forms at the junction of the lamina orbitonasalis and paranasal cartilage; 3) the maxilloturbinal is formed by an inrolling of the ventral edge of the rostral portion of the paries nasi (presumably parietotectal or paraseptal cartilage); 4) the nasoturbinal forms as a ventral process of the tectum nasi (presumably also parietotectal in origin); and 5) the atrioturbinal, when present, is either the rostral part of the maxilloturbinal (Starck, '67) or the inrolled margin of the fenestra narina (de Beer, '37). None of them enclose a lateral cavity early in ontogeny, and thus do not adhere to de Beer's ('37) definition of a concha. The nasal septum is the first structure to form, followed by the paranasal cartilage, parietotectal cartilage, and lamina orbitonasalis at about the same time; the crista and ethmoturbinal form next, and the other turbinals form much later (de Beer, '37).

The topographical relationships of these structures are somewhat variable and the discussion is based on study of *Oryctolagus cuniculus* (Fig. 18D) and *Homo sapiens*, and information extracted from the literature. The crista semicircularis is more or less directly opposite the rostral end of the nasopharyngeal duct (primary choana), and the ethmoturbinal is slightly caudal to it, the others being more rostrally situated. Ramus lateralis nasi passes through a foramen epiphaniale in virtually all major clades of extant mammals, including monotremes (Zeller,

'89); the foramen is situated just dorsal to the crista semicircularis (de Beer, '37). Although the nasolacrimal duct opens into the nasal cavity ventral to the maxilloturbinal in *Homo* and some others, this is usually regarded as a secondary opening, a derived character relative to the more rostral opening within the fenestra narina (see Starck, '67, and nasolacrimal duct discussion above). The lacrimal contacts the crista semicircularis (which ossifies as the uncinat process of the ethmoid) in *Oryctolagus* and is very close in *Homo*.

**The Similarity test.** The mode of development of the various nasal conchae and turbinals among amniotes exhibits some clear patterns. For example, the avian caudal concha, crocodilian concha, squamate concha, and mammalian crista semicircularis form at or very near the juncture of the paranasal and parietotectal cartilages, and the lamina transversalis rostralis contributes to the concha of squamates and crocodilians (the situation in turtles and *Sphenodon punctatus* is unclear). The crocodilian postconcha and mammalian ethmoturbinal both form from contributions of the paranasal cartilage and lamina orbitonasalis. Although no one has ever suggested their homology, the avian middle concha and mammalian nasoturbinal are both outgrowths of the dorsolateral portion of the tectum nasi. The mammalian maxilloturbinal is usually regarded as having the greatest similarity to the avian middle concha (Table 2), but the mammalian structure forms in a much different manner (as a continuation of the ventral margin of the paries nasi). As most other workers dating back to Gegenbaur (1873) have mentioned, the avian rostral concha exhibits no morphological similarities with structures of other amniotes, the only possibility being with the mammalian atrioturbinal (but here again they form from different components).

With regard to the timing of development, in perhaps all extant amniotes, the paranasal cartilage, parietotectal cartilage, and lamina orbitonasalis appear very early and at about the same time. The structures they combine to construct thus also appear very early. For example, the avian caudal concha, crocodilian concha, squamate concha, caudal concha of *Sphenodon punctatus*, and mammalian crista semicircularis all form very early. The mammalian ethmoturbinal also forms early. Although it is occasionally regarded as the first concha to appear in birds (e.g., Parsons,

'59; Gauthier et al., '88a), the avian middle concha always forms *after* the caudal concha. The avian rostral concha, crocodilian postconcha, rostral concha of *Sphenodon*, and mammalian maxilloturbinal (Zeller, '89) are also later-appearing structures.

The following structures enclose a lateral, extracapsular cavity, usually called the *cavum conchae*: the avian caudal concha, the crocodilian concha, and the squamate concha. There is no extracapsular *cavum* in the caudal concha of *Sphenodon punctatus*, the laterale Grenzfalte of turtles, or the crista semicircularis of mammals. The crocodilian postconcha also encloses a very large cavity, but this postconchal cavity arises from an intracapsular sinus (the post-turbinal sinus) and remains intracapsular.

The following structures are situated directly opposite the caudal portion of the (primary) choana: the avian caudal concha, avian middle concha, crocodilian concha, squamate concha (in most cases), the caudal concha of *Sphenodon punctatus*, the laterale Grenzfalte of turtles, and the mammalian crista semicircularis. The crocodilian postconcha and mammalian ethmoturbinal are caudal to it. All other structures are rostral to the (primary) choana, although in *Sphenodon* and most birds the choana is long enough that the rostral concha of the former and middle concha of the latter also are opposite the choana.

Ramus lateralis nasi passes through a foramen epiphaniale just dorsal to the following structures: avian caudal concha (although the vast majority of birds lack the foramen epiphaniale), crocodilian concha (at least in *Alligator mississippiensis*), squamate concha, possibly the caudal concha of *Sphenodon punctatus*, and the mammalian crista semicircularis. Turtles also have a foramen epiphaniale but its relationship to the nasal structures are uncertain. In birds, crocodilians, and squamates the foramen is just dorsal to the aditus conchae. De Beer and Barrington ('34; see also de Beer, '37) used this character as a landmark for determining homologies, and numerous ornithologists (e.g., Lang, '55; Müller, '61; Goldschmid, '72; de Kock, '87; Weber, '90) objected because the foramen is so rarely present in birds. Weber ('90) is correct in noting that, based on in-group comparison, presence of the foramen is probably not primitive for neornithine birds. Given its distribution in nonavian amniotes, its general absence in birds must be regarded

as an apomorphy. Most birds also have an apomorphic position of the nasal gland relative to other amniotes. Since ramus lateralis nasi carries the autonomic nerves to the nasal gland, it is possible that there is some causal association between migration of the nasal gland and loss of the foramen epiphaniale.

Gegenbaur (1873; see also Dieulaufé, '05) used the position of the nasolacrimal duct as a topographic criterion in his homologies, because the duct opens just ventral to the avian middle concha, crocodilian concha (actually the preconchal portion), and the mammalian maxilloturbinal. Gegenbaur (1873) did not indicate which mammals he sampled, but it is likely that he was drawing on human anatomy, because in humans (and some other mammals, see Starck, '67) the nasolacrimal duct indeed opens below the maxilloturbinal. However, as mentioned above, this position is probably an apomorphy within Mammalia, and a more rostral ostium having no particular association with the maxilloturbinal is likely the primitive mammalian condition. In fact, the nasal ostium of the nasolacrimal duct does not have a particularly consistent position in amniotes, other than that observed in birds and crocodilians.

