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Morphometric Changes In Semicircular Canal Shape Within Theropoda (Dinosauria: Saurischia) And Their Dietary Implications

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MORPHOMETRIC CHANGES IN SEMICIRCULAR CANAL SHAPE WITHIN THEROPODA (DINOSAURIA: SAURISCHIA) AND THEIR DIETARY IMPLICATIONS

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A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

James Logan King
B.S., University of Alabama

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Major Professor

Approved___________________________________
Department Chair

GRADUATE COMMITTEE APPROVAL

The graduate committee of James Logan King approves this thesis as meeting the partial fulfillment of the requirements for the Degree of Master of Science.

Approved____
Chair, Graduate Committee

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Committee Member

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Committee Member

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Date____________________

ABSTRACT

Theropods were a suborder of dinosaurs that displayed a large variety of dietary preferences throughout the Mesozoic and into the Cenozoic as modern birds. Being ancestrally carnivorous, many of the large-bodied early theropods were hypercarnivorous; however, members of Theropoda diversified their diets into omnivory and herbivory. Modern vertebrates with different dietary preferences have different spatial sensitivities to changes in head and body movement. In order to test if theropod diet plays a major role in the rostral (RSC), caudal (CSC), and lateral (LSC) semicircular canal shape, therizinosaurs, tyrannosaurids, ratites, an allosaurid, an ornithomimid, and a phorusrhacid were analyzed via 2D Geometric Morphometrics to see if their cross-sectional semicircular canal shapes differed based on the respective diets of each taxa. Each canal sensed the pitch (RSC), roll (CSC), and yaw (LSC) movements of the head and would allow for head and body to compensate for the movement in order to maintain balance.

This study applied a Principal Components Analysis (PCA) and Analysis of Variance (ANOVA) to test for shape change among the semicircular canals of carnivorous, herbivorous, and omnivorous dinosaurs and bird canals. Neither the LSCs nor the CSCs showed patterns that could be interpreted as diet-based groupings among all of the species tested. The RSC graphs, however, clustered the taxa into separate groups based on their trophic level. The PCA demonstrated that the cross-sectional shapes of dinosaurs, ratites, and phorusrhacids are based off of diet (PC1) and the angularity of each shape (PC2). Grouping the taxa by diet and shape angularity implies that there is a spatial sensitivity difference among the dataset based around the diet/foraging strategy of

each dinosaur and bird. The ANOVA attempted to assess the amount of variation between the carnivores, herbivores, and omnivores; however, the herbivores failed tests for normality and equality of variance. This indicates that variation among the levels of diet could not be measured. A normality and variance failure implies that the shapes of the herbivores RSCs were statistically different from the rest of the taxa sampled; however, a larger dataset should be retested to confirm that the failure did not come from sampling bias.

The clustering of the carnivores show a difference between dinosaurs that are thought to be predaceous carnivores (*Alioramus*, *Allosaurus*, and *Gorgosaurus*) and those that are thought to be scavengers or opportunistically carnivorous (*Tyrannosaurus*). *Llallawavis*, a phorusrhacid, plotted near the omnivores even though it is assumed to be a carnivore. One interpretation of this result is that *Llallawavis* was more of an opportunistic carnivore than an active predator. The omnivores (ostrich, emu, *Falcarius*, and *Struthiomimus*) grouped together in both axes of the RSC. *Falcarius* fell out closer to the carnivores in both axes while still maintaining a close proximity to the other omnivores. This pattern is interpreted as being an evolutionary holdover from *Falcarius*' carnivorous ancestry and not an indication of a carnivorous basal therizinosaur; dentition and postcranial anatomy support this interpretation based on the denticle density and size as well as the pubis in the pelvic girdle. The herbivores (cassowary, *Nothronychus*, and *Erlikosaurus*) grouped separately from the rest of the specimens in the dataset. The cassowary plotted closer to the omnivores along the y-axis; however, this was expected due to it supplementing its frugivorous diet with insects and arthropods. *Nothronychus* and the cassowary plotted next to each other supporting a specialized diet for

Nothronychus; however, no other interpretations for *Nothronychus* could be made outside of herbivory. *Erlikosaurus* grouped further away from *Nothronychus* and the cassowary by itself implying that it may be closest to a true herbivore out of all of the organisms in the study.

ACKNOWLEDGEMENTS

I would like to thank my primary advisor, Dr. Reese Barrick, and graduate committee (Dr. Laura Wilson, Dr. Keith Bremer, and Curtis Schmidt) for agreeing to advise a comparative neuroanatomy project. I would also like to thank Dr. Lindsay Zanno (North Carolina Museum of Natural History) and Dr. Stephan Lautenschlager (University of Bristol) for their assistance with therizinosaur functional morphology and unveiling some of the oddities within the lineage. A special thank you goes out to Dr. Lawrence Witmer (Ohio University) for his comments, opinions, and ideas on the endocranial research completed for this thesis. This project would not have been possible without the data provided by Dr. Stig Walsh (National Museums of Scotland) and Dr. Paul Barrett (The Natural History Museum, London).

An unfathomable amount of thanks is owed to my parents and grandmother. Their unwavering moral support (and periodic financial support) was a constant force in the writing of this thesis—even though I am positive they did not understand what I was talking about half of the time.

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INTRODUCTION

Vertebrates that undergo a trophic shift experience an abundance of anatomical modifications. These changes are evident in the dentition as well as the axial and appendicular skeleton. Theropods, a suborder of saurischian dinosaur, are comprised of a variety of both non-avian and avian organisms from a wide variety of trophic levels (Abler, 1992; Holtz et al., 1998; Zanno et al., 2009; Zanno, 2010; Zanno and Makovicky, 2011). The trophic levels of theropods diversified from hypercarnivory to omnivory and herbivory, a trait that is still present in modern birds. Few studies have investigated the impact a dietary shift has on endocranial anatomy (Smith et al., 2011)—specifically the semicircular canals of the endosseous labyrinth—of an organism. Semicircular canals are an important part of balance regulation within vertebrates and, as such, may correlate to the trophic level of an organism. The purpose of this study is to test for changes that correlate with dietary preference in the cross-sectional semicircular canal shapes of non-avian theropods and birds via a Principal Components Analysis. If so, an observation can be made on how shape changes affect the spatial sensitivity of theropod semicircular canals in respect to each organism's trophic level. Additionally, any shape change correlated with diet will be quantified via one-way Analysis of Variance to determine which axis of the semicircular canal experienced statistically significant shape change between the data categories of carnivore, herbivore, and omnivore. This study explores the interior shape variation among the semicircular canals of therizinosaurs when compared to non-avian theropods—Tyrannosauridae, Ornithomimidae, and Allosauridae—and modern Aves—Paleognathae and Phorusrhacidae.

Terminology

While the endosseous labyrinths and semicircular canals of vertebrates are functionally identical (Jones and Spells, 1963), the terminology used to describe their anatomy in humans and other branches of vertebrate biology differs from publication to publication. This paper follows the anatomical terminology used in Lautenschlager et al., 2012 and Witmer and Ridgely, 2009. The distinction between the terms used in this study, the two papers previously listed, and anatomical terminology used in other publications is that this study focuses on the position of each semicircular canal in reference to a common anatomical point instead of their positions relative to each other. While some sources refer to each semicircular canal by a specific name (e.g. Superior/Posterior/Horizontal Semicircular Canal), this study follows the naming procedure of Lautenschlager et al, (2012) to reference each canal's position to the common crus—rostrally situated (rostral canal), caudally situated (caudal canal), or laterally situated (lateral canal).

Overview of Theropoda

The suborder Theropoda (Dinosauria: Saurischia) first appeared in the Triassic, diversified during the Early Cretaceous, and continue to thrive today as birds (Alcober and Martinez, 2010; Zanno, 2010). Theropods are comprised of dinosaurs that were some of the largest terrestrial predators, many of which are popular in modern culture (e.g. *Tyrannosaurus*, *Allosaurus*, etc.), as well as some of the most derived non-avian herbivores present in the fossil record (Therrien and Henderson, 2007; Zanno and Makovicky, 2011). As theropods became more derived, the diets of some theropods changed to support a wider array of food items. Dietary specializations within dinosaurs are best observed in their teeth shape and morphology: small, tightly packed denticles in carnivores (Brink et al., 2015), larger denticles for omnivores (Holtz et al., 1998), and keratinous rhamphothecas for herbivores (Zanno and Makovicky, 2011). Predaceous theropods would use their knife-like teeth to pierce and cut muscle tissues or to help crush bones (Abler, 1992). As certain lineages of theropods became more omnivorous, their denticle sizes would increase to provide more grinding power to their teeth as a way to process more types of food thus allowing a wider range of potential prey items (Holtz et al., 1998). Herbivorous theropods lost their premaxillary teeth and developed a keratin-covered rhamphotheca which would be used as a large grinding surface for plant material (Zanno, 2010; Zanno and Makovicky, 2011).

The postcranial anatomy of theropods also changed as their diets shifted as well. Herbivorous theropods, such as the therizinosaurs, show evidence of an enlarged gut and posteriorly curved pubis that would allow for more intestinal length to process fibrous plant material (Zanno et al., 2009; Zanno and Makovicky, 2011). Similarly, therizinosaurs would have used their gastralia for respiration and supporting a larger mass of intestines as they became more derived (Claessens, 2004; Zanno and Makovicky, 2011).

Semicircular Canal Anatomy and Function in Theropoda

Semicircular canals are located dorsally on the endosseous labyrinths—the inner ear—of the skull (Cox and Jeffery, 2010) superior to the to the cochlea. In theropods, the semicircular canals are comprised of three circular to subtriangular canals (in theropods) that are situated orthogonally to one another and detect angular head movement along their respective axes (Curthoys et al., 1977; Lautenschlager et al., 2012). The rostral canal detects dorsoventral motion (pitch), caudal semicircular canals detect side-to-side motion of the skull (roll), and lateral semicircular canals interpret rotation around the vertical axis of the head (yaw) (Evans et al., 2009; Knoll et al., 2012; Lautenschlager et al., 2012). Each semicircular canal duct terminates on both sides of the canal at the ampulla. All ampulla of the semicircular canals contain the crista ampullaris (CA), which is comprised of the cupula and cilia—hair-like protrusions embedded in the cupula that detect movement (Figure 1). The cilia detect head movement when the cupula is moved by an electrolyte-rich fluid—called endolymph—as an organism's head rotates (Malinzak et al., 2012). Endolymph flows in the opposite direction of the movement of the head. This movement changes the orientation of the cupula and moves the cilia. The direction of the cilia movement is passed along as spatial orientation to the cerebellum via the vestibulocochlear nerve (Cranial Nerve VIII) and interpreted as the orientation of the skull. By determining the position of its head, an organism can orient the rest of its body and maintain an upright posture.

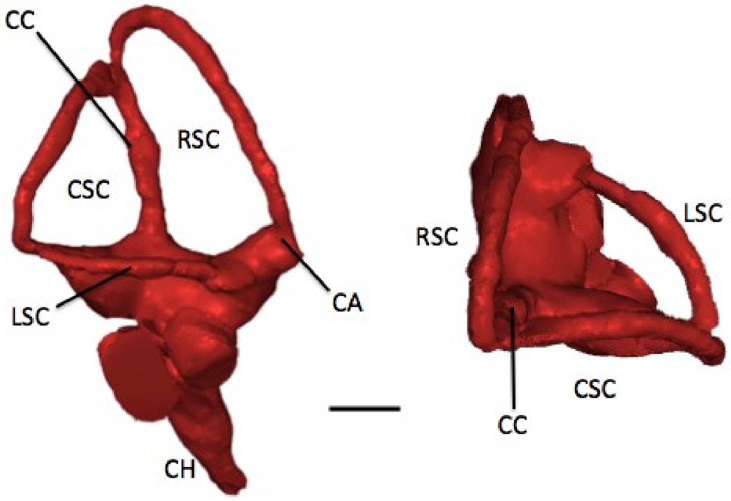

Figure 1 - Generalized anatomy of the right endosseous labyrinth of *Falcarius utahensis*. CA = crista ampullaris, CC = crus communis, CH = cochlea, CSC = caudal semicircular canal, LSC = lateral semicircular canal, RSC = rostral semicircular canal. Scale bar = 5mm

In a broader context, the semicircular canals are responsible for detecting the spatial orientation of the skull as it is moved along planes of rotation. Correlations have been made between the shape of the semicircular canals and locomotor style, and sensitivity of the canals as the head moves within Rodentia (Pfaff et al., 2015), Xenarthra (Billet et al., 2013), hominids (Spoor and Zonneveld, 1998; Spoor, 2003), non-hominid primates (Spoor et al., 2007), and some forms of birds (Hadžiselimović and Savković, 1964). All these studies have found that smaller, circular canals are associated with slower sluggish head movements in extant animals. More strongly angled shapes have been found in highly maneuverable or agile head movements in vertebrates.

The vestibulo-ocular reflex (VOR) is part of the vestibular system that maintains steady eyesight during movement (Fetter, 2007) and, as a part of the vestibular system, helps to regulate overall balance in vertebrates (Spoor and Zonneveld, 1998; Spoor et al., 2007). Eyesight is maintained by producing eye movement that is equal yet opposite of the direction of an organism's head movement and axes of eye rotation. Gaze stabilization and smooth eye movements are mediated by the floccular lobes of the brain which act as control centers for the eyesight portion of the VOR (Krauzlis and Lisberger, 1996). The VOR helps maintain balance by collecting the gaze input and head orientation from the vestibular system and interpreting the horizontal linear acceleration of the head from the utricle, the vertical linear acceleration from the saccule (Fetter, 2007), and the angular acceleration/deceleration of the head from the semicircular canals (Fetter, 2007; Cox and Jeffery, 2010; Ekdale, 2015). All of the combined sensory data is transmitted through the vestibular portion of the vestibulocochlear nerve. The VOR is interpreted within and transmitted to the rest of the body from the cerebellum.

