Journal of Paleontology, 86(1), 2012, p. 44–50
Copyright © 2012, The Paleontological Society
0022-3360/12/0086-0044$03.00

ENDOCRANIAL PETROSAL ANATOMY OF *BOTHRIOGENYS* (MAMMALIA, ARTIODACTYLA, ANTHRACOTHERIIDAE), AND PETROSAL VOLUME AND DENSITY COMPARISONS AMONG AQUATIC AND TERRESTRIAL ARTIODACTYLS AND OUTGROUPS

MAUREEN A. O'LEARY,[1] BIREN A. PATEL,[1] AND MARK N. COLEMAN[2]
[1]Department of Anatomical Sciences, HSC T-8 (040), Stony Brook University, Stony Brook, NY 11794-8081, USA,
<maureen.oleary@stonybrook.edu>; and [2]Department of Anatomy, Midwestern University, Glendale, AZ 85308, USA

ABSTRACT—We provide the first detailed endocranial description of the petrosal bone of the ear region of the anthracotheriid artiodactyl *Bothriogenys*, based on two new specimens from the early Oligocene of the Jebel Qatrani Formation, Fayum, Egypt. The new fossils have petrosals with a hyperinflated (pachyostotic) tegmen tympani (the roof over the middle ear), resembling the condition in certain cetancodontans such as hippopotamids and basal cetaceamorphans (fossil stem taxa to extant Cetacea).

The morphology of the petrosal, particularly its relative size and density, has been considered an important indicator of the ability of a marine mammal to localize sound transmitted in water, yet petrosal size (pachyostosis) and density (osteosclerosis) have not previously been quantified independent of each other. We examine the new fossils in the context of a preliminary CT-based study of petrosal density (extant taxa only) and petrosal volume (extant and extinct taxa) in a sample of artiodactyls and outgroups. In our extant comparative sample, the petrosals of cetaceans are both dense and voluminous as has been previously stated. We find, however, that the tegmen tympani is relatively voluminous (pachyostotic) without being particularly dense (osteosclerotic) in *Hippopotamus amphibius*, an extant taxon that has been documented to show some aquatic hearing behaviors, albeit less derived ones than those seen in cetaceans. A voluminous tegmen tympani, which is present in *Bothriogenys*, may have specific implications for behavior that are distinct from increases in petrosal density.

INTRODUCTION

EXTANT ODONTOCETES have been described as having both relatively dense (osteosclerotic) and relatively voluminous (pachyostotic) petrosal bones in the ear, particularly the tegmen tympani (the part of the petrosal that roofs the middle ear; Luo and Gingerich, 1999). Luo and Gingerich (1999, p. 85) stated that this combination of conditions "is almost certainly correlated with the origin of underwater hearing". Breaking down this hypothesis into component variables and quantifying those variables is important for examining any stepwise transformation, particularly one involving fossil taxa, to the derived level of underwater hearing seen in Cetacea. Specifically, separation of volume from density permits an examination of the following question: does any extant taxon that exhibits a form of derived aquatic hearing behavior lack either a voluminous or a dense petrosal?

Barklow (2004) recently reported that extant *Hippopotamus amphibius* exhibits derived underwater hearing capabilities. This observation is particularly intriguing because Hippopotamidae has been further corroborated to be the extant sister taxon to Cetacea in a recent large-scale total evidence analysis (Spaulding et al., 2009). Accordingly, quantified comparisons of petrosal volume and density among extant cetaceans, other artiodactyls, relevant fossil taxa and outgroups are highly relevant to understanding the transition to underwater hearing.

In this study, we have the opportunity to describe new data on the endocranial surface of the petrosal bone of the anthracotheriid artiodactyl *Bothriogenys* (Schmidt, 1913; Holroyd et al., 1996; Ducrocq, 1997). Anthracotheriidae is a heterogeneous, and probably paraphyletic (Fig. 1; Spaulding et al., 2009), group of artiodactyls that has been recovered from middle Eocene to late Miocene rocks of Asia, Africa, Europe and North America (Ducrocq, 1997; McKenna and Bell, 1997). The new fossils reported here come from the early Oligocene of the Jebel Qatrani Formation, Fayum, Egypt and reveal petrosals with a hyperinflated (pachyostotic) tegmen tympani. This morphology is strikingly similar to the condition in certain cetancodontans (Fig. 1), particularly hippopotamids and basal cetaceamorphans (O'Leary, 2010). A recent comprehensive combined-data phylogenetic analysis (Spaulding et al., 2009) found, however, that the hyperinflated tegmen tympani shared by *Bothriogenys* and cetancodontans is best explained as a homoplasy, having evolved at least twice in artiodactyls.

Using CT scans, we describe the ear region of two *Bothriogenys* specimens in the context of a preliminary comparative examination of volume and density of the petrosal in artiodactyls and outgroups. Quantifying whether different parts of a skull vary in material properties (including absolute mineral density of bone) has historically been difficult without destructive sampling (e.g., calculation of ash density). Radiographic techniques such as CT, however, can be applied to estimate relative (or apparent) density within and between individuals (Ciarelli et al., 1991; Snyder and Schneider, 1991; Patel and Carlson, 2007; Drum et al., 2009) without damaging original material. CT data allow 1) the assessment whether the petrosal is relatively dense compared to other parts of the skull, and 2) the construction of 3D digital models of the tegmen tympani for volume calculations and comparisons. Our sample permits preliminary comparisons of petrosal volume among different behavioral groups (e.g., marine vs. terrestrial) of artiodactyls and outgroups. We also present petrosal density comparisons limited to extant taxa only (fossil ears are excluded from density comparisons so as not to compare rock to bone).

Institutional abbreviations.—AMNH, American Museum of Natural History, Departments of Mammalogy (−M) and Vertebrate Paleontology (−VP); DPC, Duke Lemur Center Division of Fossil Primates; HGSP, Howard University-Geological Survey of Pakistan; SBU, Stony Brook University,

