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A SURVEY OF PHYLOGENETICALLY INFORMATIVE OSTEOLOGICAL CHARACTERS IN THE DIURNAL GECKOS OF THE GENUS GONATODES (REPTILIA, SPHAERODACTYLIDAE)

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by

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ABSTRACT

A SURVEY OF PHYLOGENETICALLY INFORMATIVE OSTEOLOGICAL CHARACTERS IN THE DIURNAL GECKOS OF THE GENUS GONATODES (REPTILIA, SPHAERODACTYLIDAE)

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Geckos of genus *Gonatodes* are common to areas across Central America, South America, and the Caribbean. Recent studies have shown new *Gonatodes* species continue to be recognized. Although significant to the field of biology, new species are typically described with scarce information about their basic biology, detailed aspects of their anatomy, and systematic relationships. Without this information it is not possible to infer phylogenetic relationships or to study character evolution in the context of phylogenetic trees. Advancements in DNA sequencing have been used to identify the pattern of evolution in many species. Although this approach may seem effective, there are several

factors that contribute to its inaccuracy. A separate method, which has shown to improve pre-existing phylogenetic trees, utilizes osteological features.

The aim of this study is to provide evidence that an osteological approach is useful in the study of phylogenetics. To achieve this objective, computerized tomography (CT) scans of preserved specimens *Gonatodes ceciliae*, *Gonatodes daudini*, and *Gonatodes machelae* were obtained. With the use of Drishti software, individual scans were segmented resulting in three-dimensional images of the cranial bones of these specimens of *Gonatodes*. Specific boney elements were colored for each three-dimensional scan via MeshLab. Similar characters among *G. ceciliae*, *G. daudini* and *G. machelae* were identified and compared. The evaluation of bony characters provided evidence that an osteological approach is potentially useful in the improvement of pre-existing phylogenetic trees.

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CHAPTER 1

INTRODUCTION

The genus *Gonatodes* was established in 1843 by Leopald Joseph Franz Johann Fitzinger (Kok, 2011). Species of genus *Gonatodes*, commonly known as day geckos, have been recognized in areas across Central America, South America, and the Caribbean (Schargel *et al*., 2010). There are currently 31 species recognized, several of which are found in Venezuela (Rivero-Blanco & Schargel, 2020). The first member of genus *Gonatodes* identified was *Gonatodes ocellatus* by zoologist John Edward Gray in 1831. The most recent species identified was *Gonatodes machelae* in 2020 (Rivero-Blanco & Schargel, 2020). Most of the species documented have been described in recent years (Rivero-Blanco & Schargel, 2020).

A majority of day geckos are diurnal, sexually dichromatic, and scansorial (Rojas-Runjaic *et al.* 2010). Diurnal geckos are active during the day, which allows for better foraging and visual communication (Ellingson *et al.* 1995). Sexual dichromatism is a form of sexual dimorphism, where males and females exhibit different coloration (Ellingson *et al.* 1995). In genus *Gonatodes* males are brightly colored, while females are simply gray or brown (Ellingson *et al*. 1995). Scansorial geckos are adapted for climbing (Ellingson *et al.* 1995).

Previous literature proposes the refuge model as a source of explanation for the diversity of *Gonatodes* found among Central America, South America, and the Caribbean (Gamble *et al*., 2007). It identifies climate change as a leading cause of habitat transformation and states as a consequence species are forced to seek refuge (Gamble *et al*., 2007). This isolation eventually leads to geographic separation and interferes with gene flow (Gamble *et al*., 2007). The lack of gene flow results in genetic and phenotypic divergence, and, ultimately speciation (Damasceno *et al*. 2014). The refuge model is often considered a variant of allopatric speciation (Damasceno *et al*. 2014).

Species diversification can also be explained by sympatric and parapatric speciation. In sympatric speciation, populations of species become reproductively isolated without physical separation (Coyne & Orr, 1998). Sympatric speciation may also take place when subgroups in a population begin to use different resources (Coyne & Orr, 1998). In parapatric speciation, there is some gene flow between subpopulations (Gavrilets *et al*. 2000). In comparison to allopatric speciation, sympatric and parapatric speciation is less likely among species in the genus *Gonatodes* (Schargel *et al*. 2010).

In support of the increase in diversity of genus *Gonatodes*, recent studies have shown new species continue to be recognized (Rivero-Blanco & Schargel, 2020). Recently identified species include, *Gonatodes machelae*, *Gonatodes rayito*, *Gonatodes naufragus*, and *Gonatodes rozei* (Rivero-Blanco & Schargel, 2012; Rivas *et al*. 2013; Schargel *et al*., 2017; Rivero-Blanco & Schargel, 2020). Although crucial to understand biological diversification, new species may lack proper classification (Schargel *et al*., 2017). Further examination is required to determine their relatedness to known species. The lack of taxonomic stability can often be perceived in phylogenetic analyses, which might be the case for the genus *Gonatodes* (Schargel *et al*., 2010).