One of the primary reasons the semicircular canals of fossil organisms are studied is to better understand the VOR of ancient vertebrates. While not ideal, the semicircular canals of extinct organisms are chosen over other features (such as the utricle and saccule) of the vestibular system because they are not embedded within the endosseous labyrinths. All elements of the VOR that are not visible in CT rendered images are found in the negative space within the skull. The skulls of theropods, and all skulls in the fossil record, do not preserve the soft tissue that once comprised the other organs of the VOR. Only elements located in the exterior portion of the labyrinths—such as the semicircular canals—can be used to partially reconstruct the vestibular system of a particular specimen.

MATERIALS AND METHODS

Ten non-avian theropod specimens were used for this study (Table 1, Figure 2, 3): three therizinosaurs (*Falcarius utahensis*, *Nothronychus mckinleyi*, and *Erlikosaurus andrewsi*), five tyrannosaurids (*Gorgosaurus libratus*, *Alioramus altai*, two *Tyrannosaurus rex* specimens, and CMNH 7541—a tyrannosaur of uncertain phylogenetic placement), one ornithomimid (*Struthiomimus altus*), and one allosaurid (*Allosaurus fragilis*). Dr. Stephan Lautenschlager (University of Bristol) donated the three therizinosaur braincase scans. The data from *Alioramus* were given by Dr. Gaberiel Bever (American Museum of Natural History). The ornithomimid, allosaurid, and remaining tyrannosaur data were received from Dr. Lawrence Witmer (Ohio University).

Institutional Abbreviations

AMNH – American Museum of Natural History, New York City, New York, United States; **AZMNH** – Arizona Museum of Natural History, Mesa, Arizona, United States; **CMNH** – Cleveland Museum of Natural History, Cleveland, Ohio, United States; **IGM** – Geological Institute of the Mongolian Academy of Sciences, Ulan Bataar, Mongolia; **MLP** – Museo de La Plata, La Plata, Argentina; **NHMUK** – Natural History Museum, London, United Kingdom; **ROM** – Royal Ontario Museum, Ontario, Canada; **UMNH** – Utah Museum of Natural History, Salt Lake City, Utah, United States

Table 1 - Non-avian dinosaur specimen names, numbers, diets and publication of description.

Specimen	Collection Number	Diet	Publication
Falcarius utahensis	UMNH 15000	Omnivore	Lautenschlager et al., 2012
Nothronychus mckinleyi	AZMNH-2117	Herbivore	Lautenschlager et al., 2012
Erlikosaurus andrewsi	IGM 100/111	Herbivore	Lautenschlager et al., 2012
Alioramus altai	IGM 100/1844	Carnivore	Bever et al., 2013
"Tyrannosaurid"	CMNH 7541	Carnivore	Witmer and Ridgely, 2009
Allosaurus fragilis	UMNH VP 18050	Carnivore	Witmer and Ridgely, 2009
Gorgosaurus libratus	ROM 1247	Carnivore	Witmer and Ridgely, 2009
Struthiomimus altus	AMNH FR 5355	Omnivore	Witmer and Ridgely, 2009
Tyrannosaurus rex	AMNH FR 5029	Carnivore	Witmer and Ridgely, 2009
Tyrannosaurus rex	AMNH FR 5117	Carnivore	Witmer and Ridgely, 2009

Four avian specimens from two lineages (three palaeognaths and one phorusrhacid) were used as modern analogs (Table 2, Figure 4,5): one emu, one ostrich, one cassowary, and one *Llallawavis scagliai*. The palaeognath specimens were made available by Dr. Paul Barrett (Natural History Museum, London) and Dr. Stig Walsh (National Museums, Scotland). Dr. Federico Degrange (Universidad Nacional de Cordoba) gave the *Llallawavis* data.

Table 2 - Modern avian specimen names, collection numbers, diets, and publication of description.

Specimen	Collection Number	Diet	Publication
Casarius casarius	NHMUK S/1939.12.9.964	Herbivore	Walsh et al., 2013
Dromaius novaehollandiae	NHMUK S/2001.50.1	Omnivore	Walsh et al., 2013
Llallawavis scagliai	MLP 89-III-20-1	Carnivore (?)	Degrange et al., 2015
Struthio camelus	NHMUK S/1927.2.5.1	Omnivore	Walsh et al., 2013

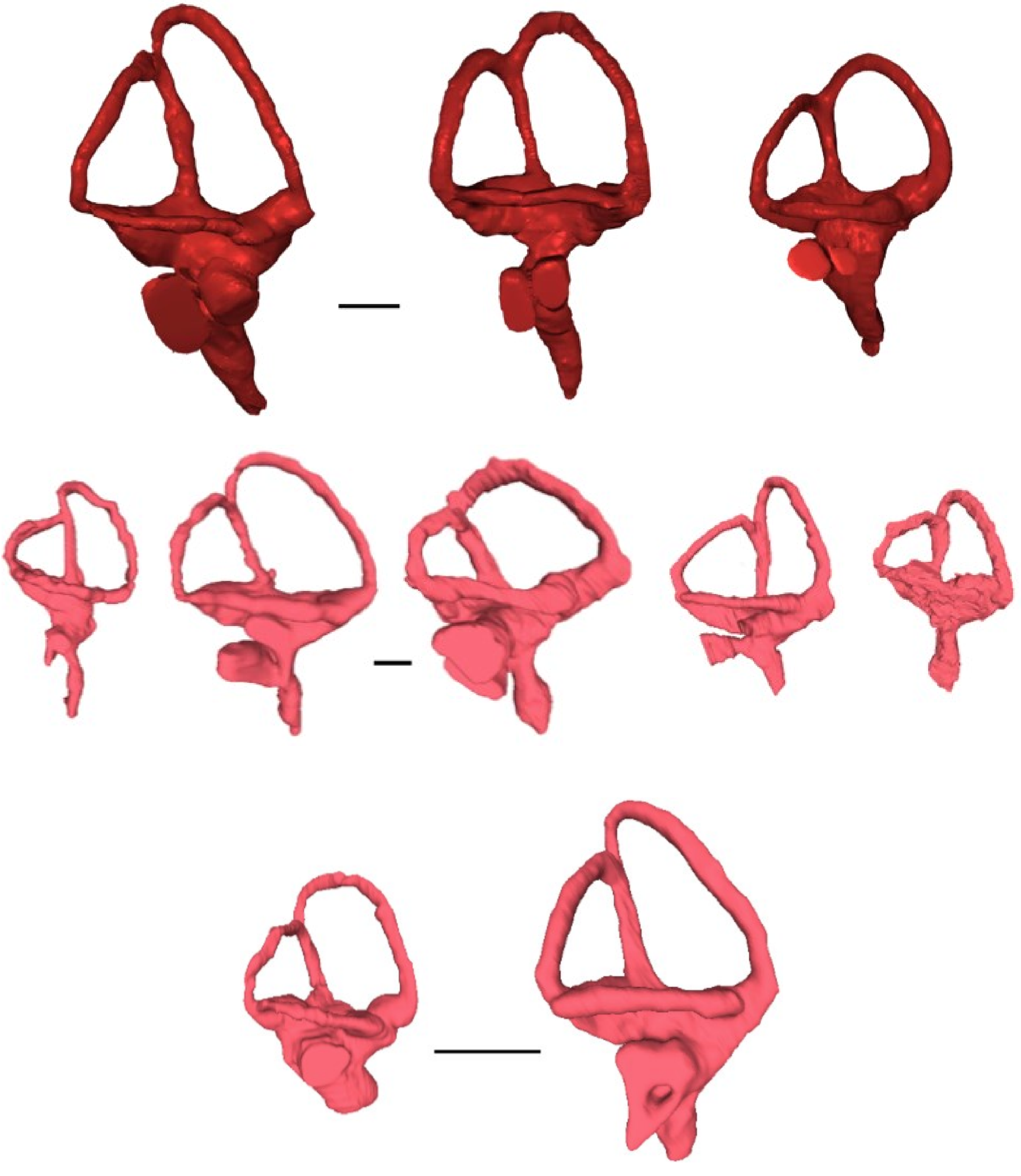

Figure 2 - Lateral views of all non-avian labyrinths used for this study. Top row (left to right): *Falcarius utahensis, Nothronychus mckinleyi, Erlikosaurus andrewsi*. Middle row: Tyrannosaurid CMNH 7541, *Tyrannosaurus rex 5029, Tyrannosaurus rex 5117, Gorgosaurus libratus, Alioramus altai.* Bottom row: *Struthiomimus altus* and *Allosaurus fragilis.* Modified from Witmer and Ridgely (2009). Scale bar = 5mm

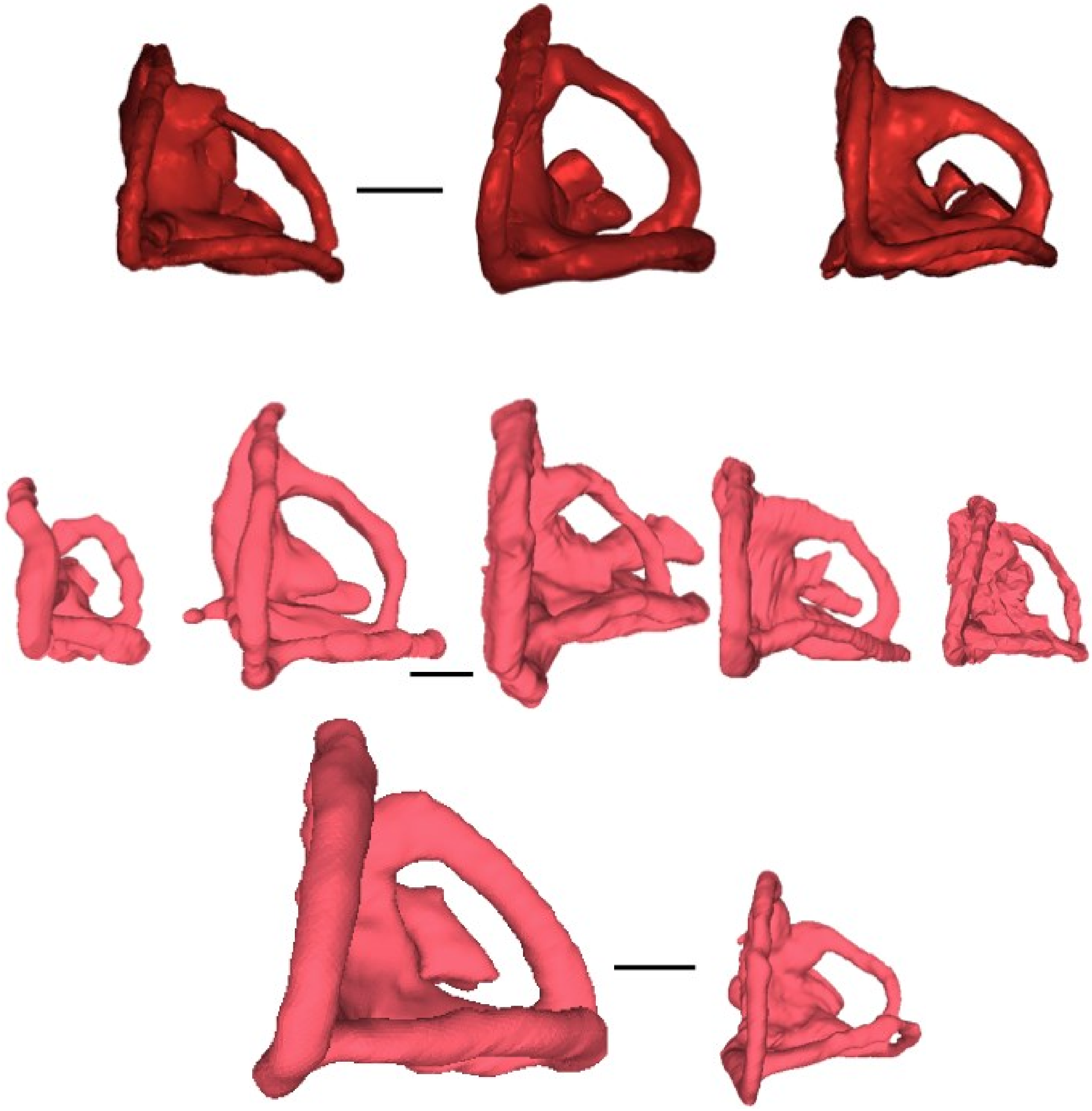

Figure 3 - Dorsal view of all non-avian labyrinths used for this study. Top row (left to right): *Falcarius utahensis, Nothronychus mckinleyi, Erlikosaurus andrewsi*. Middle row: Tyrannosaurid CMNH 7541, *Tyrannosaurus rex 5029, Tyrannosaurus rex 5117, Gorgosaurus libratus, Alioramus altai.* Bottom row: *Struthiomimus altus* and *Allosaurus fragilis.* Modified from Witmer and Ridgely (2009). Scale bar = 5mm

