

CHARACTERISTICS OF MINIATURIZATION IN SQUAMATES: A
PHYLOGENETIC PERSPECTIVE FROM CRANIAL MORPHOLOGY

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A Mariana y Manuel,

A Nacho y a Silvia,

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Con infinita gratitud.

ABSTRACT

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Miniaturization is recurrent in tetrapods, and has been widely recognized to be an evolutionary process resulting from the occupation of previously unexploited niches (Hanken and Wake, 1993; Rieppel, 1984a, 1996). In this thesis I review the process of miniaturization and its effects on the skull of squamates (lizards, snakes, and amphisbaenians). I compiled a list of characteristics previously described for squamates and summarized the main differences among higher level groups (e.g., Iguania, Gekkota or Scincomorpha). I also investigated whether observed traits linked to miniaturization are the product of convergent evolution. I used a large published morphological data set that includes 204 species of which 54 are miniaturized. I coded characters for an additional species that represent the smallest known squamates (e.g., *Sphaerodactylus ariasae* and *Brookesia micra*) and belong to taxonomic groups with minor representation in the original dataset. Analyses identified two characters that occurred in miniaturized taxa of 15 mm or less in skull length, six characteristics for species with 10 mm or less, three for species with 5 mm or less, and eight traits convergent to miniaturized head-first burrowers.

KEY WORDS: Body size, Convergence, Fossoriality, Lizards, Parsimony, Skull length, Squamata.

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CHAPTER I

Introduction

Body size impacts the way in which organisms interact with their environment. Lineages show variation in body size through time (Smith et al., 2016) and at lower and upper extremes, body size is constrained by physiological, biomechanical and environmental factors that result in changes in morphology, ecology and behavior (Smith et al., 2016; Vermeij, 2016). Morphological changes may include, for example, the reduction in hind limb bones in miniaturized salamanders (Hanken and Wake, 1993) or the reduction in egg volume in gigantic sauropod dinosaurs, particularly titanosaurids, which led to complex ontogenetic life histories (Sander et al., 2011). Some lineages can undergo a progressive increase in body size through time as is predicted by Cope's or Depréret's rule (Stanley, 1973), a trend that in some cases can lead to gigantism (Vermeij, 2016). Other lineages can go through a reduction in body size, miniaturization (Hanken and Wake, 1993). This has evolved independently in almost all major vertebrate groups (e.g., Osteichthyes, Lissamphibia, Reptilia [including Aves], and Mammalia; Hanken and Wake, 1993). Examples of extremely small body sizes in aquatic ectothermic vertebrates include cyprinid fish in the genus *Paedocypris* (Figure 1), having a mean total length of only 7.9 mm (Kottelat et al., 2006), and the microhylid frog *Paedophryne amauensis* (Figure 1), with an average total body length of 7.7 mm (Rittmeyer et al., 2012). In terrestrial ectothermic vertebrates, the smallest body sizes in amphibians or squamates are larger than in fish, which has been attributed to different physiological constraints relating to metabolism (Hanken, 1993; Rieppel, 1996; Smith et al., 2016). Among endotherms, the smallest miniaturized mammal is Kittlitz's hog-nosed bat,

Craseonycteris thonglongyai (Figure 1), with body length ranging from 29 to 33 mm (Hill and Smith, 1981), and the smallest bird is the Cuban bee hummingbird, *Mellisuga helenae* (Figure 1), with a minimum length of 64 mm (Estrada and Hedges, 1996).

Among squamates (lizards, snakes and amphisbaenians), miniaturization has occurred multiple times, and has been identified in at least 21 families (Table 1; Hanken and Wake, 1993; Rieppel, 1996) of the approximately 68 recognized squamate families (Goicoechea et al., 2016; Zheng and Wiens, 2016). Extremely miniaturized species are in the gekkotan family Sphaerodactylidae, the dwarf chameleons of the Chamaeleonidae and the blind snakes in the family Leptotyphlopidae. The Sphaerodactylidae includes the Jaragua gecko (*Sphaerodactylus ariasae*, Figure 1), whose snout-vent length (SVL) ranges from 14.1 to 17.9 mm (Hedges and Thomas, 2001), and the Virgin Island gecko (*Sphaerodactylus parthenopion*), whose SVL ranges from 12 to 17 mm (Thomas, 1965). Other examples of extreme miniaturization includes members of the iguanian family Chamaeleonidae, with the dwarf Malagasy chameleon (*Brookesia micra*, Figure 1) measuring between 15 and 19.9 mm of SVL (Glaw et al., 2012). Among squamates, the smallest snakes are in the family Leptotyphlopidae (Hedges, 2008; Feldman et al., 2016), including the species *Tetracheilostoma carlae*, with only 87–98 mm SVL. Its body length might exceed that of other miniaturized vertebrates, but its body diameter is certainly comparable. Other small snakes includes members of the family Anomalepididae represented by species such as *Liotyphlops albirostris* with a total length of 223 mm (Feldman et al., 2016; Appendix S1) and a skull length of only 4.3 mm (Rieppel et al., 2009).

Miniaturization is a common process in vertebrate evolution widely recognized to promote the occupation of new niches (Hanken and Wake, 1993; Rieppel, 1984a, 1996). To date, there is not a unifying model of miniaturization for squamates (Rieppel, 1984a), and even though there are different studies on miniaturized squamates, there is not a combined study that evaluates the convergence of miniaturization characteristics in the skull of squamates, especially considering miniaturization traits from a phylogenetic perspective. The aim of this project is to review and evaluate the characteristics associated with miniaturization from a phylogenetic perspective in a large taxonomic group. This study includes an extensive literature review and synthesis of the morphological variation associated with miniaturization in the skull of Squamata, and the identification of traits associated with miniaturization using a published morphological data set of Squamata. Because miniaturization can occur in confluence with fossoriality (Rieppel, 1984a, Lee 1998), I also attempt to identify traits that occur in miniaturized head-first burrowing and non-fossorial forms squamates.

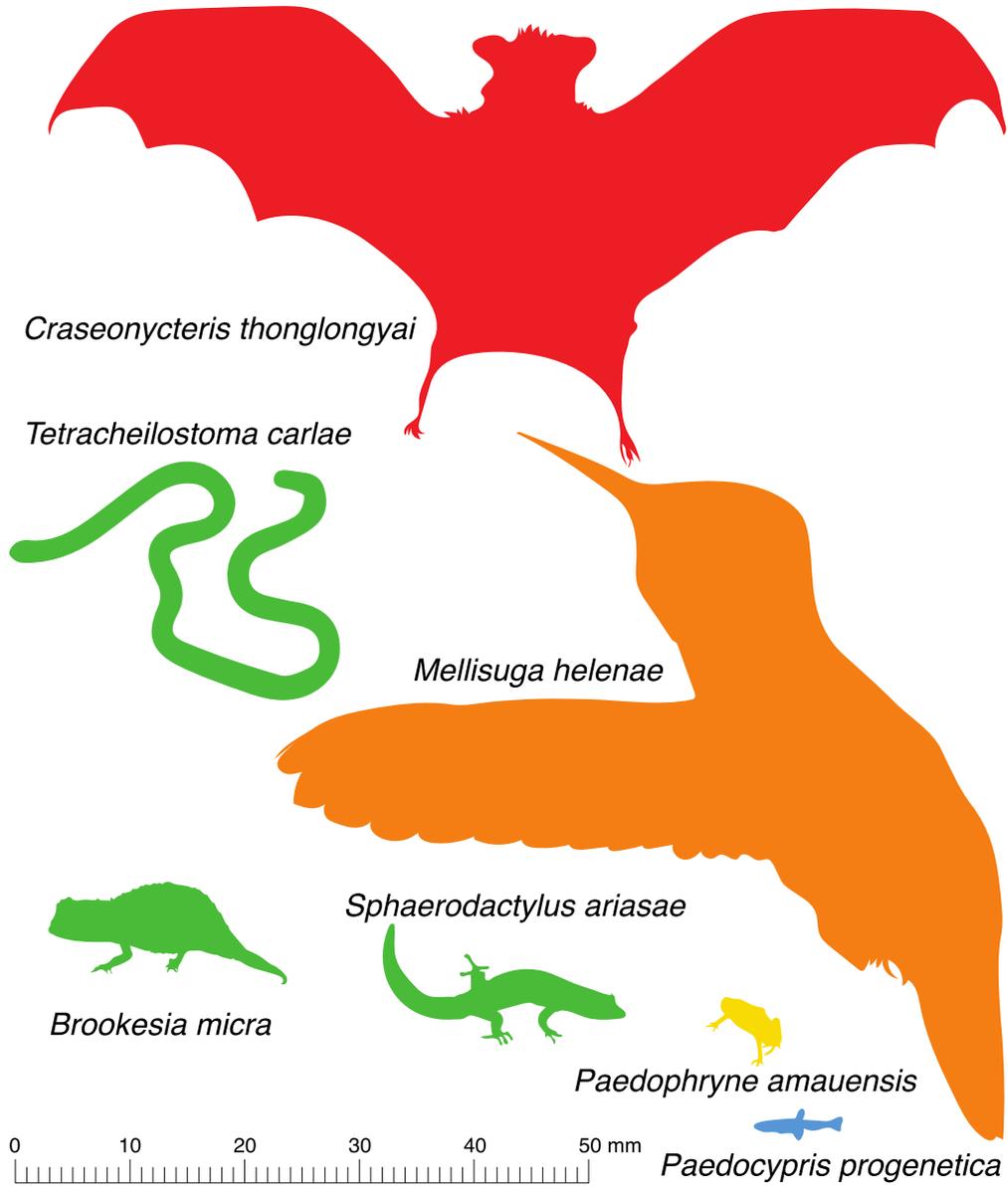


Figure 1. Silhouettes of the smallest vertebrates on record, all representatives drawn to the same scale. Blue = Actinopterygii; yellow = Amphibia; green = Reptilia; orange = Aves; red = Mammalia. Author created.

Table 1

List of families within Squamata that include miniaturized taxa.

Family	References
Amphisbaenidae	Rieppel, 1984a, b; Gans and Montero, 2008.
Anguidae	Rieppel, 1984a, b.
Anniellidae	Rieppel, 1984b.
Anomalepididae	Rieppel et al., 2009.
Anomochilidae	Rieppel and Maisano, 2007.
Bipedidae	Daza et al., 2011.
Boidae	Daza et al., 2011.
Chamaeleionidae	Rieppel and Crumly, 1997; Glaw et al., 1999.
Dibamidae	Rieppel, 1984b; Greer, 1985; Daza and Bauer, 2015.
Eublepharidae	Daza et al., 2011.
Gekkonidae	Daza et al., 2012, 2015.
Gerrhosauridae	Daza et al., 2011.
Gymnophthalmidae	Tarazona et al., 2008; Guerra and Montero, 2009; Daza and Bauer, 2015.
Lacertidae	Rieppel, 1984a; Müller, 2002.
Leptotyphlopidae	Hedges, 2008.
Opluridae	Daza et al., 2011.
Phyllodactylidae	Daza et al., 2011, 2017.
Pygopodidae	Rieppel, 1984a, b; Daza and Bauer, 2015.
Scincidae	Rieppel, 1981, 1984a, b; Griffith, 1990.
Sphaerodactylidae	Daza et al., 2008; Gamble et al., 2011; Daza et al., 2015.
Xantusiidae	Maisano, pers. comm.

CHAPTER II

A review of miniaturization in the skull of squamates

General characteristics and effects of miniaturization in tetrapods

Miniaturization is the extreme evolutionary reduction in body size of a lineage (Hanken and Wake, 1993). This is accompanied by modifications in morphology, physiology, life history, ecology and behavior (Hanken and Wake, 1993). These extreme modifications occur at different sizes, so the smallest size is taxon depended for each tetrapod group (Hanken and Wake, 1993).

The reduction in body size requires a change of structural proportions, which can be attained by the reduction of cell layers making up each tissue and sometimes even a reduction in cell volume (Rensch, 1948). As a consequence, some organs and tissues are reduced or lost (e.g., the decrease or loss of the copulatory organ in some small prosobranchs or tarsi in minute beetles), and the remaining structures are reorganized to optimize the limited available body space and compensate for their loss or reduction (Rensch, 1948). Among metazoan animals, the absolute lower limit of body size is difficult to establish due to their diversity of body plans, but phyla that include microscopic members include Rotifera, Gastrotrichia, Annelidae and Arthropoda (McClain and Boyer, 2009).

Miniaturization has been proposed to be a consequence of heterochrony, defined by Gould (1977) as a change in the relative timing of appearance and/or rate of development of characters already present in ancestors. Heterochrony can produce morphological change associated with miniaturization through two mechanisms: paedomorphism and peramorphism (Hanken, 1993; Rieppel, 1996). Paedomorphism

refers to the retention of juvenile traits in the adult (Hanken, 1993; Rieppel, 1996). Some examples include the loss of cranial elements and reduced ossification in Amphibia (Hanken, 1984), the reduction and loss of bones or structures in squamates (Rieppel, 1984a), and the loss of cranial crests in mammals (Rieppel, 1996). Peramorphism, on the other hand, refers to the extension of adult development to the level of creating new or hypertrophied structures. Some examples include the hyperossification of the parietal bones (Rieppel, 1984a, 1996), the closure of the lateral wall of the braincase in fossorial and burrowing squamates (Rieppel, 1984a, 1996; Lee, 1998; Roscito and Rodrigues, 2010), and the increase in fusion of paired elements and modification of dermatocranial bones in Gekkota (Daza et al., 2015).

