The craniofacial air sac system of Mesozoic birds (Aves)

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Birds are characterized by pneumatization of their skeletons by epithelial diverticula from larger, air-filled cavities. The diverticula—or 'air sacs'—that invade the postcranium result from outgrowths of the lungs; postcranial pneumaticity has been very well studied. Much more poorly understood are the air sacs that pneumatize the skull. Study of craniofacial pneumaticity in modern birds (Neornithes) indicates the presence of two separate systems: nasal pneumaticity and tympanic pneumaticity. The lacrimal and maxillary bones are pneumatized by diverticula of the main paranasal cavity, the antorbital sinus. There are five tympanic diverticula in neornithines that pneumatize the quadrate, articulare and the bones of the braincase. The pneumatic features of the following six genera of Mesozoic birds are examined: *Archaeopteryx*, *Enaliornis*, *Baptornis*, *Parahesperornis*, *Hesperornis* and *Ichthyornis*. Despite the 'archaic' aspect of most of these birds, many of the pneumatic features of neornithines are found in Mesozoic birds and are considered primitive for Aves. The phylogenetic levels at which most of the avian pneumatic features arose within Archosauria are uncertain. Until the phylogenetic levels at which homologous pneumatic features arose are determined, it is unwise to use most pneumatic characters in the discussion of avian origins. Within avian phylogeny, Ornithurae and Neornithes are well-supported by pneumatic synapomorphies. There is a trend towards reduction of craniofacial pneumaticity within Hesperornithiformes. Within Neornithes, four derived pneumatic characters suggest that the Palaeognathae (ratites and tinamous) is monophyletic.

KEY WORDS:—Pneumaticity – air sacs – craniofacial morphology – Mesozoic – *Archaeopteryx* – *Hesperornis* – *Ichthyornis* – phylogeny.

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INTRODUCTION

The avian skeleton has long been noted for its lightness. It often is quoted (e.g. Welty & Baptista, 1988) that the feathers of some birds actually weigh *more* than the skeleton. This lightness is achieved through pneumatization of the postcranium by non-respiratory pulmonary diverticula: the 'air sacs' of the avian lung. The English anatomist John Hunter stimulated interest in the pulmonary air sac system of birds through dramatic experiments in which he "cut the wing through the os humeri, in another fowl, and tied up the trachea as in the cock; and found that the air passed to and from the lungs by the canal in this bone . . ." (Hunter, 1774: 211). The avian pulmonary system has since received a great deal of attention and is well understood (King, 1966; King & Molony, 1971; Duncker, 1971; Brackenbury, 1987; McLelland, 1989; and references within these papers).

The skulls of birds also are characterized by air sacs. This pneumatization, however, typically does not originate from the pulmonary system but rather from the nasal and tympanic cavities. Hunter (1774: 210) was perhaps the first to note the developmental dichotomy between craniofacial and postcranial pneumaticity observing that "this supply, of the bones with air, is not wholly by means of the lung; for the cells of the bones of the head, in some birds, are filled with it . . . and [the skull] admits a considerable quantity of air, which is furnished by the Eustachian tube". With a few notable exceptions, avian craniofacial pneumaticity, in and of itself, has not been the subject of much research. Most references to it in the literature are brief and found either in general treatises that discuss avian skulls (Nitzsch, 1811; W. K. Parker, 1875; Stresemann, 1927–34; Bellairs & Jenkin, 1960) or in descriptive papers on individual taxa of birds (W. K. Parker, 1866, 1869; T. J. Parker, 1891; Pycraft, 1902 and many other papers; Suschkin, 1899; Lowe, 1926; Lang, 1955, 1956; Jollie, 1957; Müller, 1961, 1963; May, 1961; Sandoval, 1963, 1964; Toerien, 1971; Norberg, 1978; Saiff, 1974, 1976, 1978, 1981, 1982, 1983). In most cases, the descriptions of the air-filled diverticula or, more commonly, the associated bony spaces lack detail and adequate comparisons; this situation is understandable in that these were not the primary foci of the studies.

Jacquemin (1836) provided a description of the avian craniofacial air sinuses but erroneously considered all craniofacial pneumaticity to result from the tympanic air cells. In 1889, Bignon published an excellent monograph on avian craniofacial pneumaticity in which she concentrated on the "cervicocephalic" diverticulum of the antorbital sinus. The development of avian craniofacial

pneumaticity was studied peripherally in many of the papers cited above and was studied in detail for pigeons by Lurje (1906). De Beer (1937) provided an excellent summary of much of the earlier ontogenetic work. Development of nasal pneumaticity was studied in *Larus* and *Sterna* by Schüller (1939). Bremer (1940) studied the development of both nasal and tympanic pneumaticity in domestic chickens.

There is a considerable literature on the pneumatization of the skull roof of birds (primarily passeriforms). In most non-passerine birds pneumatization is complete by the time they attain adult body size, whereas in passerines pneumatization of the skull roof does not even start until after they have reached adult size (Winkler, 1979). Thus, some birds can be aged by the degree of skull pneumatization (viz. younger birds have more apneumatic 'windows'). This technique for aging birds has been known for some time (see Winkler, 1979, 1985, for an excellent review), and will not be discussed further here.

All modern birds have pneumatic skulls. Although pneumaticity is reduced in many taxa, all birds retain air-filled diverticula from the nasal and middle ear sacs. The evolution of avian craniofacial pneumaticity has never been studied. The purpose of this paper is to initiate such a study through the investigation of the pneumatic features in the skulls of Mesozoic birds. The pneumatic systems of the skulls of modern birds were studied to establish the basis for comparison necessary for any analysis of craniofacial pneumaticity in Mesozoic birds. The air-filled diverticula of modern birds were traced and the osteological correlates of the diverticula noted. The intent was to homologize these pneumatic diverticula, because the same diverticula may induce differing osteological morphologies. By determining the results of pneumatization in the dried skulls of modern birds, one then can infer the presence of diverticula in fossils (in which the diverticula are not preserved). Such determinations must be made with caution, in that (as always) the inference of soft tissues in fossils is often fraught with problems. The warning of King & King (1979) that hollow bones are not necessarily pneumatic is well taken. Although Hecht (1985: 153) suggested that "it is not possible to determine in fossils whether [observed osteological features] were true pneumatic spaces or cavities filled with tissue in the living organism", if structures exhibit the same morphology and relationships then the most parsimonious hypothesis is that they were formed through similar means. Within a morphologically consistent group like birds, this working hypothesis is sound.

The following seven genera of Mesozoic birds were examined: *Archaeopteryx*, *Gobipteryx*, *Enaliornis*, *Baptornis*, *Parahesperornis*, *Hesperornis*, and *Ichthyornis*. *Gobipteryx minuta*, an Upper Cretaceous bird from Mongolian deposits (Elzanowski, 1976, 1977), has a few features suggestive of craniofacial pneumaticity (Witmer & Martin, 1987), but the material is so equivocal in this regard that I have not included it in this study. Recent reports of a Triassic bird from the Dockum Formation of west Texas by Chatterjee (1987) have yet to be affirmed by most workers. Although Chatterjee (1987) listed several pneumatic features in the skull, it is prudent to wait for adequate documentation in print before commenting. The phylogenetic relationships and stratigraphic ranges of the remaining birds are presented in Fig. 1, which is based on the cladistic analyses of Martin (1983a, 1984) and Cracraft (1986, 1988).

Craniofacial pneumaticity was considered an ancestral avian feature by Whetstone & Martin (1979, 1981), Whetstone (1983) and Currie (1985),
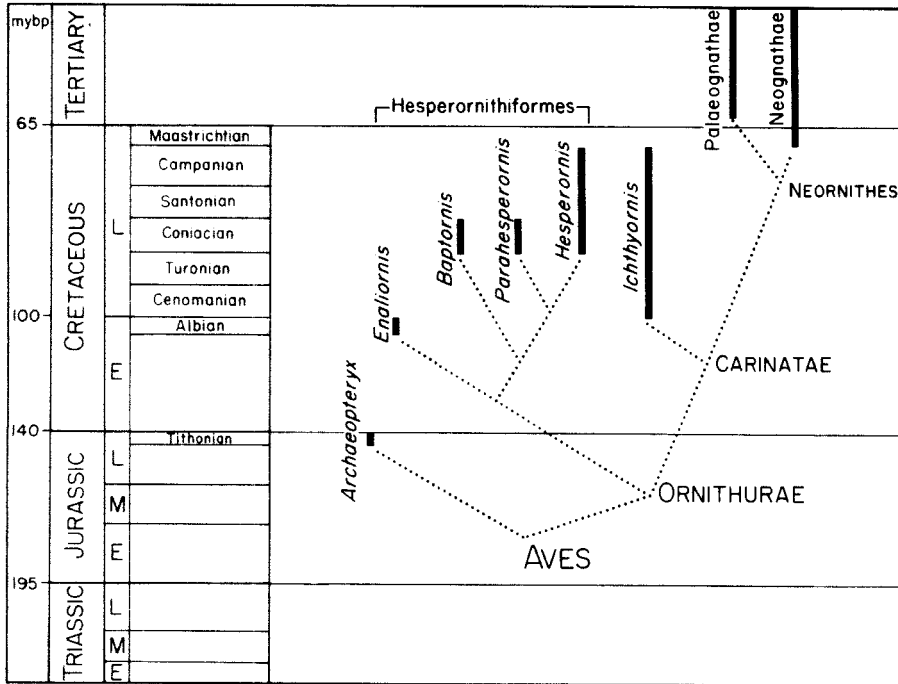
Figure 1. Phylogenetic relationships (dotted lines) and stratigraphic ranges (vertical bars) of the birds considered in this study. For character justification see Martin (1983a, 1984) and Cracraft (1986, 1988).

among others. The present study supports this assertion in that all of these birds possess at least some of the pneumatic features observed in modern birds. The details of the craniofacial pneumaticity of these birds are important for a number of reasons. Despite the references cited above, avian craniofacial pneumaticity remains poorly described, figured, and, most importantly, interpreted. How these air spaces in the skulls of birds relate to the craniofacial architecture, functional morphology, habits and systematics of birds is unknown. A first step in understanding the pattern, significance and evolution of avian craniofacial pneumaticity is to determine the 'primitive condition'. Thus, Mesozoic birds stand in a pivotal position to help elucidate the early history of avian craniofacial pneumaticity. Other techniques of determining ancestral features such as the ontogeny of modern birds and outgroup comparison with non-avian archosaurs are also important and are discussed below.

As will be elaborated later, craniofacial pneumaticity also has been important in the debate on the origin of birds. Suggestions that similarities in the pattern of air sinuses between birds and crocodilians are synapomorphic and thus indicate immediate common ancestry have been countered with reports of craniofacial pneumaticity in theropod dinosaurs, the leading contender for avian relationships (see review by Witmer, in press). Clearly, birds, crocodilians and theropods all possess pneumatic sinuses in their skulls; however, many other archosaurs also have air spaces in their skulls (Witmer, 1987). The homologies of the various pneumatic sinuses have yet to be worked out. Before features associated with pneumaticity can be used to link birds with any other group of

archosaurs, it is necessary to determine which features were present in birds ancestrally; the present study attempts to deduce this ancestral pattern. I have chosen to begin with birds because, having living representatives, the database is much larger. Also, detailed study of craniofacial pneumaticity in these most pneumatic of all archosaurs strengthens the basis for comparison with extinct archosaurs.

MATERIAL

Abbreviations of institutional names used in this work are: KUVP, Kansas University Vertebrate Paleontology; KUMNH, Kansas University Museum of Natural History; YPM, Yale Peabody Museum; FMNH, Field Museum of Natural History; USNM, United States National Museum; AMNH, American Museum of Natural History. Only the craniofacial material of the fossil specimens is discussed below.

Ichthyornis

Martin (1987) removed *Apatornis* from Ichthyornithiformes, leaving *Ichthyornis* as the sole member of the order (which thus becomes a redundant higher taxon). *Ichthyornis* was a toothed, flying form presently known only from Late Cretaceous North American deposits. Marsh (1872) erected the genus *Ichthyornis* for avian fossils discovered in Kansas. The crania of *I. dispar* (YPM 1450) and *I. victor* (YPM 1728) are badly crushed and are currently mounted in the Yale Peabody Museum of Natural History (preventing detailed study).

YPM 1775. *Ichthyornis victor* Marsh. Virtually complete left quadrate (lacking only the orbital process) and dorsal fragment of the right quadrate. These specimens were collected from the Upper Cretaceous (Senonian) Niobrara Formation of western Kansas. Marsh (1880) figured the left quadrate in four views.

YPM 6264. *Ichthyornis* sp. cf. *I. dispar*. Well-preserved articular region of the left lower jaw. It was collected in 1876 by B. F. Mudge from the Upper Cretaceous (Senonian) Niobrara Formation of Wallace County, Kansas. This specimen was described by Gingerich (1972).

YPM 1761. *Ichthyornis* sp. Articular region of the left lower jaw. This rather crushed specimen was collected from the Upper Cretaceous Niobrara Formation of western Kansas.

Hesperornithiformes

Hesperornithiformes comprises a group of birds known only from Cretaceous strata. Presently there are four described genera (Fig. 1): *Enaliornis* (Seeley, 1876), *Baptornis* (Marsh, 1877; Martin & Tate, 1976), *Parahesperornis* (Martin, 1984) and *Hesperornis* (Marsh, 1872, 1873). All of these birds were flightless, foot-propelled diving birds. Teeth are known from *Hesperornis* and *Parahesperornis*. Marsh's (1880) monographic revision of these birds united them with *Ichthyornis* in the subclass Odontornithes, based primarily on the primitive retention of teeth. Most later workers (e.g. Brodkorb, 1963) considered the Odontornithes to be an artificial grouping. Marsh's description of the skull was very brief and

made no reference to pneumatic features of the skull. Gingerich (1973, 1976) redescribed portions of the skull in his study of the palate and cranial kinesis of *Hesperornis* but also did not discuss pneumaticity. Whetstone & Martin (1979) were the first to identify any pneumatic features of *Hesperornis* and figured two of its three periotic sinuses. Of all the known Mesozoic birds, hesperornithiforms are the best known and best represented in the fossil record. The sample of preserved craniofacial bones is sufficiently large to permit a detailed analysis of craniofacial pneumaticity in these birds.

KUVP 71012. *Hesperornis regalis* Marsh. Disarticulated skull lacking only the right maxilla. This specimen was collected from the Upper Cretaceous (Coniacian to Santonian) Smoky Hill Chalk Member of the Niobrara Formation of Logan County, Kansas in 1981 by C. R. and M. C. Bonner. The skull bones are beautifully preserved and, with the exception of the relatively crushed braincase, are generally undistorted. The palate of this specimen was discussed by Witmer & Martin (1987). Bühler *et al.* (1988) discussed cranial kinesis in hesperornithids based primarily on inferences made from KUVP 71012.

YPM 1206. *Hesperornis regalis* Marsh. Complete skull. This specimen was also collected from the Niobrara Formation, probably Smoky Hill Chalk Member, in western Kansas by T. H. Russell in 1872. It was described by Marsh (1880) and Gingerich (1973) and is somewhat more damaged than KUVP 71012. YPM 1206 and KUVP 71012 are of almost identical size, which greatly facilitated comparison.

YPM 1207. *Hesperornis regalis* Marsh. Caudal fragment of the braincase. This specimen was collected by B. F. Mudge in 1875 from the same general area as YPM 1206. Although this specimen lacks most of the skull, the otic region is well preserved and is relatively uncrushed. Marsh (1880) published a drawing of this specimen, and Edinger (1951) described and figured its medial aspect.

FMNH PA 219. *Hesperornis* sp. cf. *H. regalis*. Fragment of the right side of the braincase and a fragment of the articular region of the left lower jaw. This specimen was collected from the Upper Cretaceous Boyne Member of the Vermilion River Formation of Manitoba, Canada by D. Bardack (Bardack, 1968). Although very fragmentary, this specimen is uncrushed, very well preserved, and broken in such a way that the otic region is exposed. Although Bardack (1968) considered it to be a specimen of *H. regalis*, the postcranium is slightly more gracile than the Niobrara specimens and exhibits minor differences in middle ear morphology. It is uncertain whether these differences are due to geographic variation within a single species or to interspecific differences.

USNM 4978. *Hesperornis regalis* Marsh. Fragmentary skull including the premaxilla, left lacrimal and lower jaws. The specimen was collected from the Upper Cretaceous Niobrara Chalk of western Kansas and was described by Lucas (1903). The premaxilla and lacrimal were figured by Martin (1984).

LACM 128317. *Hesperornis regalis* Marsh. Isolated left maxilla. This specimen was collected from the Niobrara Chalk of western Kansas, and compares well with maxillae of other specimens of *Hesperornis*.

KUVP 2287. *Parahesperornis alexi* Martin. Essentially complete, articulated, but crushed skull. The holotype specimen of this genus, although badly damaged in some areas, provides critical data on the braincase. It was collected from the

Upper Cretaceous (Coniacian) Smoky Hill Chalk Member of the Niobrara Formation of Graham County, Kansas by H. T. Martin in 1894. Lucas (1903) gave a brief description of the skull. Gingerich (1976) presented photographs of the entire skull and of the left pterygoid and quadrate. Martin (1984) described the skeleton, provided a reconstruction, and recognized it as a genus distinct from *Hesperornis*. *Parahesperornis* was smaller than *Hesperornis*, and KUVP 2287 (*Parahesperornis*) has some open sutures in the braincase. Thus, it is possible that the type of *Parahesperornis* is a juvenile, perhaps of *Hesperornis*. However, the skulls differ in many respects that cannot be accounted for by age differences (see below).

KUVP 24090. *Parahesperornis alexi* Martin. Fragment of the articular region of the right lower jaw. This specimen was collected by O. Bonner in 1981 from the Upper Cretaceous (Coniacian) Smoky Hill Chalk Member of the Niobrara Formation on the Andrew Bird Ranch, Gove County, Kansas.

FMNH 395. *Baptornis advenus* Marsh. Fragment of the articular region of the left lower jaw. The specimen was recovered from the Upper Cretaceous Niobrara Formation near the Smoky Hill River in western Kansas. Martin & Tate (1976) described this specimen and provided photographs and a figure.

KUVP 16112. *Baptornis advenus* Marsh. Fragment of the premaxilla. This fragment belongs to a juvenile individual. The specimen was collected in 1962 by O. Bonner from the Upper Cretaceous (Coniacian) Smoky Hill Chalk Member of the Niobrara Formation of Logan County, Kansas. This specimen was described by Martin & Tate (1976) and described and figured by Martin & Bonner (1977). Marsh (1877, 1880) related *Baptornis* to *Hesperornis* and included it in his Odontornithes. Brodkorb (1963), however, denied relationship to *Hesperornis*, and removed *Baptornis* to the Podicipediformes (grebes). Martin & Tate (1976) re-established its hesperornithiform affinities.

Enaliornis barretti Seeley. Fragment of the caudal end of the skull. This specimen is beautifully preserved and uncrushed. Many details of the braincase and middle ear are preserved. The specimen, however, is highly abraded such that even clearly broken edges are rounded and smooth. The specimen was collected in the mid-19th century from the Lower Cretaceous (Albian) Greensand deposits near Cambridge, England. Seeley (1870) provided a detailed description of the skull of *Enaliornis barretti* and figured it in four views. He initially identified it as pterosaurian despite noting that (1870: 83) "with Birds the correspondence is so close that it would be difficult to discover differences". Later, Seeley (1876) recognized his error, referred the skull to *Enaliornis*, and related the genus to "natatorial birds". Brodkorb (1963) considered *Enaliornis* to be within Gaviiformes (loons), but Martin & Tate (1976) and Martin (1983a, 1984), recognizing the derived similarities to hesperornithiforms, assigned *Enaliornis* to Hesperornithiformes. Cracraft (1982) also regarded *Enaliornis* as a basal member of Hesperornithiformes.