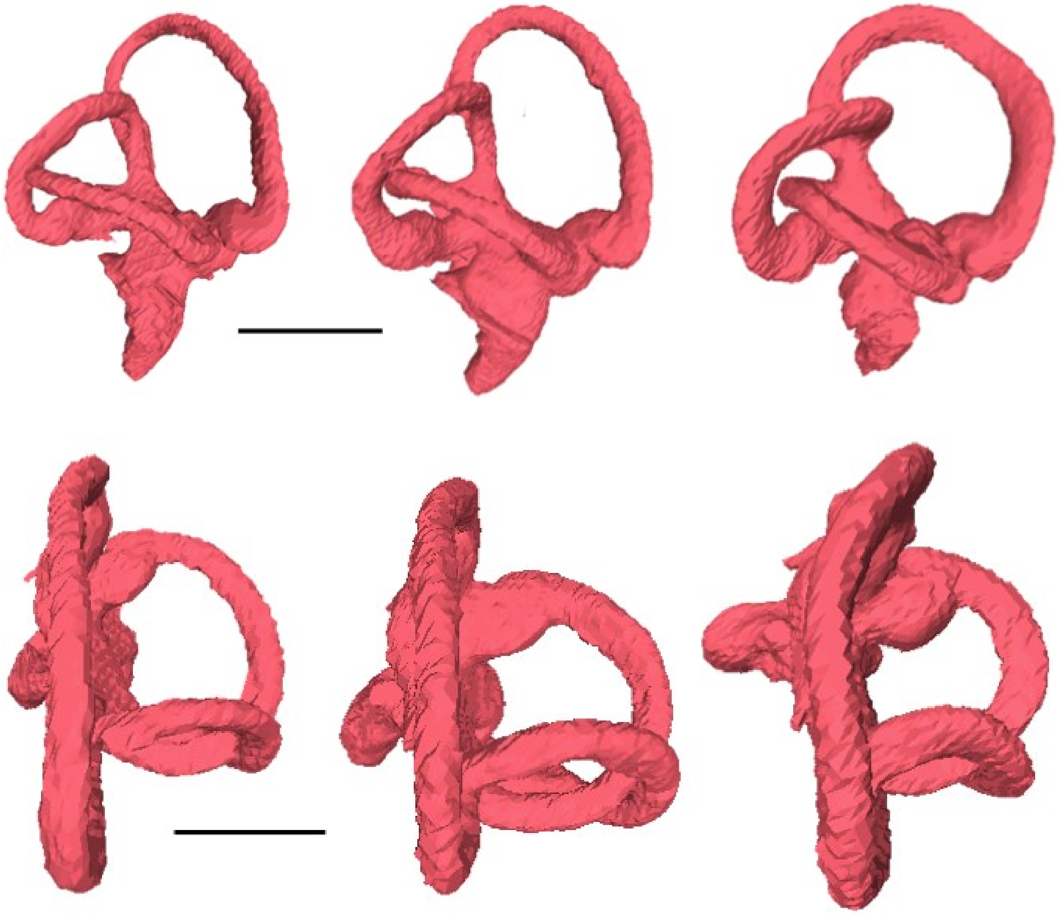

Figure 4 - Lateral (top row) and dorsal (bottom row) of all ratite labyrinths used for this study. Top and bottom row (left to right): southern cassowary (*Casuarius casuarius*), emu (*Dromaius novaehollandiae*), and ostrich (*Struthio camelus*). Modified from Walsh et al. (2013). Scale bar = 5mm

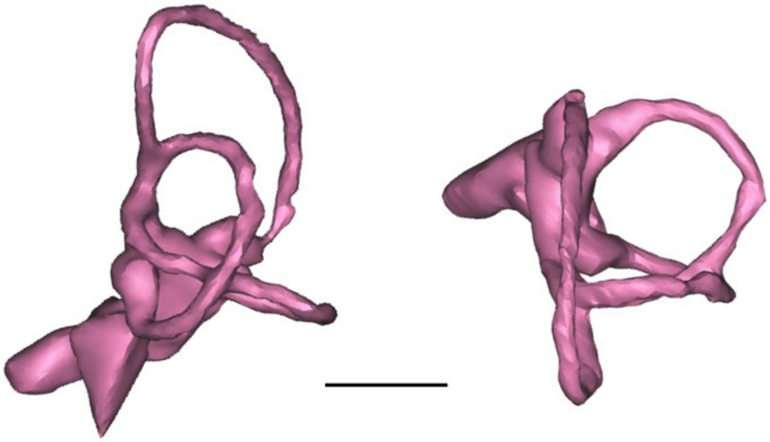

Figure 5 - Ventral (left) and dorsal (right) views of the right endosseous labyrinth from *Llallawavis scagliai*. Modified from Degrange et al. (2015). Scale bar = 10mm

Factors for Specimen Selection

Parameters for the non-avian dinosaur specimens focused on making sure locomotion styles and phylogenies (Tyrannosauridae, Therizinosauria) were homogenous. Bipedalism was kept constant in this study to ensure that no changes in the sense of balance occurred that the organisms might have experienced as they became more dependent on an obligate quadruped/facultative biped form of locomotion. Secondly, only non-avian members of Theropoda were used because they were readily available, all relatively closely related, and have extant organisms that are trophically and anatomically similar. Members of Tyrannosauroidea were used so the therizinosaur specimens could be compared to carnivores from a single lineage. Two other non-avian theropods—*Allosaurus fragilis* and *Struthiomimus altus*—were added to the data pool as single points to test against any patterns that might be related to phylogenetic relationships instead of diet. If these data points were to plot outside of a grouping that was interpreted as being related to their respective diets, a new hypothesis would have to be made that accounted for the discrepancy. The minimum body size for the non-avian theropods was dictated by *Falcarius*—no theropods smaller than *Falcarius* in body size were used in this study. Body mass and body size were not normalized within the specimens in order to test if any non-diet or non-phylogenetic related trends correlated with the shape change within therizinosaurian inner ears. This was done to test for any patterns that were related to body size or body mass instead of diet or the relationships of the two main lineages of theropods used in this study.

Parameters for the modern analogs, the ratites and the phorusrhacid, ensured that all of the avians were terrestrial and incapable of flight. The avians selected for this study were chosen due to their range in dietary preferences: herbivory (cassowary), omnivory (emu, ostrich), and assumed carnivory (*Llallawavis scagliai*). *Llallawavis* was added as a carnivorous member of Aves to test where it plotted in relation to other non-avian carnivores—similar to *Allosaurus* and *Struthiomimus* specimens in the non-avian section of the study. Additionally, a phorusrhacid was selected for this study due to the lack of large extant carnivorous terrestrial avians. Two of the avians were from a single lineage (Paleognathae) in order to keep shape change associated with phylogenetic relationships to a minimum.

Analysis Preparation

In order to statistically analyze the shapes of the pre-rendered endosseous labyrinths, 2D Geometric Morphometric shape outlines were constructed for each of the rostral, caudal, and lateral semicircular canals. These outlines were constructed by capturing a 90° cross-sectional image of each semicircular canal in MeshLab (v.1.3.3), an open source 3D mesh processing program, and saved as a .jpeg file for future research. The crus communis is the left lateral boundary and the LSC makes up the ventral boundary of the interior canal shapes in the RSC and CSC images (Figure 8). Similarly, the CSC forms the left lateral barrier of the LSC while the RSC forms the ventral border of the canal (Figure 8). These orientations were easier to manipulate when the left endosseous labyrinth was used; however, right labyrinths were mirrored and captured when the left labyrinth was not preserved.

ImageJ (v.1.48) was used to outline the interior shape of each canal with 70 semilandmarks (Figure 8). Semilandmarks were chosen over traditional anatomical landmarks due to the lack of anatomical features (e.g. skeletal sutures, protrusions) present on the models of the endosseous labyrinths. Semilandmarks were used because no anatomical points to place normal landmarks and because semilandmarks allowed for the construction of a 2D shape files of the interior portions of each semicircular canal. Choosing a greater number of landmarks would have given a more detailed outline, but would also have increased the chance of small irregularities (such as scanning artifacts) becoming outliers when analyzed during the Principal Components Analysis. The quantity of semilandmarks chosen was arbitrary and only selected because the shapes collected gave the smoothest shapes without picking up artifacts leftover from scanning. The RSCs and CSCs were outlined starting from the base of the crus communis and moving counterclockwise and clockwise (Figure 6) around the interior canal shapes. The LSCs were outlined by starting at the crus communis and continued by placing semilandmarks in a counterclockwise direction around the canal shape. Each landmark represented a point on a Cartesian plan. Once completed, the resulting shape files contained 70 values for each x and y-axis of the 2D shape for a total of 980 semilandmarks, x-values, and y-values.

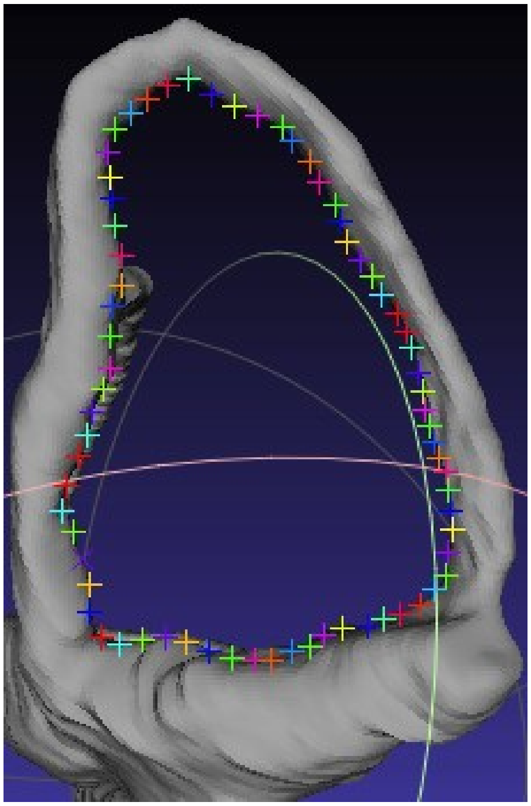

Figure 6 – Left RSC of *Gorgosaurus libratus* that has been oriented and outlined with semilandmarks along the interior canal shape. Original image modified from Witmer and Ridgely (2009)

Procrustes Superimposition

In an effort to normalize the size, translation, and rotation of the shapes within the dataset, a Procrustes Superimposition was applied via R (v.3.2.3) under the package "shapes". Normalization helps to reduce mistakes by taking all of the shapes and scaling them to a common size, rotating them so they are all oriented about a common origin, and translating them so they overlap one another. A Procrustes Superimposition rules out differences in orientation and size so true differences in object shape can be quantitatively described.

Principal Component Analysis

A Principal Component Analysis (PCA) was selected as a statistical means to observe and compare patterns of shape variation within the dataset. A PCA measures the maximum amount of variation within a group by showing the variation as principal components. Principal components are combinations of variables in the data that give the largest amount of variance (Krzanowski, 1979). Principal Component 1 (PC1) is aligned across the direction of maximum variation within the dataset. Similarly, Principal Component 2 (PC2) is aligned orthogonally to PC1 as the second greatest axis of variation. Together, PC1 and PC2 lend support to what factors influence the interior shapes of the semicircular canals of non-avian theropods and modern avians by identifying the two largest sources of variation.

A biplot was made to show if and how the canal shapes grouped together. The points on the graph are the result of using the "site scores" (=principal components) of the x-axis and y-axis of each canal from each specimen in the study. Values for the scores came from the PCA run in R (v.3.2.3) under the package "vegan". The scores from the x- and y-axes of PC1 and PC2 were plotted against each other in order to create groupings based on each individual specimen site scores. Only PC1 and PC2 were used in this study because they contained most (≥ 50%) of the variation found within all three semicircular canals.

One-Way Analysis of Variance

A one-way analysis of variance (ANOVA) was performed on the separate axes of the shapes to observe if the shapes of the canals changed more along the x-axis or y-axis among carnivores (including scavengers), herbivores, and omnivores. The ANOVA tested for normality with the Shapiro-Wilk Test and for equal variance with the Levene's Test for Homogeneity of Variance in both axes among the three conditions of data within the dataset: carnivore, omnivore, and herbivore. The ANOVA cannot distinguish how or why the changes occurred in the dataset, it does explain which changes were significant or not when compared to the conditions of the data in the study. For example, significant changes within the semicircular canals of carnivores could be compared to herbivores and omnivores along each x- and y-axis and then quantified as statistically significant or insignificant. The changes along axes relate to the members of Therizinosauria by identifying which axis of the canal was experiencing statistically significant shape change as the therizinosaurs were shifting their diet.

Shapiro-Wilk Test for Normality

The Shapiro-Wilk Test for Normality is a statistical test that checks for normal distribution within a population. If a population is normally distributed, then 95% of the data within the population is normally distributed. In this case, being statistically normal means that the probability value (p-value) is greater than 0.05. If one of the values is equal to or less than 0.05, then it is statistically significant and is not considered normal—meaning that the data is representative of 5% or less of the total population. The one-way ANOVA requires that the data being analyzed must be normally distributed for a proper analysis to be completed. For this study, pass conditions for normality are $p>0.05$ and fail conditions are set at $p\leq 0.05$.

Levene's Test for Homogeneity of Variance

Levene's Test for Homogeneity of Variance tests the samples within a dataset for equal variances. A one-way ANOVA assumes that variance is equal for the dataset; however, variance among data is not guaranteed. The Levene's test checks variance to make sure that the variance between groups is equal. Variance, by definition, is a measure of how distant each value is from the mean of the dataset. An equal variance means that all of the data used in the study varied the same amount from the mean established in the study. Failure in this study means that the variance p-value was less than 0.05. Anything less than 0.05 meant that the variance was significant and exceeded the mean variance established by the dataset as a whole. P-values were calculated in R as Pr>F scores and are recorded here as “Levene p-values”.

