ANATOMY OF THE MIDDLE EAR REGION OF THE AVIAN SKULL: SPHENISCIFORMES

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WHEN I reviewed the literature on the middle ear region of birds (Saiff 1974), it became obvious that few anatomical studies have been made on this region in birds, penguins in particular. Watson's (1883) report on the anatomy of the Sphenisciformes lacks any details on the middle ear. Walker (1888) studied quadrate morphology in a large variety of birds including Sphenisciformes. Pycraft (1898) described the skull of penguins but passed over the middle ear region save for a few brief statements regarding the quadrate, basitemporal platform, eustachian tube, and the trigeminal foramen. Shufeldt (1901) also failed to go into details of the middle ear region in his osteological study of the penguins. More recently, in a study of the evolution of penguins, Simpson (1946) described the skull of *Paraptenodytes antarcticus*, a fossil penguin. This study theorized a close relationship between the penguins and the Procellariiformes. Crompton (1953) made a further study on penguins and did an extensive developmental study of the chondrocranium. An analysis of middle ear anatomy of Procellariiformes, including a glossary of avian middle ear characters, appears in Saiff (1974). Recently Frost et al. (1975) described the circulatory system in the head of *Spheniscus demersus* in an effort to describe heat-exchange systems in penguins.

Obvious lacunae exist in the study of the middle ear of birds, including Sphenisciformes. This study describes the anatomy of the middle ear and basicrania of the Sphenisciformes and where possible makes comparisons with Procellariiformes.

MATERIALS AND METHODS

This study is based on an analysis of characters of specimens borrowed from the Bird Department of the American Museum of Natural History. Peters (1931) was used as the basis for the generic classification and Wetmore (1930) for the higher taxa.

I studied the following specimens: dried skull: *Aptenodytes forsteri* AMNH 3745. *A. patagonica* AMNH 1623, 2611, 3139, 4630, 4383, 4382. *Eudyptes chrysolophus* AMNH 5974. *E. crestatus* AMNH 3854, 5398, 5972. *E. pachyrhynchus* AMNH no number. *E. schlegeli* AMNH 5399. *Eudyptula minor* AMNH 5314, 5620, 6257. *Megadyptes antipodes* AMNH 5613, 5615. *Pygoscelis adeliae* AMNH 5041. *P. papua* AMNH 3196, 4361, 5373, 5766, 5973. *Spheniscus demersus* AMNH 1625, 1310, 3875, 4042, 4069, 4942. *S. humboldti* AMNH 2768, 4920, 4921. *S. mendiculus* AMNH 3648, 3772. Dissected: *S. demersus* AMNH 4548.

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ANATOMICAL DESCRIPTIONS

EXTERNAL.—The external auditory meatus is on the same horizontal plane as the gape. The meatus lies on the border of a white band of feathers that runs first over and then behind the eye and a dark feather patch that extends posterior to the gape onto the throa region. The feathers that cover the external meatus grow only from its anterior rim. The meatus ranges between 2.4 to 3.5 mm tall and 1.9 to 2.1 mm wide (2 ears). The rim of the meatus does not appear to be so pliable as to close completely.

The external auditory canal is directed posteroventrally. No ridges appear on the inner membranous lining of the canal. Ridges do appear with some degree of consistency in Procellariiformes (Saiff 1974) although the presence or absence of such ridges may be an effect of preservation.

Upon removal of the m. depressor mandibulae, the outer membrane covering of the external auditory canal becomes visible and when this is dissected open the tympanic membrane comes into view. The tympanic membrane is roughly circular in shape, mildly protuberant, and faces posterolaterad. It is composed of a tough, thick outer layer that is quite elastic and a thinner but equally tough inner layer. The outer layer of the tympanic membrane is a continuation of the lining of the external auditory canal while the inner layer is continuous with the epithelium lining the middle ear cavity. The inferior process of the extra-columella, covered by its ligament, lies embedded within the inner tympanic layer. Here the tympanic membrane is thickened. The tympanic membrane separates the external auditory canal from the middle ear cavity.

