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THE EVOLUTION OF SKULL MORPHOLOGY IN DIPSADINE
SNAKES ASSOCIATED WITH DIFFERENT
HABITAT ASSOCIATIONS

by

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Presented to the Faculty of the Honors College of
The University of Texas at Arlington in Partial Fulfillment
of the Requirements
for the Degree of

HONORS BACHELOR OF SCIENCE IN MICROBIOLOGY

THE UNIVERSITY OF TEXAS AT ARLINGTON

May 2020

ACKNOWLEDGMENTS

I would like to thank my faculty mentor, Dr. Corey E. Roelke, for overseeing this project and allowing me the opportunity to work in the Amphibian and Reptile Research Diversity Center under my faculty supervisor, Gregory Pandelis. I would like to thank Gregory as well, for teaching me about the museum and the importance of the work that is performed there as well as allowing me to use his work for secondary data.

May 08, 2020

ABSTRACT

THE EVOLUTION OF SKULL MORPHOLOGY IN DIPSADINE SNAKES ASSOCIATED WITH DIFFERENT HABITAT ASSOCIATIONS

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The University of Texas at Arlington, 2020

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Snakes represent a highly diverse group of vertebrates in both morphological and ecological ways, including a vast array of habitat and food sources. Snakes have exhibited special adaptations for their lifestyle that include skull morphological changes such as cranial shape, increased gape, and flexibility, which act to distinguish this clade from other vertebrates. Because snakes have evolved to be limbless due to their ability to burrow, the selective pressures on the snake skull are likely to be high. While some studies have been conducted researching the correlation between evolving skull shape and dietary specializations and habitat, little is known about skull size in relation to habitat associations and whether snakes are terrestrial, fossorial, arboreal, or marine. In this study, I look further into the relationship between habitat and habitat associations of Dipsadine snakes and ask

whether or not habitat associations are a significant ecological driver of morphological changes in snake skulls.

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CHAPTER 1

INTRODUCTION

1.1 Skull Morphology

One of the most important components of the snake skeleton is the complex structure of the skull. There are a number of joints that give snakes their gape ability which allows their ligaments to stretch and swallow prey much larger than their head. Looking into the characteristics of the cranium is critical for many reasons as it plays several roles including locomotion and ingestion for the limbless snake. When looking at cranial structure, we can look at its effect on head size and bite strength. The cranial structure can determine how strong a snake's bite is; for example, a larger head size will mean a stronger bite, but this might now have a detrimental effect on speed. Ecological associations or constraints can determine which trade off would better benefit the snake species depending if it is aquatic, arboreal, terrestrial, or fossorial (Herrel et al. 2001). Some studies suggest that locomotion can be a better predictor for head shape morphology rather than biting. For example, amphibians are effective at burrowing because of their short skulls. Although, this negatively affects their bite power, it is a tradeoff that overall works in their favor due to their environment.

1.1.1 Convergent Evolution

Physical constraints can affect morphology as evidenced by convergent evolution, in which analogous traits are found between organisms despite differing ancestors, but due to similar environmental factors. It is then fair to investigate how morphology would

differ between snakes with differing environmental factors and ecological constraints.

1.1.2 Ecological Drivers

Because snakes are so vastly different from other their lizard relatives, findings regarding snake ecomorphology are paramount and most likely unique. One unique attribute that we can further explore is a snake's ability to consume rather large prey when compared to their body size, which can be ascribed to their skull kinesis.

1.2 Dipsadinae Colubrids

The focus was narrowed to a subset of the large family of colubroid snakes called Dipsadinae. They have diversified into over 700 different types of species (Peter 2018) and are located almost everywhere in the Americas with the highest number of species in South America (Vitt and Caldwell 2014). The Dipsadinae are extremely diverse in terms of morphology and ecology. Their high population in the Western Hemisphere makes them a suitable candidate for understanding their evolutionary relationships. However, a large-scale study of the evolution of the Dipsadinae over long periods of time is still lacking, especially regarding their lifestyle. As concluded in the paper "HABITAT USE AND DIET AS DRIVERS OF MORPHOLOGICAL EVOLUTION IN DIPSADINE SNAKES", Gregory Pandelis finds that both habitat and diet play a part on skull morphology, with habitat having a substantial effect (Pandelis 2019). To further delve into this, one can look at the varying ecological factors that each habitat may provide for snake lifestyle. The habitats range from fossorial, arboreal, terrestrial, and aquatic lifestyles; all of which have their own unique environmental limitations. Foraging, burrowing and locomotion are examples of varying degrees in which differences in habitat associations may be found, as well as the type of prey that are distinctive to each habitat. All these ecological drivers

combined give us a vast amount of insight into their differing lifestyles and therefore, strongly indicates that skull morphology will also vary amongst these snakes.



