MORPHOLOGICAL CONVERGENCE ACROSS LIMB-REDUCED LIZARDS FROM

THREE CONTINENTS: AUSTRALIA, ASIA AND AFRICA

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by

Supuni Dhameera Gangani Thennakoon Mudalige Silva

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DEDICATION

To my loving *Amma* and *Thaththa* for bringing me into this beautiful world and

helping me to make my dream a reality,

To my loving teachers who taught me the ABCs in academia, and

To my loving friends for being there with me on rough days.

I'm so blessed to have y'all in my life.

With much love, Supuni

ABSTRACT

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Evolution of a serpentiform body where the body is elongated and the limbs are attenuated is a common process among squamates (lizards and snakes). Morphological convergence of this body shape might be linked to habitat preference and could be a response their peculiar locomotion mode. Although evolution of body elongation has been studied extensively, its effects on the skull anatomy remains largely unknown. Here, I quantify the skull morphological convergence of limb-reduced lizards from three continents using geometric morphometrics. Twenty seven morphological landmarks associated with the skull were studied in dorsal, lateral, and ventral views using high-resolution CT scans of the heads of surface active, limb-reduced *Paradelma orientalis* (family Pygopodidae) endemic to the Australian mainland, New Guinea and the neighbouring islands; semi-fossorial *Acontias percivali* and *Acontias meleagris* (family Scincidae, subfamily Acontinae) endemic to Sub Saharan Africa; and semi-fossorial *Nessia burtonii* and *Nessia monodactyla* (family Scincidae, subfamily Scincinae) endemic to Sri Lanka. The level of similarity of the skulls of limb-reduced lizards was quantified using three-dimensional geometric morphometric analysis, including fully-limbed and limb-reduced counterparts. PC1 versus PC2 reflected that the distribution of taxa follows a gradient that describes their nature of limbs (fully limbed, limb-reduced, limbless), which is correlated with their habitat preference (surface active, semi-fossorial and fossorial). PC1 versus PC3 also distinctly segregated the limbed and limb-reduced taxa with zero overlap. The pPCA produced visible clusters that correspond to groups of

phylogenetically related taxa further proving the embedded phylogenetic structure in the morphological data set. Semi-fossorial taxa *Acontias percivali* and *Acontias meleagris* clustered together in the PCA and pPCA plots with semi-fossorial *Nessia burtonii* and *Nessia monodactyla*. *Paradelma orientalis* diverged from *Acontias* and *Nessia* species in both morphological and phylo-morphological spaces. This supports the morphological convergence of *Acontias percivali* and *Acontias meleagris* of Sub Saharan African with *Nessia burtonii* and *Nessia monodactyla* of Sri Lanka.

KEY WORDS: Lizards, Reptiles, Cranium, Osteology, Ecology

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Last but not least, I sincerely thank my ever loving aunt Pamada Silva, and my parents Sunimal Silva and Mala Silva for their unconditional love and affection given throughout this trying process.

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CHAPTER I

Introduction

"...For animals, belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance..." Charles Darwin (1859, p. 427).

Convergent evolution, the independent acquisition of similar features in different evolutionary lineages is a common phenomenon (Conway Morris, 2010; McGhee, 2011; Currie, 2012). Although convergence itself does not necessarily indicate any particular evolutionary process the repeated appearance of similar forms contrasts with the expected pattern of divergence, and thus demands an explanation (Wake et al., 2011). Morphological and ecological similarities among phylogenetically independent lineages are considered as strong evidence of adaptation in response to the environment (Schluter, 2000). Usually, shared common ancestry results in phenotypic similarities, although similar environmental conditions could also select restricted sets of functional traits resulting in convergent evolution (Melville et al., 2006). Losos (2011) defines the term "environment" as the sum of extrinsic potential selective factors encountered by a population or species, including habitat, climate, and sympatric species. Body shape and environment are often correlated (Wainwright and Reilly, 1994; Daza et al. 2009; Losos and Mahler, 2010). Different selective pressures imposed by the environment will drive diversification within a taxon (Losos et al., 1997), but similar selective pressures could produce the same solution multiple times, leading to convergence among species of distantly related lineages. Large-scale convergence between organisms occurring in similar environments suggests that evolution can exhibit a surprising degree of

predictability and ecological factors can repeatedly and predictably shape the

evolutionary diversification (Conway Morris, 2010; Mahler et al., 2013). Thus, it is

common to observe convergent phenotypes in species from different lineages that share a

similar ecotype (Chiba, 2004; Kawahara and Rubinoff, 2013; Ingram and Kai, 2014).

Convergent evolution also occur for reasons unrelated to natural selection. First,

random evolutionary changes could cause distantly related taxa to become more similar

to each other than were their ancestors (Losos, 2011). Stayton (2008) simulated trait

evolution according to Brownian motion; convergence was high when there were higher

numbers of taxa and few traits, and the clades were diversifying only under the influence

of genetic drift.

Second, constraints on variation can also lead to convergence (Schluter, 1996).

When the production of possible variants is limited, there is a great probability for the

distantly or unrelated taxa to produce the same variations, which may then become fixed

in the population as a result of genetic drift (Losos, 2011). This can be easily

demonstrated by the evolution of DNA. Because just four states exist for a given position

of a nucleotide, the probability of independently acquiring the same change by chance is

relatively high even the taxa are distantly related (Losos, 2011).

Also, the selection on similar traits shared by multiple taxa may lead to similar

correlations between the phenotype and its environment (Moen et al., 2013). One such

classic example is the convergence of the ecomorphs of *Anolis* lizards of the Greater

Antilles (Williams, 1972; Naganuma and Roughgarden, 1990; Losos, 1992; Losos et al.,

1998). On each of the islands (Cuba, Hispaniola, Jamaica, and Puerto Rico), lizard

assemblages were composed of species that differ in habitat use, where the same set of

ecomorphs species specialized to use particular structural microhabitats occurred on each island (Williams, 1983).

Traits that improve fitness in a particular environment may have evolved initially for another reason (Gould and Verba, 1982). As a result, two species may exhibit similar phenotypes in similar selective environments, even if neither evolved the feature as an adaptation to that environment. This is the distinction between adaptation and exaptation. Adaptations evolve in response to currently detectable selective pressures. Exaptations enhance fitness in a particular environment, but evolved under different conditions than currently exist (Gould and Verba, 1982).

In summary, although phenotypic similarities of distantly related taxa that occur in similar environments are considered as strong evidence of natural selection (Schluter, 2000; Conway Morris, 2003), such converging traits can occur even in the absence of natural selection (Losos, 2011) and evolutionary ecologists have long debated the extent to which species in similar environments but different geographic regions exhibit convergence (Melville et al., 2006).

Limb reduction is a process commonly recorded in tetrapod evolution (Greer, 1987; 1990; Wiens et al., 2006; Lee et al., 2013), including mammals (Lande, 1978), amphibians (Alberch and Gale, 1985) and squamates (Underwood, 1976). Transitions from a fully quadrupedal body form to an almost or completely limbless body form have repeatedly occurred in several clades of Squamata and especially in lizards including Amphisbaenia, Scincidae, Anguidae, Dibamidae, Pygopodidae, Gymnophthalmidae, and Cordylidae (Underwood, 1976; Griffith, 1990; Greer, 1990; Shapiro et al., 2003; Wiens et al., 2006; Lee et al., 2013; Abdala et al., 2015; Miralles et al., 2015). Many lineages of

lizards have undergone limb reduction independently (Greer, 1990) ranging from the loss of a single phalanx to complete limblessness (Underwood, 1976; Greer, 1991).

The gekkotan family Pygopodidae (Figure 1) includes a group of limb-reduced, body elongated lizards endemic to the Australian mainland and some of its satellite islands, New Guinea, and the neighboring islands (Stephenson, 1961; Kluge, 1974, 1976; Cogger, 1992; Smith and Henry, 1999). Pygopodid phylogeny was first investigated by Kluge (1976), who inferred relationships among 21 extant species using 86 morphological characters. Kluge's analysis gathered strong support for four clades; *Aprasia*, *Delma*, *Lialis*, and *Pygopus* and two single-species lineages; *Ophidiocephalus taeniatus* and *Pletholax gracilis*. Today 42 species of pygopods are recognized within seven genera (Uetz et al., 2018) which have reached such a degree of morphological specialization that they no longer resemble geckos (Stephenson., 1962; Daza et al., 2009).

Pygopods move by lateral undulations of body and tail. Surface-active species of the genera *Pygopus*, *Lialis* and *Delma* are able to move through thick vegetation and litter, while the semi-fossorial *Aprasia* and *Ophidiocephalus* live in loose soil, and crawl along narrow earth cracks and insect tunnels (Kluge, 1974; Greer, 1989) and are characterized by a more subterranean existence (Parker, 1956; Kluge, 1974). *Aprasia* and *Ophidiocephalus* are even surface-active sometimes (Ehmann, 1976), but they do not climb in vegetation (Greer, 1989). As mentioned by Shea (1993), *Ophidiocephalus* sometimes uses the head as a lever to pull the body through the substrate. *Lialis*, well known for its highly specialized trophic morphology that is associated with its saurophagous habits (feeding upon lizards) (Patchell and Shine, 1986a, 1986b), exhibits

limb reduction associated with "grass-swimming" or climbing in low vegetation (Greer, 1989; Pianka and Vitt, 2003; Pianka, 2011).

Although the elongated body form of pygopods is compatible with either burrowing or climbing (Camp, 1923), cranial structure can be expected to exhibit marked differences between lizards exhibiting these two lifestyles (Daza and Bauer, 2015). Typically, fossorial squamates display a suite of specializations attributable to both mechanical and sensory adaptation (Brandley et al., 2008). On the other hand, smaller surface-active pygopods exhibit some telescoping of snout, relatively large eye size, and proportionally larger otic capsules, which are by-products of miniaturization, while larger surface-active pygopods exhibit no telescoping of snout, proportionally smaller otic capsules and generally share more "gecko-like" features (Bauer and Daza, 2016).