Unfortunately, the Cambridge Greensand deposits from which *Enaliornis* was collected yield isolated elements almost exclusively. Thus, association is a problem. Seeley (1866) named a series of avian postcranial fossils *Pelagornis barretti*; finding *Pelagornis* occupied, Seeley (1869) later proposed the name *Enaliornis barretti*. Thus, it is only an assumption that the avian skull material belongs to the avian postcranials (which are of foot-propelled divers). Although

the skull of *Enaliornis* lacks hesperornithid apomorphies, following the taxonomic treatment of others, I regard *Enaliornis* as the basal hesperornithiform. There are no cranial features that would seem to contradict this taxonomic assignment.

Archaeopteryx

Definitive specimens of *Archaeopteryx* at present are known only from the Upper Jurassic (Tithonian) Solnhofen Limestone of Bavaria, Federal Republic of Germany. Unlike the other birds employed in this study, I have not examined the original specimens of these birds. I have studied in detail, however, high-resolution casts and stereophotographs of the pertinent specimens, with the exception of the newly discovered Solnhofen specimen (Wellnhofer, 1988).

The London specimen. The holotype is housed in the British Museum (Natural History) and preserves craniofacial material. On the main slab are a well-preserved braincase (prepared from the matrix by P. J. Whybrow, 1982) and an adjacent skull bone which was identified by Walker (1985) as the right quadrate. Scattered on the counterslab are fragments of a premaxilla, maxilla, nasals, lacrimal and perhaps other skull bones. The braincase provides details of periotic pneumaticity. Whetstone (1983) and Walker (1985) discussed aspects of pneumaticity based on this specimen.

The Eichstätt specimen. Although crushed, the smaller Eichstätt specimen has the best preserved skull (Wellnhofer, 1974), which is essentially complete. It is from this specimen that aspects of nasal pneumaticity are inferred.

Most workers accept the presence of only one bird in the known fauna, *Archaeopteryx lithographica* Meyer. Recently Howgate (1985) suggested that the Eichstätt specimen was generically distinct, and proposed the name *Jurapteryx recurva*. Until Howgate's hypothesis becomes established, I will recognize only the type species. Although the presence of feathers have led most workers to comfortably place the label 'bird' on *Archaeopteryx*, several workers, such as Thulborn (1984) and Paul (1984, 1988) among others, have regarded *Archaeopteryx* as little more than a small feathered dinosaur only distantly related to birds (see discussion by Witmer, in press). These views have not attracted much support, and I join the majority in regarding *Archaeopteryx* as the basal member of Aves.

CRANIOFACIAL PNEUMATICITY IN MODERN BIRDS
Terminology and general observations

In general, the terminology is based on studies of modern birds (Neornithes) and codified in *Nomina Anatomica Avium* (NAA, Baumel *et al.*, 1979), although the anglicized forms of many terms have been substituted. Many of the terms used here that are not found in the 1979 edition of NAA will be found in the new edition.

Pneumaticity is a state in which a diverticulum from an air-filled chamber communicating with the external environment penetrates into surrounding cartilage or bone, usually inducing resorption and resulting in fossae or sinuses within the bone. The term 'pneumatization' is reserved for the developmental process producing pneumaticity. The presence of diverticula does not necessarily indicate pneumatic bones. Bremer (1940) and Sandoval (1964) were correct in

noting that in *Gallus*, for instance, despite having a typically formed diverticulum of the nasal cavity (the antorbital sinus), there is no true pneumatization of the facial bones; in other words, the diverticulum does not invade and induce resorption of osseous tissue. Sandoval (1963), however, went too far in asserting that the skull of *Gallus* is apneumatic, because the tympanic diverticula do pneumatize the braincase. No attempt will be made here to address the terminological quagmire surrounding the terms 'antrum', 'recess', 'sinus', 'space', 'sac' or 'cavity'. These all have been used as general synonyms indicating the result of pneumatization by an air-filled diverticulum. Müller (1908) suggested that 'air sac' be applied only to the pulmonary diverticula, but there seems little reason to impose this restriction. Pneumatic 'cells' are the extensions from a main sinus that invade individual osseous areas. 'Diverticulum' indicates an epithelial outgrowth of a larger cavity or sinus.

The osteological correlates of pneumatization are important in inferring the presence of air-filled diverticula in fossil taxa. Pneumatization of bone can take place either directly (intramurally) through direct communication with an air-filled diverticulum or indirectly (extramurally) through the agency of pneumatic cells within adjacent bone. For example, the squamosal is pneumatized directly while the parietal is pneumatized indirectly via the air cells in the squamosal. Unfortunately, many of the detailed studies of the craniofacial bones of birds have been performed on domestic chickens (Erdmann, 1940; Jollie, 1957; Sandoval, 1963) which, although possessing most of the air-filled diverticula, have reduced craniofacial pneumaticity and have no true pneumatization of the facial bones.

The most common osteological indication of a pneumatic diverticulum is the presence of pneumatic foramina. Usually the pneumatic foramen leads into a trabeculated cavity (sinus and recess) within the bone. Often there are no true pneumatic foramina but instead a pneumatic fossa. Pneumatic fossae exhibit characteristic excavation of the bone and usually a few bony trabeculae. Sometimes a pneumatic diverticulum is in direct contact with the bone but does not pneumatize it or produce any direct evidence of its presence; in this case, the presence of the diverticulum may be missed if only dried skull or fossil material is examined.

There are two major systems of air sacs in the avian skull (Fig. 2), one arising as an outgrowth of the nasal cavity, the other as outgrowths of the tympanic
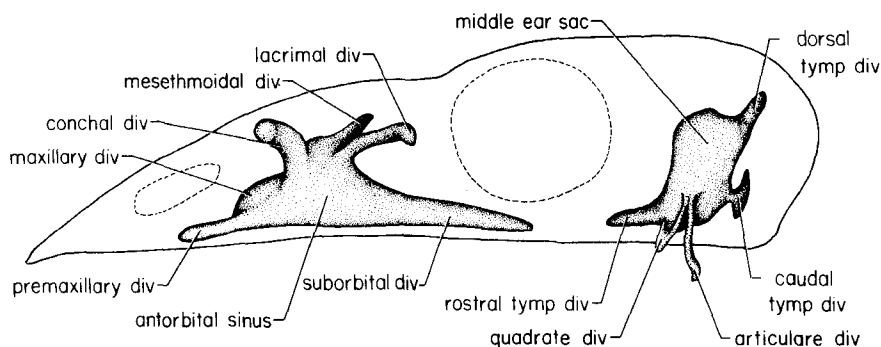

Figure 2. Diagrammatic representation of the diverticula of the antorbital sinus and middle ear sac of a nestling neognath bird. Abbreviations: div, diverticulum; tymp, tympanic.

cavity. These systems generally remain separate but occasionally merge through indirect pneumatization of the skull roof, interorbital septum and/or palatal skeleton. Bignon (1889) also described a system whereby a caudal diverticulum of the main paranasal sinus passes between soft tissue to communicate with the middle ear sac.

Nasal pneumaticity

The nasal system of air sacs communicates with the external environment via the nasal cavity and external nares. There is a single diverticulum that exits the nasal cavity; this sinus often becomes differentiated into various regional sacs (Fig. 2). The sinus begins as a pocket-shaped, dorsoventrally-compressed diverticulum at the caudal end of the middle nasal concha during the seventh (*Gallus*) or eighth (*Larus*) day of incubation (Bremer, 1940; Schüller, 1939). Various expansions of this sinus occur later in development.

This sinus has been referred to as the 'infraorbital sinus', 'subocular sac', 'orbital sinus', 'maxillary sinus', and several other terms. The sinus opens into and is enclosed by the antorbital fossa. This fossa is homologous to the antorbital fossa of non-avian archosaurs (Witmer, 1987) and has the same general relations (Fig. 3): the fossa is bounded by skin laterally (covering the antorbital fenestra), the maxilla rostrally and medially, the palatine ventrally, and the lacrimal (and, in some birds, the ectethmoid) caudally. As the avian sinus is located in the antorbital fossa, I propose the use of the term 'antorbital sinus'. In fact, use of this term has some precedence (Lang, 1955; although she later [1956] used 'orbital sinus').
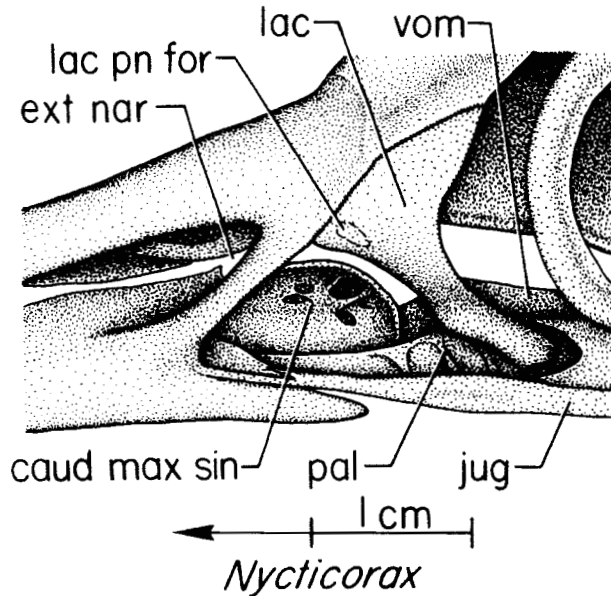

Figure 3. Osteological correlates of nasal pneumaticity. Antorbital region of *Nycticorax nycticorax* in left lateral view. Abbreviations: caud max sin, caudal maxillary sinus; ext nar, external nares; jug, jugal; lac, lacrimal bone; lac pn for, position of lacrimal pneumatic foramen; pal, palatine; vom, vomer.

As mentioned, the antorbital sinus begins as a tubular outgrowth of the caudal portion of the nasal cavity and initially occupies the antorbital fossa. Early in ontogeny the diverticulum is composed of a single layer of squamous epithelium (Bremer, 1940) that later differentiates into stratified squamous epithelium rostrally and ciliated columnar epithelium with goblet cells caudally (Jungherr, 1943). As in the mammalian paranasal sinuses, the avian antorbital sinus is non-olfactory (Negus, 1958).

In most birds, diverticula of the antorbital sinus extend throughout large portions of the skull. A number of different names have been used for the various subsidiary sinuses; their homologies are not yet clear. The confusion arises from efforts (e.g. Schüller, 1939) to utilize the terminology of the human paranasal sinuses which are not homologous with those of birds (Parsons, 1959). I employ a provisional nomenclature for the purposes of discussion; some of the names are adapted from Bignon (1889).

The antorbital sinus (Fig. 2) is initially triangular in cross section, matching the triangular boundaries of the antorbital fossa. The antorbital sinus usually does not directly pneumatize surrounding bones. In the great majority of cases, the facial bones are pneumatized by diverticula of the antorbital sinus rather than by the sinus itself.

Later in ontogeny, a dorsal diverticulum of the antorbital sinus fills the caudal nasal (olfactory) concha (Schüller, 1939). This conchal air sac is perhaps the most constant diverticulum (Bang, 1971). The caudal nasal concha is very rarely ossified in modern birds. As a result, the presence of a conchal diverticulum of the antorbital sinus is usually impossible to infer in dried skulls or fossils.

The maxillary diverticulum of the antorbital sinus is often only barely distinguishable from the medial wall of the antorbital sinus. Of all the antorbital diverticula, it is the maxillary diverticulum that most often pneumatizes bone. This diverticulum passes medially to pneumatize the palatine process of the maxilla (maxillopalatine of some authors). Among neornithine birds, neognaths and palaeognaths differ in the results of this pneumatization. In neognaths, the resulting morphology is usually a roughly vertically oriented, cup-shaped structure that is concave laterally and situated at the caudal end of the palatine process of the maxilla (Fig. 3). In palaeognaths, the maxillary diverticulum invades the rostral portion of the palatine process, producing a sometimes tubular recess within the maxilla. The maxillary diverticula of neognaths and paleognaths may not be homologous. In both cases the term 'maxillary sinus' has been used to represent the osteological results of pneumatization. Usually only a pneumatic fossa is produced, often with a number of supporting trabeculae. The simple cup-shaped maxillary sinus is perhaps the most common morphology in neognath birds. Occasionally the palatine process of the maxilla becomes inflated by the maxillary diverticulum (as in owls) resulting in pneumatic foramina. All morphological gradations lie between the inflated maxillary sinus of owls and the barely pneumatic, cup-shaped maxillary sinus of loons.

Usually there is a rostral diverticulum of the antorbital sinus that extends into the bill (primarily the premaxillary bone) lateral to the nasal cavity. It is by means of this premaxillary diverticulum (Fig. 2) that the interior of the large bills of many birds (e.g. *Pelecanus*) is formed into a vast lattice of bony trabeculae. Sometimes, as in *Sagittarius*, the maxillary and premaxillary diverticula are confluent. Usually, however, there is a separate ostium into the

premaxillary sinus rostrolateral to the maxillary sinus. Although many birds have a prominent premaxillary diverticulum, the diverticulum does not always pneumatize the bone and can only be detected through dissection or injection.

The antorbital sinus occasionally sends out a caudodorsal diverticulum that passes dorsal to the eye. A medial component, the mesethmoidal diverticulum, pneumatizes the mesethmoid and/or frontal bones. A lateral component, the lacrimal diverticulum, pneumatizes the lacrimal bone (Fig. 2). The mesethmoidal diverticulum does not usually pneumatize bone. If the mesethmoid is pneumatic, the source of the diverticulum is often the tympanic cavity (via the parasphenoid rostrum) rather than the antorbital sinus. The lacrimal is usually pneumatized directly by a separate lacrimal diverticulum. The presence of air cells within the lacrimal is widespread in birds. Usually pneumatic foramina are present dorsomedially near the bone's articulation with the skull (Fig. 3), but often there are prominent foramina laterally (e.g. *Diomedea*) and sometimes both laterally and medially (e.g. *Grus*). Communication of the air cells in the lacrimal and frontal takes place later in the ontogeny of many birds and obliterates the suture between the bones. In birds that fuse the ventral or medial surface of the lacrimal to the ectethmoid, indirect extensions from the lacrimal cells may pneumatize the ectethmoid and hence the mesethmoid, frontal and parasphenoid rostrum.

The antorbital sinus in birds is greatly influenced by the large size of the eye such that its caudal wall is concave. In many birds there is an often very large caudal diverticulum of the antorbital sinus, the suborbital diverticulum, that extends ventral to the eye and dorsal to the pterygoideus musculature (Fig. 2). This sinus and its associated diverticula have been surveyed by Bignon (1889). In some forms, such as the turkey (Cover, 1953), this caudal sac extends behind the eye, but is not very voluminous. In others, such as *Cygnus* (Bignon, 1889), the suborbital diverticulum is extensive and communicates with the contralateral diverticulum dorsal to the pterygoid, just rostral to its articulation with the parasphenoid rostrum. This sac itself often has several subsidiary diverticula. While in some birds these diverticula are small blind sacs (e.g. *Meleagris*; Cover, 1953), in other birds (Bignon, 1889) they sometimes are extensive. There are at least three subsidiary diverticula (Bignon, 1889): (1) the temporal diverticulum (e.g. *Morus*) extending between the muscles of the temporal region; (2) the perioccipital diverticulum (e.g. some psittacids) extending caudal to the head to encircle the occiput; and (3) the cervicocephalic diverticulum passing onto the neck, sometimes to communicate with the pulmonary system of air sacs (e.g. in *Cathartes* or *Buceros*).

The suborbital diverticulum, despite being the most voluminous diverticulum of the antorbital sinus in some birds, rarely pneumatizes bone. The subsidiary diverticula of the suborbital diverticulum almost never directly pneumatize bone: the temporal diverticulum is intermuscular while the perioccipital and cerivicocephalic diverticula are subcutaneous.

Tympanic pneumaticity

The tympanic air sac system communicates with the external environment via the median opening of the auditory (pharyngotympanic, Eustachian) tubes in the roof of the mouth. The auditory tube and tympanic cavity develop as

topographically differentiated portions of the first pharyngeal pouch. During ontogeny, the tympanic cavity expands and its connection with the pharynx constricts, forming the auditory tube (Arey, 1965). Although in many dried skulls there are communications between the auditory canals and adjacent pneumatic cavities (Norberg, 1978), the auditory tubes generally are thick-walled membranous conduits and do not give rise to pneumatic diverticula in the birds studied. Instead, pneumatization of the cranial bones surrounding the middle ear results from outgrowths from the tympanic cavity. While there is only a single major diverticulum of the nasal cavity (the antorbital sinus), there are numerous diverticula of the middle ear cavity (Fig. 2). The periotic air spaces are lined with the same mucous membrane that lines the tympanic cavity proper (Stresemann, 1927–34; Freye, 1952). The middle ear cavity generally is bounded by the quadate rostrally and dorsally (contrary to Freye, 1952), the paroccipital (= parotic) process and metotic strut (an ossification of the metotic cartilage which attaches to the occipital arch, basal plate, and auditory capsule; De Beer & Barrington, 1934) caudally, the otic bones medially, the parasphenoid ventrally, and the tympanic membrane laterally (Saiff, 1974). Lurje (1906), Bremer (1940) and Stork (1972) studied the development of some of the tympanic diverticula. Tympanic pneumatization begins at a later ontogenetic stage (at least in *Gallus*) than nasal pneumatization.

While some neornithine birds may lack true pneumatization of the facial bones, all have pneumatization of portions of the braincase. Birds are remarkably consistent in possessing five major tympanic diverticula. Three of these (the rostral, caudal and dorsal tympanic diverticula) invade the bones of the braincase. I employ a modified form of the terminology of Parker (1869), Suschkin (1899) and Pycraft (1902) for the corresponding spaces observed in the dried skull (that is, rostral, caudal and dorsal tympanic recesses) rather than that of Baumel *et al.* (1979) or Whetstone (1983), because the former has historical priority and is still in use by many workers (e.g. Saiff, 1983; Walker, 1985). The other two major tympanic diverticula invade the elements of the mandibular arch—the quadrate and articulare. The quadrate and arcticulare diverticula together have been termed the 'siphonial system' by some workers (e.g. Hecht & Tarsitano, 1983; Tarsitano, 1985a). Although these diverticula are indeed sometimes closely associated with each other (e.g. *Fulmarus*; Saiff, 1974), they often have no special relationship and should be considered as separate. All of these diverticula initially pass between bones and only later invade cartilaginous or osseous tissue. Although the diverticula usually begin as separate outgrowths of the middle ear sac, broad communications are typically observed in adults.