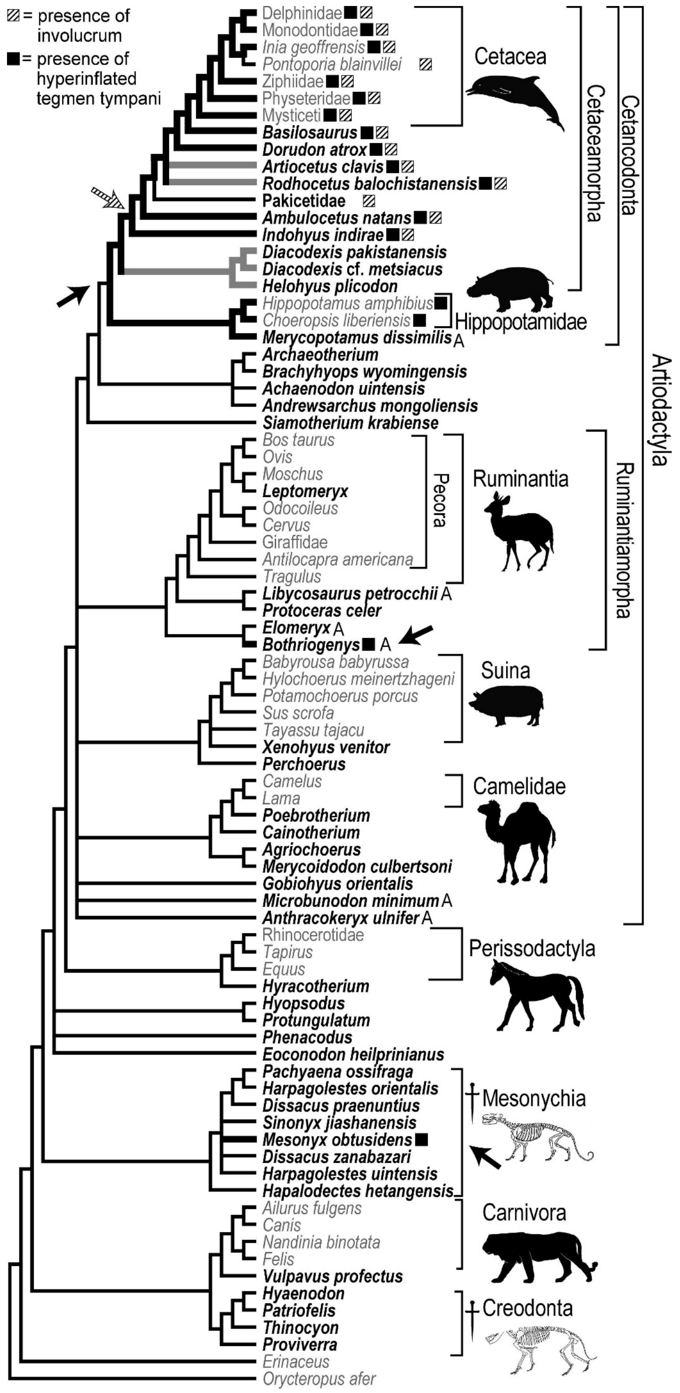

FIGURE *1*—Strict consensus of 20 trees from the phylogenetic analysis of Artiodactyla and outgroups based on phenotypic and molecular data (Spaulding et al., 2009); higher taxonomy also from that source. In all shortest trees, *Bothriogenys* is a member of Ruminantiamorpha. Optimization of the derived state, hyperinflated tegmen tympani, is overlain on tree. Black boxes indicate terminal taxa for which the hyperinflated tegmen tympani is preserved; presence of this character state is a synapomorphy of Cetancodonta (the state reverses in *Pontoporia*), and is inferred to have been present, by optimization (gray lines), for some fossil taxa for which the petrosal has yet to be described. The appearance of this condition in *Mesonyx* and *Bothriogenys* is independently derived. Striped boxes indicate the derived presence of an involucrum, a dense and voluminous scroll of bone on the medial aspect of the auditory bulla. This state appears in the common ancestor of *Indohyus* and Delphinidae (striped arrow); the character shows no homoplasy on this tree. Extinct taxa indicated in bold text. Paraphyletic Anthracotheriidae indicated by the letter "A". Both optimizations shown here on the consensus obtained in all shortest source trees. Detailed explanation of data, methods and taxonomy in Spaulding et al. (2009).

Department of Anatomical Sciences; TMM-M, Texas Memorial Museum, Mammalogy; UCM-VZ, University of California, Museum of Vertebrate Zoology; UM-GSP, University of Michigan-Geological Survey of Pakistan; UCLA, University of California, Los Angeles; UCR, University of California, Riverside; USNM, United States National Museum, Smithsonian Institution.

SYSTEMATIC PALEONTOLOGY

Repository.—Duke Lemur Center Division of Fossil Primates, Durham, North Carolina.

Order ARTIODACTYLA Owen, 1848
Family ANTHRACOTHERIIDAE Leidy, 1869
BOTHRIOGENYS cf. *GORRINGEI* Andrews and Beadnell, 1902
Figure 2

Material examined.—DPC 5248 (Fig. 2), posterior cranium with dorsally exposed left petrosal; DPC 20954 (Fig. 3) right ear region with petrosal, tympanic bulla and partial squamosal. Both specimens conditionally referred to *Bothriogenys gorringei* based on skull size and morphology (e.g., shape of bulla, cranial crests, position and shape of foramina; Schmidt, 1913). Species attribution is tentative because dentitions primarily determine taxonomy of this genus (Ducrocq, 1997; Holroyd et al., 2010), and both new specimens are edentulous.

Localities and stratigraphic context.—Locality 46 (Quarry M and the "AEC locality"), middle part of the Upper Sequence of the Jebel Qatrani Formation, Fayum, Egypt, dating to the later part of the Rupelian Stage of the early part of the Oligocene epoch (~30 mya; Bown and Kraus, 1988; Seiffert, 2006). Interpreted to be a fluvial paleoenvironment with abundant freshwater and mangrove swamps, possibly experiencing occasional marine incursions (Bown and Kraus, 1988). We note that *B. gorringei*, the species to which we tentatively attribute the new material particularly due to skull size, is more typical of Lower Sequence rocks of the Jebel Qatrani Formation (Holroyd et al., 2010; table 43.I). The full stratigraphic range of these species will be best understood when future revisions to Anthracotheriidae include expanded diagnoses with cranial characters.

Description.—DPC 5248 consists of a posterior cranium exposing the intracranial morphology. The specimen has the posterior part of both frontals, parts of both parietals and squamosals, the occipitals, both tympanic bullae, both petrosals (the right is damaged endocranialy) and the posterior parts of the basisphenoid and left alisphenoid. The individual was not fully mature at death as indicated by an unfused basioccipital-basisphenoid suture (Fig. 2.2), jagged sutures between the frontal and parietal, and an unfused suture at the parietal-squamosal contact. Description of cranial areas other than the petrosal, as well as other images of the skull, can be found on MorphoBank (Project 420).