The family Scincidae (Figure 1) includes lizards commonly referred as skinks, and has experienced limb reduction at least ten times (Wiens et al., 2006; Brandley et al., 2005). Most limb-reduced skinks are fossorial (Wiens et al., 2006), and as with other fossorial squamates, recurring borrowing adaptations like fusion of head scales and attenuate body form make phylogenetic inference intractable from a morphological perspective (Kearney and Stuart, 2004; Köhler et al., 2010; Mott and Vieites, 2009). The subfamily Acontinae is a clade of limb-reduced, burrowing skinks that inhabit sub-Saharan Africa (Figure 2; Greer, 1970). Recent molecular systematic revision of the subfamily Acontinae by Lamb et al. (2010) recognized two genera, *Acontias* and *Typhlosaurus*. These two genera have two basic morphs: *Acontias* sp. are surface-active lizards that dwell under covered objects (semi-fossorial) and have large eyes with

moveable lids while *Typhlosaurus* sp. are truly fossorial with reduced eyes (Bauer and Daza, 2016).

The genus *Nessia* (Subfamily Scincinae) is another clade of limb-reduced semi-fossorial skinks which is endemic to Sri Lanka (Figure 2). There are eight species of *Nessia* distributed in all climatic physiographic zones in Sri Lanka (Batuwita and Edirisinghe, 2017). *Nessia* is a poorly studied group as no significant contribution has been made to assess its taxonomy after some classic papers by Deraniyagala (1934, 1940, 1953, 1954, 1964) and Taylor (1950).

The head shape of lizards primarily reflects phylogeny; members of the same family cluster together in a multivariate morphological space (Openshaw and Keogh, 2014). However, morphological adaptation to a particular environment might override phylogenetic conservatism (Moen et al., 2013), enabling species who dwell in similar environments to look morphologically more similar to each other than to their ecologically different but closely related sister taxa (Mahler et al., 2013). Considering the overall morphological similarity of aforementioned species in two limb-reduced lizard taxa; Pygopodidae and Scincidae, we used novel techniques based on high-resolution computed tomography (CT) scans to document the level of morphological similarity of these taxa. Specifically, we examined the morphological similarities (and/or dissimilarities) of the skulls of four species of lizards: *Paradelma orientalis*; a surface active pygopodid from Australia, *Acontias percivali* and *Acontias meleagris*; semi-fossorial skinks of subfamily Acontinae from sub Saharan Africa, and *Nessia burtonii* and *Nessia monodactyla*; semi-fossorial skinks of subfamily Scincinae from Sri Lanka (Asia) with other pygopods and skinks.

Aims and Hypotheses

The primary aim of this study is to quantify the morphological similarities between pygopods and skinks who belong to independent evolutionary lineages (Figure 1). For that Paradelma orientalis (Pygopodidae), Acontias percivali and Acontias meleagris (Scincidae), and Nessia burtonii and Nessia monodactyla (Scincidae) were used. The specific objective of this study is to quantify the degree of similarity between members of the family Pygopodidae from Australia (Paradelma orientalis), family Scincidae from sub Saharan Africa (Acontias percivali and Acontias meleagris), and Sri Lanka (Asia) (Nessia burtonii and Nessia monodactyla) by means of three-dimensional geometric morphometric methods. I hypothesize that;

- The overall skull morphology of these three clades is convergent and has been replicated independently at least three times in three continents; Australia, Asia and Africa.
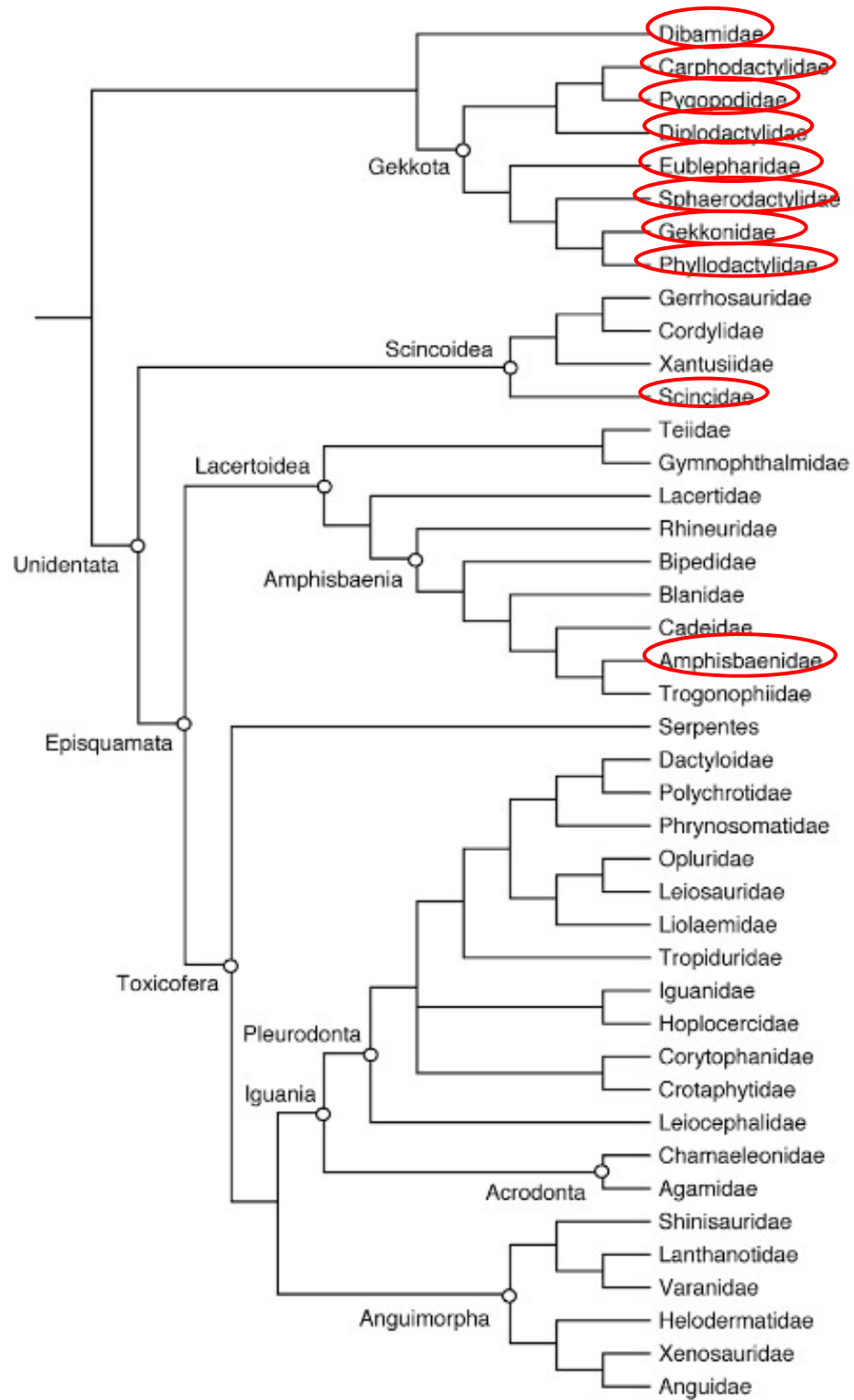
Figure 1. The phylogenetic relationship among lizard families based on Wiens et al., 2013 and Pyron et al., 2013. (Trauth et al., 2014). The families used in this study are circled in red.
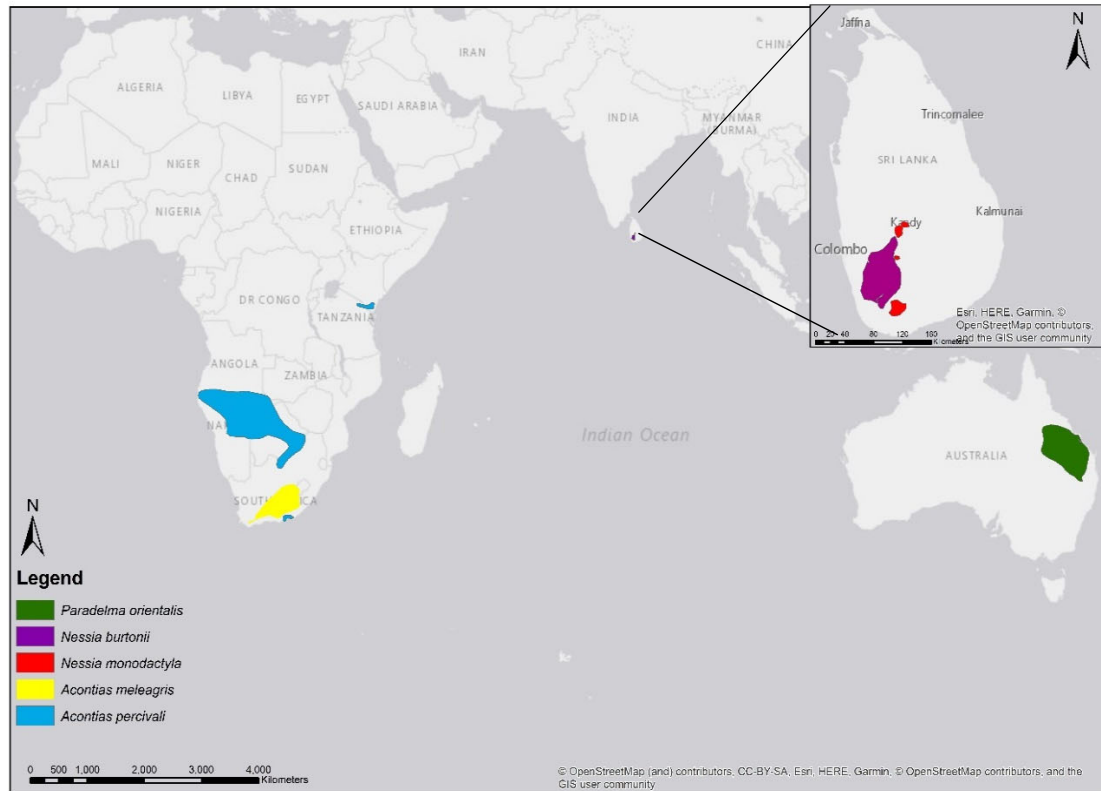
Figure 2. The distribution map of *Paradelma orientalis*, *Nessia burtonii*, *Nessia monodactyla*, *Acontias meleagris*, and *Acontias percivali*. Data were acquired from IUCN (2018) for *Paradelma orientalis* and *Acontias* sp. while *Nessia* sp. data were acquired from The Reptile Database (Uetz et al., 2018).