The dorsal tympanic diverticulum (Fig. 2) is found in all modern birds although it is a variable structure. It forms as an evagination of the wall of the middle ear sac dorsal to the columellar recess (in which lie the fenestrae ovalis and cochleae; Stresemann, 1927–34) and passes medial to the external ophthalmic artery (stapedial artery of some authors). The diverticulum passes dorsally between the prootic and squamosal bones. In doing so, it directly pneumatizes both bones. Walker (1985) noted that in many birds only a pneumatic fossa is produced on the dorsolateral surface of the prootic. Later in ontogeny the left and right diverticula may communicate within the trabeculated dermal skull roof. This communication results from the indirect pneumatization of intervening bones (e.g. the parietal). In most cases, the dorsal
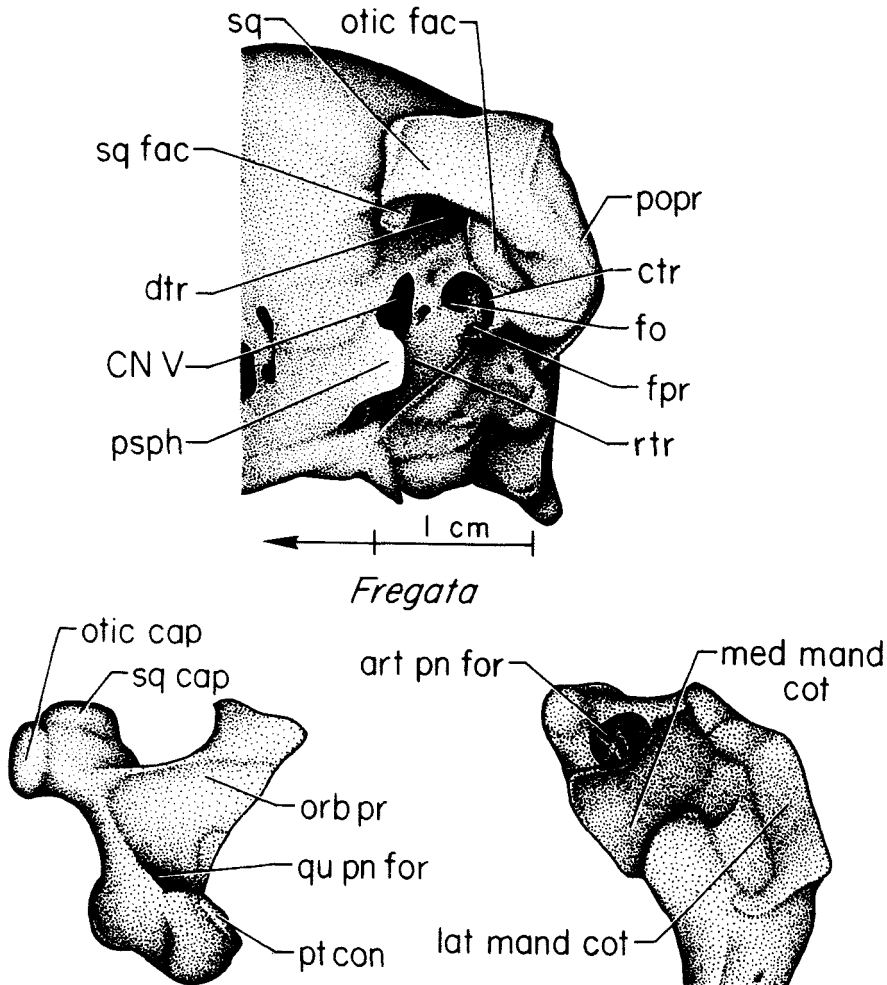
Figure 4. Osteological correlates of tympanic pneumaticity. Top, Braincase of *Fregata minor* in left ventrolateral view. Lower left, Left quadrate of same in medial view. Lower right, Articular region of left lower jaw of same in dorsal view. Abbreviations: art pn for, articulare (siphonial) pneumatic foramen; CN V, trigeminal nerve (CN V) foramen; ctr, caudal tympanic recess; dtr, dorsal tympanic recess; fo, fenestra ovalis; fpr, fenestra pseudorotundum; lat mand cot, lateral mandibular cotylus; med mand cot, medial mandibular cotylus; orb pr, orbital process of quadrate; otic cap, otic capitulum of quadrate; otic fac, otic facet of braincase; popr, paroccipital process; psph, alaparasphenoid; pt con, pterygoid condyle; qu pn for, quadrate pneumatic foramen; rtr, rostral tympanic recess; sq, squamosal; sq cap, squamosal capitulum of quadrate; sq fac, squamosal facet of braincase.

tympanic diverticulum eventually communicates with the caudal tympanic diverticulum within the paroccipital process and with the rostral tympanic diverticulum, either within the prootic bone or lateral to it. Thus, the dorsal tympanic recess occupies the prootic, squamosal and opisthotic bones through direct pneumatization, and the parietal, frontal and sometimes the epiotic and supraoccipital bones through indirect pneumatization (Fig. 4A). As Saiff (1974) noted, a few muscle fibres occasionally occupy part of the dorsal tympanic recess; in these cases the air sac is intermuscular.

Saiff (1974) also commented on the lack of vasculature passing through the dorsal tympanic diverticulum in the birds he studied. In many birds, however, the ramus occipitalis of the external ophthalmic artery, passes through this air space (Midtgard, 1984). The ramus occipitalis passes between the quadrate capitula to traverse the air space and exit the skull in a foramen between the exoccipital and the squamosal; Walker (1972, 1985) considered this occipital foramen homologous to the post-temporal fenestra of non-avian archosaurs. The ramus occipitalis is enclosed within a bony tube in some birds (e.g. *Larus* and *Grus*) as it traverses the dorsal tympanic recess. Formation of osseous tubes around structures traversing pneumatic diverticula is common (Bremer, 1940). In some birds (e.g. *Diomedea* and *Morus*), the occipital foramen also may communicate with the caudal tympanic recess.

In all modern birds, the quadrate contacts the braincase and squamosal. The separation of the otic and squamosal capitula by the dorsal tympanic diverticulum contributes to the formation of the 'double-headed' quadrate in neognath birds. In most neognaths the entrance to the dorsal tympanic recess is between the otic and squamosal facets (cotylae) for the quadrate capitula (Fig. 4A). In ratites (and indeed in some neognaths as well) the diverticulum does not separate the quadrate capitula, and the otic and squamosal facets for the quadrate capitula become continuous resulting in the 'single-headed' morphology.

In all modern birds the caudal tympanic diverticulum (Fig. 2) forms as an evagination of the caudal wall of the middle ear sac within the columellar recess, usually caudodorsal to the fenestra ovalis (= fenestra vestibularis) and fenestra pseudorotundum (= fenestra cochleae). Thus the columellar recess usually contains three foramina: the fenestra ovalis, the fenestra pseudorotundum, and the entrance to the caudal tympanic recess (Fig. 4A). Initially the diverticulum forms a roughly spherical space within the otic capsule (which ossifies as prootic, opisthotic, and usually epiotic) and is bounded approximately by the caudal semicircular canal, horizontal semicircular canal, utriculus and caudal wall of the paroccipital process. I term this space the 'proximal chamber' of the caudal tympanic recess. The 'distal chamber' of the recess forms as the diverticulum expands within the paroccipital process, sending off two subsidiary diverticula: one dorsally within the opisthotic (usually communicating with the dorsal tympanic diverticulum and thus indirectly pneumatizing the epiotic and squamosal bones), and another caudoventrally within the metotic strut (indirectly pneumatizing the basioccipital). The distal chamber of the caudal tympanic recess is roughly equivalent to the 'cavum metoticum' of Müller (1961); the latter term should be restricted to the cavity formed prior to the ossification of the metotic cartilage. Eventually, the surrounding bones usually become highly trabeculated. In dried skulls, therefore, the caudal tympanic recess can reside in the prootic, opisthotic (and perhaps exoccipital), epiotic, squamosal, and basioccipital bones.

The rostral tympanic recess exhibits a diversity of morphologies in modern birds but is never absent. It is intimately associated with the parasphenoid. The avian parasphenoid is a complex bone, and Jollie (1957) identified as many as seven centres of ossification. The portions of the parasphenoid with which we are concerned are the alaparasphenoid (tympanic wing of the basisphenoid of Erdmann, 1940; lateral wall of the presphenoid sinus of Saiff, 1974, 1978, and

other papers), the rostroparasphenoid (the parasphenoid rostrum of most authors) and the basiparasphenoid (the basitemporal platform or plate of Parker [1866] and other authors). The rostral tympanic diverticulum arises as a rostral outpocketing of the middle ear sac (Fig. 2) that passes rostromedially between the alaparasphenoid and the basisphenoid which are both directly pneumatized (Fig. 4A). The laterosphenoid (= pleurosphenoid) is also pneumatized directly by the rostral tympanic diverticulum. In most birds, the contralateral diverticula communicate ventral to the pituitary fossa and extend into the rostroparasphenoid. Medial extensions of the diverticulum often develop in the basiparasphenoid which sometimes becomes inflated. The facial nerve usually exits the braincase within or just caudal to the rostral tympanic recess and its palatine ramus must traverse the air space. Likewise, the cerebral carotid artery passes through the recess and, along with the sphenopalatine nerve and the palatine ramus of the facial nerve, is usually sheathed in bone to form a parabasal canal (Kesteven, 1925; Müller, 1963; Saiff, 1974).

The rostral tympanic recess in dried skulls (Fig. 4A) is a trabeculated conical air space with its apex directed rostromedially. The lateral wall of the recess, the alaparasphenoid, is variable in development. Sometimes it encloses the auditory tube within the recess. Rarely (e.g. *Morus*), the lateral wall is essentially lacking, there being only medial pneumatic foramina. In some birds (e.g. some procellariiforms) the alaparasphenoid is poorly ossified and the diverticulum is exposed laterally. Many birds have a complete tube, which in *Spheniscus* contacts the shaft of the quadrate. A few birds (e.g. *Gallus* and ratites), exhibit a greatly inflated alaparasphenoid.

The quadrate diverticulum (Fig. 2) exhibits a diversity of morphologies in modern birds. In some birds, mostly diving birds (such as, *Gavia*, *Spheniscus*, *Pelecanoides*, and alcids), this diverticulum does not pneumatize bone, and the adult quadrate bone is apneumatic. In *Gallus*, the quadrate diverticulum begins as a rostrodorsal expansion of the lateral portion of the middle ear sac and invades the quadrate cartilage prior to ossification (Bremer, 1940). In most birds, the diverticulum enters the quadrate ventromedially near the base of the orbital process (Fig. 4B), but other pneumatic foramina, such as dorsomedially on the shaft or on its caudal surface, are common. More than one pneumatic foramen, often combinations of these, are found in some birds (e.g. some individuals of *Larus*). All of these are considered homologous variations. A less clear case of homology is encountered when considering birds such as *Grus* in which the quadrate is pneumatized by a diverticulum dorsally between the capitula, adjacent to the dorsal tympanic diverticulum. It is not clear whether this situation represents dorsal migration of the quadrate diverticulum or loss of the quadrate diverticulum and pneumatization of the quadrate by a subsidiary diverticulum of the dorsal tympanic diverticulum.

The articulare diverticulum (or siphonium) is a caudoventral outgrowth of the middle ear sac (Fig. 2) that passes between the jaw muscles as a membranous tube to enter the mandibular (Meckel's) cartilage. In some birds, it gives off subsidiary intermuscular diverticula (Jacquemin, 1836). The position of the articulare pneumatic foramen is generally at the base of the medial process of the mandible, caudomedial to the medial mandibular facet (Fig. 4C). Additional pneumatic foramina may be present surrounding or within the jaw articulation. Although an articulare diverticulum is present in perhaps all birds, in many

(e.g. domestic fowl and the diving birds noted above) it fails to invade cartilage or bone, as witnessed by the lack of pneumatic foramina. In most cases, the articulare diverticulum is surrounded by sometimes dense connective tissue. Occasionally, this connective tissue ossifies (e.g. *Corvus*) and is termed the Os siphonium (Jollie, 1957). Nitzsch (1811) named this ossification the 'siphonium', but 'siphonium' also has come to represent the epithelial diverticulum (Bignon, 1889). I consider articulare diverticulum and siphonium to be synonyms.

CRANIOFACIAL PNEUMATICITY IN MESOZOIC BIRDS

Ichthyornis

The only facial fragments known for *Ichthyornis* are a small fragment of the maxilla (with evidence of five alveoli) from *I. dispar* and a fragment of the dorsal process of the premaxilla from *I. victor*. These fragments are insufficient to determine even presence or absence of nasal pneumaticity.

The situation regarding tympanic pneumaticity is only a little better. The two crania are so crushed that, with the present state of preparation, little can be said with confidence. Based on comparisons with *Archaeopteryx*, Whetstone (1983) identified a caudal tympanic recess in YPM 1459. Given errors in identification of several features of the otic region of *Archaeopteryx* (see below), Whetstone's interpretations of the *Ichthyornis* braincase may be incorrect.

Ichthyornis, however, clearly possessed quadrate and articulare diverticula. The quadrates of YPM 1775 were certainly pneumatic, and are modern in most regards. The left quadrate exhibits a large triangular fossa on its rostromedial surface; a large foramen is found at the base of this fossa (Fig. 5A, C). This foramen is in precisely the same position as the pneumatic foramen in the quadrates of many 'primitive' modern birds (Fig. 4B), and I consider it to be the quadrate pneumatic foramen. The foramen is large, round, and located on the ventromedial surface of the shaft at the base of the orbital process (broken in this specimen) just dorsolateral to the pterygoid condyle.

All of the known caudal fragments of the lower jaw of *Ichthyornis* exhibit characteristic evidence of an articulare diverticulum. YPM 6264 (Fig. 5B, D) and YPM 1761 both show a large, somewhat triangular foramen entering the articulare just caudal to the medial mandibular cotylus. As in modern birds, the articulare pneumatic foramen is at the base of the medial process of the mandible. Although the extent of the articulare recess cannot be determined, it must be large judging from the relatively large size of the pneumatic foramen.

Thus, *Ichthyornis* clearly possessed quadrate and articulare diverticula that pneumatized the quadrate and lower jaw, respectively (Table 1). Whether or not these birds possessed the periotic sinus system of other birds cannot be determined until detailed study of the crania is undertaken.

Hesperornithidae

As all of the facial elements are known, the antorbital fossa of *Hesperornis* can be reconstructed (Fig. 6). The maxilla forms its ventral, rostral, and medial borders, the nasal its dorsal border, and the lacrimal its caudal border; laterally the antorbital fenestra was presumably covered by skin. *Parahesperornis* probably
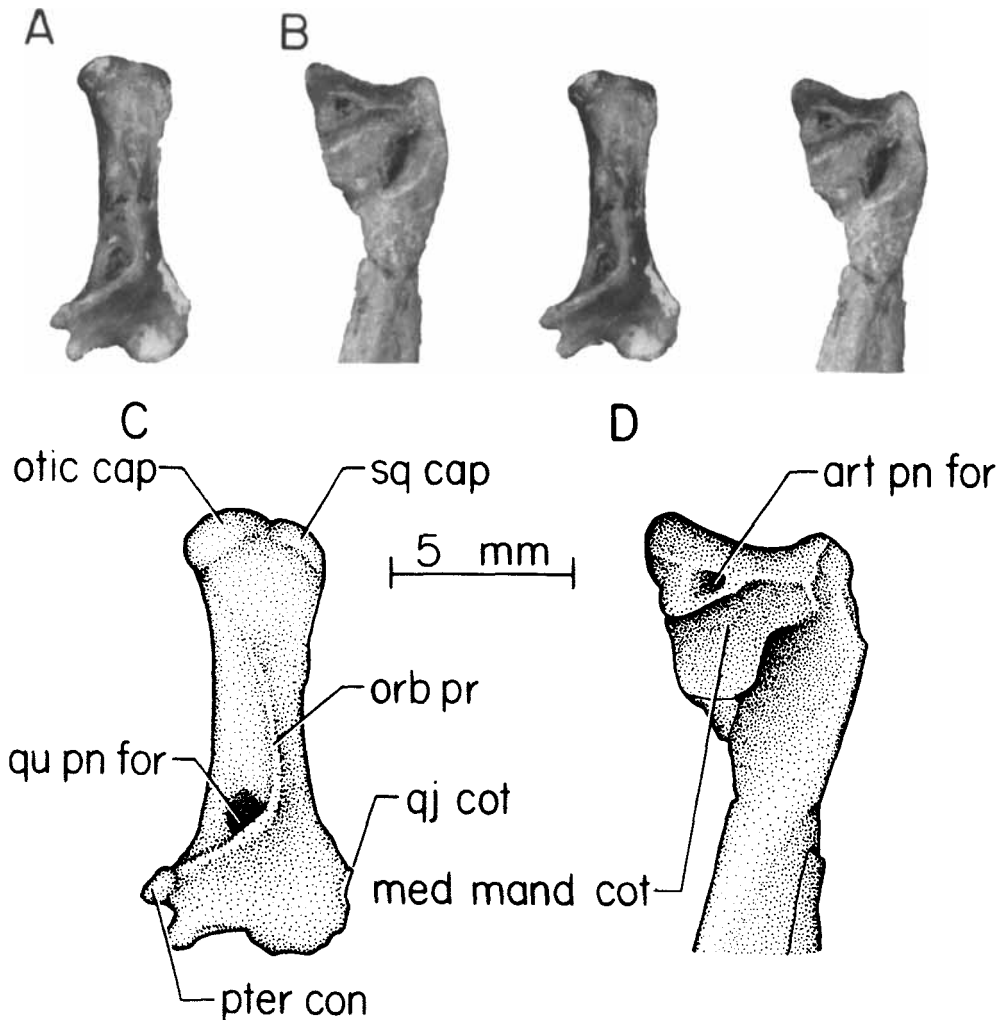
Figure 5. A, Stereophotographs of left quadrate of *Ichthyornis victor* (YPM 1775) in rostral view. B, Stereophotographs of left lower jaw of *I*. sp. cf. *I. dispar* (YPM 6264) in dorsal view. C, Drawing of A. D, Drawing of B. Abbreviations: art pn for, articulare (siphonial) pneumatic foramen; med mand cot, medial mandibular cotylus; orb pr, remains of broken orbital process of quadrate; otic cap, otic capitulum of quadrate; pter con, pterygoid condyle; qj cot, cotylus of quadratojugal; qu pn for, quadrate pneumatic foramen; sq cap, squamosal capitulum of quadrates.

exhibited similar morphology, but the maxillae are very crushed. Although the presence of an antorbital fossa might be considered insufficient evidence, in and of itself, to infer an antorbital sinus and thus nasal pneumaticity, virtually all modern birds have an antorbital fossa of comparable morphology; in these birds an antorbital sinus is present. On the basis of this comparison and the hypothesized pneumatic features discussed below, I infer the presence of an antorbital sinus in *Hesperornis* and *Parahesperornis*.