ANATOMY OF THE MIDDLE EAR REGION.—The middle ear of all six genera of penguins is characterized by a conical tympanic cavity as seen in Fig. 1 that opens to the rear of the skull medial to the quadrate. Watson (1883) clearly figured this region but did not label it. The dorsal, ventral, and anterior wall of the tympanic cavity is a curved plate of bone that extends laterally to touch the rear of the dorsal end of the quadrate; the ventral edge of this plate is bent backward horizontally to form, along with a lateral extension of the basitemporal plate, the ventral wall of the tympanic cavity.

The tympanic membrane (seen dried in place in some skulls as well as *in situ* in AMNH 4548) is stretched across the rear aperture of the tympanic cavity from the metotic process to the quadrate. On the medial wall of the tympanic cavity is the fenestra ovalis, posterior to which is a pneumatic foramen. Ventral to these two structures is the recessus scalae tympani.

The seventh nerve foramen varies among the specimens examined. A facial foramen opening within the tympanic cavity is lacking in *Eudyptes*,

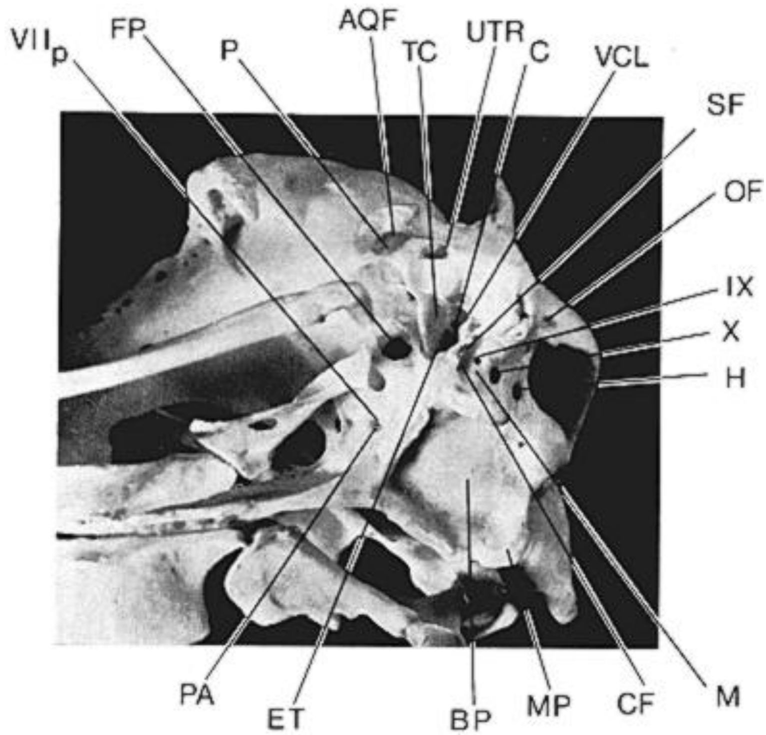

Fig. 1. *Spheniscus demersus* (AMNH 4042) oblique ventral view of the left middle ear region with quadrate removed: AQF, anterior quadrate facet; BP, basitemporal platform; C, columella; CF, carotid foramen; ET, entrance to eustachian canal; FP, foramen prooticum; H, hypoglossal foramen; IX, glossopharyngeal foramen; M, metotic process; MP, mammillary process of basitemporal platform; OF, foramen for occipital vein; P, pneumatic foramen; PA, foramen for palatine artery; SF, stapedial arterial foramen; TC, tympanic cavity; UTR, upper tympanic recess; VCL, exit point from skull of vena capitis lateralis; VIIp, foramen for palatine branch of facial nerve; X, vagal foramen.