CHAPTER II

Materials and Methods

Specimen Collection

I used high-resolution CT scans of the skull of species of limb reduced and body attenuated geckos and skinks. Additional species of fully limbed geckos and skinks were also added (Table 1). All scans were obtained at the UTCT – University of Texas – High-Resolution X-Ray CT Facility. In total the study involved 38 lizard species (Table 1), including eleven skinks, seven pygopods, and eighteen species from other gekkotan families. Two burrowing, limb reduced species were also added, one dibamid, and one amphisbaenian.

Geometric Morphometric Analysis

Landmarks. Geometric morphometric analysis is a useful tool that allows the comparison of multiple specimens to visualize the general patterns of shape variation (Daza et al., 2009). Three dimensional geometric morphometric analysis is even powerful and accurate as it allows to describe the shape changes in different planes (Navarro and Maga, 2016). For each species, I placed twenty seven anatomical 3D landmarks associated with the cranium directly on the high-resolution CT scans (Table 2, Figure 3). In the case of skinks, osteoderms were digitally removed to reveal the underlying bones. Image processing, 3D model rendering of CT scans, and landmark placement were done in Avizo Lite v. 9.5.0 software (Thermo Fisher Scientific). Voxel size was specified for each specimen as a measure of scale in the software Avizo lite v. 9.4.0. Landmark selection considered only structures that were present in all specimens, for example structures that are absent in gekkotans (e.g. supratemporal bar, and supratemporal bones

[only present in eublepharids]) were not used. Landmarks were placed (Table 2) in Avizo Lite v. 9.4.0 using the annotation option, and exported the landmark coordinates into MorphoJ v1.06 software (Klingenberg, 2011) to perform Geometric morphometric analyses in order to analyze the morphological variation and identify convergent characteristics among limb-reduced lineages. To perform a Procrustes fit, landmark coordinates were aligned by the principal axes and projected onto tangent space in MorphoJ v1.06. This procedure results in a new set of 3D coordinates (Procrustes coordinates), preserving only shape information (Weinberg et al., 2014), while centroid size as the size measure used to scale landmark configuration. Then I generated a covariance matrix and conducted a Principal Component Analysis (PCA) in MorphoJ v1.06 to visualize the evolutionary patterns of cranial shape disparity of the skulls (Figure 4 and 5). Wireframe diagrams (Figure 6) of the skull shapes were created in MorphoJ v1.06 to visualize the morphological differences of those who occupied the most extreme positive and negative PC values in each axis (PC1, PC2, and PC3) in Figure 4 and 5.

      Phylogenetic approach. The orientation of the phylogenetic principal component analyses (pPC) axes is based on the non-phylogenetic component of shape variation, but the positioning of the scores in the space retains the phylogenetic covariance (Polly et al., 2013). This aids in visualizing a hybrid of non-phylogenetic (morphological) and phylogenetic data. I used a pruned version of Zheng and Wiens (2016) phylogenetic tree, which is considered as one of the most extensive molecular analysis of squamate phylogeny. The tree was pruned using Mesquite v3.51 (Maddison and Maddison, 2018). Since *Nessia monodactyla* and *Nessia burtonii* are very poorly studied, published phylogenetic data is not available for these two species. According to the ongoing

molecular phylogenetic study of the Sri Lankan skinks, *Nessia* is found to be a sister

clade to the *Janetaescincus* and *Pamelaescincus* of Seychelles (Kanishka Ukuwela,

personal communication). Therefore, I placed *Nessia monodactyla* and *Nessia burtonii*

with *Janetaescincus* sp. and the resulting composite phylogeny (Figure 7) was used for

further analysis. To visualize the phylogenetic history of morphology, the phylogeny was

projected into the shape tangent space and a phylogenetically informed principal

components analysis (phylogenetic PCA, or pPCA) was carried out to provide a

correction for the distribution in shape space of the taxa that may be affected by

phylogenetic signal (Figure 8 and 9). The pPCA was performed using the R package

phytools v. 0.6-00 (function phyl.pca) (Revell, 2009; 2012).

       Size correction. The relationship between shape and size could be either linear or

near-linear (Klingenberg and Marugán-Lobón, 2013). The variation in shape that is

associated with variation in size (known as allometry) can affect the integration of

morphological traits (Mosimann, 1970). In geometric morphometric analysis, allometry is

widely characterized by multivariate regression of shape on size (usually centroid size or

log-transformed centroid size) (Klingenberg et al. 2001; Wellens et al. 2013). Because

the lizard skulls included in this study cover a substantial range of sizes, allometry should

also be considered before making conclusions on their morphological convergence. Here,

the inter-taxon allometric shape variability was explored in MorphoJ v1.06 by

multivariate regression with log-transformed centroid size of all 38 lizard species as the

independent variable and the PC1 (which accounted for 41.3% of the total shape

variation) as the dependent variable (Zelditch et al., 2004).
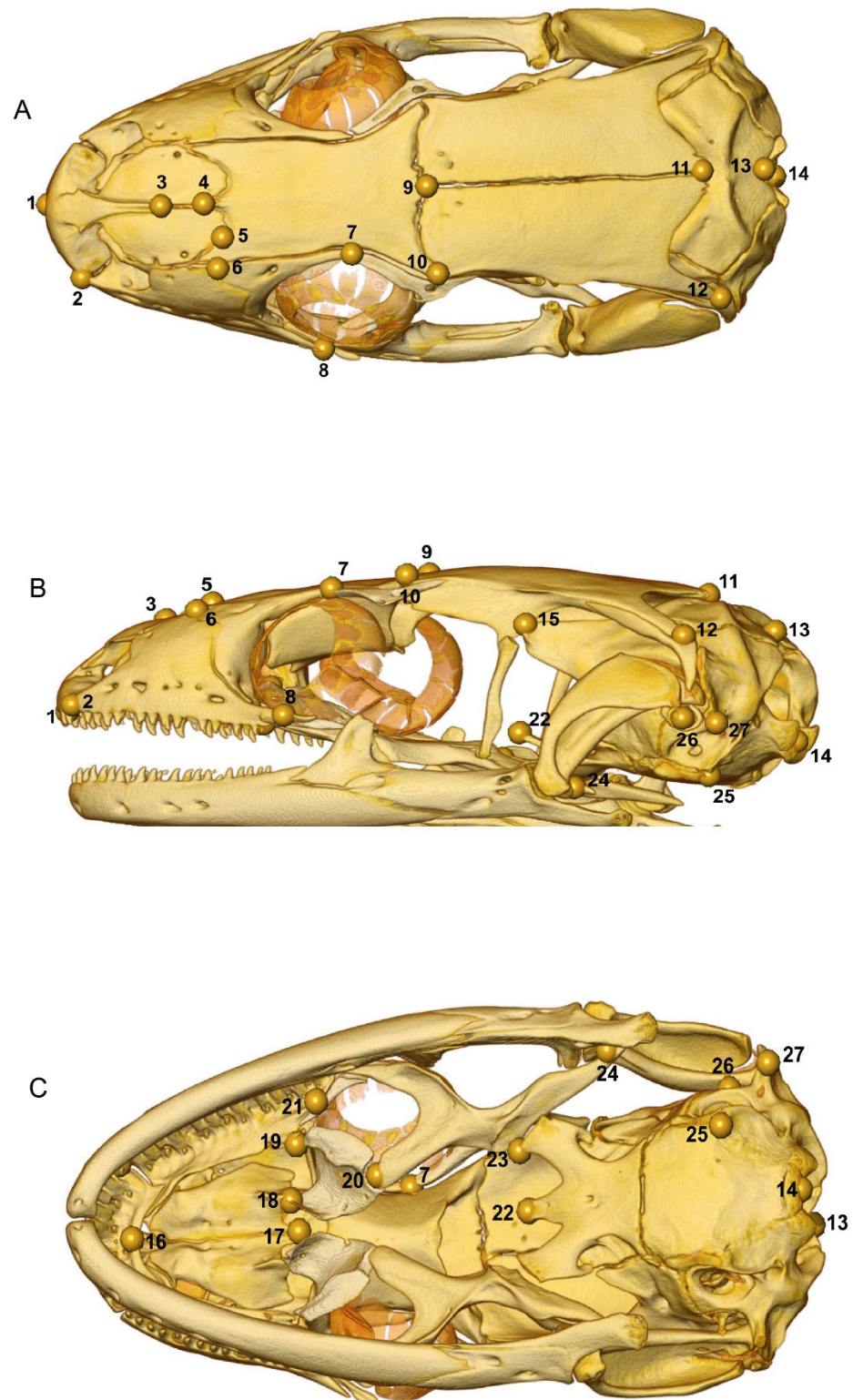
Figure 3. Positioning of the landmarks from the dorsal (A), lateral (B), and ventral (C) views of skull. The landmarks are the yellow beads embedded into skulls.

