



LIBRARY Micingan State University

This is to certify that the thesis entitled

COMPARATIVE MORPHOLOGY OF THE SKELETAL LABYRINTH IN MIOCENE-PLIOCENE FOSSIL AND RECENT SHARKS

presented by

Anna Lee Jerve

has been accepted towards fulfillment of the requirements for the

M.S. degree in <u>Geological Sciences</u> M.S. degree in <u>Geological Sciences</u> Major Professor's Signature 513107

Date

MSU is an affirmative-action, equal-opportunity employer

PLACE IN RETURN BOX to remove this checkout from your record. TO AVOID FINES return on or before date due. MAY BE RECALLED with earlier due date if requested.

DATE DUE	DATE DUE	DATE DUE
09 ¹ 1 1	D	
		2/05 c:/CIRC/DateDue.indd-p.15

COMPARATIVE MORPHOLOGY OF THE SKELETAL LABYRINTH IN MIOCENE-PLIOCENE FOSSIL AND RECENT SHARKS

By

Anna Lee Jerve

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTERS OF SCIENCE

Department of Geological Sciences

2007

ABSTRACT

COMPARATIVE MORPHOLOGY OF THE SKELETAL LABYRINTH IN MIOCENE-PLIOCENE SHARKS

By

Anna Lee Jerve

Cenozoic fossil sharks are primarily represented in the fossil record from isolated teeth, which are often difficult to use in systematic and functional studies due to problems of heterodonty and convergence. Shark prismatic cartilage has a low preservation potential in comparison to teeth, and is thus relatively rare in the fossil record. However, in some exceptional cases, delicate cartilaginous structures do preserve and can serve as a potentially rich source of data for systematic interpretations. This study reports on morphological features from five well-preserved shark otic capsules and preserved portions of the skeletal labyrinth that enclosed soft structures of the membranous labyrinth. High-resolution CT-scans of two of the specimens reveal exceptional images of the labyrinth and the relative positions of its morphological components. Resolved structures include the size and shape of the semi-circular canals and the positional relationships of the sacculus, utriculus and ampullae. Comparable CT-scan data from non-fossil lamiforms and carcharhinids reveal that the structures are homologous to the corresponding structures seen in the labyrinth of extant sharks. The morphology of all five fossil skeletal labyrinths most closely resembles that of the carcharhinid skeletal labyrinth and is distinctively different than ones from lamniforms. Thus, the morphology of the otic capsules is potentially useful for phylogenetic studies of this group, and may provide complementary data to often ambiguous tooth-based studies.

ACKNOWLEDGMENTS

First and foremost, I would like to thank my advisor, Dr. Michael D. Gottfried, and thesis committee members, Drs. Danita Brandt and Robert Anstey. A special thank you to Dr. Ralph Taggart, my honorary committee member. I would also like to thank Dr. Kevin Berger, Tracy Needham and Jeremy Williams at the MSU Radiology Clinic for volunteering their time to CT-scan the specimens used for this study.

This project would not have been possible without the contribution of specimens from Dr. John Maisey (AMNH), The National Museum of Natural History, The Calvert Marine Museum and the The Charleston Museum, Nancy Kohler (NOAA), Karen Tougas (NOAA), the Freeport Hudson Anglers, John Tyminski (Mote Marine Center for Shark Research), Ernest Scott (Dolphin Docks Deep Sea Fishing Port), Geremy Cliff (The Natal Sharks Board) and the University of Michigan Museum of Zoology.

Many thanks to those at MSU who provided support, including Dr. Sue Hill for donating a shark for exploratory dissection, Laura Abraczinskas and Dennis Lorenz for specimen preparation and cataloging, Juan Alvarez for poster formatting and Cathy Caswell for all things Fed Ex!

Special thanks to the MSU Department of Geological Sciences, The Graduate School, The International Center and the Council of Graduate Students for financial support.

Lastly, a mighty shout out to all other staff, professors, graduate students and undergraduates that have helped me along the way...you know who you are....

TABLE OF CONTENTS

LIST OF FIGURES	V
LIST OF TABLES	v i
INTRODUCTION	1
The cranium and skeletal labyrinth Anatomical abbreviations	3
MATERIALS	6
METHODS	9
DESCRIPTIONS	
Fossil Data	
PV 4173	12
PV 2698	17
PV 5849	
CMM-V-1728	22
USNM 47538	
Non-Fossil Data	
MSU 7099, 7100, 7103, 7104, 7089, 7101	
MSU 7105	
MSU 7107	
DISCUSSION	
Systematics	44
Size Estimation	
Functional Implications	53
DIRECTIONS FOR FUTURE RESEARCH	55
CONCLUSION	57
REFERENCES	58

.

LIST OF FIGURES

Number	Page
1. Shark cranial and skeletal labyrinth morphology	4
2. Photograph of specimen CMM-V-1728	7
3. Photograph of specimen USNM 47539.	8
4. Photographs of specimen PV 4173	13
5. Photographs of specimen PV 2698	18
6. Photographs of specimen PV 5849	
7. Three-dimensional surface rendered images of CMM-V-1728	23
8. Three-dimensional surface rendered images of USNM 47539	27
9. Three-dimensional surface rendered images of non-fossil carcharhinid data	33
10. Three-dimensional surface rendered images of specimen MSU 7105	37
11. Three-dimensional surface rendered images of specimen MSU 7107	41
12. Morphological comparison between carcharhinids and lamniforms	46

LIST OF TABLES

Number	Page
1. Non-fossil taxonomic information	10
2. Shared morphological characters from fossil and non-fossil specimens	49
3. Size measurements for the fossil and non-fossil specimens	52

INTRODUCTION

Much of our understanding of Cenozoic shark relationships is based on isolated teeth, primarily due to the rarity of cartilaginous skeletons in the fossil record. However, isolated teeth are often insufficient to clearly elucidate shark phylogeny (Gottfried and Fordyce, 2001) or to interpret aspects of shark paleobiology, and other morphological criteria, including jaw suspension and cranial anatomy, have in some cases proven more useful in documenting shark relationships (Maisey, 1980; 2001). These latter studies demonstrated that the braincase of sharks, specifically the skeletal labyrinth within the otic (ear) capsule (Figure 1), exhibits many informative morphological characters that can be useful for evaluating the interrelationships of sharks, as well as aspects of their sensory biology. The morphology of the labyrinth has also proven useful in delimiting ideas regarding elasmobranch mechanoreception (lateral-line system, phonoreception, feeding strategies) (Corwin, 1989; Maisey, 2001 a), which may be valuable for assessing how otic structures functioned in extinct species.

Evolutionary change in sharks is slow and results in subtle morphological changes within emerging species that are often difficult to detect, and this is compounded by evolutionary convergence, particularly when teeth are the only data set available for analysis (Hubbell, 1996). With that in mind, morphological data from the braincase and otic region of both modern and extinct sharks are valuable for future phylogenetic studies, but require novel means of data acquisition, due to the paucity of fossilized skeletal material. High-resolution CT-scanning provides a noninvasive means of studying these structures, which are not normally observed (particularly among fossils). CT-scans provide a detailed volumetric data set that can be manipulated to view threedimensional images from different angles (Lane et al., 2004).

Previous studies have applied CT-scan technology to fossil shark crania. Maisey (2004) used CT-scan images to describe the braincase of *Notorhynchus cepedianus*, a phylogenetically primitive extant neoselachian shark. Most recently, CT-scanning was applied to the braincase of *Cladodoides wildungensis*, an ancient (Devonian) basal shark (Maisey, 2001 b, 2005). In each study, the morphology was described in great detail using radiographic images obtained by CT-scanning. Maisey (2004) also identified several morphological characters that can be used for phylogenetic anaylses, as well as deciphering the function of specific structures, including the otic capsule. Both studies focused on more primitive and geologically older sharks, but were integral in establishing basic methodological protocols and affirming the utility of using CT-scanning to study fossil shark otic structures, and they laid a solid foundation for continued study using CT-scan methods.

Here, I extend previous applications of CT-scans of shark cranial anatomy to characterize the morphology of the skeletal labyrinth of the otic capsule from two wellpreserved fossil lamnid sharks from the Miocene Calvert Formation of Maryland, which were originally described and assigned to Family Lamnidae by Gottfried (1995) and then later investigated by Jerve (2006). The morphology of three well-preserved fossil shark otic capsules from the mid-Pliocene of South Carolina will also be studied. I will identify and describe otic features preserved in the fossil specimens and compare the fossil CT data with homologous data from living sharks to taxonomically assign the fossils. I will also interpret the preserved structures and compare between fossil and non-fossil material to investigate membranous labyrinth morphology. This research will provide CT-scan data for shark taxa that have not yet been studied using this technology and should spur future studies of shark otic function and evolution, as well as contribute to new hypotheses concerning shark phylogeny.

The cranium and skeletal labyrinth

Both the cranium and the skeletal labyrinth of chondrichthyans are composed of prismatic cartilage, which is a form of cartilage unique to sharks. The skeletal labyrinth houses the soft tissues of the membranous labyrinth and both are encased within the otic capsule of the cranium posterior to the orbits, with each otic capsule symmetrically arrayed on either side of the midline. See Figure 1 for an overview of shark cranial and skeletal labyrinth morphology.

