

The otic region of the skull of neognathous birds: on the homology and comparative morphology of some neurovascular and muscular foramina and other external skeletal structures

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Abstract

Even though detailed anatomical studies of the otic region exist for some avian species, there are few comparative data for most extant higher-level clades. In the present study, the external osteology of the otic region of birds is studied in a broad taxonomic context and a focus has been put on the homology of neurovascular and muscular foramina in taxa of the Neognathae. It is detailed that this part of the skull offers significant structural variation, which is of potential phylogenetic and physiological significance. The otic region of many taxa is for the first time illustrated and some osteological features are highlighted that are not or only rarely commented on in existing accounts of the otic region. These include the foramina and osseous guiding structures for the occipital ramus of arteria ophthalmica externa, as well as the skeletal correlates of ramus palatinus and ramus hyomandibularis of nervus facialis, and the foramen for musculus columellae. In addition, different conformations of the pila otica are described and some structures of unknown significance are highlighted, which require further research.

Key words

Anatomy; Aves; cranial morphology; Neognathae; osteology.

Introduction

Various aspects of the comparative osteology of birds are still insufficiently understood and this is particularly true for the otic region, that is, the middle ear and the surrounding bones. A confusing morphology with foramina and guiding structures for nerves and blood vessels as well as recesses for diverticula of the middle ear air sac makes this part of the skull one of the most complex regions of the avian skeleton.

Although several earlier authors described the anatomy of the avian otic region, most studies focused on particular taxa and had limited comparative context (CORDS, 1904; DOMBROWSKY, 1925). KESTIVEN (1925) studied the

nerve foramina of galliform birds and also undertook comparisons with a range of other taxa, but details of the otic region are difficult to discern in the illustrations accompanying the publication. Detailed descriptions of the otic region were given for the Tawny Owl (*Strix aluco*; STELLBOGEN, 1930), the Greater Rhea (*Rhea americana*; MÜLLER, 1961, 1963), domestic Galliformes (GHETIE, 1976), and the Late Cretaceous hesperornithiform *Enaliornis* (ELZANOWSKI & GALTON, 1991; these authors also commented on the distribution of some osteological features in extant birds). The comparative morphology of the otic region of the Palaeognathae and the neognathous

Turnicidae (Charadriiformes) was scrutinized by STARCK (1995), who focused, however, on hatchling morphology and soft tissue structures.

Most of the existing comparative data on the external anatomy of the otic region of adult birds were provided by Edward Saiff, who, in a series of papers, studied palaeognathous species (SAIFF, 1981, 1982, 1983, 1988), Sphenisciformes (SAIFF, 1976), Procellariiformes (SAIFF, 1974), Pelecaniformes and Ciconiiformes (SAIFF, 1978), Falconiformes and Accipitriformes (SAIFF, 2006), and Cariamiformes (SAIFF, 2011). SAIFF's studies not only cover the osteology but also describe associated soft tissue structures, especially the blood vessels and nerves that originate in the tympanic cavity or pass through it. The detailed descriptions are, however, not easily comprehended, because they pay equal attention to common features present in all birds and characteristics of certain taxa. Moreover, osteological details are difficult to discern in some of the published figures and some confusion may be caused by erroneous figure labels (e.g., SAIFF, 1978: Fig. 2 labeled the recessus tympanicus dorsalis as foramen prooticum; the foramina identified as ostia canalis carotici and canalis ophthalmici externi by SAIFF, 2006: Fig. 3 are for musculus columellae and nervus hypoglossus, respectively; the structure labeled as cotyla quadratica otici by SAIFF, 2006: Fig. 5 is the processus lateralis parasphenoidalis; SAIFF, 2011: Fig. 1 mistook the canalis caroticus cranialis for an osseous tube for nervus maxillomandibularis).

Many of the species, of which the otic region has been studied in greater detail, belong to Aequornithes, the clade including most aquatic and semiaquatic birds (MAYR, 2011a). By contrast, published data do not exist for the morphology of the otic region of the majority of other neornithine (crown group) clades, and this part of the cranium is often only briefly discussed in otherwise very detailed descriptions of the avian skull (e.g., JOHNSON, 1984). That the external morphology of the otic region of birds does offer features of phylogenetic and physiological interest is shown by the Passeriformes, for which a previously unreported derived pattern of the course of arteria ophthalmica externa was described, which characterizes a major subclade of the Passerida (MAYR, 2019).

As a consequence of the extensive pneumatization by the middle ear sac, the otic region of birds often exhibits numerous openings, recesses, and bony struts, which in some cases may be mistaken for osteological correlates of neurovascular or muscular features. To guide future research, the present study gives an overview of some of the key non-pneumatic structures in a broad taxonomic context. Because Palaeognathae were already studied by earlier authors (MÜLLER, 1961, 1963; SAIFF, 1981, 1982, 1983, 1988; STARCK, 1995) and the otic region of the Passeriformes has recently been described (MAYR, 2019), a focus was placed on non-passeriform neognathous birds. The otic region of several extant avian clades is for the first time illustrated and some structures of unknown significance are highlighted, which require further research. The main aim of this study is to present a broad overview

of the existing osteological diversity and to address the identity and homology of some non-pneumatic features. These data may serve as a basis for future studies of well-defined taxonomic subsamples, in which the evolutionary history of certain character states is traced in a robust phylogenetic framework.

General morphology of the otic region of birds

The middle ear of birds is situated in the tympanic cavity (cavum tympanicum) in the caudolateral portion of the skull, and is mainly formed by the otic bones (prooticum, opisthoticum, epioticum, metoticum) and the exoccipital bone. Laterally, the tympanic cavity is enclosed by the tympanic membrane, and acoustic signals are transmitted by the columella to the inner ear. Caudoventrally, the tympanic cavity of many birds is surrounded by a sheet-like bone, which is formed by the ala parasphenoidalis and the processus paroccipitalis of the exoccipital bone. The dorsal portion of the tympanic cavity is bounded by the cotylae for the quadrate. Apart from osteological features associated with the auditory sense, the tympanic cavity exhibits osseous guiding structures for blood vessels and nerves, as well as pneumatic recesses for diverticula of the middle ear air sac (Fig. 1).

The caudal portion of the tympanic cavity houses the fenestra vestibuli and the fenestra cochleae. These closely adjacent fenestrae are separated by an osseous strut, the promontorium tympani (Fig. 1F) and open into the cochlea, the key auditory structure of the inner ear. The fenestra cochleae is part of the exoccipital and is closed by the membrana tympanica secundaria. The fenestra vestibuli is formed by the exoccipital and prootic bones and encompasses the footplate of the columella. Just opposite of the fenestra cochleae, the medial wall of the scala tympani exhibits a foramen, the canaliculus cochleae, which opens into the fovea ganglii vagoglossopharyngealis inside the brain cavity and connects the scala tympani of the cochlea with the subarachnoid space in the brain cavity (Fig. 2E; WERNER, 1958). The fenestra vestibuli and fenestra cochleae are often situated in a deep recess, which is termed recessus columellae (Fig. 1C–F).

The middle ear sac pneumatizes the skull area around the tympanic cavity and sends off five diverticula into the surrounding bones (WITMER, 1990; STARCK, 1995; TAHARA & LARSSON, 2019a, b). Two of these pneumatize the quadrate and the mandible, whereas the other three diverticula form deep pneumatic recesses in the bones around the tympanic cavity. Based on their locations, these recesses are termed recessus tympanicus dorsalis, recessus tympanicus caudalis, and recessus tympanicus rostralis. The recessus tympanicus caudalis opens with the foramen pneumaticum caudale, which is situated caudally of the fenestra vestibuli (Fig. 1B); if a recessus columellae is present, it also encompasses the foramen pneumaticum caudale. The foramen pneumaticum dor-

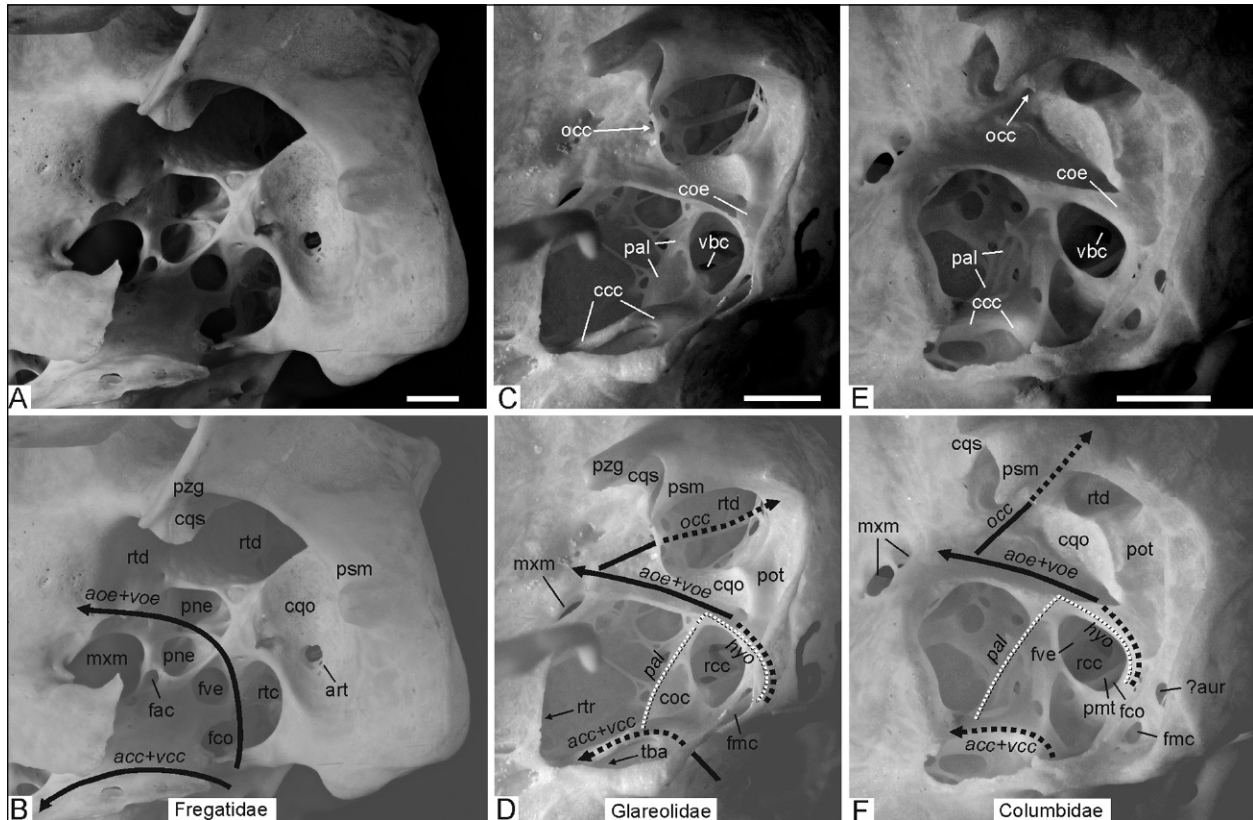


Fig. 1. Overview of major structures of the tympanic cavity (left side) in birds without (A) and with (C, E) ossified canals for the major blood vessels (canalis caroticus cranialis and canalis ophthalmicus externus). A, B, *Fregata magnificens* (Fregatidae, SMF 5389). C, D, *Rhinoptilus chalcopterus* (Glareolidae, SMF 13430). E, F, *Caloenas nicobarica* (Columbidae, SMF 17320). In B, D, and F, the images were digitally brightened and the course of major blood vessels (black lines) is indicated (dashed lines denote that the vessels travel within an osseous canal; the course of the vessels in *Fregata* is based on data in SAIFF, 1978, ramus occipitalis of arteria ophthalmica externa is not shown for this taxon). The dotted black and white lines in D and F line trace the course of the palatine and hyomandibular nerves. Abbreviations: acc, arteria carotis cerebialis; aoe, arteria ophthalmica externa; art, breakage artefact; aur, foramen for ramus auricularis of hyomandibular nerve; ccc, canalis caroticus cranialis; coc, lateral surface of cochlea; coe, canalis ophthalmicus externus; cco, cotyla quadratica otici; cqs, cotyla quadratica squamosi; fac, foramen n. facialis; fco, fenestra cochleae; fve, fenestra vestibuli; hyo, hyomandibular nerve; mxm, foramen n. maxillomandibularis; occ, ramus occipitalis of arteria ophthalmica externa; pal, palatine nerve/sulcus for palatine nerve; pmt, promontorium tympani; pot, pila otica; psm, processus suprameaticus; pzg, processus zygomaticus; rcc, recessus columellae; rtc, recessus tympanicus caudalis; rtd, recessus tympanicus dorsalis; rtr, recessus tympanicus rostralis; tba, tuba auditiva; vbc, foramen for nervus vestibulocochlearis; vcc, vena carotis cerebialis; voe, vena ophthalmica externa. Scale bars equal 2 mm.