Figure 1.1: Examples of Dipsadine Species. A – *Leptodeira septentrionalis*, a semi-arboreal frog specialist; B – *Dipsas catesbyi*, an arboreal snail-eating specialist; C – *Oxyrhopus melanogenys*, a terrestrial snake that typically feeds on reptiles; D – *Imantodes lentiferus*, an arboreal frog-eater; E – *Atractus elaps*, a small semi-fossorial snake that feeds on annelids; F – *Xenopholis scalaris*, a cryptic amphibian specialist, pictured here in a defensive flattening posture. (Photographs taken by Gregory Pandelis)

CHAPTER 2

LITERATURE REVIEW

2.1 Locomotion

In the article “The Role of Morphology in the Locomotor Performance of Arboreal Snakes”, Ronald Rozar compared a pair of closely related snakes, one arboreal and one terrestrial, in terms of climbing capabilities, vertical speed, and gap bridging. He compares snake performance under the principle that performance can be linked to fitness which can then be linked to morphology. Results confirmed that arboreal snakes performed better under arboreal environments than terrestrial snakes and vice versa. For example, arboreal snakes outperformed terrestrial snakes in climbing endurance, vertical speed, bridge gaps, and in traversing narrow diameter surfaces. However, terrestrial snakes were superior in crawling compatibility and outperformed arboreal snakes on horizontal surfaces (Rozar 2010).

2.1.1 Foraging

In the article, “Does aquatic foraging impact head shape evolution in snakes?”, results show that aquatic snakes will most likely have a skull shape that entails a narrow anterior part of the head and eyes that are dorsally placed. We can easily observe how the constraints of water have had an effect on skull shape. Obtaining food under water proves to be challenging for predators due to the fact that inertial forces are enacted on the snake’s body as seen when a snake suddenly moving towards its prey creating a wave that pushes its prey away (Segall et. al 2016).

Snakes do not have suctioning abilities and as a result, have developed a more optimal head shape as concluded by analyzing three-dimensional geometric morphometrics of a large sample of aquatic snake species. This optimal head shape includes a dorsoventral flattening, an enlarged posterior part of the head and a shorter and more curved jaw. The shape of the jaw allows the snake to continue to consume large prey while limiting the intake of the water. Dorsal positioning of the snake's nostrils allows them to breathe while partially submerged, and dorsal positioning of their eyes allows them to see better above the water. A tapered anterior of the snake head helps with speed and a broader posterior helps with carrying the captured prey. However, this was only the common pattern and there were many exceptions to these results that should further be investigated.

2.1.2 Other Snake Species

When looking at fossorial snakes, the article “Comparative Skull Morphology of Uropeltidae Snakes (Alethinophidia: Uropeltidae) with Special Reference to Disarticulated Elements and Variation”, mentions that fossorial snake skulls are quite small in size, which is quite helpful for their burrowing and underground foraging lifestyle. Other characteristics linked to the fossorial type are having an anteroposteriorly elongated skull, a small maxilla, anteriorly positioned and oriented jaw joint of the quadrate, a globular supraoccipital, a narrow palate, and a sub-rectangular premaxilla (Olori and Bell, 2012).

CHAPTER 3

METHODOLOGY

Due to the inability to physically collect data, secondary data was utilized to answer the research question. The major research article used in this study to determine whether lifestyle ecological factors are drivers of morphological change in Dipsadine snakes was “Habitat use and diet as drivers of morphological evolution in Disadine snakes” by Gregory Pandelis. As mentioned before, this study tested the predictors of food sources and habitat by quantitatively assessing morphological variation in Dipsadine snake skulls through the combinations of 3D CT scan data and natural historical data already known about this family of snakes.

3.1 Morphological Data

Micro-computed tomography scans were made up of 160 different Dipsadine species (Pandelis 2019). One representative specimen was selected for each species. Each specimen was made sure to be free of skeletal damage and adult specimens were selected if possible.