Table 1

List of species used in this study

Family	Species	Catalog Number
Scincidae	*Acontias meleagris*	YPM HERR.000851
Scincidae	*Acontias percivali*	Not available
Scincidae	*Ablepharus kitaibelii*	YPM HERR.005804
Scincidae	*Brachymeles gracilis*	FMNH 52642
Scincidae	*Chalcides ocellatus*	Not available
Scincidae	*Egernia striolata*	Not available
Scincidae	*Eugongylus rufescens*	FMNH 142306
Scincidae	*Plestiodon fasciatus*	YPM 12865
Scincidae	*Feylinia polylepis*	FMNH 120968
Scincidae	*Nessia burtonii*	CM 89394
Scincidae	*Nessia monodaclyla*	CM 89434
Pygopodidae	*Aprasia rapens*	CAS 104382
Pygopodidae	*Delma borea*	USNM 128679
Pygopodidae	*Lialis burtonis*	FMNH 166958
Pygopodidae	*Ophidiocephalus taeniatus*	Not available

(continued)

Family	Species	Catalog Number
Pygopodidae	*Paradelma orientalis*	CAS 77652
Pygopodidae	*Pletholax gracilis*	MCZ R-187676
Pygopodidae	*Pygopus lepidopodus*	CAS 135450
Gekkonidae	*Alsophylax pipiens*	CAS 143679
Gekkonidae	*Bunopus crassicauda*	CAS 140598
Gekkonidae	*Gehyra mutilata*	CAS 251893
Carphodactylidae	*Underwoodisauraus milii*	CAS 74744
Carphodactylidae	*Carphodactylus laevis*	MCZ R-35114
Carphodactylidae	*Phyllurus salebrosus*	CAS 74742
Diplodactylidae	*Diplodactylus pulcher*	CAS 75182
Diplodactylidae	*Toropuku stephensi*	CAS 47986
Diplodactylidae	*Rhynchoedura ornata*	UMMZ 124484
Phyllodactylidae	*Ptyodactylus hasselquistii*	CAS 228536
Phyllodactylidae	*Garthia gaudichaudii*	UMMZ 111574
Phyllodactylidae	*Phyllopezus lutzae*	MCZ R-46191
Sphaerodactylidae	*Saurodactylus mauritanicus*	CAS 153743

(continued)

Family	Species	Catalog Number
Sphaerodactylidae	*Euleptes europaea*	MCZ R-4463
Sphaerodactylidae	*Coleodactylus branchystoma*	UMMZ 103051
Eublepharidae	*Goniurosaurus kuroiwae*	CAS 198810
Eublepharidae	*Hemitheconyx caudicinctus*	CAS 165588
Eublepharidae	*Holodactylus africanus*	CAS 198932
Dibamidae	*Dibamus bogadeki*	YPM HERR.012715
Amphisbaenidae	*Amphisbaena caeca*	Not available

Table 2

List and definition of landmarks used in the skulls

Name	Definition
1	Anterior-most part of the premaxilla
2	Lateral edge of the premaxilla-maxilla left suture
3	Posterior most part of the ascending nasal process of the nasal
4	Posterior most part of the ascending jugal process of the premaxilla
5	Posterolateral tip of the nasal
6	Posterolateral tip of the maxilla
7	Posterolateral tip of the prefrontal
8	Edge of the posterior process of the maxilla
9	Middle point of the frontoparietal suture
10	Lateral edge of the frontoparietal suture
11	Posterior edge of the posteromedial process of the parietal
12	Postorbitofrontal, where anterior and posterior process met. In specimens with rounded lateral edge, the landmark was placed in the middle of the curvature
13	Posterior end of the supraoccipital bone

Name	Definition
14	Intercondylar space at the basioccipital bone
15	Anterior end of the crista alaris of the left prootic
16	Posterior border of premaxilla palatal shelf
17	Posteromedial edge of vomer
18	Anterior border of vomerine process of palatine
19	Anterolateral process of palatine
20	Anterior border of ectopterygoid
21	Lateromedial edge of palate-pterygoid suture
22	Parabasisphenoid rostrum
23	Anterior edge of basipterygoid process
24	Pterygoid-quadrate joint
25	Spheno-occipital tubercle
26	Stapes footplate
27	Parooccipital process

CHAPTER III

Results and Discussion

Morphological variation of skulls

Principal component analysis (PCA) performed on Procrustes coordinates of skulls from 38 adult squamate species generated 37 principal components. I explored the morphospace defined by the first three principal components, PC1 (41.3%), PC2 (11.5%) and PC3 (10.9%), which together accounted for 63.7% of the total shape variation. All other subsequent principal components explain individually less of the 7% of the variation (Table 3 and Appendix A).

The first two PCs, PC1 and PC2 (52.7% of the variation) produced a trait gradient where five main morphological groups are distinguished with almost no overlap: 1) limbed gekkotans, 2) limbed skinks, 3) limb-reduced gekkotans (i.e. pygopods), 4) limb-reduced skinks, and 5) fossorial groups. (Figure 4). The two gekkotan groups and the two skink groups did not appear positioned adjacent to each other in the morphospace. Both gekkotan and skink groups are separated with a similar gap between them, and do not converge in the same morphospace. Another way to describe this is that limbed skinks are clustered between limbed gekkotans and limb-reduced gekkotans, and limb-reduced skinks are clustered between limb-reduced gekkotans and fossorial forms (Figure 4).

Although this is an analyses based on skull morphology, PC1 and PC2 (Figure 4) reflects the distribution of taxa following a gradient that described their nature of limbs (fully limbed, limb-reduced, limbless), which is correlated with their habitat preference (surface active/cursorial, semi-fossorial and fossorial). The PC1 described a gradient of limb reduction – taxa with negative PC1 values are fully limbed and are associated with

surface active/cursorial taxa such as *Ptyodactylus hasselquistii*, *Carphodactylus laevis* and *Phyllurus* salebrosus, while positive values on PC1 are associated with limb-reduced lizards and fossorial forms such as *Amphisbaena caeca*. Limb-reduced, surface active taxa such as *Paradelma orientalis* and *Lialis burtonis*, and limb-reduced, semi-fossorial taxa such as *Nessia monodactyla*, *N. meleagris*, *Acontias percivali*, and *A. meleagris* occupied intermediate positions of the morphological space along the PC1 gradient. The PC2 described a gradient in the snout length and brain case height. The limbless skink *Feylinia polylepis* falls in the extreme lower right, noticeably isolated from all other, corresponding to the most negative value of PC2. The semi-fossorial and limbless *Dibamus bogadeki* (Family Dibamidae) lies closer to the limb-reduced, semi-fossorial *Acontias meleagris* and *Acontias percivali*, while *Nessia monodactyla* and *Nessia burtonii*, two Sri Lankan endemic, semi-fossorial, limb-reduced skinks make another cluster with another semi-fossorial, limb-reduced skink, *Brachymeles gracilis* endemic to Philippines (Figure 4).

In the plot of PC1 versus PC3 (Figure 5), there is a distinct segregation of limbed lizards (gekkotans and skinks) and limb-reduced lizards with zero overlap, where almost all the limbed lizards are in the negative PC1 values while all the limb-reduced ones are in the positive PC1 values. The semi-fossorial, limbless *Dibamus bogadeki* forms a cluster with the semi-fossorial, limb-reduced skinks –*Acontias percivali* and *A. Meleagris* (same as in PC1 vs PC2), *Nessia monodactyla and N. burtoii*, and *Brachymeles gracilis*. Interestingly, *Ophidiocephalus taeniatus*, a semi-fossorial pygopod appeared to occupy the same cluster, and the fossorial species *Amphisbaena caeca* is also located relatively closer to this cluster (Figure 5). All fully limbed, surface active lizards formed a cluster

associated with negative values on PC1 axis, while almost all the fossorial or semi-fossorial, limb-reduced taxa occupy positive values on PC1 axis. The fully limbed skinks *Egernia striolata*, *Eugongylus rufescens*, and *Eumeces fasciatus* are the exceptions for this pattern, which occupy lower negative PC1 values (Figure 5).

Wireframe diagrams represent the skull shape variations based on the landmarks selected (Figure 6); taxa corresponding to most positive values on PC1 axis (i.e. *Amphisbaena caeca*) reflect a depressed braincase, and a short and ventrally directed snout, accentuating a cylindrical shape, while the taxa corresponding to most negative values on PC1 axis (i.e. *Ptyodactylus hasselquistii*) indicate both a flattened snout and a tall braincase, including a prominent crest on the parietal bone (Figure 6). In this regard, limbed gekkotans have taller skulls than limbed skinks, and limb-reduced gekkotans have taller skulls than limb-reduced skinks. Taxa in extreme PC2 positive values (i.e. *Aprasia repens*) reflect lateral closure of the braincase, and reduction of the snout length, producing an increase in the posterior extension of premaxilla, making the general snout shape more bullet shaped (Figure 6). Extreme PC2 negative values reflect an open laterally and taller braincase, and longer snout derived from the increase in the length of the maxillary and nasal bones (Figure 6). Extreme positive PC3 values reflect changes in the skull of *Lialis* where the skull is basically wedge shaped, with a very low skull and a long robust snout derived from a large expansion of both maxillary and nasal bones (Figure 6). Taxa in negative PC3 values reflect a more rounded skull, with a shortened snout, and taller skull (braincase). Both positive and negative extreme points along the PC3 axis were pygopods, which is the group that exhibit the highest morphological differences in the analysis.

Phylogenetic history of skull morphology

In the present study, the projection of the phylogenetic tree (Figure 7) into the morphospace generated 37 phylogenetic principal components (Appendix B). I explored the phylogenetic-morphospace defined by the first three phylogenetic principal components, pPC1, pPC2 and pPC3, which together account for 50.5% of the total phylogenetic-shape variation. The pPCA resulted visible clusters that correspond to groups of phylogenetically related taxa (Figures 8 and 9) further proving the embedded phylogenetic structure in the morphological data set. As example, in Figure 8 of pPC1 versus pPC2, *Carphodactylus laevis*, *Underwoodisaurus milii*, *and Phyllurus salebrosus* (Family Carphodactylidae) are occupying the most positive pPC2 values together with other gekkotans, still isolated on the same branch (Figure 8). Also, *Diplodactylus pulcher*, *Toropuku stephensi*, and *Rhynchoedura ornata* (Family Diplodactylidae) are on the same branch leftwards below carphodactylids. However, despite the distant phylogenetic relatedness, all limb-reduced taxa (Scincidae, Pygopodidae, Dibamidae, and Amphisbaenidae) occupy the pPC2 negative values or slightly positive values. This result clearly demonstrates how two Carphodactylidae and Pygopodidae (which are sister groups) have diverged extremely in morphology by being in opposite ends of the pPC2 spectrum, in fact diplodactylid geckos, who are sister to the clade formed by Carphodactylidae and Pygopodidae were clustered in between these two groups, together with other limbed gekkotan families.