sale, for the recessus tympanicus dorsalis, is usually situated between the quadrate cotylae and pneumatizes the squamosum and adjacent bones (Fig. 1B). The recessus tympanicus rostralis opens with the foramen pneumaticum rostrale and forms a deep, funnel-shaped and rostro-medially directed cavity (Fig. 1D), which pneumatizes the basioccipital, basisphenoid, and parashenoid bones. The recessus tympanicus rostralis is situated dorsal of the tuba auditiva (Fig. 1D), which opens with the ostium canalis tubae auditivae and connects the cavum tympani with the pharynx.

Four major blood vessels pass through the tympanic cavity and are associated with osteological structures (Fig. 1): the arteria carotis cerebialis and vena carotis cerebialis as well as the arteria ophthalmica externa and vena ophthalmica externa (a. carotis cerebialis was identified as a. carotis interna by MAYR, 2019, who followed earlier authors, such as SAIFF, 1978; the term a. carotis interna refers, however, to the section of the artery before it enters the tympanic cavity). In most birds, these ves-

sels enter (in the case of the arteries) or exit (in the case of the veins) the tympanic cavity through openings in the fossa parabasal, which are designated as ostium canalis carotici and ostium canalis ophthalmici externi, respectively (Fig. 4). The two arteries derive from arteria carotis interna, which divides into a. carotis cerebialis and a. ophthalmica externa shortly before or directly after entering the tympanic cavity. Arteria carotis cerebialis enters the tympanic cavity through the ostium canalis carotici in the cranioventral portion of the fossa parabasal. Within the tympanic cavity, a. carotis cerebialis usually runs within an osseous canal, the canalis caroticus cranialis, which also encompasses v. carotis cerebialis and traverses the ventral section of the tympanic cavity. The external ophthalmic artery and vein, by contrast, take a semicircular course along the caudodorsal side of the recessus columellae or the fenestra vestibuli and foramen pneumaticum caudale in taxa without this recess. Arteria ophthalmica externa and vena ophthalmica externa supply the rete ophthalmicum in the area of the fossa tempo-

ralis, a heat exchange structure that cools the brain and mitigates heat loss through the large eyes of birds (MIDTGÅRD, 1984). Both vessels enter or exit the tympanic cavity through the ostium canalis ophthalmici externi in the fossa parabasalis (Fig. 4). An unusual derived condition occurs in the passeriform taxon Passerida, in which a. ophthalmica externa is separated from v. ophthalmica externa by the recessus columellae; it was hypothesized that this derived morphology is of physiological significance and constitutes an adaptation for reducing heat loss of the arterial blood before it reaches the eye and the brain (MAYR, 2019). Arteria ophthalmica externa often sends off a dorsal branch, the ramus occipitalis, which enters the skull through a foramen near the foramen pneumaticum dorsale and exits it through a foramen on the caudal surface of the cranium near the crista nuchalis transversus (Fig. 4G, H; MAYR & WALSH, 2018).

The prooticum is perforated by two nerves, nervus facialis (cranial nerve VII) and nervus vestibulocochlearis (cranial nerve VIII; BUBIÉN-WALUSZEWSKA, 1981; DUBBELDAM, 1993). These nerves exit the brain cavity through five or six foramina in the fossa acustica interna on the medial surface of the prooticum within the braincase (MAY, 1961; WEBER, 1990). Most of these foramina are for the rami (branches) of nervus vestibulocochlearis, which innervate the cochlea and the utriculus and ampullae of the labyrinth and leave the braincase through four or five foramina (MAY, 1961; MÜLLER, 1961; BUBIÉN-WALUSZEWSKA, 1981; WEBER, 1990). Although some foramina for n. vestibulocochlearis are visible through the fenestra vestibularis and fenestra cochleae (Fig. 1), the nerve does leave traces in the tympanic cavity itself. Nervus facialis is the only cranial nerve, which travels through the tympanic cavity and the nerve primarily innervates muscles of the jaw apparatus, the eye and the supraorbital gland (BUBIÉN-WALUSZEWSKA, 1981). The foramen nervi facialis is the rostralmost of the foramina in the fossa acustica interna (MAY, 1961) and penetrates the prooticum to exit on the lateral surface of the bone. After having left the braincase, the nerve divides into a palatine and a hyomandibular ramus, which are termed palatine nerve (ramus palatinus of nervus facialis) and hyomandibular nerve (ramus hyomandibularis of nervus facialis), respectively. Detailed descriptions of the course of nervus facialis and its derivatives were given for the Strigidae (STELLBOGEN, 1930), domestic Galliformes (GHETIE, 1976), taxa of the waterbird clade (Aequornithes; SAIFF, 1978), and for palaeognathous birds (STARCK, 1995). The palatine nerve runs rostroventrally and enters the canalis caroticus cranialis to join the arteria carotis cerebralis along a short distance (Fig. 1D, F; FREYE, 1952). Within the canalis caroticus cranialis it connects with the sphenopalatine nerve to form the vidian nerve, which exits the ventral surface of skull in a small foramen next to the opening of arteria palatina; the portion of the canalis caroticus cranialis, which guides the vidian nerve, is termed canalis parabasalis (MÜLLER, 1963; BAUMEL & WITMER, 1993: 83 erroneously synonymized the entire canalis caroticus cranialis with the parabasal canal). The

hyomandibular ramus travels a short distance dorsally and then bends caudally and joins the vena et arteria ophthalmica externa (Fig. 1D, F; STELLBOGEN, 1930; SAIFF, 1978). It runs together with these blood vessels in the canalis ophthalmicus externus, or the corresponding part of the tympanic area in taxa without this canal, and exits the skull in the fossa parabasalis. Before leaving the tympanic cavity, the hyomandibular nerve gives off a ramus auricularis, which passes through a small opening next to the foramen musculi columellae (STELLBOGEN, 1930; GHETIE, 1976). Another thin strand of the hyomandibular nerve, the chorda tympani, innervates the salivary gland (BUBIÉN-WALUSZEWSKA, 1981), but osteological correlates of this nerve can not be identified through macroscopic inspection of macerated skulls. Caudovertrally of the tympanic cavity, the exoccipitale exhibits foramina for nervus glossopharyngeus (cranial nerve IX), n. vagus (cranial nerve X), and nervus hypoglossus (cranial nerve XII; see BUBIÉN-WALUSZEWSKA, 1981; MAYR, 2018). None of these nerves enters the tympanic cavity, but the foramen n. glossopharyngeus is sometimes situated in the fossa parabasalis (Fig. 4D) and may be confused with one of the openings for the nerves and vessels entering or exiting the tympanic cavity.

The sole muscle associated with osteological structures in the tympanic cavity is musculus columellae (STARCK, 1995). As detailed by POHLMANN (1921) and STELLBOGEN (1930), the musculus columellae of birds is likely to be homologous to the mammalian musculus stapedius. Even though the existence of a musculus columellae in birds was altogether doubted by GEORGE & BERGER (1966), various earlier authors provided detailed descriptions (STELLBOGEN, 1930; MÜLLER, 1963), and ELZANOWSKI (1987) noted that it is present in most taxa. Musculus columellae originates outside the tympanic cavity on the caudal surface of the skull, close to the fossa parabasalis (STELLBOGEN, 1930). The muscle inserts on the extracolumellar cartilage and enters the tympanic cavity through the foramen musculi columellae, which is not to be confused with the foramen for the glossopharyngeus nerve or other nerve foramina that are situated within or close to the fossa parabasalis (Fig. 4). Neither musculus columellae nor foramen m. columellae are listed in the Nomina Anatomica Avium (BAUMEL *et al.*, 1993), where the foramen m. columellae appears to be subsumed under the term hiatus subtympanicus, which was introduced for a “[d]eficiency (notch or fenestra) in the junctional area between the Ala parasphenoidalis and the margin of the Proc. paroccipitalis” (BAUMEL *et al.*, 1993: 70); KESTEVEN (1925) erroneously considered the foramen m. columellae to be a ligamental foramen.

Material and methods

This study is based on the examination of macerated skulls in the collection of Senckenberg Research Institute Frankfurt, Germany (SMF). The following species