Phylogenetics offers information about the evolutionary history of species (Wiley & Lieberman 2011). Its goal is to provide a complete description of speciation and character evolution (Wiley & Lieberman 2011). Phylogenetic trees are diagrams that depict evolutionary relationships of organisms (Wiley & Lieberman 2011). A clade is a section of phylogeny that includes an ancestral lineage and all of its descendants (Wiley & Lieberman 2011). Genus *Gonatodes* belongs to the clade Gekkota, which include geckos and pygopods (Gamble *et al*. 2008). The first phylogenetic analysis of *Gonatodes* was performed by Rivero-Blanco (1979). The resulting phylogeny, however, was not based on a quantitative analysis.

Recent studies have utilized advancements in DNA sequencing to construct phylogenetic trees in the Gekkota (Bauer *et al*., 2018). Evolutionary related species share a common ancestor and thus contain similar DNA sequences (Nadler, 1995). Those that are closely related contain a small number of differences in their sequences compared to species that are distantly related (Nadler, 1995). The first molecular phylogeny of *Gonatodes* was conducted by Gamble *et al*. (2008). It, however, analyzed only 12 out of the 20 recognized species of *Gonatodes* at that time.

Although a molecular approach may seem effective in constructing phylogenetic trees, there are several disadvantages. Prior to phylogenetic analysis, corresponding genes in different lineages must be aligned to determine homology (Nadler, 1995). Nucleotide substitution or insertion-deletion events can lead to variation among genes and thus positional homology (Nadler, 1995). Molecular phylogenies rely on the comparison of orthologous gene sequences, which may be incompatible with the evolutionary history of species (Nadler, 1995). Varying rates of evolution among lineages can lead to contrasting gene sequences (Nadler, 1995). Phylogenetic trees composed from molecular data should be viewed as provisional hypotheses that may be altered when additional information becomes available (Peterson & Seberg, 1998).

Studies have also noted an osteological approach to develop phylogenetic trees (Mounce *et al*., 2016). By comparing differences in bone structures, evolutionary relationships can be identified (Mounce *et al*., 2016). A majority of osteological trees are generated from characters describing the skull (Mounce *et al*., 2016). The skull yields characters with stronger phylogenetic signals and is more widely available (Mounce *et al*., 2016).

The species used for this study are *Gonatodes ceciliae*, *Gonatodes daudini*, and *Gonatodes machelae*. *G. ceciliae* is one of the largest species of genus *Gonatodes* and endemic to northeastern Venezuela and Trinidad and Tobago islands (Schargel *et al*. 2010). *G. daudini* is endemic to Union Island in the Grenadines (Rivas *et al*. 2013). *G. machelae* is one of the smallest species of genus *Gonatodes* and is endemic to Margarita Island, Venezuela (Rivero-Blanco & Schargel, 2020). Osteological variability among the skull of the species are identified and described. The aim of this research is to provide evidence and support that osteology is a useful data source to reconstruct phylogenetics trees, specifically in genus *Gonatodes*.

CHAPTER 2

MATERIALS AND METHODS

2.1 Drishti 2.6.4

Prior to experimentation *G. ceciliae*, *G. daudini*, and *G. machelae* were collected and photographed with computerized tomography (CT). CT images obtained were of the head and neck. Data analysis began by filtering these scans though a software named Drishti, an open-source volume rendering system that delivers high quality three-dimensional images (Limaye, 2012). Some of Drishti's features include volume rendering, volume shaping, animations, and mesh generation (Limaye, 2012). Drishti ultimately provides an interface for developing animations (Limaye, 2012). It includes three standalone programs: Drishti Import, Drishti Paint, and Drishti (Limaye, 2012). Drishti Import converts volume data into 8-bits per voxel, a format that Drishti Render can read (Limaye, 2012). Drishti Paint allows users to perform slice-by-slice segmentation (Limaye, 2012).

2.1.1 Drishti Import

CT scans of *G. ceciliae*, *G. daudini*, and *G. machelae* were opened in Drishti Import by loading a standard image directory. A usable signal from the scan was selected with the histogram provided. The information generated was saved to a .pvl.nc file format for subsequent loading into Drishti Paint. Slice zero was saved as the top slice and the raw file was not saved along with a preprocessed volume. There was no subsampling in Z or XY.

The final volume grid size was saved with the default numbers provided. The voxel unit for each scan was set to mm/voxel and the voxel size was set to the numbers provided by each CT scan.

2.1.2 Drishti Paint

Individual .pvl.nc files for *G. ceciliae*, *G. daudini*, and *G. machelae* were loaded into Drishti Paint for segmentation. The subsampling level was set to 2. Individual voxels were determined and defined by adjusting the transfer function. Bony elements were 'tagged' for each .pvl.nc file. The final data was exported as a .ply mesh file for subsequent use in MeshLab.

2.2 MeshLab

MeshLab is an open source mesh processing system (Cignoni *et al*. 2008). Some of MeshLab's features include tools for measuring, cleaning, healing, and inspecting images (Cignoni *et al*. 2008). MeshLab results in three-dimensional images available for color management (Cignoni *et al*. 2008).