In ventral view of the ear region, the bulla and petrosal do not contact the basioccipital or basisphenoid. The foramen ovale, which is contained entirely within the alisphenoid (Fig. 2.2), opens posteriorly into a piriform fenestra (partially obscured by the auditory bulla). The piriform fenestra, basicapsular fissure and small, open jugular notch are all continuous. The stylomastoid foramen is technically a notch, open medially such that it is continuous with the jugular notch. The tympanic bulla (Fig. 2.2) has a distinctive crest on its ventromedial side running anteromedially to posterolaterally, which comes to a single point anteriorly and a double point posteriorly. The bulla is otherwise spherical. The bulla lacks an involucrum, the dense and large medial wall seen in

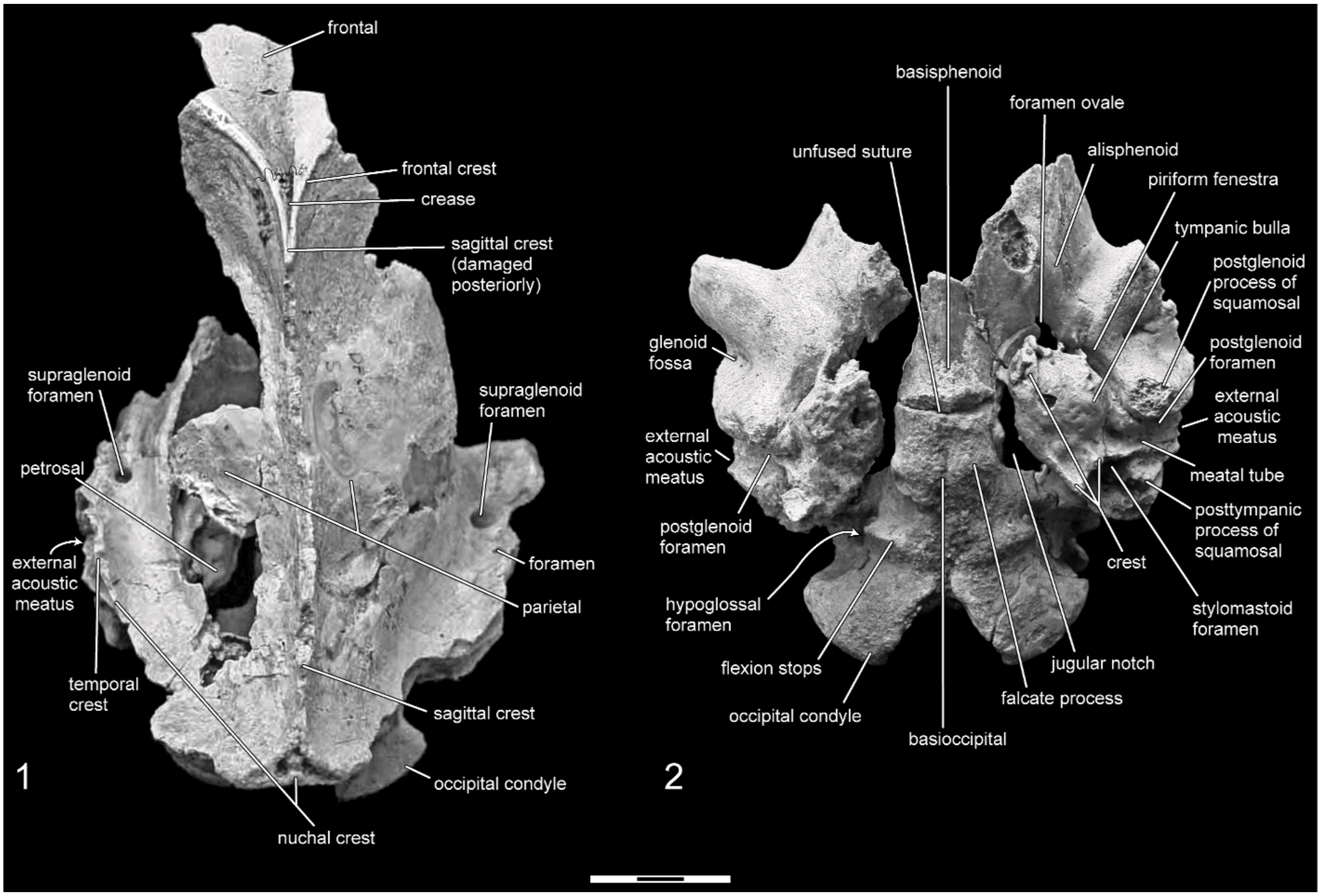

FIGURE 2—New fossil anthracotheriid skull (DPC 5248) in *1*, dorsal; and *2*, ventral views, referred to *Bothriogenys* cf. *gorringei* Andrews and Beadnell, 1902. The petrosal is visible through the dorsal aspect of the skull where the calvarium is broken. Other images of this skull are available on www.MorphoBank.org (Project 420).

cetaceans and *Indohyus* (Thewissen et al., 2007). The bony meatal tube is longer mediolaterally than the bulla is wide. In dorsal view (Fig. 2.1) the petrosal is visible due to damage to the posterior calvarium. The petrosal exhibits a hyperinflated tegmen tympani with a prefacial commissure fossa as discussed below for DPC 20954 (Fig. 3).

DPC 20954 provides endocranial views of the petrosal and the internal view of the tympanic bulla. Delicate trabeculae line the bulla internally (see also Fig. 4.2; also preserved in DPC 5248, left side), and may have entirely filled the bulla. The endocranial surface of the petrosal exhibits fully preserved foramina acusticum superius and inferius set within a deep-walled internal acoustic meatus. The prefacial commissure has a raised, knob-like shape. The hiatus Fallopii is a large hole positioned fully endocranially (also visible in DPC 5248). This specimen has a hyperinflated tegmen tympani such as has been described in detail for hippopotamids (O'Leary, 2010) and cetaceamorphans (Luo and Gingerich, 1999; O'Leary, 2010). The posterior aspect of the petrosal endocranially has a large prefacial commissure fossa (also a feature of hippopotamids and cetaceamorphans; O'Leary, 2010). Between the inflated tegmen tympani and the adjacent squamosal is a narrow space (containing some matrix).

Comparison of petrosals (gross anatomy).—O'Leary (2010) provided detailed descriptions of a comparative sample of artiodactyl petrosals. In Figure 4 we supplement this by comparing a few key features of the petrosal of *Bothriogenys* (not figured in O'Leary, 2010) in coronal cross section and in endocranial view. Particularly important is the relative size of the tegmen tympani in *Bothriogenys* compared to the rest of the petrosal. *Tayassu* has a moderately inflated tegmen tympani, a condition that is both plesiomorphic and widespread among terrestrial artiodactyls (O'Leary, 2010). By contrast, both hippopotamid species and *Bothriogenys* have a relatively voluminous tegmen tympani particularly similar to that of extinct cetaceamorphans (e.g., *Basilosaurus*) and even slightly larger than that of many extant cetaceans (e.g., *Tursiops*). Cetaceamorphans, hippopotamids and *Bothriogenys* also share a well-developed prefacial commissure fossa. *Elomeryx* (figured in O'Leary, 2010), a North American anthracotheriid does not, however, exhibit the same endocranial ear region similarities to Cetancodonta as are observed in *Bothriogenys*.