RESULTS

Rostral Semicircular Canal

Principal Component Analysis

The x and y-axis of PC1 explained 51.05% and 42.05% of the total shape variation of each RSC, respectively. The x and y-axis of PC2 explained a much smaller amount of total shape variation with 8.48% and 18.88%, respectively.

When the x-axes were plotted together, they produced groupings of data that were spread out over the entirety of the graph but retained distinct dietary groupings (Figure 7). The y-axes were equally as spread out but could be divided into two main groups based on a diagonal divide among specimens in the dataset (Figure 8).

One-Way ANOVA

The majority of x and y-values for PC1 passed both the Shapiro-Wilk test for normality and the Levene Test of Equal Variance—with the exception of the x-axis for PC1. All of the p-values for PC1—for both axes of carnivores, herbivores, and omnivores—were well above the significance value of 0.05. <F_X = 5e-05, F_Y = 1.5283, Df_X = 2,11, Df_Y = 2,11, $p_{X,Y}$ = Table 3>

The y-values for all diets in PC2 passed the Shapiro-Wilk test for normality but failed the Levene Test of Equal Variance. P-values for the x-axis of the carnivores and omnivores were above the accepted significance level for the study. The carnivores and omnivores passed the Shapiro-Wilk test as well as the Levene Test of Equal Variance; however, the herbivores failed the Shapiro-Wilk test. All of the diets for the y-values of PC2 were well above the significance level of the study. <F_X = 4.1692, F_Y = 0.2135, Df_X = 2,11, Df_Y = 2,11, $p_{X,Y}$ = Table 4>

Table 3 - Table of ANOVA and Levene p-values for the x and y-axis of PC1 for the rostral semicircular canals. Calculated in R with the package "car".

Diet	X-axis	Y-axis
Carnivore	0.3829	0.6943
Herbivore	0.1699	0.2552
Omnivore	0.8597	0.2502

	X-axis	Y-axis
Levene p-values	0.9995	0.2596

Table 4 - Table of ANOVA and Levene p-values for the x and y-axis of PC2 for the rostral semicircular canals. Calculated in R with the package "car". Failed p-values have been *italicized*.

Diet	X-axis	Y-axis
Carnivore	0.3693	0.2794
Herbivore	*0.0323*	0.1269
Omnivore	0.8871	0.5932

	X-axis	Y-axis
Levene p-values	*0.0449*	0.8110

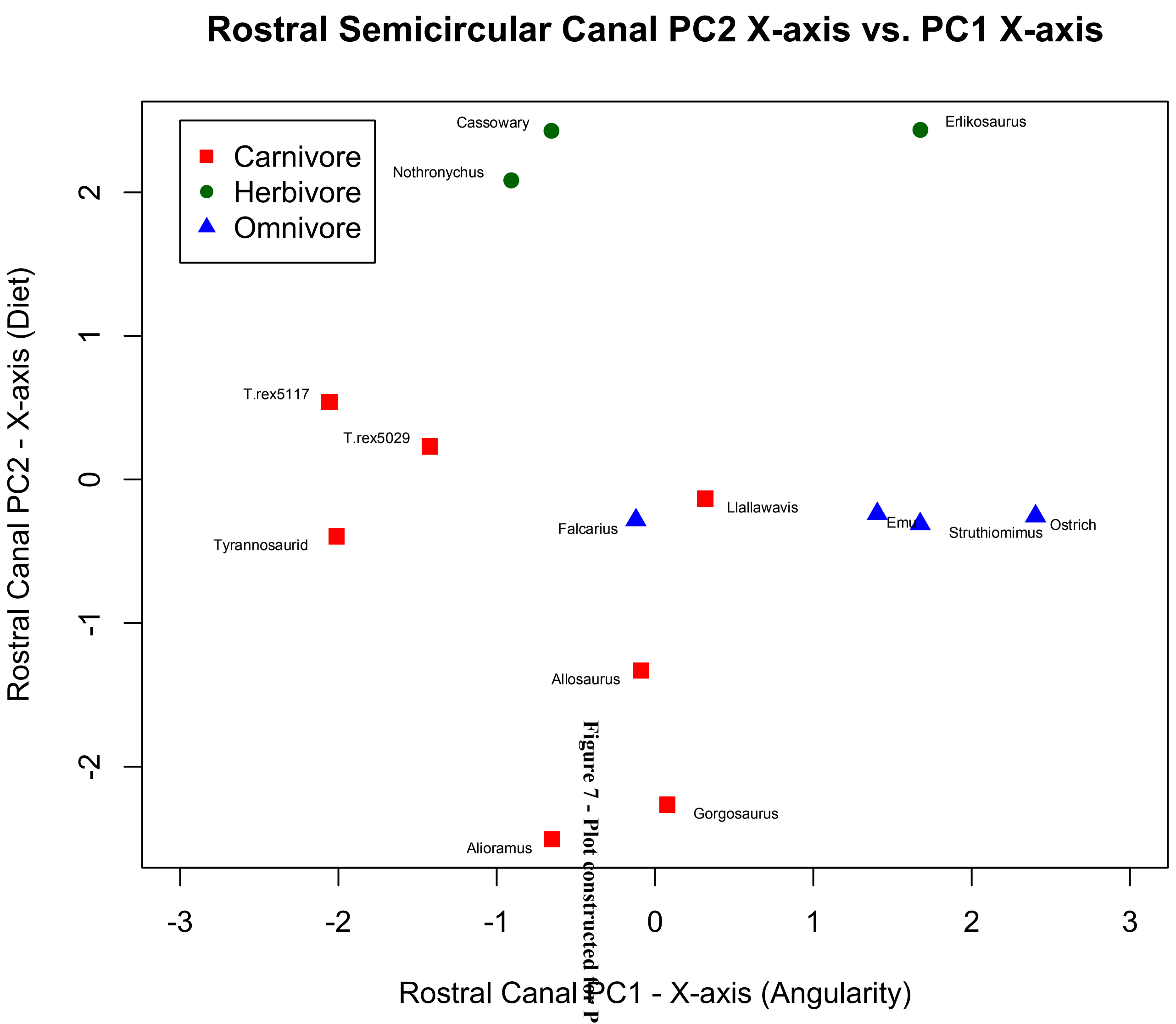

Figure 7 - Plot constructed for PC1 and PC2 of the

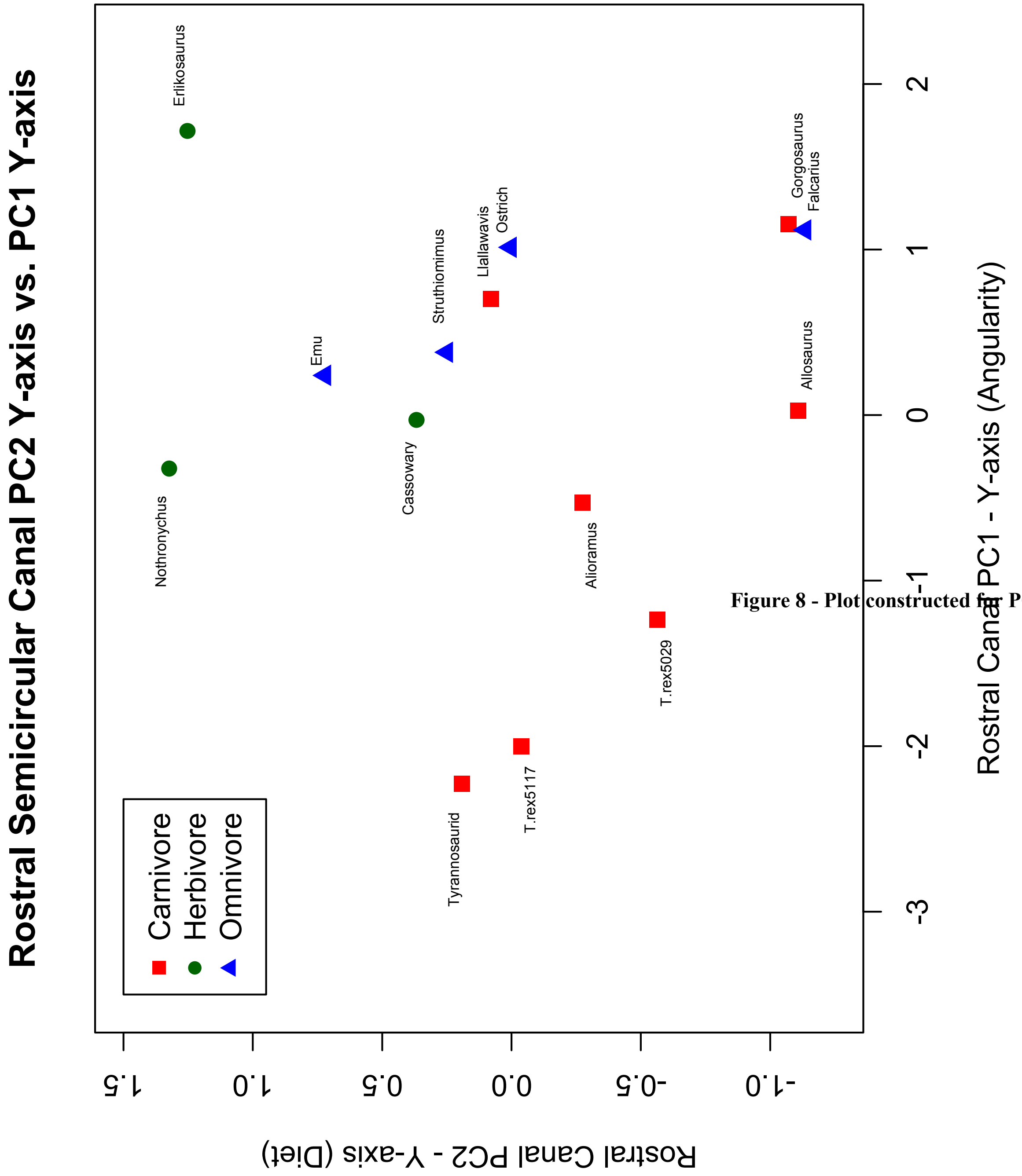

Figure 8 - Plot constructed for PC1 and PC2

Caudal Semicircular Canal

Principal Component Analysis

The x and y-axis of PC1 explained 35.49% and 44.08% of the total shape variation of each CSC, respectively. PC2 for the x and y-axes of the CSCs were explained by 23.51% and 18.83%, a notably larger amount of explanation than PC2 of the RSCs.

When the x and y-axes of both PC1 and PC2 were respectively plotted against each other, no apparent patterns could be found. All of the specimens in the dataset were seemingly randomly oriented (Figure 9, 10).

One-Way ANOVA

The x-values for PC1 passed both the Shapiro-Wilk test for normality and the Levene Test of Equal Variance; however, the y-values failed the Levene test. All of the p-values for PC1 of the x-axis and y-axis for all diet categories were well above the significance level of 0.05. <$F_X = 0.6176$, $F_Y = 0.4884$, $Df_X = 2{,}10$, $Df_Y = 2{,}10$, $p_{X,Y}$ = Table 5>

The x and y-values for PC2 passed both the Shapiro-Wilk test and Levene Test of Equal Variance. All of the p-values for PC2 of both the x and y-axis of the carnivores, herbivores, and omnivores were well above the significance value of 0.05. <$F_X = 1.1523$, $F_Y = 0.6176$, $Df_X = 2{,}10$, $Df_Y = 2{,}10$, $p_{X,Y}$ = Table 6>

Table 5 - Table of ANOVA and Levene p-values for the x and y-axis of PC1 for the caudal semicircular canals. Calculated in R with the package "car".

Diet	X-axis	Y-axis
Carnivore	0.4219	0.2766
Herbivore	0.8798	0.8325
Omnivore	0.1001	0.9408

Levene p-values	X-axis	Y-axis
	0.5735	0.3545

Table 6 - Table of ANOVA and Levene p-values for the x and y-axis of PC2 for the caudal semicircular canals. Calculated in R with the package "car".