Eudyptula, Megadyptes, and *Spheniscus*. Crompton (1953) studied the developmental process involved in this arrangement in *Spheniscus*. The palatine nerve enters the carotid canal through a foramen on its dorsomedial surface in order to run forward along with the carotid artery. The section of the carotid canal where the palatine nerve and carotid artery travel together represents the parabasal canal. At the anterolateral edge of the parabasal canal is a foramen for the forward continuation of the palatine nerve. Just anterior to this palatine nerve foramen is a larger foramen for the palatine artery. The hyomandibular branch of the facial nerve exits from a foramen located posterodorsal and lateral to the fenestra ovalis and then leaves the middle ear region with the stapedial artery through the stapedial arterial foramen. One specimen of *Eudyptula* (AMNH 5314) I examined had a foramen only on the right side of the inner wall of the tympanic cavity. This foramen is covered over by a membrane and is probably pneumatic.

Aptenodytes has a facial foramen. Dorsal and lateral to the facial foramen is an overhang of bone that is a forward continuation of the lateral wall of a canal that curves posterodorsally above the fenestra ovalis and opens posteriorly into the middle ear cavity. The posterior opening is directed toward the foramen housing the stapedial artery. It seems reasonable to assume that the hyomandibular nerve travels within this bony canal up to the stapedial canal and leaves the middle ear region via the stapedial canal and the stapedial arterial foramen. Anteroventral to the facial foramen a foramen enters the carotid canal from the tympanic cavity. Presumably the palatine nerve travels along the wall of the tympanic cavity to enter the carotid canal through this foramen.

The presence of a facial foramen opening into the middle ear of *Pygoscelis* cannot be determined without a dissection. Anterolateral to the fenestra ovalis in *Pygoscelis* are two fossae separated by a vertical ridge of bone. On this ridge is a foramen that is patent only on the left side in one of the specimens examined here (AMNH 5766) and in none of the others. It is not possible to tell whether this foramen is for the facial nerve, and if so, for which branch. It is doubtful, though, that the palatine branch would exit from this foramen. If it did, it would have to travel posteriorly for almost the entire length of the tympanic cavity in order to enter the carotid canal as there is no foramen that leads into the carotid canal from the tympanic cavity as is present in *Aptenodytes*.

All species examined had a bony canal for the stapedial artery dorsal to the columella, deep to the tympanic cavity. Posterior to entry into the middle ear, the stapedial canal runs medial to a vertical bar of bone (the lateral edge of the metotic process) connecting the rear of the paroccipital process to the rear of the basitemporal platform.

Running anteriorly in the ventrolateral portion of the tympanic cavity are two bony canals: a lateral canal for the eustachian tube, and a more dorsomedial carotid canal. These two canals are separated by a thin plate of bone referred to by Pycraft (1898) as a downgrowth from the alisphenoid wing of the parasphenoid. Anteriorly, the tympanic cavity is blind. The blind area presumably represents the presphenoid sinus of several Procellariiformes, Pelecaniformes, and Ciconiiformes (Saiff 1973).

In all penguins examined the carotid artery enters the carotid canal through the carotid foramen, which is located ventromedial to the tympanic cavity. The carotid artery is never exposed within the tympanic cavity. Just before entering the middle ear, the carotid artery gives off a dorsal branch, the stapedial artery, which lies dorsal to the columella. Deep to the stapedial artery, and also dorsal to the columella is the vena capitis lateralis. Together the stapedial artery complex of vessels and that of the vena capitis lateralis form a rete mirabile located lateral to the foramen prooticum. The vena capitis lateralis leaves the middle ear through a notch in the anterodorsal edge of the tympanic cavity just deep to the quadrate.

In *Megadyptes* and *Aptenodytes* a large dorsally directed pneumatic foramen enters into the braincase posterior to the dorsal rim of the tympanic cavity and deep to the point of entry of the stapedial artery into the middle ear. None of the other genera has such an opening.

All forms have a foramen just anterior to the articulatory surface for the head of the quadrate in the paroccipital process. This foramen takes the form of an elongate slit and appears to be the true upper tympanic recess. Anterior to the upper tympanic recess is an opening in much the position of the upper tympanic recess of the Diomedeidae and Procellariidae (Saiff 1974); this opening in penguins enters the brain cavity and appears to be pneumatic. In the Procellariiformes, Pelecaniformes, Sphenisciformes, and Ciconiiformes, the true upper tympanic recess is separated from the brain cavity by an imperforate wall of bone (Saiff 1973).