Among tetrapods, three major generalized consequences of miniaturization have been identified: 1) structural simplification or reduction; 2) emergence of morphological novelties; and 3) increase in intraspecific morphological variation (Hanken and Wake, 1993). Each of these consequences are discussed below.

Structural simplification or reduction, in which some organs or systems are reduced or completely lost, is the best-documented consequence of miniaturization. It has been identified in the modifications of the skull of tetrapods (Rieppel, 1996), salamanders (Hanken, 1984), non-fossorial squamates (Rieppel, 1984a; Rieppel and Crumly, 1997; Daza et al., 2008; Gamble et al., 2011; Daza et al., 2011; Daza and Bauer, 2015), and fossorial squamates, particularly head-first burrowers (Rieppel, 1984b; Rieppel and Maisano, 2007; Guerra and Montero, 2009; Tarazona et al., 2008; Rieppel et al., 2009; Daza and Bauer, 2015). Structural simplification also has been described in the appendicular skeleton, for example the unique carpal rearrangement of the miniaturized

salamanders of the genus *Thorius* (Hanken, 1985), and the reduction of tarsals and carpals in small chameleons (Diaz and Trainor, 2015). Special senses organs and the central nervous system, particularly the eye, hearing apparatus and the brain, are larger relative to other structures in miniaturized salamanders (Hanken, 1983; Roth et al., 1990). Most morphological modifications are observed in the skull because it contains important organs (e.g., brain, inner ear, eyes, tongue), which to remain functional, cannot decrease in size beyond a limit, as is the particular case of the otic capsules in miniaturized and fossorial squamates (Rieppel, 1981; Hanken, 1993).

Development of morphological novelties appears to compensate for the loss or reduction of elements of vital function (Hanken, 1993). For example, in miniaturized geckos the jaw adductor muscles are modified and might play a role in closing the posterior border of the orbit, and the neck extensor muscles shift anteriorly onto the parietal bone, increasing the area covered by the muscle (Daza et al., 2008).

Increased morphological intraspecific variability is directly related to morphological novelties and structural simplification (Hanken, 1993). When present, it can be the result of truncated development, like the formation of the septomaxilla in the plethodontid salamander *Thorius*. Hanken (1993) evaluated the degree of development of this bone in five species of this genus and found a great variability within each species. In some individuals the septomaxilla is absent whereas in others it is small or large. But intraspecific morphological variation can also emerge because of the early development of structures. Hanken (1993), considering that phalangeal arrangement is set during early stages of development, demonstrated that the number and arrangement of digits within species of the genus *Thorius* is highly variable.

Characteristics and effects of miniaturization in the skull morphology of Squamata

There are several miniaturized groups among squamate reptiles (lizards, snakes and amphisbaenians, Table 1) and there are some convergent characteristics associated with it. Miniaturization is associated with change in the shape of the skull in which the neurocranium (braincase) comes to lie at the same level of the dermatocranium (bones of the skull roof) (Figure 2); this structural change is due to the relative size increase of the braincase (Rieppel, 1984a).

A fundamental indicator of miniaturization is the decrease in skull length. Rieppel (1984a) considered miniaturized squamates to have a skull length of 15 mm or less. This value was not determined arbitrarily, but it was estimated based on the proportional increase in the diameter of the otic capsules and neurocranium with respect to the decrease of the dermatocranium diameter as body size decreases. Based on the work of Jones and Spells (1963) on the physical dimensions and functionality of the semicircular canals in tetrapods, Rieppel (1984a) established the relationship between the skull length and the internal transverse diameter of the otic capsules. Based on the measurements of different lizard species, it is determined that at approximately at 15 mm, the diameter of the neurocranium increases, which indicates that the inner ear retains a proportionally large neurocranium.

At this minimum size, several morphological changes occur (Figures 2, 3, 4) including: 1) the proportional increase in size of the otic capsules, especially in fossorial species, where the neurocranium size increases along with the brain and otic capsules as the skull decreases its size (Rieppel, 1984a, 1996); 2) the closure of the post-temporal fenestra and occiput, especially in fossorial species (Rieppel, 1984a, 1996; Hanken, 1993;

Daza et al., 2008); 3) rearrangements of the jaw adductor muscles (Rieppel, 1984a, 1996; Daza et al., 2008); 4) elongation of the skull (Daza et al., 2011); 5) in most cases the widening of the snout relative to its length (Daza et al., 2011); 6) shifting of the occipital condyle to the posterior-most margin of the skull (common in squamates except in *Brookesia*, Daza et al., 2011); and 7) reduction of the paroccipital process (Daza et al., 2011).

The characteristics presented above are frequently found in miniaturized squamates independent of their lifestyle; however, miniaturization is often linked to fossoriality (Rieppel, 1996). Convergent evolution among fossorial forms, particularly head-first burrowers, is associated with other morphological changes such as body elongation, limb reduction and cranial consolidation (Lee, 1998). There are important morphological differences between the skull of non-fossorial and head-first burrowers which, independently have developed a convergent reinforced skull with reduced mobility (i.e., kinesis; Rieppel, 1984a, 1984b, 1996; Hanken and Wake, 1993; Lee, 1998). Several head-first burrowers have been extensively studied and some characteristics of miniaturization are associated with fossoriality (Rieppel, 1984b, 1996; Hanken and Wake, 1993; Lee, 1998; Roscito and Rodrigues, 2010; Daza and Bauer, 2015), like the closure of the occiput (Rieppel, 1984a) and lateral wall of the braincase (Figure 2; Rieppel, 1984a, 1996; Hanken and Wake, 1993; Lee, 1998), loss of the upper temporal arcade and squamosal, and the supratemporal becoming fully incorporated in the posterolateral braincase (Figure 3; Rieppel, 1984a). Other morphological features related to small body size in fossorial amphisbaenians, snakes, and dibamids are the loss of the lacrimal and jugal bones, fusion of postdentary bones (prearticular, articular and

surangular) into a compound element, and modification of quadrate suspension to become directly attached to the otic capsules (Lee, 1998). In amphisbaenians and dibamids, two additional traits are identified: the loss of postfrontals and reduction of the crista prootica (Lee, 1998: character 23, page 413 described loss of prefrontals, but this is a *lapsus calami* because the prefrontal bone is actually one of the most consistently present bones among reptiles).

Overall, there are characteristics of miniaturization that are exclusive to head-first burrowers and characteristics that are general for Squamata; however not all of the miniaturized groups share all of the characteristics and consequently there is not a single pattern of miniaturization (Rieppel, 1984a).

Characteristics of miniaturization in major clades of Squamata

The study of miniaturized squamates, has provided a general overview of the morphological variation of the skull in miniature taxa. However, additional characteristics are found among each of the major higher level clades (Iguania, Gekkota, Scincomorpha, Anguimorpha, Dibamidae, Amphisbaenia, Serpentes).

Iguania. Within Iguania, Chamaeleonidae includes several genera of ground and leaf dwellers that are well known for their miniaturized species. These species represent some of the most extreme examples of body size reduction within Squamata (Rieppel and Crumly, 1997; Glaw et al., 2012; Branch et al., 2014). The dwarf chameleons belong to the genera *Chamaeleo*, *Rhampholeon*, *Rieppeleon* and *Brookesia* (Rieppel and Crumly, 1997; Matthee et al., 2004; Glaw et al., 2012; Branch et al., 2014). The smallest size is attained in the Malagasy genus *Brookesia* from the minima group, which includes six species with a maximum total length of 45 mm: *B. minima*, *B. peyrierasi*, *B. tuberculata*,

B. micra, *B. dentate* and *B. ramanantsoai*. The first three were recognized as species based on their hemipenial morphology (Glaw et al., 1999) and later, a combined analysis of morphology and molecular data was used to infer the relationships among members of the group (Glaw et al., 2012). The smallest species is *Brookesia micra* with an average SVL of 15.3 mm in males and 19.9 mm in females (Glaw et al., 2012). Unfortunately there has not been a detailed description of the cranial morphology of this species that allows the evaluation of the miniaturization patterns and comparisons with other miniaturized species of squamates, especially sphaerodactyl geckos (including *Sphaerodactylus ariasae*) that have a very similar mean SVL.

Skull descriptions and comparisons with other chameleons are available in the literature (Rieppel, 1987; Rieppel and Crumly, 1997). A closure or reduction of the supratemporal fenestra is one of the most remarkable features in miniaturized squamates (Rieppel, 1996), but in small chameleons this fenestra remains open and unreduced. Instead, it is always surrounded by the postorbitofrontal and the squamosal in *Brookesia*, and is incomplete in some species of *Rhampholeon* (*R. kerstenii* and *R. brachyurus*) and small species of *Chamaeleo* (*C. nasutus*, and *C. gallus*) where the posterior end of the squamosal fails to close the fenestra due to a reduction in its ascending process. This characteristic is considered paedomorphic and thus related to miniaturization (Rieppel, 1987; Rieppel and Crumly, 1997).

Another possible paedomorphic trait related to miniaturization is the absence of a connection between the prefrontal and the maxilla that usually would separate the prefrontal fontanelle and the external naris. This connection is not present in some species of *Rhampholeon* (*Rhampholeon* type II of Rieppel, 1987 or *Rieppeleon* Matthee

et al., 2004: *R. brevicaudatus*, *R. marshalli*, *R. nchisiensis*, *R. platyceps*, *R. spectrum*, and *R. temporalis*), and in *Chamaeleo nasutus* and *C. willsii*. Additional poorly ossified structures (paedomorphic characteristics) are found in the floor of the braincase and in the margin of the orbit in the skull roof (Rieppel, 1987; Rieppel and Crumly, 1997).

Additional modifications associated with paedomorphism and small size are found in the morphology of the otic region, particularly in the size and orientation of the fenestra ovalis (Rieppel and Crumly, 1997). The snout is also modified in small forms, some changes include the narrowing of the premaxilla, fusion of nasals and increased suturing of the nasals with the frontal (Rieppel, 1987).

Gekkota. Gekkota is one of the better-studied groups in terms of miniaturization, with examples of miniaturization coming from the families Sphaerodactylidae, Pygopodidae, Gekkonidae and Phyllodactylidae. The family Sphaerodactylidae is characterized by its small size and only three of the 12 genera that comprise it have large and small forms: *Aristelliger*, *Teratoscincus* and *Pristurus*. The smallest sizes are found in the subfamily Sphaerodactylinae, which has 6 miniaturized genera: *Gonatodes*, *Lepidoblepharis*, *Sphaerodactylus*, *Pseudogonatodes*, *Coleodactylus* and *Chatogekko* (Daza et al., 2008; Gamble et al., 2011). These genera are geographically restricted to the circum-Caribbean and northern South America (Gamble et al., 2008) and are primarily diurnal (Gamble et al., 2015). The SVL in sphaerodactylines does not exceed 80 mm (Feldman et al., 2016, Appendix S1; Griffing et al., 2018). The smallest species is *Sphaerodactylus ariasae* (Hedges and Thomas, 2001); however, *Sphaerodactylus parthenopion* (Thomas, 1965) and *Sphaerodactylus elasmorhyncus* (Hedges and Thomas, 2001) have similar body sizes.

Besides reduced body size, evidence of miniaturization in Sphaerodactylidae is observed in the high degree of overlap between bones of the skull, especially the muzzle unit (Daza et al., 2008). Usually there are different kinds of cranial sutures: open contacts (e.g., fronto-parietal suture); overlapping or *butt-lap* contacts that cause a reduction in the thickness of the bones (found in nasal-frontal and maxilla-prefrontal contact); and closed contacts, found in the bones that form the braincase (Daza et al., 2008). In this family, overlap contacts provide valuable information for taxonomy and for understanding miniaturization, from the shape of the contact, its size and the degree of overlap. An example can be found in the overlap between the ascending nasal process of the premaxilla and the nasal bone (Daza et al., 2008). In *Sphaerodactylus* the nasals are anteriorly separated and underly the nasal process of the premaxilla. The overlap of the nasal by the premaxilla is $\frac{1}{2}$ to $\frac{3}{4}$ the length of the nasal, whereas in *Gonatodes* the overlap is $\frac{1}{2}$ to $\frac{1}{4}$, about $\frac{1}{2}$ in *Lepidoblepharis*, and the shortest ascending nasal process of the premaxilla is found in *Coleodactylus* which overlaps approximately $\frac{1}{4}$ of the nasals (Daza et al., 2008; Gamble et al., 2011). The most extreme case of overlap between the premaxilla, nasals and frontal is seen in some populations of *Chatogekko* where the nasal process of the premaxilla is in contact with the frontal and, as a consequence, the nasals are completely separated (Gamble et al., 2011; Daza, pers. comm, 2018).

Another characteristic associated with miniaturization in Sphaerodactylidae is the reduction in size of the paroccipital process. Usually, this process is short and stout in all Sphaerodactylidae, but in *Chatogekko* and *Pseudogonatodes*, the process is completely hidden by the semicircular canals and the otooccipital bulge (Gamble et al., 2011; Daza and Bauer, 2012a; Bauer et al., 2018). The reduction of the paroccipital process has been

found in other miniaturized squamates (Daza et al., 2011; Daza and Bauer, 2012a) as well as the reduction in height of the coronoid process, which is lower than the contour of the mandible in sphaerodactylids (Rieppel, 1984a; Daza et al., 2008; Gamble et al., 2011), and the reduction of the sphenoccipital tubercle in all miniaturized genera except *Gonatodes* (Daza and Bauer, 2012a).