Diet	X-axis	Y-axis
Carnivore	0.9962	0.2475
Herbivore	0.5488	0.2550
Omnivore	0.4638	0.6695

Levene p-values	X-axis	Y-axis
	0.6275	0.5586

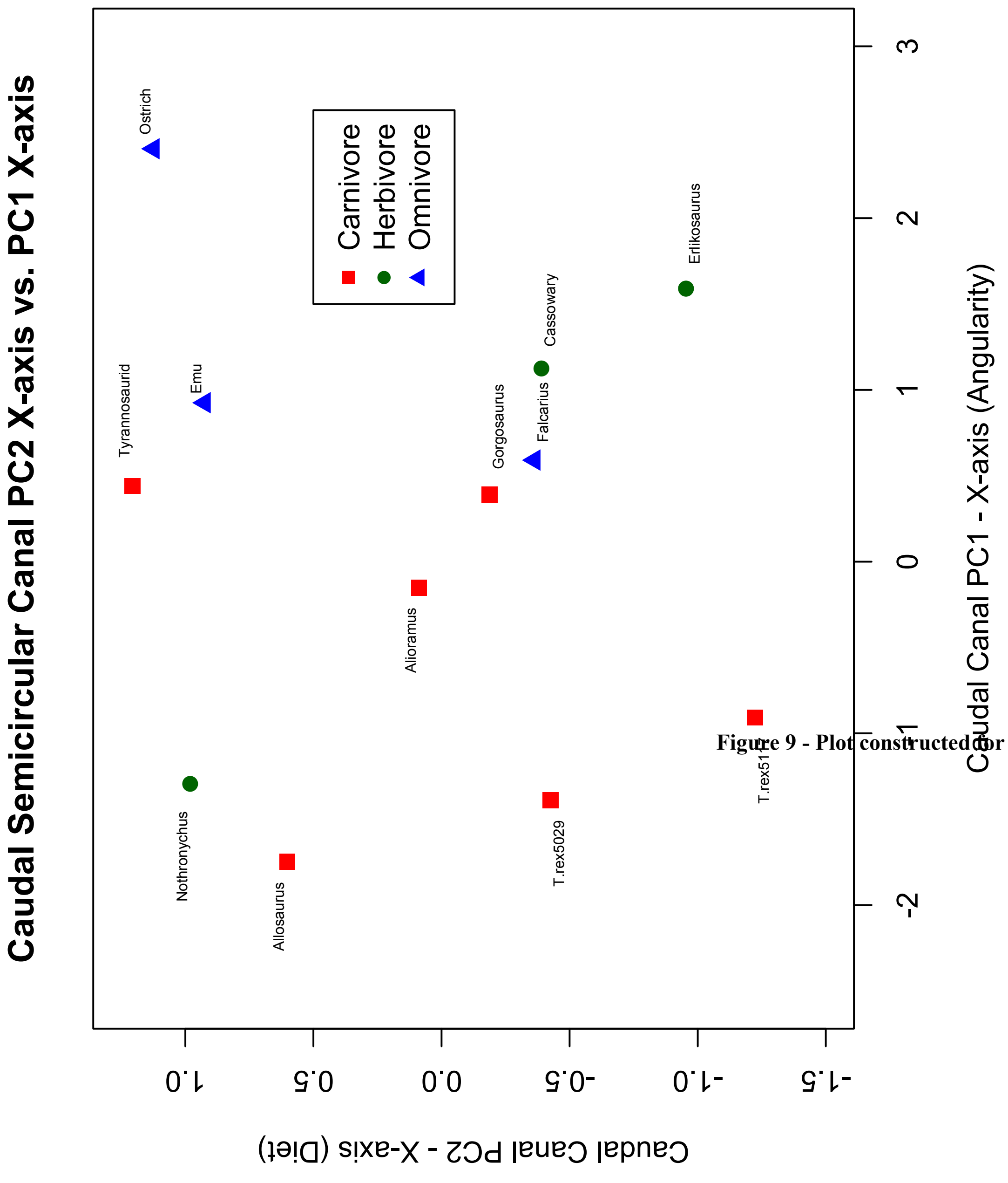

Figure 9 - Plot constructed for PC1 and PC2 o

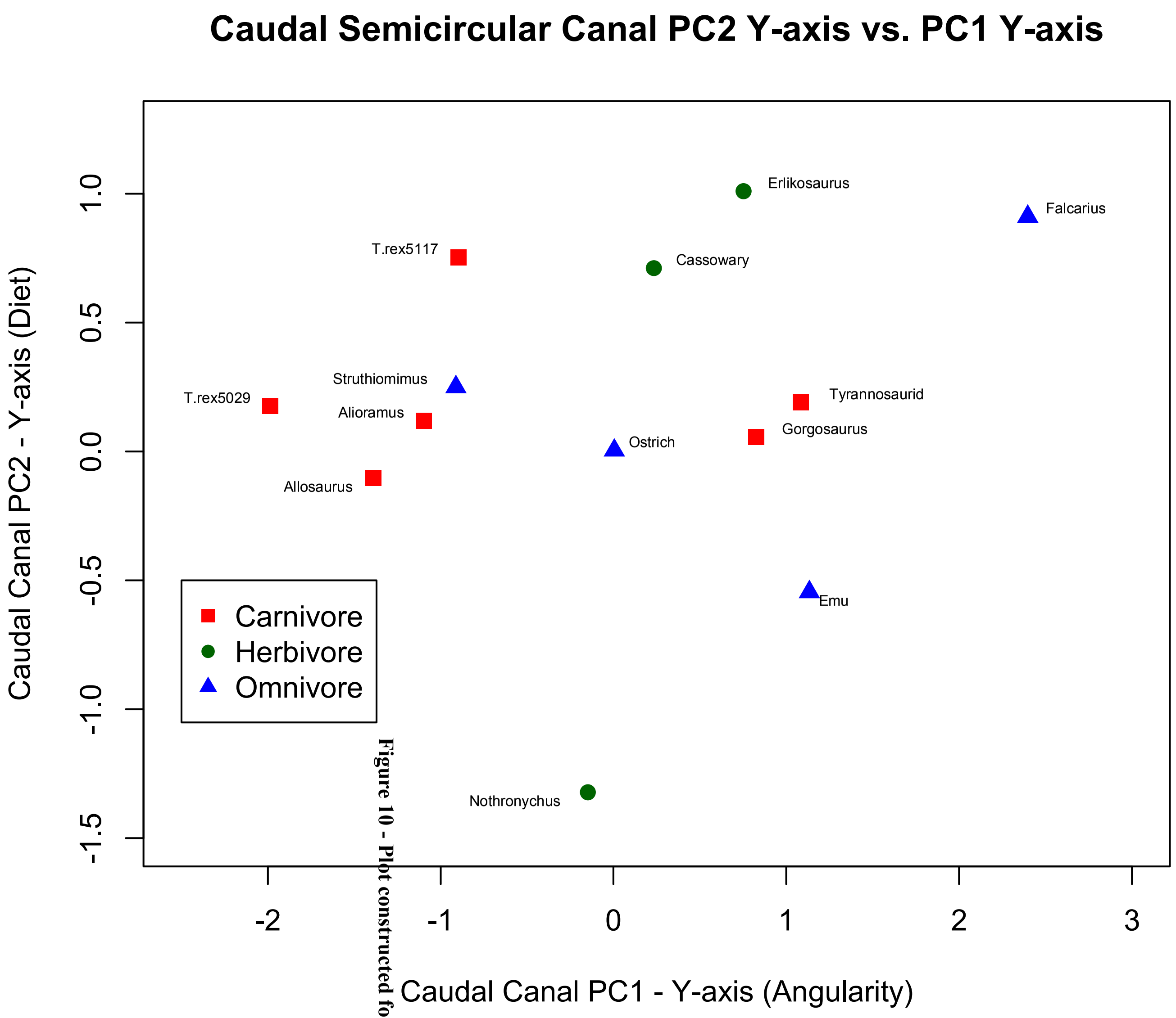

Figure 10 - Plot constructed for PC1 and PC2

Lateral Semicircular Canals

Principal Component Analysis

The axes of PC1 explained 43.49% and 35.44% of the total shape variation among the LSCs, respectively. Similarly, the x and y-axes of PC2 explained 14.29% and 20.17% of the respective total shape variation among the LSCs

When the x and y-axes of both PC1 and PC2 were respectively plotted against each other, no apparent patterns could be found. All of the specimens in the dataset were once again seemingly randomly oriented (Figure 11, 12).

One-Way ANOVA

The x and y-values for PC1 passed both the Shapiro-Wilk test for normality and the Levene's Test of Equal Variance. All of the p-values for x and y-values for the carnivores, herbivores, and omnivores of PC1 were well above the significance value of 0.05. <$F_X = 1.2834$, $F_Y = 0.8462$, $Df_X = 2,11$, $Df_Y = 2,11$, $p_{X,Y}$ = Table 7>

Both the x and y-values for PC2 passed the Shapiro-Wilk test for normality but only the y-values passed the Levene's Test of Equal Variance. All of the p-values for x and y-values for the carnivores, herbivores, and omnivores of PC2 were well above the significance value of 0.05. <$F_X = 0.4574$, $F_Y = 0.7747$, $Df_X = 2,11$, $Df_Y = 2,11$, $p_{X,Y}$ = Table >

Table 7 - Table of ANOVA and Levene p-values for the x and y-axis of PC1 for the lateral semicircular canals. Calculated in R with the package "car".

Diet	X-axis	Y-axis
Carnivore	0.9457	0.8738
Herbivore	0.8103	0.2532
Omnivore	0.7969	0.5492

	X-axis	Y-axis
Levene p-values	0.3155	0.4552

Table 8 - Table of ANOVA and Levene p-values for the x and y-axis of PC1 for the lateral semicircular canals. Calculated in R with the package "car".

Diet	X-axis	Y-axis
Carnivore	0.1804	0.2274
Herbivore	0.5762	0.5349
Omnivore	0.0599	0.2079