COMPARATIVE CT EXAMINATION OF EAR REGIONS

Materials.—Both *Bothriogenys* specimens were CT scanned along with a comparative sample of artiodactyls and marine and terrestrial extant and fossil outgroups (Table 1).

Methods.—Serial CT scans were collected of each skull (or isolated petrosal) in the coronal plane using either 1) a conventional medical CT scanner (GE Lightspeed CT scanner, 120 kV, 70 mA, 0.625 mm slice thickness) at SBU Medical Center yielding digital images saved as 16-bit DICOM files, or 2) a micro CT scanner at the University of Texas at Austin High Resolution X-ray CT Facility yielding digital images saved as 16-bit TIFF files. Both *Bothriogenys* specimens were subjected

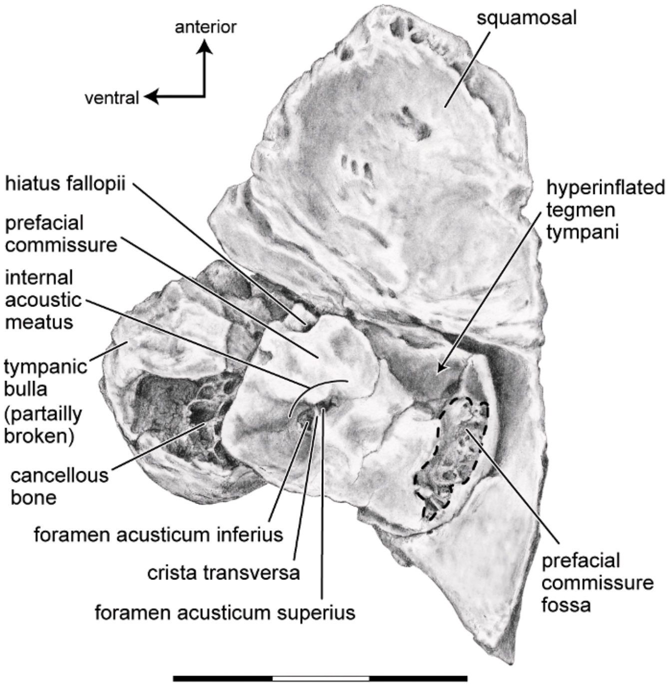

FIGURE *3*—Drawing of medial (endocranial) view of right ear region of *Bothriogenys* (DPC 20954). Tympanic bulla is partially broken exposing cancellous interior. The hyperinflated tegmen tympani has a damaged endocranial surface (encircled by dotted line). A slit-like space exists between the tegmen tympani and the adjacent squamosal (see also Fig. *4.2*). Note that *Bothriogenys* lacks an involucrum, a dense ridge found on the ventromedial surface of the tympanic bulla, known in many cetaceamorphans.

to micro-CT; scans for DPC 5248 had voxel dimensions of 74 × 74 × 82 µm, and those for DPC 20954 had voxel dimensions of 68 × 68 × 63 µm. Several micro-CT scans were also obtained directly from the Digimorph database.

We examined CT scans of a skull of one individual of 15 extant species in the coronal plane to evaluate relative *radiological* density of the petrosal. We imported each DICOM/TIFF stack of serial CT scans into ImageJ software and isolated homologous regions of the skull for density comparisons between species. We selected a single slice corresponding to the middle of the cochlea for density evaluation. Two regions of interest (ROI) were determined (Fig. 5.1): 1) pixels encompassing the entire petrosal, and 2) pixels encompassing the basioccipital. Following convention, we determined relative density of the petrosal by obtaining the brightest pixel value (Hounsfield Units) in the petrosal ROI and scaling that to the brightest pixel value in the basioccipital ROI. We considered brighter pixels (those with larger Hounsfield Unit values) in a CT image to be denser.

As a preliminary attempt to quantify tegmen tympani volume in aquatic and terrestrial artiodactyls and outgroups, we examined CT data collected from an isolated petrosal (either actual bone or a high resolution cast) of one individual from 14 species. Each DICOM stack described above was imported into Amira 5.2 software to generate 3D digital models of each specimen. We saved each digital model as a PLY file, then imported them into Geomagic Studio 8 software to measure volume. We measured two different volumes: 1) total volume of the reconstructed petrosal excluding the mastoid region (the latter may vary greatly in artiodactyls and is not the focus of our comparison), and 2) volume of the tegmen tympani portion alone. It is also