Some characteristics associated with miniaturization in the geckos of the family Sphaerodactylidae are also present in geckos of other families. Within Gekkonidae, the diurnal Namibian festive gecko (*Narudasia festiva*) reaches a maximum SVL of 32 mm (Daza et al., 2012). *Narudasia festiva* also has several of the characteristics of miniaturized geckos like the overlap of the nasal by the premaxilla along about $\frac{1}{2}$ of its total length, but in contrast with sphaerodactyl geckos, the nasal process of the premaxilla is narrow (Daza et al., 2012). In addition, the relative size of the neurocranium is larger than that of the dermatocranium, and the supraoccipital is exposed (Daza et al., 2008, 2012). Interestingly, there are many other morphological features that do not follow the miniaturization patterns of other geckos with similar ecological characteristics; for example, the post-temporal fenestra remains open (Rieppel, 1984a, 1996; Daza and Bauer, 2012b; Daza et al., 2012). In a similar way, in *Homonota* and *Garthia*, two southern South American geckos of the family Phyllodactylidae, some characteristics resemble those of sphaerodactylids: the braincase is proportionally big, the snout is short, and the proportion between the muzzle unit and the parietal unit is 1:1. However, there is not an extensive overlap of the premaxilla and nasal. The muzzle overlap in these taxa is not extensive because there is a significant reduction in size of the jugal, maxilla and nasal. The most extensive reduction is observed in the jugal, a condition that is believed

to be related to small body size (Daza et al., 2017). Another difference is that the paroccipital process is not short and stout as in other miniaturized squamates (Sphaerodactylidae, Daza et al., 2011). Instead, in the miniaturized Phyllodactylidae, and in the gekkonid *Narudasia* (Daza et al., 2012) the joint of the quadrate with the otooccipital resembles that of large geckos, moving the quadrate-otooccipital joint to a more posterolateral position, rather than an anterior position as in miniaturized sphaerodactylids (Daza et al., 2017).

Another family of Gekkota that provides a good example of miniaturization is the Pygopodidae. The biology, ecology and general body plan of this family is different from that of all other Gekkota families; all members are limb reduced, have elongated bodies, and two genera became fossorial or semifossorial (*Aprasia* and *Ophidiocephalus*; Daza and Bauer, 2015). These differences determine the miniaturization pattern in Pygopodidae, which has several genera with extremely reduced body sizes and has been studied in detail (McDowell and Bogert, 1954; Rieppel, 1984a, 1984b, 1996; Evans, 2008; Daza and Bauer, 2015). Members of the family have a paedomorphic premaxilla with two ossification centers, and a suturing between the ascending nasal process of the premaxilla and the nasals that helps reinforce the snout (Daza and Bauer, 2015). In *Pletholax* the ascending nasal process of the premaxilla is convergent with *Chatogekko*, where the premaxilla is sutured to the frontal, separating the nasal bones (Gamble et al., 2011; Daza and Bauer, 2015). The post-temporal fenestra is reduced to a fissure between parietal and supraoccipital in *Pletholax* whereas in *Aprasia* it is completely closed. In both genera the descending process of the parietal is enlarged and in the same plane as the crista alaris of the prootic, closing the lateral wall of the skull as in other fossorial and

miniaturized species (Rieppel, 1984a; Daza and Bauer, 2015). Among all genera of miniaturized pygopods, *Aprasia* represents the smallest. This genus also includes some fossorial and semi-fossorial forms, with a skull length that ranges from 4 to 5 mm (Rieppel, 1984a; Daza and Bauer, 2015). *Aprasia* displays a combination of features that are associated with miniaturization and fossoriality similar to the ones described for other fossorial miniaturized squamates like *Dibamus* (Dibamidae) and some scolecophidians. *Aprasia* resembles *Dibamus* in the loss of the squamosal and supratemporal, similar but not identical quadrate suspension, the structure of the trabecula communis, and the absence of an interorbital septum in the chondrocranium. (Rieppel, 1984a, 1984b; Daza and Bauer, 2015).

Miniaturization has been extensively associated with paedomorphism (Hanken and Wake, 1993; Rieppel, 1996), and in the Gekkota there are several traits considered paedomorphic, including the paired premaxilla (in some genera) and parietals, amphicoelous vertebrae, notochordal canal, and large eye size compared to the length of the skull (Kluge, 1967; Werner, 1971). However, these characteristics are not exclusive to miniaturized geckos, and some are found less frequently in miniaturized taxa, for example, the premaxilla becomes fused in small forms (*Chatogekko amazonicus* and *Sphaerodactylus roosevelti*; Daza et al., 2008; Gamble et al., 2011), while it remains paired in larger geckos (Kluge, 1962; Daza and Bauer, 2012a). Another important trait that needs to be evaluated in detail is eye size relative to skull length. Ongoing research using ontogenetic series of gekkotans supports that the large eye of geckos is not a paedomorphic feature, but instead follows a negative allometric scaling relationship with the skull (Daza, pers. comm.).

Dibamidae. Dibamidae is a family of limbless, elongated, head-first burrowing squamates, currently classified in two genera: *Anelytropsis*, a monotypic genus found in northeastern Mexico (Greer, 1985); and *Dibamus* from northeast Asia (Greer, 1985) with 23 species currently recognized (Uetz et al., 2018). All species in the family are small with SVL ranging from 52 to 203 mm in the genus *Dibamus* and 77 to 180 mm in the genus *Anelytropsis* (Greer, 1985). Skull length in *Dibamus* can be as short as 5 mm (Rieppel, 1984b). Miniaturization in this family has been proposed to be the consequence of burrowing (Rieppel, 1984a) and therefore several convergent characteristics are found with other head-first burrowers (Gasc, 1968; Rieppel, 1984b; Greer, 1985; Lee, 1998).

In *Dibamus*, characteristics associated with burrowing and therefore with miniaturization include: the loss of the supratemporal fenestra and the reduction of the post-temporal fenestra (Gasc, 1968; Rieppel, 1984a, 1984b); reduction of the crista alaris, which is formed by an anterior extension of the prootic, contributing to the lateral wall of the braincase (Rieppel, 1984b); and a shallow sella turcica, with loss of the dorsum sellaris (convergent as in the anguimorph *Anniella*; Rieppel, 1984b). In addition, resembling the condition found in *Anniella* and fossorial skinks, the lateral aperture of the recessus scala tympani is closed (Rieppel, 1984b). As in amphisbaenians and snakes, the jaw adductor muscles are rearranged in Dibamidae, and particularly *Dibamus*, where the branches of the jaw adductor muscles extend onto the parietal (Gasc, 1968; Rieppel, 1984b). Miniaturized geckos also have a rearrangement of these muscles but it differs from that described for *Dibamus* (Rieppel, 1984b; Daza et al., 2011). The reduction of body size in *Dibamus* affects the orientation and organization of the jaw adductor

muscles fibers, which results in a mechanical disadvantage, but this is compensated by the increase in height of the coronoid eminence (Rieppel, 1984b).

Additional characteristics of miniaturization and burrowing found in *Anelytropsis* and *Dibamus* are the fusion of the postdentary bones of the jaw: surangular, angular, prearticular and articular (Rieppel, 1984b; Greer, 1985). Gasc (1968) describes the presence of a splenial bone in *Dibamus novaeguineae* but the presence of the bone was not confirmed in subsequent papers (Rieppel, 1984b; Greer, 1985); in one HRCT scan available of *Dibamus bogadeki* (YPM HERR 612715, Table 2), I could not determine if there was a discrete splenial bone, or a fused element with postdentary bones. One thing that is certain is that there is a bony structure occupying the position where the splenial should be.

The fusion of postdentary bones is convergent among burrowing miniaturized squamates (Lee, 1998), and this trait in dibamids is consistent with the predicted simplification or loss of structures in miniaturized animals (Hanken and Wake, 1993). Other characteristics of the dibamid skull should be examined in order to determine their relation to miniaturization.

Other characteristics reported for *Dibamus* include the late fusion of the bones of the braincase, especially otic and occipital regions (Greer, 1985). The skull of dibamids also undergoes simplification due to the loss or reduction of multiple bones, including the lacrimal, jugal, splenial, postorbital, supratemporal, squamosal, and epipterygoid (Rieppel, 1984b; Greer, 1985). In *Anelytropsis*, there is also a trend to reduce these elements, although a remnant of the temporal or squamosal was reported by Greer (1985), the epipterygoid is well developed, and the postorbital is highly reduced but a

remnant is present (Rieppel, 1984b; Greer, 1985). In the specimen of *Dibamus bogadeki* (YPM HERR 612715, Table 2) there was a postfrontal clasping the frontoparietal suture. It cannot be ruled out that many of these bones that have been reported as lost may indeed be an artifact of specimen preparation.

The snout in dibamids differs considerably from other miniaturized squamates such as geckos (*Aprasia*) and chameleons (Rieppel and Crumly, 1997; Daza et al., 2008). The ascending nasal process of the premaxilla is short and narrow, separating the nasals for about ½ of their length in *Anelytropsis*, while in *Dibamus*, the nasal process barely reaches the anterodorsal surface of the snout. In dibamids, the nasal bones separate the premaxilla and the frontal bone (Greer, 1985).

Scincomorpha. Within Scincomorpha, the best-studied examples of miniaturization are in the family Gymnophthalmidae. This family includes many small forms with elongated bodies and reduced limbs that lack external ear openings (Tarazona et al., 2008). There are several members of this group that are miniaturized, and that are strictly fossorial or sandswimmers, including *Bachia bicolor* (Ramos-Pallares et al., 2015; Tarazona et al., 2008), *Calyptomatus nicterus*, *Scriptosaura catimbau*, and *Nothobachia ablephara* (Roscito and Rodriguez, 2010), and species that are forest dwellers like *Potamites eupleopus* (Bell et al., 2003) or leaf litter dwellers and semifossorial like *Vanzosaura rubricauda* (Guerra and Montero, 2009).

One common trait of miniaturization in the Gymnophthalmidae is the elongation of the ascending nasal process of the premaxilla, which is sutured to the anterodorsal surface of the frontal bone, thus separating the nasals (Tarazona et al., 2008; Guerra and Montero, 2009; Roscito and Rodriguez, 2010). In *Bachia bicolor*, the nasal contacts the

frontal, and has a medial shelf that is overlapped by the ascending nasal process of the premaxilla (Tarazona et al., 2008). In *Scriptosaura catimbau* and *Nothobachia ablephara* the overlapping of the ascending nasal process of the premaxilla of the nasals is more extensive than in the sand swimmer *Calyptomatus nicterus* (Roscito and Rodriguez, 2010). In *Potamites ecleopus* the ascending nasal process of the premaxilla is short and does not contact the frontal or separate the nasals (Bell et al., 2003).

Evidence of miniaturization comes also from the circumorbital region of the skull. The lacrimal bone is very small in *Bachia bicolor* (Tarazona et al., 2008) and lost in *Calyptomatus nicterus*, *Scriptosaura catimbau* and *Nothobachia ablephara* (Roscito and Rodriguez, 2010). In *Vanzosaura rubricauda* and *Potamites ecleopus*, the lacrimal is absent, but review of specimens of different developmental stages revealed an incomplete suture between the lacrimal and the prefrontal indicating that the former is not lost but rather fused (Bell et al., 2003; Guerra and Montero, 2009).

The skull roof and the neurocranium of miniaturized gymnophthalmids are highly variable. The closed supratemporal fenestra is recognized by Rieppel (1996) as one of the characteristics of miniaturization and fossoriality, however, the supratemporal fenestra is open in *Bachia bicolor* (Tarazona et al., 2008) and narrow and elongated in *Vanzosaura rubricauda* (Guerra and Montero, 2009) and *Potamites ecleopus* (Bell et al., 2003). The post-temporal fenestra shows variability as well, being closed in adult specimens of *Bachia* and some specimens of *Scriptosaura catimbau* where the parietal is sutured to the supraoccipital (Tarazona et al., 2008; Roscito and Rodriguez, 2010), and open in *Vanzosaura*, *Calyptomatus* and *Nothobachia* (Guerra and Montero, 2009; Roscito and Rodriguez, 2010). In *Calyptomatus* hypertrophied ventral parietal process fits between

the epipterygoid and the braincase, enclosing entirely the brain cavity (Roscito and Rodriguez, 2010). In *Bachia* the parietal partially closes the brain cavity and contacts the alar process of the prootic posteriorly (Tarazona et al., 2008), or partially closes the braincase in front of the epipterygoid in *Scriptosaura* (Roscito and Rodriguez, 2010). In other species, the lateral wall of the brain cavity is not be well developed, for example in *Vanzosaura*, *Nothobachia* or *Potamites ecleopus* (Bell et al., 2003; Guerra and Montero, 2009; Roscito and Rodriguez, 2010).

Synostosis of the braincase in adult stages is common in miniaturized gymnophthalmids such as *Vanzosaura rubricauda*, *Nothobachia ablephara* and *Scriptosaura catimbau* (Guerra and Montero, 2009; Roscito and Rodriguez, 2010). In other species such as *Calypptomatus nicterus* and *Bachia bicolor* the braincase is not completely fused in adults and the sutures are visible especially between the parabasisphenoid, basipterygoid and prootic (Tarazona et al., 2008; Roscito and Rodriguez, 2010). In neonates of *Bachia*, these bones are sutured by cartilage (Tarazona et al., 2008).