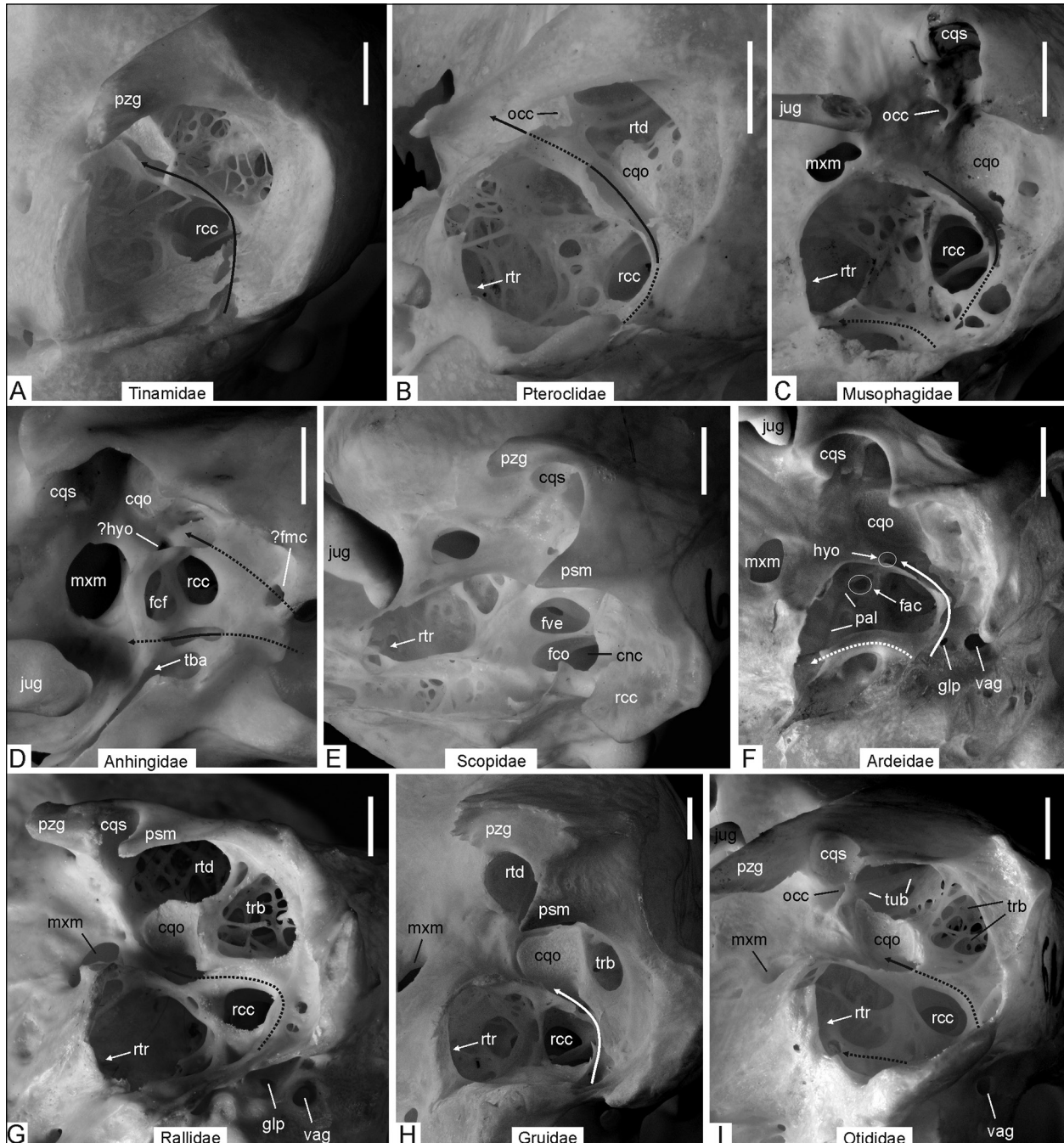


Fig. 2. Different conformations of the otic region. A, *Crypturellus undulatus* (Tinamidae, SMF 2149) as an example of a palaeognathous bird. B, *Pterocles quadricinctus* (Pteroclididae, SMF 15865), in which the canalis ophthalmicus externus reaches far rostrally. C, *Corythaixoides concolor* (Musophagidae, SMF 10769), in which the foramen for the ramus occipitalis of arteria ophthalmica externa is well visible. D, *Anhinga anhinga* (Anhingidae, SMF 9967), which is a member of Aequornithes with a canalis ophthalmicus externus. E, *Scopus umbretta* (Scopidae, SMF 13592), which lacks a recessus columellae and a canalis ophthalmicus externus. F, *Egretta gularis* (Ardeidae, SMF 13576), a representative of the Aequornithes with a canalis caroticus cranialis. G, *Gallirallus australis* (Rallidae, SMF 18691), a species with a trabeculate surface of the pila otica. H, *Balearica regulorum* (Gruidae, SMF 336), in which the pila otica forms a distinct recess. I, *Tetrax tetrax* (Otididae, SMF 11770), another species with a trabeculate surface of the pila otica. The black lines denote the presumed course of arteria carotis cerebialis and arteria ophthalmica externa (dashed lines indicate that the artery travels in the canalis caroticus cranialis or canalis ophthalmicus externus, respectively). Abbreviations: cnc, canaliculus cochleae; cco, cotyla quadratica otici; cqs, cotyla quadratica squamosi; fac, foramen for nervus facialis; fco, fenestra cochleae; fmc, foramen musculi columellae; fve, fenestra vestibuli; glp, foramen for nervus glossopharyngeus; hyo, foramen for hyomandibular nerve; jug, caudal end of jugal bar; mxm, foramen n. maxillomandibularis; occ, opening for ramus occipitalis of arteria ophthalmica externa; pal, sulcus for ramus palatinus of nervus facialis; psm, processus suprameaticus; pzg, processus zygomaticus; rcc, recessus columellae; rtd, recessus tympanicus dorsalis; rtr, recessus tympanicus rostralis; tba, tuba auditiva; trb, trabeculate/recessed surface of pila otica; tub, osseous tube for ramus occipitalis of arteria ophthalmica externa; vag, foramen for nervus vagus. Scale bars equal 2 mm.

and specimens were examined for a detailed study of osteological structures (nomenclature and classification follow the IOC World Bird List at <http://www.world-birdnames.org>): Rheidae: *Rhea americana* (SMF 4237); Tinamidae: *Crypturellus undulatus* (SMF 2149); Megapodiidae: *Alectura lathami* (SMF 14286); Cracidae: *Ortalis canicollis* (SMF 14247); Numididae: *Guttera edouardi* (SMF 14283); Odontophoridae: *Colinus virginianus* (SMF 8950); Phasianidae: *Meleagris gallopavo* (SMF 9971), *Syrnaticus soemmerringii* (SMF 14637); Anseranatidae: *Anseranas semipalmata* (SMF 11276); Anatidae: *Somateria mollissima* (SMF 15797); Podicipedidae: *Tachybaptus ruficollis* (SMF 14234); Phoenicopteridae: *Phoenicopterus chilensis* (SMF 5803); Gaviidae: *Gavia stellata* (SMF 14210); Spheniscidae: *Spheniscus humboldti* (SMF 383); Fregatidae: *Fregata magnificens* (SMF 5389); Sulidae: *Sula dactylatra* (SMF 11912); Anhingidae: *Anhinga anhinga* (SMF 9967); Phalacrocoracidae: *Phalacrocorax carbo* (SMF 13664); Pelecanidae: *Pelecanus onocrotalus* (SMF 5378); Balaenicipitidae: *Balaeniceps rex* (SMF 6293); Scopidae: *Scopus umbretta* (SMF 13592); Ardeidae: *Nycticorax nycticorax* (SMF 13330), *Egretta gularis* (SMF 13576); Threskiornithidae: *Platalea leucorodia* (SMF 17688), *Geronticus eremita* (SMF 13339); Ciconiidae: *Ciconia ciconia* (SMF 7774); Procellariidae: *Bulweria bulwerii* (SMF 7798), *Lugensa brevirostris* (SMF 10256); Diomedidae: *Diomedea melanophris* (SMF 5388); Oceanitinae: *Oceanites oceanicus* (SMF 9968); Recurvirostridae: *Himantopus himantopus* (SMF 14791); Burhinidae: *Burhinus capensis* (SMF 10767); Haematopodidae: *Haematopus ostralegus* (SMF 13725); Charadriidae: *Charadrius leschenaultii* (SMF 17277), *Vanellus vanellus* (SMF 15994), *Pluvialis apricaria* (SMF 14175), *Oreopholus ruficollis* (SMF 13419); Scolopacidae: *Calidris ferruginea* (SMF 14135), *Scolopax rusticola* (SMF 13672), *Numenius arquata* (SMF 13767); Rostratulidae: *Rostratula benghalensis* (SMF 16060); Jacanidae: *Jacana jacana* (SMF 13420); Thinocoridae: *Thinocorus rumicivorus* (SMF 12875); Turnicidae: *Turnix castanota* (SMF 13267); Glareolidae: *Rhinoptilus chalcopterus* (SMF 13430); Dromadidae: *Dromas ardeola* (SMF 13418); Chionidae: *Chionis alba* (SMF 5910); Stercorariidae: *Stercorarius skua* (SMF 16925); Sternidae: *Thalasseus bengalensis* (SMF 13798); Laridae: *Larus argentatus* (SMF 14383), *L. hyperboreus* (SMF 10154); Alcidae: *Alca torda* (SMF 13988), *Synthliboramphus antiquus* (SMF 8385); Rallidae: *Gallirallus australis* (SMF 18691), *Aramides saracura* (SMF 2153), *A. ypecaha* (SMF 13386); Heliornithidae: *Podica senegalensis* (SMF 11877); Aramidae: *Aramus guaranauna* (SMF 9970); Gruidae: *Balearica regulorum* (SMF 336); Otididae: *Tetrax tetrax* (SMF 11770); Pteroclididae: *Pterocles quadricinctus* (SMF 15865); Columbidae: *Caloenas nicobarica* (SMF 17320), *Treron waalia* (SMF 17110); Mesitornithidae: *Monias benschi* (SMF 4206); Rhynchoetidae: *Rhynchoetos jubatus* (SMF 2717); Eurypygidae: *Eurypyga helias* (SMF 3939); Phaethontidae: *Phaethon lepturus* (SMF 4697); Cuculidae: *Centropus senegalensis* (SMF 12501); Musophagidae: *Corythaix-*

oides concolor (SMF 10769), *Musophaga violacea* (SMF 12549); Opisthocomidae: *Opisthocomus hoazin* (SMF 1550); Steatornithidae: *Steatornis caripensis* (SMF 1738); Podargidae: *Podargus strigoides* (SMF 2503); Nyctibiidae: *Nyctibius griseus* (SMF 5394); Caprimulgidae: *Caprimulgus europaeus* (SMF 12071); Aegothelidae: *Aegothales cristatus* (SMF 237); Apodidae: *Apus apus* (SMF 17575); Trochilidae: *Phaethornis malaris* (SMF 5579); Cariamidae: *Cariama cristata* (SMF 2462); Cathartidae: *Coragyps atratus* (SMF 12266); Sagittariidae: *Sagittarius serpentarius* (SMF 11960); Accipitridae: *Circus approximans* (SMF 12178); Falconidae: *Milvago chimango* (SMF 12274), *Falco tinnunculus* (SMF 16038); Strigiformes: *Tyto alba* (SMF 13693); *Strix aluco* (SMF 14411); Psittacidae: *Nestor notabilis* (SMF 2844), *Pionus fuscus* (SMF 14821), *Ara macao* (SMF 14616), *A. severa* (14815); Leptosomidae: *Leptosomus discolor* (SMF 5438); Coliidae: *Urocolius macrourus* (SMF 13282); Trogonidae: *Apaloderma narina* (SMF 12035), *Harpactes oreskios* (SMF 12031); Coraciidae: *Coracias garrulus* (SMF 12723); Alcedinidae: *Alcedo atthis* (SMF 12822); Meropidae: *Merops apiaster* (SMF 11494); Picidae: *Picus viridis* (SMF 14354); Megalaimidae: *Psilopogon australis* (SMF 11147); Indicatoridae: *Indicator indicator* (SMF 12968); Bucconidae: *Monasa nigrifrons* (SMF 1557); Upupidae: *Upupa epops* (SMF 12580); Bucerotidae: *Tockus erythrorhynchus* (SMF 12521). Note that the above list denotes specimens, in which the middle ear is intact and well macerated. For most of the studied species, the Senckenberg collection includes multiple specimens, and critical anatomical observations have been verified based on more than one individual. For specific features, cursory examinations of other species were furthermore performed (these species are listed in the text).

Anatomical terminology follows BAUMEL & WITMER (1993), BAUMEL (1993), and DUBBELDAM (1993). Table 1 compares the terminology employed in the present study with that used by other authors. If not indicated otherwise, the course of vessels shown in some the figures was deduced from the position and morphology of the osseous guiding structures. The phylogenetic framework used in the present study is shown in Fig. 3.

Results

Guiding structures for blood vessels

In most neognathous taxa, the major blood vessels within the tympanic cavity are at least partially enclosed in bony tubes (SAIFF, 1978; WITMER, 1990). In the Fregatidae, however, which were chosen to illustrate features of the otic region in the Nomina Anatomica Avium (BAUMEL *et al.*, 1993), this is not the case and both, a canalis caroticus cranialis and a canalis ophthalmicus externus, are absent (Fig. 1A, B). The morphology of the otic region therefore distinctly differs from that of taxa with both canals

Table 1. Terminology of the *Nomina Anatomica Avium* (BAUMEL *et al.*, 1993), which is used in the present study, compared with the terminology of other authors.