Small (miniaturized) limbed forms such as *Ablepharus kitabelii* (skink), *Saurodactylus mauritanicus* and *Coleodactylus brachystoma* (gekkotans) are clustered closer to the limb-reduced lizards which indicates cranial skull convergence between

miniaturized groups and semi-fosorial/fossorial taxa. This similarity was also found previously between gekkotans in a 2D Geometric moprhotric analyses (Daza et al., 2009). Interestingly, *Dibamus bogadeki* – a limbless lizard endemic to China falls closer to *Acontias meleagris* and *Acontias percivali* – two limb-reduced skinks endemic to Sub Saharan Africa. This pattern was common for all the PCA and pPCA plots.

Determining the convergence in the skull morphology using geometric morphometric analysis

This study used a geometric morphometric analysis in a comparative context to explore the evolutionary convergence of limb-reduced lizard species from three continents and to compare the evolutionary integration in the skull of limb-reduced taxa vs non limb-reduced taxa. I hypothesized that *Paradelma orientalis* (Family Pygopodidae), *Acontias percivali* and *Acontias meleagris* (Family Scincidae), and *Nessia burtonii* and *Nessia monodactyla* (Family Scincidae) from Australian, African and Asian continents, respectively, are showing convergence in their skull morphology. If morphological convergence has occurred among taxa, morphologically similar species occupy a similar position in the morphospace in the multivariate ordinations (PCA) (Ricklefs et al., 1981; Winemiller et al., 1995; Mitteroecker et al., 2005; Montaña and Winemiller, 2013; Da Silva et al., 2018). Given the great variety of skull shapes in lizards, it is not surprising that they covered a wide range of morphospace (Figures 4 and 5). However, the working hypothesis was only partially supported, since only *Acontias percivali* and *Acontias meleagris* clustered together in the PCA and pPCA plots with *Nessia burtonii* and *Nessia monodactyla*. Though *Paradelma orientalis* does not fall anywhere closer to these two-skink species in PCA analysis, it is closer to *Nessia burtonii*

in pPCA (Figure 8), suggesting some higher degree of convergence when the phylogenetic information is included. Though the dorsal view of the skull of *Paradelma orientalis* is very similar to *Acontias meleagris* (Bauer and Daza, 2008), results reveals that the overall 3D skull morphology is not similar. These groups are probably segregated by information on the vertical axis, which might not be capture by a 2D analysis.

If environmental conditions impose constraints on adaptation, and these constraints are simultaneously expressed in morphology, then the ecological niches can be predicted using the morphological data and vice versa (Kerr and James, 1975). Habitat use is found to be an important factor shaping the body in lizards (Daza et al., 2009). Surface active species have relatively taller heads and trunks compared to climbing species (Vanhooydonck and Van Damme, 1999).

In the case of *Paradelma orientalis*, *Acontias percivali,* and *Acontias meleagris*; and *Nessia burtonii* and *Nessia monodactyla* from Australian, African and Asian continents, respectively, the morphological convergence between *Acontias* and *Nessia* species indicates that these two lineages have evolved independently in two continents to fill similar ecological niches. Despite occurring in different biogeographic regions, these lizards are similar in their body form (limb-reduced), and habitat use (semi-fossorial). Though literature does not provide enough information about the climatic data (temperature, rainfall etc.) and topography (elevation, soil type etc.) of the regions inhabited by *Acontias* and *Nessia* species, I assume them to live under similar conditions (in loose and wet soil in higher elevations), filling the same ecological niche in in Sub Saharan Africa and Sri Lanka. Their semi-fossorial habitat might have resulted similar skull morphologies, suggesting that habitat use plays an important role in their

morphology (and vice versa). On the other hand, *Paradelma orientalis* is not only phenotypically different from *Acontias* and *Nessia* species, but also a surface active lizard. This might have resulted *Paradelma orientalis* to exhibit a different skull morphology in 3D structure.

The regression analysis on inter-taxon allometric shape variability of 38 lizard species (Figure 10) suggested a very weak correlation between the size and shape (r^2 = -0.11). Also, the log transformed centroid sizes of skulls of *Acontias meleagris*, *Acontias percivali*, *Nessia monodactyla*, and *Nessia burtonii* are similar (Figure 10) and smaller than that of *Paradelma orientalis*. This further confirms that the findings made from PCA and pPCA is consistent. For example, *Acontias meleagris* and *Acontias percivali* of Sub Saharan Africa are morphologically converged with *Nessia monodactyla* and *Nessia burtonii* of Sri Lanka.

My findings are consistent with those reported in other studies revealing a correlation between morphology and habitat. This observation is similar to the example of the ecomorphs of *Anolis* lizards on the Caribbean islands (Williams, 1972; Naganuma and Roughgarden, 1990; Losos, 1992; Losos et al., 1998), where similar ecomorphs were observed in different islands.
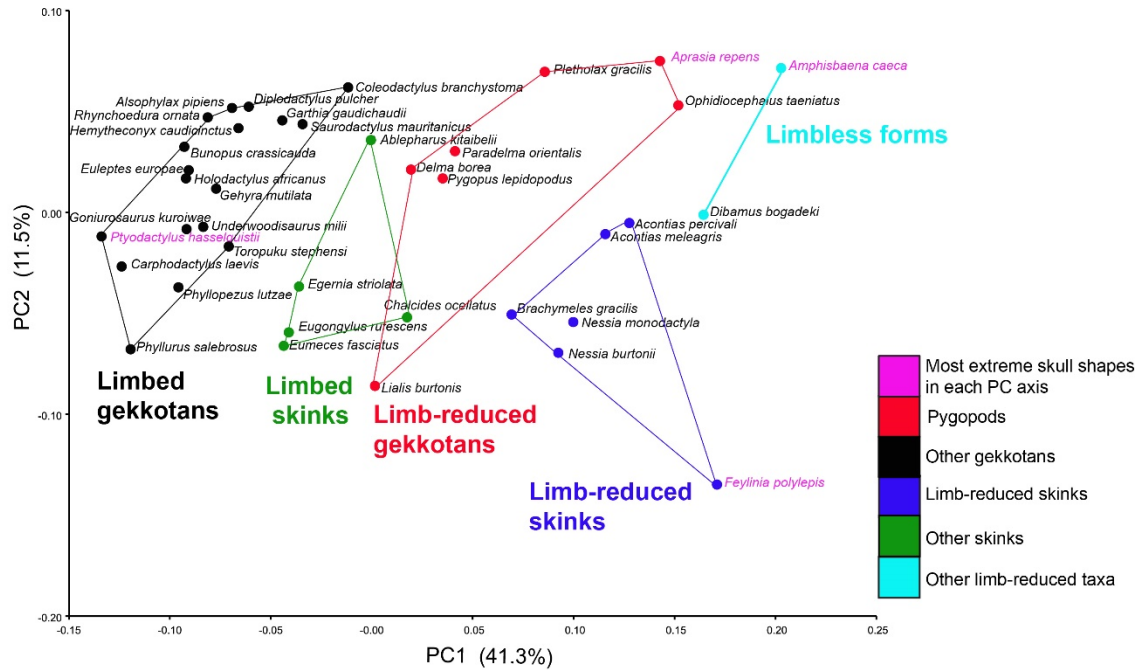
Figure 4. Two axes of Principal component analysis (PC1 vs PC2) of 38 gekkotan and skink species based on 27 morphological landmarks. Numbers in parenthesis indicate the percentage of variance explained by each PC axis.