The lacrimal bone attaches to or is very close to the avian caudal concha, crocodilian concha (at least prior to nasal rotation), and mammalian crista semicircularis. The lacrimal is absent in turtles and *Sphenodon punctatus* and is generally very reduced or absent in extant squamates.

In summary, based on the above 1:1 correspondences in ontogenetic development and topographic relationships of morphological structures, the following hypothesis of homology passes the similarity test: avian caudal concha, crocodilian concha (including the pre-concha), squamate concha, caudal concha of *Sphenodon punctatus*, and mammalian crista semicircularis. In all these cases, the structure 1) forms at or very near the juncture of the paranasal and parietotectal cartilages (unknown for *Sphenodon*), 2) is the earliest conchal structure to form, 3) is situated (at least early in ontogeny) directly opposite the caudal portion of the (primary) choana (also true for the laterale Grenzfalte of turtles), 4) is just ventral to the foramen epiphaniale which transmits ramus lateralis nasi (the foramen is rare in birds but the nerve takes the same course), and 5) contacts the lacrimal bone (the bone is absent in turtles, *Sphenodon*,

and reduced or absent in most squamates). Furthermore, in birds, crocodilians, and squamates, the structure encloses an extracapsular sinus, the *cavum conchae*. For the sake of discussion, this variably named structure will be termed the "primary concha," borrowing the usage from Peter ('06). The crocodilian postconcha and mammalian ethmoturbinal pass the similarity test of homology on the basis of being 1) formed by both paranasal cartilage and lamina orbitonasalis and 2) located caudal to the primary choana. No other structures have enough 1:1 correspondences to survive the similarity test.

**The Congruence Test.** The congruence test requires that the putative homolog characterize a monophyletic group. At first glance, this is clearly the case with regard to the primary concha—the primary concha characterizes and is indeed a synapomorphy of Amniota. However, turtles present a problem because they lack a structure that passed the similarity test. On the basis of strict parsimony and assuming monophyly of Sauropsida, two equally parsimonious solutions obtain: 1) Absence of a primary concha in turtles is a reversal (i.e., a derived absence) such that presence of a primary concha is indeed the ancestral amniote condition (Fig. 20A), or 2) the absence in turtles is truly the primitive condition such that a very similar structure arose independently in Mammalia and Diapsida (Fig. 20B).

Strictly in cladistic terms, these two alternatives cannot be resolved. The second alternative might seem more likely in that the mammalian crista semicircularis simply "looks different" from the structure in diapsids: The crista is inconspicuous and is literally "overshadowed" by the much more prominent turbinals surrounding it (Fig. 18D). However, the numerous detailed similarities between the crista and the structures in diapsids are compelling when taken together, and on this basis it seems likely that the original hypothesis that these structures are homologous and characterize Amniota is correct. The nasal cavity of extant turtles is apomorphically greatly reduced in size relative to other amniotes and even relative to the Triassic turtle *Proganochelys quenstedti* (Gaffney, '90). Given this apomorphy and the numerous other craniofacial apomorphies characterizing extant turtles (Gaffney and Meylan, '88), it is not unreasonable to regard the absence of the primary concha in turtles as a derived absence (Fig. 20A). Gauthier et

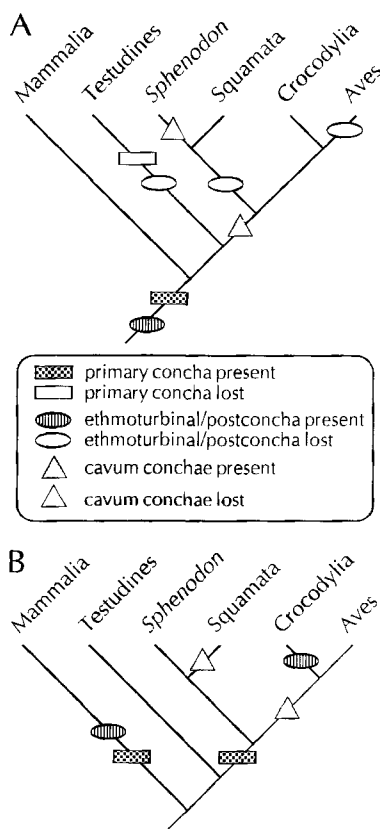


Fig. 20. Cladograms summarizing the congruence of hypotheses of homology of nasal conchae and associated structures with the phylogeny of extant Amniota. **A:** Cladogram favoring losses over parallelisms. **B:** Cladogram favoring parallelisms over losses.

al. ('88a, p. 127), who also discussed the problems presented by turtles in establishing conchal homologies, suggested that the laterale Grenzsfalte might be a primary concha, "albeit of a sort peculiar to turtles." The analysis presented here offers no support either way as to the status of the laterale Grenzsfalte.

The primary conchae of extant diapsids other than *Sphenodon punctatus* exhibit an extracapsular cavity, the *cavum conchae*. Its absence in *Sphenodon* presents precisely the same problem as turtles did above. Presence of a *cavum* may characterize Diapsida, such that its absence in *Sphenodon* is scored as a derived loss (Fig. 20A), or, equally parsimonious in cladistic terms, *Sphenodon* may retain the truly primitive condition (also manifested by mammals) such that a *cavum* con-

chae is derived independently in squamates and archosaurs (Fig. 20B). Deciding between these two alternatives on morphological grounds is not as easy as in the previous situation, and largely depends on whether one prefers reversals or parallelisms (i.e., accelerated or delayed transformation, respectively, in the jargon of character optimization; see Swofford and Maddison, '87). On the strength of the similarities of the primary conchae in squamates and archosaurs, my opinion is that a cavum conchae was present in the ancestral diapsid and has been lost in *Sphenodon* (Fig. 20A). *Sphenodon* remains poorly known with regard to many of the important features, and new studies could have an impact on this issue.

Finally, it is impossible with the data at hand to deduce whether the ancestral amniote enclosed a cavum within its primary concha. Without outgroups possessing homologous primary conchae, presence and absence of a cavum conchae cannot be polarized. It is equally parsimonious to regard either mammals or diapsids as having the primitive condition.