Nomina Anatomica Avium	Other authors
fenestra vestibuli	fenestra ovalis (SAIFF, 1974, 1978)
fenestra cochleae	recessus scalae tympani (SAIFF, 1974, 1978)
recessus columellae	recessus stapediale (WERNER, 1958)
promontorium tympani	processus interfenestralis (SAIFF, 1974), crista interfenestralis (ELZANOWSKI & GALTON, 1991)
canaliculus cochleae	aquaeductus cochleae (MÜLLER, 1961), apertura medialis (WEBER, 1990; STARCK, 1995), perilymphatic foramen (SAIFF, 1974)
canalis ophthalmicus externus	canalis fallopiæ (STELLBOGEN, 1930), stapediale canal (PORTER & WITMER, 2016)
ostium canalis ophthalmici externi	foramen stylomastoideum (STELLBOGEN, 1930)
ostium canalis carotici	foramen jugulare (CORDS, 1904)
fovea ganglii vagoglossopharyngealis	fossa metotica (WERNER, 1958)
canalis caroticus cranialis	parabasal canal (SAIFF, 1974, 1976, 1978)
tuba auditiva	eustachian tube (SAIFF, 1974, 1976, 1978)
recessus tympanicus rostralis	presphenoid sinus (SAIFF, 1974, 1976, 1978)
recessus tympanicus dorsalis	upper tympanic recess (SAIFF, 1974, 1976, 1978)
arteria ophthalmica externa	stapedial artery (SAIFF, 1974, 1976, 1978, 1988; PORTER & WITMER, 2016)
vena ophthalmica externa	vena capitis lateralis (SAIFF, 1974, 1978, 1988), stapediale vein (PORTER & WITMER, 2016)
arteria carotis cerebialis	arteria carotis interna (SAIFF, 1988; MAYR, 2019)
foramen nervi facialis	foramen tympanicum faciale (GHETIE, 1976)

(Fig. 1C–D), and identification of some osteological features is not straightforward if this standard anatomical literature is used.

Fregatidae belong to the Aequornithes, the clade including the majority of aquatic and semiaquatic avian taxa (Fig. 3; MAYR, 2011a). Most other neognathous birds without a canalis caroticus cranialis are likewise part of Aequornithes, and in addition to the Fregatidae, the Procellariiformes, Ciconiidae (Fig. 5C), Pelecanidae, Scopidae (Fig. 2E), Balaenicipitidae, Sulidae, and Phalacrocoracidae (Fig. 5B) lack a canalis caroticus cranialis (Tab. 2). Because the canal is present in other taxa of the Aequornithes (Gaviidae [Fig. 5A], Spheniscidae, Threskiornithidae, Ardeidae [Fig. 2F]) and is partially ossified in the Anhingidae (Fig. 2D), the reduction of an ossified canal either occurred several times within Aequornithes or some taxa secondarily regained an ossified canal. Outside the Aequornithes, a canalis caroticus cranialis is only absent in the Phaethontidae. Most other Neognathae exhibit a fully ossified canalis caroticus cranialis, but in some taxa the canal is incompletely ossified, with the lateral portion being open (e.g., Sternidae). The canalis caroticus cranialis of the Cariamidae was mistaken for an ossified canal for nervus maxillaris and n. mandibularis by SAIFF (2011: Fig. 1 and p. 30), but in the Cariamidae and all other birds these latter nerves emerge from the foramen maxillomandibularis and do not traverse the tympanic cavity.

In all taxa that lack the canalis caroticus cranialis, an ossified canalis ophthalmicus externus is likewise absent (Tab. 2). In addition, a canalis ophthalmicus externus is

absent or largely reduced in the Phoenicopteridae and the charadriiform Lari (Chionidae, Dromadidae, Stercorariidae, Sternidae [Fig. 5F], Laridae, and Alcidae [Fig. 5D]). In a number of neognathous birds, the canalis ophthalmicus externus is only partly ossified, being laterally open over varying sections (e.g., Gruidae, Podicipedidae, Musophagidae, Pteroclididae [Fig. 2B], Cathartidae, Sagittariidae, Bucerotidae). A fully ossified canalis ophthalmicus externus is found in many only distantly related groups and is present in, e.g., the Anhingidae [Fig. 2D], Cuculidae [Fig. 6E], the charadriiform Scolopaci, Strisores (the clade including “caprimulgid” and apodiform birds), and in most taxa of the Telluraves, the clade including the majority of the arboreal land birds. However, the length of this canal shows considerable variation, and whereas it usually does not reach beyond the cotyla quadratica otici, its rostral opening is situated outside the tympanic cavity in phasianid Galliformes and in the Pteroclididae (Fig. 2B).

The arteria carotis interna divides into a. carotis cerebialis and a. ophthalmica externa either immediately before entering the tympanic cavity or the split occurs within the tympanic cavity. Often, the morphology can be deduced from the shape of the ostium canalis ophthalmici externi, which is a single opening (for vena ophthalmica externa) in taxa, where the split occurs within the tympanic cavity. By contrast, the ostium forms two openings (for arteria and vena ophthalmica externa) in taxa, where a. carotis interna divides outside the tympanic cavity. The position of this split differs in closely related taxa, and SAIFF (1978: 360) noted that it occurs within the tympanic cavity in the Phaethontidae,

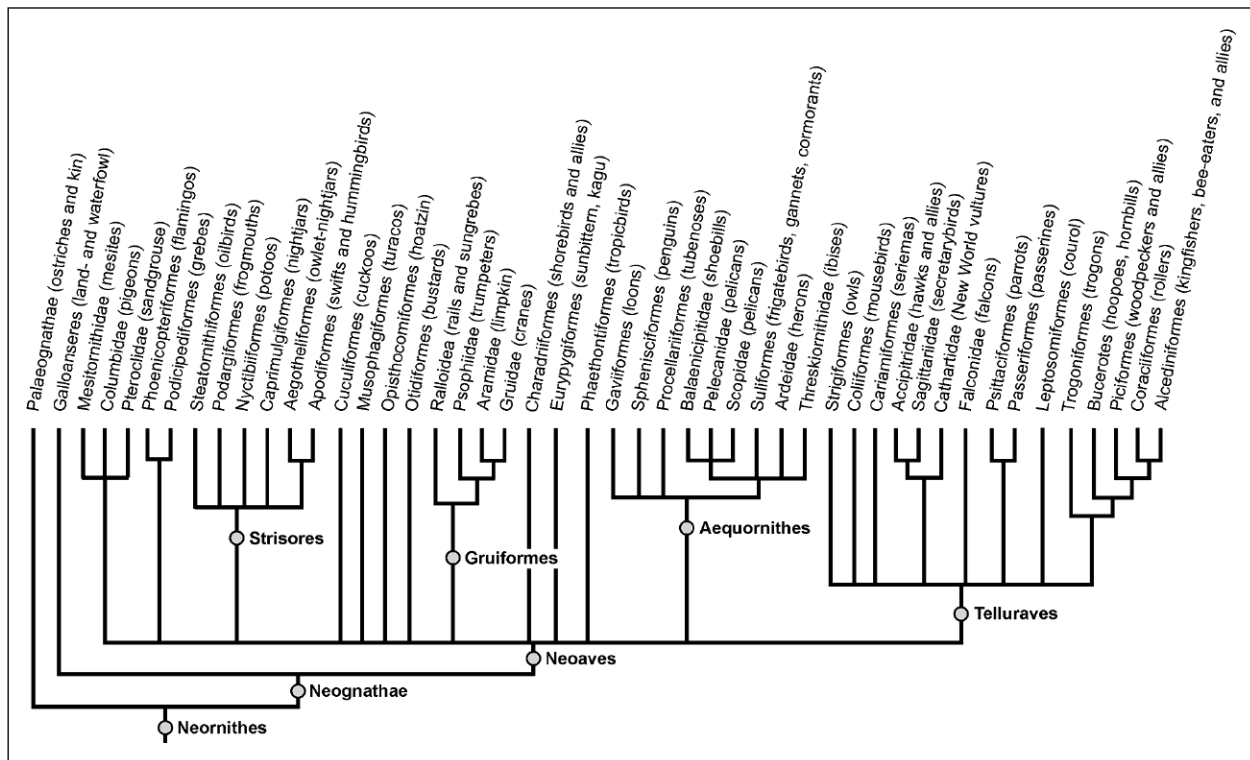


Fig. 3. Phylogenetic framework for neornithine birds used in this study (based on HACKETT *et al.* 2008; JARVIS *et al.*, 2014; PRUM *et al.*, 2016).

Sulidae, Anhingidae, and Phoenicopteridae, but caudal of the tympanic cavity in the Ciconiidae, Pelecanidae, Scopidae, Phalacrocoracidae, Ardeidae, and Threskiornithidae. In *Falco tinnunculus* (Falconidae) and *Strix aluco* (Strigidae), the ostium canalis ophthalmici externi forms two confluent large openings, which indicate that a. carotis cerebialis and a. ophthalmica externa divide outside the tympanic cavity, with a. ophthalmica externa entering the ostium canalis ophthalmici externi together with vena ophthalmica externa. Two distinct openings for a. carotis cerebialis and a. ophthalmica externa are likewise visible in *Eolophus roseicapillus* (Psittacidae; Fig. 4F). In *Apus apus* (Apodidae; Fig. 4E) and *Numenius arquata* (Scolopacidae), by contrast, a. carotis interna seems to divide after entering the ostium canalis ophthalmici externi and certainly this is also the case in those taxa of the passeriform Passerida, in which a. ophthalmica externa travels rostral of the recessus columellae (MAYR, 2019).

The foramen through which ramus occipitalis of a. ophthalmica externa enters the skull is present in many distantly related taxa, but it has not been illustrated by previous authors studying the otic region of birds. If present, this foramen is located between the cotyla quadratica squamosi and the cotyla quadratica otici (Figs. 2C, 4A–F). Often, the vessel travels within a bony tube in the recessus tympanicus dorsalis (MIDTGÅRD, 1984), and such an ossified tube for ramus occipitalis of a. ophthalmica is present in, e.g., the Podicipedidae, many charadriiform birds (Fig. 5E), Aramidae, Gruidae, Steatornithidae, Apodidae, Trochilidae, Pteroclididae, Falconi-

dae, Coraciidae (Fig. 5G), and Meropidae. A foramen for the ramus occipitalis of a. ophthalmica externa occurs in all taxa, in which this vessel travels in an osseous tube through the recessus tympanicus dorsalis. By contrast, this foramen is usually absent in taxa, in which an osseous tube for ramus occipitalis of a. ophthalmica externa is absent (e.g., Anatidae, Laridae, Rallidae, Strigiformes, Columbidae, Nyctibiidae, Coliidae, Trogonidae, Alcedinidae, Indicatoridae, and Upupidae). For Spheniscidae and Gaviidae, probing of the exit opening near the crista nuchalis transversa with a bristle shows that ramus occipitalis of a. ophthalmica externa enters the skull through the small foramen pneumaticum dorsale. This is also true for *Egretta gularis* (Ardeidae), in which the exit opening near the crista nuchalis transversa is visible through the foramen pneumaticum dorsale. In other taxa of the Aequornithes (Ciconiidae, Phalacrocoracidae, and Scopidae) as well as in the Podicipedidae, an osseous tube is likewise absent, but the entry opening of ramus occipitalis is separated from the foramen pneumaticum dorsale by a narrow bony bridge (Fig. 5B). However, several taxa that lack an entry foramen of ramus occipitalis of a. ophthalmica externa also lack the exit foramen of this artery near the crista nuchalis transversa (e.g., *Syrnaticus soemmerringii* [Phasianidae], *Aramides ypecaha* [Rallidae], *Harpactes oreskios* [Trogonidae], *Urocolius macrourus* [Coliidae]), and it needs to be determined through anatomical dissections if the occipital ramus is reduced in these birds. That the occipital ramus of arteria ophthalmica externa is indeed genuinely absent in galliform birds is suggested by the studies of PORTER & WITMER