2.2.1 Mesh Generation

Mesh files for *G. ceciliae*, *G. daudini*, and *G. machelae* were loaded into MeshLab. Image colors were altered to fit a gray scale with the vertex color thresholding filter. The Z painting tool was used to color similar characters among each species. Snapshots were taken and saved with an alpha transparent background and screen multiplier of 1. Angles include: dorsal, ventral, and right lateral.

2.3 Image Labeling

Bones of *G. ceciliae*, *G. daudini*, and *G. machelae* were labeled in Microsoft Word. Snapshots of similar angles for *G. ceciliae*, *G. daudini*, and *G. machelae* were combined and labeled in Microsoft Word. Rivero-Blanco's PhD dissertation (1979) was used as a guide to determine the names of characters identified.

CHAPTER 3

RESULTS

3.1 Overall Description of the Skull

The skull of genus *Gonatodes* is composed of five single bones (premaxilla, frontal, phenoid, basiooccipital, and supraoccipital) and seventeen paired bones (maxillae, prefrontals, jugals, palatines, pterygoids, prevomers, septomaxillae, ectopterygoids, nasals, postfrontals, parietals, squamosals, epipterygoids, quadrates, prootics, opisthotics, and exoccipitals) (Rivero-Blanco, 1976). The dorsal, ventral, and right lateral view of *G. ceciliae*, *G. daudini*, and *G. machelae* displayed all bones listed above (Figs. 3.1, 3.2, 3.3). From the osteological features listed above four characters were selected for comparison. These characters were: (1) postfrontal - posterior end wide or narrow, (2) ectopterygoid - anterior basal process wide or narrow, (3) palatine - posterolateral corner angular or rounded, and (4) squamosal – straight, curved, or very curved. The skulls of *G. ceciliae*, *G. daudini*, and *G. machelae* appeared to be longer than wide and wedge shaped. The anterior margin of each skull was formed by the premaxilla and the posterior margin was formed by the semicircular canals of the braincase. The anterior portion of each skull was narrow with a tapered snout. The snout of *G. daudini* appeared to be more pointed than the snouts of *G. ceciliae* and *G. machelae*. The posterior portion of each skull was significantly wider than the anterior portion. The jaw of each skull had a slight curvature towards the center.