Older morphological descriptions of the shark otic region often lack detailed accounts of the skeletal labyrinth. More focus has been placed on its position relative to other cartilaginous structures of the cranium and often it is only the soft tissues of the membranous labyrinth that are described (Vilstrüp 1950, 1951). Denison (1937) used transverse sections taken in one-centimeter increments to describe the cranial morphology of a whale shark (*Rhincodon*), and provided a short description of some otic structures, but he did not elaborate on the morphology of the calcified structures surrounding the semicircular canals. There have been several descriptions of membranous labyrinths from elasmobranchs to add to our knowledge of the structure and



FIGURE 1. Shark cranial and skeletal labyrinth morphology. The cranium from *Isurus oxythyrchus* (MSU 7105) to illustrate the basic morphology of the neurocranium in (a) lateral and (b) dorad views. The otic region is designated by the dotted black line. (c) illustrates the soft anatomy of the most posterior region of the brain, otic capsules and relative positions of the cranial nerves VIII. X and X. Also shown is the position of the membranous labyrinth inside the otic capsule, which is illustrated as a dark structure (membranous labyrinth) surrounded by light grey (the skeletal labyrinth). (d) Shows the external morphology of the membranous labyrinth, indiving the (a)a laneiror ampulla. (sc) anterior semicircular canal). (a) lateral ampulla, (lsc) lateral semicircular canal). (pa) posterior ampulla. (gsc) posterior semicircular canal, cac's asccutus. (ur) utriculus and (end d) endolymphatic ducd. Structures not included are the preampullary canal (pac) and perlymphatic fenestra (p fen). (e-d) modified from Gilbert, 1973.

function of different morphologies within the group (see Maisey, 2001 [Squalus and Notorhynchus] and Schaeffer, 1981 [Xenacanthus]).

More recently, it was recognized that the morphology of the shark skeletal labyrinth is an informative tool for systematic purposes (Maisey, 2004). The skeletal labyrinth has been studied via the use of CT-scanning to investigate the gross morphology in fossil and Recent chondrichthyans and it has been noted that endocranial and labyrinth morphology are useful for providing morphological characters for systematic purposes, regardless of how closely they correspond to the morphology of their soft tissues. Thus, employing CTscanning to acquire morphological data has provided some of the more detailed accounts of the skeletal labyrinth (Maisey, 2005).

Anatomical Abbreviations

The Membranous and Skeletal Labyrinth

aa	anterior ampulla
asc	anterior semicircular canal
la	lateral ampulla
end d	endolymphatic duct
lsc	lateral semicircular canal
Inc	lateral wall of the neurocranium
pa	posterior ampulla
pac	preampullary canal
p fen	perilymphatic fenestrae
psc	posterior semicircular canal
sac	sacculus
ur	utriculus

Cranial Nerves (CN)

VIII	auditory nerve foramen, auditory nerve canal
IX	glossopharyngeal nerve foramen, glossopharyngeal nerve canal
Х	vagus nerve foramen, vagus nerve canal

MATERIALS

Fossil shark otic capsule specimens obtained from the National Museum of Natural History (USNM), Calvert Marine Museum (CMM-V) and the The Charleston Museum (PV) form the basis of the fossil portion of this study. USNM 47538 was collected from the Miocene Calvert Formation in Calvert County, Maryland, and includes a partial fossilized left otic capsule that is preserved three-dimensionally in siltstone to very fine-grained sandstone matrix that contains bivalve and gastropod hash. The specimen is encased in sediment and too fragile to separate from the matrix. CMM-V-1728 (Figure 2) was collected from the Miocene Choptank Formation, Calvert County, Maryland, and includes a partial fossilized left otic capsule in-filled with a medium-grained clastic matrix similar to that in USNM 47538 (Figure 3).

The three isolated fossil otic capsules from the Charleston Museum (PV 4173, PV 2698 and PV 5849; Figures 4, 5, 6), are mid-Pliocene in age and were each collected from the Goose Creek Limestone from or near the Magnolia Phosphate Mine in Charleston County, South Carolina. PV 4173, a right otic capsule, is the most complete, and PV 2698 and PV 5849 are both partial left otic capsules in-filled with fine-grained sandstone.



FIGURE. 2. Photographs of fossilized left otic capsule CMM-V-1728 in (a) Lateral and (b) dorsal views. Arrows indicate the anterior (A) and ventral (V) directions. Scale bar equals 1 cm.



FIGURE 3. Photograph of the ventral view of fossilized right otic capsule USNM 47528 in matrix. Arrows indicate the anterior (A) and lateral (L) directions. Scale bar equals 1 cm.

Non-fossil crania used for comparative purposes were acquired through donations from several organizations, including the Center for Shark Research at Mote Marine Laboratory (FL), the Freeport Hudson Anglers Deep Sea Fishing Club (NY), the National Marine Fisheries Service (RI) and Dolphin Docks Deep Sea Marine Fishing Port (TX). All crania were prepared and catalogued in to the collections of the the Michigan State University Museum (MSU). Specimens represent the orders Carcharhiniformes and Lamniformes (Table 1) and include crania from juvenile specimens of *Carcharhinus limbatus* (MSU 7099) and *Carcharhinus leucas* (MSU 7100), and three prenatal *Carcharhinus falciformis* (MSU 7103, 7104, 7089), *Carcharhinus acronotus* (MSU 7101), *Isurus oxyrhyncus* (MSU 7105) and *Alopias vulpinus* (MSU 7107).

METHODS

The non-fossil neurocrania were prepared by hand using warm water maceration and dissection, and are stored in 70% ethanol. Specimens that did not produce clear initial images of the skeletal labyrinth were CT-scanned after the skeletal labyrinth was filled with Gastrografin, a radio-opaque liquid that is used to create high contrast images of the gastrointestinal tract when x-rayed, to yield comparable fossil and non-fossil images. The Gastrografin was introduced into the otic capsule by injection through the endolymphatic foramen, and/or though a hole pierced just laterally to the foramen using18 gauge hypodermic needles. The injected fluid was held within the cranium by closing all of the open foramina in the skull with wax and super-glue.

MSU Cat #	Order	Family	Species	Age
7100	Carcharhiniformes	Carcharhinidae	Carcharhinus leucas	juvenile
7099	Carcharhiniformes	Carcharhinidae	Carcharhinus limbatus	juvenile
7101	Carcharhiniformes	Carcharhinidae	Carcharhinus acronotus	adult
7103	Carcharhiniformes	Carcharhinidae	Carcharhinus falciformis	neonat
7104	Carcharhiniformes	Carcharhinidae	Carcharhinus falciformis	neonat
7089	Carcharhiniformes	Carcharhinidae	Carcharhinus falciformis	neonat
7105	Lamniformes	Lamnidae	Isurus oxyrhynchus	adult
7107	Lamniformes	Alopiidae	Alopias vulpinus	adult

TABLE 1. Catalogue numbers and other taxanomic information for all non-fossil specimens.

All specimens were CT-scanned at the Michigan State University Radiology Clinic on a GE Discovery ST medical scanner with a 16-slice capability. Scan data were taken using a helical rotational speed of 0.8 mm per second with slices taken every 0.625 mm and interleaf slices recorded in 0.562 mm intervals. Non-fossil specimens were oriented on the scanning bed in dorsal-ventral "resting" position with the rostrum facing anteriorly and slices were taken on the frontal and coronal planes. Fossil specimens were similarly positioned and with respect to the relative orientation of the otic capsule inside the cranium (right or left). Surface-rendered images were processed using an AW work station and viewed using a GE Centricity DICOM viewer software. The data were also processed and manipulated using OsiriX Medical Imaging software, version 2.7. All measurements were done via caliper (PV fossils) or by the measurement tool on the OsiriX imaging software. On the cranium, length was measured from the tip of the rostrum to the back of the cranium, near the foramen magnum. The skeletal labyrinth was oriented in life position and measured in a similar way.

DESCRIPTIONS

Fossil Specimens

PV 4173 (Figure 4) preserves the cartilaginous portions of the right side of the skeletal labyrinth that, in life, would have contained soft tissue structures of the membranous labyrinth. The specimen as preserved (Figure 4) measures 6.79 cm in total length, 5.38

cm wide and 4.89 cm in height. The prismatic nature of the cartilage is clearly evident, with a distinct stippled appearance on the external surfaces where the ends of the prisms are exposed. The fossil and its sedimentary in-fill are black in color, which possibly reflects post-burial phosphatization.

The sacculus of PV 4173 is ovoid, with a flattened ventral surface, and the entire structure tapers posteriorly to a somewhat rounded point (Figure 4 c). There is a crack (an artifact of preservation) running across the surface of the prismatic cartilage. The cartilage is pinched in at the point where the semicircular canals and ampullae become confluent with each other and the sacculus. The dorsal surface of the sacculus exhibits a smooth, kidney-shaped indentation that is approximately 2.09 cm in length (Figure 4 a, c). The posterior half of this feature is longer than the anterior half, measuring 1.06 mm in the posterior half and 0.87 cm in the anterior half. The anterodorsal extremity of the sacculus, which is located immediately posterior to the anterior semicircular canal, comes to a rounded point that rises slightly higher than where the two structures conjoin. The mediodorsal portion of the sacculus is irregular where the posterior semicircular canal,



FIGURE 4. Photograph of the right otic capsule PV 4173 in a (a) dorsal, (b) ventral, (c) lateral, (d) medial, (e) anterior and (f) posterior views with major stuctures labeled in each orientation. Scale bar equals 1 cm.

posterior ampulla and preampullary canal rest on the sacculus, and in addition the sacculus bulges slightly where it connects with the lateral semicircular canal. The cartilage where the posterior semicircular and preampullary canals meet is missing, which reveals the location of the endolymphatic duct and perilymphatic foramen (Figure 4 a). Two distinct canals that connect the anterior ampulla and the utriculus to the sacculus are also evident, and the cartilage just posterior to those canals is smooth and flat, indicating where the skeletal labyrinth may have come in contact with the neurocranium.