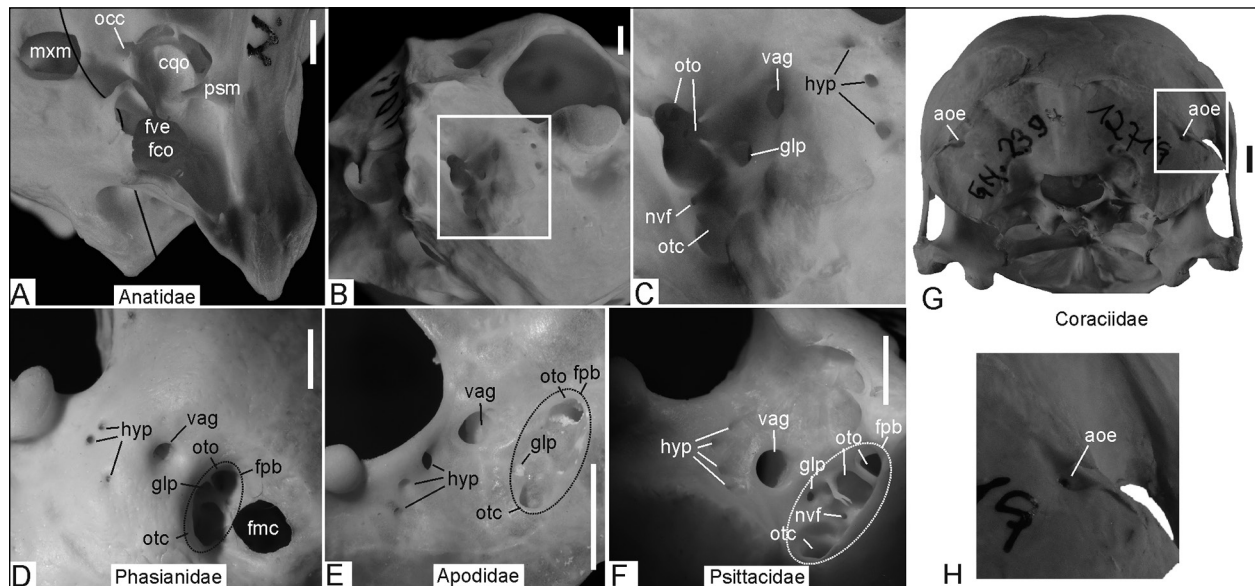


Fig. 4. Structures outside the tympanic cavity that relate to features of the otic region. A, *Somateria mollissima* (Anatidae, SMF 15797), left otic region in lateral view, the bristle indicates the course of the nerve canal in the fossa parabasal, which is indicated as “nvf” in C. B, C, *S. mollissima* (SMF 15797), basicranial area of left side with fossa parabasal, the frame denotes the position of the detail shown in C. D, *Gallus gallus* (Phasianidae, SMF 32329), basicranial area of right side with fossa parabasal. E, *Apus apus* (Apodidae, SMF 17575), basicranial area of right side with fossa parabasal. F, *Eolophus roseicapillus* (Psittacidae, SMF 14626), basicranial area of right side with fossa parabasal. G, H, *Coracias garrulus* (Coraciidae, SMF 12719), skull in caudal view to show the caudal opening for ramus occipitalis of arteria ophthalmica externa; the frame indicates the position of the detail shown in H. Abbreviations: aoe, caudal foramen for ramus occipitalis of arteria ophthalmica externa; cco, cotyla quadratica otici; fco, fenestra cochleae; fmc, foramen muscoli columellae; fpb, fossa parabasal (dashed circle); fve, fenestra vestibuli; glp, foramen for nervus glossopharyngeus; hyp, foramina for nervus hypoglossus; mxm, foramen n. maxillomandibularis; nvf, unidentified nerve foramen; occ, foramen for ramus occipitalis of arteria ophthalmica externa; otc, ostium canalis carotici; oto, ostium canalis ophthalmici externi; psm, processus suprameaticus; vag, foramen for nervus vagus. Scale bars equal 2 mm.

(2016), who did not identify this vessel in their detailed account of the vascular anatomy of the turkey skull.

Caudal of the cotyla quadratica otici, a vein exits the skull, which was termed “vena auris” by STELLBOGEN (1930), who considered its homology to be uncertain. The corresponding foramen was labeled as “foramen orale v. auris interna” by GHETTE (1976: 269). It was also identified as a venous foramen by SAIFF (1978: 320) for the Phalacrocoracidae, who described an “occipital vein” for ciconiiform and pelecaniform birds. PORTER & WITMER (2016: Fig. 10) associated this vein with the occipital sinus. The foramen is well visible in the Gaviidae, Podicipedidae, Ciconiidae, and Scopidae. In other taxa, it is often concealed by the canalis ophthalmicus externus, but in the Jacanidae (Fig. 6C) and Upupidae (Fig. 5I) the caudodorsal area of the tympanic cavity is poorly ossified and an osseous tube for the vein is exposed.

Foramina and guiding structures for the branches of nervus facialis

The opening of nervus facialis is situated rostrally of the fenestra vestibuli, between the latter and the foramen n. maxillomandibularis. In many cases, identification of the foramen n. facialis is straightforward, since it opens into the fossa acustica interna within the brain cavity and can therefore be distinguished from surrounding pneumatic openings by probing with a fine bristle. Foramen

n. facialis is very large in most taxa of the Aequornithes (except Scopidae, Fregatidae, Sulidae) and in the Phoenicopteridae. Especially amongst taxa of the Strisores and Telluraves, the foramen n. facialis is concealed by the fact that nervus facialis runs within an osseous canal. In some taxa, nervus facialis splits into a palatine and a hyomandibular ramus before exiting the foramen n. facialis and the nerve therefore leaves the braincase through two foramina, which were reported present in, e.g., the Cathartidae and Sagittariidae (SAIFF, 2006). According to SAIFF (1978), the foramen n. facialis is situated in a deep fossa in the Anhingidae (“fossa facialis”); a foramen next to the rostral opening of the canalis ophthalmicus externus is therefore likely to be for the hyomandibular nerve (Fig. 2D).

Often, a shallow sulcus on the lateral surface of the prootic bone denotes the course of the palatine nerve along its way to the canalis caroticus cranialis, and a foramen on the dorsal surface of the canalis caroticus cranialis indicates the site, where the palatine nerve joins the a. carotis cerebialis. The sulcus for the palatine nerve is, for example, present in *Rhinoptilus* (Glareolidae; Fig. 1C), *Sterna* (Sternidae; Fig. 6A, B), *Centropus* (Cuculidae; Fig. 6E, F), and *Caloenas* (Columbidae; Figs. 1E, 5G, H). By contrast, the palatine nerve is conducted by an osseous tube in the Tinamidae (SAIFF, 1988), some Anatidae (*Branta leucopsis*) and Columbidae, as well as in the Rallidae (*Gallinula*), Aramidae, Gruidae, the charadriiform Scolopaci (Jacanidae [Fig. 6C, D], Thino-

coridae, Scolopacidae), Musophagidae, Steatornithidae, Caprimulgidae, Upupidae, and the Coliidae. In other taxa, the nerve is guided by a very fine osseous trabecula (e.g., Bucerotidae).

In some taxa, a groove for the hyomandibular nerve is visible, which runs from the foramen nervi facialis to the canalis ophthalmicus externus or the corresponding area in taxa without this canal. Often a tiny opening for the hyomandibular nerve can be discerned in the ventral portion of the canalis ophthalmicus externus (Figs. 2F, 5F).

In various species, a small foramen for the ramus auricularis of the hyomandibular nerve is present in the osseous sheet that delimits the ventral border of the tympanic cavity. This foramen was described for the Strigiformes by STELLBOGEN (1930) and is situated caudally of the foramen musculi columellae in *Strix aluco* (Strigidae; Fig. 7H). As to be expected, the nerve foramen is smaller than that for the muscle in *S. aluco*, but in other taxa the situation is less clear (see next section).

In many birds, there is a tiny foramen in the fossa parabasalis, between the ostium canalis carotici and the ostium canalis ophthalmici externi and next to the foramen for nervus glossopharyngeus (Fig. 4C, F). In the studied Anseriformes and in the Indicatoridae, this foramen leads into a canal within the osseous strut rostral of the recessus columellae and is connected with the foramen for the hyomandibular nerve (Fig. 4A). Possibly, this foramen in the fossa parabasalis is therefore for a branch of the hyomandibular nerve which travels ventrally through the tympanic cavity and communicates with the glossopharyngeus nerve (BUBIÉN-WALUSZEWSKA, 1981).

Foramen musculi columellae

The foramen musculi columellae is located in the osseous sheet forming the caudoventral border of the tympanic region, close to the recessus columellae, or to the fenestra cochleae in birds without a recessus columellae (Fig. 7). The foramen m. columellae opens near the fossa parabasalis (Fig. 4D), next to which musculus columellae has its origin. It has been described for the Strigidae by STELLBOGEN (1930), who identified another, smaller, and more caudally situated foramen as that for the ramus auricularis of the hyomandibular nerve.

Comparative data for the foramen m. columellae have not yet been published. In some taxa its identification is straightforward by comparison with the Strigidae, and the foramen for the tendon of musculus columellae is often accompanied by a smaller caudal foramen, presumably for ramus auricularis of the hyomandibular nerve (e.g., Alcedinidae; Fig. 7K).

However, in some taxa the two foramina have reverse sizes and a small foramen is situated rostral of a larger one (e.g., *Centropus senegalensis*, Cuculidae; Fig. 7G). Because the foramen for the tendon of musculus columellae is expected to be larger than that for a thin nerve, the opening for the auricular ramus of nervus hyoman-

dibularis appears to be situated rostral of the foramen nervi columellae in these birds. In some species, such as *Numenius arquata* (Scolopacidae, Fig. 7F) and *Indicator indicator* (Indicatoridae, Fig. 7J), both foramina appear to be confluent and form a large, irregularly-shaped opening. In all of the above instances, an unambiguous identification of these foramina is, however, only possible through examination of the soft tissue anatomy.

The size of the foramen m. columellae is variable. It is tiny in the studied Cuculidae (Fig. 7G), Trogonidae (Fig. 7I), and Alcedinidae (Fig. 7K), where it seems to conduct only the tendon of musculus columellae. By contrast, the foramen m. columellae is very large in the Galliformes (Fig. 7A, B), some Charadriiformes (Fig. 7F), the Upupidae (Fig. 6L), and the piciform Indicatoridae (Fig. 7J). Just by examination of macerated skulls it can not be determined, whether in these latter taxa the size of the foramen is constrained by soft tissue, and anatomical dissections are also required to assess whether a part of the muscle itself is encompassed by the foramen in taxa with a large foramen m. columellae.

A foramen m. columellae is absent in taxa, in which the osseous sheet surrounding the caudoventral part of the tympanic cavity is reduced. This is the case in most taxa of the Aequornithes as well as in the Podicipedidae, Phoenicopteridae, and some Charadriiformes. In some taxa, there is a fenestra of uncertain identity close to the fenestra cochleae, which may or may not represent a foramen m. columellae (e.g., Anhingidae [Fig. 2D], Phoenicopteridae [Fig. 7D]).