A Nikon XT H225ST μ CT machine was used to obtain micro-CT scans with the following parameters ranging from 10-30 μ m voxel size, 85-100 kV, 80-200 mA, 1-2 frame averaging, and 500-1600 projections (Pandelis et al. 2019). Proprietary Nikon CT pro 3D software was utilized to reconstruct tomograms from radiographic projections on the Nikon XT H225ST machines and then Avizo was used to create 3-dimensional surface models where landmarks could be placed (Pandelis et al. 2019) on the (n=73) landmark location

(Figure 3.1). Landmarks were placed on each side of the cranium for the purpose of encouraging the Genetically Modified (GM) analyses accuracy as there is proof that landmarking single halves of bilateral and symmetrical structures does this (Cardini 2016). Landmarking was done only on the right side of the cranium in disjoint trophic structures that were viewed on their own (Pandelis 2019).

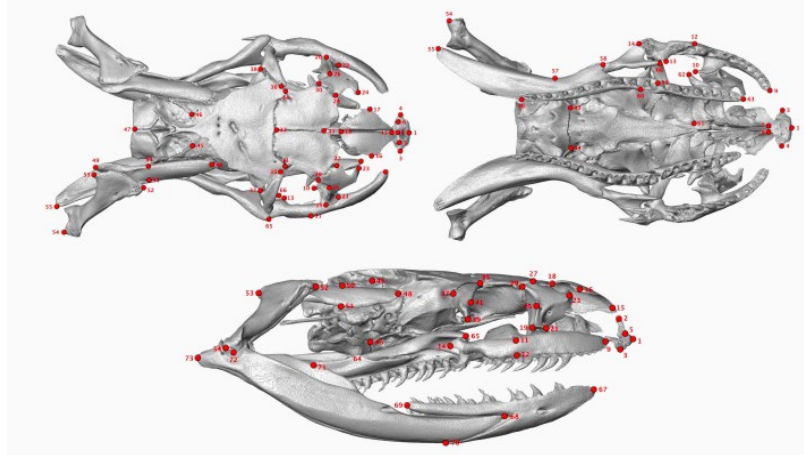


Figure. 3.1. Landmark Locations. Note that symmetrical sides of the cranium were landmarked; trophic structures that were independently analyzed were landmarked right side only.

3.1.1 Ecological Data

Natural, historical literature surveys were used to obtain habitat data and the 160 Dipsadine species were qualitatively determined as being terrestrial, semi-arboreal, arboreal, semi-aquatic, aquatic, semi-fossorial and cryptozoic (Pandelis et al. 2019).

The first method used to obtain dietary data was only used for the smaller species subset (n=68) and was categorized through quantitative assessment by the form of proportion of each prey category consumed. For the second method, a combined quantitative and qualitative approach measured the form of the main prey category through diet. This method was used for the entire dataset (n=160). Quantitative dietary data was extracted using a Grundler unpublished database obtaining predator-prey interactions for

more than 600 snake species (Pandelis 2019). The database records were obtained through both museum specimen dissections and published literature. For each single observation, a prey item ingested by a snake is represented. Out of the 160 specimens in this study, the database had quantitative dietary data for 129 of the species. Amongst these species, 68 of them had over 10 dietary records. The data for these 68 species were assembled by a proportion of prey consumed by each species in the following categories: amphibians, reptiles, birds, mammals, fish, reptile eggs, bird eggs, annelids, and mollusks. This pattern closely followed prey taxonomy and additionally, primary diet was determined categorically for the entire dataset.

3.1.1.1 Phylogenetic Framework

Methods to obtain the phylogenetic structure in the data acted to compare phylogenetic relationships, and geometric morphometric data was used as well (Pandelis et al. 2019). The new molecular phylogeny used was created through the supermatrix approach in a maximum likelihood framework and was used for all analyses (Zaher et al. 2019). The projection of specimens into morphospace was done on the entire dataset (160 species).

3.1.1.2 Analyses

After removing the effects of rotation and size in the landmark data, skull shape variation in the dataset was quantified and visualized. The following skull elements were analyzed: non-trophic elements (braincase, postorbitals, prefrontals, nasals, and premaxilla), maxilla, ectopterygoid, supratemporal, quadrate, mandible, pterygoid, and palatine as shown in Figure 3.1 (Pandelis 2019). The most mobile elements of the snake skulls were aligned and analyzed separately. Using the packages “geomorph v.3.1.3”