Ventral to the perforation into the brain cavity and anterior to the tympanic cavity is the foramen prooticum. Pycraft (1898) described the morphology of the foramen prooticum as well as that of the pneumatic foramen dorsal to it.

At the base of the skull posterior to the tympanic cavity are the glossopharyngeal, vagal, and hypoglossal foramina, which Crompton (1953) described. The glossopharyngeal and vagal foramina are located in the metotic process. Pycraft (1898) described the posterior aspect of the skull and the basitemporal platform, the former being variable among the genera while the latter is constant. The basitemporal platform as seen from below is triangular and concave. The eustachian tubes make the lateral edges curl ventrally, hence the concavity. At the rear of the basitemporal platform on each side is a weak mamillary process. "In all genera but *Spheniscus* there is a well-marked precondylar fossa" (Pycraft 1898). In all respects, save the mamillary process, the basitemporal platform (Table 1) of Sphenisciformes is very similar to that of Procellariiformes, especially *Diomedea* (Saiff 1974).

In all the genera of penguins the eustachian tubes are at least partly covered by bone. In *Eudyptes*, *Spheniscus*, and *Megadyptes* the bony covering extends to near the anterior end of the basitemporal platform

TABLE 1

COMPARISON OF SEVERAL STRUCTURES IN THE GULL, DIOMEDEIDAE, PROCELLARIIDAE, AND SPHENISCIDAE

Structure	*Larus argentatus*	Diomedeidae	Procellariidae	Spheniscidae
Presphenoid sinus	Closely approaches lateral edge of basitemporal platform below eustachian tube	Free	Free except at anterior end where it fuses with edge carotid canal	Fuses with free edge of basitemporal platform below eustachian tube
Carotid canal	Complete osseous structure running length of middle ear	Open laterally	Open laterally	Complete osseous structure running length of middle ear
Metotic process	Strong; perforated by vascular foramina and glossopharyngeal foramen	Weak; lacks vascular notches or foramina; lacks glossopharyngeal foramen	Weak; lacks vascular notches or foramina; glossopharyngeal foramen present but close to lateral edge	Strong; perforated by vascular foramina and glossopharyngeal foramen
Basitemporal platform	Weak mamillary processes	Strong mamillary processes	Strong mamillary processes	Weak mamillary processes
Angle between basitemporal platform and foramen magnum	110°	120°	118°	113°

while in *Eudyptula*, *Aptenodytes*, and *Pygoscelis* it covers only the posterior half of the eustachian tube.

QUADRATE AND ITS RELATION TO THE MIDDLE EAR.—Pycraft (1898) described the quadrate of the penguins. The quadrate articulates near the anterior end of the paroccipital process by two heads. The articulation is strengthened by a broad ligament connecting the paroccipital process and the lateral edge of the curved articulatory surface of the outermost head of the quadrate. A portion of this ligament extends to the dorsalmost lip of the tympanic cavity. The vena capitis lateralis runs just deep to this portion of the ligament. The angle of articulation is approximately at right angles with the long axis of the head. Posterior to the point of articulation a ventral curve of the paroccipital process extends about halfway down the level of the tympanic cavity.

The quadrate itself exhibits a deep capitular groove separating the prootic and squamosal-opisthotic articular heads with the paroccipital process. The facets for these articular heads in the paroccipital process are quite distinct from each other. A line drawn through these facets intersects the long axis of the skull at approximately a 45-degree angle. The upper tympanic recess is located anterior to these two facets. The penguins show some slight variability with regard to the orbital process. That of *Eudyptula*, *Eudyptes*, and *Spheniscus* is curved slightly upward with the superior border sharper than the inferior. In *Pygoscelis* the orbital process is similar in shape but longer. In *Aptenodytes* and *Megadyptes* the orbital process is taller than those described above although of the same approximate length as the *Eudyptula* grouping.