Immediately ventral to the the smooth cartilage and preampullary canal, the sacculus is incomplete and reveals three foramina. The most anterior foramen indicates the path of the utricular canal and is less than 1 mm in diameter. The second foramen is located dorsoposteriorly relative to the first. The path of this foramen is more difficult to resolve, but it appears to enter the sacculus in a diagonal ventral-dorsal direction. The third foramen is located dorsoposteriorly relative to the second foramen and appears to be apart of a larger canal that is directed laterally into the sacculus, and to another canal located adjacent to the first that runs posteriorly along the length of the preampullary canal. The portion of cartilage between the incomplete part of the sacculus and the bend in the preampullary canal creates an irregularly-shaped, deep sulcus that houses two more foramina, both directed laterally and with one located more dorsal to the other. There is a small shelf of cartilage located immediately anterior to the dorsal foramen, which appears to be the incomplete outer wall of a canal. The irregularity in the overall shape of the sulcus is created partly by the aforementioned cartilaginous shelf and canal running

ventral to the preampullary canal. Immediately dorsal to this pair of foramina there is a larger foramen that is only made evident by a 4.5 mm remnant piece of cartilage that connects the preampullary canal and sacculus.

The three semicircular canals are incomplete, with sediment in-fill preserving the general shape of the canals where cartilage is missing. The anterior semicircular canal is the shortest of the three canals (Figure 4 e). The canal itself has a diameter of 1.10 cm where the canal connects with the sacculus and 1.25 cm where the canal and anterior ampulla become confluent. The anterior semicircular canal does not contact the cartilage of the sacculus. The cartilage of the dorsoventral part of this canal is incomplete. The lateral semicircular canal is the longest of the three canals and is appressed to the lateral mid-section of the sacculus and the diameter decreases posteriorly to the point where the structure enters the sacculus (Figure 4 c). The posterior end of the lateral semicircular canal is rounded with a maximum diameter of 1.37 cm. It smoothly wraps around the sacculus for 2.17 cm, the diameter then rapidly decreases to 1.24 cm, which creates a rounded point when the specimen is viewed dorsally. Another, more pronounced, rounded point is created roughly 2.06 cm anterior to the first when the diameter decreases to 1.14 cm. The diameter then increases slightly as the canal enters the lateral ampulla.

The posterior semicircular canal is approximately 4.5 cm in length with 1.54 cm of the anterior part of the canal missing and represented by a thin, 0.26 cm wide ridge of cartilage that leads to the opening of the endolymphatic duct (Figure 4 a, d, f). The posterior end of this canal is incomplete with in-fill representing the dorsal surface, and what cartilage still exists is smooth in appearance which suggests that it had some contact

with cartilage of the neurocranium. The posterior canal wraps around the dorsal part of the sacculus and the cartilage comes in contact with the cartilaginous surface of the sacculus along its entire length excluding a 0.94 cm long area just anterior to the point where the canal overlaps the site at which the position of where the lateral semicircular canal enters the sacculus. The preampullary canal begins at the perilymphatic foramen and ends at the posterior ampulla. It is generally v-shaped and is approximately 3.6 cm in total length. It faces medially and becomes wider posteriorly until it merges with the posterior ampulla creating two arms: one flat, thin arm, 0.48 cm in diameter, that has the same smooth texture as other areas that may have come in contact with the neurocranium and a thicker arm, 0.88 cm in diameter. The ventral surface of the point at which the two arms meet is incomplete with in-fill representing the general shape of the canal.

The ampullae are incomplete but sufficiently well-preserved to interpret some aspects of their morphology. The anterior ampullae measures 1.19 cm in height and 1.84 cm wide and is an enlargement at the point where the anterior semicircular canal enters the utriculus (Figure 4 e). It is dorsal to the utriculus, anterior to the sacculus and medial to the lateral ampulla. In medial view, the anterior ampulla extends posteriorly, following the length of the utriculus. The lateral ampulla measures 1.61 cm in height and approximately 0.89 cm in length. In external view, it is the ventral half of the anterior end of the lateral semi-circular canal that appears to enter the utriculus, while the anterior semi-circular canal meets the utriculus along the full extent of the anterior end. The posterior ampulla is connected ventrally to the posterior semicircular canal and posteriorly to the preampullary canal, and is marked by an increase in the diameter, which measures 1.51 cm in length and 1.38 cm in height. Scan data do not resolve internal details of this portion of the labyrinth.

Specimen PV 2698 (Figure 5) preserves incomplete cartilaginous portions of the left side of the skeletal labyrinth. The sacculus is similar in shaped to that of PV 4173, but its overall size is smaller measuring 6.23 cm in total length, 4.22 cm wide and 4.75 cm in height. The majority of the cartilage of the dorsolateral part of the sacculus is missing, which exposes clastic sediment in-fill. The dorsal half of the sacculus is less complete that the ventral half, but it preserves cartilaginous structures not preserved in PV 4173, including the cartilage surrounding the endolymphatic duct, which is located immediately dorsal to the dorsolateral part of the sacculus (Figure 5 c). The medial side of the sacculus is almost completely covered by smooth cartilage that rested on the neurocranium. Only a portion of cartilage that is medial to the posterior semicircular canal is observable and no distinct morphological features are preserved similarly to the posteriorly positioned rounded point in PV 4173. The ventral half of the sacculus is rounded anteriorly and comes to a point posteriorly. The sacculus is missing an ovalshaped piece of cartilage immediately below the utriculus and utricular canal (Figure 5 e). A deep indentation is located directly dorsal to the missing cartilage and appears to reveal the position of two foramina, one traveling out laterally and the other running posteriorly. There is a bulge in the sacculus posterior to the missing cartilage, which is interpretable due to the sediment in-fill.

Cartilage is missing from external surfaces of the anterior and lateral semicircular canals, but the general morphology is still intact due to remnant cartilage and sediment





in-fill. The anterior semicircular canal is the shortest, becoming wider near where it becomes confluent with the anterior ampulla. The anterior canal and the external surface of the sacculus are not appressed and create a small gap (Figure 5 d). The lateral semicircular canal is the longest measuring 5.05 cm in length and approximately 1.00 cm in diameter. The overall shape of the lateral canal resembles that of PV 4173; it travels slightly dorsolaterally outward from where the anterior and lateral ampullae join with the utriculus, at which point the canal becomes directed more posteriorly until it slightly curves around the posterior end of the sacculus and ends adjacent to the position of the posterior ampulla (Figure 5 c). The nature of the lateral semicircular canal is somewhat angular and anteriorly tapered when viewed from a dorsal perspective. The posterior semicircular canal is incomplete and what structures do exist are partially covered by the cartilage housing the endolymphatic duct. The ventral cartilage surrounding part of the posterior semicircular canal and the preampullary canal remains intact, but does not reveal details of the internal morphology of the structure.

The lateral and anterior ampullae of specimen PV 2698 are well-preserved, but the posterior ampulla is missing and is represented by indentations in the cartilage where the structure was located. The anterior ampulla is wider than it is tall and the cartilage where the lateral part of the anterior ampulla meets the utriculus is pinched. The medial part of the anterior ampulla is elongated and extends posteriorly along the length of the utriculus for 1.00 cm until it enters the sacculus. The lateral ampulla is marginally wider than the diameter of the lateral canal, which is 1.25 cm in width and 0.77 cm in height. As in PV 4173, the ventral half of the anterior end of the lateral semi-circular canal appears to enter

directly into the utriculus, while the anterior ampulla overlaps the dorsal half of the lateral ampulla, thereby obscuring the connection point of the lateral ampulla and utriculus. The utriculus is well-preserved, relatively large and appears to be overlapped by the anterior ampulla. The ventral and medial surface of the utriculus reveal a smaller canal that extends medially until it merges with the sacculus (Figure 5 d, e).

Specimen PV 5849 (Figure 6) is incomplete and preserves portions of a right skeletal labyrinth. This specimen is approximately the same size as PV 4173 and is 6.9 cm long. This specimen is slightly lighter in color and more weathered than PV 4173 and PV 2698, but the prismatic nature of the cartilage is still evident. The sacculus is nearly complete, lacking ventral portions next to the lateral semicircular canal, utriculus and lateral ampulla (Figure 6 b, c). Posterior to the junction between the lateral ampulla and utriculus there is a circular section of smooth cartilage, 0.5 cm in diameter, on the surface of the sacculus. Lateral to this surface, there is a piece of cartilage resting on the surface of the sacculus that possibly shows where the structure rested against the neurocranium.

The semicircular canals are either missing or incomplete on specimen PV 5849. The anterior semicircular canal is completely missing, and only parts of the lateral semicircular canal remain intact, including the lateral surface of the cartilage that rests against the sacculus and outlines the former shape of the canal (Figure 6 a, c, f). The posterior canal is incomplete and the only part of the structure that remains intact is located at the contact between the posterior ampulla. This structure appears to overlap the lateral ampulla as in PV 2698 and PV 4173. The preampullary canal and posterior



FIGURE 6. Photographs of fossilized right otic capsule PV 5849 in (a) dorsal, (b) ventral, (c) lateral, (d) medial, (e) anterior and (f) dorsoposterior views with major stuctures labeled in each orientation. Scale bare equals 1 cm.

ampulla are partially complete where the cartilage is intact or where sediment in-fill has been exposed. The anterior ampulla is missing, but its contact with the utriculus can be identified by the presence of the canal that contacts the medial side of the utriculus. The lateral ampulla is partially complete and the lateral cartilage of the posterior ampullae is missing, but sediment in-fill retains the general morphology of the structure. The general shape of the posterior ampulla is stomach-shaped and it is difficult to discern where the preampullary canal begins (Figure 6 f). The cartilage housing the utriculus is missing, but the utricular canal is completely intact.