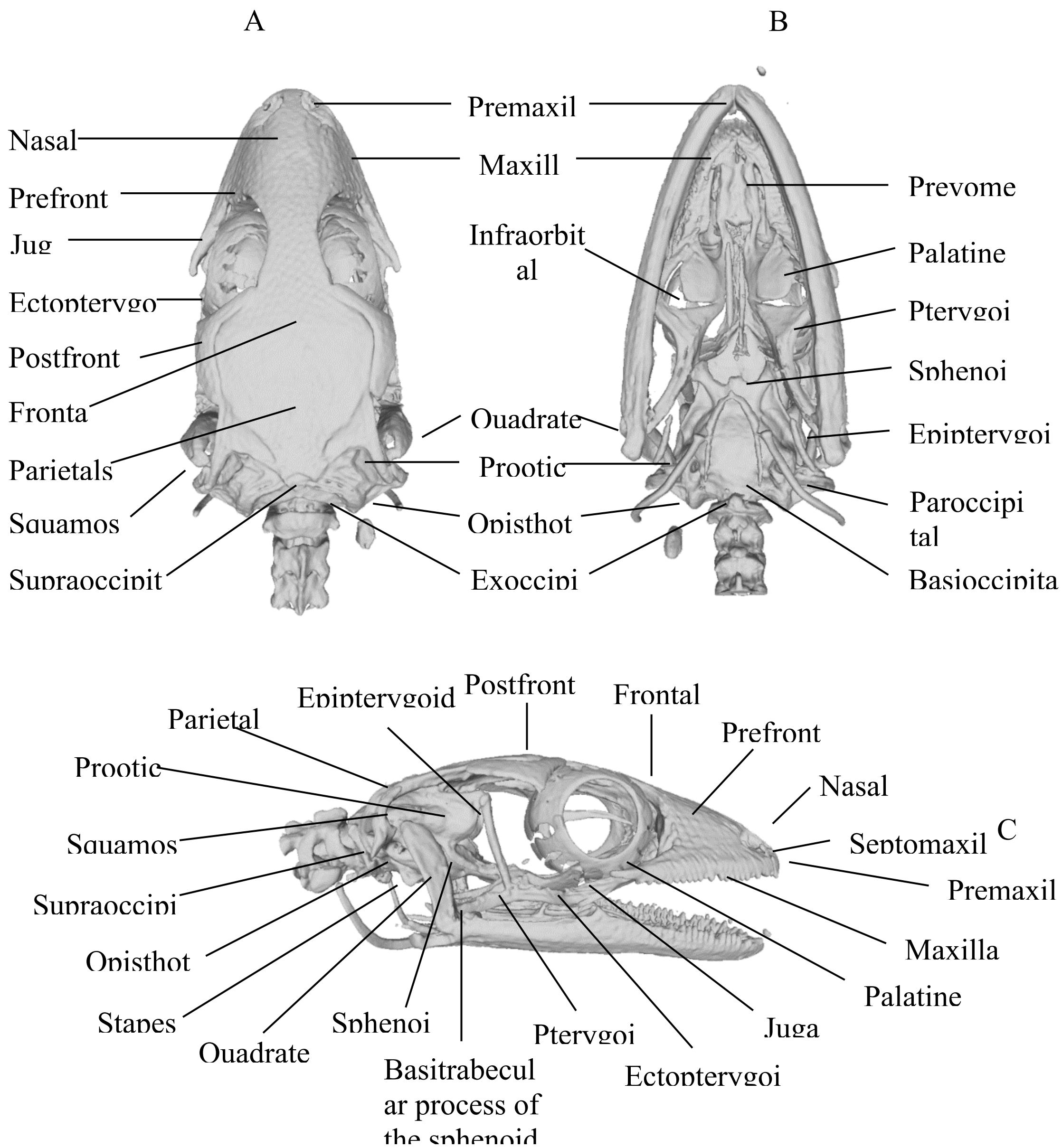


Figure 3.1: Descriptive view of the skull of *Gonatodes machelae* (A) dorsal; (B) ventral; (C) right lateral

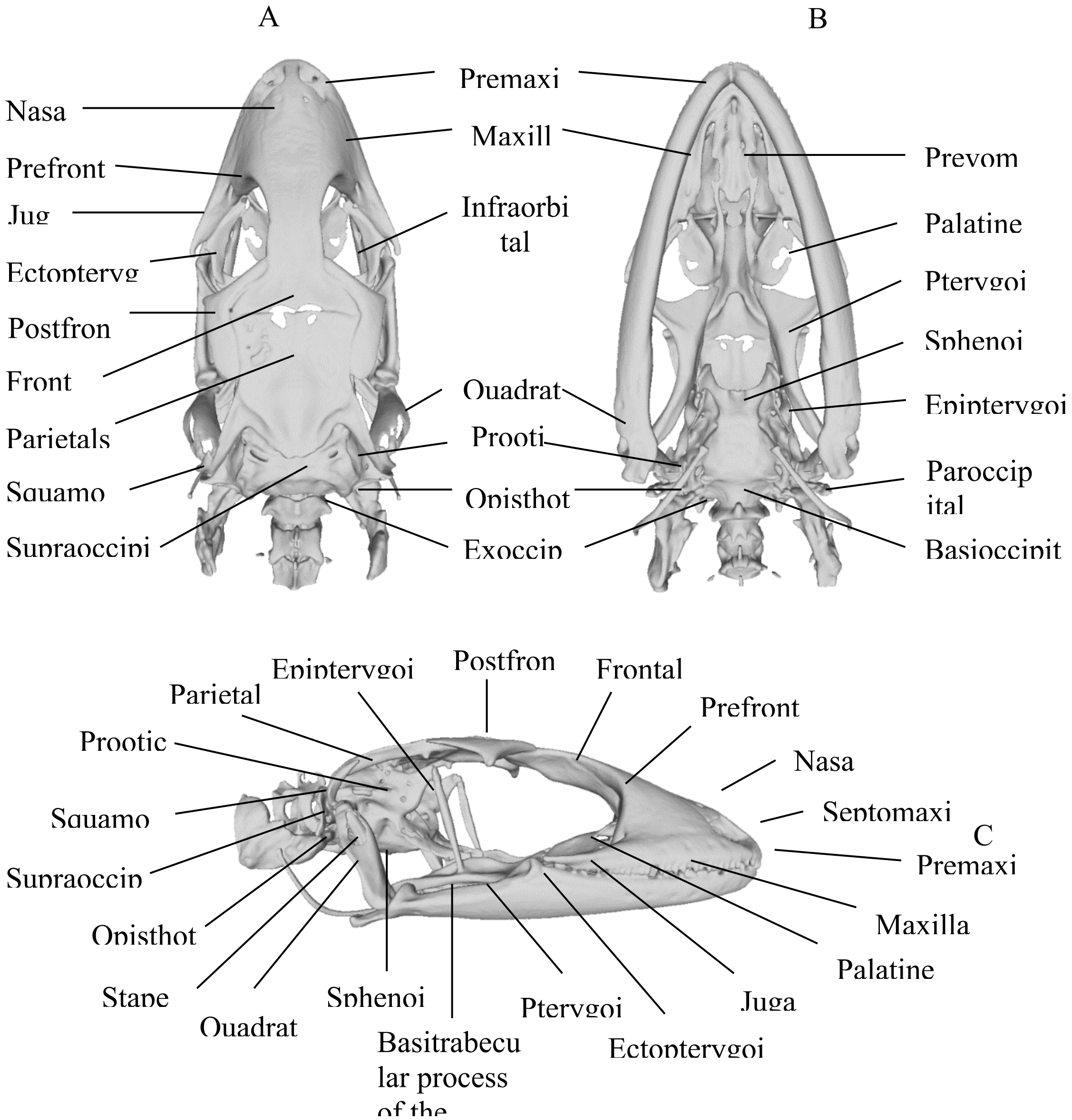


Figure 3.2: Descriptive view of the skull of *Gonatodes ceciliae* (A) dorsal; (B) ventral; (C) right lateral