The nasal conchae of hesperornithids are not preserved, probably due to a lack of ossification. Thus, it is not possible to identify the position of the
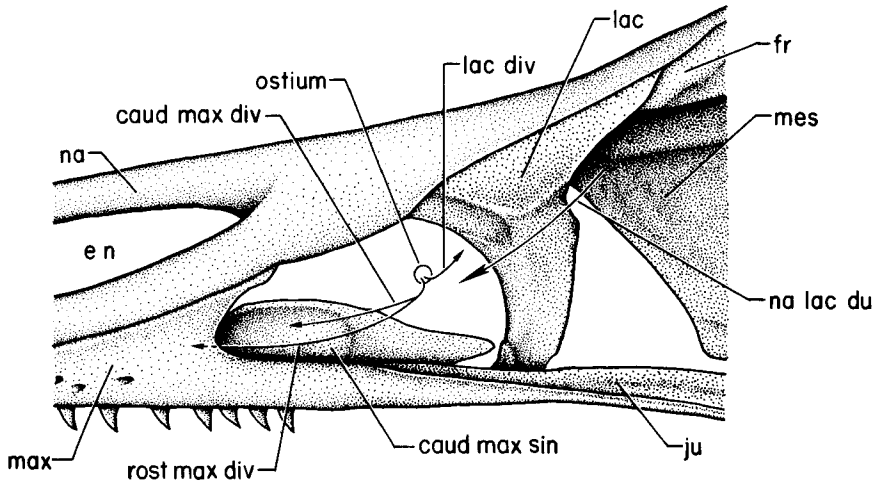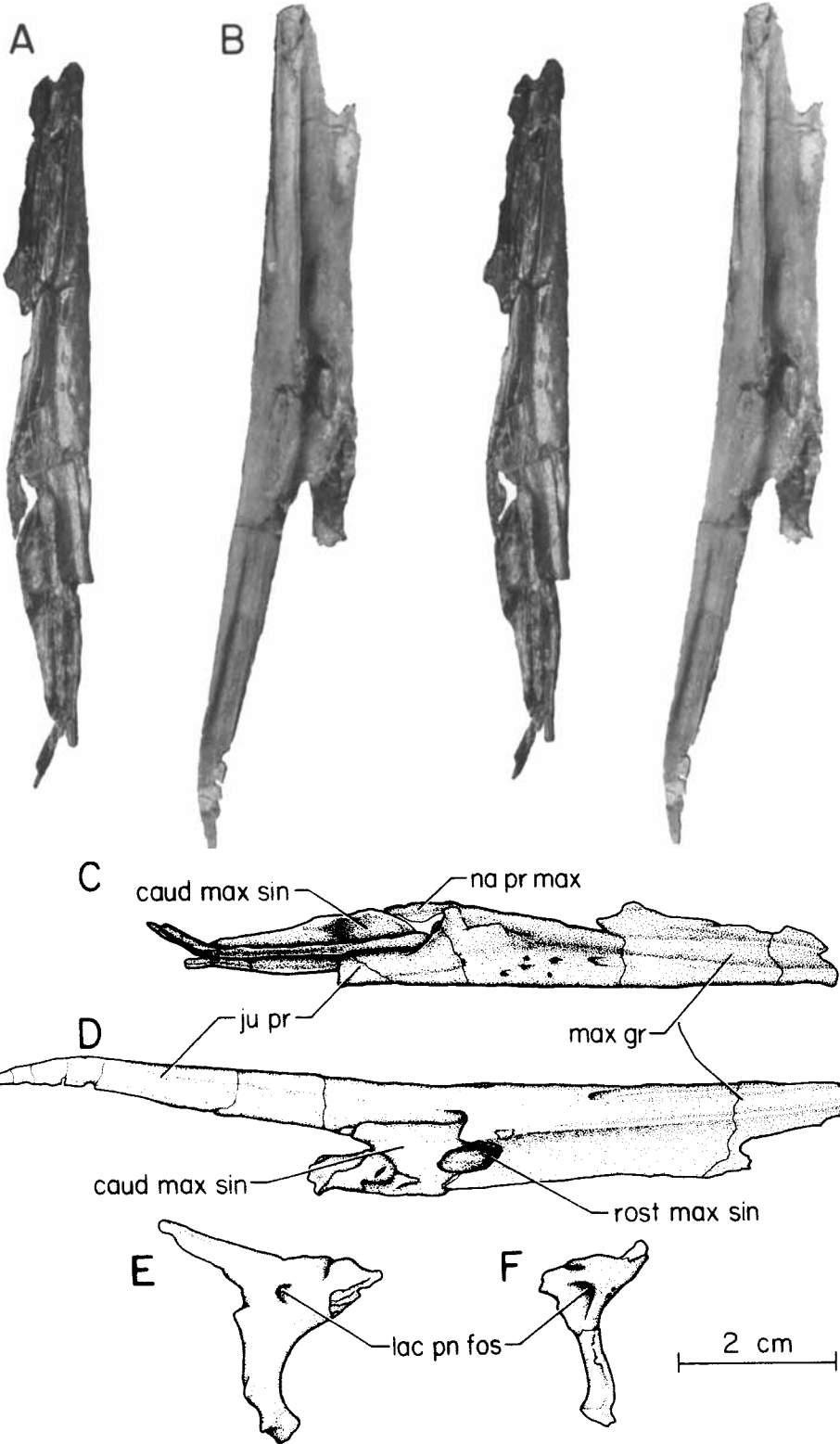
Figure 6. Reconstruction of antorbital fossa of *Hesperornis regalis* in left lateral view. Abbreviations: caud max div, position of caudal maxillary diverticulum; caud max sin, caudal maxillary sinus; e n, external nares; fr, frontal; ju, jugal; lac, lacrimal; lac div, position of lacrimal diverticulum; max, maxilla; mes, mesethmoid; na, nasal; na lac du, course of nasolacrimal duct; ostium, position of ostium of antorbital sinus; rost max div, position of rostral maxillary diverticulum.

antorbital sinus ostium into the nasal cavity. Likewise, the presence of a conchal diverticulum pneumatizing the caudal (olfactory) concha cannot be inferred.

None of the preserved hesperornithid premaxillae exhibit pneumatic features. Thus, there is no positive evidence to indicate the presence of a premaxillary diverticulum. Although such an air sac might have been present but did not pneumatize bone, it remains that hesperornithid premaxillary bones were apneumatic. Reduced pneumaticity or apneumaticity is a prediction of the hypothesis that the extensive pachyostosis observed in the hesperornithid postcranium (Martin, 1983a) extended into the skull. This hypothesis is tested further below.

The mesethmoid bone in *Hesperornis* and *Parahesperornis* is solid and clearly apneumatic. Thus, there is no positive evidence of a mesethmoidal diverticulum. Recall that most modern birds also lack a mesethmoidal diverticulum of the antorbital sinus. In hesperornithids the palatal skeleton is apneumatic, and as a result there is no reason to infer the presence of a suborbital diverticulum or any of its subsidiary diverticula.

There are, however, pneumatic features in the antorbital region of hesperornithids. Evidence of a lacrimal diverticulum is best expressed in *Parahesperornis* (KUVP 2287). On the medial aspect of its lacrimal, dorsally near the bone's articulation with the frontal, there is a large fossa (Fig. 7F). This fossa opens rostromedially towards the antorbital fossa and is directed caudodorsally into the bone. At the caudal apex of this conical recess are two foramina. It is likely that these foramina connect with two foramina on the caudal surface of the bone. This fossa is almost certainly a pneumatic fossa. Its relations are very similar to those in neornithines. An important difference, however, is that in *Parahesperornis* the body of the bone itself is not pneumatized and trabeculated. For this reason, I have identified a pneumatic fossa rather than a pneumatic

Figure captions with labels:

C — caud max sin, na pr max

D — ju pr, max gr, caud max sin, rost max sin

E, F — lac pn fos

2 cm

foramen. Another difference is in the presence of caudal foramina communicating with the lacrimal recess. Although uncommon, this situation.is not unknown in modern birds (e.g. *Diomedea*, KUMNH 67080).

Despite the caudal foramina, it is likely that the lacrimal fossa of *Parahesperornis* is associated with pneumaticity rather than with either the nasolacrimal duct or nasal gland duct. In virtually all modern birds the nasolacrimal duct passes *lateral* to the lacrimal bone before emptying into the respiratory region of the nasal cavity ventral to the middle concha (Bang & Wenzel, 1985). Although a few ratites send thin, lateral processes that almost enclose the duct, the nasolacrimal duct rarely, if ever, passes directly through the body of the lacrimal bone. Instead, most birds have a lateral groove on the lacrimal for the nasolacrimal duct. Both hesperornithids have broad lateral grooves for passage of the nasolacrimal ducts (Fig. 6). These birds also have prominent supraorbital grooves on the dorsal surface of the frontal bones indicating well-developed nasal salt glands (not surprising in marine diving birds). As with the nasolacrimal duct, the nasal gland duct of neornithines does not pierce the lacrimal on its way to the nasal cavity, but rather passes medial to the bone (Marples, 1932).

The two hesperornithids differ in the degree of lacrimal pneumaticity. They agree in having a dorsomedial pneumatic fossa and caudal foramina, but differ greatly in the size of the fossa. In *Parahesperornis* the pneumatic fossa is large and expands within the bone. In *Hesperornis* (Fig. 7E), on the other hand, the fossa is very shallow. It is presently impossible to polarize this feature; the lacrimals of plesiomorphic hesperornithiforms (*Baptornis* and *Enaliornis*) are unknown and the only other described lacrimal of a Mesozoic bird (that of *Archaeopteryx*) is too poorly preserved. Martin (1984), however, suggested that *Parahesperornis* is a less specialized member of Hesperornithiformes than is *Hesperornis*. Perhaps, then, *Parahesperornis* simply retains the plesiomorphically less pachyostotic condition of the lacrimal, and *Hesperornis* is derived in reducing lacrimal pneumaticity associated with increased pachyostosis. Other craniofacial features (discussed below) support this assessment.

The maxillae of hesperornithids also show evidence of pneumaticity. The morphology of the maxilla of *Hesperornis* is quite modern—despite the presence of teeth. As in palaeognaths, the maxilla of *Hesperornis* has broad palatine processes (Fig. 7B, D). The dorsal surface of the rostral portion of the palatine process in KUVP 71012 is strongly concave. The caudal end of this portion, however, seems to have a small cavity directed rostrally for a short distance. This cavity may be homologous with that in *Casuarius* where it becomes a greatly inflated, tubular structure housing the maxillary diverticulum. *Struthio* and *Dromaius* are more similar to *Hesperornis* in having a smaller cavity (Fig. 8).

The caudal portion of the palatine process of the maxilla also shows evidence of pneumaticity in *Hesperornis* (e.g. YPM 1206: Fig. 7A, C). The caudal portion of the palatine process is relatively vertical and is drawn out into a tapering,

Figure 7. A, Stereophotographs of right maxilla of *Hesperornis regalis* (YPM 1206) in lateral view. B, Stereophotographs of left maxilla of same (KUVP 71012) in dorsal view. C, Drawing of A. D, Drawing of B. E, Left lacrimal of *H. regalis* (KUVP 71012) in medial view. F, Right lacrimal of *Parahesperornis alexi* (KUVP 2287) in medial view. Abbreviations: caud max sin, caudal maxillary sinus; ju pr, jugal process; lac pn fos, lacrimal pneumatic fossa; max gr, maxillary groove for premaxilla and nasal; na pr max, nasal process of maxilla; rost max sin, rostral maxillary sinus.
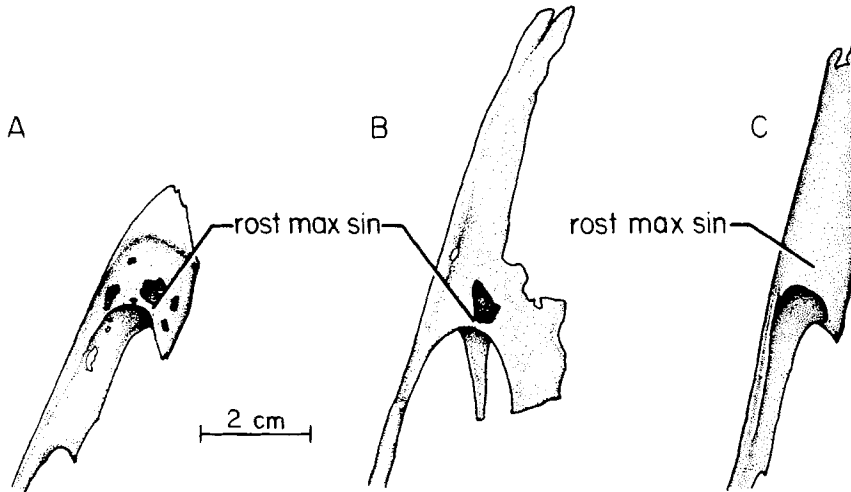
Figure 8. Dorsal views of left maxillae of ratites showing rostral maxillary sinuses and lack of caudal maxillary sinuses. A, *Dromaius*. B, *Struthio*. C, *Casuarius*. Abbreviation: rostr max sin, rostral maxillary sinus.

pointed structure. The vertical portion is excavated, forming an oval depression that is concave laterally. This fossa corresponds well with the vertically oriented, cup-shaped 'maxillary sinus' of modern neognath birds (Fig. 3). I refer to it as the 'caudal maxillary sinus' in *Hesperornis* to distinguish it from the 'rostral maxillary sinus' in the rostral portion of the palatine process. The caudal maxillary sinus is really only a pneumatic fossa in that the bone is modified by the air sac but not invaded by it. This situation is similar to that in some other diving birds (such as penguins) where the maxillary diverticulum fails to resorb and trabeculate osseous tissue in the palatine process.

Nasal pneumaticity, therefore, is well represented, though not extensive, in hesperornithids (Table 1). There was a lacrimal diverticulum of the antorbital sinus that produced a prominent lacrimal pneumatic fossa in *Parahesperornis*; this fossa is perhaps somewhat reduced in *Hesperornis*. A maxillary diverticulum was also present in *Hesperornis*, resulting in a small pneumatic recess in the rostral

TABLE 1. Summary of major pneumatic features of Mesozoic birds. Abbreviations: +, presence; −, absence; ?, unknown or equivocal; ARCH, *Archaeopteryx*; ENAL, *Enaliornis*; BAPT, *Baptornis*; PARA, *Parahesperornis*; HESP, *Hesperornis*; ICHTH, *Ichthyornis*; NEORN, Neornithes

	ARCH	ENAL	BAPT	PARA	HESP	ICHTH	NEORN
Nasal pneumaticity							
Maxillary sinus	+	?	?	?	+	?	+
Lacrimal sinus	?	?	?	+	+	?	+
Tympanic pneumaticity							
Dorsal tympanic recess	+	+	?	+	+	?	+
Caudal tympanic recess	+	+	?	+	+	?	+
Rostral tympanic recess	+	+	?	+	+	?	+
Quadrate sinus	−?	?	−	−	−	+	+
Articulare sinus	?	?	+	+	−	+	+

portion of the palatine process (the rostral maxillary sinus) and a more prominent cup-shaped pneumatic fossa in the caudal portion (the caudal maxillary sinus). Unfortunately the maxillae of *Parahesperornis* are poorly known.

As with nasal pneumaticity, tympanic pneumaticity is well represented in hesperornithids and is in fact more extensive than in most modern diving birds. Four of the five principal tympanic diverticula can be inferred in hesperornithids. The exception is the quadrate diverticulum.

Evidence for a dorsal tympanic recess is preserved in all specimens preserving relevant portions of the braincase. The dorsal tympanic diverticulum passed rostral to the quadrate's articulations with the braincase, as shown by the disposition of the cotylae for the quadrate capitula. For *Hesperornis* these are best preserved in KUVP 71012. The squamosal and otic cotylae are at the caudal margin of the tympanic cavity. They are not confluent (as in some of the ratites), but are separated by a non-articular intercotylar depression. The entrance to the dorsal tympanic recess is fully rostral to these facets, much as in many modern birds, such as *Fregata* (Fig. 4A) and *Diomedea*. Marsh (1880) considered the quadrate of *Hesperornis* to be 'struthious' in that he interpreted it as 'single-headed'. As discussed earlier, this is a function of the entrance to the dorsal tympanic recess. The dorsal tympanic diverticulum did not significantly separate the quadrate capitula resulting in a negligible intercapitular sulcus. There are distinct capitula, however, contrary to Marsh's (1880) assertion; this observation is corroborated by the presence of the intercotylar depression noted above.

The large entrance to the dorsal tympanic recess is best seen in detail in *Parahesperornis* although the same general pattern can be observed in the specimens of *Hesperornis*. The rostrolateral margin of the entrance in *Parahesperornis* (formed by the squamosal and probably the laterosphenoid) is undercut by the recess. The caudal margin is formed by the intercotylar depression (broken in KUVP 2287 but intact in KUVP 71012) and the quadrate cotylae. The ventral portion of the entrance to the dorsal tympanic recess is formed by the prootic bone. FMNH PA 219 (*Hesperornis*) clearly shows this ventral portion of the entrance (Fig. 9). The diverticulum passed dorsally rostromedial to the prootic portion of the otic cotyla, producing a pneumatic fossa on the rostrolateral surface of the prootic. These relationships are virtually identical to those in sea birds such as procellariiforms and pelecaniforms.

An unobstructed view of the dorsal tympanic recess itself cannot be observed in its entirety in any of the specimens due to crushing and persistent matrix. X-Rays of KUVP 71012 (*Hesperornis*) show a cavity in the region of the recess that continues medially a short distance under the intercotylar depression. Similarly, X-rays of KUVP 2287 (*Parahesperornis*) show larger cavities that extend dorsally and caudally. Owing to fortuitous preservation and breakage, the cavity of the dorsal tympanic recess can be directly observed in other *Hesperornis* material (FMNH PA 219). In this specimen (Fig. 9A, B) the bone dorsolateral to the recess (part of the squamosal) has been lost, revealing a roughly hemispherical cavity within the prootic and probably opisthotic bones. The recess extends ventrally a short distance caudal to the entrance. These bones enclosed the diverticulum but were not trabeculated (i.e. the walls of the recess are smooth and lack bony struts). In contrast, most modern birds have a highly trabeculated dorsal tympanic recess. *Spheniscus* and the juveniles of many other birds, however, show a similar morphology. There are a few small foramina
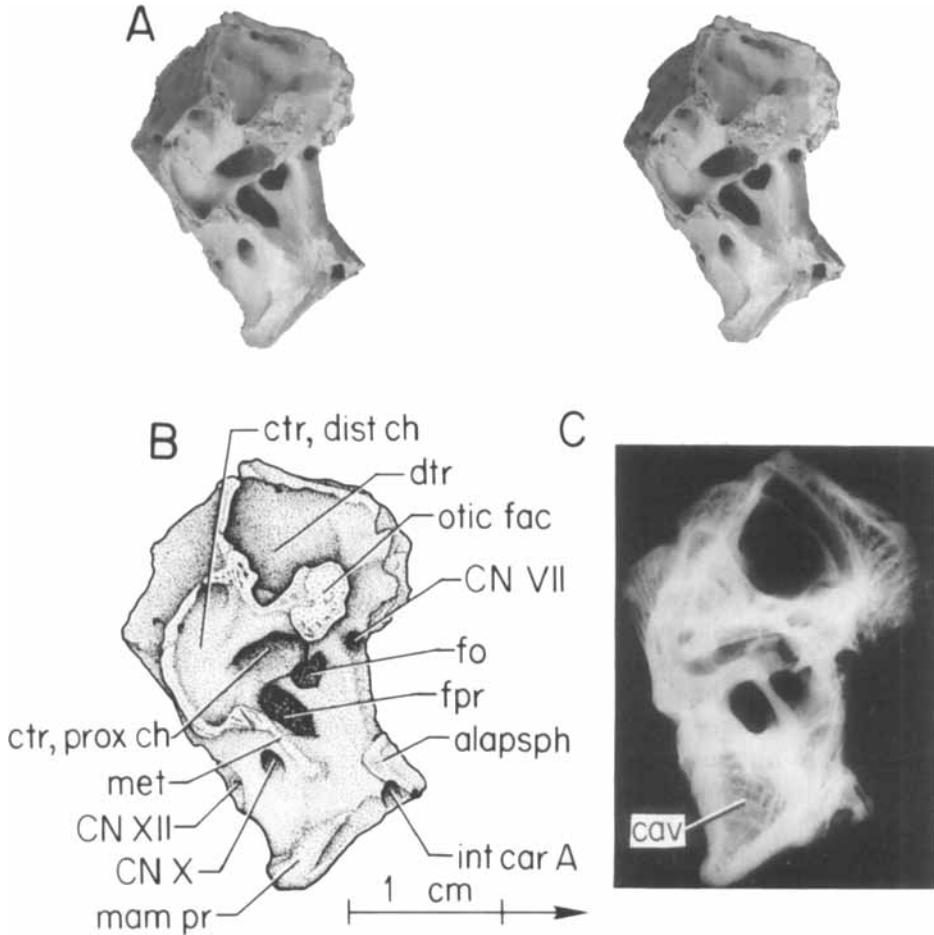
Figure 9. Fragment of right otic region of *Hesperornis* (FMNH PA 219) in lateral view. A, Stereophotographs. B, Drawing of A. C, X-Ray. Abbreviations: alapsph, alaparasphenoid fragment; aud tub, auditory tube foramen; cav, pneumatic cavity in caudal portion of basicranium; CN VII, foramen for facial nerve (CN VIII); CN X, foramen for vagus nerve (CN X); CN XII, foramen for hypoglossal nerve (CN XII); ctr, dist ch, distal chamber of caudal tympanic recess; ctr, prox ch, proximal chamber of caudal tympanic recess; dtr, dorsal tympanic recess; fo, fenestra ovalis; fpr, fenestra pseudorotundum; int car A, foramen of internal (cerebral) carotid artery; mam pr, mamillary process; met, broken metotic strut; otic fac, otic facet.

within the dorsal tympanic recess of FMNH PA 219 that appear to be vascular rather than pneumatic.