Other characteristics subject to variation with the ontogeny of *Bachia* are the ossification of the skull roof, which follows the pattern described by Rieppel (1996) where, in neonates, the only parts of the skull roof that are completely ossified are the lateral wall of the parietal and the frontals (Tarazona et al., 2008). The observation of specimens at different stages of development in *Potamites ecleopus* also indicates that the fusion of the braincase is a continuous process that starts with the fusion of the exoccipital and the opisthotic in the neonates and ends with the complete fusion of the

braincase when specimens have reached about 95% of their expected adult size (Bell et al., 2003).

The jaw shows several similarities in miniaturized gymnophthalmids. The coronoid process is low (Tarazona et al., 2008; Guerra and Montero, 2009; Roscito and Rodriguez, 2010), similar to the condition in miniaturized geckos (Daza et al., 2008) but differing from *Dibamus* (Rieppel, 1984a). Other similarities are found in the post-dentary bones. The splenial and angular are present as discrete elements, even though the angular is very small in *Bachia bicolor* (Tarazona et al., 2008) and there is a fused compound bone (Tarazona et al., 2008; Guerra and Montero, 2009; Roscito and Rodriguez, 2010). However, the bones that fuse to make the compound bone vary (Tarazona et al., 2008; Guerra and Montero, 2009; Roscito and Rodriguez, 2010). In *Bachia bicolor* and *Vanzosaura rubricauda* the fusion occurs between the articular and the surangular (Tarazona et al., 2008; Guerra and Montero, 2009) while in *Calypotomatus nicterus*, *Scriptosaura catimbau* and *Nothobachia ablephara* the surangular is an isolated bone and the prearticular and articular are fused (Roscito and Rodriguez, 2010). In *Potamites ecleopus* the surangular is partially fused to the prearticular-articular complex and the angular is a small bone restricted to the ventral part of the lower jaw (Bell et al., 2003).

Characteristics associated with miniaturization are also found in other families within Scincomorpha like Lacertidae and Scincidae. A detailed description of the skull of *Parvilacerta parva* (Müller, 2002), a small lacertid with a skull length of approximately 13 mm and jaw length that ranges from 8.7 to 11.8 mm, exposes some of the characteristics associated with miniaturization described by Rieppel (1984a, 1996) such as the enlargement of the neurocranium that is at the same level of the skull roof of the

dermatocranium, not below it, and the post-temporal fossa and supratemporal fenestra are closed (Müller, 2002). Additionally, as in some gekkotans (Daza et al., 2018) it has an elongated ascending nasal process of the premaxilla, which separates the nasals approximately $\frac{1}{2}$ of their length, however, the process does not contact the frontals (Müller, 2002).

Within the Scincidae there is a large taxonomic diversity and a great variability of body size (Vitt and Caldwell, 2014). In this family, body elongation is common and its relation to miniaturization and morphological changes in the axial skeleton has been reviewed for *Eumeces* where the number of presacral vertebrae is greater than in the smallest species (Griffith, 1990). However, the skull anatomy of this non-fossorial skink needs to be evaluated.

Regarding cranial morphology, the best examples of miniaturization come from head-first burrowers. Rieppel (1984a) recognized three miniaturized genera within the subfamily Acontinae and recognized miniaturization as a result of fossoriality. The three genera are *Acontias*, with only one species of non-miniaturized adult skull size that retains the upper temporal arcade (*Acontias plumbeus*; Rieppel, 1981), *Feylinia* and *Typhlosaurus*. All members of these genera have species with skull lengths of less than 15 mm and the general characteristics of miniaturized fossorial lizards.

The supratemporal fenestra is highly variable: it can be open as in *Feylinia* (Rieppel, 1981); open but narrow as in *Typhlosaurus* (Rieppel, 1981, 1984a); or the upper temporal arcade is lost and the fenestra reduced as in *Acontias* (Rieppel, 1981). The post-temporal fenestra is very reduced in *Feylinia* (slit-like) and completely closed in *Acontias percivali* and *Typhlosaurus* (Rieppel, 1981).

The lateral wall of the braincase is completely closed by the extension of the descending process of the parietal and the extension of the crista alaris of the prootic. The descending process of the parietal is more extensive in *Typhlosaurus* than in *Acontias*; in *Feylinia* this process is reduced to a narrow projection (Rieppel, 1981).

The ascending nasal process of the premaxilla is not elongated in this group of head-first burrowing skinks; this process does not extend posteriorly, and does not contact the frontals (Rieppel, 1981, 1984a). In *Typhlosaurus* the premaxilla remains unfused anteriorly but it is fused posteriorly in the ascending nasal process of the premaxilla, as in the gekkotan *Aprasia* (Daza and Bauer, 2015). In both *Typhlosaurus* and *Aprasia*, the ascending nasal process is short and does not contact the frontals.

Loss, reduction or fusion of bones is common in miniaturized Dibamidae (Greer, 1985) and Gymnophthalmidae (Bell et al., 2003; Guerra and Montero, 2009). Bone reduction or loss is also common in the Acontinae: in the genus *Acontias* the lacrimal is reduced; in *Typhlosaurus* the jugal and lacrimal are extremely reduced; and the jugal and lacrimal have been described as lost in *Feylinia* (Rieppel, 1981). All lower jaw bones are present; however, the angular is reduced and restricted to the ventral side in *Typhlosaurus* and the coronoid is low in *Feylinia*.

Amphisbaenians. Amphisbaenians are a group of exclusively fossorial squamates currently classified in six families (Amphisbaenia, Bipedidae, Blanidae, Cadeiae, Rhineuridae and Trogonophidae; Uetz et al., 2018). All are specialized head-first burrowers and most are limbless, except Bipedidae which retain the forelimbs (Gans, 1978). The high degree of specialization of amphisbaenians and the type of substrate they excavate are responsible for the variety of head shapes (Gans and Montero, 2008) and

overall, four different head morphotypes are recognized: shovel-headed, round-headed, keel-headed and spade-headed. These head shape types are associated with a particular mode of excavation rather than phylogeny (i.e., *Diplometopon zarudnyi*, Trogonophidae, has the spade-head morphotype and uses an oscillatory movement of the head to excavate through loose aeolian sands; Maisano et al., 2006).

Cranial morphology of amphisbaenians is very different from that of other squamates, and the increased modifications found in the skull represent a challenge for deciphering the evolutionary history of this group (Gans, 1978). Some of these characteristics include: the interlocking sutures in members of Amphisbaenidae, especially between the frontal and the parietal; a completely fused braincase in the otic-occipital complex; fusion of bones in the mandible; posterior extension of the dentary; lack of temporal arches; reduced kinesis of the skull; lack of palatal and suborbital fenestra; the parietal wall completely closing the braincase; and a secondary palate (Gans and Montero, 2008).

Some of these characteristics, such as the fusion and closure of the braincase or the lack of temporal arches, are characteristics of miniaturized squamates (Rieppel, 1984a, 1996); however these are synapomorphies of the amphisbaenians regardless of their skull size. In addition, many amphisbaenians have small skull length (see Appendix 1 and Table 3.1 in Gans and Montero, 2008). Therefore, assessing miniaturization in this group of squamates that have highly modified skulls is more complicated.

Gans and Montero (2008) evaluated changes in the skull pattern in large and small species of the genus *Amphisbaena* (Amphisbaenidae) and they found changes are transitional between small and large species with transitional stages. The smallest species

in their analysis are *Amphisbaena lumbricalis* with a skull length of 6.0 mm and *Amphisbaena slevini* with 5.8 mm (Gans and Montero, 2008). Among the characteristics associated with a reduction of skull length are: equal width between the snout and the otic-occipital region; sagittal crest absent or very low; decreased interdigitation in the frontoparietal and interfrontal sutures; anterior supraoccipital process short; reduced flexion of snout with respect to pterygoid plate; absent or small basipterygoid; and quadrate thin and tilted (Gans and Montero, 2008).

In summary, previous descriptions of many different squamate groups indicate that similar characteristics have been developed independently. Additional traits of the skull related to a reduction in body size in major clades of squamates will be revised and contrasted among miniaturized squamates in the next chapter. I will test some of these traits in a phylogenetic framework to determine and identify additional possible cranial characteristics of miniaturized squamates.

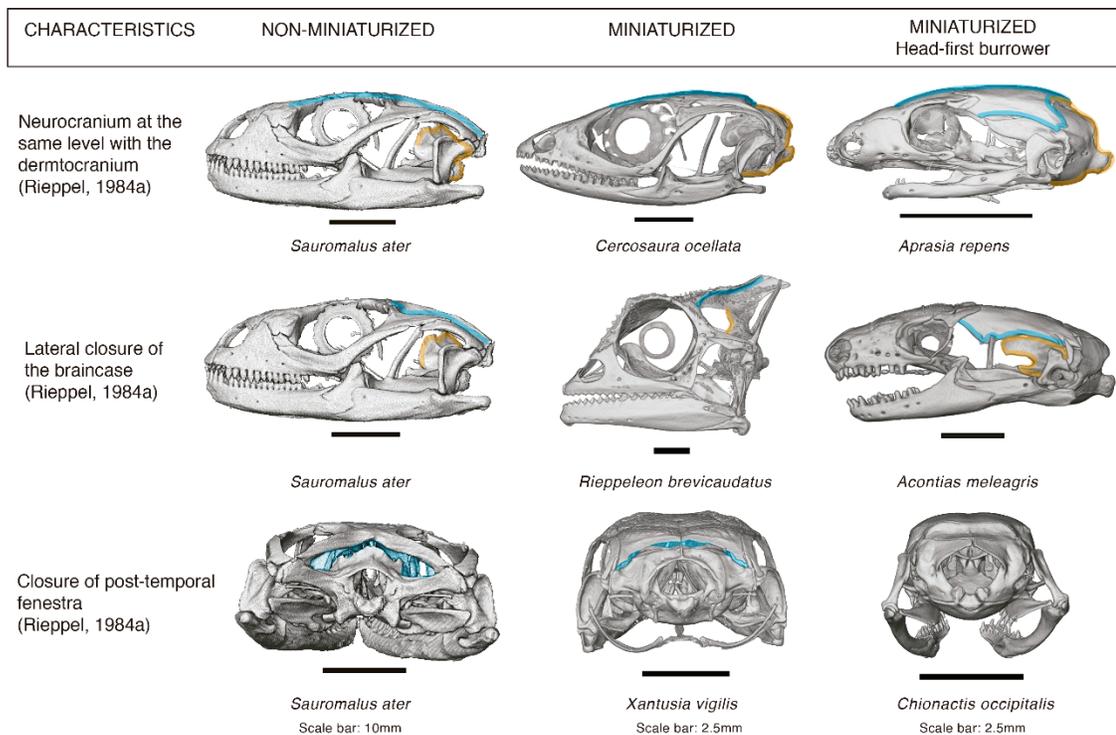


Figure 2. Characteristics of miniaturization in the skull of squamates, part one. Comparison of a non-miniaturized species, the Iguanian *Sauromalus ater* (column1), with miniaturized species of different groups. First two rows show the skulls in lateral view and the third row shows skulls in posterior view. *Sauromalus ater* images from DigiMorph.org. Author created.

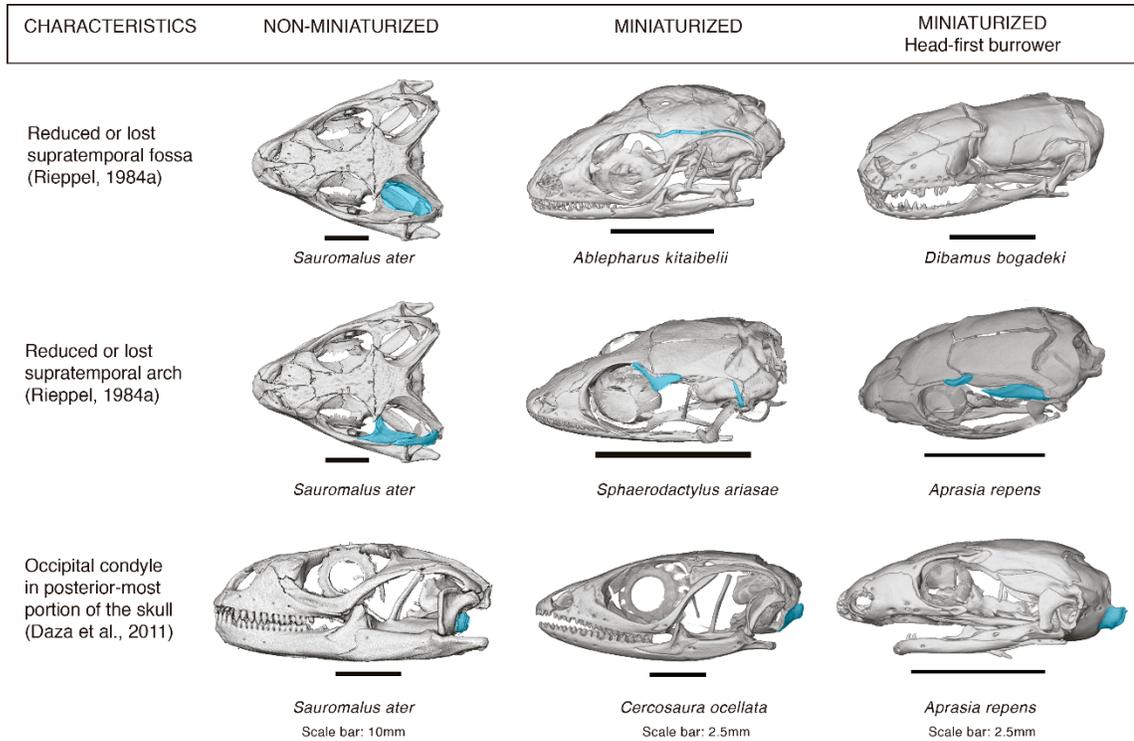


Figure 3. Characteristics of miniaturization in the skull of squamates, part two. Comparison of a non-miniaturized species, the Iguanian *Sauromalus ater* (column 1), with miniaturized species of different groups. In first two rows the skull of *Sauromalus ater* in dorsal view, all other species in dorso-lateral view. Third row shows skulls in lateral view. *Sauromalus ater* images from DigiMorph.org. Author created.