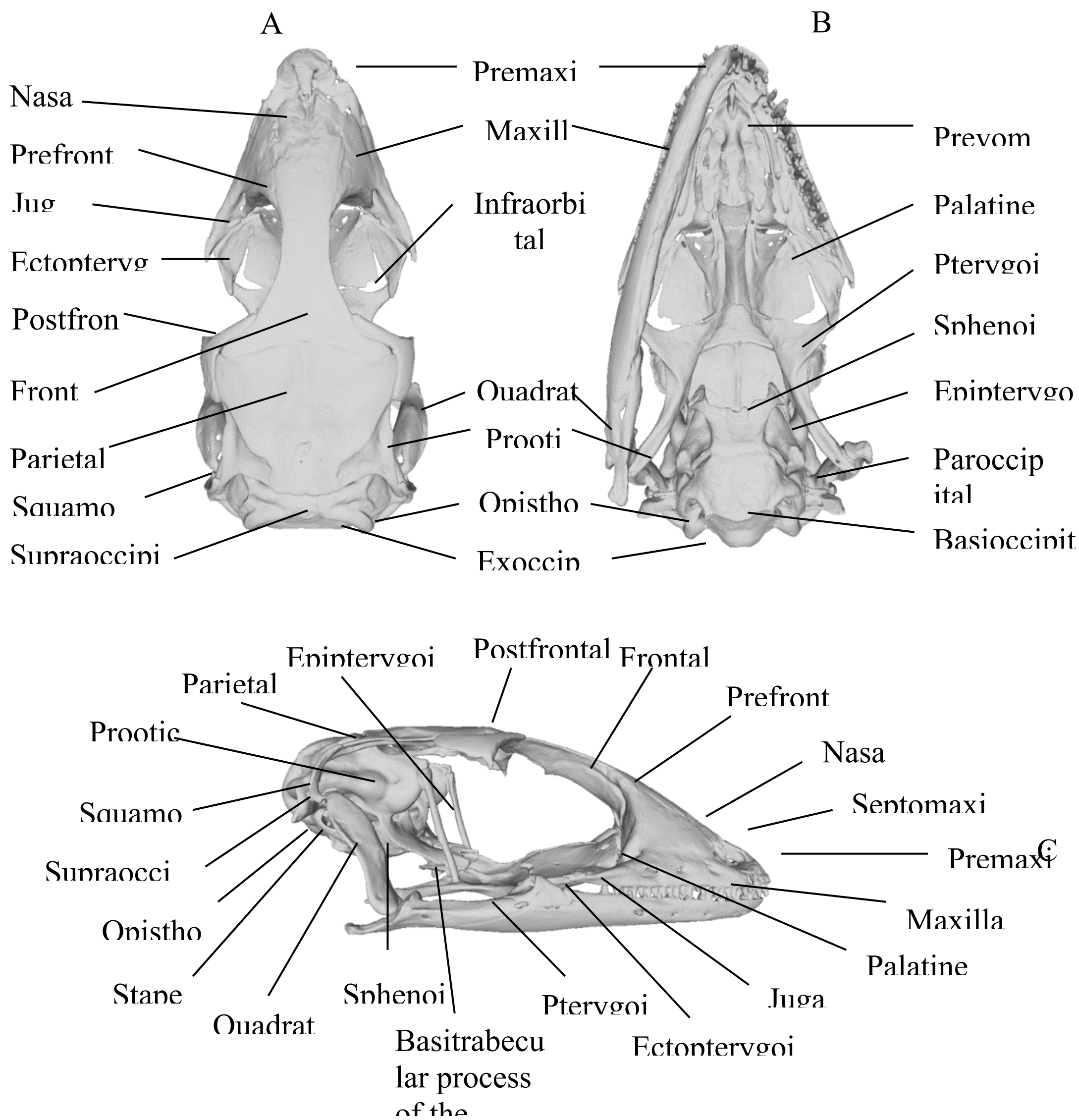


Figure 3.3: Descriptive view of the skull of *Gonatodes daudini* (A) dorsal; (B) ventral; (C) right lateral

3.2 Description of Isolated Bones

3.2.1 Postfrontal

A prominent osteological character of the dorsal skull of *G. ceciliae*, *G. daudini*, and *G. machelae* was the postfrontal: a boomerang-shaped bone that connects with the frontal and parietal bones via its inner margins (Fig. 3.4). The posterior process of this bone is flat and usually twice as wide as the club-shaped anterior process. The postfrontal bone in *G. daudini* was smaller in comparison to the postfrontal bone in *G. machelae* and *G. ceciliae*. The posterior end of the postfrontal bone was wide in *G. ceciliae* and *G. machelae* and narrow in *G. daudini.* The anterior and posterior ends were similar in size in *G. daudini*.