Hesperornithids possessed large occipital foramina (post-temporal fenestrae). In both KUVP 71012, YPM 1206, and KUVP 2287, the foramina are oval, oriented transversely, and located medial to the zygomatic process on the occipital surface caudal to the transverse nuchal crest. These foramina are large—relatively much larger than in most modern birds—and clearly enter the dorsal tympanic recess. Their large size may have resulted from incomplete ossification, the primitive retention of a larger post-temporal fenestra, resorption of surface bone through pneumatization, or the passage of large blood vessels.

There is no evidence for communication of the left and right dorsal tympanic recesses in any of the specimens of *Hesperornis* or *Parahesperornis*. X-Rays of the University of Kansas specimens show little medial extension of these spaces, and
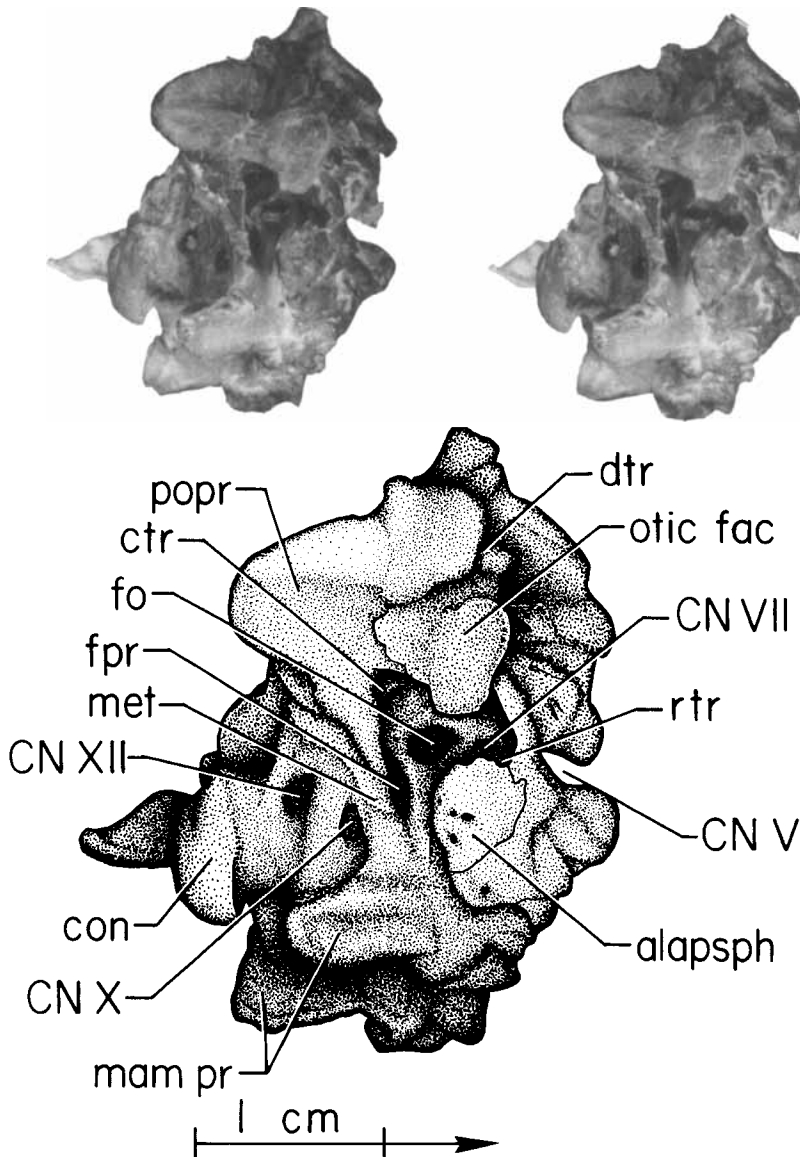
Figure 10. Fragment of braincase of *Hesperornis regalis* (YPM 1207) in right caudoventrolateral view. Abbreviations: alapsph, alaparasphenoid; CN V, trigeminal nerve (CN V) foramen; CN VII, facial nerve (CN VII) foramen; CN X, vagus nerve (CN X) foramen; CN XII, hypoglossal nerve (CN XII) foramen; con, occipital condyle; ctr, entrance of caudal tympanic recess; dtr, entrance of dorsal tympanic recess; fo, fenestra ovalis; fpr, fenestra pseudorotundum; mam pr, mamillary process; met, metotic strut; otic fac, otic facet; popr, paroccipital process; rtr, rostral tympanic recess.

FMNH PA 219 preserves at least part of the dorsomedial wall precluding this connection. Furthermore, there is no indication of the trabeculated skull roof that allows this communication in modern birds; known skull roof fragments (parietal and supraoccipital bones) exhibit a dense, solid morphology.

The caudal tympanic recess is best observed in specimens of *Hesperornis* (YPM 1207 and FMNH PA 219) although enough of it is preserved in *Parahesperornis* to be confident of its similarity to *Hesperornis*. In YPM 1207 (Fig. 10), the entrance to the caudal tympanic recess is well preserved and undistorted except for a

small fracture in the lateral portion of the right metotic strut which has resulted in dorsal displacement of the lateral part of the right paroccipital process. The entrance is within the weakly-developed columellar recess, caudodorsal to the fenestra ovalis and fenestra pseudorotundum. The entrance is bounded medially by the smooth 'threshold' (*sensu* Walker, 1985) which is continuous with the crista interfenestralis (which separates the fenestra ovalis and f. pseudo-rotundum). The prootic peduncle of the otic facet forms the rostral margin of the entrance. A curved horizontal ramus of the opisthotic/exoccipital running between the metotic strut and the otic facet forms the lateral margin. The caudal margin is formed by the dorsal part of the metotic strut. Finally, the entrance to the caudal tympanic recess is open ventrally and confluent with the middle ear cavity. This entrance is large relative to modern birds.

Caudodorsally, the proximal and distal chambers of the large caudal tympanic recess can be seen expanding within the paroccipital process of YPM 1207 but are best observed in FMNH PA 219 where the lateral wall is broken away (Fig. 9A, B). The proximal chamber of the caudal tympanic recess in *Hesperornis* (FMNH PA 219) is an oval, horizontally-oriented depression with a conical caudomedial extension. As in many modern birds, the proximal chamber undercuts the prootic peduncle of the otic facet both medially and ventrally.

The distal chamber of the caudal tympanic recess is reniform and vertically oriented. The ventral portion of the distal chamber extends caudoventral to the main chamber and caudal to the metotic strut; at the ventral apex are a few small foramina reaching into the metotic strut. This ventral portion of the distal chamber is homologous with that portion of the caudal tympanic recess that extends into the basioccipital in many modern birds. It is possible that the caudal portion of the basicranium was pneumatized by the caudal tympanic recess in *Hesperornis*. X-Rays of FMNH PA 219 (Fig. 9C) show a large trabeculated cavity within the region of the mamillary process; it is likely that the foramina noted above are pneumatic foramina. The dorsal portion of the distal chamber extends up to just caudolateral to the dorsal tympanic recess, from which it is separated by a wall of bone. As with the dorsal tympanic and lacrimal recesses, this recess is not characterized by trabeculation of the bone, much like modern diving birds and the young of most other birds.

The rostral tympanic recess, preserved in some form at least in all the specimens, is well developed in hesperornithids. As mentioned previously for modern birds, the rostral tympanic recess is a rostromedially-directed cavity lying between the alaparasphenoid and basisphenoid (Fig. 4). The alaparasphenoid forms the lateral wall of this recess (best preserved in YPM 1207; Fig. 10). The alaparasphenoid is thick—not the thin lamina of most modern birds—but is not pneumatically inflated as in ratites. It is rough and pitted ventrally, exhibiting numerous small foramina, while dorsally it is somewhat thinner and smoother. This morphology is unlike most modern birds and may have resulted from either extensive vascularization or incomplete ossification or both; the other specimens show similar morphology. The extensive alaparasphenoid in hesperornithids runs from the basicranial facet (basipterygoid process of Marsh, 1880 and Gingerich, 1973) up to the margin of the squamosal or laterosphenoid (at least in *Parahesperornis*) and extending medial and almost caudal to the quadrate shaft. Thus, the alaparasphenoid provided a lateral covering to most of the middle ear. In fact, the caudolateral

tip of the alaparasphenoid may well have contacted the shaft of the quadrate (as in some penguins).

Medial to the alaparasphenoid is the rostral tympanic recess. Within the rostromedially-directed recess there are two ridges or struts on the prootic. The facial foramen is directly rostroventral to the intersection of the two ridges. The vertical ridge provides a faint demarcation of the columellar recess caudally and the tympanic recess rostrally. The horizontal strut divides the recess into a smaller, dorsal space and a larger, ventral space. In FMNH PA 219, this ventral subcavity of the recess pneumatized the basisphenoid, producing a strutted pneumatic cavity within the bone rostral to the precondylar fossa.

There is good evidence for communication of the contralateral rostral tympanic recesses ventral to the hypophysial fossa. In *Parahesperornis* the alaparasphenoid is very thin near its attachment to the rostroparasphenoid (parasphenoid rostrum). There is clearly a cavity between the endocranial floor (basisphenoid) and the ala-/rostroparasphenoid complex, suggesting that the left and right rostral tympanic diverticula communicated. X-Rays corroborate these findings, indicating that the recess may have extended a short distance into the rostroparasphenoid as well. *Hesperornis* probably also has this communication as indicated by KUVP 71012 in which the base of the rostroparasphenoid is broken away revealing a cavity between the endocranial floor and parasphenoid.

The quadrate diverticulum of the middle ear sac of hesperornithids, if present, did not pneumatize the quadrate, because all known quadrates of *Hesperornis* and *Parahesperornis* are apneumatic. In these birds, there is a large fossa in the position of the quadrate pneumatic foramen observed in *Ichthyornis*, but no foramina enter the bone (Fig. 11D); as the quadrate portion of M. protractor quadrati et pterygoidei inserts in this area (Hofer, 1950; Zusi & Storer, 1969), the fossa may have been for muscle attachment.

The development of an articulare diverticulum is variable in hesperornithids. *Parahesperornis* has a large siphonial foramen on the dorsal surface of the articulare just caudal to the medial mandibular cotylus and rostral to a transverse
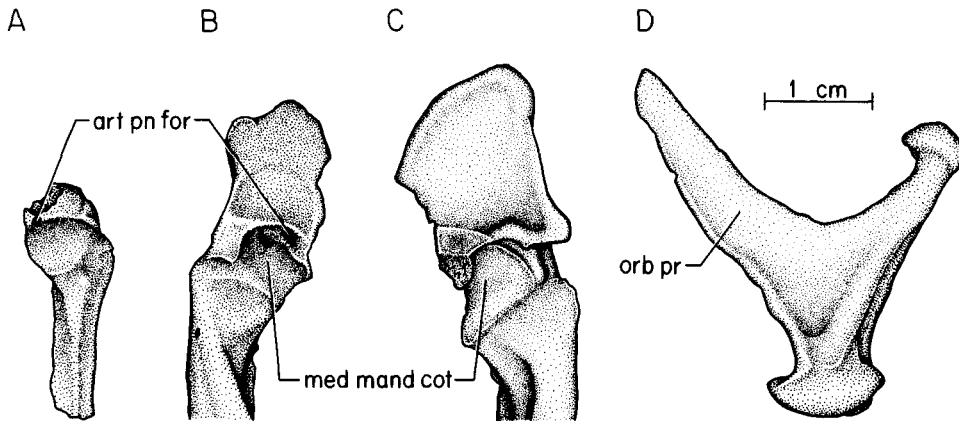

Figure 11. Dorsal views of articular region of lower jaws of A, *Baptornis advenus* (FMNH 395), left side; B. *Parahesperornis alexi* (KUVP 2287), right side; and C, *Hesperornis regalis* (KUVP 71012), left side. D, Right quadrate of *H. regalis* (KUVP 71012) in medial view. Abbreviations: art pn for, articulare (siphonial) pneumatic foramen; med mand cot, medial mandibular cotylus; orb pr, orbital process of quadrate.

crest separating the retroarticular process and the jaw articulation (Fig. 11B). In another specimen of *Parahesperornis*, KUVP 24090, there is also a portion of the chorda tympani canal (in oblique section). There is not, however, a large air space within the articulare.

Hesperornis, on the other hand, appears to totally lack articulare pneumaticity. There is an oval depression in the same position as the pneumatic foramen of *Parahesperornis*, but it does not penetrate the bone (Fig. 11C). This depression is similar to that found in modern birds that lose articulare pneumaticity and transform the diverticulum into a ligamentous structure, such as penguins, loons, alcids and some individuals of *Gallus* (Bremer, 1940). Thus, as we observed earlier regarding lacrimal pneumaticity, *Hesperornis* exhibits a (perhaps apomorphically) more pachyostotic condition than does its sister taxon *Parahesperornis*. These differences reinforce the assertion that these are indeed different species. That is, these differences cannot be ascribed to age. In not only modern birds but also crocodilians, pneumaticity generally increases with age. The differences between *Parahesperornis* and *Hesperornis* demonstrate precisely the *opposite* trend if one considers the former to be a juvenile of the latter. The type specimen of *Parahesperornis* may indeed be a juvenile, but not of *H. regalis*. It seems certain that there were two hesperornithids in the Niobrara sea, and the differences between these two taxa help elucidate the evolution of this group.

In summary (Table 1), the hesperornithids *Hesperornis* and *Parahesperornis* appear to have had an antorbital sinus, with lacrimal and maxillary diverticula pneumatizing bone. In the middle ear region, four of the five tympanic diverticula were present—only the quadrate diverticulum could not be inferred. In *Parahesperornis* but not *Hesperornis*, the articulare diverticulum pneumatized bone. The tympanic recesses of hesperornithids are large and well developed relative to some modern diving birds. The dorsal tympanic diverticulum produced cavities in the prootic, opisthotic and squamosal; the contralateral diverticula do not appear to have communicated within the skull roof. The caudal tympanic diverticulum entered the paroccipital process where it pneumatized the prootic, opisthotic (plus exoccipital) and probably the caudal portion of the basicranium. The caudal and dorsal tympanic diverticula did not communicate. The rostral tympanic diverticulum excavated the prootic, alaparasphenoid, basisphenoid, and probably the rostroparasphenoid. The contralateral rostral tympanic diverticula apparently communicated with each other.

Baptornis

The craniofacial anatomy of *Baptornis* is very poorly known. Study of the known premaxilla yields no positive evidence for the presence of a premaxillary diverticulum of the antorbital sinus in *Baptornis*. Premaxillary diverticula also could not be inferred for either *Hesperornis* or *Parahesperornis*. As the maxilla and lacrimal are not preserved in any specimens of *Baptornis*, nasal pneumaticity cannot be discussed further.

Martin & Tate (1976) noted that *Baptornis* possesses a quadrate fossa like that in hesperornithids and likewise that the quadrate was apneumatic.

A caudal fragment of the left lower jaw of FMNH 395 (Fig. 11A) provides the *only evidence* of tympanic pneumaticity in *Baptornis*. Caudal to the medial

mandibular cotylus on the dorsal surface of the articulare is a foramen in the same position as the articulare pneumatic foramen of *Parahesperornis* and other birds. I consider this foramen to be evidence for an articulare diverticulum in *Baptornis*.

Enaliornis

Braincases represent the only known craniofacial material of *Enaliornis*, and thus nothing can be said about nasal, quadrate or articulare pneumaticity. The best braincase provides detailed data on tympanic pneumaticity. The middle ear is large. As in modern birds and hesperornithids, the dorsal tympanic diverticulum in *Enaliornis* passed caudodorsally between the prootic and squamosal bones. Like hesperornithids, the squamosal and otic cotylae for the quadrate are at the caudal margin of the tympanic cavity and the entrance to the dorsal tympanic recess was rostral to these facets (Fig. 12). As preserved, there does not appear to be a non-articular intercotylar depression between the facets, in contrast with the hesperornithids. Thus, the entrance to the recess may have extended a short distance between the facets, suggesting that the diverticulum may have produced a small separation of the quadrate capitula,
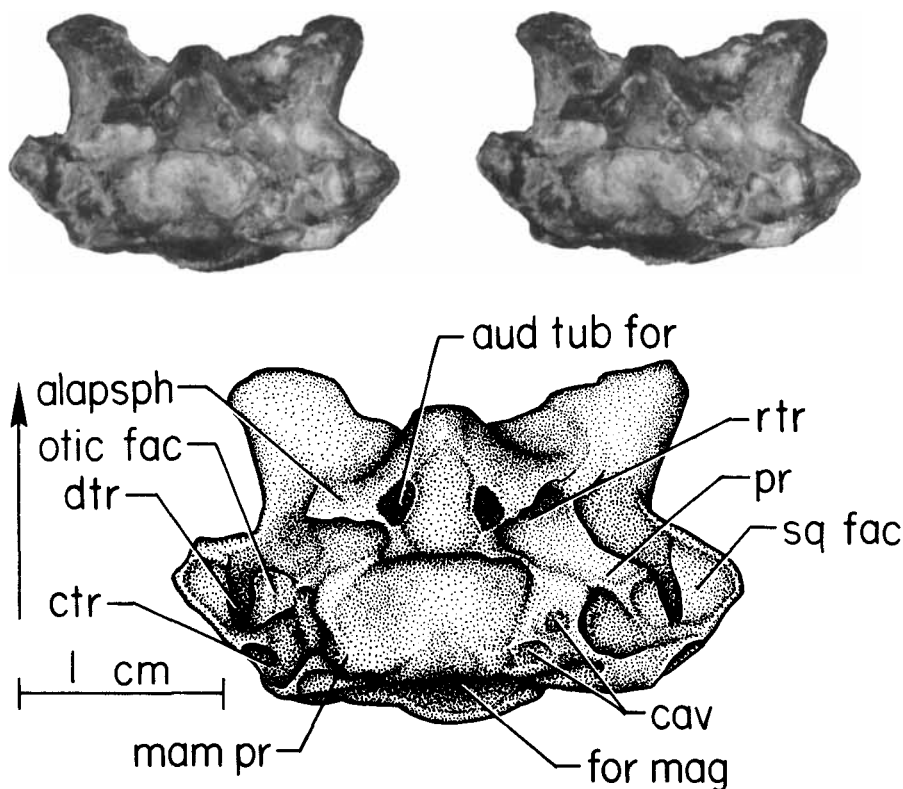