CMM-V-1728 (Figure 7) is incomplete and preserves portions of a left otic capsule. The structure is extremely fragile and is in-filled with sediment, but CT-scans reveal a number of structures including the sacculus, cranial nerve openings, lateral and posterior semicircular canals, preampullary canal, endolymphatic duct and perilymphatic fenestra. The specimen is 7.81 cm long, 6.45 cm tall and 6.02 cm wide, is composed of primatic cartilage and is light brown in color.

The sacculus is generally ovoid with the intact ventral portion coming to a rounded point postriorly. A large portion of the lateral wall of the sacculus is missing, which reveals the internal morphology of the medial wall of the sacculus (Figure 7 c). This is overlain by cartilaginous fragments of the neurocranium with exception to a portion bordering the preampullary canal, posterior ampulla and posterior semicircular canal. Much of the dorsoanterior surface of the sacculus is completely missing, except the areas that border larger structures (endolymphatic duct, perilymphatic foramen and posterior semicircular canal). Part of the lateral surface on the ventral portion of the sacculus is



FIGURE 7. Three-dimensional surface rendered images of fossilized left otic capsule CMM-V-1728 in (a) dorsal, (b) ventral, (c) lateral, (d) medial, (e) anterior and (f) posterior views with major stuctures labeled in each orientation. Scale bar equals 1 cm.

incomplete, but it is still possible to discern the general shape, which is rounded with a more acuminate posterior end and a flatter anterior end, similar to specimens PV 4173 and PV 2698. There is a small piece of cartilage from the neurocranium appressed to the anteroventral surface of the sacculus, but the ventral surface is otherwise featureless (Figure 7 b).

The specimen has only two intact semicircular canals; the anterior semicircular canal is missing, the lateral canal is present, but incomplete and the posterior canal is surprisingly complete (Figure 7 c). The lateral semicircular canal is only represented by 3.07 cm of the lateral wall, and an outline of the remainder of the structure is observed on the medial wall on the sacculus extends for 2.22 cm. The posterior canal overlaps the point where the lateral canal enters the sacculus, causing a slight bulge. The posterior semicircular canal is slender and tapers dorsally, with the diameter almost doubling in size where the structure merges with the posterior ampulla. Together, the posterior semicircular canal, posterior ampulla and preampullary canal wrap around the sacculus in a U-shape pattern. The posterior to the where the structure merges with the sacculus for 3.15 cm, beginning immediately posterior to the where the structure merges with the sacculus and ending just before the canal overlaps the lateral semicircular canal. The most dorsolateral wall of the canal is incomplete and exposes the the location of the perilymphatic fenestra, which is anterior to where the canal enters the sacculus.

The posterior ampulla is designated here as beginning ventral to where the posterior canal overlaps the lateral canal (Figure 7 a, d). It is 1.42 cm in diameter at its widest point. However, the boundary between it and the preampullary canal is unclear as there

are no distinct external morphological changes that mark the boundary. The preampullary canal then slightly tapers as it enters the sacculus and at its smallest point measures 0.90 cm in diameter. Another canal-like triangular "sac" that is interpreted as housing the glossopharyngeal nerve (CN IX) originates immediately ventral to the preampullary canal (Figure 7 d). The canal/sac consists of two branches; one directed anteriorly and another laterally that merge into the larger canal. The anterodorsal portion of this canal is fragmented and exposes one large and one small circular foramina, in addition to an oval opening into the preampullary canal which may or may not be due to preservation and taphonomic processes. The smaller foramen measures 0.18 cm and enters the sacculus laterally. The larger foramen follows the posterior path of the glossopharyngeal nerve canal, but it is unclear if the foramen is an anatomical structure or a preservational artifact.

Directly anterior to the nerve canal there is a triangular hollow that shows where the preampullary and nerve canals enter the sacculus. Before entering the sacculus, it appears as if the nerve canal branches into two short canals, one entering the sacculus dorsal to the other. It also appears as though there is another small foraminal canal running posteriorly and dorsal to the branching nerve canal, which may be one of the pathways of the auditory nerve. There is a large opening anterior to the triangular opening, which may have been the main compartment for the auditory nerve. The origin of the small nerve canal is located in the posterior wall of this opening. None of the ampullae, nor the utricular sac, were preserved on this specimen. However, the canal that runs posteriorly and connects the utriculus to the sacculus is exposed and can be traced

along the outer wall of the sacculus and connects to the large opening for the auditory nerve (Figure 7 d).

The internal morphology of the sacculus is clearly illustrated due to the absence of the lateral wall of the sacculus and lateral semicircular canal. The posterior internal surfaces are smooth and slightly bulge where other structures merge with the main cavity of the sacculus. The more anterior half that is near to the cranial nerve openings is irregularly shaped. The medial wall of the sacculus appears to thicken the height of the sacculus where the perilymphatic fenestra and endolymphatic duct enter the cavity. The thickened cartilage expands anteriorly and ventrally until it becomes a flat sheet with long openings that go through to the large openings on the medial side of the sacculus (Figure 7 d).

USNM 47538 (Figure 8) preserves the dorsal portion of a left otic capsule and has a total length of 8.69 cm. This specimen is completely encased in sediment, but the outline of the structure is easily observed due to its distinct, darker brown color and the prismatic nature of the cartilage comprising the otic capsule. The actual specimen is exposed in ventral view as oriented in the block of sediment. The specimen is too fragile to prepare out of matrix and so CT-scanning was employed to create surface-rendered images of the external and internal morphology. Scan data reveal that many of the intact surfaces of the otic capsule are obscured by cartilaginous fragments of the surrounding neurocranium with some surfaces more fragmented and worn near the exposed edges. The external morphology reveals major structures including the partially preserved utriculus, anterior semicircular canal, anterior ampulla, lateral ampulla, lateral semicircular canal, sacculus and posterior semicircular canal. In addition, the opening to the endolymphatic duct and



FIGURE 8. Three-dimensional surface rendered images of fossilized otic capsule USNM 47538 in (a) dorsal, (b)ventral, (c) lateral, (d) medial, (e) anterior and (f) posterior views and indicates the major stuctures in each orientation. Scale bar equals one centimeter.

perilymphatic foramen is also present, but the perilymphatic foramen is difficult to locate (Figure 8 a).

The majority of the dorsal half of the sacculus is intact and measures maximum dimensions of 5.31 cm in length, 3.35 cm in width and 3.63 cm in height. The sacculus is generally rounded, but when viewing the specimen dorsally it appears to be slightly laterally compressed, which is further supported by the presence of small dorsal-ventral overlapping fractures on the posteromedial portion of the sacculus, located between the posterior semicircular canal and the cranial cartilage on the medial side of the skeletal labyrinth. The dorsal portion of the sacculus is covered by cartilage fragments, and extends onto the lateral surface of the sacculus (Figure 8 c). This cartilage is slightly kidney-shaped and is positioned similarly to the smooth indentation on PV 4173, but completely appressed to the outside surface. The medial side of the sacculus is almost entirely covered by a shield-like sheet of cartilage from the neurocranium (Figure 8 d). The medially positioned sheet of cartilage is broad, flares dorsally and ventrally, and measures a maximum length of 5.49 cm and a width of 3.97 cm. A poorly developed, wide, short tube is located near the midpoint of the dorsal portion of the sacculus and lining the shield. Sections of this opening appear to be confluent with the sacculus, but other sections appear to be so closely appressed to the fragmented cartilage and the side of the neurocranium, making it difficult to determine whether the structure is part of the combination of cranial cartilage and the skeletal labyrinth, or of the skeletal labyrinth only. The large opening appears to connect to the posterior semicircular canal which may be the reason for its large size, and based on its position, the opening most likely houses the openings for the endolymphatic duct and perilymphatic foramen. However, the internal morphology is fragmented and incomplete resulting in the absence (in dorsal view) of the cartilage surrounding the endolymphatic duct. A U-shaped notch is located at roughly half the length of the ventral portion of the shelf and measures 0.83 cm wide. The notch flattens ventrally and reveals an oval-shaped foramen, which enters into the sacculus in a diagonal path that is anterior to the perilymphatic foramen.

Internally, the dorsal portion of the sacculus is a D-shaped hollow with the flatter side located medially (Figure 8 b). The cavity is incomplete, the cartilage is fractured and is sightly visible on the outer surface of the specimen which is perhaps due to the compression that affected the integrity of the cartilage immediately adjacent to the medial side of the sacculus and anterior semicircular canal. The internal morphology of the medial wall of the sacculus is much more morphologically informative; it becomes thicker at its midpoint (posterior to the notch) and reveals a surface with what appears to be four foramina, positioned in a squarish orientation. Upon closer inspection, it is more difficult to trace the path of the two medial foramina following a dorsal-ventral path that leads to the large opening in the dorsal surface of the sacculus. The more anteriorly positioned foramen most likely represents the path of the endolymphatic duct (see Maisey, 2005). The much larger foramen is located immediately posterior, the perilymphatic fenestra, and appears to be set slightly obliquely in the skeletal labyrinth.