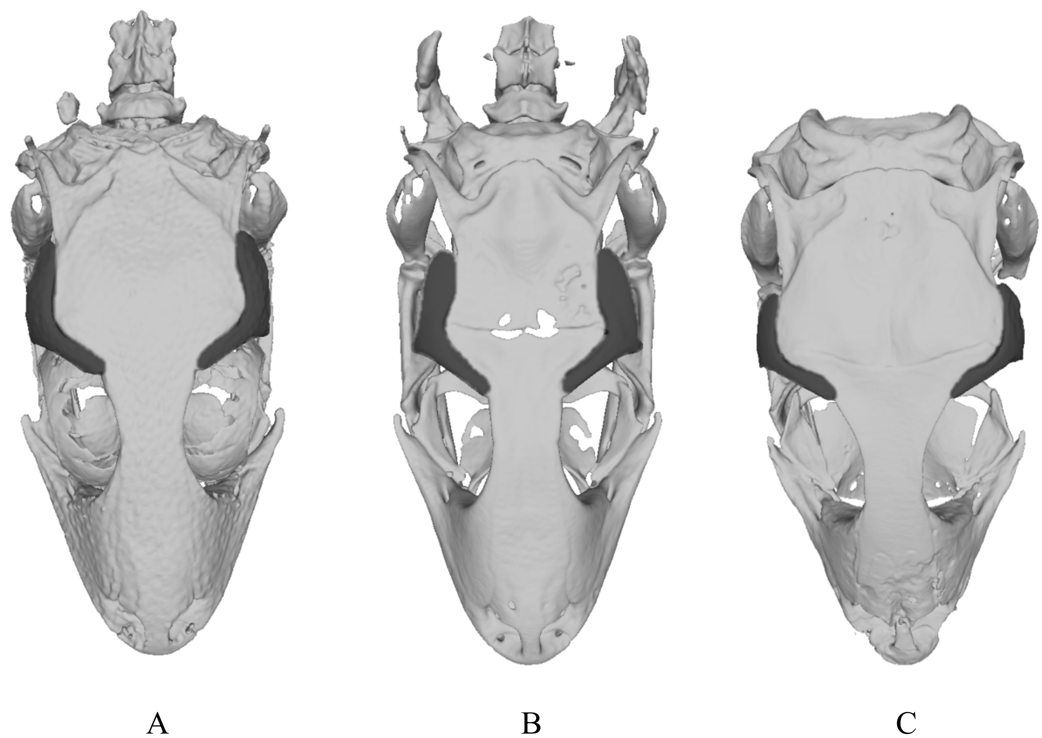
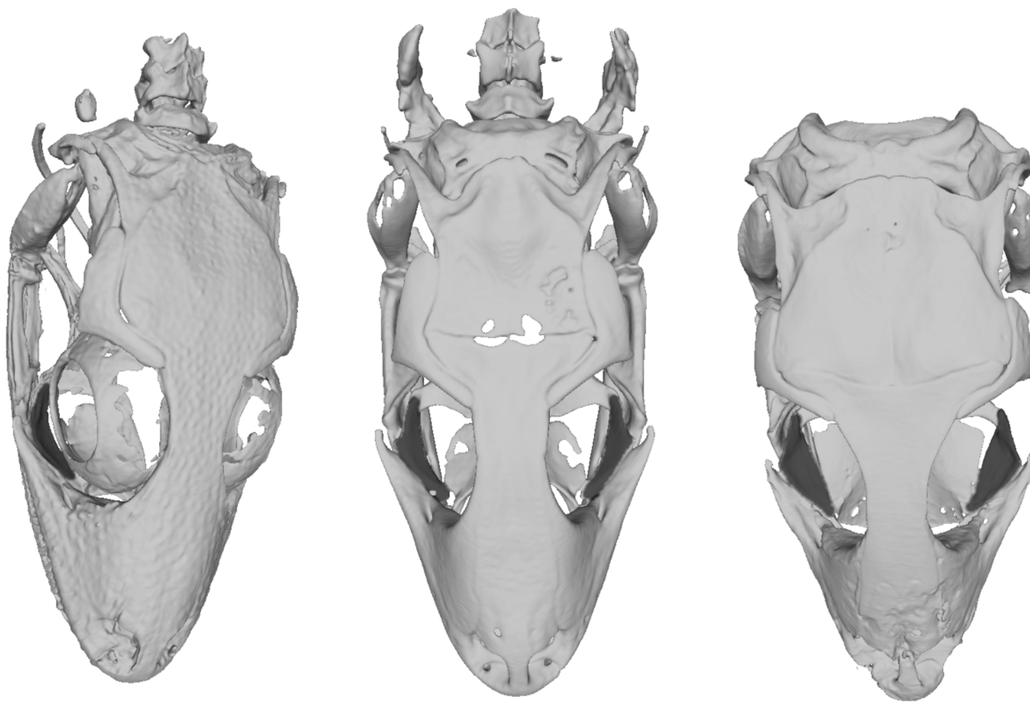


Figure 3.4: Dorsal skull of (A) *Gonatodes machelae*; (B) *Gonatodes ceciliae;* (C) *Gonatodes daudini* with postfrontal colored

3.2.2 Ectopterygoid

A second prominent osteological character of the dorsal skull of *G. ceciliae*, *G. daudini*, and *G. machelae* was the ectopterygoid: a crescent-shaped bone that connects with the pterygoid, maxilla, and palatine. It completes the lateral border of the inferior orbital foreman. When viewed from the side its basal process is directed anteriorly and articulates in the jugal-maxilla groove. The posteriorly directed dorsal and ventral processes are equal in length. In *G. machelae* and *G. ceciliae* the anterior basal process was wide. In *G. daudini* the anterior basal process was narrow.