The pterygoid articulatory surface lies ventral and medial to the orbital process. The quadrato-jugal articulatory surface is at the base of the quadrate shaft on its lateral aspect just dorsal to the mandibular articulatory surface. Little variability among the several genera of Spheniscidae exists in the mandibular articulatory surface. Pycraft (1898) failed to describe this portion of the quadrate. The penguin has a shallow trochlear groove separating the inner and outer condylar pairs and no groove to distinguish the two condyles of the outer condylar pair from each other save for a shallow depression in *Eudyptula* and *Megadyptes*. The two condyles of the inner condylar pair are distinct from each other but the groove separating them is much shallower than in *Diomedea* (Saiff 1974).

The quadrate of penguins lacks a pneumatic foramen.

DISCUSSION

PRESPHENOID SINUS.—The anatomical literature makes little mention of this structure. Watson (1883) figured it in his description of the osteology of the penguins and Pycraft (1898) made some mention of it. There seems little doubt that the presphenoid sinus is pneumatic. In the Sphenisciformes it is shallow, poorly developed, and directed anteromedially. Its lateral wall fuses ventrally with the free edge of the basitemporal platform and is in close contact posteriorly with the quadrate shaft. The downward extension offers lateral protection to the carotid artery and eustachian tube (Table 1). Such protection is absent in the Diomedeidae although it is present to varying degrees in other Procellariiformes (Saiff 1974). Only in *Daption capensis* among the Procellariiformes does the hind portion of the lateral wall of the presphenoid sinus come into contact with the quadrate, a condition also seen in penguins.

UPPER TYMPANIC RECESS.—The position of the entrance to the upper tympanic recess with respect to the facets for the head of the quadrate has been used as a taxonomic character in birds (Lowe 1926, Saiff 1974). All the Sphenisciformes have a small, slit-shaped entrance to the upper tympanic recess that lies anterior to the paired quadrate facets. In the Diomedeidae, Pelecanoididae, and Procellariidae of the Procellariiformes the entrance is much larger than in the penguins but the position with respect to the quadrate facets is the same. The entrance to the upper tympanic recess in the Hydrobatidae of the Procellariiformes is small and located between the quadrate facets and not anterior to them (Saiff 1974).

FACIAL FORAMEN.—*Aptenodytes* is the only Sphenisciform that has a facial foramen opening within the middle ear. The palatine ramus continues forward to the parabasal canal; the hyomandibular ramus passes through a foramen in the ventral wall of a canal that continues posterodorsally to join the stapedial arterial canal. Presumably the hyomandibular nerve passes into the stapedial arterial canal and then leaves the middle ear through the stapedial arterial foramen. Crompton (1953) gave an account of the early development of the chondrocranium of *Spheniscus demersus* including a description with figures of the ontogeny of the facial foramen, its subsequent closing over, and the path ultimately taken by the facial nerve.

METOTIC PROCESS.—Crompton (1953) discussed much of the literature concerned with this structure, as well as its development in *Spheniscus demersus*. All the Sphenisciformes have a strong metotic process perforated by vascular foramina as well as foramina for the glossopharyngeal, vagus, and hypoglossal nerves. In many respects the metotic process of the penguins is markedly different from that of the Procellariiformes (Saiff 1974). The metotic process of the Diomedeidae is weak and lacks even a separate glossopharyngeal foramen. Also lacking are vascular foramina as in all the Procellariiformes I previously examined (Saiff 1974).

ENTRY OF CIRCULATION INTO THE HEAD.—In the single specimen that was dissected, the relative position of the foramen magnum with respect to the basitemporal platform shows that the carotid artery and vena capitis lateralis do not have to bend to enter the head from the neck. Frost et al. (1975) figure this in their recent paper. This is a different arrangement from that in the Procellariiformes (Saiff 1974). Even so, the vena capitis lateralis, stapedial artery, and carotid artery of penguins pass through foramina in the metotic process, as in the Pelacaniformes (Saiff 1973), rather than entering the middle ear in front of the metotic process as in the Procellariiformes.