The semicircular canals of USNM 47538 are incomplete and somewhat fragmented, but do still reveal general information about the general morphology of these structures. The anterior semicircular canal rests against the anterodorsal surface of the sacculus, and it bends around the sacculus until it becomes confluent with the anterior ampulla. In lateral view, the canal is thin at its contact with the sacculus and greatly increases in size anteriorly until it meets the ampulla. There is also clear evidence for compression on the anterior portion of the anterior semicircular canal, where the lateral cartilage appears to be slightly overlapping the medial surface. Thus, diameter size of the anterior canal may not increase to that extent, but instead may be an artifact of compression.

Almost all of the lateral semicircular canal is missing from the specimen, with a small, angular portion of cartilage connected to the lateral ampulla as the only trace of the structure. The fragmented wall of the lateral canal that lines the sacculus appears to travel away from the lateral ampulla at a consistent angle and then slightly changes direction before terminating. The posterior semicircular canal is also incomplete, but much more remains intact than the lateral canal. The ventral part of the canal is broken and does not reveal information regarding the relationship of the posterior canal to the posterior ampulla. It is unclear how much of the canal is missing dorsally, but it appears that the canal may not rest on the surface on the sacculus immediately posterior to the opening for the endolymphatic duct and perilymphatic canal.

Only two of the ampulla are intact; the anterior ampulla is poorly preserved, the lateral wall is missing or covered by cartilaginous fragments from the neurocranium, but the interior morphology is adequate to illustrate its relationship to the anterior semicircular canal, utriculus and lateral ampulla. The anterior semicircular canal gradually merges with the anterior ampulla. Although it is unclear where the exact point of convergence is

for the two structures, the ampullar cavity becomes wider distally and laterally. The medial portion of the anterior ampulla constricts and extends posteriorly and runs parallel to the utriculus and enters the sacculus. There is a definite cartilaginous boundary between the anterior and lateral ampullae that creates a "shelf" of cartilage interiorly and suggest an external lateral wall, that connects the two structures and pinches at their boundary (and is covered by cartilage from the neurocranium). This boundary is marked by the cartilaginous shelf also marks where the anterior and lateral ampullae merge with the utriculus.

The majority of the utriculus is missing and also appears to have undergone some compression suggested by the presence of a heavily folded fragment of cartilage. The dorsal half of the utriculus is represented and suggests an overall rounded shape. The lateral external surface of the utriculus is pinched where it connects to the lateral ampulla. The majority of the surface of the lateral ampulla is obscured by cartilage from the neurocranium, but a subtle change in the external cartilage suggests that the overall size of the lateral ampulla is slightly wider than the lateral semicircular canal. The interior morphology is fairly straighforward; the more complex parts of the structure center on the aforementioned nature of how the lateral ampulla connects with the utriculus and borders the anterior ampulla.

Non-fossil Data

MSU 7099, 7100, 7103, 7104, 7089 and 7101 (Figure 9), which are all members of the Family Carcharhinidae (Carcharhinus falciformis (MSU 7089, 7103, 7104), C. limbatus (MSU 7100), C. leucas (MSU 7099), C. acronotus (MSU 7101)), share a number of similarities in skeletal labyrinth morphology. The shared gross morphology will be discussed here with notable morphological differences, if any, described individually. Following convention, descriptions of non-fossil specimens are based on the morphology of the left skeletal labyrinth, except where noted. Corresponding structures on the right side are mirror images. The shape and proportion of the structures of the skeletal labyrinth from the specimens listed above are comparable across specimens and measurements of the overall length of the skeletal labyrinth are found on Table 3. The general shape of the sacculus is ovoid, with the anterodorsal and posteroventral extremeties coming to rounded, blunt ends in lateral view. The dorsal and ventral surfaces of the sacculus are rounded and typically covered by cartilage from the neurocranium. The posteromedial surface of the sacculus bulges slightly immediately adjacent to where the posterior canal overlaps the lateral canal.

The semicircular canals vary in size and shape on each specimen, but all are of similar proportions. The anterior canal enters the sacculus anterodorsally and is the shortest of the three semicircular canals. The medial side of the skeletal labyrinth reveals that a small gap forms from where the anterior canal wraps around the sacculus, suggesting that this canal may extend laterally throught the sacculus. In lateral view, there is evidence for a small gap ventral to the point where the anterior canal and ampulla connect, but this



FIGURE 9. Lateral view of three-dimensional surface renderings of the skeletal labyrinth of the non-fossil specimens (a) Carcharhinus acronotus (MSU 7101), (b-d) Carcharhinus faciformis (MSU 7104, 7089, 7103), (e) Carcharhinus Imbatus (MSU 7099) and (f) Carcharhinus leucas (MSU 7100). Structures present on the specimens include the sacculus; anterior, lateral and posterior semicircular canals; anterior and lateral ampullae, urticulus and the canal for the glossopharyngeal nerve (CN IN). Specimens are not to scale.

may be an artifact of the scans. The lateral canal is the longest of the three semicircular canals and is somewhat upwardly inclined dorsoposteriorly. The posterior end of the lateral canal is typically wider than the anterior end (which becomes enlarged where the canal merges with the lateral ampulla). The posterior end of the lateral ampulla pinches where the structure meets the border of the posterior semicircular canal, but continues medially and causes a slight bulge in the sacculus. The posterior semicircular canal is slender and long. It extends from the most dorsal part of the sacculus and connects to the posterior ampullae, which here, is located begin just posterior to the position of the point of overlap between posterior and lateral semicircular canals.

A large medially directed opening is situated anterior to where the posterior canal enters the sacculus, exposing two foramina. Both foramina are relatively small, one apparently larger and much more prominent than the other. The larger foramen is here identified as the opening for the endolymphatic duct and the smaller one is the opening for the perilymphatic fenestra.

The anterior ampulla is typically the largest of the three ampullae. It is rounded with the boundary between the ampulla and anterior canal is not easily resolved but likely indicated by the location of the small gap caused by where the canal winds around the sacculus. The anterior ampulla extends laterally extends as far as the dorsal portion of the lateral ampulla and the cartilage constricts where the two meet (though the anterior ampulla sits higher than the lateral ampulla, thus making it appear to be wider). The medial side of the anterior ampulla appears to extend posteriorly into the sacculus. The anterior ampulla meets the utriculus along the full extent of the anterodorsal side. The lateral ampulla is difficult to discern within the overall structure of the lateral semicircular canal, but is ultimately indicated by a slight increase in the overall diameter. The ventral portion of the lateral ampulla meets the utriculus and is marked by a pinched area of cartilage. The posterior ampulla is obscured by the canal for the vagus nerve, but if the cartilage is removed, the general outline of the structure can be observed. The ampulla becomes wider and it is difficult too discern where it merges with the preampullary canal. Nevertheless, these two structures are the widest part of this posterior set of structures.

The preampullary canal merges with the sacculus immediately dorsal to where the glossopharyngeal nerve enters. The utriculus is flattened, but still relatively round. The majority of the utriculus is often covered by cartilage from the neurocranium, but when partially exposed, the cartilage of the skeletal labyrinth is smooth with a small bulge traveling posteriorly and ventral to the posteriorly directed bulge of the anterior ampulla. Openings for the auditory nerve are usually positioned posterior to the utriculus, on the medial side of the skeletal labyrinth. The openings are subtle and are often obscured by cartilage, but can be located on at least four of the specimens.

The canal for the vagus nerve is positioned over the posterior ampulla on the medial side of the skeletal labyrinth. In an anteromedial view, the canal is a single opening and is overall slightly inclined ventroposteriorly. It is relatively large with respect to the size of the openings for the auditory nerve (CN VIII), which can be difficult to locate on the CT-images. The opening for the glossopharyngeal nerve (CN IX) is located laterally on the posteroventral surface of the sacculus. It is a large opening, comparable in diameter

to the glossopharyngeal foramen. The duct for the nerve opening tapers medially where it rests against the ventral surface of the preampullary canal and then enters the sacculus approximately midway across the medial wall.

MSU 7105 (Isurus oxyrhynchus) (Figure 10) has a skeletal labyrinth morphology that is notably different than that of those specimens belonging to Family Carcharhinidae. In contrast to the uniform morphology of the carcharhinid skeletal labyrinth, lamniform labyrinths exhibit distinct morphologies within the order. The sacculus, ampullae and utriculus of specimen MSU 7105 are smaller in proportion to the size of the semicircular canals. The sacculus is so small in proportion to the anterior semicircular canal, that the point at which the two merge is difficult to resolve on the external surface of the skeletal labyrinth. The sacculus is generally ovoid, but narrow and wider at the bottom, and measures 3.34 cm in length, 3.05 cm in height and 2.45 cm wide. The spacing and nature of the manner in which the anterior and posterior semicircular canals enter the structure creates a dimple that gives it a heart-shaped dimpled appearance when viewed laterally. The medial wall of the sacculus is, for the most part, covered by a smooth sheet of cartilage that is interrupted at intervals around the perimeter by large openings and also the canals for the cranial nerves. Only a small, flattened section of the ventral part of the sacculus extends below the lateral semicircular canal.