Turning to the homologies of the other structures, the crocodilian postconcha and mammalian ethmoturbinal passed the similarity test of homology (although barely so, and only on two criteria). This hypothesis clearly fails the congruence test. If the postconcha and ethmoturbinal were homologous (a possibility raised by de Beer and Barrington, '34; Table 2), then this homology would have to characterize Amniota, necessitating independent loss in turtles, lepidosaurs, and birds (Fig. 20A). Thus, on the basis of parsimony, these structures are judged as independent acquisitions and nonhomologous (Fig. 20B). Likewise, most of the other conchal structures that over the years have been regarded as homologous in various amniotes are judged on similar grounds as neomorphs in this analysis: the avian rostral concha, avian middle concha, crocodilian postconcha, rostral concha of *Sphenodon punctatus*, laterale Grenzfalte of turtles, and all the mammalian turbinals. Only a single structure, the primary concha, can be homologized between any of the major clades.

The osteological correlates of the nasal capsule and conchal structures are remarkably few. Although mammals and a few avian species ossify some or all of their conchae, this is not the case in extant nonavian sauropsids and indeed the majority of birds. The

presence of various bony ridges within the nasal cavities of several nonmammalian therapsid synapsids have suggested to many workers that turbinals predate the origin of Mammalia (reviewed by Miao, '88; see also Hillenius, '92, '94), but these are absent from basal synapsids (Romer and Price, '40). A concerted—often less than conservative—effort to find such correlates in Sauropsida revealed no consistent bony features that could be used to infer conchae in dried skull or fossil material. The only indication of the cartilaginous nasal capsule is the presence in many fossil archosaurs of a ridge for the paries nasi on the palatine bone in the vicinity of the choana (see Witmer, '94, in press). Thus, the congruence of the above hypotheses of homology with the phylogeny of both extinct as well as extant amniotes cannot be tested adequately.

In summary, the Gegenbaur/Matthes scheme, although the most popular and repeated hypothesis for conchal homologies among amniotes, is no longer tenable—it fails both the similarity and congruence tests. The only component of it that survives is the homology of the squamate and crocodilian conchae. Ironically, both Matthes ('34, p. 926) and Müller ('61, p. 253) regarded the homology of the avian middle concha and mammalian maxilloturbinal as the best-supported aspect of the hypothesis and “undisputed” (they even both used “unbestritten”), yet both structures prove to be neomorphs. On the other hand, the hypothesis of homology advocated here for the primary conchae among amniotes is precisely that suggested by de Beer ('37; see also de Beer and Barrington, '34). It differs from de Beer's in that the similarity tests involve many more criteria and de Beer never tested congruence. The absence of a congruence test led him to suggest the homology of structures that are here regarded as neomorphs. Although some uncertainties remain as a result of conflicting information from turtles and *Sphenodon punctatus*, the one point about which there is absolutely no doubt is that the primary conchae of extant archosaurs (i.e., the avian caudal concha and crocodilian concha) are homologous.

#### *Antorbital cavity*

The antorbital cavity is a little different from the other structures whose homology is being tested here because it is a compartment rather than a bone or soft-tissue element. But since the significance (even exis-

tence) of this cavity has not been appreciated, it is discussed here. A simple definition of antorbital cavity was offered earlier and applied to both birds and crocodilians. It is the space rostral to the orbit, external to the nasal capsule, and internal to the surface of the snout. But definitions, when applied typologically, can lead to erroneous interpretations as was just demonstrated in the case of Gegenbaur's (1873) conception of a Nasenmuschel. The question then becomes, what is the history of the antorbital cavities of extant archosaurs? That is, are they homologous? In both birds and crocodilians, the antorbital cavity is a large space readily discernable in dried skulls. It is surrounded by the maxilla, lacrimal, and palatine, with the jugal and prefrontal also taking part in birds and crocodilians, respectively. The cavities in both taxa have a variety of contents: the nasolacrimal duct, the nasal gland and/or its ducts (although the gland sometimes fails to reach the cavity in some crocodilians), the maxillary neurovasculature, ramus lateralis nasi, often a portion of the dorsal pterygoideus musculature, and a paranasal air sac.

The antorbital cavity is virtually absent in nonarchosaurian sauropsids, because the cartilaginous nasal capsule in general completely fills the preorbital portion of the snout (Plate, '24; Matthes, '34; Parsons, '59). Of course many of the same structures (e.g., ramus lateralis nasi, the nasolacrimal duct, etc.) must pass rostrally from the orbit between the nasal capsule and roofing bones, but in lepidosaurs and turtles they pass through a very small potential space. It might seem justifiable to regard the antorbital cavity as present but very small in nonarchosaurian sauropsids. However, in comparison, the cavity in extant archosaurs is so well developed and so well demarcated osteologically that it seems overly pedantic to consider lepidosaurs and turtles as having an antorbital cavity. Most mammals, on the other hand, have an extracapsular space, often accommodating many of the same structures as in archosaurs; this space is best developed in prenatal material (Mihalkovics, 1898), with many of the contents of the space later becoming enclosed within bone.

Although the resemblance is not great, one could consider the mammalian extracapsular space and the antorbital cavities of birds and crocodilians as passing the similarity test of homology. According to the phylogeny of extant amniotes, however, it is more parsimoni-

ous to regard the cavities as having been acquired independently in Mammalia and Archosauria (i.e., no homology); homology would require the less parsimonious assumption of independent loss in Testudines and Lepidosauria. In either case, the antorbital cavities of birds and crocodilians are judged as homologous.

If this hypothesis is also congruent with archosaur phylogeny, then the osteological correlates of the antorbital cavity will be present in at least the basal members of all the major clades of archosaurs, both fossil and extant. These osteological correlates were mentioned above: 1) a cavity surrounded by a particular group of bones, 2) the course of the nasolacrimal canal, 3) a muscular fossa on the palatine, and 4) evidence for the position of the cartilaginous paries nasi (e.g., crests associated with the choanal portion of the palatine bone). The homology of most of these correlates was demonstrated in previous sections.