Recessus columellae and canaliculus cochleae

A deep recessus columellae is present in, e.g., the Galliformes, many Anseriformes, Anhingidae (Fig. 2D), Rallidae (Fig. 2G), Pteroclididae (Fig. 2B), Columbidae (Fig. 1E, F), Alcedinidae (Fig. 7K), and Passeriformes (Mayr, 2019). Occurrence of a recessus columellae is variable in the Charadriiformes, with a recess being present in the Scolopaci (Scolopacidae, Rostratulidae, Jacanidae, and Thinocoridae), some Charadrii (e.g., *Vanellus vanellus* [Fig. 7E], *Charadrius leschenaultii*, *Burhinus capensis*), and some Lari (Turnicidae and Glareolidae), but being absent in other Charadrii (e.g., Haematopodidae, Recurvirostridae) and Lari (Stercorariidae, Sternidae, Laridae, Alcidae). A recessus columellae is also absent in most Aequornithes except for the Ardeidae and Threskiornithidae. Whether a recessus columellae is formed depends, among others, on the degree of ossification of the canalis ophthalmicus externus, which constitutes the dorsal border of the recess, and in taxa with a well-ossified canalis ophthalmicus externus, a recessus columellae is usually present (except for Gaviidae, Spheniscidae, and Anhingidae). There exist, however, gradual differences in the transition from species with a well-defined, deep recessus columellae (e.g., Columbidae; Fig. 1E, F) to those, in which the fenestrae vestibuli and cochleae are

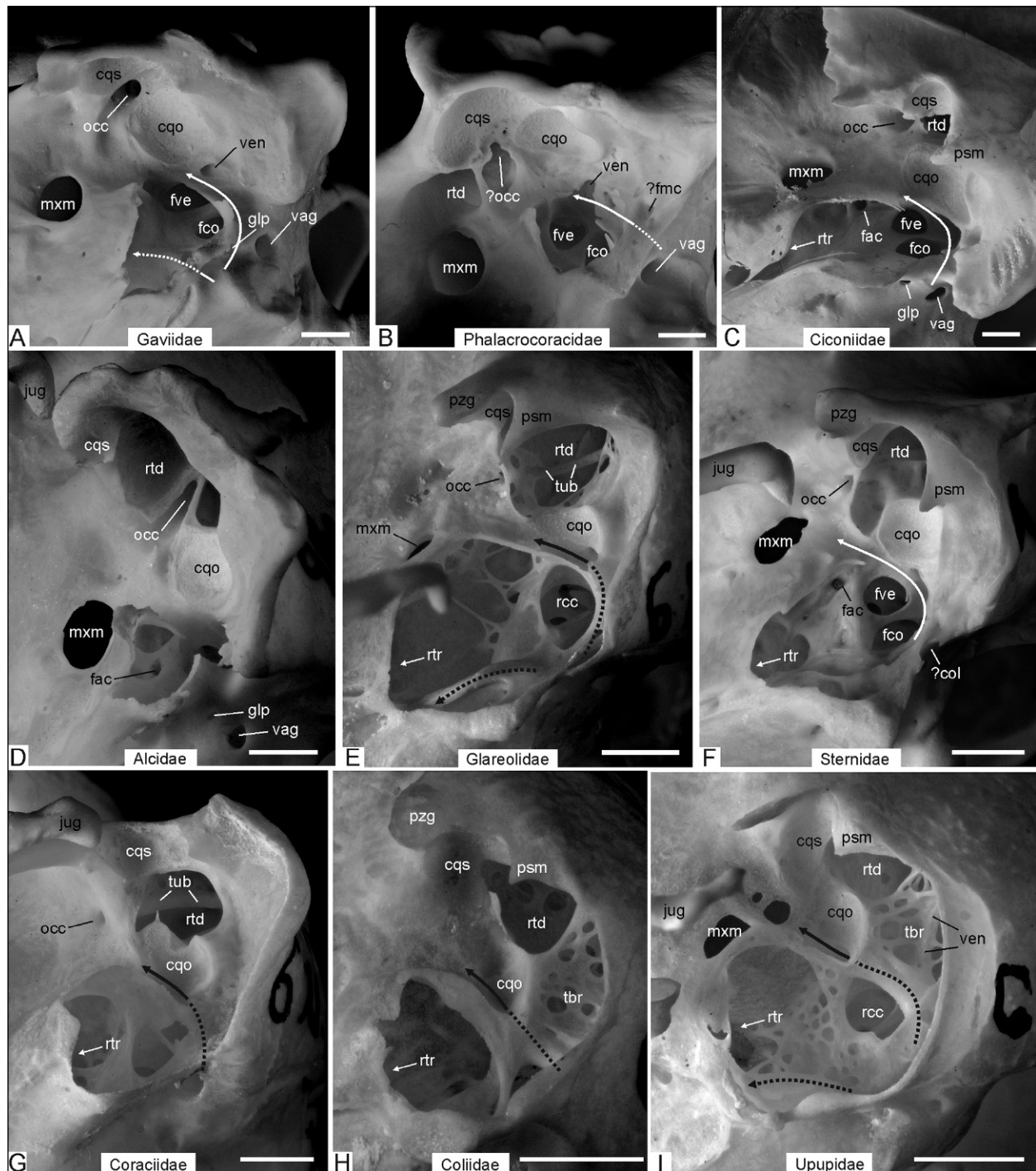


Fig. 5. The left otic region of various taxa to show the opening and osseous guiding structures for ramus occipitalis of arteria ophthalmica externa and the foramen for the occipital vein. A, *Gavia stellata* (Gaviidae, SMF 14210). B, *Phalacrocorax carbo* (Phalacrocoracidae, SMF 13664). C, *Ciconia ciconia* (Ciconiidae, SMF 7774). D, *Alca torda* (Alcidae, SMF 13988). E, *Rhinoptilus chalyptopterus* (Glareolidae, SMF 13430). F, *Thalasseus bengalensis* (Sternidae, SMF 13798). G, *Coracias garrulus* (Coraciidae, SMF 12723). H, *Urocolius macrourus* (Coliidae, SMF 13282). I, *Upupa epops* (Upupidae, SMF 12580). The black lines denote the presumed course of arteria carotis cerebialis and arteria ophthalmica externa (dashed lines indicate that the artery travels in the canalis caroticus cranialis or canalis ophthalmicus externus, respectively). Abbreviations: col, notch for musculus columellae; cco, cotyla quadratica otici; cqs, cotyla quadratica squamosi; fac, foramen n. facialis; fco, fenestra cochleae; fmc, foramen muscoli columellae; fve, fenestra vestibuli; jug, caudal end of jugal bar; mxm, foramen n. maxillomandibularis; psm, processus suprameaticus; pzg, processus zygomaticus; rtd, recessus tympanicus dorsalis; rtr, recessus tympanicus rostralis; tbr, trabeculate surface of pila otica; tub, osseous tube for ramus occipitalis of arteria ophthalmica externa; ven, foramen/ossified tube for occipital vein. Scale bars equal 2 mm.

fully exposed and not situated in a recess (e.g., Scopidae; Fig. 2E), so that an unambiguous categorization is sometimes not possible.

In neornithine birds, the canaliculus cochleae (“perilymphatic foramen” of SAIFF, 1974: 219) is usually a small canal, which opens into the fovea ganglii vagoglos-

Table 2. Some features of potential phylogenetic significance and their distribution across neognathous higher-level clades.

Character state	Taxa that show this character state
canalis ophthalmicus externus not ossified	Phaethontidae, Gaviidae, Diomedidae, Oceanitidae, Hydrobatidae, Procellariidae, Ciconiidae, Fregatidae, Sulidae, Phalacrocoracidae, Pelecanidae, Scopidae, Balaenicipitidae, Phoenicopteridae, Dromadidae, Stercorariidae, Sternidae, Laridae, Alcidae
canalis caroticus cranialis not ossified	Phaethontidae, Diomedidae, Oceanitidae, Hydrobatidae, Procellariidae, Ciconiidae, Fregatidae, Sulidae, Phalacrocoracidae, Anhingidae, Balaenicipitidae
canaliculus cochlea forming large window-like opening	Anseranatidae, some Anatidae, Phaethontidae, Phoenicopteridae, Gaviidae, Spheniscidae, Fregatidae, Sulidae, Anhingidae, Phalacrocoracidae, Pelecanidae, Balaenicipitidae, Scopidae, Threskiornithidae, Ciconiidae, Diomedidae, Oceanitidae, Hydrobatidae, Procellariidae, Rostratulidae, Recurvirostridae, Burhinidae, Haematopodidae, some Charadriidae, Glareolidae, Sternidae, Laridae, Alcidae, Heliornithidae, Aramidae, Gruidae, Cathartidae
pila otica with trabeculate lateral surface	Rallidae, Psophiidae, Aramidae, Gruidae, Scolopacidae, Rostratulidae, Jacanidae, Thinocoridae, Turnicidae, Cuculidae, some Musophagidae, Otididae, Pteroclididae, Mesitornithidae, some Columbidae, Eurypygidae, Rhynchotidae, Caprimulgidae, Coliidae, Trogonidae, Upupidae, Phoeniculidae, Bucconidae, Passeriformes

sopharyngealis (WERNER, 1958), but in some taxa it forms a large opening, which reaches the size of the fenestra cochleae (Tab. 2). A very large, window-like canaliculus cochleae was reported by WERNER (1958) for the Anatidae, Gruidae, Ciconiidae, Threskiornithidae, Phalacrocoracidae, Cathartidae, and some Psittacidae (*Ara*). Here it is noted that a large canaliculus cochleae was found in all examined taxa of the Aequornithes except for the Ardeidae. The size of the canaliculus cochleae is variable in the Anseriformes, and a large canaliculus is present in the Anseranatidae and some Anatidae (e.g., *Branta leucopsis*, *Somateria mollissima*), whereas it is absent in other Anatidae (*Amazonetta brasiliensis*, *Sarkidiornis melanotos*, *Tadorna tadornoides*, *Anas smithii*). In the Charadriiformes, a large canaliculus cochleae is present in most Charadrii (except *Vanellus*) and in the Lari, whereas it is small in most Scolopaci except for the Rostratulidae. WERNER (1958) reported a large canaliculus cochleae for “*Ara*” (a species was not specified), but I found it to be small in *Ara severa*, *A. macao*, and *Pionus fuscus* (Psittacidae).

Pila otica, quadrate cotylae, and other osteological structures

The cotyla quadratica otici, which articulates with the otic condyle of the quadrate, is often situated on a peduncle-like structure termed pila otica. In a number of taxa, the pila otica has a trabeculate lateral surface and sometimes it bears a distinct recess (Tab. 2). A trabeculate pila otica is present in palaeognathous birds, as well as in several only distantly related taxa of the Neognathae, such as the charadriiform Scolopaci, many gruiform birds (Rallidae [Fig. 2G], Aramidae, Psophiidae, Gruidae [Fig. 2H], but not Heliornithidae), Otididae (Fig. 2I), Cuculidae (Fig. 6E), some Musophagidae, Mesitornithidae, and several taxa of the Telluraves (Coli-

idae [Fig. 5H], Trogonidae [Fig. 7I], Upupidae [Fig. 5I], Bucerotidae, and the piciform Bucconidae, Ramphastidae, and Indicatoridae [Fig. 7J]). Amongst Charadriiformes, a trabeculate pila otica occurs in all studied taxa of the Scolopaci (Scolopacidae [Fig. 7F], Rostratulidae, Jacanidae [Fig. 6C], and Thinocoridae), but it is absent in the Charadrii and all Lari except the Turnicidae. MAYR & CLARKE (2003) also listed the presence of a trabeculate pila otica for the Opisthocomidae, Cariamidae, and Balaenicipitidae, but in these taxa the pila otica has an irregularly textured surface (Opisthocomidae, Cariamidae) or bears pneumatic foramina (Balaenicipitidae), with these conformations being of questionable homology to the trabeculate pila otica in other taxa.