The anterior semicircular canal curves around and tapers ventrally toward the anterior ampulla, which creates a circular gap 0.20 cm in diameter where the canal is unattached to the sacculus. The cartilage composing the ventral portion of the anterior semicircular canal is only in contact with the anterior ampulla. The lateral canal is somewhat



FIGURE 10. Three-dimensional surface renderings of the skeletal labyrinth of the *lsurus oxythynchus* (MSU 7105) specimen in (a) lateral, (b) posteromedial and (c) anterior view. (b, c) are missing the cranial nerve canals illustrated in (a). Scale bar equals one centimeter.

vertically compressed and is 2.46 cm long, 0.77 cm tall and 0.96 cm wide at its thickest section on MSU 7105. The canal tapers anteriorly, which results in a small lateral ampulla that merges with the sacculus and along the full extent of the posterior end of the urticulus. The posterior semicircular canal is on roughly the same plane as the anterior semicircular canal, and shares a similar morphology. The posterior semicircular canal is not as wide as the anterior canal, but is relatively wider than the carcharhinid posterior semicircular canal. The canal is roughly 3.22 cm long and much more uniform in diameter (0.63 cm) than the other canals. It overlaps the lateral semicircular canal, which creates a small gap 323.98 microns in diameter, but otherwise rests against that surfaces of the sacculus and lateral canal. Cartilaginous fragments from the neurocranium partially rest atop the dorsal surfaces of the anterior and posterior semicircular canals. Removing the fragments in OsiriX causes large gaps within the walls of the cartilage, which suggests that the cartilage of the canals is closely and tightly appressed to the neurocranium.

The ampullae are quite small in MSU 7105 and their exact dimensions are difficult to measure. It appears as if the anterior ampulla begins immediately ventral to where it becomes confluent with the anterior semicircular canal. The anterior ampulla then extends posteroventrally on a slight incline until it merges with the utriculus. The lateral ampulla is indistinguishable from the lateral semicircular canal, due to the canal tapering anteriorly. The ventral part of the ampulla comes in contact with the utriculus, but enters the sacculus without resting on any other structures anteriorly. The posterior semicircular canal and ampulla are located behind the cranial nerve canals. The structures are revealed

to have similar dimensions as the posterior semicircular canal when the cranial canals are removed digitially. There is little morphological change in the size and shape of the posterior ampulla, which makes it difficult to precisely identify the exact identification of a preampullary canal.

The endolymphatic duct is located on the dorsal surface of the sacculus, between the anterior and posterior semicircular canals. It is relatively long and prominent, measuring 1.13 cm in length and tapers slightly until it opens to an irregularly oval-shaped endolymphatic foramen that is 0.22 cm by 0.36 cm in diameter. Just anterior to the endolymphtic duct, there is another smaller canal-like structure that has no discernible opening and does not appear to be hollow when viewed in cross-section. This "canal" measures 0.57 cm long and roughly 0.27 cm in diameter. This structure appears to be associated with the most anterior region of the sacculus. There is no indication as to exactly where the perilymphatic fenestra is located.

The nerve openings of MSU 7105 are quite large and are both directed slightly dorsoposteriorly. The canal that houses the glossopharyngeal nerve (CN IX) measures approximately 4.15 cm long and tapers anteriorly and posteriorly, entering the sacculus immediately posterior to the same place as the posterior ampulla and preampullary canal. The opening itself is oval with the diameter of the long axis 0.56 cm. This canal merges with the canal for the vagus nerve for 1.25 cm at its widest point. The canal for the vagus nerve is incomplete, as the outer wall is missing. The path of the canal begins approximately where the posterior semicircular canal connects with the dorsal part of the sacculus. The canal is marked by a foramen that measures 0.47 cm in diameter and

travels posteriorly on a slight ventroposterior incline and increasing in size until it ends with an opening 0.69 cm wide. One more opening is located adjacent to the utriculus on the medial side of the sacculus. It appears as though the opening leads to the main compartment of the sacculus and may house a branch of the glossopharyngeal nerve.

MSU 7107 (Figure 11) also belongs to the order Lamniformes (*Alopias vulpinus*) and has a drastically different skeletal labyrinth morphology from all other non-fossil specimens. Initial CT-scans of the specimen did not yield usable images of the skeletal labyrinth and so the otic capsule was injected with Gastrografin. The most dorsal regions of the labyrinth are not interpretable, and the specimen is described from the left side. The skeletal labyrinth of this specimen is 4.25 cm in length, 3.89 cm in height and 2.6 cm wide. In lateral view, the sacculus of MSU 7107 is pear-shaped and in ventral view, the sacculus iskidney-shaped, but with the indentation pointing medioposteriorly instead of on the rounded ventral surface as on carcharhinid specimens.

The semicircular canals of MSU 7107 are large in size, but seem to be more proportioned relative to the size of the sacculus here than on specimen MSU 7105. The anterior and posterior canals are incomplete with the most dorsal regions missing and directed slightly dorsolaterally (giving the overall appearance of the two being pushed toward each other). The majority of the anterior semicircular canal is missing, which suggests that it is most likely the shortest of the three canals. Due to its narrow nature, the anterior canal does not contact the dorsal half of the sacculus anywhere along its length. Instead, the canal curves around the anterior end of the skeletal labyrinth to



FIGURE 11. Three-dimensional surface renderings of the skeletal labyrinth of the *Alopias vulpinus* (MSU 7107) specimen in (a) lateral and (b) medial views. Scale bar equals one centimeter.

create a large gap. The lateral semicircular canal is large and is of comparable length as the posterior semicircular canal. The lateral semicircular canal travels posteriorly with on a steep incline until it merges with the sacculus. The posterior end of the lateral canal becomes slightly thicker, and as a result, it appears to tapers slightly anteriorly until it contacts the lateral ampulla. The ventral portion of the posterior semicircular canal is intact and it appears as though the posterior canal overlaps the posterior most end of the lateral canal and is positioned around the sacculus to create a long, large oval-shaped gap. The posterior semicircular canal appears to enter the sacculus ventral lower to where the anterior canal enters, and in anterior view, the direction of the canal changes from being positioned almost vertically to medioposteriorly to include the perilymphatic foramen. The endolymphatic duct is located anteriorly to the perilymphatic foramen. The endolymphatic duct is a thin tube that is slightly smaller in length than that of MSU 7105, emanating from the mediodorsal midpoint of the sacculus.

The anterior ampulla is shaped like a lima bean and narrows slightly where it joins with the utriculus. The lateral ampulla appears to join with both the urticulus and anterior ampulla, although it is difficult to locate the exact position of where the structure merges with the lateral canal. In ventral view, it is clear that the lateral ampulla connects to the utriculus via a small canal and appears to connect to the sacculus and anterior ampulla along its full extent. The posterior ampulla appears to become wider, but it is unclear where it separates from the semicircular canal. It also appears as though there is either an extremely short or no preampullary canal and that the posterior ampulla directly connects to the medial wall of the sacculus immediately ventral to where the lateral canal enters the sacculus. The utriculus is a rounded triangular structure. The scan data also reveal that, in addition to being connected to the anterior and lateral ampullae, that there is another canal running medioventrally that enters into an oval opening with two foramina that possibly show the location of the auditory nerve travels with respect to the labyrinth. Both foramina are fairly large; one directed laterally into the utriculus and the other is directed slightly posterolaterally into the sacculus.

The canals for the glossopharyngeal (CN IX) and vagus (CN X) nerves are easy to locate, with the opening for the glossopharyngeal nerve does not appressed to the side of the sacculus as it is in the carcharhinid specimens, but instead directed more laterally than posteriorly, as is the vagus nerve. Both openings are large, with the vagus nerve opening being much larger than the glossopharyngeal. The glossopharyngeal nerve canal appears to connect with the medioventral portion of the sacculus and this area is marked by two cartilaginous "bumps", one larger than the other.

DISCUSSION

Systematics

Images from the scans of the skeletal labyrinth from all of the known non-fossil carcharhinids share similar morphological characters including:

a. an ovoid sacculus that terminates in rounded points anterodorsally and

posteroventrally

- b. an anterior semicircular canal that is significantly shorter than the lateral and posterior canals
- c. a triangular gap on the medial surface where a small section of the anterior semicircular canal does not rest against the sacculus
- d. the smooth, but angled path traveled by the lateral semicircular canal when viewed dorsally
- e. slight tapering of the lateral semicircular canal anteriorly
- f. a long, slender posterior canal that rests against much of the surface of the sacculus and winds around it in a U-shape ventroanteriorly to connect to the posterior ampulla and preampullary canal
- g. an anterior ampulla whose width slightly bulges and is difficult to discern from the anterior semicircular canal.
- h. a posterior extension of the anterior ampulla on the medial side of the sacculus
- *i.* pinching of the lateral ampulla along the shared surfaces of both the anterior ampulla and utriculus

44

- *j*. a lateral ampulla that is difficult to discern from the lateral semicircular canal; it bulges slightly in size.
- k. a stomach-shaped posterior ampulla
- *l*. an obvious canal extending posteriorly on the medial side of the urticulus.
- *m*. the low-set, medially directed position of the perilymphatic foramen located posteriorly to the endolymphatic duct and emanating from the posterior semicircular canal
- *n*. the low-set, medially directed position of the endolymphatic duct
- *o*. laterally-directed opening for the glossopharyngeal nerve on the posteroventral surface of the sacculus.

The above carcharhinid characters significantly differ from those exhibited from the lamniform specimens (Figure 12). Moreover, the range of morphology within the order itself is also markedly different. In general, the lamniform skeletal labyrinth appears to be somewhat elongated and vertically flattened in comparison to those belonging to the carcharhinid specimens. The sacculus in the lamniforms usually tapers dorsally, whereas the shape of this structure in charcharhinids is more evenly disposed dorsally and ventrally. Furthermore, the lamniform lateral semicircular canal tends to be inclined on a smaller angle and the folding on the medial side of the structure created from the anterior semicircular canal and ampulla and its resulting gap is larger and rounder. Similarly, the gap where the posterior canal is not resting against the sacculus is larger and rounder. The posterior semicircular canals are larger, more prominent and appear to be positioned



FIGURE 12. Morphological comparison of the skeletal labyrinth from (a) Order Lamniformes (*Isurus oxyrthynchus*. MSU 7105) and (b) Family Carcharthinidae (*Carcharthinus acronotus* MSU 7101). more anteriorly. The ampullae, especially the lateral and posterior ampulla, tend to be less well-defined and do not pinch in the same way along the boundaries between other structures as they do in carcharhinids. It remains unclear if the preampullary canal is present, but extremely small, or missing from the lamniform specimens due to the lack of a definite shape to the posterior ampulla. Arguably the preampullary canal should be present and is described as a character for the elasmobrach inner ear (Schaeffer, 1981), but it has not always been identified on some specimens (Maisey, 2005).