When fossil archosaurs are sampled for these features (see Witmer, in press), it becomes apparent not only that the presence of a large antorbital cavity is indeed an ancestral feature of Archosauria (affirming its homology in extant forms), but also that extant birds more closely approximate the primitive archosaurian condition (Witmer, '87, '90, '92, in press). In birds, the antorbital cavity is open laterally in the skull via the external antorbital fenestra, and the maxilla and lacrimal usually exhibit fossae associated with the cavity (i.e., antorbital fossae; Fig. 7). This basic morphology is widely distributed in fossil archosaurs, including basal crocodylomorphs (e.g., *Sphenosuchus acutus*, Walker, '90; *Protosuchus richardsoni*, Crompton and Smith, '80; see Witmer, in press). In fact, antorbital fenestrae and fossae are traditionally regarded as diagnostic features of Archosauria (e.g., Romer, '66; Carroll, '88; among many others). Thus, extant crocodilians are apomorphic in secondarily closing the external antorbital fenestra, while retaining the antorbital cavity (Witmer, in press).

#### Air sacs

##### Historical background

The homology of the paranasal air sacs of extant amniotes has received little formal treatment in the literature. Gegenbaur (1873) briefly considered the possibility that the avian antorbital sinus is homologous to the crocodilian postconchal sinus, but rejected it because, in effect, the former is extracapsular

whereas the latter is intracapsular. Solger (1876), however, retained the possibility of their homology, suggesting that perhaps in the ancestors of birds (or in early avian ontogeny) the sinuses were intracapsular, and became extracapsular during the course of phylogeny (or ontogeny) owing to regression of the cartilage. Matthes ('34) and Bertau ('35) sided with Gegenbaur (1873) in denying the homology. Bleicher and Legait ('32) suggested the homology of the avian antorbital and mammalian maxillary sinuses, but this idea was refuted by Stadtmüller ('36) and received little further attention. Otherwise, the only other issue receiving much analysis was the homology of the crocodilian paranasal sinuses to those of mammals. For example, Meek ('06, '11) homologized the crocodilian caviconchal sinus to the mammalian maxillary sinus. Bertau ('35) and Parsons ('70) dismissed this hypothesis with little discussion. In its place, Bertau ('35) suggested that the crocodilian caudolateral recess is homologous to the mammalian maxillary sinus, although this hypothesis was based entirely on the supposed homology of the crocodilian postconcha with the mammalian nasoturbinal (both of which were regarded as neomorphs in a previous section).

#### Extant amniotes

As described above, birds have a single epithelial extracapsular diverticulum of the nasal cavity, whereas crocodilians have five different types of diverticula. The questions remain, which, if any, of the crocodilian diverticula are homologous to the avian antorbital sinus, and do any other amniotes have such a sinus? Three main criteria will be used to assess the similarity of these air sacs: 1) the timing of appearance of the diverticulum, 2) the position and topographic relationships of the sinus ostium, and 3) the topographic relationships of the air sac to surrounding structures. Birds and then crocodilians will be analyzed first, followed by a discussion of the status of paranasal air sinuses in other amniotes. Any hypotheses of homology surviving the similarity test then will be tested for congruence with amniote and archosaur phylogeny (including extinct taxa).

*Birds.* The avian antorbital sinus appears very early in ontogeny, during the first third of embryonic development in the birds studied here (see also Lurje, '06; Schüller, '39; Bremer, '40). The ostium of the antorbital sinus has the following almost invariant

topographic relationships (Figs. 8, 9, 10A): 1) just ventral or slightly caudoventral to the caudal concha and rostral to the lamina orbitonasalis (later in ontogeny, with caudal expansion of the middle concha ventral to the caudal concha, the ostium may come to lie between the two conchae), 2) just ventral to the olfactory epithelium (Bang, '71), 3) directly opposite (i.e., dorsal to) the caudalmost portion of the choana, 4) just medial to the maxillary nerve and accompanying vessels (the diverticulum usually eventually surrounds the nerve), and 5) well caudal to the opening of the nasolacrimal duct. The sinus expands nearly to fill the antorbital cavity; among all the contents of the cavity, the antorbital sinus is the most voluminous. Within the antorbital cavity, the diverticulum in most birds (Bang, '71) penetrates the aditus and cavum conchae and fills (pneumatizes) the caudal concha. The lacrimal bone forms just caudal to the sinus in the region of the aditus, and later assumes a relatively more rostral position owing to pressure from the orbital contents and subsequent caudal growth of the nasal capsule (see above). The sinus is situated just lateral to the nasal capsule, just deep to the skin, and is lodged rostrally in the maxillary bone which is usually pneumatized by the sinus. The bones comprising the external antorbital fenestra (see above) form initially as splints surrounding the antorbital sinus and associated with particular portions of the nasal capsule. As a result, the fenestra is viewed correctly as an embryonic fontanelle that never closes rather than as a "hole" that opens up ontogenetically. Finally, the nasolacrimal duct passes dorsomedially around the sinus, the two coming into direct contact for much of the course of the duct.

*Crocodilians.* In crocodilians, the only one of the diverticula that consistently appears during embryonic development is the caviconchal sinus. In *Alligator mississippiensis*, the sinus arises just after the first third of the embryonic period, at about the same time the conchal structures are beginning to form. The caviconchal sinus ostium has the following topographic relationships (Figs. 10B, 12C-E, 17): 1) just caudoventral to the root of the concha, 2) immediately ventral to the olfactory epithelium (Bertau, '35), 3) directly opposite the caudalmost portion of the primary choana, and 4) caudal to the opening of the nasolacrimal duct. Early in ontogeny, the caviconchal sinus projects laterally beneath

(*Alligator*; Figs. 15, 17) or perforates (*Crocodylus* spp.) the paries nasi and is directed toward the maxillary nerve and vessels; it eventually reaches the neurovasculature where it expands, perhaps following the heterogeneity provided by these structures. The sinus expands within the antorbital cavity in the area of the fontanelle between the developing maxilla, lacrimal, nasal, and prefrontal, here named the fonticulus antorbitalis (Fig. 15). The caviconchal sinus occupies the cavum conchae, with the fonticulus antorbitalis progressively closing around the aditus conchae. The ascending ramus of the maxilla subsequently closes the fonticulus, probably in association with nasal rotation. Most of the caviconchal sinus eventually occupies a bony cavity within the maxilla, the caviconchal recess, passing through a bony aperture (Fig. 12C-E) that forms around the diverticulum as it expands. The nasolacrimal duct passes dorsomedially over the caviconchal sinus, the two contacting each other briefly (at least in adults) before the latter enters the caviconchal recess (Fig. 13).