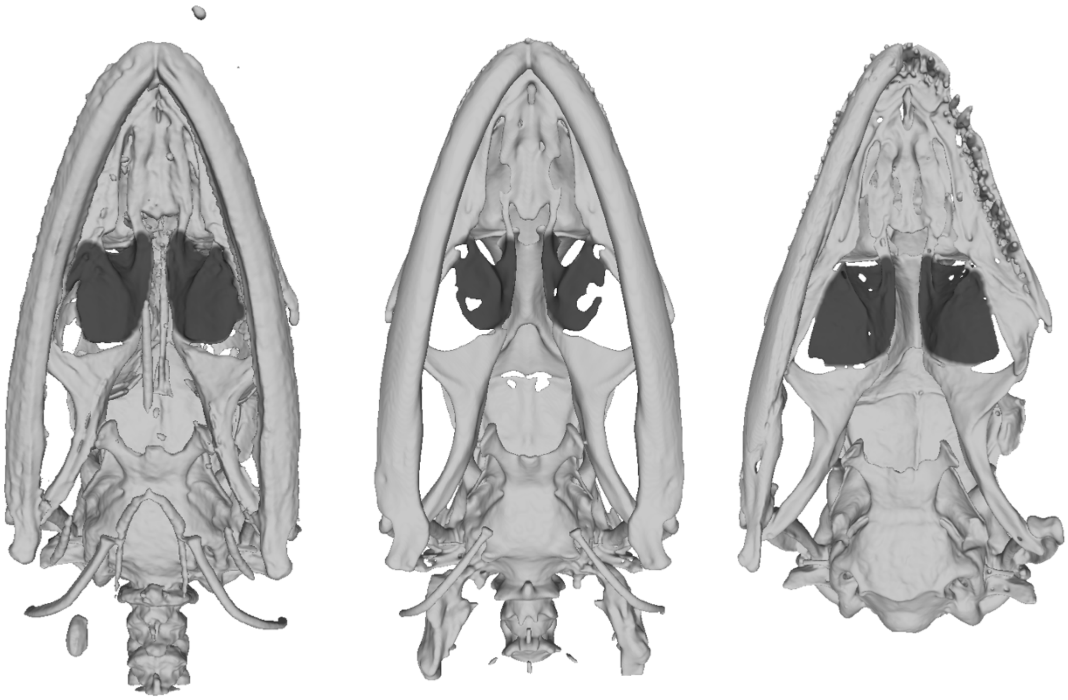
A B C

Figure 3.5: Dorsal skull of (A) *Gonatodes machelae*; (B) *Gonatodes ceciliae;* (C) *Gonatodes daudini* with ectopterygoid colored

3.2.3 Palatine

A prominent osteological character of the ventral skull of *G. ceciliae*, *G. daudini*, and *G. machelae* was the palatine: a scroll-like bone that connects with prevomer, maxilla, prefrontal, pterygoid, and ectopterygoid. In ventral view, the palatine is concave and forms to processes that project anteriorly. The medial process overlaps the provomer and the lateral process contacts the lower portion of the prefrontal. The palatine forms the anterior and medial boundaries of inferior orbital foramen laterally. Its posterolateral edge is rounded, irregularly serrated, and well separated from the pterygoid. In *G. machelae* and

G. daudini the posterolateral corner was angular. In *G. ceciliae* the posterolateral edge was rounded. The palatine of *G. daudini* was similar to the palatine of *G. machelae*.



A B C

Figure 3.6: Ventral skull of (A) *Gonatodes machelae*; (B) *Gonatodes ceciliae;* (C) *Gonatodes daudini* with palatine colored

3.2.4 Squamosal

A prominent osteological character of the right lateral skull of *G. ceciliae*, *G. daudini*, and *G. machelae* was the squamosal: a small bone that connects with the posterior process of the parietal, the anterior surface of the paroccipital, and the dorsal head of the quadrate. It curves along the parietal and is the only bony elements supporting to roof of the skull. The squamosal of *G. machelae* and *G. ceciliae* appeared to be almost straight. The squamosal of *G. daudini* was slightly curved.