Figure 12. Braincase of *Enaliornis barretti* in ventral view. Abbreviations: alapsph, alaparasphenoid; aud tub for, auditory tube foramen; cav, pneumatic cavity in left mamillary process; ctr, caudal tympanic recess; dtr, entrance of dorsal tympanic recess; for mag, foramen magnum; mam pr, mamillary process; otic fac, otic facet; pr, prootic; rtr, rostral tympanic recess; sq fac, squamosal facet.
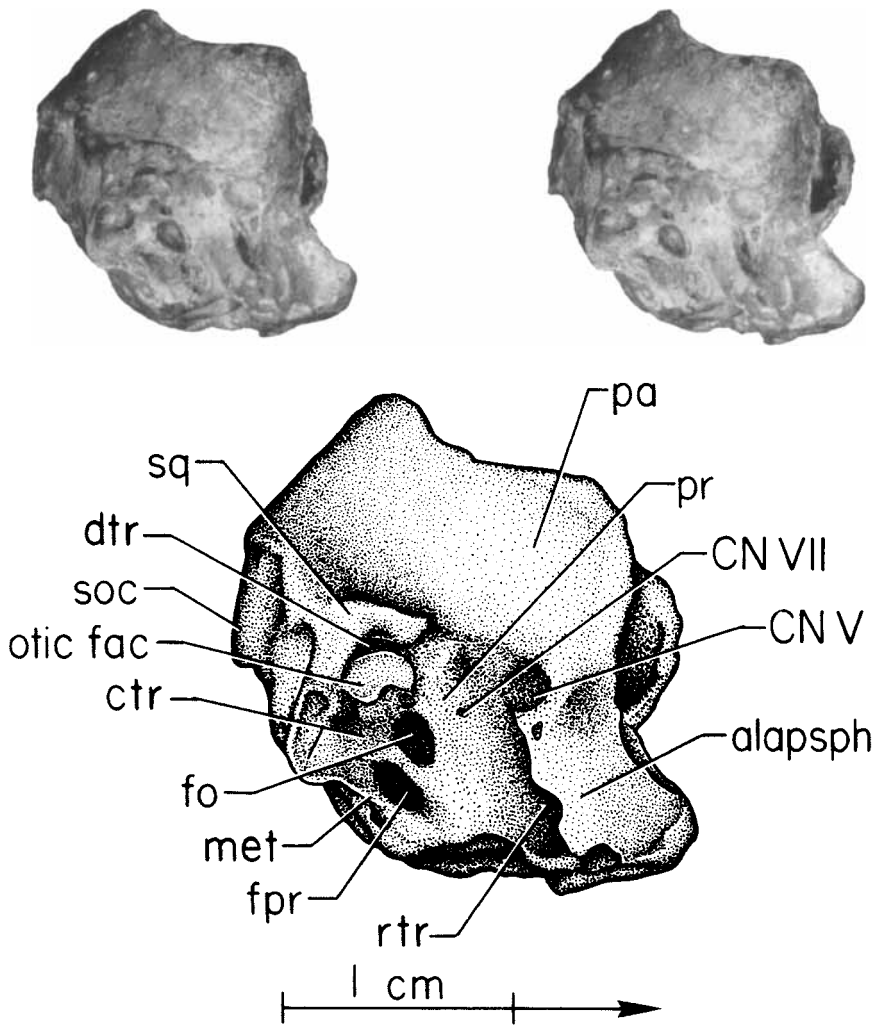
Figure 13. Braincase of *Enaliornis barretti* in right lateral view. Abbreviations: alapsph, alaparasphenoid; CN V, trigeminal nerve (CN V) foramen; CN VII, facial nerve (CN VII) foramen; ctr, caudal tympanic recess; dtr, entrance of dorsal tympanic recess; fo, fenestra ovalis; fpr, fenestra pseudorotundum; met, metotic strut; otic fac, otic facet; pa, parietal; pr, prootic; rtr, rostral tympanic recess; soc, supraoccipital; sq, squamosal.

resulting in a 'double-headed' quadrate similar to many modern birds. The entrance to the dorsal tympanic recess passes medial to the prootic peduncle of the otic cotylus which is excavated rostromedially (Fig. 13). The entrance is roofed by a horizontal crest of the squamosal.

Preserved on the left side of the skull is an occipital foramen. It is located laterally on the occiput, just caudal to the transverse nuchal crest. It is not as large as that in hesperornithids but would communicate with the dorsal tympanic recess. On the right side, there is a smaller, more lateral foramen that may communicate with the caudal tympanic recess, much as in some neornithines that also have multiple caudal foramina penetrating into the dorsal and caudal tympanic recesses.

Based on the distance between the endocranial wall and the external wall of the squamosal and also on the small size of the squamosal, the volume of the dorsal tympanic recess appears to be moderate—comparable to that of the hesperornithids. It seems very unlikely that the contralateral dorsal tympanic recesses communicate since both the supraoccipital and parietal bones are very thin medially, and the broken rostral edge of the parietal is solid and not strutted. Lack of a communication between the contralateral recesses therefore is common to both hesperornithids and *Enaliornis*.

The caudal tympanic recess of *Enaliornis* (Figs 12, 13) is remarkably similar to that of *Hesperornis* and strengthens the identification of this bird as a hesperornithiform. As in other birds, the entrance to the caudal tympanic recess is caudodorsal to the fenestrae ovalis and pseudorotundum (Fig. 13). The columellar recess is only weakly developed, as in *Hesperornis*. The 'threshold' to the recess, which forms the medial wall of the entrance, is smooth and continuous with the crista interfenestralis (as in *Hesperornis* and most modern birds). The entrance is roofed dorsally by the otic cotylus. Rostroventrally, the recess communicates broadly with the tympanic cavity. The lateral wall of the recess and hence the lateral wall of the entrance has been lost through abrasion.

The proximal chamber of the caudal tympanic recess is roughly spherical and undercuts the otic cotylus medially and especially caudally. There is a medial extension of this chamber, as in *Hesperornis*, but it does not appear to pass as deeply. The distal chamber of the recess is somewhat reniform and is more strongly divided into dorsal and ventral portions than in *Hesperornis*. The distal and proximal chambers are broadly confluent. The distal chamber extends dorsomedially to lie as a circular depression caudal to the otic cotylus and is separated from the dorsal tympanic recess; thus, these two recesses do not appear to communicate. The ventral portion of the distal chamber extends within the paroccipital process caudal to the fenestra pseudorotundum.

In many neornithines and apparently *Hesperornis*, the caudal tympanic recess extends ventrally to pneumatize the basioccipital. Although the occipital condyle has been lost through abrasion, the portion of the basioccipital flooring the endocranial cavity is preserved. This portion seems to be apneumatic. However, inside the left mamillary process (which has been opened up through abrasion; Fig. 12), there appear to be two cavities separated by a small beam of bone. These cannot be associated with the hypoglossal or vagus foramina as these foramina are well preserved on the right side and are situated as in hesperornithids and neornithines. These cavities compare well with the pneumatic recess within the mamillary process of *Hesperornis* (FMNH PA 219) and probably were formed by pneumatization by the caudal tympanic diverticulum via the metotic strut.

The rostral tympanic recess was well developed and large in *Enaliornis* (Figs 12, 13). It extended rostroventromedially from the middle ear. The alaparasphenoids, although preserved only rostromedially, probably extended much further caudally, at least to a position ventral to the trigeminal foramen. The alaparasphenoids are thin and do not exhibit the dimpling seen in *Hesperornis*. Within the recess there are only faint hints of the vertical and horizontal crests observed in *Hesperornis* (YPM 1207), and may not have been divided into dorsal and ventral portions.

It is very likely that the contralateral rostral tympanic diverticula

communicated in life. There is clearly a large space between the floor of the endocranial cavity and the parasphenoid below. Communicating with this cavity are two large ventral foramina in the parasphenoid. Seeley (1870) considered these to be for the carotid artery, but in modern birds the artery passes through the rostral tympanic recess medial to the alaparasphenoid. Alternatively, the foramina agree well with the auditory tube openings of ratites. If this identification is correct, then this supports their being an air-filled cavity dorsally.

In summary (Table 1), the dorsal tympanic diverticula of *Enaliornis* were much like those of hesperornithids and did not communicate with each other or the caudal tympanic diverticula. The caudal tympanic diverticula were very similar to those of *Hesperornis* and pneumatized the paroccipital process, otic capsule, and probably the mamillary processes of the basicranium. The rostral tympanic diverticula were well developed, and there was contralateral communication. As in the hesperornithids, there was little if any trabeculation of the walls of the recesses, which exhibit a smooth morphology.

Archaeopteryx

Of the four specimens of *Archaeopteryx* in which craniofacial material is preserved, the Berlin and Eichstätt specimens provide the best evidence of nasal pneumaticity in this bird. Among the few details that can be observed in the Berlin skull is the presence of a triangular antorbital fenestra (Heilmann, 1927; Ostrom, 1976). Unfortunately, the specimen is so damaged that no internal anatomy can be made out in this region. The Eichstätt specimen, however, exhibits a well-preserved, albeit crushed, antorbital fossa (Fig. 14). The antorbital fenestra is bounded by the maxilla ventrally, rostrally and dorsally (although the nasal may also take part in the dorsal margin). The lacrimal (including the 'prefrontal' of Wellnhofer, 1974) forms the caudal and caudodorsal boundaries of the fenestra. Such an antorbital fenestra—bounded principally by lacrimal and maxilla—is the ancestral archosaurian condition.

The nasal process of the maxilla consists of two rami: a triangular ventral ramus bordering the external nares and projecting dorsally to contact the subnarial process of the nasal, and a dorsal ramus extending caudally from the ventral ramus to contact the nasal and lacrimal. Whetstone (1983) considered this dorsal ramus to be the mesethmoid bone but it is clearly part of the maxilla and not a median element. The dorsal ramus of the nasal process of the maxilla is slightly recessed (Wellnhofer, 1974) such that the nasal overhangs this region. Cracraft (1986) noted that this dorsal ramus is a primitive feature of *Archaeopteryx*, and that loss of the dorsal ramus is synapomorphic for ornithurine birds. The fact that in *Archaeopteryx* this dorsal ramus of the nasal process is recessed, allowing the nasal to partially bound the antorbital fenestra, may indicate an intermediate condition to that in ornithurine birds in which the dorsal ramus is lost and the nasal alone forms the dorsal margin of the fenestra. The ventral ramus of the nasal process of the maxilla in *Archaeopteryx* is almost certainly the homologue of the nasal process of the maxilla in ornithurine birds.

Descending from the dorsal ramus of the nasal process are two struts of bone (the central portions of the struts are found on the counterslab); these struts contact the palatine process of the maxilla just medial to the labial (dentigerous)
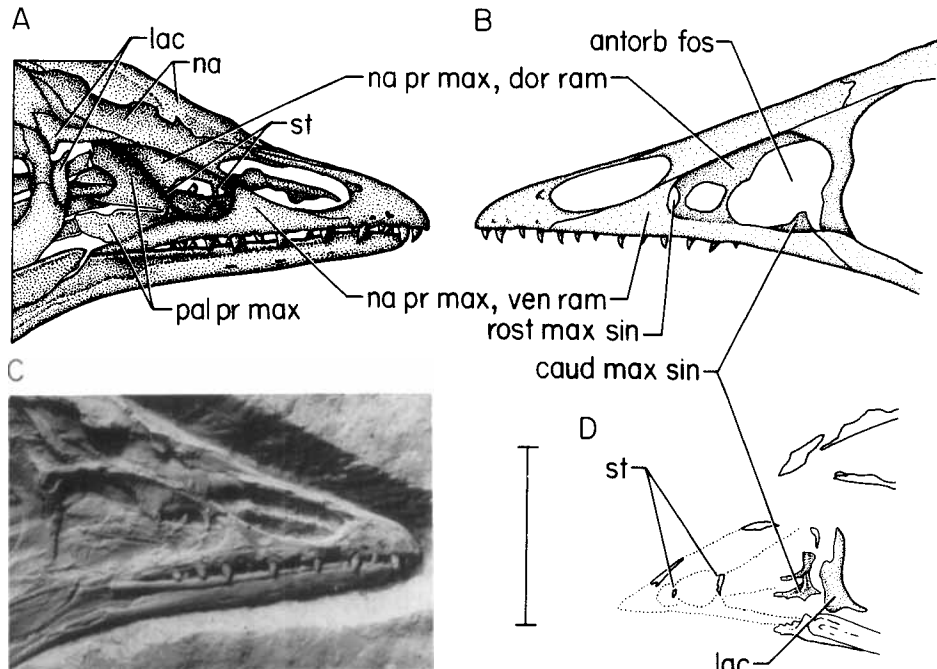
Figure 14. Antorbital region of the Eichstätt specimen of *Archaeopteryx*. A, Antorbital region in right lateral view. B, Reconstruction in left lateral view. C, Photograph of main slab. D, Antorbital bones found on counterslab. Abbreviations: antorb fos, antorbital fossa; caud max sin, caudal maxillary sinus; lac, lacrimal; na, nasal; na pr max, dor ram, dorsal ramus of nasal process of maxilla; na pr max, ven ram, ventral ramus of nasal process of maxilla; pal pr max, palatine processes of maxilla; rost max sin, rostral maxillary sinus; st, struts. B and D adapted from Wellnhofer (1974).

process (Fig. 14A–C). Wellnhofer (1974) considered these struts to parition off subsidiary antorbital fenestrae within the maxilla. The antorbital fossae of all the other birds considered thus far housed an air-filled sinus from the nasal cavity. Thus, I consider this strutting of the maxilla in *Archaeopteryx* to be a result of pneumatization by a diverticulum of the antorbital sinus. Pneumatic strutting of the maxilla occurs in crocodilians (Wegner, 1957) and many modern birds (Witmer, 1987). The closest similarity to the condition in *Archaeopteryx*, however, is found in theropod dinosaurs. In fact, Gauthier (1986) regarded this condition as a synapomorphy of Theropoda. Osmólska (1976, 1985) considered the cavities around the antorbital fossa of the peculiar theropod *Oviraptor* to be of pneumatic origin, as did Stovall & Langston (1950) for the carnosaur *Acrocanthosaurus*.

As a result of pneumatization, there are two chambers within the rostral portion of the maxilla. The larger caudal chamber lies between the two struts, the dorsal ramus of the nasal process, and the palatine process. The smaller rostral chamber lies rostral to the front strut, passes medial to the ventral ramus of the nasal process, and is floored by the palatine process. The rostral chamber is thus in the same topographic location as the rostral maxillary sinus of *Hesperornis* and ratites and may be its homologue. Loss of the dorsal ramus of the nasal process of the maxilla in ornithurine birds opened up the caudal chamber observed in *Archaeopteryx* such that the enclosed air space became confluent with the antorbital sinus.

There also may be some evidence for the caudal maxillary sinus observed in *Hesperornis* and neognaths. On the counterslab of the Eichstätt specimen (Fig. 14D) are a pair of bone fragments rostral to the lacrimal in the antorbital region. These fragments are somewhat L-shaped, with a rostral horizontal process and a caudal vertical process. Wellnhofer (1974) described them as being concave; the convacity is directed rostrolaterally. Wellnhofer (1974) tentatively identified these bones as Ossa uncinata, rare secondary ossifications that run from lacrimal to palatine in a few neornithines. These bony fragments, however, are in such a position that it is almost certain that they instead attached to the medial edge of the palatine processes of the maxillae. Witmer & Martin (1987) suggested that these maxillary fragments were associated with the maxillary diverticulum and homologized them with the cup-shaped (caudal) maxillary sinus of *Hesperornis* and neognaths. Although the structures in *Archaeopteryx* are not cup-shaped, their morphology (roughly vertically-oriented and concave laterally) and position (on the medial margin of the palatine process) are comparable to the structures seen in non-ratite ornithurines.

A final consideration is lacrimal pneumaticity in *Archaeopteryx*. The avian lacrimal is usually pneumatized medially near the articulation of the lacrimal with the skull. The medial aspect of the Eichstätt lacrimal is not exposed, and there are no other foramina visible. De Beer (1954) figured an isolated lacrimal found on the London counterslab; it was one of his "unidentified skull bones". Martin (1984) correctly identified the bone as a lacrimal. This lacrimal is more or less complete, but no pneumatic features are apparent (although further preparation may change this situation).

Tympanic pneumaticity was developed in *Archaeopteryx*. Details of the braincase are found primarily in the London cranium, with a few relevant points coming from the Eichstätt specimen. Recent papers dealing with the braincase of *Archaeopteryx* by Whetstone (1983) and especially Walker (1985) eliminate the necessity of detailed description here. Both Whetstone (1983) and Walker (1985) cited the presence of a depression on the prootic as evidence for a dorsal tympanic diverticulum (Figs 15, 16). This depression is found on the lateral surface of the dorsal part of the prootic and is bordered rostrally by the laterosphenoid, dorsally by the parietal, and caudally by the opisthotic/exoccipital and a tongue of the parietal. This depression is very similar to that occurring on the prootics of many juvenile neornithines, *Hesperornis*, and perhaps *Enaliornis*, where it results from pneumatization by the dorsal tympanic diverticulum. Because the post-temporal fossa (occipital foramen) communicates with the dorsal tympanic recess in *Enaliornis*, *Hesperornis*, and many modern birds, the apparent communication of the prootic depression with the post-temporal fossa in *Archaeopteryx* (Walker, 1985) provides further evidence for the prootic depression being a pneumatic fossa.

The only difficulty in this assessment is the 'problem of the squamosal' of *Archaeopteryx*. In the other birds considered thus far, the squamosal roofs the dorsal tympanic recess and hence roofs the prootic depression. Numerous fragments have been suggested for the squamosal of *Archaeopteryx*. Without entering into the debate, the important fact is that, as both Whetstone (1983) and Walker (1985) noted, it is unlikely that the squamosal of *Archaeopteryx* could have completely roofed the dorsal tympanic recess.
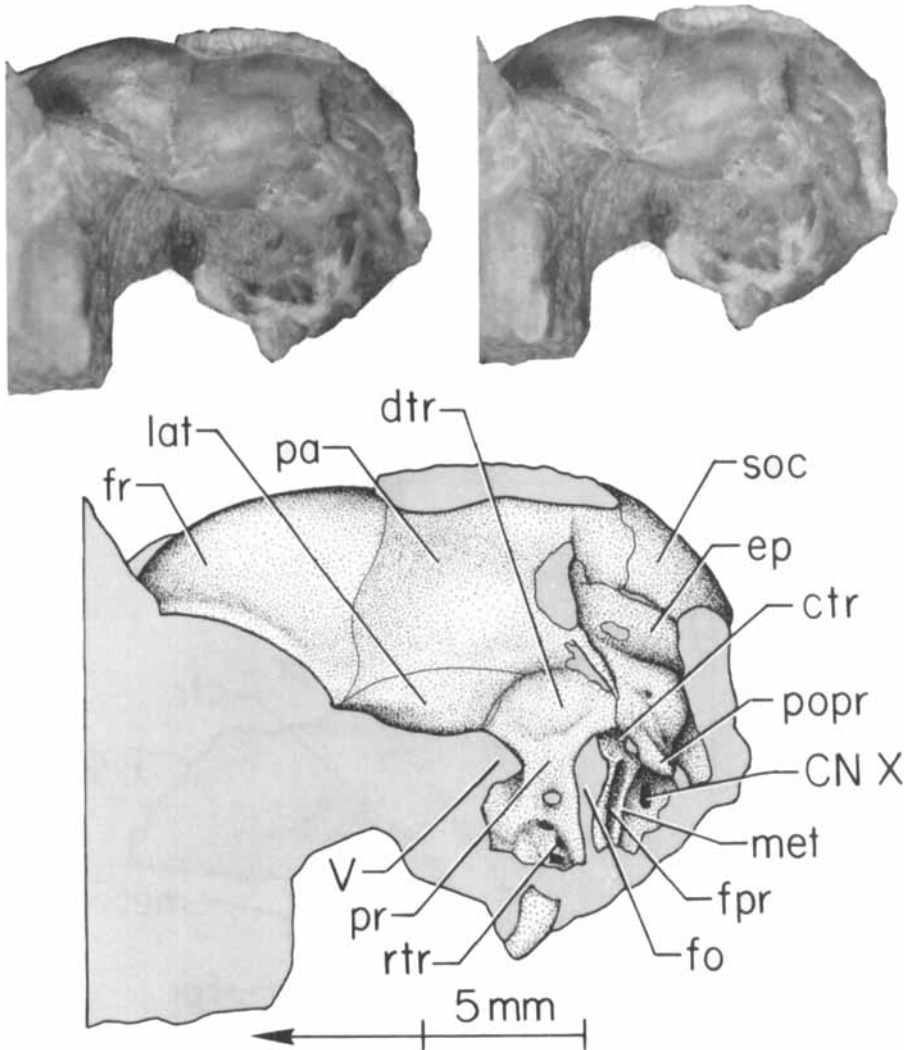
Figure 15. London cranium of *Archaeopteryx* in left lateral view. Abbreviations: V, trigeminal nerve (CN V) foramen; CN X, vagus nerve (CN X) foramen; ctr, caudal tympanic recess; dtr, dorsal tympanic recess; ep, epiotic; fo, fenestra ovalis; fpr, fenestra pseudorotundum; fr, frontal; lat, laterosphenoid; met, metotic strut; pa, parietal; popr, paroccipital process; pr, prootic; rtr, rostral tympanic recess; soc, supraoccipital.