In both lamniform specimens, the endolymphatic duct extends dorsally as a long canal leading from the main body of the sacculus to the endolymphatic foramen on the dorsal part of the cranium. This shape of the endolymphatic duct is drastically different from the almost nonexistent endolymphatic duct in carcharhinids. The location of the perilymphatic foramen is either missing or could not be interpreted from scan data on MSU 7105, as there is no indication of a canal protruding from the same area as the posterior semicircular canal as has been identified by Maisey (2005). This leads to the question of whether the enigmatic long, closed canal that is located anteriorly on MSU 7105 is the actual location of the endolymphatic duct. There is no supporting literature for a perilymphatic canal with a wider diameter and positioned so far anteriorly. Gilbert (1976) illustrated the cranial nerves leading into the otic region and showed the auditory nerve (CN VIII) entering the dorsal part of the sacculus near the location of the endolymphatic duct. Thus, this canal may have housed a branch of the auditory nerve, but this possibility cannot be confirmed without further detailed study of shark neuroanatomy.

On the basis of the descriptions from all of the specimens, it is apparent that the gross morphology of the fossils PV 4173, PV 2698 and PV 5849 most closely resembles the skeletal labyrinth of the extant carcharhinids (Table 2). More interestingly, these data also reveal that the morphology of the CMM and USNM specimens is also more similar to the carcharhinid skeletal labyrinth and not to members of the Order Lamniformes as earlier speculated by Gottfried (1995). With the exception of PV 5849, the most incomplete of the South Carolina specimens, the PV fossils have skeletal labyrinth morphology that share many of the characteristics displayed by the non-fossil carcharhinids. Some characteristics still remain unresolved and will require further examination, including those related to the position of the cranial nerves, the shape of the posterior semicircular canal and ampulla and the exact nature of the endolymphatic duct and perilymphatic foramen.

Specimen USNM 47539 is also considered a carcharhinid skeletal labyrinth and due to the nature and morphology of the dorsal portion of the skeletal labyrinth. There are almost no differences between fossil and extant data in the dorsal morphology, with the exception of the cartilaginous shield on the medial side of the labyrinth. Otherwise, the relative shapes and proportions (with exceptions that can be attributed to the minor degree of lateral compression) are consistent with the other carcharhinid characters mentioned above.

Although the more informative lateral and anterior portions of CMM-V-1728 are missing, there are still many characters that align this specimen with the Carcharhinidae, including the shape of the sacculus, posterior semicircular canal, posterior ampulla,

	a	b	С	d	θ	f	g	h	i	j	k	ł	m	n	0	1
Fossil Specimens																
PV 4173	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х		Х
PV 2698	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х		Х	—	
PV 5849	?	Х	?			—	?		—		Х	Х			—	—
CMM-V-1728	X	Х	?				Х			_	Х	?		Х	_	-
USMN 47538	?		?		—	—			Х	Х	—			Х	—	Х
Non-fossil Specimens																
MSU 7089	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	_
MSU 7099	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	
MSU 7100	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	
MSU 7101	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	—
MSU 7103	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	
MSU 7104	X	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	?	Х	Х	—
MSU 7105			—		_						_	_		_	_	
MSU 7107		_				_	—				_	_	—		—	

TABLE 2. Shared morphological characters of the skeletal labyrinth from fossil and non-fossil specimens. An X represents the presence of characters, a question mark (?) indicates that the presence of shared characters is based on incomplete morphology and a dash (-) denotes absence of characters in the specimens. Letters on the horizontal axis refer to the character list in the main body of the paper--and a short summary of the morphology is as follows, (a) an ovoid sacculus, terminating in rounded points, (b) short anterior semicircular canal, (c) presence of a triangular gap, (d) smooth, but angled lateral semicircular canal, (e) slight tapering of the lateral semicircular canal anteriorly, (f) U-shaped posterior semicircular canal, posterior ampulla and preampullary canal, (g) slightly bulging anterior ampulla, (h) posteriorly directed extension of the anterior ampulla, (i) pinching where the lateral ampulla shares surfaces with the anterior ampulla and utriculus, (j) slightly bulging lateral ampulla, (k) stomach-shaped posterior ampulla, (l) posteriorly directed utricular canal on the medial surface of the skeletal labyrinth, (m) low-set, medially directed perilymphatic fenestra, (n) low-set, medially directed endolymphatic fenestra, (o) laterally directed opening for the glossopharyngeal nerve (CN IX) and (1) kidney-shaped indentation on the dorsal half of the sacculus

utricular canal, and the nature and position of the glossopharyngeal nerve canal. The exact location of the endolymphatic duct and perilymphatic fenestra is not completely resolved. However, the large opening that outlines where the posterior semicircular canal enters the sacculus has the same general shape as in the extant carcharhinids, and so those structures theoretically should be present. CMM-V-1728 also possesses a curious foramen that was not observed on any of the other specimens. If this specimen is indeed a skeletal labyrinth belonging to a carcharhind, this foramen could simply be yet another example of where the auditory nerve enters the sacculus, but further studies are required to confidently label it as such.

CMM-V-1728 differs from the extant carcharhinids in that the majority of the posterior semicircular canal does not rest against the surface of the sacculus. This trait is less extensively developed on specimen PV 4173. In addition, the fossils show evidence of where the neurocranium rested against the skeletal labyrinth. Each PV specimen, in addition to the CMM specimen, has a small fragment of cartilage or a smooth indentation (PV 4173) where cartilage once rested on the anteroventral surface of the sacculus. The kidney-shaped indentation on PV 4173 has not yet been observed on any of the non-fossil specimens because that area is usually covered by cartilage. However, this feature is also observed on USNM, but appears to be a part of a cartilaginous fragment from the neurocranium that is resting against the skeletal labyrinth.

Each fossil slightly differs from the generalized description of the carcharhinid skeletal labyrinth and each has at least one character that it shares with another fossil specimen. The former may mean that the fossils exhibit characteristics that are unique to

lower taxonomic groups (genus, species). The latter could indicate that the fossils can be united taxonomically on the basis of shared characters that may be synapomorphic for the Carcharhunidae. However, as some of these characters have not yet been observed on the non-fossil specimens, this argument is not completely supported and this issue will require additional comparative material to be fully resolved.

Size Estimation

The size of the cranium to which the fossils belonged can be inferred by calculating the percentage of the total length of the skeletal labyrinth to the total length of the nonfossil shark crania (Table 3). PV 4173 and PV 2698 are the most complete and therefore yield the more accurate measurements. These two specimens are on the smaller end of the size spectrum of fossils examined for this study, but are significantly longer than many of the labyrinths from the extant crania. Size estimates for the total length of the crania that once housed these fossils are 22.63 cm for PV 5173, and 17.93 cm for PV 2698. The anterior side of CMM-V-1728 is missing and so a total length measurement is not possible, but a minimum estimate for cranium, based on the preserved portion is 25.80 cm long. Likewise, PV 5849 and USNM are incomplete, but a minimum size estimate for cranium of PV 5849 is around 23 cm and the approximation for the USNM specimen, 28.97 cm, places it as by far, the largest of the fossils. This cranial size range is not unusual or unexpected for members of the represented groups (Kent, 1994).

Non-fossil specimens	TL cranium	TL skeletal labyrinth	%
MSU 7089	8.75	2.89	33
MSU 7099	8.68	2.54	29
MSU 7100	8.78	3.26	37
MSU 7101	13.69	4.2	31
MSU 7103	8.45	2.77	33
MSU 7104	8.36	2.69	32
MSU 7105	23.68	3.34	14
MSU 7107	15.09	4.25	28
Fossil specimens			
PV 4173	22.6	6.79	
PV 2698	17.9	5.38	
PV 5849	23.0	6.9	
CMM-V-1728	25.8	7.74	
USMN 47538	29.0	8.69	

TABLE 3. Size measurements for fossil and non-fossil specimens. The total Length (TL) of the cranium was measured along with the total length of the skeletal labyrinth to determine the what percentage of the cranium the skeletal labyrinth encompassed. All measurements are in centimeters.

Size estimates for the fossil crania are high if this percentage remains somewhat consistent within the family and is irrespective of age. On average, the skeletal labyrinth from the non-fossil data was approximately 30 % of the total length of the cranium, with the exception to MSU 7105, in which the percent of the cranium occupied by the skeletal labyrinth was significantly smaller (14 %) and MSU 7100 which falls slightly outside the upper range, at 37 %. Because these fossils share more morphological characteristics with carcharhinid skeletal labyrinths, MSU 7105 and MSU 7107, which are lamniforms, will not be considered in subsequent comparisons, so the anomalously small value for MSU 7105 can be explained by taxonomic differentiation. The slightly higher percentage of MSU 7100 may be explained by intra-specific variation, in which this particular individual has a shorter rostrum in proportion to its cranium, thereby decreasing the overall length of the cranium.