The other paranasal air sinuses of crocodilians generally appear after hatching. Exceptions may include the caudolateral sinus in *Melanosuchus niger*, which seems to appear in late embryonic development (Bertau, '35), although the same sinus always appeared posthatching in the *Alligator mississippiensis* material studied here. Similarly, Meek (1893) described the formation of a maxillary cecal recess in a *Crocodylus porosus* embryo that was probably about one-half to two-thirds of the way through embryonic development. The postvestibular and prefrontal sinuses in *Alligator* do not appear until some time after the 1st week and several months posthatching, respectively. The caudolateral recess forms ventral to the postconcha and hence caudal to the concha and caviconchal recess ostium; it eventually pneumatizes the palatine bone in at least some alligatorids (Fig. 12C; see above for variations). As indicated earlier, the maxillary cecal recesses are very variable in number, always evaginating the lateral wall of the nasal cavity proper rostral to the concha; they usually are rostral to the nasolacrimal duct aperture but one or two may be caudal to it (Figs. 12E, 16). The postvestibular sinus ostium is within the maxillary bone caudal to the vestibule and well rostral to the opening of the nasolacrimal duct (Fig. 12C,D). The prefrontal sinus ostium is located at the caudomedial corner

of the nasal cavity proper and thus far caudal to all of the other structures mentioned here; it leads directly into the prefrontal bone (Fig. 12C,D).

*Summary of extant archosaurs.* Comparing crocodilians and birds, it is clear that the avian antorbital sinus shares a number of 1:1 correspondences with the crocodilian caviconchal sinus: 1) It forms very early in embryonic development; 2) the sinus ostium has virtually identical relationships to the homologous (primary) concha, olfactory epithelium, primary choana, and the aperture of the nasolacrimal duct; 3) the sinus has an intimate relationship with the maxillary neurovasculature; 4) the sinus is lodged within the antorbital cavity and is the largest of the contents of the cavity; 5) the sinus enters the cavum conchae; 6) the sinus is just rostral to the lacrimal bone where the latter borders the aditus conchae (at least early in crocodilian development); 7) the sinus occupies a large cavity within the caudal portion of the maxillary bone; and 8) the nasolacrimal duct contacts and passes dorsomedially over the sinus. Furthermore, the caviconchal sinus is the only sinus that has been found to be present in all extant crocodilian species that have been sampled for these attributes. Thus, the hypothesis of homology of the avian antorbital sinus and crocodilian caviconchal sinus passes the similarity test, whereas Solger's (1876) and Bertau's ('35) hypotheses fail the test.

*Lepidosauria.* Judging from the literature and my dissections, Lepidosauria in general (if not in toto) lack extracapsular paranasal air sinuses. Among the few workers who have identified them is Mihalkovics (1898) who labeled the extraconchal recess of *Lacerta agilis* as a "maxillary sinus." The extraconchal recess is an intracapsular space lined with nasal epithelium (Parsons, '70) that in some squamates (e.g., lacertids) is exposed by a deficiency in the capsular wall called the fenestra lateralis nasi. Although it may have the appearance of a paranasal sinus in some transverse sections (e.g., Mihalkovics, 1898, Fig. 14), it is clearly part of the nasal cavity proper. Even though Nemours ('30) could not find any such sinuses in his squamate material, he considered that they indeed were present on Mihalkovics' (1898) authority. The closest thing to a true paranasal air sinus in Lepidosauria is probably the recessus extracapsularis described for *Varanus niloticus* by Malan ('46) and figured for *V. monitor* by

Bellairs and Kamal ('81). This structure is similar to the one described by Mihalkovics (1898) in that it is clearly also part of the extraconchal recess, but here it almost reaches the cavum conchae and thus approaches the condition in birds and crocodilians (Malan, '46). However, its topographic relationships to surrounding structures are otherwise very different, and given the phylogenetic position of *Varanus* within Squamata (Estes et al., '88), it is clearly an apomorphy of the genus. Thus, Lepidosauria can be regarded as lacking a paranasal air sinus homologous to the one observed in birds and crocodilians.

**Turtles.** Mihalkovics (1898) also reported a "maxillary sinus" for turtles and was again echoed by Nemours ('30). This structure is clearly the recessus ducti nasopharyngei of Parsons ('59; see Fig. 18C). As its name implies, Parsons ('59) regarded this small epithelial cavity as deriving from the nasopharyngeal duct and not the nasal cavity proper. The recessus generally has a thick columnar-to-cuboidal epithelium rather than the thin squamous epithelium of the paranasal air sinuses of archosaurs. It does not pneumatize bone or have any osteological correlates in the material studied here or, judging from the photographs published by Gaffney ('79), probably any other turtles. It does resemble the archosaur sinus, however, in being located close to the juncture of the nasal cavity proper and the caudal border of the primary choana and in appearing before hatching. Since extant turtles lack unambiguous primary conchae, nasolacrimal ducts, and antorbital cavities (which were important landmarks in archosaurs), the status of the recessus ducti nasopharyngei as a potential homolog of the avian antorbital sinus and crocodilian caviconchal recess is problematic and can be regarded as having failed the test of similarity. Parsons ('70) denied its homology with the mammalian maxillary sinus.

**Mammals.** Of all the mammalian paranasal sinuses (Paulli, 1900), only the maxillary sinus has the potential to be homologous to the main paranasal sinus of extant archosaurs. The maxillary sinus appears earliest in ontogeny, prenatally in at least dogs, sheep, and humans, although the ethmoidal sinus sometimes appears at about the same time (Dieulafé, '05; Peter, '06). The maxillary sinus ostium is more or less opposite the primary choana (Fig. 18D). The ostium is cau-

dal or caudodorsal to the crista semicircularis (which is probably a primary concha); this relationship is actually a little different from archosaurs where the ostium is never at all dorsal to the primary concha, but it remains a potential resemblance. The maxillary nerve passes close to the ostium in *Oryctolagus cuniculus* and through the sinus in *Homo sapiens*. Finally, as its name implies, the sinus excavates the maxilla. Thus, given these 1:1 correspondences (and the homology of the crista semicircularis to the archosaur primary concha), the mammalian maxillary sinus, avian antorbital sinus, and crocodilian caviconchal sinus could be viewed as passing the similarity test of homology.