	X-axis	Y-axis
Levene p-values	0.6444	0.4844

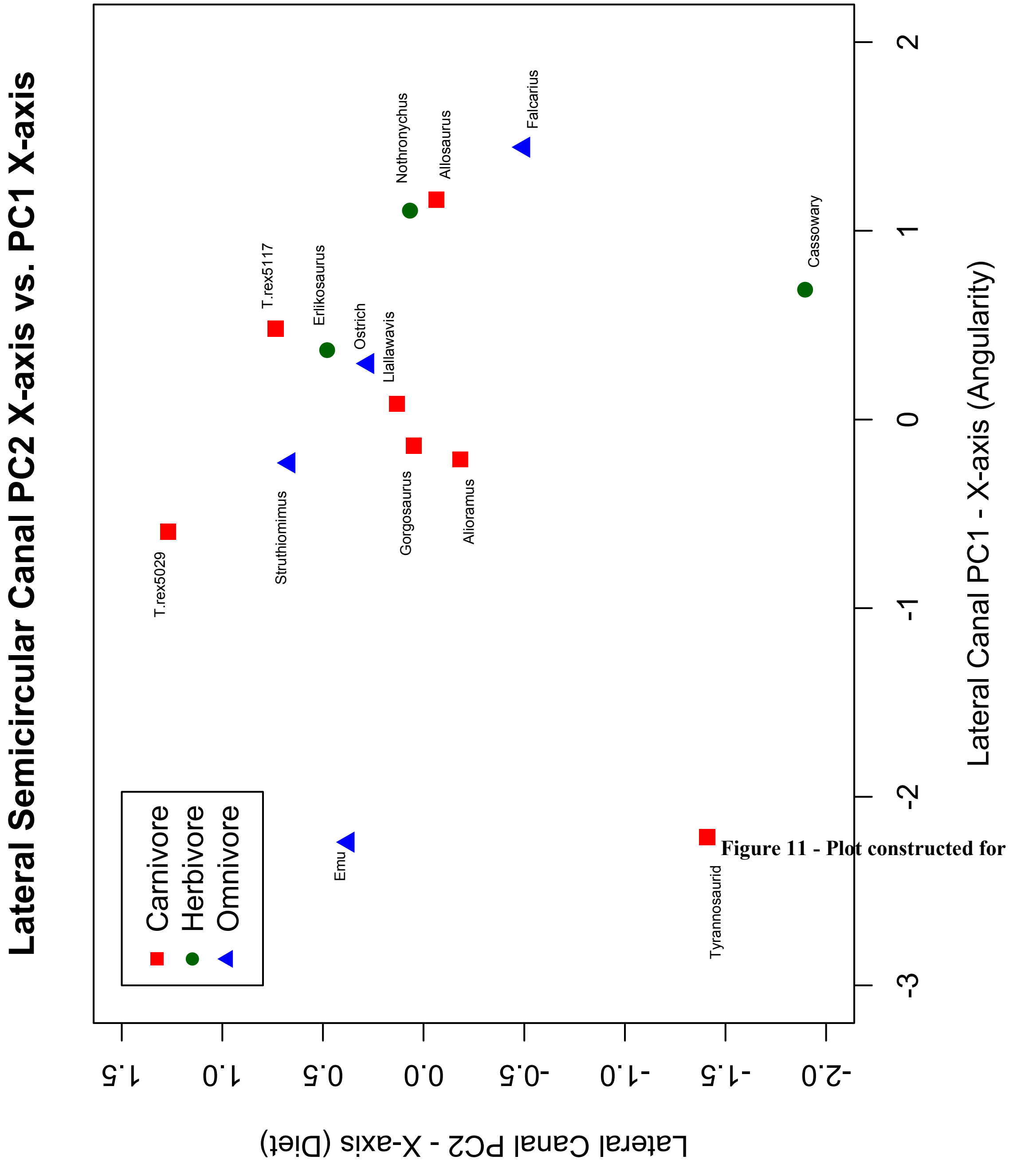

Figure 11 - Plot constructed for PC1 and PC2

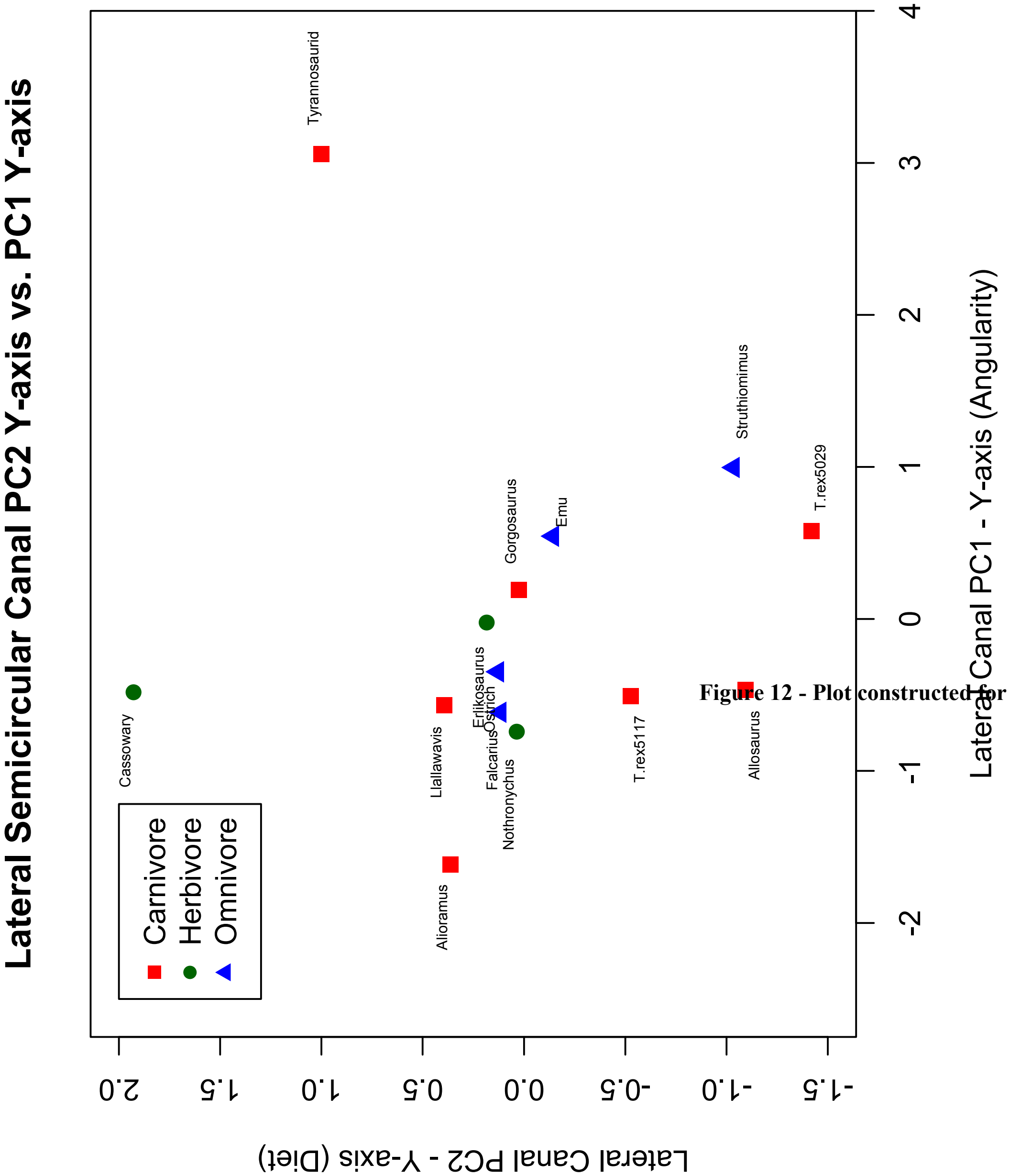

Figure 12 - Plot constructed for PC1 and PC2 o

DISCUSSION

Implications

Broad Impact

This study provides evidence that the dorsoventral spatial sensitivity in theropods is directly related to the shape of the rostral semicircular canals and the diet of each organism (Figure 13, 14). Overall, the shape of the rostral canal changes with the trophic level of each organism used within this study. A loss of angular shapes matches up with diets that do not require rapid head movements during foraging or browsing. These observations are reflected in the inner ears of modern animals as well: agile animals that utilize rapid head movements or regularly move their heads along planes of rotation have more angular canal shapes than those that move their heads more slowly. However, it is not clear if the angularity of the rostral canals corresponds solely with the cranial spatial sensitivity of each dinosaur or if it also correlates with each dinosaur's body agility/vertebral flexibility. It is feasible that the canals indicate how sensitive the head was to rotation, how flexible the head was compared to the body, how agile the animal was overall, or possibly a combination of balance, agility, and vertebral flexibility. More research will have to be conducted on theropodian postcranial anatomy to analyze how agile each theropod was when compared to their semicircular canal angularity and diet. Other head movements (roll and yaw) are not linked to a specific trophic level nor related to a specific dietary preference or foraging strategy.

Predaceous theropods move their heads more frequently along the rostral plane than other non-avian dinosaurs—especially during feeding movements and pursuit/alert positioning of their heads. The feeding ecology of predaceous theropods is dependent on them finding prey items, bringing them down, and repeatedly moving their heads dorsoventrally during prey consumption; their inner ears are more angular to distinguish between small changes in head posture.

Less specialized carnivores (such as the proposed scavengers/opportunists) would not be as dependent on having a finely tuned sense of spatial awareness; however, they still required the ability to repeatedly move their heads up and down while scavenging without becoming disoriented. A rounded angular rostral canal allowed for spatial recognition without dulling their spatial sensitivity. Similarly, omnivores have a wider range of dietary options—some of which do not require fast head movements to track or catch prey items. Much like the opportunistic/scavenging carnivores, omnivorous forms of theropods and birds are able to move their heads up and down the vertical plane without losing their spatial orientation.

Unlike the other dietary niches described, herbivorous forms of non-avian theropods and avians do not need to move their heads during feeding as much. Modern herbivores rapidly move their heads up or down to achieve an alert position when they perceive danger (i.e. as they were being hunted). Otherwise, herbivores do not move their heads much during browsing/foraging or they are not agile with quick head movements. Generally speaking, herbivores do not require a head capable of rapid changes in orientation; however, this does not mean that their sense of spatial orientation was weak. Herbivorous theropods and modern birds only have a sluggish movement when compared to the hypercarnivorous predators based on the circular rostral semicircular canals.

Therizinosaurs

The therizinosaurs reflect a change in diet during their lineage's evolution based on how the rostral canal shapes grouped together along both x and y-axes. *Falcarius*, an omnivorous form of therizinosaur, plots differently than the more derived herbivorous therizinosaurs: *Nothronychus* and *Erlikosaurus* (Figure 10, 11). This indicates that the changes observed in the canal shapes are related to the trophic level of each therizinosaur. This observation is supported by the postcranial anatomy and dentition of the therizinosaurs used within the study.

Members of Therizinosauria experienced a dietary shift based on postcranial anatomical adaptations and dentition specializations (Zanno, 2010; Zanno and Makovicky, 2011). An increase in gastralia robusticity and posterior curving of the pubis facilitates an increased intestinal length—thus allowing for more fibrous food to be ingested and supported within derived therizinosaurs (Zanno and Makovicky, 2011). The dentition of *Falcarius* differs from *Nothronychus mckinleyi* and *Erlikosaurus andrewsi* in that it has a higher denticle density and smaller denticle size per tooth (Kirkland et al., 2005; Zanno and Makovicky, 2011; Hedrick et al., 2015). The smaller denticles along *Falcarius*' lanceolate teeth are less specialized than the ones found in derived therizinosaurs. Large denticles are used to grind fibrous food up during mastication while smaller, tightly packed denticles produce more of a cutting edge and are less useful for herbivory (Holtz et al., 1998; Brink et al., 2015). Therizinosaurs lose the small tightly packed denticles as they become more derived throughout their lineage (Zanno, 2010). Derived therizinosaurs also become edentulous along their premaxilla in order to maximize the grinding surfaces in their mouths (Zanno et al., 2009; Zanno and Makovicky, 2011). For example, the edentulous premaxilla of *Nothronychus* was covered in keratinous rhamphotheca that allowed for processing of plant material (Hedrick et al., 2015).

While the postcranial data support an omnivorous diet for *Falcarius*, the shape along the x and y-axis of the rostral canals supports a more opportunistically carnivorous strategy. Interpreting the data based solely on the RSCs would mean that *Falcarius* has a carnivorous dietary preference with omnivorous tendencies based on the overall shape and sensitivity of the rostral canal; however, further dietary data can be found in the dentition of Falcarius. The denticles on *Falcarius*' teeth are thicker than those generally found in predaceous non-avian carnivores (Holtz et al., 1998). This indicates that the teeth were used more for grinding plant material than slicing through prey items—thus supporting a more omnivorous lifestyle for *Falcarius*. Another interpretation of *Falcarius*' position relative to the carnivores is that the shape of the rostral canal along the y-axis is a holdover from its carnivorous maniraptoran ancestors. This would indicate that endocranial anatomy of *Falcarius* does not adapt to dietary changes as quickly as the dentition and postcranial anatomy does—which has merit as a valid interpretation since the shape of the rostral canal in *Falcarius* groups with the other omnivores within the dataset along the x-axis.

Additionally, the trophic level for *Erlikosaurus* falls out as a traditional herbivore; however, *Nothronychus* may have had a specialized form of herbivory much like the cassowary. Cassowaries are frugivores that supplemented their diet with insects and arthropods (Bradford et al., 2008). While difficult to ascertain, *Nothronychus* may have had a similar dietary preference that focused on herbivory but was supported with another such as insectivory or scavenging.

Ratites, Llallawavis, *and* Struthiomimus

The ratites used in this study—the ostrich, emu, and cassowary—grouped as expected for a dietary based grouping. Emus and ostriches feed primarily on seeds and vegetation during wet seasons in their respective habitats. They shift their diets to include more insects and small vertebrates during times of drought or when their normal preferred food items are not available. Since their diets have a large amount of variation, the ostrich and emu used in this study grouped near each other along both axes and near other omnivorous organisms. The cassowary's diet is different from the emu and the ostrich and it grouped differently in the PCA. Cassowaries are primarily frugivorous but will also eat plants, seeds, and the occasional insect or arthropod. The cassowary's position along the y-axis is interpreted as a similar shape based on the omnivorous similarities between the cassowary, emu, and ostrich. The y-axis places the cassowary in near the top of the graph near among the derived therizinosaurs. This placement is interpreted to show the frugivorous dietary preference of the cassowary and how it is more similar, dietarily, speaking, to herbivorous dinosaurs than it is to modern omnivorous ratites.

The ornithomimid in the dataset, *Struthiomimus*, grouped between two of the modern analogs, the ostrich and the emu. This placement has implications for the diet of *Struthiomimus* based on the observed diets of ostriches and emus. There is evidence for herbivory/omnivory in ornithomimids that is based around rhamphotheca and gastric mill in well preserved ornithomimids (Barrett, 2005). As with derived therizinosaurs, a rhamphotheca provides a larger grinding surface and allows for mastication of fibrous material. A gastric mill allows for further processing of plant material by using muscles and gastroliths within the gastric mill to grind plant materials before sending it to the stomach for digestion. Both ostriches and emus have both toothless rostrums and gastric mills and will eat seeds, plants, insects, and small vertebrates based on what is available. Since *Struthiomimus* plots between or near the ostrich, emu, and cassowary (Figure 10, 11), its diet is assumed to be more omnivorous than carnivorous or herbivorous. Furthermore, it is feasible that *Struthiomimus* may have adapted its diet to include more invertebrates and small vertebrates as needed.

Llallawavis falls near the predaceous carnivores along the x-axis and near the dietary divide along the y-axis, one interpretation for its dietary habits could be that *Llallawavis* was a carnivore with omnivorous tendencies. This interpretation is reflected in today's ratites that have a preferred trophic level but will modify their diets based on the resources available. *Llallawavis* has been assumed to be a carnivore based on its phorusrhacid ancestry. Phorusrhacids are presumed to be predators based on the strongly curved tip of the rostrum, the calculated bite force from fossil specimens, and neck flexibility (Degrange et al., 2010; Tambussi et al., 2012). The tip of the rostrum and bite force would have helped to remove flesh from prey items; however, other large non-phorusrhacid birds with similar body characteristics, such as *Diatryma*, are placed in dubious trophic levels throughout the fossil record thus making their diets difficult to determine (Witmer and Rose, 1991). Additionally, other terrestrial post-Cretaceous birds (e.g. *Gastornis*) have diets that are based more around herbivory or omnivory than phorusrhacids based on isotopic evidence (Angst et al., 2014). This provides evidence that multiple terrestrial birds have had similar anatomical builds but different diets. Similarly, modern large-bodied terrestrial birds exhibit a wide array of dietary preferences and foraging techniques and are comparable anatomically speaking. Ostriches and emus are omnivores but their diets are influenced by seasonal weather patterns. Cassowaries are primarily herbivores that obtain most of their nutritional intake from fruits and supplement their diets with insects. Since the Phorusrhacidae are extinct and have few modern analogs, the carnivorous diet/foraging strategy of *Llallawavis* is almost impossible to observe by comparing the RSCs since their diets may have depended on the environment at any given time. Alternatively, the placement of the *Llallawavis* RSC could be an artifact of earlier, more omnivorous ancestor. However, this interpretation is less parsimonious than the former because it assumes the existence of an omnivorous or herbivorous phorusrhacid and all of the members of Phorusrhacidae are assumed to be carnivorous. Since most lineages change from carnivory to herbivory or omnivory, it can be assumed that *Llallawavis* is a carnivore that is trending more towards omnivory. The diet change assumption is made for *Falcarius*, a maniraptoran, due to its hypercarnivorous ancestry and postcranial evidence for a trophic shift between the Early Cretaceous and Late Cretaceous. Phorusrhacids are all assumed to be carnivores and no known diet shifts have occurred before *Llallawavis*. Since evolutionary trends do not support a change from omnivory/herbivory to carnivory, *Llallawavis* is interpreted as being a carnivore with omnivorous tendencies based on the sensitivity of its rostral canal.