Figure 5. Two axes of Principal component analysis (PC1 vs PC3) of 38 gekkotan and skink species based on 27 morphological landmarks. Numbers in parenthesis indicate the percentage of variance explained by each PC axis.
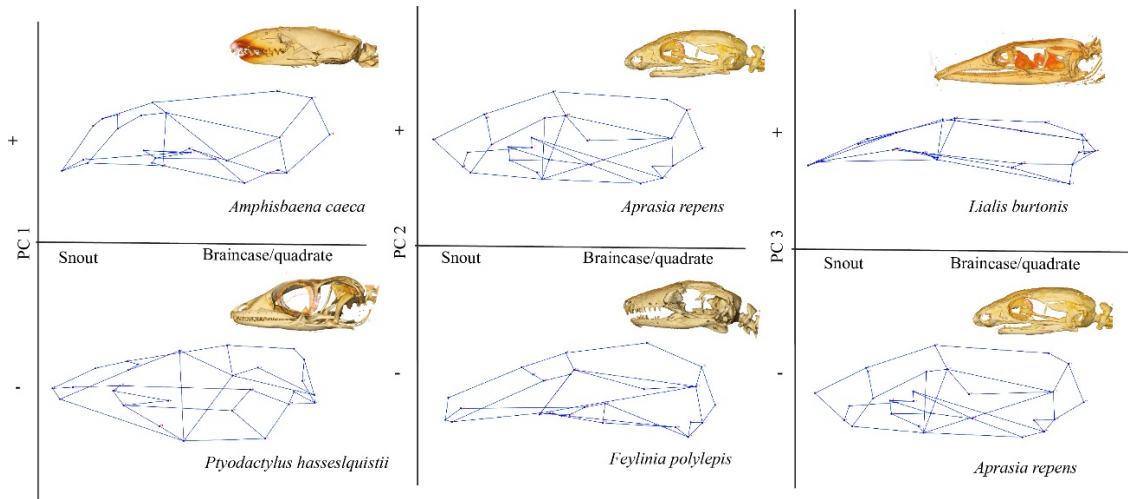
Figure 6. The wireframes displaying the extreme skull shapes (with species names) of gekkotan and skink species at positive (+) and negative (−) values of each PC axis based on 27 morphological landmarks. The 3D-rendered skulls corresponding to the observed extreme species in both positive and negative directions on each PC axis (PC1 in the left, PC2 in the right, and PC3 in the left) are also shown**.**
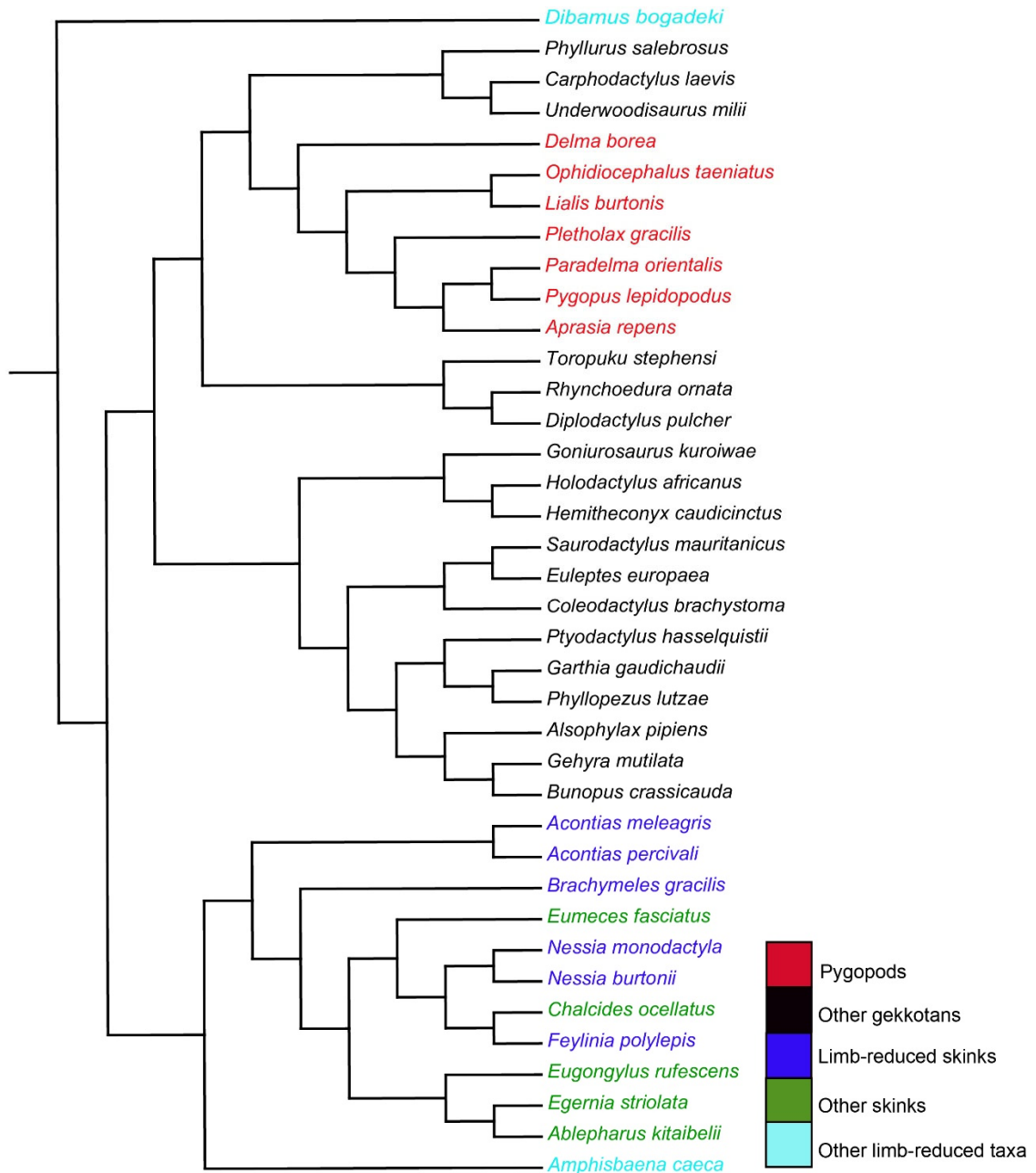
Figure 7. Simplified phylogenetic relationship among 38 species used in the study adapted from Zheng and Wiens (2016). As Zheng and Wiens (2016) tree did not have phylogenetic information on *Nessia* sp., two *Nessia* species were placed on the phylogeny as a sister clade to the *Janetaescincus* and *Pamelaescincus* of Seychelles (Kanishka Ukuwela, personal communication).
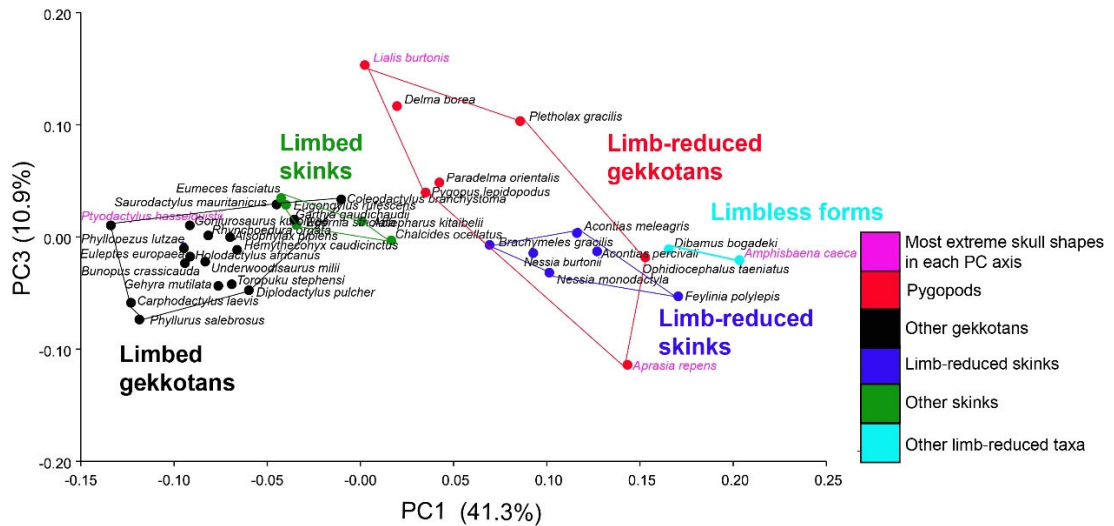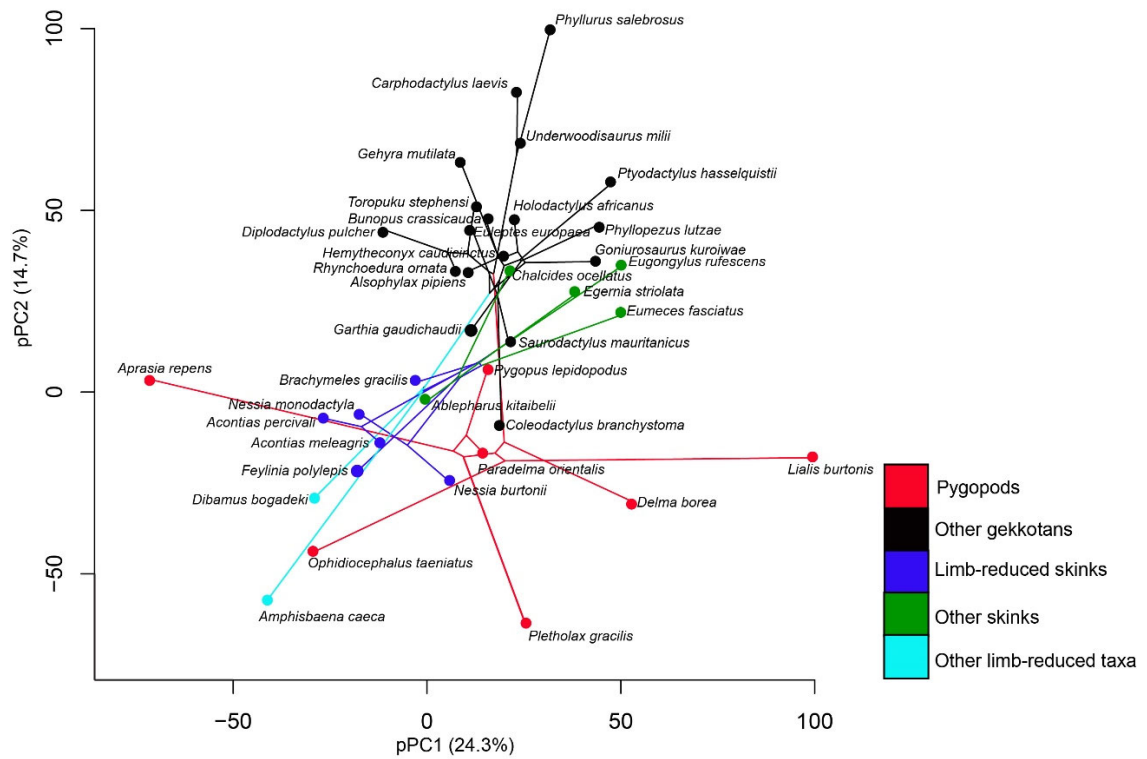
Figure 8. Two axes of phylogenetic Principal component analysis (pPC1 vs pPC2) of 38 gekkotan and skink species based on 27 morphological landmarks and their phylogeny according to Zheng and Wiens (2016). Numbers in parenthesis indicate the percentage of variance explained by each pPC axis.
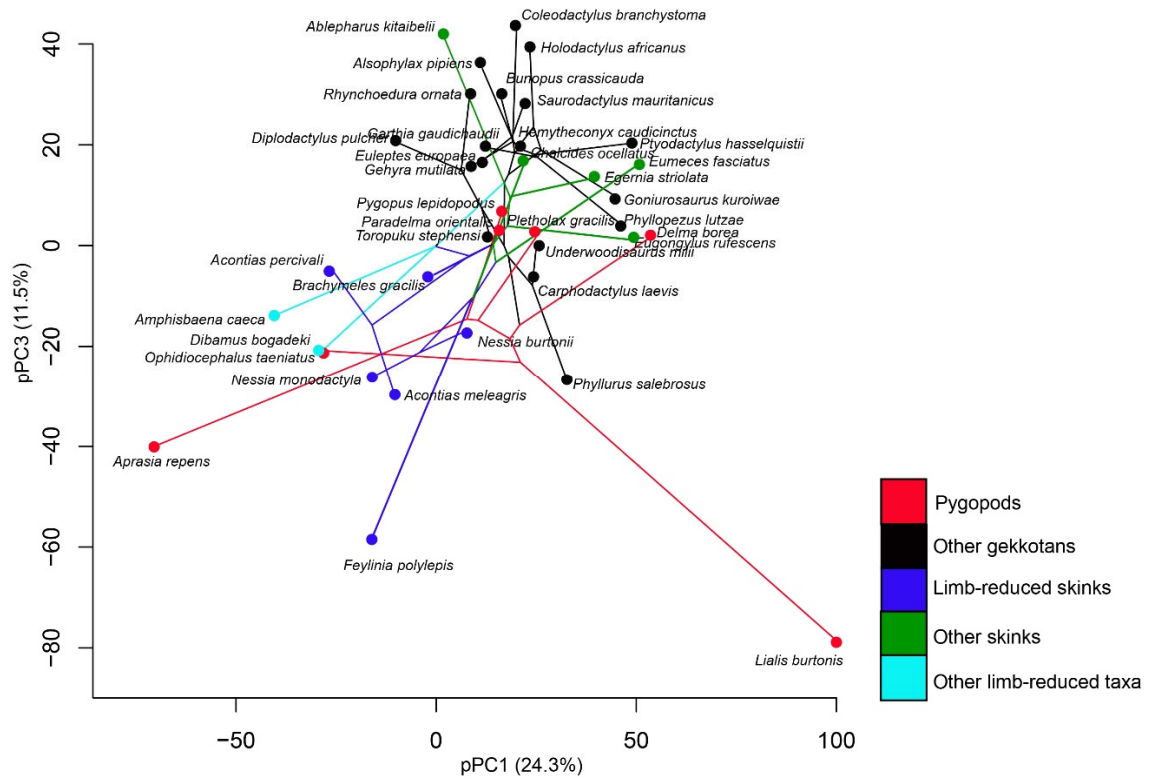
Figure 9. Two axes of phylogenetic Principal component analysis (pPC1 vs pPC3) of 38 gekkotan and skink species based on 27 morphological landmarks and their phylogeny according to Zheng and Wiens (2016). Numbers in parenthesis indicate the percentage of variance explained by each pPC axis.
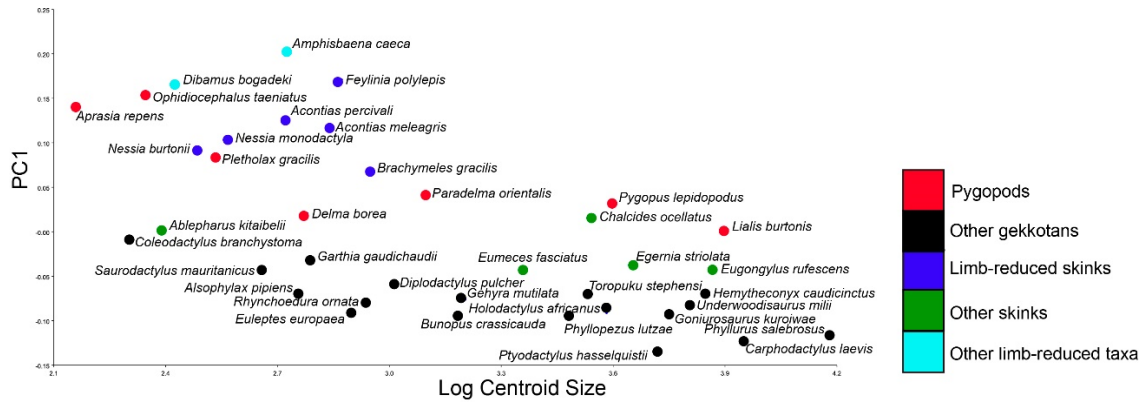
Figure 10. Multivariate regression of shape on log-transformed centroid size of 38 gekkotan and skink species. The PC1 is the shape variable which accounts for 41.3% of the total variance, and its relationship to log-transformed centroid size indicates the strength of allometry.