Functional Implications

Detailed morphological descriptions of the skeletal labyrinth in sharks are not common because much of the literature is devoted to the functional aspects of the membranous labyrinth and how it relates to acoustics and equilibrium (see Corwin, 1989; Tester, et al. 1972; Vilstrüp 1950, 1951). Popper and Faye (1977) showed that the shark (and elasmobranchs, in general) inner ear is adapted for low frequency semi-directional phonoreception. The semicircular canals (specializing in detecting angular accelerations) and other organs like the macula neglecta (composed of thousands of sensory cells) are responsible for detecting vibratory motion, vertical movement and possible auditory functions (Corwin, 1977, 1981). The sensory cells located within the structures of the membranous labyrinth work in conjunction with internal compact and solid structures called otoliths, which are principally composed of aragonite and are sensitive to acceleration and gravitational changes (Popper and Coombs, 1980). Sharks also incorporate statoliths into their otic capsule (Parsons and Cardell Jr., 1965 and Vilstrüp, 1951). These structures are usually composed of small grains of calcite and quartz taken in from their external environment and incorporated in the membranous labyrinth to serve a function similar to that of otoliths (Maisey, 1980).

Fossils typically do not preserve the soft structures that compose the membranous labyrinth and our knowledge of the function of the skeletal labyrinth in fossils is limited. However, the shape of the skeletal labyrinth usually corresponds to the general shape of the membranous labyrinth, and changes to the membranous labyrinth will be reflected in the morphology of the of the skeletal labyrinth itself. Therefore, the modifications in the function of the membranous labyrinth should be reflected in the morphology of the skeletal labyrinth should be reflected in the morphology of the skeletal labyrinth should be reflected in the morphology of the skeletal labyrinth should be reflected in the morphology of the skeletal labyrinth should be reflected in the morphology of the skeletal labyrinth that directly relates to functional adaptations and identified characters to support the idea that phonoreception is prevalent in elasmobranchs.

Unfortunately, just as there are few studies that describe the morphology of the skeletal labyrinth, there is a paucity of work dealing with the functional implications of varying skeletal labyrinth morphologies and more research must be completed to understand the functional intricacies the skeletal labyrinth exhibits.

54

DIRECTIONS FOR FUTURE WORK

Variations in the morphology of the skeletal labyrinth may provide insight into habitat and behavior. Recent studies focusing on the functional morphology of the membranous labyrinth show that the morphology does indeed change with respect to habitat and lifestyle (see Witmer, et al., 2003). It has been postulated, for example, that the architecture of human and ape labyrinths, in addition to changes in the muscular anatomy, suggest differences in locomotory adaptations (Bramble and Lieberman, 2004).

But can we say anything about the differences in the habitat and lifestyle of sharks based on the morphology of the skeletal labyrinth? Do any of the morphological characters on the skeletal labyrinth represent behavioral differences? For example, does the compact and more uniform morphology of the three semi-circular canals reflect the coastal habitat of many of the carcharhinid species, while the more open morphology of the canals in lamniforms correspond with an open ocean, pelagic environment? Are there any characters on the skeletal labyrinth that reflect the jumping behavior observed in certain sharks, such as the thresher shark (MSU 7107) and white shark (*Carcharodon carcharias*) (Compagno, 2001; Hubble, 1996)? In that sense this could be taken one step further in developing hypotheses encompassing broader paleoecological implications (i.e., feeding strategies).

However, such questions require more basic research to decipher the intricacies of skeletal labyrinth morphology in both fossils and extant specimens. Efforts to increase the taxonomic sample of morphological data sets from fossil and extant shark crania are imperative for effective comparisons between groups. It is also necessary to increase the number of documented specimens in order to understand how the skeletal labyrinth varies within taxanomic groups. Understanding the anatomical variability is essential to use such data as a tool for studying not only functional morphology, but also phylogeny and systematics. Ontogenetic change and variation should also be considered, especially because available samples may leave one with a wide age distribution. Consequently, such paleoecological and behavioral implications are well beyond the scope of this study.

CONCLUSIONS

I. Several morphological characteristics have been identified on the skeletal labyrinth of non-fossil material that distinguish between members of Family Carcharhinidae (Order Carcharhiniformes) and Order Lamniformes (Families Alopiidae and Lamnidae).

2. The morphology of the skeletal labyrinth in carcharhinids tends to be uniform within the family, with small variations possibly indicating genus/species characters. Similarly, the architecture and relative proportions of otic structure (and with respect to the cranium) seems to remain constant over ontogeny.

3. The comparative morphology of the fossil and extant material implies that the fossil otic capsules most likely belong to Family Carcharhinidae. This assessment challenges the original assignment of the fossil otic capsules CMM-V-1728 and USNM 47538 to Family Lamnidae by Gottfried (1995) as they actually share very few of the general characteristics of Lamniform sharks.

4. Size estimates based on the proportion of the total length of the skeletal labyrinth to the total length of the cranium shows that the overall size of the cranium for the fossil specimens is within the normal range of adult carcharhinid sharks.

5. Detailed studies that add to our knowledge and understanding of skeletal labyrinth morphology have potential for further deciphering functional and paleoecological aspects of shark evolution.

REFERENCES

- BRAMBLE, D.M. and LIEBERMAN, D.E. 2004. Endurance running and the evolution of *Homo*. Nature 432: 345-352
- COMPAGNO, L.J.V. 2001. Sharks of the World: An annotated and illustrated catalogue of shark species known to date, volume 2. FAO Species Catalogue for Fishery Purposes 1 (2): 269 pp.
- CORWIN, J.T. 1977. Morphology of the macula neglecta in sharks of the genus *Carcharhinus*. Journal of Morphology 152: 341-362
- CORWIN, J.T. 1989. Functional anatomy of the auditory system in sharks and rays. The Journal of Experimental Zoology Suppl. 2: 62-74
- DENISON, R.H. 1937. Anatomy of the head and pelvic fin of the Whale Shark, *Rhineodon*. Bulletin of the American Museum of Natural History 73(5): 477-515
- GILBERT, S.G. 1973. Pictorial anatomy of the dogfish. University of Washington Press. p. 41.
- GOTTFRIED, M.D. 1995. Morphology of the membranous labyrinth and associated structures in Miocene shark chondrocrania. Journal of Vertebrate Paleontology 15 (3)
- GOTTFRIED, M.D. and FORDYCE, E. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. Journal of Vertebrate Paleontology 21(4): 730-739
- HUBBLE, G. 1996. Using tooth structure to determine the evolutionary history of the white shark; pp. 9-18 in A. Klimely and D. Ainley (eds.), Great White Sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego.

- JERVE, A. 2006. Morphology of the skeletal labyrinth of Miocene lamnid sharks as revealed by CT-scanning. Journal of Vertebrate Paleontology 26 (3) suppl. 82A
- KENT, B.T. 1994. Fossil sharks of the Chesapeake Bay region. Egan Rees & Boyer, Inc. Columbia, Maryland.
- LANE. J.I., WITTE, R.J., DRISCOLL, C.L.W., CAMP, J.J., and ROBB, R.A. 2004. Imaging microscopy of the middle and inner ear: Part I: CT Microscopy. Clinical Anatomy 17: 697-612
- MAISEY, J.G. 1980. An evaluation of jaw suspension in sharks. American Museum Novitates 2706: 17 pp.
- ----- 1987. Cranial anatomy of the lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. American Museum Novitates 2878: 1-39
- ----- 2001a. Remarks on the inner ear of elasmobranchs and its interpretation from skeletal labyrinth morphology. Journal of Morphology 250: 236-264
- ----- 2001b. CT-scan reveals new cranial features in Devonian chondrichthyan "Cladodus" wildungensis. Journal of Vertebrate Paleontology 21(4): 807-810
- ----- 2004. Morphology of the braincase in the Broadnose Sevengill Shark *Notorhynchus* (Elasmobranchii, Hexanchiformes), based on CT Scanning. American Museum Novitates 3429: 52 pp.
- ----- 2005. Braincase of the upper Devonian shark *Cladodoides wildingesis* (Chondrichthyes, Elasmobranchii), with observations on the braincase in early chondrichthyans. Bull. Amer. Mus. Nat. Hist. 288: 104 pp.

- PARSONS, J. AND CARDELL JR., R.R. 1965. Analysis of statoliths by x-ray diffraction and emission spectroscopy. Transactions of the American Microscopical Society 84 (3): 415-421
- POPPER, A.N. and COOMBS, S. 1980. Auditory mechanisms in teleost fishes. American Scientist 68: 429-440.

POPPER, A.N. and FAY, R.R. 1977. Structure and function of the elasmobranch auditory system. American Zoologist 17 (2): 443-452

- SCHAEFFER, B. 1981. The braincase of *Xenacanthus*, with comments on elasmobranch monophyly. Bull. Amer. Mus. Nat. Hist. 164 (1): 3-66
- TESTER, A.L., KENDALL, J.I. AND W.B. MILISEN. 1972. Morphology of the ear of the shark genus *Carcharhinus* with particular reference to the macula neglecta. Pacific Science 26: 264-274
- VILSTRÜP, J. 1950. Studies on the structure and function of the semicircular canals. Copenhagen: Munksgaard.
- VILSTRÜP, J. 1951. Structure and function of the membranous sacs of the labyrinth in *Acanthias vulgaris*. Copenhagen: Munksgaard.
- WITMER, L.M., CHATTERJEE, S., FRANZOSA, J. and ROWE, T. 2003. Neuroanatomy of flying reptiles and implications for flight posture and behaviour. Nature 425: 950-953

	BORGAR FIATE UNTERNET LINAMES 3 1293 02845 7665	