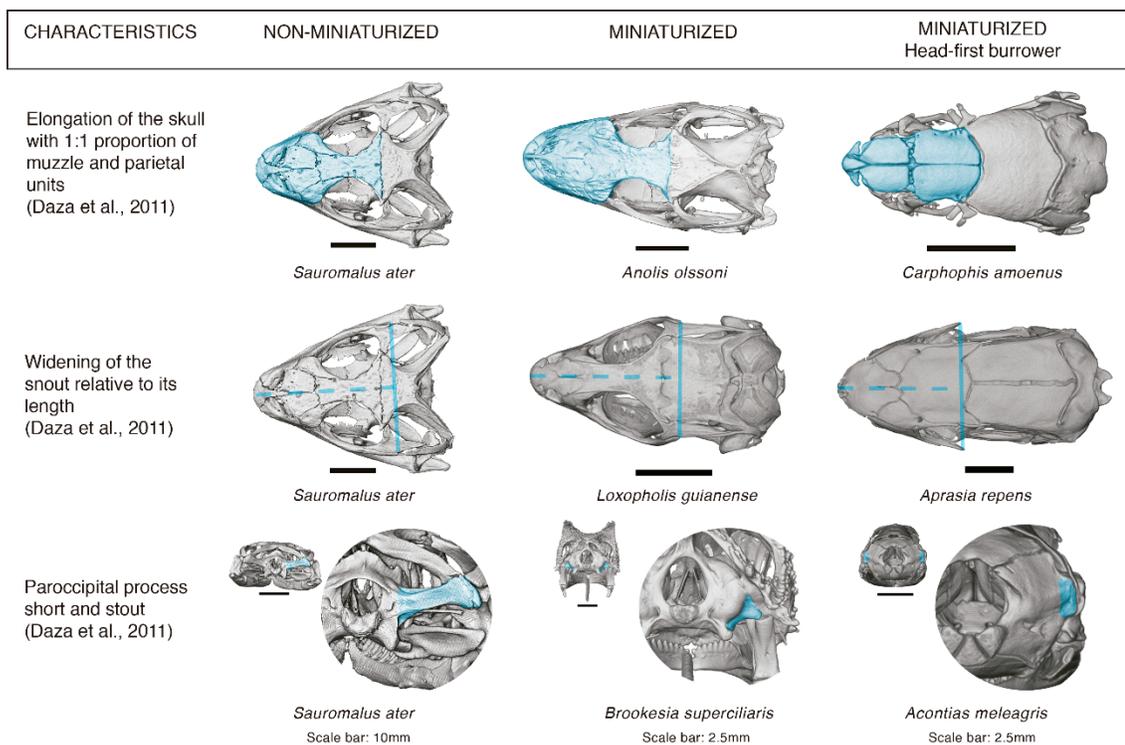


Figure 4. Characteristics of miniaturization in the skull of squamates, part three. Comparison of a non-miniaturized species, the Iguanian *Sauromalus ater* (column 1), with miniaturized species of different groups. First two rows show skulls in dorsal view. Third row shows skulls in posterior view with an enlarged image with detail. *Sauromalus ater* images from DigiMorph.org. Author created.

Table 2

List of Specimens used in this project.

Family	Species	Catalog number
Chamaeleonidae	<i>Brookesia micra</i>	ZSM uncatalogued
Chamaeleonidae	<i>Brookesia minima</i>	YPM HERR.010232
Chamaeleonidae	<i>Brookesia superciliaris</i>	YPM HERR.010233
Chamaeleonidae	<i>Rieppeleon brevicaudatus</i>	YPM HERR.011665
Colubridae	<i>Chionactis occipitalis</i>	YPM HERR.018232
Colubridae	<i>Carphophis amoenus</i>	YPM HERR.013611
Dactyloidae	<i>Anolis olssoni</i>	YPM HERR.003101
Dibamidae	<i>Dibamus bogadeki</i>	YPM HERR 612715
Gymnophthalmidae	<i>Anadia ocellata</i>	YPM HERR.017102
Gymnophthalmidae	<i>Loxopholis guianense</i>	YPM HERR.015357
Gymnophthalmidae	<i>Cercosaura ocellata</i>	YPM HERR.016695
Pygopodidae	<i>Aprasia repens</i>	YPM HERR 014702
Scincidae	<i>Ablepharus kitaibelii</i>	YPM HERR.005804
Scincidae	<i>Acontias meleagris</i>	YPM HERR.000851
Scincidae	<i>Scincella assatus</i>	YPM HERR.012314
Scincidae	<i>Isopachys gyldenstolpei</i>	YPM HERR.011914
Scincidae	<i>Janetaescincus vesevfitzgeraldi</i>	YPM HERR.006085
Scincidae	<i>Menetia greyii</i>	YPM HERR.013675
Sphaerodactylidae	<i>Sphaerodactylus ariasae</i>	USMN 541810
Xantusiidae	<i>Xantusia vigilis</i>	YPM HERR.017170

CHAPTER III

Materials and Methods

Identification of miniaturized taxa

This project uses as base information a published dataset of morphological characteristics for squamates (lizards, snakes and amphisbaenians) (Gauthier et al., 2012, and additions in Longrich et al., 2012; Martill et al., 2015). The dataset contains a total of 205 fossil and extant species of squamates and includes miniaturized and non-miniaturized groups. The data matrix includes 642 phenotypic characters, of which 437 are related to skull morphology.

I used a cutoff value of 15 mm skull length (SL) to classify species as miniaturized or not. This value was estimated in a previous study (Rieppel, 1984a) and its rationale is explained in the previous chapter. Skull length was measured from the anterior tip of the premaxilla to the posterior part of the occipital condyle in all specimens used in Gauthier et al. (2012), Longrich et al. (2012) and Martill et al. (2015). The measurements were taken from the available high-resolution computed tomographies (HRCT) at The University of Texas High-Resolution X-ray CT Facility (UTCT), and the Digital Library of Morphology (DigiMorph.org, from www.digimorph.org/) using the inspeCTor tool. For specimens where HRCT were not available, SL was obtained from publications or published images of the species. The list of taxa, their measurements, and the references from which those measurements were taken or estimated are reported in Appendix 1.

Considering that some of the smallest squamates were not included in the initial datasets and that the inclusion of those species is fundamental for addressing the

evolution of miniaturization in Squamata, HRCT for several miniaturized species were acquired at UTCT. Seven additional species were added in the phenotypic data sets, including five specimens from the Yale Peabody Museum of Natural History (Table 2, Chamaeleonidae: *Brookesia minima*, YPM HERR.010232; *B. superciliaris*, YPM HERR.010233; *Rieppeleon brecivaudatus*, YPM HERR.011665; Pygopodidae: *Aprasia repens*, YPM HERR 014702; and Dibamidae: *Dibamus bogadeki*, YPM HERR 012715). The smallest gekkotan (Sphaerodactylidae: *Sphaerodactylus ariasae*, USMN 541810) is deposited in the National Museum of Natural History Smithsonian Institution in Washington DC. One specimen of one of the smallest chameleons (Chamaeleonidae: *Brookesia micra*, ZSM uncatalogued) is deposited in the Bavarian State Collection of Zoology in Munich Germany.

Tomograph image stacks of specimens were loaded into the computer software Avizo Lite version 9.4. (Thermo Fisher Scientific, Waltham, MA). Three dimensional model renderings were used to obtain the skull morphological characters of each species and include them in the dataset of Martill et al. (2015). A total of 437 morphological characters of the skull were scored for each of the additional species (Appendix 2). Postcranial data were left as missing data.

Phylogenetic analysis using parsimony and identification of convergent characteristics

The new data set was analyzed with the computer program TNT 1.5 (Goloboff and Catalano, 2016) using the new technology option and the search strategy specified in Daza et al. (2016).

Additionally, to identify possible new characters exclusive of all miniaturized taxa, I performed four additional phylogenetic analyses after implementing a series of constraints: 1) all miniaturized taxa (i.e., skull length of 15 mm or less) were constrained to be monophyletic; 2) all miniaturized taxa with skull length of 10 mm or less (intermediate miniaturization), were constrained to be monophyletic; and 3) all miniaturized taxa with skull length of 5 mm or less (extreme miniaturization) were constrained to be monophyletic. These three constraints were made to detect what traits were possibly affected with different levels of size reduction. Finally, a fourth analysis was done forcing the monophyly of all the miniaturized head-first burrowers.

Each constrained analysis was performed using a new technology search with the command “xmult” with 1000 replicates until the most parsimonious tree was found 50 times. I searched for the strict consensus tree and used it to identify convergent characteristics of each constrained group by mapping the synapomorphies of each node. I only used those synapomorphies that were optimized for the node of the constrained group. I calculated the consistency index for each character that supported the constrained node using Mesquite version 3.31 (Maddison and Maddison, 2018). In this case the consistency index was interpreted as a measure of how “homoplastic” a character was, but keeping in mind that the groups found with these analyses are not natural.

Finally, all characteristics identified for miniaturized squamates, including described traits in the literature, and the constrained analyses, were tested in an additional sample of 20 miniaturized species of squamates (Table 2). The characteristics were observed from HRCT of these specimens.

Testing the similarities or dissimilarities of convergent data

To test the similarity of the identified convergent characters for miniaturized squamates I performed a Principal Coordinate Analysis (PCoA) in the software PAST3 (Hammer et al., 2001) version 3.19. This analysis indicates the similarity between the miniaturized species and the non-miniaturized species by means of the identified characteristics for miniaturization. A PCoA analysis was performed using the traits identified for each category with the constrained analysis (15 mm and below, 10 mm and below, 5 mm and below, and head-first burrowers). For the analysis, all characters were set as ordinal data.

In these analyses, I excluded all the fossil taxa (55 species, Appendix 1) because of the large amount of missing data these species incorporated in the analysis. For extant species, inapplicable data were scored as belonging to a different category (8) because PCoA analyses do not allow missing values.

Evolution of the skull size among squamate reptiles

To evaluate the evolution of skull length in Squamata, I performed a phylogenetic analysis using Parsimony TNT 1.5 (Goloboff and Catalano, 2016) using the same search strategy used by Daza et al. (2016). The strict consensus tree was used to reconstruct the ancestral state of skull length. The reconstruction was done in Mesquite version 3.31 (Maddison and Maddison, 2018) using a parsimony model of reconstruction for unordered characters. The skull lengths of the species were taken from the list of species and measurements, which are listed in Appendix 1.

CHAPTER IV

Results

Skull length measurements and categories of miniaturization

I was able to acquire skull length data for 205 species (Appendix 1) from the phenotypic data set (Martill et al., 2015). Eight species were excluded because it was not possible to measure their skull length with accuracy (i.e., HRCT data were not available, and/or accurate illustrations, photographs or measurements were not available in the literature). The remaining 197 species include 47 that fall within the miniaturization category (i.e., SL equal to or shorter than 15 mm). After including seven of the smallest squamates in the dataset (*Brookesia micra*, *Brookesia minima*, *Brookesia superciliaris*, *Rieppeleon brecivaudatus*, *Dibamus bogadeki*, *Aprasia repens* and *Sphaerodactylus ariasae*), the total number of species included in the analysis is 204, of which 54 are miniaturized (Appendix 1).

To evaluate if additional convergent characteristics are exclusive to all miniaturized members, I established three categories of miniaturization according to skull length. The first category includes all miniaturized squamates that have a skull length of 15 mm or less (54 species), the intermediate category includes species with skull lengths of 10 mm or less (26 species), and the last category of extreme miniaturization includes species that have 5 mm or less of skull length. Of the five species in the category of extreme miniaturization, three are head-first burrowers (*Typhlops squamosus*, *Liotyphlops albirostris*, and *Aprasia repens*) and two are leaf litter dwellers (*Brookesia micra* and *Sphaerodactylus ariasae*).

For all the miniaturized species in the dataset, the lifestyle was recorded and organized into two categories: head-first burrower or not. Of the 54 miniaturized species, 23 were head-first burrowers (Appendix 1).

Identification of convergent characteristics of miniaturization using phylogenetic methods

In the search for possible convergent characteristics among miniaturized squamates, three phylogenetic analyses with different constrained groups were performed. Character numbering in this section follows previous studies (Gauthier et al., 2012; Longrich et al., 2012; and Martill et al., 2015).

Overall, eleven characteristics related to skull morphology and one characteristic of the hyoid apparatus were identified. The first analysis induced monophyly of all species with a skull length equal to or smaller than 15 mm (54 species in total; Appendix 1). After finding the minimum tree length 50 times (50 hits), 410 most parsimonious trees were saved with a best score of 6541. The strict consensus was calculated using all the trees (Figure 5), and in the figure the constrained group of all miniaturized species is highlighted.

In the constrained tree miniaturized and head-first burrowing species were nested within Iguania. An interesting unexpected result is that within the constrained group, Iguania was not recovered as monophyletic although other major clades in of miniaturized or head-first burrowers were resolved in groups concordant with unconstrained analysis (Figure 5).