Table 3

Eigenvalues and % variance of first ten PCs

PC	Eigenvalues	% Variance
1	0.00923595	41.276
2	0.00257690	11.516
3	0.00244685	10.935
4	0.00142652	6.375
5	0.00106794	4.773
6	0.00080349	3.591
7	0.00066871	2.989
8	0.00052431	2.343
9	0.00044826	2.003
10	0.00037859	1.692

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APPENDIX A
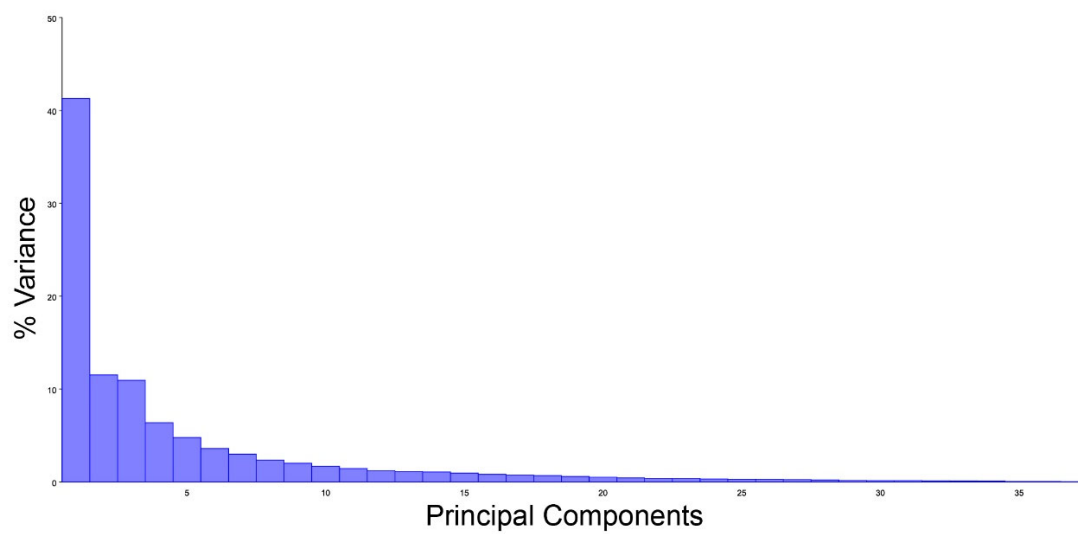
Variance (%) explained by each Principal component in the Principal components

analysis of gekkotan and skink species based on 27 morphological landmarks.

APPENDIX B

% Variance explained by each Phylogenetic principal component in the Phylogenetic principal component analysis of gekkotan and skink species based on 27 morphological landmarks and their phylogeny

pPC	% Variance	pPC	% Variance
1	24.28673422	20	0.75743520
2	14.68191071	21	0.68367719
3	11.49497721	22	0.59108554
4	7.84143790	23	0.50388403
5	6.29218658	24	0.44353418
6	4.59838367	25	0.36880243
7	3.85839983	26	0.33817911
8	3.27869539	27	0.33290188
9	2.98483563	28	0.26892248
10	2.46493216	29	0.23412467
11	2.07444406	30	0.19375036
12	1.97017233	31	0.19044783
13	1.55727768	32	0.15976328

(continued)

pPC	% Variance	pPC	% Variance
14	1.51182330	33	0.14585118
15	1.39026673	34	0.11415984
16	1.22838667	35	0.08215780
17	1.07081036	36	0.07536861
18	1.00724967	37	0.06353189
19	0.85949843		

VITA

SUPUNI DHAMEERA GANGANI THENNAKOON MUDALIGE SILVA

EDUCATION
- **MS in Biology**, Sam Houston State University, Huntsville, Texas, USA (**GPA - 4.00**)
  Thesis Title - Evolutionary Convergence across limb-reduced lizards from three continents; Australia, Asia and Africa. Advisor – Dr. Juan D. Daza
- **BS in Environmental Conservation and Management (Honors)** Degree, University of Kelaniya, Sri Lanka. (2015) **First Class Honors** (GPA - 3.78)
  Thesis Title - Trends in the invasiveness of *Najas marina*, Linnaeus 1753 (Family: Najadaceae) in the Ramsar Wetland of Madu Ganga Estuary, Sri Lanka. Advisor – Prof. M. J. S. Wijeyaratne
- **Graduate Chemist (Second Class Honors)**, Institute of Chemistry, Ceylon. (2013)

RESEARCH INTERESTS
- Nutrient dynamics, food-web dynamics, and habitat restoration of Marine and Estuarine Ecosystems, especially coral reefs, mangrove habitats, and sea grasses
- Geometric morphometrics of evolutionary independent lineages
- Marine and Coastal Resources Management

CAREER AND TEACHING EXPERIENCE
- **Graduate Teaching Assistant** attached to the Department of Biological Sciences, University of North Texas, Texas, USA (August 2018- Present)
- **Assistant Curator of Freshwater Mussel Collection** at the Sam Houston State Natural History Collections, Sam Houston State University, Texas, USA (June 2017- Present)
- **Graduate Teaching Assistant** attached to the Department of Biological Sciences, Sam Houston State University, Texas, USA (August 2016- Present)
- **Graduate Teaching Assistant** attached to the Research Services Centre, Faculty of Science, University of Kelaniya, Sri Lanka (January 2016- July 2016)
- **Graduate Teaching Assistant** attached to the Department of Zoology and Environmental Management, Faculty of Science, University of Kelaniya, Sri Lanka (February 2015- December 2016)
- **Intern** at Chemical Industries Colombo Limited (CIC), Sri Lanka (January 2014- February 2014)

PUBLICATIONS
- Montaña, C. G., **Silva, S. D. G. T. M.**, Hagyari, D., Wagner J., Tiegs, L., Sadeghian C., Schriever, T. and Schalk, C. M. *In preparation (In review).* Revisiting 'What do tadpoles really eat?': A ten-year perspective. Target Journal: ***Freshwater Biology.***

- **Silva, S. D. G. T. M.**, Dahanayaka, D. D. G. L. and Wijeyaratne, M. J. S. (*In review*). A remote sensing approach for assessing the invasion of *Najas marina* Linnaeus, 1753 (Family Najadaceae) in the Ramsar Wetland of Madu Ganga Estuary in Sri Lanka. Target Journal: ***Biological Invasions***.
- Barclay, D., **Silva, T. M. S. D. G.**, Kim, H. and Godwin, W. B. 2017. New Record of the Freshwater Mussel *Lanceolaria gladiola* Heude, 1877 (Family: Unionidae) from South Korea. ***International Journal of Fisheries and Aquatic Studies.*** 5(5): 202-204.
- **Silva, T. M. S. D. G.** and Wijeyaratne, M. J. S. 2017. Environmental factors contributing to the invasion of *Najas marina* L in Madu Ganga Estuary, a Ramsar Wetland in Sri Lanka. ***Sri Lanka Journal of Aquatic Sciences***. 22(2): 109–116.