#### Congruence with extant amniote phylogeny

Congruence of these features within the context of extant amniote phylogeny reveals a complex pattern. The following structures are potentially homologous: the avian antorbital sinus, crocodilian caviconchal sinus, and the mammalian maxillary sinus. It should be noted that although it has been referred to above as the "mammalian" maxillary sinus, it reportedly is absent from extant monotremes and is apparently restricted to *Phascogalea cinereus* among extant Marsupialia where it has rather different topographic relationships and may not be homologous (Paulli, 1900; see also Moore, '81; Wible, '91; Novacek, '93). Taking monotremes and marsupials into account, the avian antorbital sinus and crocodilian caviconchal sinus are homologous, being congruent with other evidence that they comprise a monophyletic Archosauria, but the maxillary sinus of placental mammals and the paranasal air sinus of Archosauria are seen as independent acquisitions (Fig. 21).

#### Congruence with the phylogeny of extinct and extant amniotes

According to the above analysis, parsimonious application of Hennig's ('66) auxiliary principle argues for homology of the main paranasal air sacs of birds and crocodilians. However, given the uncertain status of the sinus in most nonarchosaurian amniotes, it would be reassuring to know that the sinus indeed characterizes all archosaurs and did not evolve independently in extant birds and crocodilians. Furthermore, consideration of other fossil amniotes may shed light on the status of the maxillary sinus of placental mammals and the recessus ducti nasopharyngei of turtles.



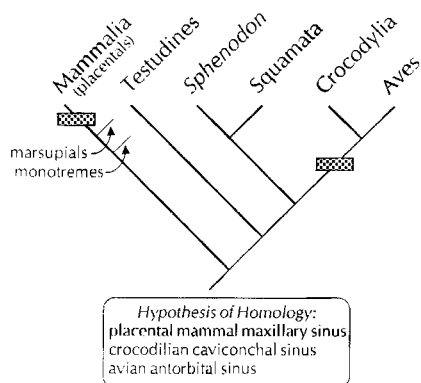


Fig. 21. Cladogram summarizing the congruence of a hypothesis of homology of paranasal air sinuses with amniote phylogeny. Parsimony dictates that the mammalian maxillary sinus is not homologous to the antorbital sinus of archosaurs.

The following shared osteological correlates of the avian antorbital sinus and crocodilian caviconchal sinus are potentially observable in fossils (see Witmer, in press, for more extensive discussion): 1) An antorbital cavity is present in the area of the skull lateral to the nasal cavity and formed principally by the maxilla, lacrimal, and palatine; 2) a fossa or recess is excavated within the maxilla; 3) the antorbital cavity is located directly opposite the primary choana; and 4) the nasolacrimal canal indicates that the nasolacrimal duct passed dorsomedially around the cavity. Fossil archosaur taxa were surveyed for these attributes and are discussed in detail elsewhere (Witmer, in press). The results of the survey indicate that at least the basal members of all major clades of archosaurs manifest these osteological correlates of paranasal pneumaticity. As just one rather typical example, the Triassic crurotarsan *Ornithosuchus longidens* (Fig. 22; Walker, '64; Sereno, '91; Witmer, in press) has a very large antorbital cavity formed by the maxilla, lacrimal, and jugal and partially floored by the palatine. There is an extensive, smooth-walled antorbital fossa excavated into not only the maxilla but also the lacrimal and jugal. The antorbital cavity and internal antorbital fenestra are situated directly opposite the caudalmost portion of the choana. The nasolacrimal canal passes dorsomedial to the cavity, probably running between the prefrontal and lacrimal bones (its rostral portion could not be traced). Thus, given the phylogenetic distribution of the osteological corre-

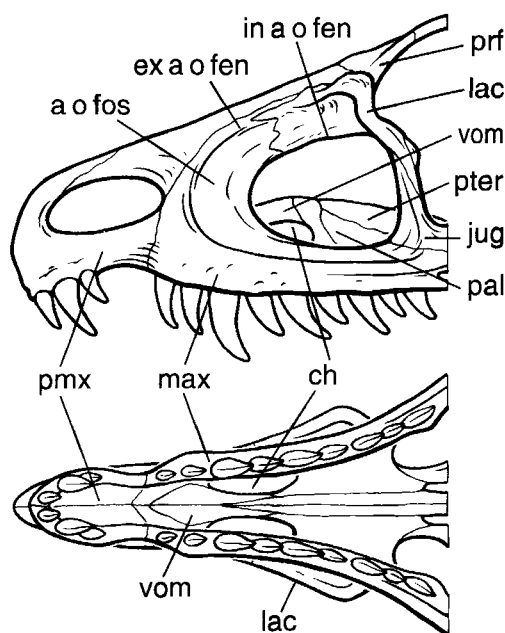


Fig. 22. *Ornithosuchus longidens*. Skull in left lateral view, showing features of the antorbital cavity. Modified after Walker ('64), Sereno ('91), and specimens.

lates of the paranasal air sinus, an air sac can be inferred with little speculation in fossil archosaurs (Witmer, in press). The hypothesis of homology of the avian antorbital sinus and crocodilian caviconchal sinus therefore survives the congruence test over all of archosaur phylogeny and is indeed strongly corroborated.

To my knowledge, paranasal air sinuses have not been reported in any extinct lepidosauromorphs, which is consistent with their absence in the extant members of the clade. Likewise, sinuses resembling those of archosaurs have not been described in any fossil turtles, including *Proganochelys quenstedti* (Gaffney, '90). As in extant turtles, if the recessus ducti nasopharyngei was present in fossil turtles, it did not pneumatize bone. In fact, the only evidence for any sort of paranasal pneumaticity in turtles is restricted to *Meiolania platyceph*, which has a small cavity within the nasal and maxilla in the region of the naris; this nasomaxillary sinus, if indeed pneumatic, would thus be a diverticulum of the vestibule rather than the nasal cavity proper (Gaffney, '83).

The phylogenetic level within Synapsida at which the maxillary sinus appears is unclear.

Rowe ('88) listed the presence of ethmoidal, frontal, and sphenoidal sinuses as a synapomorphy of therian mammals, implying their absence in more basal synapsids, but did not comment on the maxillary sinus. Wible ('91, p. 13) subsequently excluded Rowe's ('88) "pneumatic sinuses" character from his analysis, because, based on Pauli's (1900) study, "paranasal air sinuses do not occur widely in taxa other than placentals." However, a number of workers have identified "maxillary sinuses" in various nonmammalian therapsids (Fourie, '74; Kemp, '69, '79, '80, '82; Kermack et al. '81; Sues, '85), suggesting an earlier origin of this structure. In some cases (e.g., *Morganucodon watsoni*, Kermack et al., '81), the structure really is little more than a depression on the floor of the nasal cavity, whereas in others (e.g., *Luangwa drydalli*, Kemp, '80) the bony cavity is large and connected to the nasal cavity proper via a relatively small ostium. Furthermore, in most cases the structure has a close relationship with the maxillary nerve (Kemp, '82; Sues, '85), and in the gorgonsopsian *Arctognathus* sp. the pterygoideus musculature is even reconstructed as encroaching on the cavity (Kemp, '69).