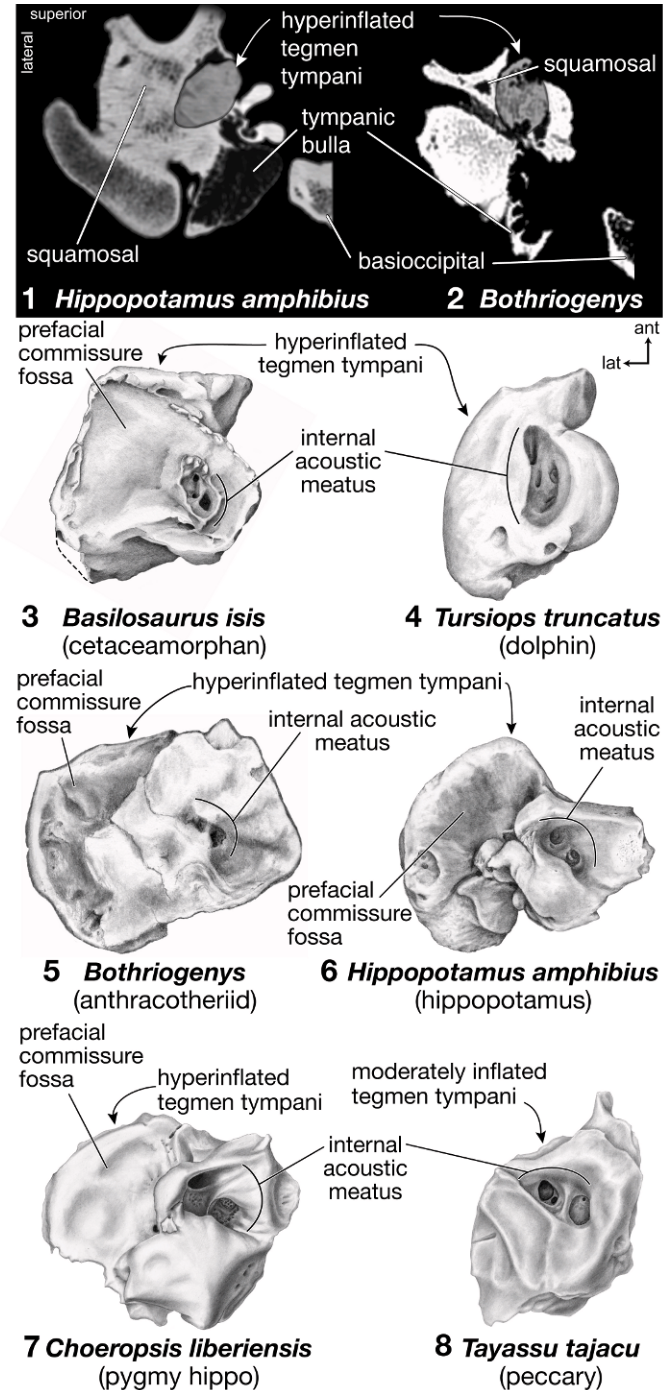

FIGURE *4*—Comparisons of the relative shape of the petrosal bone of the ear in terrestrial, aquatic and semiaquatic artiodactyls. *1*, *2*, CT scans of left ear region in coronal view: *1, Hippopotamus amphibius* (AMNH 53769); *2*, the anthracotheriid *Bothriogenys* cf. *gorringei* (DPC 5248), indicating similar hyperinflation of the tegmen tympani of the petrosal. Note the small separation between the inflated tegmen tympani of the petrosal and the squamosal bone lateral to it. The relatively thin bone of the ventral tympanic bulla (absence of an involucrum, see text) is also apparent; *3*–*8*, left petrosal bones (endocranial views) of artiodactyls; *3*–*7*, exhibit hyperinflation of the tegmen tympani: *3*,*4*, fossil and living cetaceamorphans; *5*, extinct anthraocotheriid; *6*, *7*, hippopotamids; *8*, *Tayassu* is fully terrestrial and lacks hyperinflation of the petrosal. Specimens are: *Basilosaurus isis* (UM-GSP 97507; mastoid region not shown); *Tursiops truncatus* (AMNH-M 184930); *Bothriogenys* cf. *gorringei* (DPC 20954); *Hippopotamus amphibius* (AMNH-M 24289); *Choeropsis liberiensis* (USNM 464982); *Tayassu tajacu* (USNM 52128). *3*–*8*, reprinted from O'Leary (2010). The prefacial commissure fossa is absent in the extant cetacean *Tursiops* and in the suid *Sus*.

TABLE *1*—CT data for comparative sample. Relative petrosal density is not reported for extinct taxa (n/a) because they are lithified making a comparison to bone unreliable. Volume of the tegmen tympani alone is standardized against volume of the petrosal, excluding the mastoid region, which can vary enormously in Artiodactyla. Further details can be found in the text.

Taxon	Specimen number	Item scanned (skull, isolated petrosal, or both)	CT type	Relative tegmen tympani volume	Volume category	Relative petrosal density
Basilosaurus isis	UM-GSP 97507	petrosal (cast)	medical CT	.81	5	n/a
Bothriogenys cf. *gorringei*	DPC 2054	skull	micro CT	**.47**	**3**	n/a
Bothriogenys cf. *gorringei*	DPC 5248	skull	micro CT	**.47**	**3**	n/a
Callorhinus ursinus	UCM-VZ 175109	skull	micro CT	n/a	n/a	1.13
Camelus dromedarius	SBU MAR 31	both	medical CT	.12	1	1.49
Canis lupus	TMM M-1701	both	micro CT	.18	1	1.26
Cephalophus callipygus	SBU MAR 9	skull	medical CT	n/a	n/a	1.48
Cervus elaphus	UC-MVZ 13434	petrosal	medical CT	.38	2	n/a
Choeropsis liberiensis	UCR 3116	petrosal	medical CT	.62	4	n/a
Choeropsis madagascariensis	SBU MAR 33	skull	medical CT	n/a	n/a	1.43
Delphinus delphis	SBU MCT 1	both	medical CT	.23	2	1.88
Dorudon atrox	UM 94812	petrosal (cast)	medical CT	.65	4	n/a
Enhydra lutra	UCLA SO 2951-98	skull	micro CT	n/a	n/a	1.10
Giraffa camelopardalis	UCM-VZ 55146	both	medical CT	.25	2	1.67
Hippopotamus amphibius	AMNH 53769 and 24289	both	medical CT	.62	4	1.24
Kogia breviceps	AMNH 36592	petrosal	medical CT	.35	2	n/a
Lama glama	TMM-M-2052	skull	micro CT	n/a	n/a	1.23
Macaca mulatta	SBU OMC 12	skull	medical CT	n/a	n/a	1.51
Merycoidodon sp.	AMNH-VP Lusk 0781572	petrosal	medical CT	.14	1	n/a
Mesonyx obtusidens	AMNH-VP 12643	petrosal	medical CT	.18	1	n/a
Odocoileus virginianus	SBU MAR 20	petrosal	medical CT	.21	2	n/a
Phoca vitulina	SBU MM 118	skull	medical CT	n/a	n/a	1.29
Sus scrofa	TMM-M-454	skull	micro CT	n/a	n/a	1.21
Ursus arctos	TMM-M-2749	skull	micro CT	n/a	n/a	1.87
Zalophus californicus	UCLA 252	skull	micro CT	n/a	n/a	1.15

important to note that our 3D models of petrosals were hollow volumes and do not take into account the morphology and volume of any sub-volumes (if they exist). Furthermore, because of absolute size differences in the analyzed specimens, as well as potential methodological errors from either making the 3D models (i.e., thresholding challenges) or isolating the tegmen tympani, we classified our percent volume measures into five volume categories (1: 0–20%; 2: 21–40%; 3: 41–60%; 4: 61–80%; 5: 81–100%) to present our comparative results. This is a relative comparison of the volume of the tegmen tympani alone.

Results.—All extant species examined have relatively dense petrosal bones compared to the basioccipital (relative density values>1.0; Fig. 5.1; Table 1). Relative density is, however, greatest in the odontocete, *Delphinus*, corroborating statements from Luo and Gingerich (1999) that odontocetes have relatively dense (osteosclerotic) petrosal bones compared to many terrestrial mammals. Hippopotamids, although semi-aquatic, have petrosals that are relatively less dense, with values comparable to those of terrestrial mammals. Similarly, aquatic carnivorans (e.g., *Enhydra*, *Zalophus*, *Callorhinus*) also do not exhibit particularly dense petrosal bones. Again we refrain from attributing comparative significance to ear region density in *Bothriogenys*, or other fossils, because comparing relative density in fossils, which are lithified, is unreliable.