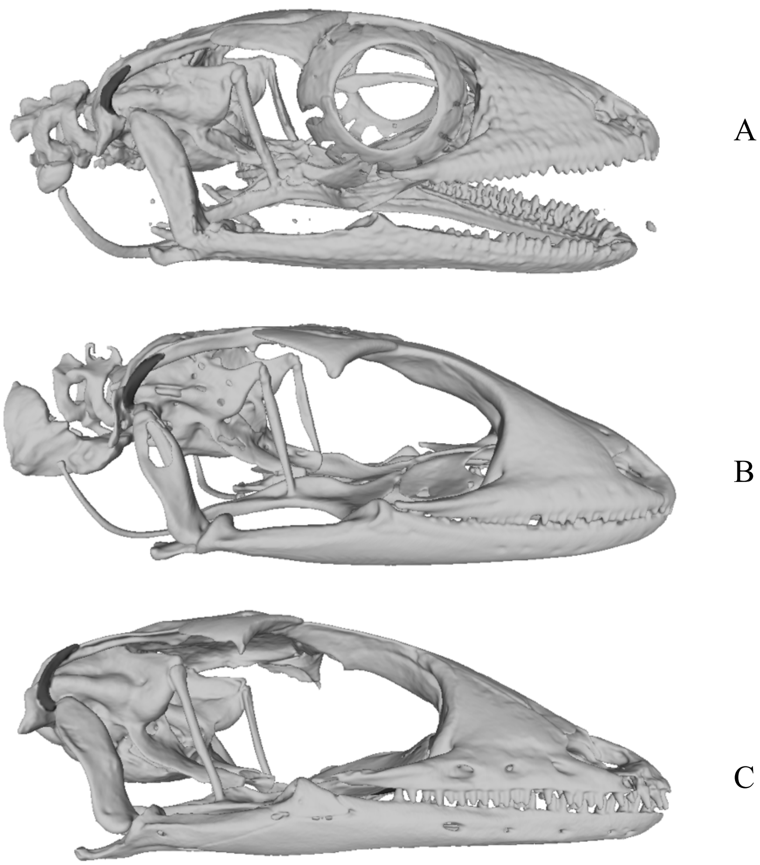


Figure 3.7: Right lateral skull of (A) *Gonatodes machelae*; (B) *Gonatodes ceciliae;* (C) *Gonatodes daudini* with squamosal colored

3.3 Character State Relationships

By using character state data, a table of similarity between *G. machelae*, *G. ceciliae*, and *G. daudini* was developed (Table 3.1). *G. machelae* and *G. ceciliae* shared three-character states: squamosal, ectopterygoid, and postfrontal. *G. machelae* and *G. daudini* shared one-character state: palatine. *G. daudini* and *G. ceciliae* did not share any character states.

Table 3.1: Character states shared between *Gonatodes machelae*, *Gonatodes ceciliae*, and *Gonatodes daudini*

	G. ceciliae	*G. daudini*
G. machelae	3	1
G. daudini	0	

CHAPTER 4

DISCUSSION

The species studied in this paper represent only about 10% of the known species and therefore do not give a complete picture of the overall relationships of genus *Gonatodes*. However, by using character state data, similarities between *G. ceciliae*, *G. daudini*, and *G. machelae* were identified. *G. machelae* and *G. ceciliae* shared more character states than *G. machelae* and *G. daudini*. *G. machelae* and *G. ceciliae* both had small postfrontal posterior ends, wide anterior basal ectopterygoid processes, and an almost straight squamosal bone. Literature suggests species that share a large number of character states are more closely related (Rivero-Blanco, 1976). This indicated *G. machelae* and *G. ceciliae* were more closely related to each other than to *G. machelae* and *G. daudini* and *G. ceciliae* and *G. daudini*. Despite *G. ceciliae* and *G. daudini* not sharing characters they are still related to one another by the simple fact they are a part of the same genus.

Despite much attention in recent years, our understanding of the phylogenetic relationships of species of *Gonatodes* remains incomplete. This is due at least in part to the fact that several species have been discovered in recent years. The data obtained in this work, however, is consistent with the pre-existing phylogenetic trees and suggests that osteology is a character system with good potential for phylogenetic analyses. The osteology suggests *G. machelae*, *G. ceciliae*, and *G. daudini* all share a common ancestor (Schargel *et al*. 2010). *G. machelae* and *G. ceciliae*, however, share a more recent common ancestor relative to *G. daudini* (Schargel *et al*. 2010). My survey of osteological features of the skull is still, however, preliminary and more species will need to be included and other bony elements examined in detail.

Skull variability of *G. ceciliae*, *G. daudini*, and *G. machelae* provided evidence that osteology is a suitable data source to construct phylogenetic trees of genus *Gonatodes* and should be used in conjunction with molecular data. Factors such as nucleotide substitution or insertion-deletion events and varying rates of evolution among lineages can pose limitations to molecular approaches to constructing phylogenetic trees (Nadler, 1995). Using additional data from osteology can complement molecular datasets and help overcome these limitations. Osteology may also be used as a way to confirm the data in pre-existing phylogenetic trees. Future research should include a larger data set and compare additional bony elements of the skull genus *Gonatodes*. It may also be beneficial to scan other portions of the osteology of the geckos in genus *Gonatodes*.

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BIOGRAPHICAL INFORMATION

Macey spent a majority of her childhood in El Paso, Texas. She moved to Arlington, Texas in 2016 to attend the University of Texas at Arlington. She quickly became interested in the field of biology. In Fall 2017, she joined an undergraduate research group organized by Professor Corey Roelke. During this time, she studied the habitat and activity of *Scincella lateralis*, a common lizard species in the Eastern half of the United states. Her work resulted in a paper discussing competing thermoregulatory models in *S. lateralis*, which was submitted for publication.

Macey will graduate in May 2020 with an Honors Bachelor of Biology and a minor in Biochemistry and Theatre Arts. After graduation, she plans on attending medical school in Texas. Macey aspires to be an oncologist.