In this study, the RSCs of ostriches, emus, *Llallawavis*, and *Struthiomimus* generally grouped together in both axes. The cassowary plotted differently along the y-axis due to its herbivorous nature but plotted near the other ratites, phorusrhacid, and ornithomimid in the x-axis. This is interpreted as a generally omnivorous diet for ostriches, emus, *Llallawavis*, and *Struthiomimus* that allowed for dietary modification based on what was available at the time. Cassowaries, while predominantly herbivorous, will also ingest invertebrates

Tyrannosaurs and Allosaurus

Tyrannosaurids and the *Allosaurus* used in the dataset were interpreted as carnivores for this study. In the PCA, *Alioramus*, *Gorgosaurus*, and *Allosaurus* grouped together as predaceous carnivores while the two *Tyrannosaurus* specimens and the "Cleveland specimen", a specimen that is often referred to as a juvenile *Tyrannosaurus* (Carr, 1999), grouped together separately. Generally speaking, this is being interpreted as two separate groups of carnivores: predators (carnivores that actively pursued prey) and opportunists (carnivores that were capable of bringing down live prey but may have scavenged carcasses as well). This observation was independent of the epoch in which the specimens lived as well as how they were related to one another.

The predaceous tyrannosaurids—*Alioramus* and *Gorgosaurus*—and *Allosaurus* shared a similar morphospace that exclusively included them. All of the predaceous carnivores are being considered predaceous based on key differences in anatomy between themselves and the opportunists: body size, tooth morphology, and brain development. *Alioramus*, *Gorgosaurus*, and *Allosaurus* are all more lightly built than the *Tyrannosaurus* specimens. The smallest predator, *Alioramus*, reached a size of approximately 6 meters and was a more gracile tyrannosaurid from Mongolia (Brusatte et al., 2012). The largest of the predators, *Gorgosaurus*, could reach 9 meters (Russell, 1970); however, the size of the largest *Gorgosaurus* is still smaller than the most complete *Tyrannosaurus*, 12.3 meters (Hutchinson et al., 2011). *Allosaurus*, a non-tyrannosaurid predator, averaged approximately 9 meters and could potentially grow to be larger (Smith, 1999). This smaller size would have made all of the predators better suited for speed than *Tyrannosaurus* and would have allowed for a more active predatory lifestyle. Smaller specimens of *Gorgosaurus* have larger tibia-to-fibula ratios suggesting that they were capable of running regardless of the fact that they were closely related to *Tyrannosaurus* (Hutchinson et al., 2011).

The dentition of the predators differs from the opportunists in size and denticle size. Predaceous tyrannosaurids have ziphodont teeth that are characterized by a flattened blade-like appearance along the crown with small denticles that act as serrations along the mesial and distal edges of each tooth (Brink et al., 2015). Serrations allow for the cutting and holding of muscle tissues during the bite (Abler, 1992). *Alioramus*, *Gorgosaurus*, and *Allosaurus* have teeth that are characterized as ziphodont. *Tyrannosaurus* and the Cleveland specimen have reduced serrations along their mesial and distal margins but have broader massive teeth that are more useful for crushing than slicing when used in tandem with a large bite force (Farlow and Holtz, 2002). This difference in tooth morphology is indicative of a difference in prey acquisition—ziphodont teeth for active predators and bone-crushing teeth for less active carnivores.

The endocasts of the carnivores indicate subtle differences between the specimens. The *Tyrannosaurus* specimens (and the other tyrannosaurids) are more similar to modern birds in that their cerebral lobes are expanded (Brochu, 2000). The brain of *Allosaurus* favors the brains of archosaurs more than birds, which is not unusual due to its more distant relationship to Aves (Rogers, 1999). Even with the differences in brain morphologies, some lobes of the brain can be compared between specimens. *Alioramus* and *Gorgosaurus* have reduced olfactory bulbs when compared to

Tyrannosaurus (Witmer and Ridgely, 2009; Bever et al., 2013a). *Allosaurus* has a well-developed olfactory bulb that implies an acute sense of smell—much like tyrannosaurs (Rogers, 1999). All of the tyrannosaurs and *Allosaurus* have well-developed senses of smell that can be used during predation; however, the large olfactory bulbs of *Tyrannosaurus* and the Cleveland specimen have been associated with specialized hunting techniques or scavenging (Zelenitsky et al., 2009). The evolutionary trend of tyrannosaurs towards binocular vision, however, indicates that the use of vision was important as the lineage progressed through the Late Cretaceous, a trait that would not be useful for a scavenger (Stevens, 2006). Based on evidence from the brain, *Tyrannosaurus* and the Cleveland specimen were equipped to detect movement and smell prey as well, if not better, than the rest of the tyrannosaurs and *Allosaurus*. The difference in endocranial anatomy between carnivorous specimens is the shape of the rostral canal, which indicates the sensitivity of head movements. Since the *Tyrannosaurus* specimens grouped with the omnivores, their spatial sensitivity is interpreted as being lesser than those of the other tyrannosaurids. Based on the olfactory, visual, and spatial abilities of *Tyrannosaurus*, it is assumed that it is an opportunist instead of a more active predator. This interpretation would account for why the carnivores in the dataset grouped into two different areas despite their relationship to each other and the large temporal range that they all represent.

Data from the body size, tooth morphology, and brain anatomy indicates that the carnivores can be divided up into two sections: predaceous carnivores and opportunistic/scavenging carnivores. The *Tyrannosaurus* specimens have visual capabilities that were not expected in an organism that subsists purely on scavenging.

Excellent visual and olfactory abilities are interpreted as characteristics of an organism that opportunistically hunts live organisms but could also locate and scavenge carcasses as needed. *Alioramus*, *Gorgosaurus*, and *Allosaurus* are all well-balanced, medium-sized carnivores that could actively chase down prey items and did not utilize scavenging as a main source of nutrition.

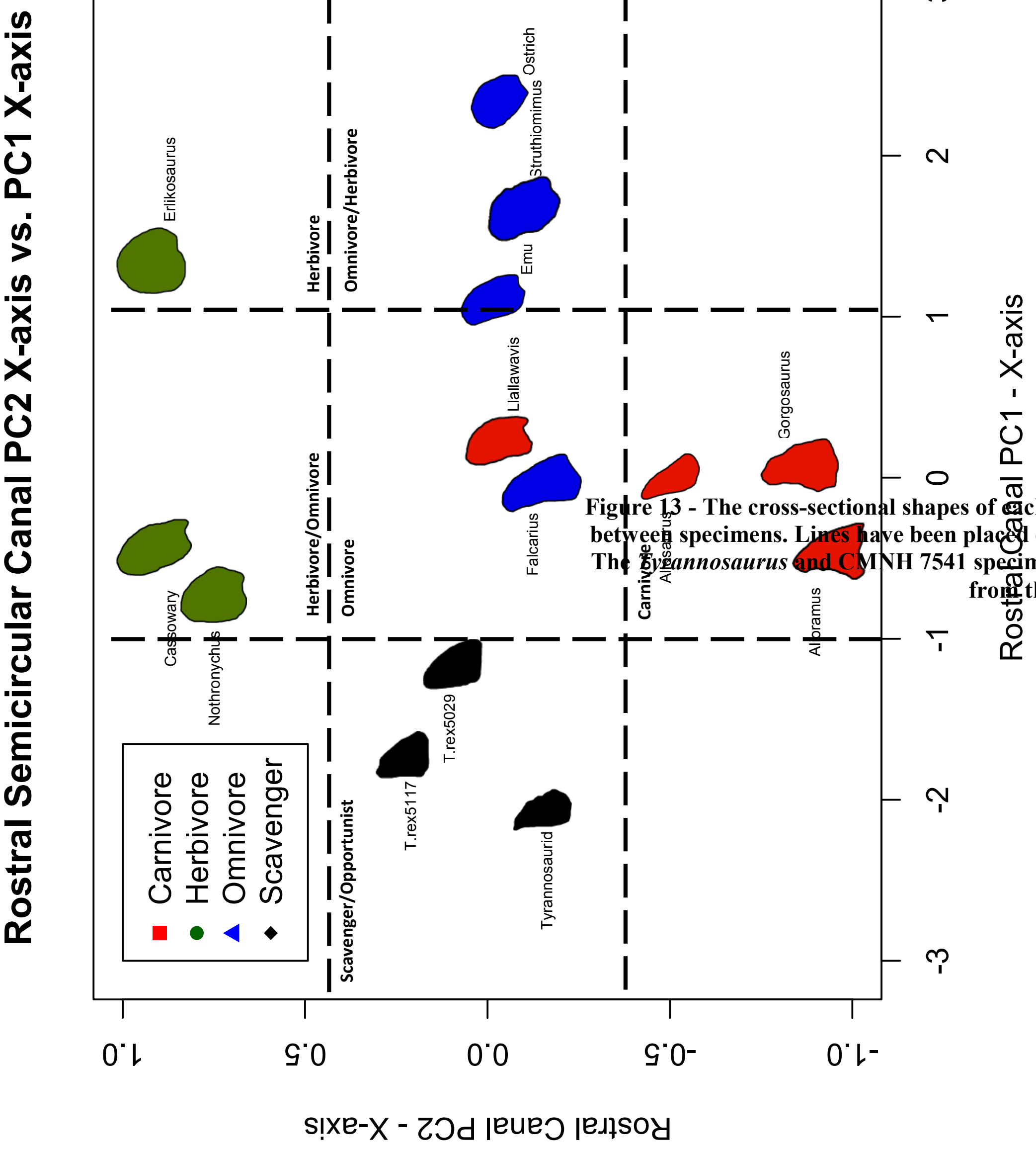

Figure 13 - The cross-sectional shapes of each canal have been overlain
between specimens. Lines have been placed over the plot to show how
The *Tyrannosaurus* and CMNH 7541 specimens have been coded as “s
from the predaceous carnivores.

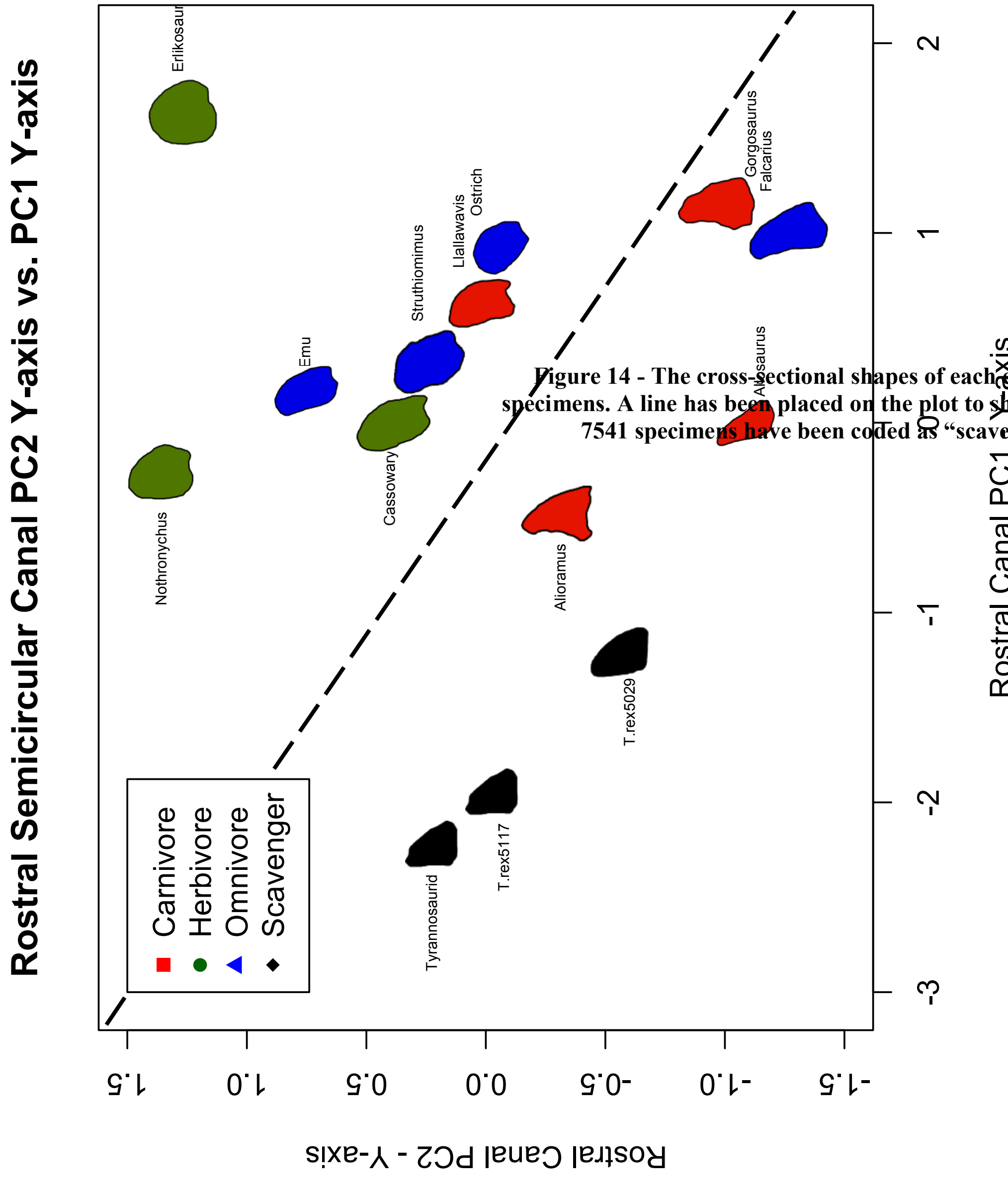

Figure 14 - The cross-sectional shapes of each canal have been overlain to
specimens. A line has been placed on the plot to show the split between group
7541 specimens have been coded as "scavengers" to show to separate

CONCLUSIONS

A PCA showed the most dynamic angularity differences along the x-axis of the rostral canals (up to 51.05% shape variation explained) with the y-axis still showing dietary preference but in much less detail (up to 18.88% shape variation explained). The caudal and lateral semicircular canals did not express patterns that could be interpeted as being shape change related to diet. Principal Component 1 was associated with the diet of the taxa used in the study while Principal Component 2 correlated with the angularity of the shapes of the semicircular canals. This means that since each dietary group was plotted along PC1 then a large percentage of variation found in the first component can be explained as being linked directly to the diet-related spatial sensitivity of the rostral canal. A one-way ANOVA was attempted but failed due to the herbivores not being normally distributed and lacking equal variances. While the ANOVA failed, the results gathered showed that a statistically significant difference was present in the cross-sectional shapes of the rostral semicircular canals. However, the statistically significant difference between diets could be caused by the low number of samples or by the disproportionate number of samples in each dietary category. Ideally, the test would be retried with a larger number of equal amounts of samples for each diet.