(Adams et al. 2019), “RRPP v0.5.0” (Collyer and Adams 2019, 2018), “ape v.5.3” (Paradis et al. 2018), and “nlme v3.1-143” (Pinheiro et al. 2019), analyses were performed in R. Using functions from “diversitree v.0.9-11”, specific visualizations were also created (FitzJohn 2012). Using Generalized Procrustes Analysis (Gower 1975), all the landmarks for each skull in the full dataset were aligned and the size effect was removed. All aligned modules were analyzed with principal components with the principal components (PC) scores 1 and 2 being plotted with a color based on primary diet and habitat. The mean shape was acquired and then re-shaped for the full non-trophic skull module dataset. For the subset of species diet data (n=68), principal component analyses were also performed, and skull modules were aligned. In morphospace, PC 1 and 2 scores were plotted on a pie chart. Generalized least squares (PGLS) with permutation was utilized to test habitat use and diet effects on skull shape. Analysis was done through geomorph using the function “procD.pgls” (Adams 2014, Adams and Collyer 2015, 2018). Using a Brownian motion model of evolution, the covariance across the dataset was calculated.

Another PGLS with permutation was performed and the generalized function “gls” was used in the nlme package and an evolutionary covariance matrix was specified using the Brownian motion under the “corBrownian” function (Pandelis et al. 2019).

Two-block partial least squares in a phylogenetic context (PPLS) was used to correlate the diet data and skull shape. The “phylo.integration” function in geomorph was used to implement PPLS (Adams and Felice 2014, Adams and Collyer 2018).

CHAPTER 4

DISCUSSION

While selecting the specimens to represent the species to be studied, the reason behind choosing adult Dipsadine snakes if possible was because there are great differences in the juvenile skull shape in the Dipsadine snake, *Hydrodynastes gigas* (Murta-Fonseca and Fernandes 2016) which could lead to an inaccurate analysis of skull morphology between species.

The reason the landmark locations (n=73) were chosen was because they represented easily identifiable and homologous locations on skull elements that were seen and unambiguous in Dipsadine snakes as shown in Figure 3.1 (Pandelis 2019). The number and position of landmarks were also chosen for the same reason as these positions allowed the most morphological variation amongst all species to be shown.

An overwhelming proportion of studies have adopted a 2-D approach (Davis et al. 2016, dos Santos 2016, Klaczko et al. 2016, Ruane 2015). This is primarily because collecting 3D data is much more difficult and much less cost-effective than the 2D approach. The reason that a 3-D GM approach to this study was incorporated was because the inability of 2-D GM to capture crucial variation in 3-dimensional objects like skulls has been shown to significantly affect the outcomes of hypothesis tests (Buser et al. 2017).

Regarding the phylogenetic framework, the species chosen to do not represent independent comparable data points because the reason behind species morphology is

related to sharing evolutionary history (Felsenstein 1985, Huey 1987, Harvey and Pagel 1991, Ridley 1983). Therefore, comparing was done using geometric morphometric data.

For the analyses, the reason behind aligning the most mobile elements of the snake skull individually was because there are various kinetic elements in the skull that can rotate and translate. For this reason, if we were to view the overall skull shape with these elements included, the shape would be confounded due to the arbitrary position it would be in. Recently, there has been growth in this area of research showing newly developed methods that remove the effects of translation and arbitrary rotation in 3-dimensional structures (Vidal-García et al. 2018). However, since the snake skull is composed of extremely loose structural components, implementing this method would only hinder the skull and overall be ineffective. By performing kinesis prior to formalin fixation on the snake skull, the arbitrary rotation element was successfully removed.

When plotting the PC scores, they were differentiated by color based on the habitat and diet which acts to visualize the variance in skull shape regarding these variables. The purpose behind warping the skull shape was to represent the shape extremities in the plotted PC axes. By doing this, the principal components axis allows the interpretation of the shape variation to be tracked. As far as the results for the PC axes, the PC1 made up 27.2% of shape variation while PC2 made up 19.08% (Fig 4.1). Broad skulls showed low PC1 values while narrow skulls showed high PC1 values. PC2 represented the extent to which expansion of the anterior position of the skull was seen and whether the landmarks were concentrated anteriorly (Pandelis et al. 2019). Narrow anterior portions of the skull had low PC2 values while a severely expanded anterior region had high PC2 values as shown in Figure 5 (Pandelis et al. 2019).