MIDDLE EAR ARTERIES.—The carotid artery of the Sphenisciformes is completely encased in a bony tunnel as it traverses the middle ear. The stapedial artery is also protected on its lateral, medial, and ventral sides. This protection results from the close proximity of the quadrate and the lateral wall of the presphenoid sinus, which form a canal for the stapedial artery.

RETE MIRABILE.—In this study I dissected only a single specimen, and it had a rete mirabile. Frost et al. (1975) also found a rete mirabile in his dissections of *S. demersus*. Saiff (1973) described the presence or absence of the structure in several other birds. As far as can be determined no physiological or behavioral feature distinguishes the forms possessing a rete mirabile from those that lack one. Frost et al. (1975) discussed the literature concerning retia mirabile as heat-exchange systems. Certainly further studies involving dissections of more species are in order.

EUSTACHIAN TUBE.—This structure runs from the anteroventral region of the middle ear cavity to a median opening in the rear of the palate, which it shares with its fellow from the other side of the head. The eustachian tube of the Sphenisciformes runs along the edge of the basitemporal platform in a long canal that is at least partly protected by bone on all sides in all genera.

QUADRATE.—Pycraft (1898) and Shufeldt (1901) described quadrate structure in penguins. The sphenisciform quadrate is at right angles with respect to the long axis of the skull (in lateral view), and an extensive capitular groove separates the paired condyles of the quadrate head. Dorsal to the capitular groove in the paroccipital process a wide ridge of bone separates the facets for the quadrate head. These facets are perpendicular to the long axis of the skull. The upper tympanic recess is just anterior to a line drawn between the two facets.

The orbital process of the several species of penguins varies a bit but none is significantly different from that of the albatross (Saiff 1973). The arrangement of condyles of the mandibular articulatory surface is also as in *Diomedea* (Saiff 1973), but the condyles of the penguins are separated by grooves that are quite a bit shallower and less elongated than in the albatross.

CONCLUSIONS

Although a number of authors, notably Murphy (1936), Murphy and Harper (1921), and Simpson (1946), have held the Sphenisciformes to be closely related to the Procellariiformes, the middle ear gives no confirmation of it. Indeed, a cursory examination of five of the characters covered in this work indicates that the middle ear of the gull, *Larus argentatus*, comes closer to the penguins than do those of the Diomedeidae or Procellariidae (Table 1). At the same time several other characteristics are shared by several Procellariiformes and Sphenisciformes, such as ridges on the walls of the external auditory canal, the presence of a rete mirabile, basitemporal platform save the mammillary process, and position of upper tympanic recess with respect to the quadrate facets.

Wetmore (1930), Peters (1931), Murphy (1936), Simpson (1946), and Storer (1960, 1971) agree that the Spheniscidae are composed of six genera, which my data confirm. The Sphenisciformes are easily distinguished from the Procellariiformes (Saiff 1973, 1974) and the Pelecaniformes and Ciconiiformes (Saiff 1973) by the penguins' wide presphenoid sinus, which has a lateral wall that fuses to the basitemporal platform and is in close contact with the medial edge of the quadrate shaft, though the presphenoid sinus extends only a short distance rostrad.

All the penguins save *Aptenodytes* lack a facial foramen. Perhaps this is another character indicating the primitiveness of that genus among the Sphenisciformes. Many workers have studied the ancestry of extant penguins and do not agree on which genus is the most primitive and nearest to the ancestral form. Pycraft (1898) favored *Eudyptula* based on his osteological analysis of temporal fossae, upper jaw, quadratojugal bar, sternum and pectoral limb, while Wilson (1907), based on color characters of the head plumage, believed *Aptenodytes* closest to the primitive form.

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SUMMARY

The osteology and soft anatomy of the middle ear region of the skull are described for the Sphenisciformes with particular emphasis on the foramina for nerves and blood vessels. Also discussed is the morphology of the

basicranium and the quadrate. Comparative analysis of the characters are used to assess taxonomic conclusions. Little support is added to the theory that the penguins are closely related to the Procellariiformes.

The paper is part of a series that attempts to allow an assessment of evolutionary relationships within the Aves based on the anatomy of the middle ear region.

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