Some Galliformes exhibit a previously unrecorded variation in the position of the cotyla quadratica otici, which, owing to a rostrally stretched pila otica, reaches farther rostrally than the processus supraceuticus in the Odontophoridae and Phasianidae (Fig. 8). In these latter two taxa, the cotyla quadratica otici is therefore situated outside the tympanic cavity, whereas it is in a more caudal position in the Numididae, Cracidae, and Megapodiidae, which is here considered to be the plesiomorphic condition for crown group Galliformes. In the Odontophoridae and Phasianidae, the pila otica furthermore bears a window-like opening (Fig. 8C).

To a large degree, the morphology of the otic region of birds is shaped by features related to the extensive pneumatization by the diverticula of the middle ear air sac, which results in a considerable variation in the configuration of bony struts, recesses, and pneumatic openings. It is beyond the scope of the present study to give an account of these pneumatic features, which requires an examination of soft tissue structures. Here it is only noted that the Steatornithidae constitute the only non-aquatic avian taxon, which lacks a foramen pneumaticum dorsale (even in diving birds, such as the Gaviidae and Spheniscidae, a small foramen pneumaticum dorsale is usually

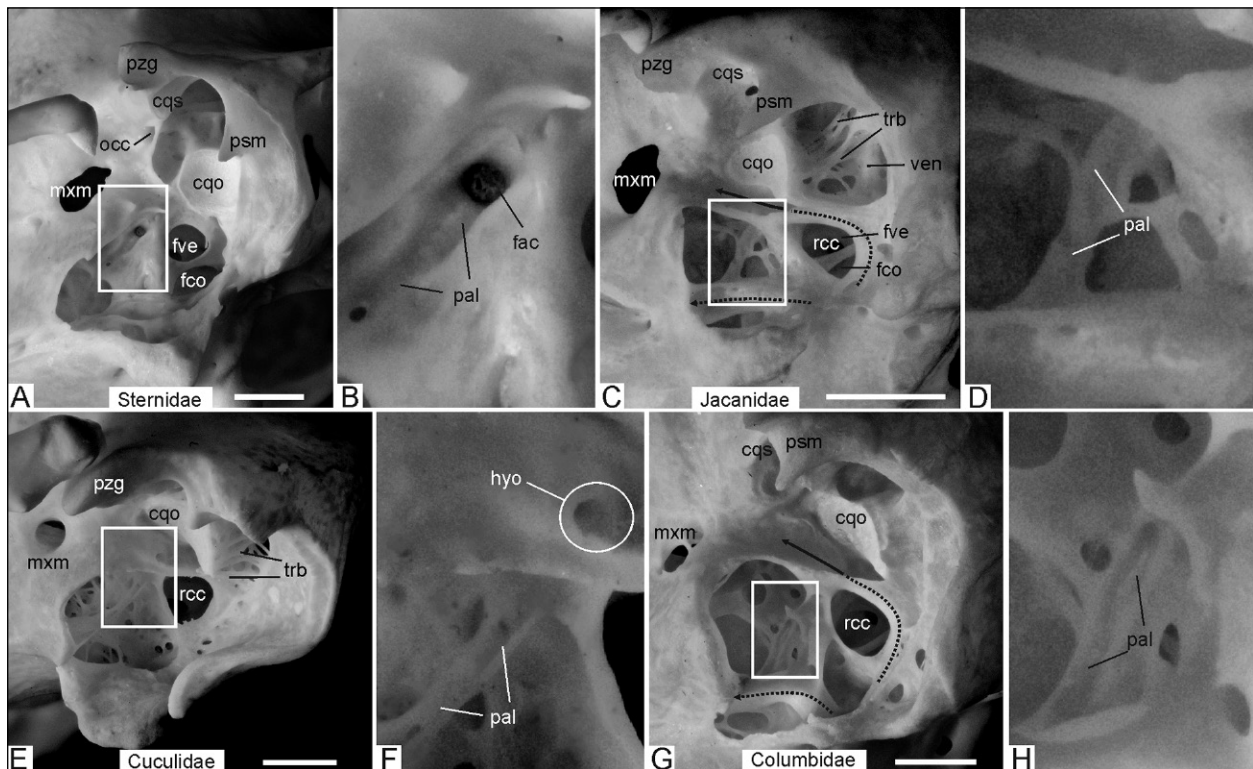


Fig. 6. Osseous structures associated with the palatine and hyomandibular nerves (left side, lateral view). A, B, *Thalasseus bengalensis* (Sternidae, SMF 13798). C, D, *Jacana jacana* (Jacanidae, SMF 13420). E, F, *Centropus senegalensis* (Cuculidae, SMF 12501). G, H, *Caloenas nicobarica* (Columbidae, SMF 17320). The black lines denote the presumed course of arteria carotis cerebialis and arteria ophthalmica externa (dashed lines indicate that the artery travels in the canalis caroticus cranialis or canalis ophthalmicus externus, respectively). The framed areas show the position of the details depicted in B, D, F, and H. Abbreviations: cqs, cotyla quadratica squamosi; fac, foramen for nervus facialis; fco, fenestra cochleae; fve, fenestra vestibuli; hyo, foramen for hyomandibular nerve; mxm, foramen n. maxillomandibularis; occ, opening for ramus occipitalis of arteria ophthalmica externa; pal, sulcus (B, F, H) or osseous tube (D) for palatine nerve; psm, processus suprameaticus; pzg, processus zygomaticus; rcc, recessus columellae; trb, trabeculate surface of pila otica; ven, ossified tube for occipital vein. Scale bars equal 2 mm.

present). The dorsal tympanic recess therefore does not seem to pneumatize the squamosum in these birds, and this unusual morphology may be related to the echolocation capabilities of oilbirds (SUTHERS & HECTOR, 1985).

Discussion

Even though the otic region of neognathous birds offers some anatomical variation of potential phylogenetic significance, presumably derived features evolved convergently in distantly related taxa. In galliform birds, a derived morphology of the pila otica (see above and Fig. 8), supports the results of molecular analyses, which recover a clade including the Odontophoridae and Phasianidae to the exclusion of the Numididae (KRIEKS *et al.*, 2007; WANG *et al.*, 2013). Otherwise, however, I could not identify immediate character evidence for a phylogenetic placement of higher-level clades, and presumably closely related taxa can show very different conformations of the otic region. Such is, for example, true for the Phaethontiformes and Eurypygiiformes (Eurypygidae and Rhynochetidae), which in current molecular analyses are recovered as sister taxa (e.g., JARVIS *et al.*, 2014;

PRUM *et al.*, 2015), but which distinctly differ in the morphology of the otic region. Whereas the otic region of the marine and highly aerial Phaethontidae resembles that of other birds with a similar ecology (e.g., Fregatidae, Diomedidae), the otic region of the Eurypygiiformes is more similar to that of gruiform birds.

With regard to non-pneumatic osteological structures, major differences in the otic region of birds occur in the degree of ossification of the bony tubes encasing blood vessels, the development of the recessus columellae, and the morphology of the pila otica. These structures serve different functions and their morphology is the result of multiple physiological constraints. A correlation with auditory capabilities is likely for the formation of a recessus columellae and the morphology of the foramen musculi columellae, but has also been assumed for features related to the vascular anatomy.

ELZANOWSKI (1995: 48) noted that a canalis ophthalmicus externus and a canalis caroticus cranialis are mainly absent in seabirds and proposed that “bony arterial tubes provide acoustic insulation of the middle ear”. He further hypothesized that because “sea birds are permanently exposed to high levels of background noise from wind and waves [...] reducing the endogenous noise, arterial or otherwise, may be of less importance” (ELZANOWSKI,

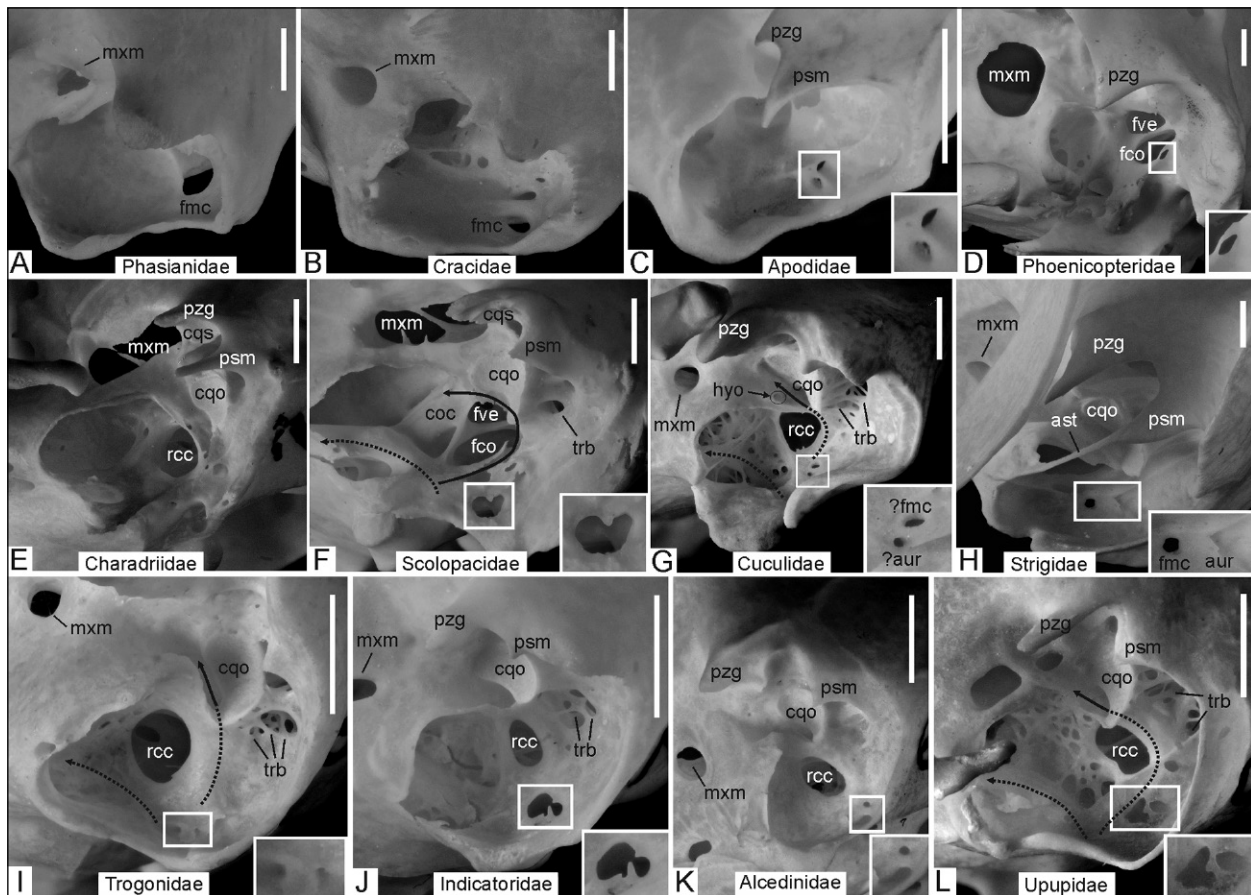


Fig. 7. The left otic region of neognathous taxa in laterodorsal (A–D, H) and lateral (E–G, I–L) view to show the different conformations of the foramen musculi columellae and the foramen for ramus auricularis of the hyomandibular nerve. A, *Syrnaticus soemmerringii* (Phasianidae, SMF 14637). B, *Ortalis canicollis* (Cracidae, SMF 14247). C, *Apus apus* (Apodidae, SMF 17575). D, *Phoenicopterus chilensis* (Phoenicopteridae, SMF 5803). E, *Vanellus vanellus* (Charadriidae, SMF 15994); this species lacks a foramen musculi columellae. F, *Nu-menius arquata* (Scolopacidae, SMF 13767). G, *Centropus senegalensis* (Cuculidae, SMF 12501). H, *Strix aluco* (Strigidae, SMF 14411). I, *Harpactes oreskios* (Trogonidae, SMF 12031). J, *Indicator indicator* (Indicatoridae, SMF 12968). K, *Alcedo atthis* (Alcedinidae, SMF 12822). L, *Upupa epops* (Upupidae, SMF 12580). The framed areas show the position of the enlarged details, which depict the foramen musculi columellae and/or the foramen for ramus auricularis of hyomandibular nerve (in most cases a clear distinction of these foramina is not possible in macerated skulls). The black lines denote the presumed course of arteria carotis cerebialis and arteria ophthalmica externa (dashed lines indicate that the artery travels in the canalis caroticus cranialis or canalis ophthalmicus externus, respectively). Abbreviations: ast, annulus tympanicus (bony bridge connecting processus suprameaticus with ala parasphenoidalis in strigiform birds; see STELLBOGEN, 1930); aur, foramen for ramus auricularis of hyomandibular nerve; coc, lateral surface of cochlea; cco, cotyla quadratica otici; cqs, cotyla quadratica squamosi; fco, fenestra cochleae; fmc, foramen musculi columellae; fve, fenestra vestibuli; hyo, foramen for hyomandibular nerve; mxm, foramen n. maxillomandibularis; psm, processus suprameaticus; pzo, processus zygomaticus; rcc, recessus columellae; trb, trabecles/recess on pila otica. The scale bars equal 2 mm.