In contrast, in more basal synapsids (i.e., "pelycosaurs"), there is no indication of any of the maxillary pneumaticity observed in therapsids (Romer and Price, '40; personal communication from A.S. Romer to T.S. Parsons: see Parsons, '59, '70). In fact, medial views of the maxillae of most basal synapsids reveal a relatively simple morphology (Romer and Price, '40; Reisz, '72, '75). It is thus very unexpected to find a basal synapsid with an antorbital fenestra—the Permian varanopsid *Varanodon agilis* (Olson, '65). As in archosaurs the fenestra in *Varanodon* is bounded by the maxilla and lacrimal, but unlike archosaurs, the premaxilla, septomaxilla, and nasal also bound the fenestra. The soft-tissue relations of this structure are unknown. Given its perhaps unique occurrence in Synapsida, it is almost certainly an autapomorphy of *V. agilis*.

Thus, synapsids present a very complicated picture with regard to the evolution of paranasal pneumaticity. Basal synapsids appear to lack any of the osteological correlates, except for one form that has an antorbital fenestra. Some nonmammalian therapsids seem to have pneumatic maxillae that might pass the similarity test with archosaurs and placentals, whereas others do not. And fi-

nally, among extant Mammalia, only placentals seem to have a maxillary sinus. Clearly, more work is necessary to determine the homologies of these structures *within* Synapsida. Taken together, however, these data suggest that paranasal air sinuses were not present in Synapsida ancestrally, but instead appeared later, perhaps even more than once.

## Summary

In summary, with the additional evidence from the fossil record, some of the former uncertainty can be resolved. There is good evidence that the maxillary sinus arose within Synapsida and the antorbital/caviconchal sinus arose within Sauropsida. Thus, the paranasal air sinus of archosaurs clearly is not homologous with the maxillary sinus of placentals: The hypothesis may pass the similarity test, but it fails the congruence test. Moreover, there really is no longer any reason to entertain the notion of homology of the recessus ducti nasopharyngei of turtles with either the mammalian or archosaur sinus: It passes only the most superficial of similarity tests and is not congruent with amniote phylogeny.

Paranasal pneumaticity in sauropsids, however, probably did indeed originate somewhat earlier than the common ancestor of Archosauria—but not much earlier. The major osteological correlates of paranasal pneumaticity are present in the immediate outgroups of Archosauria: Proterochampsidae, *Euparkeria capensis* (Fig. 1), Erythrosuchidae, and Proterosuchidae (Witmer, in press). These basal archosauriforms have not been emphasized here because they fall outside of the extant phylogenetic bracket of birds and crocodilians. According to the methodology for inferring soft tissues in fossils (see Witmer, '95, for details), since basal archosauriforms fall outside of the bracket, soft-tissue inferences must be more tentative for them because the causal associations between soft and hard tissues are not directly testable by study of extant forms. Nevertheless, given the compelling morphological evidence provided by the osteological correlates of paranasal pneumaticity, there is a sound basis to speculate that a homologous paranasal air sac characterizes a somewhat more inclusive group than just Archosauria.

## SUMMARY AND CONCLUSIONS

Perhaps the most significant general conclusion arising from the foregoing analysis is

that, for many questions in evolutionary biology, the dichotomy between paleontology and neontology is not only artificial but actually may impede an investigator's arrival at appropriate inferences. Paleontology is traditionally the domain of only hard parts, whereas neontology theoretically can examine virtually any aspect of an organism. This dichotomy thus presents a problem for paleontologists because certain critical information (e.g., soft-tissue attributes) is seemingly out of reach. For researchers focusing on living groups of organisms, this problem seemingly disappears because all tissues theoretically are available for study. Actually, the neontologist neither may be able to escape this problem in that all organisms have an evolutionary history, and many questions ostensibly posed about extant taxa in fact require information from phylogenetically relevant taxa known only as fossils.

Thus, in order to correctly interpret both extinct and extant organisms, we are challenged to expand the domains of traditional osteology or paleontology and to recover whatever relevant soft anatomical information we can from fossils. Gauthier et al. ('88a) effectively demonstrated "the importance of fossils" in phylogeny reconstruction. The Extant Phylogenetic Bracket approach advocated here and elsewhere (Witmer, '95) is in some respects the other side of the same coin in that it emphasizes "the importance of extant taxa" in paleobiology. Only organisms living today provide the detailed evidence for causal interactions between soft and hard tissues, and, when the appropriate extant taxa are sampled (i.e., minimally the first two extant outgroups), they constrain all inferences about the soft-tissue conformation of the anatomical systems of extinct organisms.

Reconstructing soft tissues in fossils is conceptually similar to reconstructing ancestral or nodal characters and, given that organic evolution occurs, is founded on nothing more complex than the homology relation. Evidence of the causal association between a soft-tissue element and its osteological correlates is provided by extant taxa. When studied within a comparative framework, a hypothesis can be formulated that similarities in these associations among taxa are due to inheritance of the association from a common ancestor, that is, that the associations are homologous. The hypothesis predicts that the common ancestor will pass this association on to all of its descendants. Thus, we

may test this hypothesis by surveying these other (in this case, fossil) descendants—i.e., test for the congruence of the hypothesis with a specified phylogenetic pattern. The hypothesis passes the congruence test if the osteological correlates are found in the fossils. If the association between the soft tissue and its osteological correlates is indeed causally based in the extant forms, then there is a sound basis for inferring the same, homologous soft-tissue element in the fossil form.

This basic approach has been employed above to probe the facial anatomy of extant archosaurs (birds and crocodilians) for homologous causal associations between soft and hard tissues in the hopes of shedding light on the morphology of fossil archosaurs. In particular, the goal has been to elucidate the soft-tissue relations of the antorbital fenestra and cavity, structures that always have been diagnostic for archosaurs yet enigmatic in function. The three previous suggestions for the primary soft-tissue contents of the antorbital fenestra and cavity have been a gland, a portion of the pterygoideus muscle, and a paranasal air sac. Extant birds retain antorbital fenestrae and cavities that generally resemble those of most fossil archosaurs, but extant crocodilians lack any such openings in the surfaces of their snouts. Thus, the question was, what are the soft-tissue contents of the cavity and fenestra in birds, and are there any related features that can be homologized with crocodilians and hence all archosaurs?