Another persistent problem is where the quadrate of *Archaeopteryx* articulated on the skull (Whetstone, 1983; Walker, 1985; Haubitz *et al.*, 1988). This debate again is peripheral to the present focus. In all cases the dorsal tympanic recess would be rostral to the articulation of the quadrate with the skull, as in *Enaliornis, Parahesperornis, Hesperornis* and many modern birds.

A communication between the contralateral dorsal tympanic diverticula within the skull roof in *Archaeopteryx* seems impossible. The dorsal tympanic diverticulum apparently did not pass between and within bones, and there are no pneumatic foramina in the skull roof.
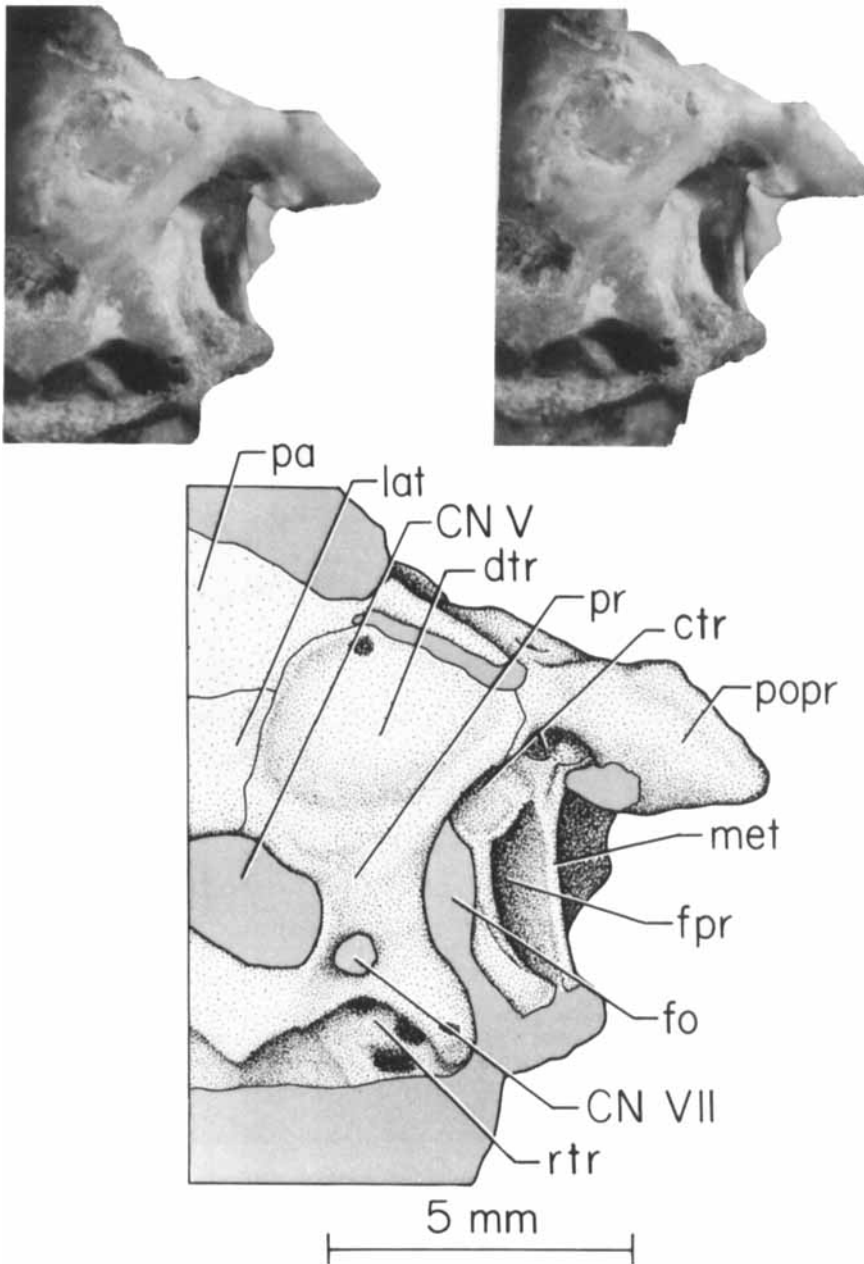
Figure 16. London cranium of *Archaeopteryx* in left rostrolateral view. Abbreviations: CN V, trigeminal nerve (CN V) foramen; CN VII, facial nerve (CN VII) foramen; ctr, caudal tympanic recess; dtr, dorsal tympanic recess; fo, fenestra ovalis; fpr, fenestra pseudorotundum; lat, laterosphenoid; met, metotic strut; pa, parietal; popr, paroccipital process; pr, prootic; rtr, rostral tympanic recess.

The caudal tympanic recess in *Archaeopteryx* (Figs 15, 16) is much like that of other birds. Whetstone (1983) identified the fenestra pseudorotundum as the entrance to the caudal tympanic recess (his 'antrum pneumaticum centrale') but Walker (1985) corrected this mistake. The entrance to the recess is caudodorsal to the fenestrae ovalis and pseudorotundum within the columellar recess (Fig. 16). The entrance is bounded medially by the 'threshold' (Walker, 1985) which is continuous with the crista interfenestralis. Horizontal processes from the prootic and opisthotic/exoccipital form the dorsal margin of the entrance. The metotic strut forms the ventrolateral margin of the entrance. The recess appears to expand within the paroccipital process but to an unknown extent. The paroccipital process looks somewhat inflated caudally but there is no positive evidence of the contralateral communication observed in some modern birds. Likewise, the basioccipital is not preserved, and there is no way to determine if it was pneumatized by the caudal tympanic diverticulum.

Both Whetstone (1983) and Walker (1985) suggested that a rostral tympanic recess may have been present in *Archaeopteryx*. There is a fossa containing three foramina in the prootic bone ventral to the facial foramen (Fig. 16). The fossa continues rostrally ventral to the trigeminal foramen where it can no longer be traced. The three foramina within the fossa were considered pneumatic by both Whetstone and Walker. Thus, the prootic bone was pneumatized by both the dorsal and rostral tympanic diverticula as in many neornithine birds. The basisphenoid, which is not preserved, was probably also pneumatized because the pneumatic fossa appears to have continued ventrally as well as rostrally. Whether there was an alaparasphenoid lateral to the rostral tympanic diverticulum as in the other birds considered thus far is unknown. There is also no way of knowing if the contralateral rostral tympanic diverticula communicated.

An articulare diverticulum cannot be inferred positively for *Archaeopteryx*. The articular bone is preserved in the Berlin and Eichstätt specimens, but the appropriate dorsomedial view is not available with the present state of preparation. Walker (1985) identified one of the isolated skull bones found on the London specimen as the right quadrate. He neither reported nor figured any pneumatic foramina in this bone. The computed tomography study of Haubitz *et al.* (1988) also did not find any quadrate pneumatic foramina. *Archaeopteryx* thus may be tentatively scored as lacking a pneumatic quadrate.

In summary (Table 1), *Archaeopteryx* possessed both nasal and tympanic pneumaticity, but of somewhat different morphology than in the ornithurines. The maxillary diverticulum of the antorbital sinus was present, including possible precursors of the rostral and caudal maxillary sinuses. Lacrimal pneumaticity remains a question. Tympanic pneumaticity was present. The quadrate bone appears to be apneumatic, but articulare pneumaticity cannot be assessed. The dorsal tympanic diverticulum excavated a typical pneumatic fossa on the prootic but, atypically, may not have been roofed by the squamosal. The caudal tympanic diverticulum was similar to those of ornithurines. The rostral tympanic diverticulum pneumatized the ventrolateral portion of the prootic and probably also the basisphenoid. No communications between any of the tympanic diverticula—either contralateral or ipsilateral—are indicated.

DISCUSSION

Nasal pneumaticity

The presence of an antorbital sinus is inferred for *Archaeopteryx* and the hesperornithids *Hesperornis* and *Parahesperornis*. All neornithine birds have the sinus. Thus, an antorbital sinus is primitive for Aves. The two most common diverticula of this sinus in neornithines—the maxillary and lacrimal diverticula—were present in the hesperornithids, but only the maxillary diverticulum can be inferred in *Archaeopteryx*. Although the facial region of *Ichthyornis* is unknown, phylogenetic analysis predicts that an antorbital sinus with lacrimal and maxillary diverticula was present in *Ichthyornis* (unless it was apomorphically reduced or lost). The basis for this prediction is that the outgroups of *Ichthyornis* (Neornithes, Hesperornithiformes and *Archaeopteryx*) possessed antorbital sinuses, lacrimal diverticula (except perhaps *Archaeopteryx*), and maxillary diverticula. Thus, these features were ancestral for the taxon including at least *Archaeopteryx* and Ornithurae. This same reasoning applies for those aspects of tympanic pneumaticity for which we lack data for *Ichthyornis*.

Hesperornis and *Archaeopteryx* have both rostral and caudal maxillary sinuses. The rostral maxillary sinus is located between the palatine process, the ventral ramus of the nasal process, and a dorsal lamina of the maxilla. The caudal maxillary sinus is located just lateral to a vertical, concave-lateral portion of the palatine process. These two maxillary diverticula pneumatizing different portions of the maxilla had not been previously identified but may be primitive for all birds. This situation has implications for the systematics of modern birds. Virtually all neognaths have a cup-shaped caudal maxillary sinus (or an obvious transformation of it) that is very similar to that of *Hesperornis* (compare Fig. 3 with Fig. 7A, C). Based on outgroup comparison with *Archaeopteryx*, this cup shape may be considered a synapomorphy of ornithurine birds. Palaeognaths, however, all clearly lack this cup-shaped structure at the caudomedial portion of the palatine process (Fig. 8). Given the topology of Fig. 1, this absence must be considered an apomorphic loss.

The maxillae of palaeognaths clearly exhibit pneumatic features (Fig. 8). Palaeognaths retain the broad palatine processes of the maxilla observed in *Hesperornis* and *Archaeopteryx*. Ratites (tinamous are equivocal on this point) also appear to retain the rostral maxillary sinus of these Mesozoic birds, showing, in particular, a morphology similar to *Hesperornis*. Most neognaths, on the other hand, show a greatly reduced palatine process of the maxilla. Concomitant with this reduction of the palatine process is the reduction of the rostral maxillary sinus. This sinus is lost in most neognaths. Only a small foramen which transmits the nasal ramus of the nasopalatine nerve (a branch of the maxillary nerve) and a twig of the palatine branch of the maxillary artery (a branch of the external carotid artery) usually remains. These vessels and nerves traverse the antorbital fossa. Presumably these structures were present in the Mesozoic toothed birds where they probably serviced the teeth, suggesting their homology with the dorsal alveolar nerves and arteries of other toothed amniotes. However, some neognaths (such as procellariiforms) retain some pneumaticity in this region. Loss of the rostral maxillary sinus occurs at an unknown level within Neognathae. However, reduction or loss of the rostral maxillary sinus remains as a synapomorphy of Neognathae.

Dorsal tympanic recess

The dorsal tympanic diverticulum of the middle ear sac pneumatized bone in all of the Mesozoic birds studied and is almost certainly an ancestral feature of Aves. *Enaliornis*, *Parahesperornis* and *Hesperornis* all exhibit a dorsal tympanic recess between and within the squamosal and prootic bones. The lack of a squamosal roof to the recess may be an autapomorphy of *Archaeopteryx lithographica*. However, this last point is problematic in that the morphology is controversial and outgroup comparison is inconclusive for this character (see below).

The contralateral dorsal tympanic diverticula apparently did not communicate via the dermal skull roof in any of the Mesozoic birds studied. The communication in many neornithine birds is therefore derived. Although phylogenetics dictates assignment of the plesiomorphic condition to the hesperornithiforms, it is possible that such a communication in these birds had been lost. The Hesperornithiformes were highly pachyostose pursuit diving birds. Essentially all modern pursuit diving birds also lack communication between the contralateral dorsal tympanic diverticula. As this communication is probably a synapomorphy of Neornithes, lack of a communiction in neognath divers must be considered a reversal—no doubt connected with increased pachyostosis. However, as indicated above, we have no reason to think that an apneumatic skull roof is anything but a primitive feature of hesperornithiforms.

The position of the entrance to the dorsal tympanic recess relative to the cranial facets for the quadrate capitula and also the size of the entrance have been used as systematic characters (Lowe, 1925, 1926; Saiff, 1974; Cracraft, 1985). Lowe (1925) considered the primitive condition to be a small entrance between the cranial cotylae for the quadrate, and the derived condition to be a large entrance rostral to the cotylae. Saiff (1974 and later papers) and Cracraft (1985) followed Lowe's character analysis. The present study, however, reverses this polarity. In *Archaeopteryx*, *Enaliornis*, *Parahesperornis* and *Hesperornis*, the entrance to the dorsal tympanic recess is fully rostral to the articulation of the quadrate with the cranium. In the hesperornithiforms this entrance is large, despite extreme pachyostosis. This polarity is corroborated in the phylogeny of the Neognathae. Among clades commonly thought by systematists (Mayr & Amadon, 1951; Wetmore, 1960; Cracraft, 1981) to have branched early in neognath phylogeny (Gaviiformes, Sphenisciformes, Procellariiformes, Pelecaniformes), the entrance to the dorsal tympanic recess is rostral to the cranial cotylae for the quadrate and is (at least in those forms that are not pursuit divers) moderately to very large.

Caudal tympanic recess

Of all the pneumatic systems surveyed in this study, the morphologic relationships of the caudal tympanic recess are the most constant. In all known birds—both fossil and recent—the caudal tympanic diverticulum enters the paroccipital process caudodorsal to the fenestrae ovalis and pseudorotundum. In many neornithine birds, the contralateral diverticula communicate via the pneumatic cells in the epiotic and supraoccipital. None of the Mesozoic birds show any evidence of having such a communication. Another feature of many

modern birds is indirect pneumatization of the caudal portion of the basicranium via the metotic strut. *Enaliornis* and *Hesperornis* appear to show evidence of such pneumatization of the caudal basicranium, suggesting that this may be an ancestral feature of at least ornithurine birds.

Rostral tympanic recess

Presence of a rostral tympanic diverticulum of the middle ear sac is inferred for all the Mesozoic birds in which relevant portions of the braincase are preserved. Evidence ranges from the few pneumatic foramina on the rostroventral surface of the prootic of *Archaeopteryx* to the well-preserved and very modern recesses of the hesperornithiforms. The rostral tympanic diverticulum pneumatized the basisphenoid and prootic in most, if not all, Mesozoic birds.

A characteristic of the rostral tympanic recess of modern birds is the presence of the alaparasphenoid. A well-developed alaparasphenoid is present in basal ornithurines (Hesperornithiformes). However, *Archaeopteryx* shows no evidence of having this lateral wall, probably due to the fortunes of preservation. Nevertheless, the possibility remains that an alaparasphenoidal ossification had not yet evolved. In the ontogeny of the domestic chicken, the alaparasphenoid is the last parasphenoidal centre to ossify (Erdmann, 1940; Jollie, 1957; Sandoval, 1963). Perhaps the absence of an alaparasphenoid in *Archaeopteryx* is real, indicating a relationship between ontogeny and phylogeny. Additional fossil material of these birds is necessary to test this hypothesis.

Another important feature of the rostral tympanic diverticula of modern birds is their contralateral communication. The diverticula are directed rostromedially from the middle ear and communicate ventral to the hypophysial fossa; median extensions into the rostroparasphenoid often occur in this region. Among Mesozoic birds, the hesperornithiforms *Enaliornis*, *Parahesperornis*, and *Hesperornis* can be shown to have such a communication and perhaps also a small air space in the parasphenoid rostrum. Again, preservational problems prevent the inference of this communication in *Archaeopteryx*. Until additional data suggest otherwise, I will consider communication of the contralateral diverticula to be a synapomorphy of ornithurine birds.

Quadrate pneumaticity

The quadrate diverticulum was present in *Ichthyornis*. This bird possesses a large pneumatic foramen in the medial surface of the quadrate at the base of the orbital process. The presence of quadrate pneumaticity is a synapomorphy of at least Carinatae. I consider the position of the quadrate pneumatic foramen ventromedially at the base of the orbital process (Fig. 4B) to be primitive for this clade. This position is found in procellariiforms, basal pelecaniforms, among others. The dorsal position of the quadrate pneumatic foramen on the shaft may be a synapomorphy of palaeognaths. This character exhibits a great deal of homoplasy in Neognathae.

The hesperornithiforms *Baptornis*, *Parahesperornis* and *Hesperornis* and apparently also *Archaeopteryx* lack quadrate pneumatic foramina. Plesiomorphic absence of quadrate pneumaticity is surprising in hesperornithiforms, because their braincases and quadrates are modern in most other respects. It is tempting

to assert that their lack of quadrate pneumaticity is instead an apomorphic loss—simply another manifestation of a trend to increase pachyostosis. Most modern pursuit diving birds (e.g. loons, penguins, alcids, etc.) also apomorphically lose quadrate pneumaticity. Nevertheless, we simply have no good phylogenetic reason to suggest that quadrate pneumaticity was lost in hesperornithiforms.

Articulare pneumaticity

Presence of an articulare diverticulum (siphonium) is a synapomorphy of Ornithurae. Among the Mesozoic birds, articulare pneumatic foramina are known for the hesperornithiforms *Baptornis* and *Parahesperornis* and *Ichthyornis*. In all cases the foramen is located dorsally within the articulare bone just caudal to the medial mandibular cotylus. In *Ichthyornis* the foramen and enclosed cavity are large. In hesperornithiforms, articulare pneumaticity is greatly reduced and is characterized by small pneumatic foramina and very small air spaces within the articulare bones. This is another derived feature uniting at least those hesperornithiforms above *Enaliornis*. This trend culminates in *Hesperornis* which lacks articulare pneumaticity. This trend is probably another indication of the development of pachyostosis, as most modern pursuit divers also lose articulare pneumaticity.

When attempting to infer the presence of a siphonial foramen in any archosaur, it is important to distinguish between the putative pneumatic foramen and the foramen for the chorda tympani nerve. In most non-synapsid amniotes the chorda tympani nerve passes rostroventrally through a foramen in the region of the jaw articulation, usually between the articulare and prearticular bones. In turtles and many squamates, there is a chorda tympani foramen in a similar position to the avian siphonial foramen. In birds, the chorda tympani nerve does not pierce the articulare but travels along its medial border, enters the mandibular canal, and fuses with a branch of the mandibular nerve (Gentle, 1984, personal communication). Thus, there is little possibility that pneumatic and nerve foramina were confused in this study.