Figure 5.2 shows the relative volume (pachyostosis) of the tegmen tympani as five categories (see also Table 1). The relatively largest volume of the tegmen tympani is seen in extinct cetaceamorphans (e.g., *Dorudon*, *Basilosaurus*) and extant hippopotamids. *Bothriogenys* has a tegmen tympani volume that technically ranks in category 3; however, due to breakage of the petrosal (Fig. 3), we consider the value for *Bothriogenys* to be an underestimate; its full volume was certainly larger and most likely in category 4. Inflation of the tegmen tympani in extant odontocetes (category 2; e.g., *Delphinus* and *Kogia*), which has not previously been quantified, is actually somewhat low by comparison with extinct cetaceamorphans. In category 2 are also three terrestrial ruminant artiodactyls. This suggests that when measuring volume in three dimensions (as opposed to gross inspection, e.g., Luo and Gingerich, 1999; Spaulding et al., 2009; and O'Leary, 2010), it becomes apparent that artiodactyls, such as *Cervus* and *Giraffa*, have a more voluminous tegmen tympani than was previously appreciated. Similarly, Luo and Gingerich (1999) emphasized that inflation of the tegmen tympani of the petrosal was shared by cetaceans and mesonychians based on visual inspection; however *Mesonyx*, differs greatly from cetaceamorphans in this variable when it is quantified. Comparing both graphs, it is apparent that relative tegmen tympani inflation (pachyostosis) can occur independent of increases in petrosal density (osteolsclerosis), such as in hippopotamids.

CT scanning also allowed us to make new observations on the relationship between the petrosal and squamosal bones of the skull. In both hippopotamids and *Bothriogenys*, a small but potentially functionally significant separation (Fig. 4.1, 4.2) exists between the petrosal and the squamosal. Luo and Gingerich (1999) emphasized the importance of spaces for isolating the ear bones from cranial vibrations. The CT scans also confirm that both hippopotamids and *Bothriogenys* lack an involucrum (Fig. 4.1, 4.2). The hippopotamid bulla is instead a fragile, almost transparent, shell of bone that is strikingly different from the thick-walled bullae of cetaceans, and even thinner than that of *Bothriogenys*.

IMPLICATIONS FOR RECONSTRUCTING HEARING BEHAVIOR

Among members of the clade Artiodactyla, particularly within Cetaceamorpha (Fig. 1), the ear region underwent major anatomical modifications, as certain species transitioned from

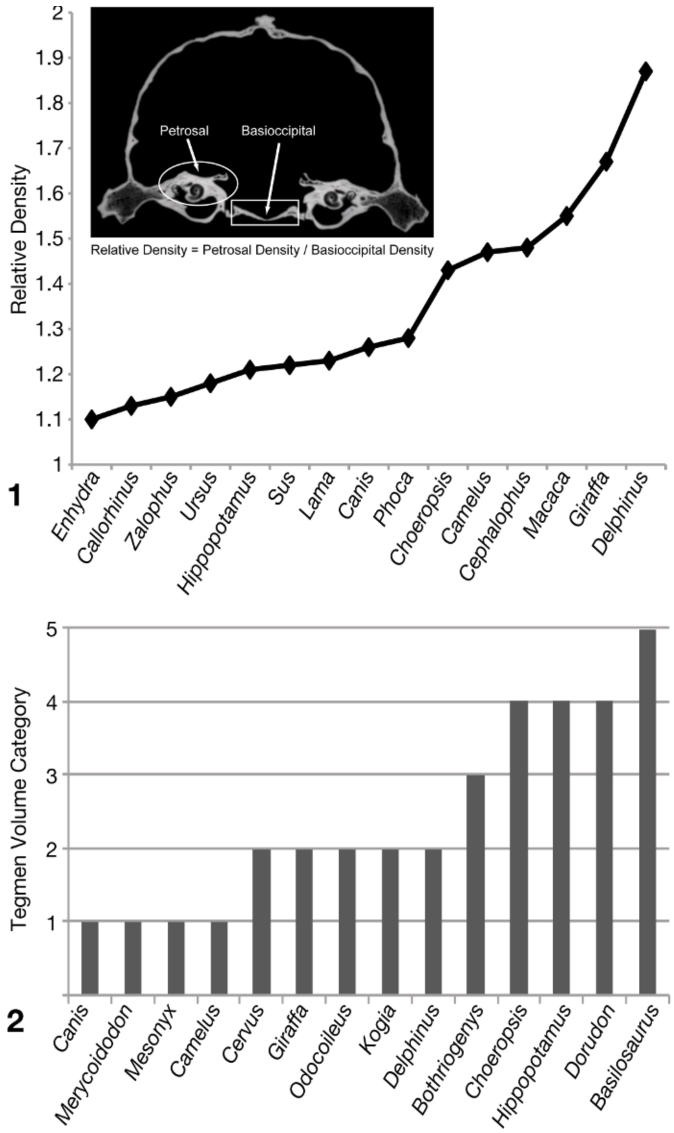

FIGURE *5*—CT-based comparisons of relative petrosal density and volume. *1*, bones under comparison; and *2*, relative density (i.e., radiological density) of the petrosal compared to a standard reference (basioccipital bone) in one individual each of 15 species: of aquatic taxa (*Delphinus delphis* [SBU MCT 1], *Phoca vitulina* [SBU MM118], *Callorhinus ursinus* [UCM-VZ 175109], *Enhydra lutra* [UCLA SO 2951-98], *Zalophus californicus* [UCLA 252]); semi-aquatic taxa (*Hippopotamus amphibius* [AMNH 53769]); and terrestrial taxa (*Lama glama* [TMM-M 2052], *Choeropsis madagascariensis* [SBU MAR 33], *Ursus arctos* [TMM-M-2749], *Sus scrofa* [TMM M-454], *Giraffa camelopardalis* [UCM-VZ 55146], *Cephalophus callipygus* [SBU MAR 9], *Camelus dromedarius* [SBU MAR 31], *Macaca mulatta* [SBU OMC 12], and *Canis lupus* [TMM M-1701]). All species have petrosals that are more dense than the adjacent basioccipital bone (values>1.0). Relative density is greatest in the odontocete, *Delphinus*. Semi-aquatic-terrestrial taxa have petrosals that are relatively less dense than those of *Delphinus* and more similar to densities found in terrestrial mammals. Comparative volume of the tegmen tympani of the petrosal standardized to total petrosal volume excluding the mastoid region for 14 species. Results are arranged into five categories of volume (see Table 1). Hippopotamids and extinct cetaceamorphans each have a particularly voluminous tegmen tympani. The volume estimate for *Bothriogenys* is an underestimate due to breakage of the fossil; this taxon likely had a volume comparable to that of hippopotamids. Specimens are: extinct cetaceamorphans (*Dorudon atrox* [UM 94812], *Basilosaurus isis* [UM-GSP 97507]); extinct artiodactyls (*Merycoidodon* sp. [AMNH-VP Lusk 0781572] and *Bothriogenys* cf. *gorringei* [DPC 5248]); and an extinct mesonychian (*Mesonyx obtusidens* [AMNH-VP 12643]); aquatic cetaceans (*Delphinus delphis* [SBU MCT 1] and *Kogia breviceps* [AMNH-M 36592]); a semi-aquatic artiodactyl, *Hippopotamus amphibius* (AMNH 24289); and several terrestrial taxa (*Choeropsis liberiensis* [UCR 3116], *Camelus dromedarius* [SBU MAR 31], *Odocoileus virginianus* [SBU MAR 20], *Giraffa camelopardalis* [UC-MVZ 55146], *Cervus elaphus* [UC-MVZ 134134].