Having sampled all the major organ systems comprising the facial portion of the head and having established their homologies over all amniotes or at the very least among sauropsids, we are now in a better position to assess the function of the antorbital cavity of archosaurs. First of all, although extant crocodilians lack a fenestra in the side of their snouts, they retain a homologous bony antorbital cavity internally that compares well with that of birds, albeit in crocodilians it is highly modified in association with skull flattening and nasal rotation. Turning to the three major candidates for the soft tissue lodged in the cavity, birds and crocodilians share a homologous nasal gland with all sauropsids (perhaps all tetrapods), a homologous *m. pterygoideus, pars dorsalis* (which may be an archosaur apomorphy), and a homologous paranasal air sinus (again, probably an innovation of archosaurs). Furthermore, all three structures at least reach

the antorbital cavity in most birds and crocodilians and therefore may be classed as "contents" of the cavity. Thus, the three major hypotheses for the function of the archosaurian antorbital cavity all remain valid on these counts.

What are the homologous osteological correlates of these soft-tissue elements? With respect to the nasal gland, homologous bony evidence for the gland is scant but tends to involve grooving of the maxilla and nasal in the vicinity of their suture; thus, the osteological correlates of the nasal gland do not involve the external antorbital fenestra in birds, and it is a minor component of the cavity in both extant clades. The major homologous osteological correlate of the dorsal pterygoideus muscle is a muscular fossa on the palatine. In birds the muscle is never associated with the antorbital fenestrae and is a minor component of the cavity. A muscular fossa is found in fossil archosaurs as well, yet there is very good evidence (Witmer, in press) that, as in birds, the muscle was restricted to the caudoventral portion of the cavity and did not attach to the antorbital fenestra or fossae. Finally, the homologous osteological correlates of paranasal pneumaticity include the antorbital cavity itself, its morphology (e.g., excavations of the maxilla and/or lacrimal), and its relationship to the primary choana and bony nasolacrimal canal. In both birds and crocodilians, the paranasal air sinus is the largest component of the antorbital cavity, and in birds it extends to the margins of the external antorbital fenestra. The presence of these osteological correlates in fossil archosaurs suggests that they also had a large paranasal air sac filling their antorbital cavities. In summary, based on careful study of all aspects of facial anatomy in extant and fossil archosaurs and the determination of the homologies of particular soft-tissue attributes and their osteological correlates, the problem of the function of the antorbital fenestra and cavity of archosaurs is solved—the structures functioned primarily to house a paranasal air sac.

It also was emphasized earlier that an approach such as this benefits the interpretation not only of fossil organisms but also extant organisms, for the simple reason that extant taxa have a phylogenetic history. Thus, the findings reported in the last paragraph impact on our interpretations of modern birds and crocodilians. For example, as indicated above, birds are primitive in retaining an

external antorbital fenestra, yet this fenestra is relatively small in comparison to other archosaurs, particularly relative to nonavian theropods which tend to have enormous external fenestrae. This reduction in the size of the external fenestra (and indeed of the cavity as a whole) is probably another manifestation of the apomorphic expansion of both the vestibular portion of the nasal cavity and the eyeball and its adnexa and the apomorphic reduction in the size of the maxilla.

Furthermore, the analysis reaffirms that crocodilians have lost the external antorbital fenestra. Extant crocodilians plesiomorphically retain the paranasal air sac and the antorbital cavity, but the embryonic fonticulus antorbitalis—the embryonic structure most comparable to the external antorbital fenestra of other archosaurs—becomes closed laterally (almost certainly due to nasal rotation), thus internalizing the antorbital cavity. Extant birds retain a large internal antorbital fenestra, which is largely occluded by the cartilaginous paries nasi. The internal antorbital fenestra is retained in extant crocodilians as well, at least in part, and is at least the rostromedial portion of the maxillary aperture to the bony caviconchal recess (Fig. 12C–E). In both birds and crocodilians, the internal antorbital fenestra transmits only the epithelial air sac.

A final matter relates to the causal nature of the associations between particular soft and hard tissues and suggests avenues of further research. Although "causal associations" have been stressed throughout, causation remains an assumption in most cases and has not been specifically tested by, say, experimentation. Nevertheless, the causal nature of many of the associations seems relatively straightforward. For example, the dorsal pterygoideus muscles probably indeed cause fossae on the palatine bone, and the antorbital and caviconchal air sacs indeed cause pneumatic cavities via pneumatically induced processes of resorption. The very existence of the antorbital cavity in extant archosaurs well may be caused by the presence of the paranasal air sac. For example, in birds, as mentioned earlier, many of the facial elements form around the air sac such that the external antorbital fenestra can be viewed as an embryonic fontanelle that fails to close. It is virtually certain that the air sac does not provide the inductive interaction triggering ossification because other sauropsids, which lack the air sac, retain the bones;

the bones probably ossify as a result of inductive interactions involving the nasal capsule, oral epithelium, etc. However, evagination of the air sac slightly precedes the onset of ossification of the facial bones, and subsequent expansion of the sac probably is a major factor in determining the position and form of the bones. In crocodylians, the morphogenetic process of nasal rotation apparently "overrides" the competency of the air sac to prevent apposition of the facial bones, and the external antorbital fenestra subsequently closes. A final association that seems to be causally based is the relationship of the ostium of the air sac to the primary choana. In both clades of extant archosaurs, the air sac and choana are tightly linked, starting from the earliest appearance of the air sac and continuing throughout ontogeny, despite subsequent ontogenetic transformation of surrounding structures. The morphogenetic reason for this association of air sac and choana remains obscure, but is probably real.

In summary, by studying fossil archosaurs in light of the information provided by their extant relatives, it is possible to recover from the fossils a great deal of important evidence for the existence and form of various soft tissues. Reciprocally, these insights impact on our interpretation of the modern taxa. Determination of the homologous causal associations between soft tissues and their osteological correlates indicates that the antorbital cavity and fenestrae of fossil archosaurs were associated primarily with an epithelial diverticulum of the nasal cavity (i.e., an air sac), and the nasal gland and dorsal pterygoideus muscles were only minor components of the cavity.

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Edward Heck executed Figure 22.

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