1995: 48). ELZANOWSKI'S (1995) hypothesis is plausible, but does not explain the absence of an ossified canalis ophthalmicus externus in some non-aquatic taxa that do not live in environments with a high background noise, such as the Ciconiidae and Scopidae. Because the external ophthalmic vessels supply the rete ophthalmicum, a major heat exchange structure of the avian skull (MIDTGÅRD, 1984), their encasement in a bony canal may also have an insulating function and possibly reduces heat loss into the recessus pneumaticus dorsalis. In taxa where it is present, the canalis ophthalmicus extensorius furthermore contributes to the formation of a recessus columellae, so that a correlation with auditory acuity and vocal capabilities also needs to be considered.

Of Mesozoic birds outside the avian crown group, the otic region has only been described for the Cretaceous

hesperornithiforms *Enaliornis* and *Hesperornis* (WITMER, 1990; ELZANOWSKI, 1991; ELZANOWSKI & GALTON, 1991). Both taxa lack a canalis ophthalmicus externus and a canalis caroticus cranialis, and the otic region of *Enaliornis* resembles that of extant seabirds, especially the Phaethontidae, Fregatidae, and Diomedidae (ELZANOWSKI & GALTON, 1991). Based on comparisons with *Enaliornis* and *Hesperornis*, ELZANOWSKI (1995) considered the lack of ossified canals for the major vessels in the otic region to be plesiomorphic for Neornithes (crown group birds). However, a canalis caroticus cranialis is only absent in the Phaethontidae and in taxa of the Aequornithes, and because these birds are phylogenetically nested within Neognathae, the lack of a canalis caroticus cranialis is more likely to be derived for neognathous birds. Being present in the Galloanseres and many distantly related

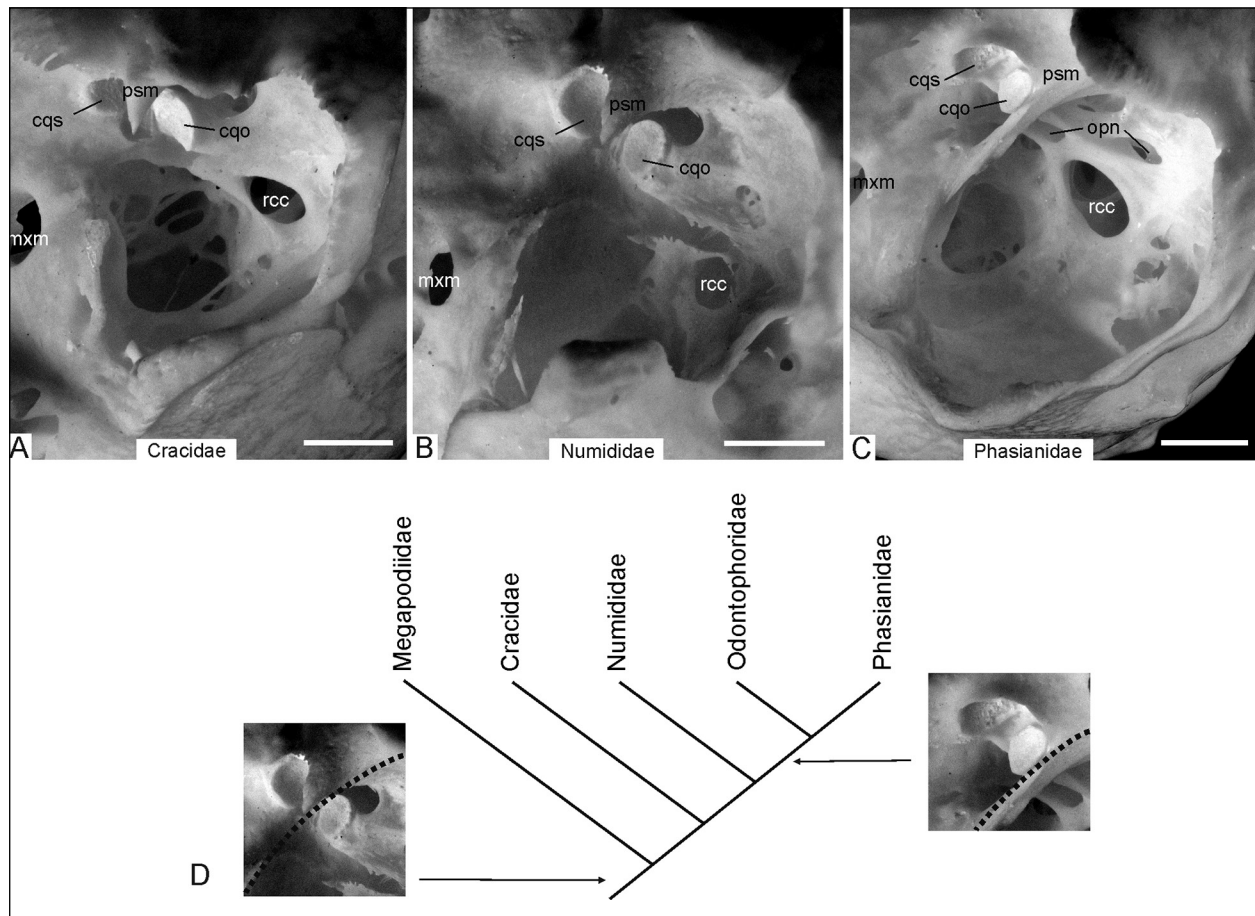


Fig. 8. The otic region of galliform birds (left side, lateral view) to show the different extent of the pila otica. A, *Ortalis canicollis* (Cracidae, SMF 14247). B, *Guttera edouardi* (Numididae, SMF 14283). C, *Syrnaticus soemmerringii* (Phasianidae, SMF 14637). D, phylogenetic interrelationships of crown group Galliformes, the left image (a detail from B) shows the plesiomorphic condition for crown group Galliformes, the right one (a detail from C) depicts the derived morphology found in the Odontophoridae and Phasianidae; the dashed lines indicate the rostral margin of the tympanic cavity. Abbreviations: cco, cotyla quadratica otici; cqs, cotyla quadratica squamosi; mxm, foramen n. maxillomandibularis; opn, window-like opening on pila otica; psm, processus suprameaticus; rcc, recessus columellae. Scale bars equal 2 mm.

neoavian taxa, such as the Opisthocomidae, Cuculidae, or Passeriformes, an ossified canalis ophthalmicus externus is probably likewise plesiomorphic for neognathous birds.

The size of the foramen nervi facialis reflects the diameter of the nervus facialis and, hence, the number of efferent and afferent fibers of this nerve. The foramen is particularly large in taxa of the Aequornithes, which may relate to the fact that these birds have well-developed jaw muscles and supraorbital glands that are innervated by nervus facialis. Why the palatine nerve is enclosed in a bony tube in some taxa defies an immediate explanation, but encasement of this fine nerve may provide some mechanical protection.

The functional significance of other features of the otic region likewise remains elusive. This is, for example, true for the presence of a large canaliculus cochleae, which is mainly found in aquatic or semi-aquatic birds (Anseriformes, Aequornithes, and Charadriiformes), but also occurs in a few non-aquatic taxa, such as the Cathartidae. A window-like canaliculus cochleae is present in many large-sized birds, but in the Procellariiformes and

Charadriiformes it also occurs in small species, so that its formation does not seem to be primarily related to the size of the bird.

A conspicuous feature of some taxa is a trabeculate surface of the pila otica, which sometimes forms a distinct recess (e.g., Gruidae [Fig. 2H]). This morphology appears to be correlated with the length of the pila otica and with the exception of the Phoenicopteridae, a trabeculate surface is mostly found in taxa, in which the pila otica forms a distinct peduncle (the presence of small foramina in the Phoenicopteridae may indicate a secondary shortening of the pila otica). A trabeculate pila otica was listed as an apomorphy of the Gruiformes by CRACRAFT (1988: 351) and the feature was also included in the character matrix of MAYR & CLARKE (2003). However, the wide distribution of this character diminishes its phylogenetic significance. Occurrence of a trabeculate pila otica in palaeognathous birds (Fig. 2A) may suggest that it is plesiomorphic for neornithine birds and was convergently lost in some neognathous clades. On the other hand, a trabeculate pila otica is absent in the Galloanseres and within Neoaves, its occurrence is mainly restricted to the

Gruiformes, the charadriiform Scolopaci and Turnicidae, the Columbaves sensu PRUM *et al.* (2015), and some taxa of the Strisores (Caprimulgidae) and Telluraves (Trogonidae, Coliidae, Upupiformes; Tab. 2). It is therefore equally possible that this feature evolved several times independently within Neornithes and is apomorphic for some neognathous clades. Even within Charadriiformes, which show some variation concerning the feature and whose phylogenetic interrelationships are well resolved (e.g., MAYR, 2011b), an unambiguous decision is not possible. With Scolopaci and Lari being sister groups and Turnicidae being the sister taxon of all other Lari, it is equally parsimonious to assume that a trabeculate pila otica is an apomorphy of the clade (Scolopaci + Lari), which was lost in all Lari other than the Turnicidae, or that it evolved convergently in the Scolopaci and Lari. The functional significance of this feature is unknown, but a relation to the middle ear air sac seems likely and a trabeculate pila otica may have a thermoregulatory function, facilitating heat exchange from the braincase.

Clearly, the structural variation found in the otic region of birds remains significantly underexplored, and various features of unclear identity or homology require further research. This is particularly true for the small nerve foramen in the fossa parabasis (Fig. 4C, F) and for the identity of the vessel caudal of the cotyla quadratica otici (Fig. 5I). A potential absence of the ramus occipitalis of arteria ophthalmica externa in some taxa also needs to be verified through anatomical dissections or soft tissue imaging. It is to be hoped that the present study will serve as a basis for future studies, which address these issues and provide further information on the distribution of some of the above-discussed features of the avian otic region. However, even the limited data presented here suggest that this part of the skull offers much variation in osteological structures that may improve our knowledge of avian physiology and phylogeny. Once a better understanding of the features of the otic region is reached, they have the potential to inform palaeornithologists on ecological attributes of fossil birds, thereby complementing data derived from endocranial (e.g., PROFFITT *et al.*, 2016) and inner ear morphology (e.g., WALSH *et al.*, 2009).

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