terrestrial to aquatic life over 50 million years ago (Luo and Gingerich, 1999; O'Leary, 2010). Terrestrial mammals typically hear by processing sound transmitted through air to the eardrum, where mechanical transduction stimulates auditory neurons. Head and body tissues have greater density than air, thus these tissues largely deflect airborne sounds. The eardrum (tympanic membrane) of a typical terrestrial mammal vibrates independently of other cranial structures, and transmits these vibrations through the ossicular chain to the inner ear where they are translated (or transduced) into neurological impulses. A mammal determines the direction of a sound primarily by neurologically comparing differences in acoustic stimuli between the two independent ears (Reysenbach de Haan, 1960).

Terrestrial mammals, however, have great difficulty determining the direction of underwater sounds (Wainright, 1958; Reysenbach de Haan, 1960; Tonndorf, 1968) because the acoustic impedance of sound propagating through water is similar to that of tissues of the head (Smith, 1969; Ketten, 1997; Nummela, 1999; Nummela et al., 2004). When a terrestrial mammal receives a waterborne sound, its entire skull, not the tympanic membranes alone, vibrates in response to sound waves. Directional cues from underwater sounds are thus highly limited for most mammals adapted to life on land because both ears are stimulated at approximately the same time (Reysenbach de Haan, 1960).

Cetaceans have been recorded to comprehend underwater sound (e.g., Nachtigall et al., 2000). Luo and Gingerich (1999, p. vii) postulated that the presence of a "pachyostotic and osteosclerotic" petrosal conferred "substantial capacity for directional hearing in water". They argued that osteosclerosis increased the density contrast between bones of the ear and surrounding structures, thereby increasing the reflection of interfering sound waves that could potentially pass through adjacent tissues (Luo and Gingerich, 1999). By limiting the transmission of skull vibrations to the ear region, underwater-directional hearing is possible by confining the pathway of incoming sound waves to specialized, directionally specific channels (Ketten, 1994).

It was separately discovered, however, that a derived ability to hear underwater sound, albeit not necessarily to the degree observed in Cetacea, is also present in *Hippopotamus amphibius.* Barklow (2004) reported that *H. amphibius* responds readily to the directionality of underwater sound while retaining the ability to hear fully airborne sounds. We show here that *Hippopotamus* apparently exhibits this ability to hear underwater in the absence of osteosclerosis of the petrosal or bulla, and only in the presence of a relatively inflated (pachyostotic) tegmen tympani. This inflation is also present in the extinct anthracotheriid *Bothriogenys* and in extinct cetaceamorphans *Basilosaurus* and *Dorudon*. The functional role of inflation is not known but it may represent an intriguing transitional morphology also related to underwater hearing. Inflation of the tegmen tympani is apparently secondarily reduced in more derived cetaceans (e.g., *Delphinus* and *Kogia*).

CONCLUSIONS

The fossil anthracotheriid, *Bothriogenys,* has a hyperinflated tegmen tympani of the petrosal bone in the ear, most similar to the condition seen in extant hippopotamids and extinct cetaceamorphans (*Basilosaurus* and *Dorudon*). The most recent comprehensive cladistic analysis (Fig. 1; Spaulding et al., 2009) indicated that this hyperinflated condition developed convergently within Artiodactyla: in *Bothriogenys* and also at the base of Cetancodonta (the clade of hippopotamids + cetaceans). Extant cetancodontans, from hippopotamids (Barklow, 2004) to cetaceans (Ketten, 1994; Luo and Gingerich, 1999; Nachtigall et al., 2000), exhibit a range of abilities to process sound underwater. Only among more highly nested cetaceamorphans, those ranging from *Indohyus* to Delphinidae, does the ear region become osteosclerotic in both the petrosal and the bulla. This group of species also does not exhibit the greatest degree of inflation (pachyostosis). This morphology is instead found in hippopotamids and basal cetaceamorphans. Our preliminary CT-based observations suggest, therefore, that the shared ability for extant cetancodontans to interpret sound underwater (to differing degrees), such as seen in *Hippopotamus* (Barklow, 2004) and cetaceans (Luo and Gingerich, 1999), is a behavior that can appear in the absence of an osteosclerotic petrosal and bulla (involucrum), both of which hippopotamids lack.

A separate study on oxygen isotopes in *Bothriogenys* (Clementz et al., 2008) supports the hypothesis of an aquatic lifestyle for this taxon. A key new area of investigation should be the functional significance of the hyperinflation of the petrosal alone for aquatic hearing, and whether this morphology indicates a type of aquatic hearing specialization. Such a discovery would suggest that *Bothriogenys*, which, as noted above, is currently hypothesized to be phylogenetically outside of Cetaceamorpha (Spaulding et al., 2009), also exhibited some ability for underwater directional hearing. In the context of the current phylogenetic hypothesis, this would further suggest the presence of multiple, independent transitions to a semiaquatic/aquatic life within Artiodactyla. Critical to such an investigation would be a study of the pachyostosis seen in the ruminants sampled here.

The derived petrosal morphology found in *Bothriogenys*, is absent in a different anthracotheriid taxon, North American *Elomeryx* (O'Leary, 2010). This difference indicates that the African anthracotheriids studied so far share a larger number of gross morphological features of the ear region with cetancodontans than do North American anthracotheriid species. Petrosal data that will be essential for testing this hypothesis, have not yet been reported for the majority of named anthracotheriid genera (McKenna and Bell, 1997).