Non-avian archosaurs, pneumaticity and the origin of birds

Craniofacial pneumaticity appears to be widespread in archosaurs, although the precise phylogenetic levels at which most of the features appear remains uncertain. Nasal pneumaticity may be an ancestral feature of archosaurs (Witmer, 1987). The maxillae, palatines and pterygoids of modern crocodilians are pneumatized by diverticula of the nasal cavity (Wegner, 1957). Air-filled diverticula of the nasal cavity also can be inferred reliably for lambeosaurine hadrosaurs (Weishampel, 1981), ankylosaurs (Maryanska, 1977), pterosaurs and theropods. Some 'thecodonts', such as ornithosuchians and rauisuchians, exhibit characteristics suggestive of pneumaticity in their antorbital regions. The avian rostral maxillary sinus is probably homologous to the rostral cavities within the maxillae of non-avian archosaurs (Witmer, 1987). On the other hand, nothing directly comparable to the caudal maxillary sinus of birds is known in non-avian archosaurs. Lacrimal diverticula can be inferred for most theropods. At least one genus, *Troodon* (Currie, 1985), displays a pneumatic foramen within the lacrimal in the avian position (medially near the lacrimal's articulation with the frontal).

Tympanic pneumaticity has become an important issue in the discussion of the origin of birds. Several workers have considered similarities in the craniofacial air spaces of birds and crocodylomorphs to be indicative of unique common ancestry (Walker, 1972; Whetstone & Martin, 1979, 1981; Bellairs & Kamal, 1979; Martin et al., 1980; Whetstone & Whybrow, 1983; Martin, 1983a, b; Witmer, 1984; Tarsitano, 1985a, b). Although these similarities had been known for some time (Parker, 1883), this sudden interest in craniofacial air spaces stimulated the search for these pneumatic features in theropod dinosaurs—the leading candidate for avian relationships. With the exception of Moodie (1915), few people had noticed the potentially pneumatic features of *Tyrannosaurus* (Osborn, 1912). Recently, however, several theropods have been shown to have pneumatic cavities in their braincases. Russell (1970), Osmólska et al. (1972), Barsbold (1974), Molnar (1985), Currie (1985, 1987) and Raath (1985) have described pneumatic features in a variety of theropods. As mentioned previously, birds, crocodylomorphs, and theropod dinosaurs are not alone among archosaurs in possessing air-filled cavities in their skulls. Additional analysis is required to determine the homologies of these features.

Dorsal tympanic air spaces have been described only for crocodylomorphs among non-avian archosaurs. The crocodylomorph sinus is similar to the avian one in that it passes dorsally between prootic and squamosal and communicates with the post-temporal fossa. This sinus has not yet been reported in any other archosaur. According to P. Currie (personal communication), the theropod *Troodon* also possesses a dorsally directed pneumatic sinus, but this sinus appears to be connected with an air space in the paroccipital process (that is, caudal to the avian and crocodylomorph dorsal sinus). If birds are considered theropods, then the similarities in the dorsal sinus of birds and crocodylomorphs must be considered convergent.

Tarsitano (1985a, b) suggested that contralateral communication of the dorsal air sacs of birds and crocodylomorphs (his intertympanic sinus) is a synapomorphy uniting these two taxa. As we have seen, however, such a communication is not the ancestral condition for birds in that no Mesozoic bird exhibits this communication. Instead, contralateral communication of the dorsal tympanic diverticula is a synapomorphy of Neornithes. Thus, this character must have arisen convergently in birds and crocodylomorphs.

Pneumatic sinuses within the paroccipital process have been reported for both crocodylomorphs and theropods. The crocodylomorph *Dibothrosuchus* has a large foramen in the paroccipital process caudodorsal to the fenestra ovalis and fenestra pseudorotundum (Wu, 1986); the position is similar to the avian entrance to the caudal tympanic recess. This condition refutes the claim of Whetstone & Whybrow (1983) that 'sphenosuchians' (Benton & Clark, 1988, recently showed Sphenosuchia to be paraphyletic) lack this cavity. Eusuchian crocodilians also exhibit a tympanic diverticulum into the paroccipital proccess (Müller, 1967). Kurzanov (1976) and Molnar (1985) identified cavities in the paroccipital processes of the carnosaurian theropods *Itemirus* and *Tyrannosaurus*, respectively. The ornithomimid *Gallimimus* (Osmólska et al., 1972) possesses pneumatic foramina opening into its hollow paroccipital process (Whetstone & Whybrow, 1983). Likewise, the troodontid *Saurornithoides* (Barsbold, 1974) exhibits similarly placed pneumatic foramina in its paroccipital process (Currie,

1985). As alluded to previously, *Troodon* has a pneumatic space in its paroccipital process that extends dorsally some distance as in many neornithine birds (personal observations; Currie, personal communication). Thus, contrary to Whetstone & Whybrow (1983), the presence of an 'antrum pneumaticum centrale' (caudal tympanic recess) in birds and crocodylomorphs is not unique to these two taxa.

The greatest area of uncertainty regards the homology of the basicranial sinuses of archosaurs. Numerous archosaurs (including a number of 'thecodonts') exhibit a large median ventral sinus within the basioccipital and especially the basisphenoid. In many forms it is difficult to determine if it communicates with the middle ear or even if it is pneumatic. These sinuses are very well developed in most theropods although the median ventral opening has been lost in troodontids (Currie, 1987). The sinus is in a very similar topographic position to the 'median auditory opening' (foramen intertympanicum of Simonetta, 1956, and Müller, 1967) in crocodylomorphs (Taquet & Welles, 1977). Tarsitano (1985a) raised the possibility of these basicranial sinuses being homologous in theropods and crocodilians.

Tarsitano (1985a, b) considered the pneumatic basicranium of birds to be homologous to the crocodilian condition and used this median ventral opening (his 'hypophysial-basicranial fenestra') as a synapomorphy. However, birds appear to lack such a median ventral opening. Most neornithine birds do indeed exhibit pneumatic basioccipitals and basisphenoids, but ontogenetically the sources of the pneumaticity are usually different for the two bones: the basioccipital is pneumatized by the caudal tympanic diverticulum while the basisphenoid is pneumatized by the rostral tympanic diverticulum. In adults the air spaces often merge. There are only two median ventral openings in the avian basicranium: (1) the median opening of the paired auditory tubes (which is a derived condition uniting neognaths in that palaeognaths and *Enaliornis* lack such a median opening), and (2) the craniopharyngeal canal which is a narrow tube (usually obliterated in adults) that contains the epithelial stalk of the embryonic invagination of Rathke's pouch and extends into the pituitary fossa (Wingstrand, 1951). The invagination of Rathke's pouch never becomes filled with air or pneumatizes bone in birds (Wingstrand, 1951). Neither of these median ventral openings in birds seems the likely homologue of the intertympanic sinus system (*sensu* Simonetta, 1956 and Müller, 1967) of crocodilians and perhaps theropods. The basicranium of birds is pneumatized by diverticula of the middle ear while, as noted by Müller (1967), the basicranium of crocodilians is pneumatized by an air-filled diverticulum of the pharynx that only later in ontogeny gains communication with the tympanic cavity. Further research on this problem clearly is merited.

A few theropods, such as ornithomimids (Osmólska *et al.*, 1972) and troodontids (Barsbold, 1974; Currie, 1985, 1987), may have something similar to the rostral tympanic recess of birds. In these forms, there is a large 'parasphenoid capsule' that appears to have contained a diverticulum from the middle ear sac. The cerebral carotid artery passes through this sinus as in birds (Currie, 1985). Although the parasphenoid is reduced in crocodylomorphs, many primitive crocodylomorphs also appear to have had such a diverticulum. The basipterygoid process of 'sphenosuchians' were pneumatized by this diverticulum

(Walker, 1972; Wu, 1986). Early crocodilians possess elaborate air sinuses rostral to and in direct communication with the tympanic cavity (Crompton & Smith, 1980; Busbey & Gow, 1984).

Crocodylomorphs, like birds, have pneumatic quadrates and articulares; these have been used by Whetstone & Martin (1981), Witmer (1984) and Tarsitano (1985a; only pneumatic articulares) as synapomorphies delimiting a bird/crocodylomorph clade. Molnar (1985), however, is correct in noting that the theropod *Tyrannosaurus* also possesses pneumatic quadrates and articulares. This is true for other tyrannosaurids as well, but is unknown in other theropods. In fact, many advanced theropods, such as *Oviraptor*, *Caenagnathus*, *Deinonychus*, *Dromaeosaurus* and *Ornitholestes*, can be shown to lack pneumatic quadrates and/or articulares. Just where pneumatic quadrates and articulares appear in the phylogeny of theropods is uncertain.

This last point brings up a general problem in that theropods are an extremely diverse group. We simply do not know the distribution of the various pneumatic features within Theropoda. In fact, this same difficulty occurs when considering the larger taxon Archosauromorpha. None of the pneumatic features proposed as synapomorphies of birds and crocodilians are unequivocal, unique characters. At present, it seems unwise to use any pneumatic characters to link birds with any particular group of archosaurs. Similarities are informative, but knowledge of the distribution and precise morphology of these similarities in all relevant taxa is imperative if we hope to distinguish synapomorphy from homoplasy.

CONCLUSIONS

Craniofacial pneumaticity is an ancestral feature of birds, and we are now in a position to understand its evolution within birds. However, uncertainties remain as to where in the phylogeny of archosaurs these features arose. Many pneumatic features clearly were inherited from their non-avian ancestors. Some of the pneumatic characters, however, still may be synapomorphic for birds, depending on the choice of non-avian outgroups. Given the bird/crocodylomorph hypothesis of Whetstone & Martin (1979), perhaps no pneumatic characters (broadly interpreted) are unique to birds, but instead originated in the common ancestor of birds and crocodylomorphs. On the other hand, if birds are considered theropods (Fig. 17), then a dorsal tympanic diverticulum is synapomorphic for birds, regardless of which theropods are closer to birds. Important differences result when different theropods are considered the sister group of birds (see Witmer, in press, for a discussion of the diversity of opinion). For example, troodontids and ornithomimids (Thulborn, 1984; Currie, 1985, 1987) shows the closest similarity to birds in pneumatic features: a well-defined middle ear cavity, an air sinus sheathed laterally by parasphenoid, a pneumatic basioccipital, and an air sinus in the paroccipital process. Tyrannosaurids have a virtually modern avian system of pneumatic sinuses in their quadrates and articulares. Dromaeosaurids, although usually considered the theropods closest to birds (Ostrom, 1976; Gauthier, 1986), exhibit few of the pneumatic features of birds. The phylogenetic level at which these features arose within Theropoda or Archosauria as a whole, again, are uncertain.

Phylogenetic relationships within Aves (Fig. 17) are based on the extensive analyses of Martin (1983a, 1984) and Cracraft (1986, 1988). Pneumatic
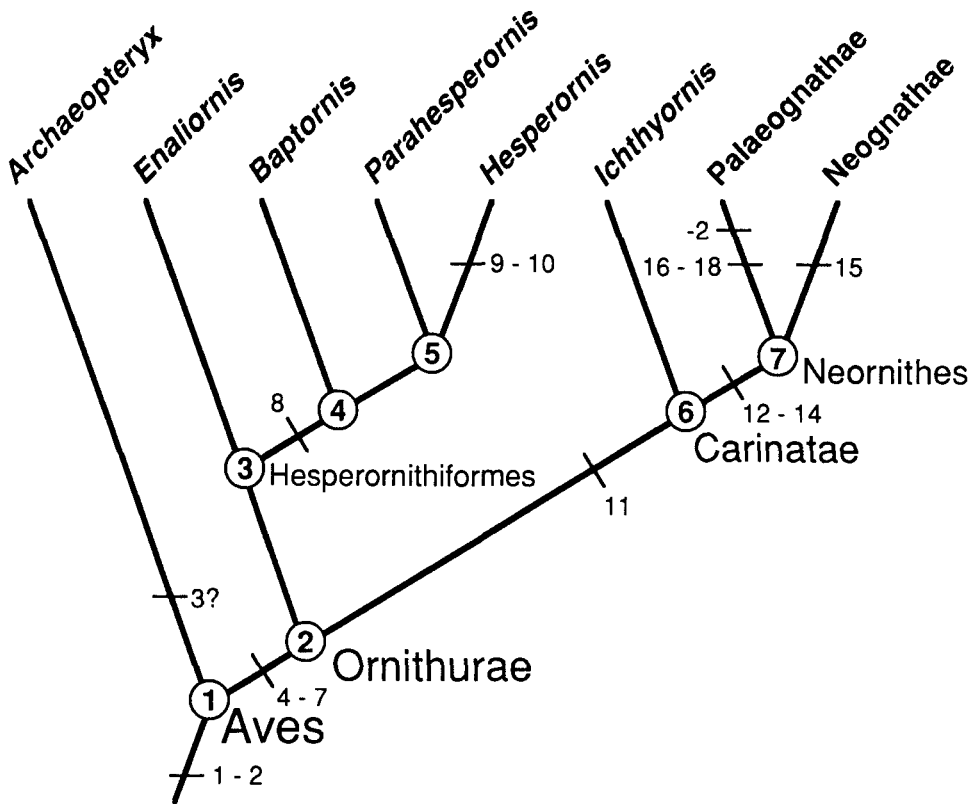
Figure 17. Cladogram of some Mesozoic birds. The topology is fixed based on the analyses of Martin (1983a, 1984) and Cracraft (1986). Pneumatic characters 1–18 are plotted over this cladogram. See text for discussion.

characters plotted on this highly corroborated tree entirely support this topology. Detailed character analysis can be found in the preceding sections. As mentioned, regardless of which specific theropods are used as non-avian outgroups, the presence of a dorsal tympanic diverticulum and recess (character 1; Fig. 17) stands as a synapomorphy of Aves (Node 1). In *Archaeopteryx* and Hesperornithiformes the large entrance to the dorsal tympanic recess is restricted to being only rostral to the quadrate's cranial articulation. Some neornithines apomorphically close the rostral entrance due to alterations in the relative positions of the quadrate and middle ear, diverting the dorsal tympanic diverticulum caudal to the quadrate articulation. Another synapomorphy of birds is a caudal maxillary sinus (character 2), a feature that is otherwise unknown in archosaurs. *Archaeopteryx* appears to be unique in lacking a squamosal roof to the dorsal tympanic recess (character 3?). A question mark has been appended to this character because of uncertainties of both morphology and polarity assessment.

The typical cup-shaped caudal maxillary sinus (character 4) first appears in the common ancestor of Ornithurae (Node 2). Another ornithurine synapomorphy is the extension of the caudal tympanic recess into the caudal portion of the basicranium (character 5), which is found in *Enaliornis, Hesperornis*

and Neornithes. The appearance of articulare pneumaticity (character 6) also is placed at the Ornithurae node. Also supporting the monophyly of the Ornithurae is the communication of the contralateral rostral tympanic diverticula (character 7). It should be noted that *Archaeopteryx* is unknown with respect to characters 5–7, and thus these characters actually may have originated at high phylogenetic levels. In fact, character 7 is known in several non-avian archosaurs (Witmer, 1988), and may have to be applied to a more inclusive level in the future.

Within Hesperornithiformes, articulare pneumaticity is reduced (character 8) in the taxon *Baptornis* + Hesperornithidae (Node 4). The polarity of this character is equivocal in that there is no phylogenetic basis for choosing between either a reduction in articulare pneumaticity in hesperornithiforms or an increase in articulare pneumaticity in Carinatae. However, judging from the general pachyostosis of hesperornithiforms, the former is the better guess. The articulares of *Enaliornis* are unknown, preventing assessment of this character. It is possible that this trend began in the common ancestor of Hesperornithiformes (Node 3). Within the Hesperornithidae (Node 5), *Hesperornis* is characterized by the loss of articulare pneumaticity (character 9) and reduction of lacrimal pneumaticity (character 10). Again, these changes may reflect a trend towards greater pachyostosis in *Hesperornis*.

As *Ichthyornis* is so poorly known craniofacially, there is only one pneumatic feature supporting Carinatae (Node 6): the presence of quadrate pneumaticity (character 11). Neornithes (Node 7) is characterized by three pneumatic characters that reflect an increase in the extent of tympanic pneumaticity: 12, communication of the contralateral dorsal tympanic diverticula within the dermal skull roof; 13, communication of the contralateral caudal tympanic diverticula within the cranium; and 14, communication of the ipsilateral dorsal and caudal tympanic diverticula. These three characters and also character 7 (communication of the contralateral rostral tympanic diverticula) exhibit a great deal of homoplasy within Neognathae where loss of one or more of these communications occurs independently in many lineages.

In Neognathae, the rostral maxillary sinus is reduced or absent (character 15). There are four characters supporting the monophyly of Palaeognathae. Palaeognaths have lost the caudal maxillary sinus, and thus show a synapomorphic reversal of character 2. As the cup-shaped caudal maxillary sinus of *Hesperornis* is identical to that of many neognaths, its loss is a strong character uniting the Palaeognathae. In palaeognaths, the quadrate pneumatic foramen is much more dorsally situated on the shaft relative to its position in *Ichthyornis* and basal neognaths (character 16). Although convergent deviations from the primitive position of the quadrate pneumatic foramen are common in the Neognathae, it is assumed that it evolved only once in the common ancestor of Palaeognathae. Cracraft (1986, 1988) suggested that the rostral wall of the middle ear being 'thickened and cancellous', is a synapomorphy of palaeognaths, but lacked adequate outgroup comparison. The present study supports his suggestion in that in all palaeognaths the alaparasphenoid is inflated by the rostral tympanic diverticulum (character 17) while in hesperornithiforms and neognaths (except galliforms) the alaparasphenoid is not inflated. Cracraft (1986, 1988) also postulated that pneumatization of the bone immediately caudal to the cranial articulation of the quadrate (character 18) is

synapomorphic for palaeognaths; this character is also found in some neognaths, notably most Gruiformes.

In summary, most of the major pneumatic features of the skulls of modern birds were present in Mesozoic birds and probably in their non-avian ancestors as well. Modern birds (Neornithes), however, exhibit much more tympanic pneumaticity (characters 12–14). With the exception of the contralateral communication of the rostral tympanic recesses, Mesozoic birds generally appear to lack much indirect pneumatization of bone, and hence lack the often broad communications of neornithines. In other words, the air-filled diverticula tended to pneumatize only those bones immediately surrounding the main air cavity and did not extend into and trabeculate more distant bones. In many ways, the extent of tympanic pneumaticity in Mesozoic birds corresponds to a juvenile stage of pneumatization of neornithine birds. In this respect, phylogeny parallels ontogeny in that the indirect pneumatization that produces the extensive communications of neornithines occurs as terminal additions in ontogeny.

All birds—both fossil and recent—exhibit air-filled diverticula in their skulls. Despite this ubiquity, these air sacs are only beginning to be understood in an evolutionary context. The findings presented here have permitted the deduction of the ancestral pattern of avian craniofacial pneumaticity and allowed its early evolution to be traced—from the relatively restricted, smooth-walled bony sinuses of *Archaeopteryx* and hesperornithiforms to the expansive, interconnected and highly-strutted spaces of neornithines. Equipped with a knowledge of the 'primitive condition', phylogenetic analysis of the 9000 species of living neornithine birds is both elucidated and facilitated. More broadly, an understanding of the basal avian pattern strengthens and clarifies the comparison with non-avian archosaurs, which in turn yields insights on pneumaticity in birds and its bearing on avian origins and relationships.

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