The Gekkota was recovered as a monophyletic group, as was the “fossorial group” (Gauthier et al., 2012) including dibamids, amphisbaenians and snakes. These

were recovered together as a cluster, although the Jurassic fossil snake *Diablophis gilmorei* fell outside this group. The fossorial group was recovered as sister to *Anniella pulchra*, which is the only miniaturized member of Anguimorpha within the dataset. The snakes are divided into two major clades, the Scolecophidia and Alethinophidia (Figure 5).

The constrained group is supported by one convergent characteristic from the hyoid apparatus, the absence of a second ceratobranchial opposed on midline (Character 448, state 0). It is worth mentioning that in the data set 130 species out of the 204 are scored as missing data (?) for this character, and the second ceratobranchial opposed on the midline is only present in some iguanids, regardless of their skull size. At the subsequent node, after the iguanian *Uta stansburiana*, two additional convergent characteristics of the skull were optimized (Figure 6): the posterior termination of the dentary coronoid process is below the level of the coronoid apex (Character 364, state 0, CI=0.077) and the number of dentary teeth is between 10 – 20 (Character 421, state 2, CI=0.069).

The constrained group of the intermediate size category of miniaturization included 26 species with skull lengths of 10 mm or less. The phylogenetic analysis with this constrained group and all the other non-miniaturized species retained 18 most parsimonious trees with a best score of 6226 with 50 hits. I calculated the strict consensus tree (Figure 7).

The general topology of the constrained group supports some of the squamate groups at the familial level, but the relationships among the families are different from unconstrained analysis. The constrained miniaturized clade is nested within the

Scincomorpha. Within the constrained group, the scincomorphs are not closely related to each other and Gekkota forms a monophyletic group that is grouped together with xantusiids. Head-first burrowers including *Acontias percivali* are grouped with the miniaturized anguimorph *Anniella pulchra* and other species. Dibamids formed a clade sister to a clade of amphisbaenians. Iguanians, represented by two chameleon species, are sister to a clade of snakes. As in the previous analyses, snakes are divided into the two major clades: Scolecophidia and Alethinophidia (Figure 7).

Six convergent characteristics for the constrained node were identified for the analysis of 10 mm or less of skull length (Figure 8): suborbital margin of the maxilla suborbital process at the jugal articulation slopes smoothly towards the tip of the process (Character 123, state 0, CI=0.166); prefrontal orbitonasal margin slopes ventromedially (Character 128, state 2, CI=0.129); ectopterygoid posterior process absent (Character 283, state 2, CI=0.105); epipterygoid located entirely anteriorly to prootic (Character 291, state 1, CI=0.05); median maxillary tooth absent (Character 413, state 0, CI=0.03); and maxilla tooth row ends anterior to midorbit (Character 418, state 1, CI=0.09).

The analysis constraining the monophyly of extreme miniaturization (5 mm or less) included 5 such species. From this analysis 249 trees were retained, with a best score of 5869 with 50 hits. I calculated the strict consensus tree (Figure 9). The constrained node with the five miniaturized species is sister to a clade of snakes. Within the constrained node, there place the is a clade including two scolecophians, *Liotyphlops albirostris* and *Typhlophis squamosus*, sister to a clade including *Brookesia micra*, which is also sister to a clade formed by the two gekkotans, *Aprasia repens* and *Sphaerodactylus ariasae*.

The group with extreme miniaturization is supported by three convergent characters (Figure 10): premaxilla internal process size very reduced or absent (Character 14, state 1, CI=0.143); nasals fused (Character 17, state 1, CI=0.125); and splenial absent (Character 374, state 1, CI=0.22).

The constrained analysis with the fossorial group included 23 head-first burrower species, and recovered 442 most parsimonious trees with a best score of 5968 with 50 hits. In this analysis the constrained group is nested within snakes (Figure 11). Within the miniaturized head-first burrower group, the snakes are not grouped together, and therefore the two major groups (Scoleophidia and Alethinophidia) are not recovered. Dibamids and amphisbaenians are sister to each other.

The miniaturized head-first burrower group has ten convergent characteristics, two of which are not related to the skull but are associated more with limblessness: absence of the pubis (Character 510, state 1, CI=0.125); and absence of the femur (Character 548, state 1, CI=0.125). The remaining eight characters are related to skull morphology (Figure 12): suture between the frontal and the parietal is lightly interdigitated or there is simple abutment (Character 56, state 1, CI=0.174); postorbital lost (Character 68, state 1, CI=0.09); parietal sagittal crest absent (Character 93, state 0, CI=0.09); parietal supratemporal process is reduced and represents less than 25% of the parietal width (Character 101, state 1, CI=0.125); maxilla narial margin rises at a high angle (Character 118, state 0, CI=0.2); parabasisphenoidal keel absent (Character 326, state 0, CI=0.2); medial aperture of the recessus scala tympani (MARST) entirely on opisthotic (Character 344, state 1, CI=0.087); and retroarticular process present (Character 404, state 1, CI=0.067).

To test the characters identified in these analyses and those mentioned in literature (see Chapter 1), I compiled a list of 21 characters. I scored only these traits in 20 additional miniaturized squamates (Table 2) to evaluate their presence (Table 3); however, none of the identified traits are present in all of these miniaturized species. There are characteristics present in most of them, and usually the exceptions are Iguanians (Chamaleonidae and Dactyloidae). Characters that are present in the vast majority of miniaturized squamates included the following. The occipital condyle in the posterior-most portion of the skull (Daza et al., 2011) is absent only in the chameleon *Rieppeleon brevicaudatus*. The paroccipital process is short and stout (Daza et al., 2011) in the majority of miniaturized squamates, except in some Iguanians (*Rieppeleon brevicaudatus* and *Anolis olssoni*). The skull being longer than wide (Daza et al., 2011) is not found in *Brookesia micra* and *Brookesia minima*, two species characterized by a short snout that is ventrodorsally oriented. Features that are found in 15 of the miniaturized species include: the jaw muscle attachment shifted posterodorsally (Rieppel, 1984a); the muzzle unit/parietal-braincase complex ratio equal or nearly 1:1 (Daza et al., 2008); and the fusion of postdentary bones (Lee, 1998).

The two species that have most of the evaluated traits are the gecko *Sphaerodactylus ariasae*, with 19 out of 21 traits present, and the skink *Menetia greyii*, which exhibits 17 out of 21 traits. In both species the characteristics that are not found are the prefrontal-orbitonasal margin sloping ventromedially, reduction in the premaxilla internal process and the fusion of the nasals. In addition to these, *Menetia greyii* does not have an increased overlapping of bones in the muzzle unit. The iguanians, and

particularly *Anolis olsoni*, *Rieppeleon brevicaudatus* and *Brookesia micra*, were the species that have the lowest number of miniaturization traits.

Not all characteristics identified here as being correlated with miniaturization are found in all miniature species as was evident from the constrained group analyses, since the CIs were generally very low. Additionally, some of the traits are more common than others (Table 3).

Table 3

Characteristics of miniaturization. Evaluation of the traits associated with miniaturization from the literature review and from the constrained analysis.

Family	Species	Skull Length (mm)	Characteristic																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Chamaeleonidae	<i>Brookesia micra</i>	4.08						•	•	•	•							•		•	•	•	•
Chamaeleonidae	<i>Brookesia minima</i>	5.5					•	•	•			•						•	•	•	•	•	•
Chamaeleonidae	<i>Brookesia superciliaris</i>	11.1				•		•	•			•	•					•			•	•	•
Chamaeleonidae	<i>Rieppeleon breviceaudatus</i>	11.5				•	•		•			•	•					•		•			
Colubridae	<i>Chionactis occipitalis</i>	6.72	•	•	•	•		•	•	•			•	•				•		•		•	•
Colubridae	<i>Carphophis amoenus</i>	7.75	•	•	•	•		•	•	•			•	•				•		•		•	•
Dactyloidae	<i>Anolis olssoni</i>	12.9			•	•		•	•						•	•			•				•
Dibamidae	<i>Dibamus bogadeki</i>	7.1	•	•	•	•	•	•	•	•	•	•			•	•			•			•	•
Gymnophthalmidae	<i>Anadia ocellata</i>	9.8	•	•	•	•		•	•	•	•	•			•	•	•		•				•
Gymnophthalmidae	<i>Loxopholis guianense</i>	8.5	•	•	•	•	•	•	•	•	•				•	•							
Gymnophthalmidae	<i>Cercosaura ocellata</i>	10.9	•	•	•	•		•	•	•	•				•	•							•
Pygopodidae	<i>Aprasia repens</i>	4.0	•	•	•	•	•	•	•	•	•				•	•			•		•	•	•
Scincidae	<i>Ablepharus kitaibelii</i>	4.2		•	•	•		•	•	•	•	•	•		•	•	•	•	•			•	•
Scincidae	<i>Acontias meleagris</i>	10.6	•	•	•	•		•	•	•	•		•	•	•	•	•	•	•			•	
Scincidae	<i>Scincella assatus</i>	8.5	•	•	•	•		•	•	•	•	•			•	•	•	•					
Scincidae	<i>Isopachys gyldenstolpei</i>	10.1	•			•	•	•	•	•	•	•				•	•	•	•				•
Scincidae	<i>Janetaescincus vesevfitzgeraldi</i>	6.5	•	•	•	•		•	•	•	•	•			•	•	•	•					•
Scincidae	<i>Menetia greyii</i>	6.5	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•				•	•
Sphaerodactylidae	<i>Sphaerodactylus ariasae</i>	4.22	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•				•	•
Xantusiidae	<i>Xantusia vigilis</i>	9.8	•	•	•	•		•	•	•	•	•	•	•		•		•					

Note(1) Reduction of skull diameter, neurocranium and dermatocranium positioned at the same level (Rieppel, 1984a); (2) Posttemporal fossa open or obliterated (Rieppel, 1984a); (3) Jaw muscles attachment shifted posterodorsally (Rieppel, 1984a); (4) Skull longer than wide (Daza et al., 2011); (5) Wide snout (Daza et al., 2011); (6) Occipital condyle located in the most posterior margin of the skull (Daza et al., 2011); (7) Paroccipital process short and stout (Daza et al., 2011); (8) Increased overlapping of bones in the muzzle unit (Daza et al., 2008); (9) Muzzle unit/ parietal-braincase complex ratio equal or similar to 1:1 (Daza et al., 2008); (10) Dentary coronoid process posterior termination below or anterior to level of coronoid apex (Gauthier et al., 2012); (11) Dentary tooth count between 10-20 (Gauthier et al., 2012); (12) Suborbital margin of the maxilla suborbital process at the jugal articulation slopes smoothly towards the tip of the process (Gauthier et al., 2012); (13) Prefrontal orbitonasal margin slopes ventromedially (Gauthier et al., 2012); (14) Ectopterygoid posterior process absent (Gauthier et al., 2012); (15) Epipterygoid in resting position located entirely anterior to prootic (Gauthier et al., 2012); (16) Median premaxillary teeth absent (Gauthier et al., 2012); (17) Maxilla tooth row extends behind midorbit (Gauthier et al., 2012); (18) Premaxilla internal process size very reduced or absent (Gauthier et al., 2012); (19) Nasals fused (Gauthier et al., 2012); (20) Splenial absent (Gauthier et al., 2012); and (21) Postdentary bones fused (Lee, 1998). The black dots denote the presence of the character in the species.

Testing the similarities or dissimilarities of convergent data

To see if the proposed characteristics of miniaturization were more similar among phylogenetic groups or were more similar in miniaturized taxa I performed a Principal Coordinate Analysis (PCoA) for each of the categories of miniaturization (15 mm of skull length or less; intermediate with 10 mm or less; and extreme with 5 mm or less) and for the head-first burrowers.

The PCoA of all the miniaturized taxa was done using the two traits related to skull morphology found in the constrained analysis. The comparison between miniaturized and non-miniaturized taxa (Figure 13) shows that most snakes group together and form a group morphologically distinct from lizards. Within other groups of lizards, gekkotans grouped together in two different clusters, and these clusters did not include other groups of lizards. *Aprasia repens* plotted separately from all other taxa. Miniaturized species, which are represented by red symbols in Figure 13, do not cluster together. In combination, these results indicate that the traits of miniaturization found with the constrained analysis are highly variable among squamates and are not unique for miniaturized species. This result is consistent with data derived from the literature review and constrained analyses.

The PCoA with the characteristics of intermediate miniaturization (Figure 14) produced less well defined groups than the previous analysis. In this analysis was recovered a cluster that includes some snake species in the second quadrant of the plot, but other snakes were found in other areas of the plot. Most species of lizards were clumped together in the first quadrant of the plot, but there are no major differences between the major clades. Some miniaturized species fell within this group, but others

were found in other areas of the plot. This plot does not show major differences between miniaturized and non-miniaturized species. Instead, the PCoA showed a high degree of variability among the traits for the two categories (miniaturized and non-miniaturized).

Similar results were found with the PCoA that resulted using the characteristics recovered in the extreme miniaturized constrained analysis (Figure 15). This PCoA includes three characteristics and shows that species of Amphisbaenia, Anguimorpha and one Scincomorpha are different from the other groups of Squamates. Miniaturized species were not grouped independently from the rest of the non-miniaturized species.

The PCoA analysis of the identified traits for head-first burrowers identified three clusters (Figure 16). One cluster, in the third quadrant that includes most of the snake species, also includes a few miniaturized head-first species. Another cluster in the first quadrant includes some Scincomorpha and some miniaturized head-first burrowers (snakes, amphisbaenians, and gekkotans). The last cluster, in the fourth quadrant, includes other miniaturized head-first burrowers such as amphisbaenians and snakes. These clusters are not exclusive of either fossorial or miniaturized forms.