ACKNOWLEDGMENTS

We thank E. Simons, E. Seiffert, T. M. Bown, and P. Chatrath for access to the new fossils (DPC publication number 1196), the AMNH and USNM for access to important comparative material, J. Gatesy for reading an earlier version of this manuscript, and P. Holroyd for discussions on taxonomy. J. Groenke prepared the *Bothriogenys* specimens. We gratefully acknowledge J. Maisano and T. Rowe of Digimorph (and NSF grants IIS-9874781 and IIS-0208675) for providing microCT data, and NSF grant IOB 0517748 to B. Van Valkenburgh, which funded some of the scans used here. Medical CT scanning was facilitated by the staff in the Department of Radiology at Stony Brook University Medical Center. The paper was greatly improved by reviews from T. Deméré and one anonymous reviewer. Research was supported by NSF grants DEB-9903964, EAR 0116517, and DEB 0629836 to M. A. O'Leary, and recent paleontological fieldwork in the Fayum area was supported by NSF grants to E. Simons and E. Seiffert, and grants from The Leakey Foundation to E. Seiffert.

REFERENCES

ANDREWS, C. W. AND H. J. L. BEADNELL. 1902. A preliminary note on some new mammals from the upper Eocene of Egypt. Survey Department, Public Works Ministry, Cairo, p. 1–9.

BARKLOW, W. E. 2004. Amphibious communication with sound in hippos, *Hippopotamus amphibius*. Animal Behavior, 68:1125–1132.

BOWN, T. M. AND M. J. KRAUS. 1988. Geology and paleoenvironment of the Oligocene Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. U.S. Geological Survey Professional Papers, 1452:1–60.

CIARELLI, M. J., S. A. GOLDSTEIN, J. L. KUHN, D. D. CODY, AND M. B. BROWN. 1991. Evaluation of orthogonal mechanical properties and density of human trabecular bone from the major metaphyseal regions with materials testing and computed tomography. Journal of Orthopaedic Research, 9:674–682.

CLEMENTZ, M. T., P. A. HOLROYD, P. L. KOCH. 2008. Identifying aquatic habitats of herbivorous mammals through stable isotope analysis. Palaios, 23:574–585.

DRUM, M. G., C. M. LES, R. D. PARK, R. W. NORRDIN, C. W. MCILWRAITH, AND C. E. KAWCAK. 2009. Correlation of quantitative computed tomographic subchondral bone density and ash density in horses. Bone, 44:316–319.

DUCROCQ, S. 1997. The anthracotheriid genus *Bothriogenys* (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: Phylogenetical and paleobiographical relationship. Stuttgarter Beitrage zur Naturkunde. Series B, 250:1–44.

HOLROYD, P. A., E. L. SIMONS, T. M. BOWN, P. D. POLLY, AND M. J. KRAUS. 1996. New records of terrestrial mammals from the upper Eocene Qasr El Sagha Formation, Fayum Depression, Egypt. Palaeovertebrata, 25:175–192.

HOLROYD, P. A., F. LIHOREAU, G. F. GUNNELL, AND E. R. MILLER. 2010. Anthracotheriidae, p. 843–851. *In* L. Werdelin and W. J. Sanders (eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley.

KETTEN, D. R. 1994. Functional analysis of whale ears: Adaptations for underwater hearing. I.E.E.E. Proceedings in Underwater Acoustics, 1:264–270.

KETTEN, D. R. 1997. Structure and function in whale ears. Bioacoustics, 8:103–135.

LEIDY, J. 1869. Notice of some extinct vertebrates from Wyoming and North Dakota. Proceedings of the Academy of Natural Sciences of Philadelphia, 21:63–67.

LUO, Z. AND P. D. GINGERICH. 1999. Terrestrial Mesonychia to aquatic Cetacea: transformation of the basicranium and evolution of hearing in whales. University of Michigan Papers on Paleontology, 31:1–98.

MCKENNA, M. C. AND S. K. BELL. 1997. Classification of mammals above the species level Columbia University Press, New York.

NACHTIGALL, P. E., D. W. LEMONDS, AND H. L. ROITBLAT. 2000. Psychoacoustic studies of dolphin and whale hearing, p. 330–363. *In* W. W. L. Au, A. N. Popper, and R. R. Fay (eds.), Hearing in whales and dolphins. Springer-Verlag, New York.

NUMMELA, S. 1999. Scaling and modeling of the mammalian middle ear. Ph.D. dissertation, University of Helsinki, Finland.

NUMMELA, S., J. G. M. THEWISSEN, S. BAJPAI, S. T. HUSSAIN, AND K. KUMAR. 2004. Eocene evolution of whale hearing. Nature, 430: 776–778.

O'LEARY, M. A. 2010. Anatomical and phylogenetic study of the osteology of the petrosal of extant and extinct artiodactylans (Mammalia) and relatives. Bulletin of the American Museum of Natural History, 335:1–206.

OWEN, R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds discovered in the Eocene deposits on the N.W. coast of the Isle of Wight. Quarterly Journal of the Geological Society of London, 4:103–141.

PATEL, B. A. AND K. J. CARLSON. 2007. Bone density spatial patterns in the distal radius reflect habitual hand postures adopted by quadrupedal primates. Journal of Human Evolution, 52:130–141.

REYSENBACH DE HAAN, F. W. 1960. Some aspects of mammalian hearing under water. Proceedings of the Royal Society of London, B, 152B:54–62.

SCHMIDT, M. 1913. Uber Paarhufer der fluviomarinen Schichten des Fajum: Odontographisches und osteologisches Material. Geologische und Palaeontologische Abhandlungen, 11:153–264.

SEIFFERT, E. R. 2006. Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. Proceedings of the Academy of Natural Sciences, Philadelphia, 103:5000–5005.

SMITH, P. F. 1969. Underwater hearing in man: I. Sensitivity. Navy Submarine Medical Center Report, 659:1–23.

SNYDER, M. S. AND E. SCHNEIDER. 1991. Estimation of mechanical properties of cortical bone by computed tomography. Journal of Orthopaedic Research, 9:422–431.

SPAULDING, M., M. A. O'LEARY, AND J. GATESY. 2009. Relationships of Cetacea (Artiodactyla) among mammals: Increased taxon sampling alters interpretations of key fossils and character evolution. PloS One, 4:1–14.

THEWISSEN, J. G. M., L. N. COOPER, M. T. CLEMENTZ, S. BAJPAI, AND B. N. TIWARI. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature, 450:1190–1194.

TONNDORF, J. 1968. A new concept of bone conduction. Archives of Otolaryngology — Hand and Neck Surgery, 87:595–600.

WAINRIGHT, W. N. 1958. Comparison of hearing thresholds in air and water. Journal of the Acoustical Society of America, 30:1025–1029.

ACCEPTED 12 AUGUST 2011