In this study, a single model was used containing two independent variables which were habitat use and primary diet and one dependent variable which was skull shape. Both of these variables were modeled together for the purpose of being able to compare the predictive strength of these two ecological variables on skull morphology. There is an evident pattern seen in regards to habitat within the non-trophic module as shown in Figure 4.1 (Pandelis et al. 2019). To the right of PC1, the semi-fossorial snakes are grouped together indicating narrower skulls with the most extreme in the figure being *Apostolepis*, *Phalotris*, and *Elapomorphus*. The exceptions were *Heterodon* and *Xenodon dorbignyi* as they are the only outliers out of the semi-fossorial species as seen in the far left of PC1. The aquatic snakes all cluster very closely together, which indicates very similar morphologies. It's also important to note that the cryptozoic species follow the semi-fossorial morphospace much more as compared to other groups.

The PGLS test acted to assess how the independent variables affected the dependent variable whereas in PPLS, directly tested the degree of correlation between these two variables (Rohlf 2000). This is because PPLS acts to assess the significance of the degree to which two sets of variables covary phylogenetically and this is done with a permutation test (also called a randomization test) which is a common tool used in statistics that acts to compile sample distributions (Sampson et al. 1989, Streissguth et al. 1993). From Table 1, using procD.pgls, the most statistically significant predictor of skull shape in all modules was seen to be habitat but it also showed some variation between the modules in terms of predictor variable strength. Similar results are seen when comparing multivariate shape analyses when looking at the PGLS data, as habitat use did predict shape immensely shown in PC1 in specifically the quadrate, maxilla, and pterygoid.

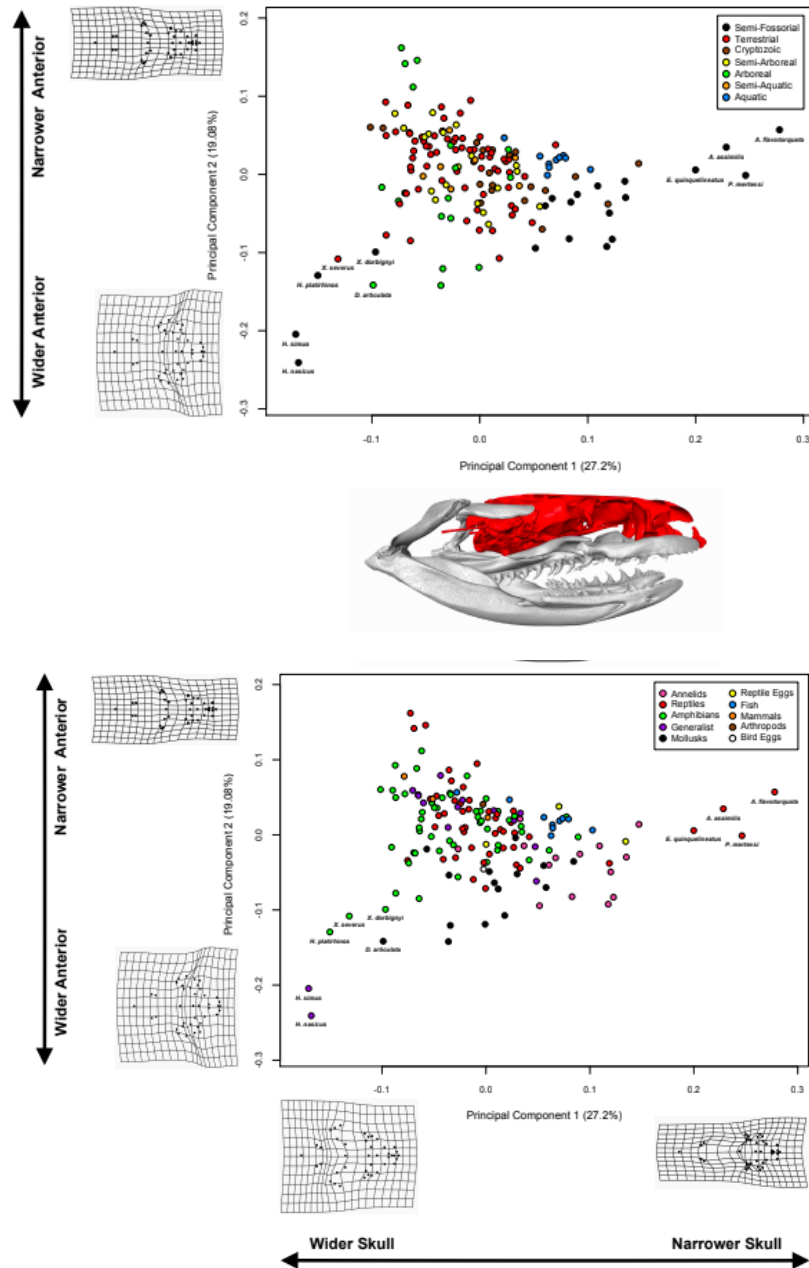


Figure 4.1. The non-trophic module shape plotted with respect to habitat use (top) and diet (bottom) in the principal components analysis.