Evolution of the skull size among squamate reptiles

An important component of miniaturization is the phylogenetic history of species or clades that are miniaturized. Hanken and Wake (1993) proposed that miniaturization is a process that implies an important body size reduction compared to that of the ancestor. In squamates, an accurate indicator of body size and of miniaturization is skull length, therefore, in order to evaluate the evolution of miniaturization in Squamata it is important to look at the evolution of skull length.

Squamata is a highly diverse group and previous studies have tried to quantify body size in this group and have produced large data sets (Meiri, 2008; Feldman et al., 2016). Here the analysis considers a minor proportion of squamates diversity, but the sample includes both fossil and living taxa and is a first attempt to analyze skull size variation within squamate reptiles. Furthermore, as mentioned earlier, skull length is a better descriptor of size than SVL as the latter might be misleading under some circumstances (i.e., animals with nearly identical SVL might have extremely different skull proportions).

The reconstruction of skull length in squamates (Figure 17,18 and 19) shows that almost all major clades within Squamata have miniaturized species, with the exception of Mosasauria and Varanoidea. The latter is clearly an effect of taxon sampling because there are actually living representatives of the genus *Varanus* that fall in the miniaturized category, such as the pygmy goanna, *Varanus brevicauda*, from Western Australia, with a maximum SVL of 42 to 126 mm and mean head length of 13.45 mm in females and 14.24 mm in males (King and Pianka, 2007). There is also a possible varanoidean preserved in burmite amber (99 MYA) which could represent the smallest member of this group ever recorded (~19.1 mm SVL; Daza pers. comm.).

In the fossorial group, there is a predominance of miniaturized forms (e.g., Dibamidae) and in some groups within this clade there are some important changes towards large size (e.g., Amphisbaenia). In other squamate clades there is great variation in skull size, for example within Gekkota, Scincomorpha and Serpentes. The analysis indicates that in Gekkota there are at least two instances of miniaturization in the Sphaerodactylidae and the Pygopodidae, but in both of these families there are some

species with a large skull size. It is also known that in other gekkotan families there are members that are miniaturized, such as the Gekkonidae (Daza et al., 2012), Phyllodactylidae (Daza et al., 2017), and Eublepharidae (Kluge, 1962). Within Scincomorpha, skull length is highly variable and there are a few miniaturized clades, which are represented by mainly head-first burrowers and xantusiids. Within snakes, some of the relationships are not defined, but some clades have a small skull length of 15 mm or less. This is certainly true for the Scolecophidea, where miniaturization is a common process.

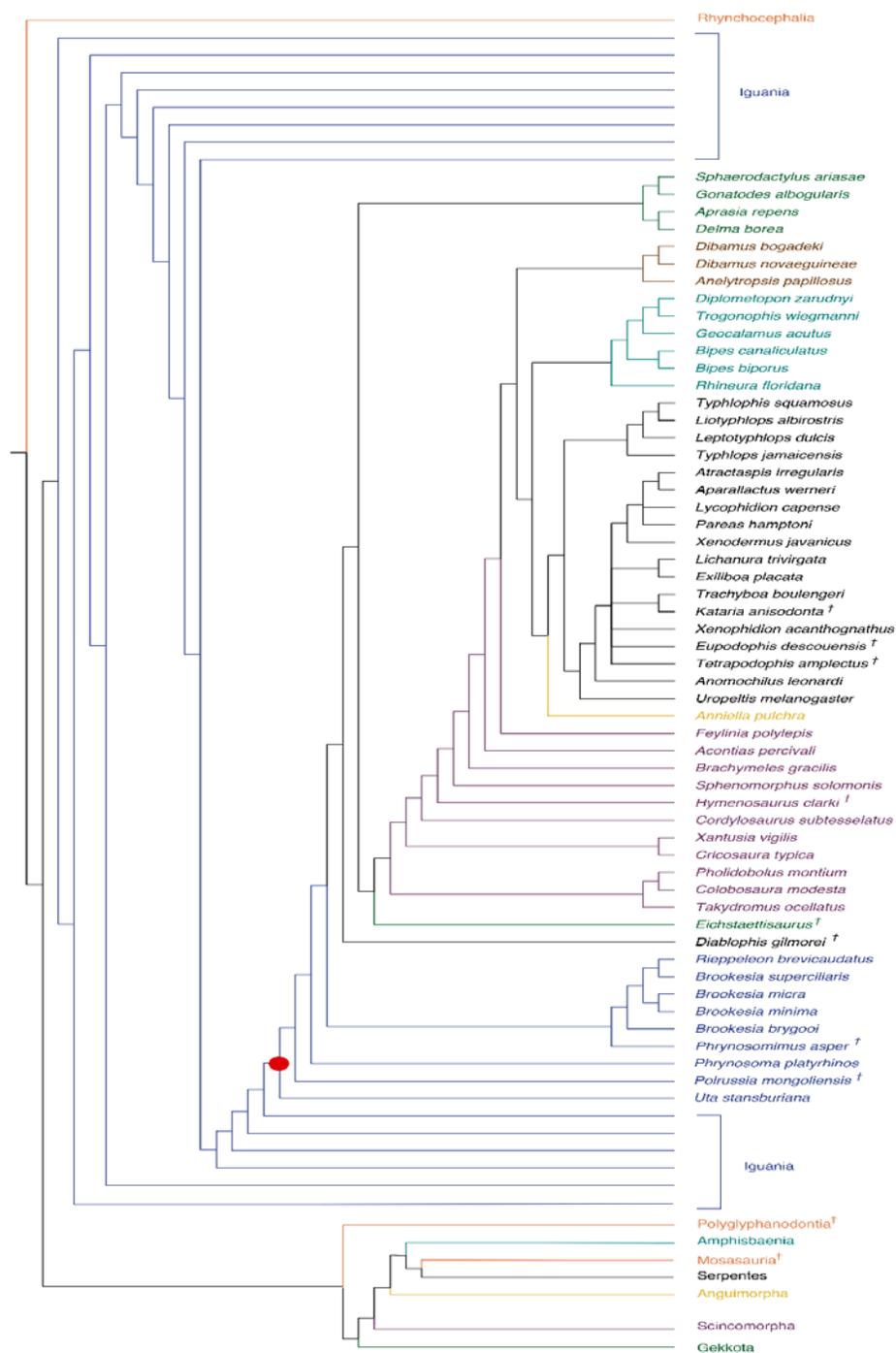


Figure 5. Cladogram of the analysis with a constrained group of all miniaturized species. The node of the constrained group of all miniaturized squamates with a skull length of 15 mm or less is indicated with a red dot. The tree is color coded by major groups: Iguania = blue, Gekkota = green, Scincomorpha = purple, Anguimorpha = yellow, Serpentes = black, Amphisbaenia = aquamarine, Dibamidae = brown, Polyglyphanodontia, Mossasauria and Rhynchocephalia = orange. Fossil species or groups are indicated with a dagger. Author created.

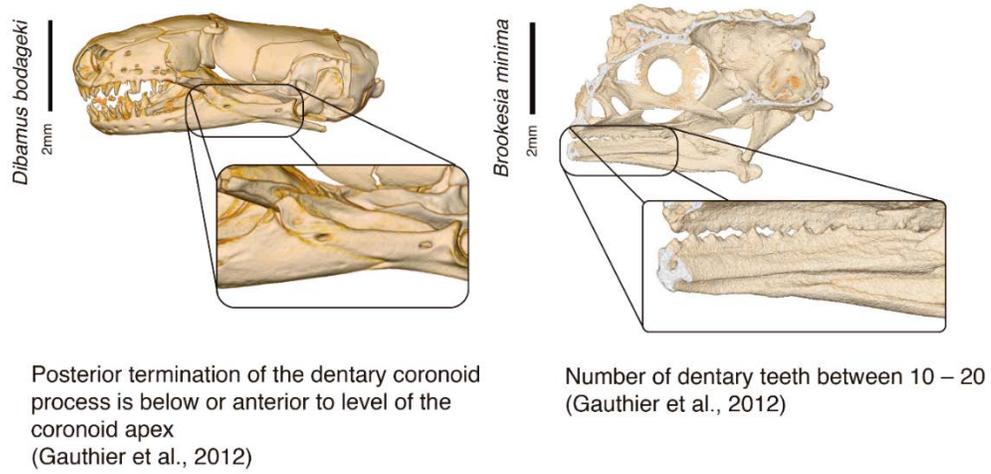


Figure 6. Convergent characteristics of all miniaturized squamates with skull length of 15 mm or less obtained from the constrained analysis. Author created.

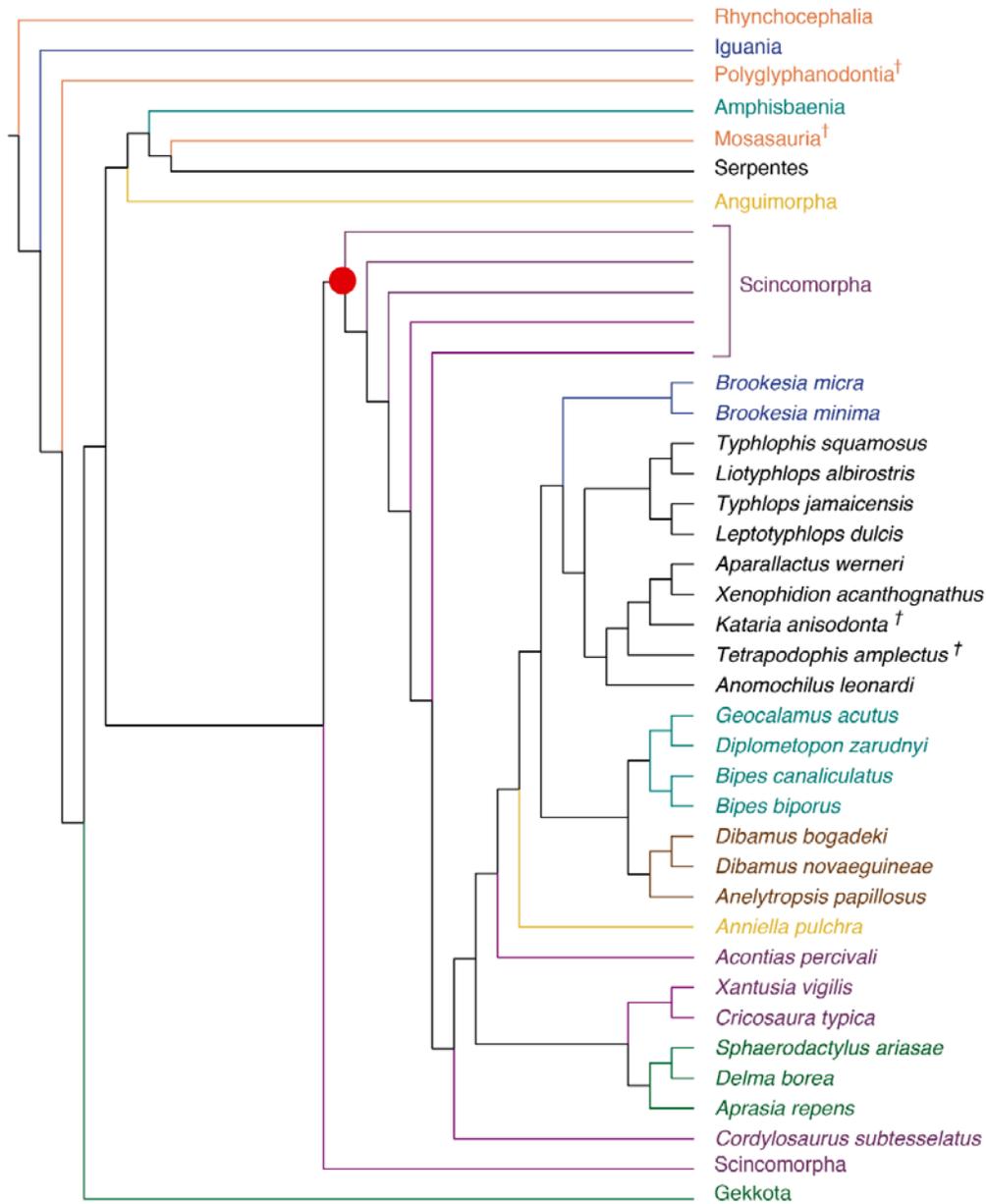


Figure 7. Cladogram of the analysis with a constrained group of intermediate miniaturized species. The node of the constrained group of all miniaturized squamates with a skull length of 10 mm or less is indicated with a red dot. The tree is color coded by major groups: Iguania = blue, Gekkota = green, Scincomorpha = purple, Anguimorpha = yellow, Serpentes = black, Amphisbaenas = aquamarine, Dibamidae = brown, Polyglyphanodontia, Mossasauria and Rhynchocephalia = orange. Fossil species or groups are indicated with a dagger. Author created.