The patterns exhibited in PC1 and PC2 of the rostral semicircular canals are supported by the dentition and postcranial anatomy of the fossil specimens and by the observable dietary preferences of the modern specimens. Herbivores (cassowary, *Nothronychus*, and *Erlikosaurus*) grouped near the top of each biplot. Predaceous carnivores (*Allosaurus*, *Alioramus*, and *Gorgosaurus*) gropued opposite of the herbivores at the bottom of each graph. Opportunistic predators/scavengers (the two *Tyrannosaurus* individiuals and the Cleveland specimen) plotted with each other on the left of each graph—separate from closely related predaceous carnivores (*Alioramus* and *Gorgosaurus*). The omnivores always plotted in the middle of the herbivores and carnivores with some overlap. *Struthiomimus*, *Falcarius*, ostrich, and emu gropued on the right of the graphs for each axis of the RSC. These groups are expected for a graph that plotted organisms based on their dietary preference. Even though two of the specimens, *Falcarius* and *Llallawavis*, grouped differently than expected, potential explanations for their placement were provided. *Falcarius* grouped near the predaceous carnivores due to its hypercarnivorous ancestry—meaning that its endocranial anatomy did not change as fast as its postcranial anatomy and dentition. *Llallawavis* was assumed to be a predaceous carnivore, an assumption that is challenged by its grouping. Since *Llallawavis* groups within the omnivores in both axes, it is likely that it was a opportunistic carnviore with omnivorous tendencies based on the shape of its rostral canal.

FUTURE WORK

In the future, the same techniques will be applied to more diverse groups of non-avian dinosaur fauna. The inclusion of more non-avian theropods, ornithopods, sauropods, and extant avians with varying diets will help to test for any other ecomorphological clues to non-avian dinosaur behavior outside of locomotor style and spatial awareness. Additionally, applying this technique with extant aquatic and volant birds will test to see if locomotion type affects the results found within the rostral semicircular canals. By testing the internal cross-sectional canal shapes in birds with varying locomotion types, this study can move from just observing changes in the semicircular canals to how the canals change in resepect to the floccular lobes of the brain as diet and locomotion styles change between lineages.

REFERENCES

Abler, W. L. 1992. The Serrated Teeth of Tyrannosaurid Dinosaurs, and Biting Structures in Other Animals. Paleobiology 18:161–183.

Alcober, O. A., and R. N. Martinez. 2010. A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina. ZooKeys 55–81.

Angst, D., C. Lécuyer, R. Amiot, E. Buffetaut, F. Fourel, F. Martineau, S. Legendre, A. Abourachid, and A. Herrel. 2014. Isotopic and anatomical evidence of an herbivorous diet in the Early Tertiary giant bird *Gastornis*. Implications for the structure of Paleocene terrestrial ecosystems. Naturwissenschaften 101:313–322.

Barrett, P. M. 2005. The Diet of Ostrich Dinosaurs (Theropoda: Ornithomimosauria). Palaeontology 48:347–358.

Bever, G. S., S. L. Brusatte, T. D. Carr, X. Xu, A. M. Balanoff, and M. A. Norell. 2013a. The Braincase Anatomy of the Late Cretaceous Dinosaur *Alioramus* (Theropoda: Tyrannosauroidea). Bulletin of the American Museum of Natural History 376:1–72.

Bever, G. S., S. Brusatte, T. D. Carr, X. Xu, A. M. Balanoff, M. Norell, M.-A. M. P. Project, and M. S. U. Akademi. 2013b. The braincase anatomy of the late Cretaceous dinosaur *Alioramus* (Theropoda, Tyrannosauroidea). (Bulletin of the American Museum of Natural History, no. 376). .

Billet, G., D. Germain, I. Ruf, C. de Muizon, and L. Hautier. 2013. The inner ear of *Megatherium* and the evolution of the vestibular system in sloths. Journal of Anatomy 223:557–567.

Bradford, M. G., A. J. Dennis, and D. A. Westcott. 2008. Diet and Dietary Preferences of the Southern Cassowary (*Casuarius casuarius*) in North Queensland, Australia. Biotropica 40:338–343.

Brink, K. S., R. R. Reisz, A. R. H. LeBlanc, R. S. Chang, Y. C. Lee, C. C. Chiang, T. Huang, and D. C. Evans. 2015. Developmental and evolutionary novelty in the serrated teeth of theropod dinosaurs. Scientific Reports 5:12338.

Brochu, C. A. 2000. A Digitally-Rendered Endocast for *Tyrannosaurus rex*. Journal of Vertebrate Paleontology 20:1–6.

Brusatte, S. L., T. D. Carr, and M. A. Norell. 2012. The Osteology of *Alioramus*, A Gracile and Long-Snouted Tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. Bulletin of the American Museum of Natural History 1–197.

Carr, T. D. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). Journal of Vertebrate Paleontology 19:497–520.

Claessens, L. P. A. M. 2004. Dinosaur gastralia; origin, morphology, and function. Journal of Vertebrate Paleontology 24:89–106.

Cox, P. G., and N. Jeffery. 2010. Semicircular canals and agility: the influence of size and shape measures. Journal of Anatomy 216:37–47.

Curthoys, I. S., R. H. I. Blanks, and C. H. Markham. 1977. Semicircular Canal Functional Anatomy in Cat, Guinea Pig and Man. Acta Oto-Laryngologica 83:258–265.

Degrange, F. J., C. P. Tambussi, K. Moreno, L. M. Witmer, and S. Wroe. 2010. Mechanical Analysis of Feeding Behavior in the Extinct “Terror Bird” *Andalgalornis steulleti* (Gruiformes: Phorusrhacidae). PLOS ONE 5:e11856.

Degrange, F. J., C. P. Tambussi, M. L. Taglioretti, A. Dondas, and F. Scaglia. 2015. A new Mesembriornithinae (Aves, Phorusrhacidae) provides new insights into the phylogeny and sensory capabilities of terror birds. Journal of Vertebrate Paleontology 35:e912656.

Ekdale, E. G. 2015. Form and function of the mammalian inner ear. Journal of Anatomy.

Evans, D. C., R. Ridgely, and L. M. Witmer. 2009. Endocranial anatomy of lambeosaurine hadrosaurids (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. Anatomical Record (Hoboken, N.J.: 2007) 292:1315–1337.

Farlow, J. O., and T. R. Holtz. 2002. The fossil record of predation in dinosaurs. Paleontological Society Papers 8:251–266.

Fetter, M. 2007. Vestibulo-Ocular Reflex; pp. 35–51 in A. Straube and U. Büttner (eds.), Developments in Ophthalmology. vol. 40. KARGER, Basel.

Hadžiselimović, H., and L. Savković. 1964. Appearence of Semicircular Canals in Birds in Relation to Mode of LIfe. Cells Tissues Organs 57:306–315.

Hedrick, B. P., L. E. Zanno, D. G. Wolfe, and P. Dodson. 2015. The Slothful Claw: Osteology and Taphonomy of *Nothronychus mckinleyi* and *N . graffami* (Dinosauria: Theropoda) and Anatomical Considerations for Derived Therizinosaurids. PLOS ONE 10:e0129449.

Holtz, T. R., Jr., D. L. Brinkman, and C. L. Chandler. 1998. Denticle Morphometrics and a Possibly Omnivorous Feeding Habit for the Theropod Dinosaur *Troodon*. Gaia 15:159–166.

Hutchinson, J. R., K. T. Bates, J. Molnar, V. Allen, and P. J. Makovicky. 2011. A Computational Analysis of Limb and Body Dimensions in *Tyrannosaurus rex* with Implications for Locomotion, Ontogeny, and Growth. PLoS ONE 6:e26037.

Jones, G. M., and K. E. Spells. 1963. A Theoretical and Comparative Study of the Functional Dependence of the Semicircular Canal upon Its Physical Dimensions. Proceedings of the Royal Society of London B: Biological Sciences 157:403–419.

Kirkland, J. I., L. E. Zanno, S. D. Sampson, J. M. Clark, and D. D. DeBlieux. 2005. A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. Nature 435:84–87.

Knoll, F., L. M. Witmer, F. Ortega, R. C. Ridgely, and D. Schwarz-Wings. 2012. The Braincase of the Basal Sauropod Dinosaur *Spinophorosaurus* and 3D Reconstructions of the Cranial Endocast and Inner Ear. PLoS ONE 7.

Krauzlis, R. J., and S. G. Lisberger. 1996. Directional organization of eye movement and visual signals in the floccular lobe of the monkey cerebellum. Experimental Brain Research 109:289–302.

Krzanowski, W. J. 1979. Between-Groups Comparison of Principal Components. Journal of the American Statistical Association 74:703–707.

Lautenschlager, S., E. J. Rayfield, P. Altangerel, L. E. Zanno, and L. M. Witmer. 2012. The Endocranial Anatomy of Therizinosauria and Its Implications for Sensory and Cognitive Function. PLoS ONE 7:e52289.

Malinzak, M. D., R. F. Kay, and T. E. Hullar. 2012. Locomotor head movements and semicircular canal morphology in primates. Proceedings of the National Academy of Sciences 109:17914–17919.

Pfaff, C., T. Martin, and I. Ruf. 2015. Bony labyrinth morphometry indicates locomotor adaptations in the squirrel-related clade (Rodentia, Mammalia). Proceedings of the Royal Society B: Biological Sciences 282.

Rogers, S. W. 1999. *Allosaurus*, crocodiles, and birds: evolutionary clues from spiral computed tomography of an endocast. The Anatomical Record 257:162–173.

Russell, D. A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. National Museum of Natural Sciences Publications in Paleontology. 1–34.

Smith, D. K. 1999. Patterns of size-related variation within *Allosaurus*. Journal of Vertebrate Paleontology 19:402–403.

Smith, D. K., L. E. Zanno, R. K. Sanders, D. D. DeBlieux, J. I. Kirkland, and J. J. Kirkland. 2011. New Information on the Braincase of the North American

Therizinosaurian (Theropoda, Maniraptroa) *Falcarius utahensis*. Journal of Vertebrate Paleontology 31:387–404.

Spoor, F. 2003. The Semicircular Canal System and Locomotor Behavior, with Special Reference to Hominid Evolution. Cour. Forsch. Senckenberg 243:93–104.

Spoor, F., and F. Zonneveld. 1998. Comparative review of the human bony labyrinth. American Journal of Physical Anthropology 107:211–251.

Spoor, F., T. Garland, G. Krovitz, T. M. Ryan, M. T. Silcox, and A. Walker. 2007. The primate semicircular canal system and locomotion. Proceedings of the National Academy of Sciences 104:10808–10812.

Stevens, K. A. 2006. Binocular vision in theropod dinosaurs. Journal of Vertebrate Paleontology 26:321–330.

Tambussi, C. P., R. de Mendoza, F. J. Degrange, and M. B. Picasso. 2012. Flexibility along the Neck of the Neogene Terror Bird *Andalgalornis steulleti* (Aves Phorusrhacidae). PLOS ONE 7:e37701.

Therrien, F., and D. M. Henderson. 2007. My theropod is bigger than yours … or not: estimating body size from skull length in theropods. Journal of Vertebrate Paleontology 27:108–115.

Walsh, S. A., A. N. Iwaniuk, M. A. Knoll, E. Bourdon, P. M. Barrett, A. C. Milner, R. L. Nudds, R. L. Abel, and P. D. Sterpaio. 2013. Avian Cerebellar Floccular Fossa Size Is Not a Proxy for Flying Ability in Birds. PLoS ONE 8:e67176.

Witmer, L. M., and K. D. Rose. 1991. Biomechanics of the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life. Paleobiology 17:95–120.

Witmer, L. M., and R. C. Ridgely. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. Anatomical Record (Hoboken, N.J.: 2007) 292:1266–1296.

Zanno, L. E. 2010. A taxonomic and phylogenetic re-evaluation of Therizinosauria (Dinosauria: Maniraptora). Journal of Systematic Palaeontology 8:503–543.

Zanno, L. E., and P. J. Makovicky. 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. Proceedings of the National Academy of Sciences 108:232–237.

Zanno, L. E., D. D. Gillette, L. B. Albright, and A. L. Titus. 2009. A new North American therizinosaurid and the role of herbivory in "predatory" dinosaur evolution. Proceedings. Biological Sciences / The Royal Society 276:3505–3511.

Zelenitsky, D. K., F. Therrien, and Y. Kobayashi. 2009. Olfactory acuity in theropods: palaeobiological and evolutionary implications. Proceedings of the Royal Society of London B: Biological Sciences 276:667–673.