Author changed her professional name from Thennakoon Mudalige Supuni Dhameera Gangani Silva (T. M. S. D. G. Silva) to Supuni Dhameera Gangani Thennakoon Mudalige Silva (S. D. G. T. M. Silva) in 2018.

CONFERENCE ACTIVITY/PARTICIPATION

Conferences Organized

- ICTSD 2016: International Symposium on ICT for Sustainable Development, Department of Zoology and Environmental Management, University of Kelaniya, Sri Lanka and KISSEL Group, Ibaraki University, Japan (2016)
- URS-ENCM 2015: Undergraduate Research Symposium on Environmental Conservation and Management, Department of Zoology and Environmental Management, University of Kelaniya, Sri Lanka (2015)
- 10th ANet: International network for myrmecology (ant research) in Asia, Department of Zoology and Environmental Management, University of Kelaniya, Sri Lanka (2015)
- ICTSD 2014: International Symposium on ICT for Sustainable Development, Department of Zoology and Environmental Management, University of Kelaniya, Sri Lanka and KISSEL Group, Ibaraki University, Japan (2014)

Oral and Poster Presentations

- **Silva, S. D. G. T. M**., Daza, J., D., and Bauer, A. M. (2018) Morphological (Osteological) Convergence across surface active and limb-attenuated lizards from three continents: Australia, Asia and Africa. The International Research Symposium on Pure and Applied Sciences (IRSPAS) 2018. Faculty of Science, University of Kelaniya, Sri Lanka. (Talk)
- Montaña, C. G., Schalk, C. M., Schriever, T., **Silva, T. M. S. D. G.**, Hagyari, D., Wager, J., Tiegs, L., and Sadeghian, C. (2018) Revisiting 'What do tadpoles really

eat?': A ten-year perspective. Joint Meeting of Ichthyologists and Herpetologists, Rochester, New York. (Talk)

- **Silva, T. M. S. D. G**. and Wozniak, J. R. (2017). Determining benthic nitrogen fluxes along a hydrological gradient in saltwater ponds of coastal Texas. Proceedings of 2017 Texas Bays and Estuaries Meeting, The University of Texas Marine Science Institute, Port Aransas, USA. p. 40. (Poster)

- **Silva, T. M. S. D. G.** and Wijeyaratne, M. J. S. (2017). Trophic condition of Madu Ganga Estuary, a Ramsar Wetland in Sri Lanka. 18th Annual Ecological Integration Symposium, Texas A&M University, College Station, USA. (Talk)

- **Silva, T. M. S. D. G.** and Wozniak, J. R. (2016). Benthic biogeochemical responses to changing hydrology in coastal saltwater ponds of Texas. 6th Annual Marine Science Graduate Student Organization Student Research Forum, Texas A&M University, Corpus Christi, USA. (Talk)

- Kodituwakku, K. A. R. K., Wazir, S. R., Aththanayake, A. M. H. L., **Silva, T. M. S. D. G.**, Malshani, E. M. S., Partheepan, K., Thevendran, K., Udayanga, N. W. B. A. L., Sumanapala, A. P., Jayanga, B. H. N. and Chandrasekara, W. U. (2016). Management of coastal resources: Lessons learnt from two coastal communities occupying the west coast of Sri Lanka. Proceedings of the International Research Symposium on Pure and Applied Sciences (IRSPAS 2016), Faculty of Science, University of Kelaniya, Sri Lanka. p. 105. (Talk)

- **Silva, T. M. S. D. G.** and Wijeyaratne, M. J. S. (2015). Factors affecting the invasion of *Najas marina,* Linnaeus 1753 (Family Najadaceae) in the Ramsar Wetland of Madu Ganga Estuary, Sri Lanka. Proceedings of the Twenty-first Scientific Sessions of the Sri Lanka Association for Fisheries and Aquatic Resources, May 2015. Sri Lanka Association for Fisheries and Aquatic Resources, Colombo, Sri Lanka. p.10. (Talk)

- **Silva, T. M. S. D. G.**, Dahanayaka, D. D. G. L. and Wijeyaratne, M. J. S. (2015). Assessment of invasion of *Najas marina*, Linnaeus 1753 in Madu Ganga Estuary, Sri Lanka using ASTER data of Terra satellite. Proceedings of the Thirty Fifth Scientific Sessions of Institute of Biology, Sri Lanka, September 2015. Institute of Biology, Sri Lanka. p.32. (Talk)

SERVICE TO PROFESSION
- **Editorial committee member -** Student Environment & Nature Magazine "Cynosure" 5th Edition (2013)

DEPARTMENTAL AND UNIVERSITY SERVICE
- **Vice President** – Biological Sciences Graduate Student Organization, Sam Houston State University, Texas, USA (2017)

- **Resource person** – Practical Training Program for GCE Advanced Level Biosystems Technology Teachers conducted by Ministry of Education, Sri Lanka and Research Services Centre, Faculty of Science, University of Kelaniya, Sri Lanka (2015)
- **Organizing committee member** – CHEMEX 2012 Exhibition, Institute of Chemistry, Ceylon, Sri Lanka (2012)
- **Organizing committee member** – CHEMEX 2011 Exhibition, Institute of Chemistry, Ceylon; held at the Bandaranaike Memorial International Conference Hall, Colombo, Sri Lanka (2011)
- Represented the Faculty of Science, University of Kelaniya, Sri Lanka at the Inter Faculty Modeling Competition, "Stylish Marketer 2011", and emerged 1st Runners up (2011)
- **Student Coordinator** – Level one at Institute of Chemistry, Ceylon (2010)
- Regular **Compere** at the National and International Conferences organized by the University of Kelaniya, Sri Lanka

SCHOLARSHIPS AND GRANTS
- **Graduate Student Tuition Benefit Program** - Department of Biological Sciences, University of North Texas, Texas, USA (2018 Fall) $ 3,670
- **Mary Beth Baird Health Assistance Scholarship** - Department of Biological Sciences, University of North Texas, Texas, USA (2018 Fall) $1, 200
- **Special Graduate Student Scholarship** - College of Science and Engineering Technologies, Sam Houston State University, Texas, USA. (2018 Spring) $1,500
- **Graduate Studies General Scholarship** - Office of Graduate Studies, Sam Houston State University, Texas, USA. (2017 Fall) $1,000
- **Special Graduate Student Scholarship** - College of Science and Engineering Technologies, Sam Houston State University, Texas, USA. (2017 Fall) $1,500
- **Leadership Scholarship** - Office of Graduate Studies, Sam Houston State University, Texas, USA. (2017 Fall) $500
- **Special Graduate Student Scholarship** - College of Science and Engineering Technologies, Sam Houston State University, Texas, USA. (2017 Spring) $1,500
- **Travel Grant -** Marine Science Graduate Student Organization, Texas A & M University, Corpus Christi, USA. (2016) $400

HONORS AND AWARDS

- **Student Spotlight of the Week** – Featured in Leadership Initiatives, Sam Houston State University, Texas, USA (2017)

CERTIFICATIONS AND PROFESSIONAL QUALIFICATIONS
- Professional Association of Diving Instructors (PADI) **Open Water Diver** (License no. 1504AZ9276)
- Foundations of Coaching (Level 1) in **USA Swimming and American Swimming Coaches Association** (ASCA)
- Foundation Course (2009) and Certificate Course (2010) in **Human Resources Management** at Institute of Personnel Management, Sri Lanka

LEADERSHIP, VOLUNTEER, COMMUNITY AND OTHER EXPOSURE
- **Gardener (Volunteer)** at **Bearkats Community Garden**, Sam Houston State University, Texas, USA (2016 and 2017)
- **Leadership training** organized by the Office of Graduate Studies, Sam Houston State University, Texas, USA. (2017)
- **Diver (Volunteer)** in the **annual coral reef monitoring program** organized by the Holcim (Lanka) Limited in collaboration with IUCN which involved monitoring the artificially constructed coral reef at Unawatuna, Sri Lanka (2016)
- **Animal Rescuer (Volunteer)** in the **animal rescue program** organized by the Holcim (Lanka) Limited in collaboration with IUCN which involved the rescue of vulnerable species from the proposed quarry site, Aruwakkalu, Sri Lanka (2015)
- **National Participant** in the "World Wide Views on Climate and Energy" - the largest ever global citizen consultation on climate and energy (2015)
- Attended the workshop on "Identifying & conducting outreach activities to enhance soft skills of Environmental Conservation and Management graduates" funded by Higher Education for the Twenty First Century project (2014)
- **Headed the volunteer group** at the conduction of Sri Lankan Biology Olympiad 2014 organized by the Institute of Biology, Sri Lanka
- Embellished front pages of national newspapers and magazines as an award winning, successful model (**Finalist at Model of the Year 2011**, organized by Lou Ching Wong Studio, Sri Lanka)
- **Rapporteur** in the "The Future Leaders Summit" organized by Channel 1 MTV, Sri Lanka (2007)

LANGUAGE COMPETENCE

Language	Reading	Writing	Speaking
Sinhalese	Excellent	Excellent	Excellent
English	Excellent	Excellent	Excellent
Tamil	Good	Good	Fair

PROFESSIONAL AFFILIATIONS
- Member of Ecological Society of America
- Associate Member of the Institute of Chemistry, Ceylon