CHAPTER 5

CONCLUSION

In the study, it was shown that habitat use was indeed a significant ecological predictor of shape in various skull modules across all data. There was also evidence indicating that ecological factors had some part of responsibility in driving the skull shape diversification in the Dipsadine mega-radiation. This is consistent since there are adaptive peaks through the lifestyle exhibited by Dipsadine snakes correlated with the speciated ecological factors of Dipsadine snakes. Factors like whether the snake is arboreal, terrestrial, fossorial or marine does play into the evolution of the skull structure and, eventually, function.

Habitat use was a greater predictor of shape than diet and as we are focusing on lifestyle constraints that Dipsadine snakes exhibit, we will only draw conclusions from this data. We can conclude that the reason being is due to stronger selective pressures that habitat and environment impose. Out of all species, the aquatic and semi-fossorial snakes were consistent in being outliers compared to the other ecological groups. This was expected as many studies have noted widespread convergence amongst these snakes (Savitsky 1983). There have been several studies that have even noted morphological convergence in skull elongation in aquatic or piscivorous snakes (Fabre et al. 2015, Hampton 2011, Herrel et al. 2008). However, it was shown that this was not due to a response caused by lifestyle constraints of the aquatic medium. The tight clustering of these aquatic snakes in the non-trophic module indicates development of an adaptive response

to a piscivorous diet or aquatic habitat use constraints. Overall, the data suggests strong morphological constraints or a narrow adaptive peak in the phylogenetically disparate aquatic snakes as seen by their tendency to cluster closely in both morphospace analyses.

In the non-trophic module analysis, the semi-fossorial group (excluding the two outlier species) were consistent in clustering away from other groups indicating a narrow skull shape. This is consistent with a previous study that noted convergence in fossorial snakes suggesting that since fossorial snakes exhibit burrowing, they are apt to have a more narrow, rigid skull (Savitzky 1983). We can conclude this is because a fossorial snake's habitat is composed of dense soil medium and therefore, lifestyle constraints and selective pressures will act to allow a more effective penetration with decreased resistance when the skull is smaller. This is also consistent with Olori and Bell's 2012 comparative study mentioning that fossorial snake skulls are quite small, which is helpful for their burrowing and underground foraging. They also noted how fossoriality and miniaturization often occur together however, the phenomena is still unknown and needs further study.

5.1 Application

Based of Pandelis' original study, we can conclude there is a strong correlation between habitat association and snake skull morphology as selective pressures are high. Further study of the relationship between habitat association/constraints and habitat is necessary to understand this correlation. Better ecological data is necessary to test between other hypotheses about the significance of adaptation and how that ecologically correlates in snakes. Basic ecological information is lacking due to the inherent cryptic nature of snakes, the well-known difficulties associated in locating them (Durso et al. 2011) and their previous infamous history of not being the most efficient study model (Mullin and Siegel

2009). However, the data remains vital in order to address the dynamic issue of adaptation patterns and the characteristics and ecological correlations on a macroevolutionary level. In the future, novel methods for utilizing snakes as model organisms efficiently and effectively should be developed further, as there are some starting to emerge (Mullin and Siegel 2009). This will assuredly allow herpetologists and ecologists to gain a more detailed comprehension of the nature of adaptive evolution and ecology of snakes.

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BIOGRAPHICAL INFORMATION

Sierra Lee is obtaining an Honors Bachelor of Science in Microbiology with a minor in Biochemistry and plans to apply to medical school in the 2020 cycle. She has a deep interest in Child Abuse Pediatrics and has shown this throughout her years of being Volunteer Coordinator of UT Arlington's Student National Medical Association – Minority Association of Premedical Students. She was recognized at the Leadership Recognition Ceremony in 2019 for her work with DFW's homeless community and other volunteer outreach programs. In her professional career, her main area of focus will be serving underserved communities like children, under-represented minorities, low socioeconomic families, the homeless population, and the elderly. Her mission is to bridge the gap of socioeconomic health disparities and obtain healthy equity for all.