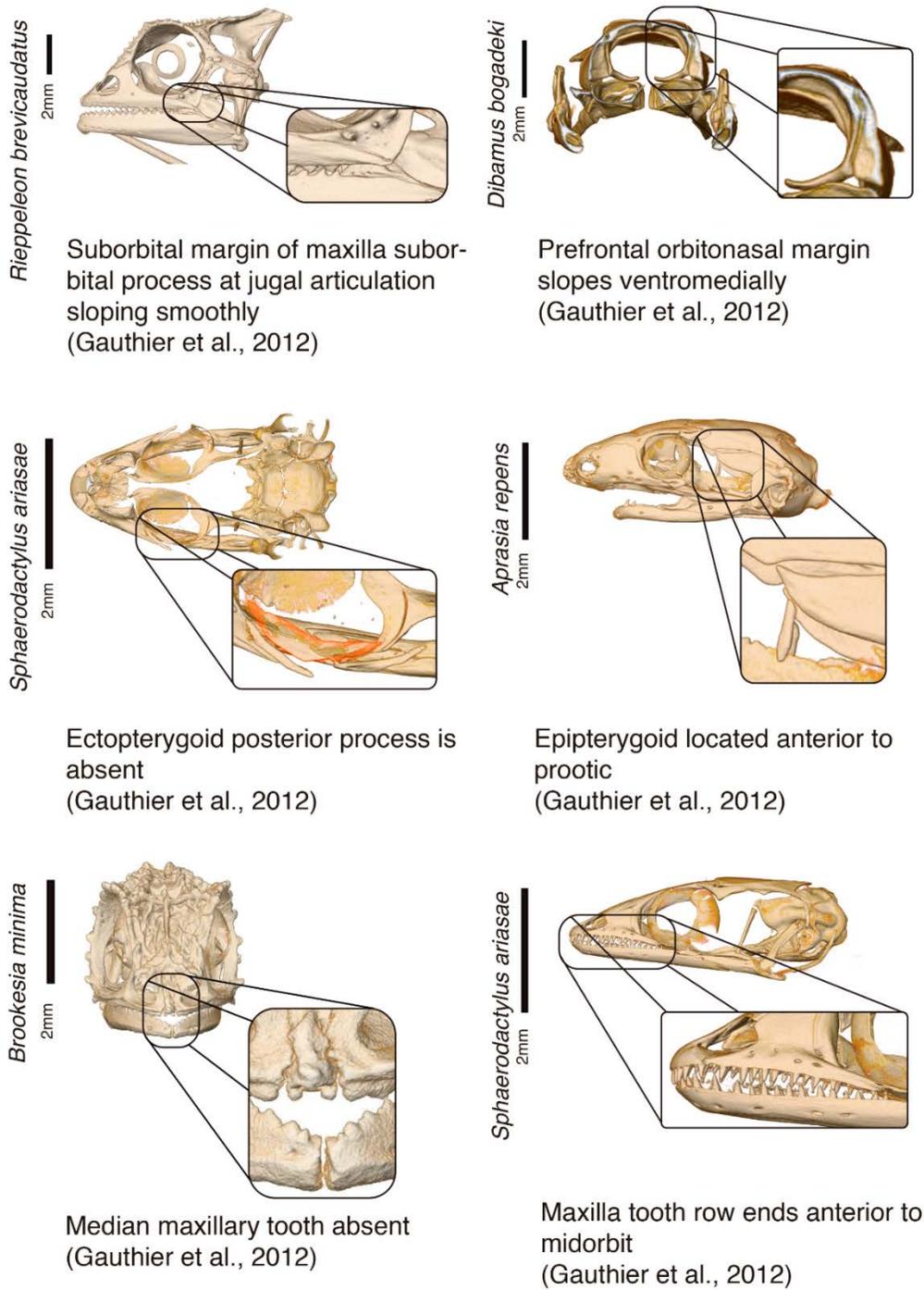


Figure 8. Convergent characteristics of intermediate miniaturized squamates with skull length of 10 mm or less obtained from the constrained analysis. Author created.

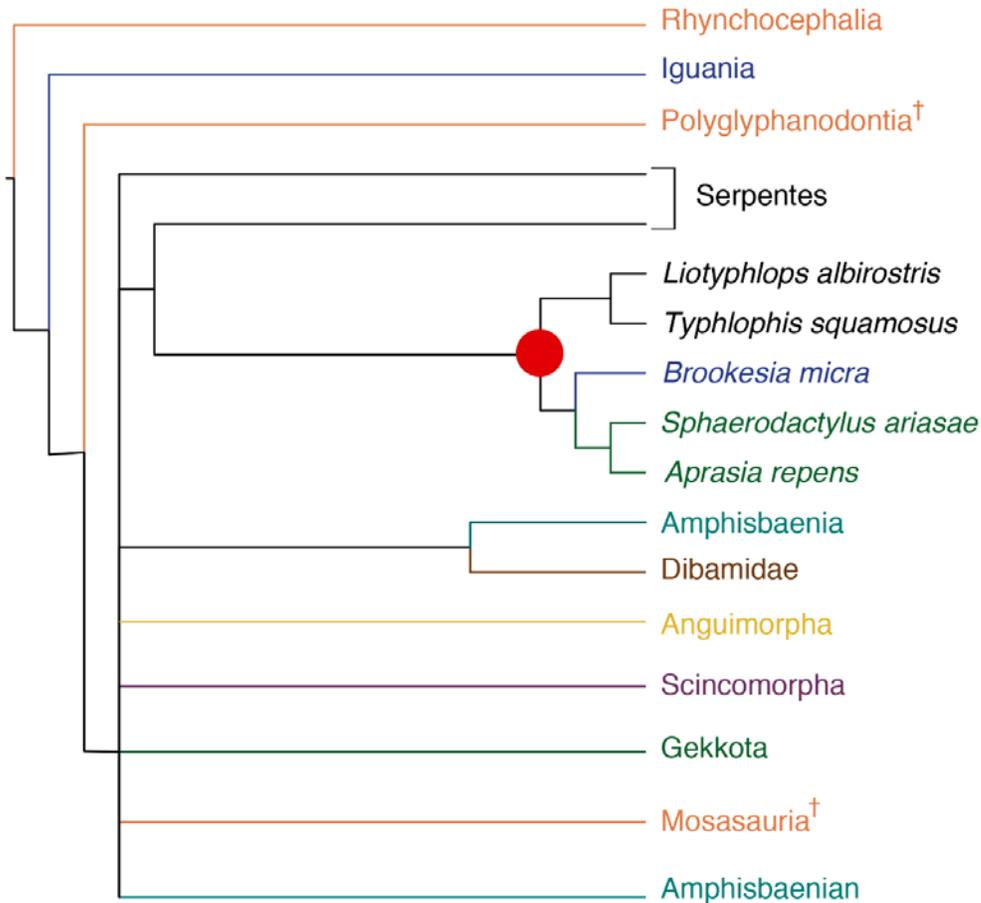
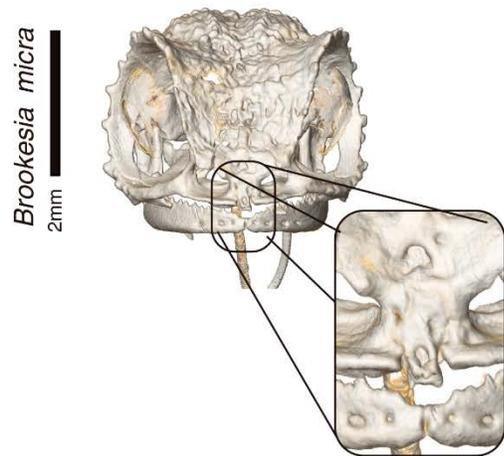
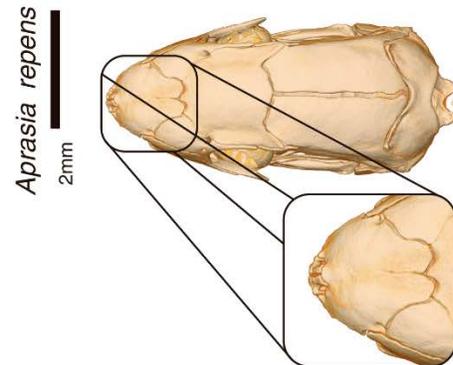


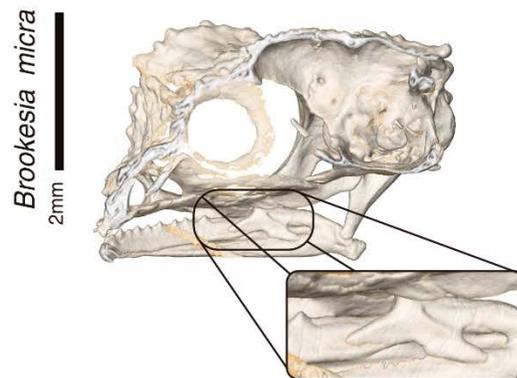
Figure 9. Cladogram of the analysis with a constrained group of extreme miniaturized species. The node of the constrained group of all miniaturized squamates with a skull length of 10 mm or less is indicated with a red dot. The tree is color-coded by major groups: Iguania = blue; Gekkota = green; Scincomorpha = purple; Anguimorpha = yellow; Serpentes = black; Amphisbaenia = aquamarine; Dibamidae = brown; Polyglyphanodontia, Mosasauria and Rhynchocephalia = orange. Fossil species or groups are indicated with a dagger. Author created.



Premaxilla internal process size
very reduced or absent
(Gauthier et al., 2012)



Fused nasals
(Gauthier et al., 2012)



Splenial absent
(Gauthier et al., 2012)

Figure 10. Convergent characteristics of extreme miniaturized squamates with skull length of 5 mm or less obtained from the constrained analysis. Author created.

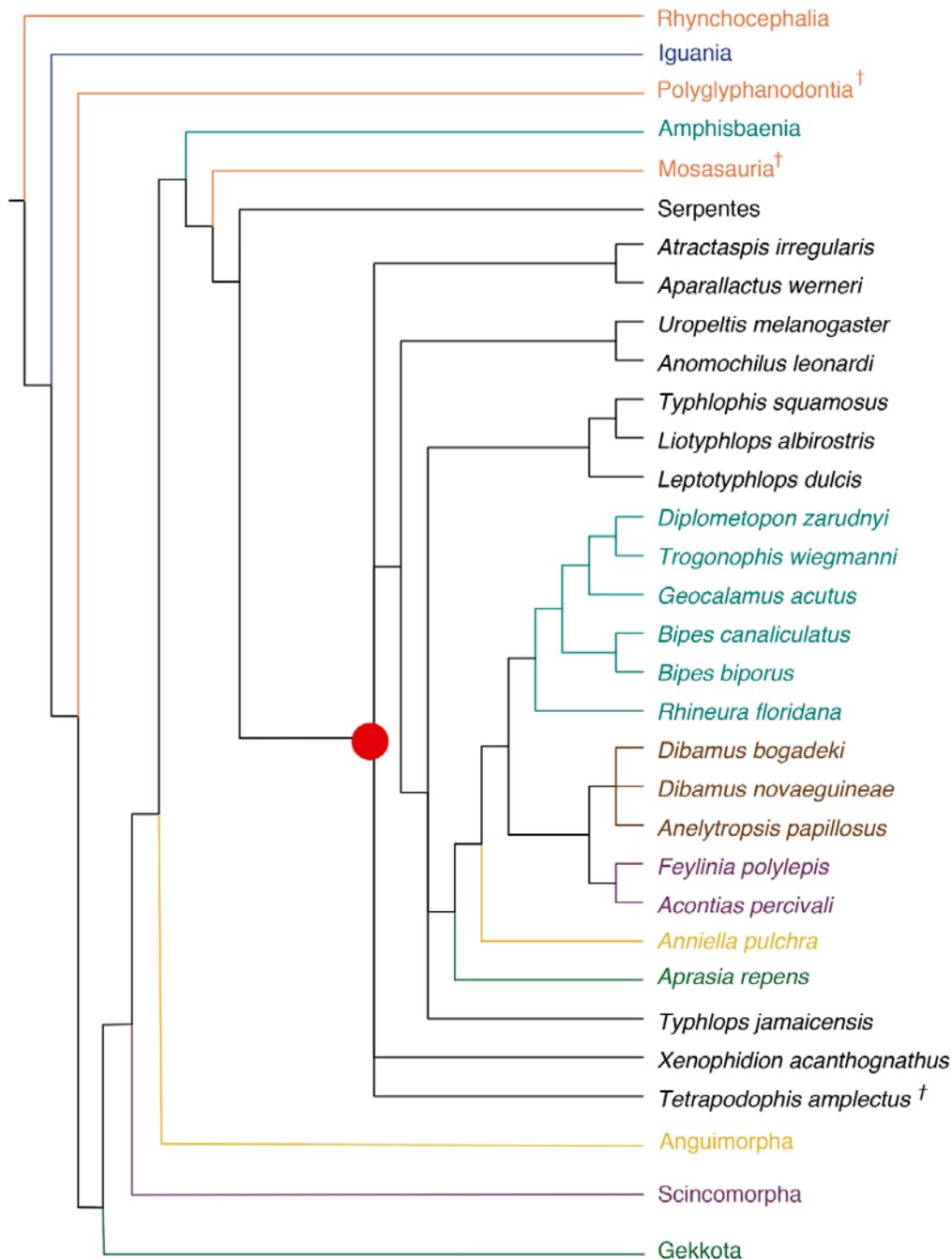


Figure 11. Cladogram of the analysis with a constrained group of head-first burrower miniaturized species. The node of the constrained group of all miniaturized squamates that are strict head-first burrowers is indicated with a red dot. The tree is color-coded by major groups: Iguania = blue; Gekkota = green; Scincomorpha = purple; Anguimorpha = yellow; Serpentes = black; Amphisbaenia = aquamarine; Dibamidae = brown; Polyglyphanodontia, Mosasauria and Rhynchocephalia = orange. Fossil species or groups are indicated with a dagger. Author created.

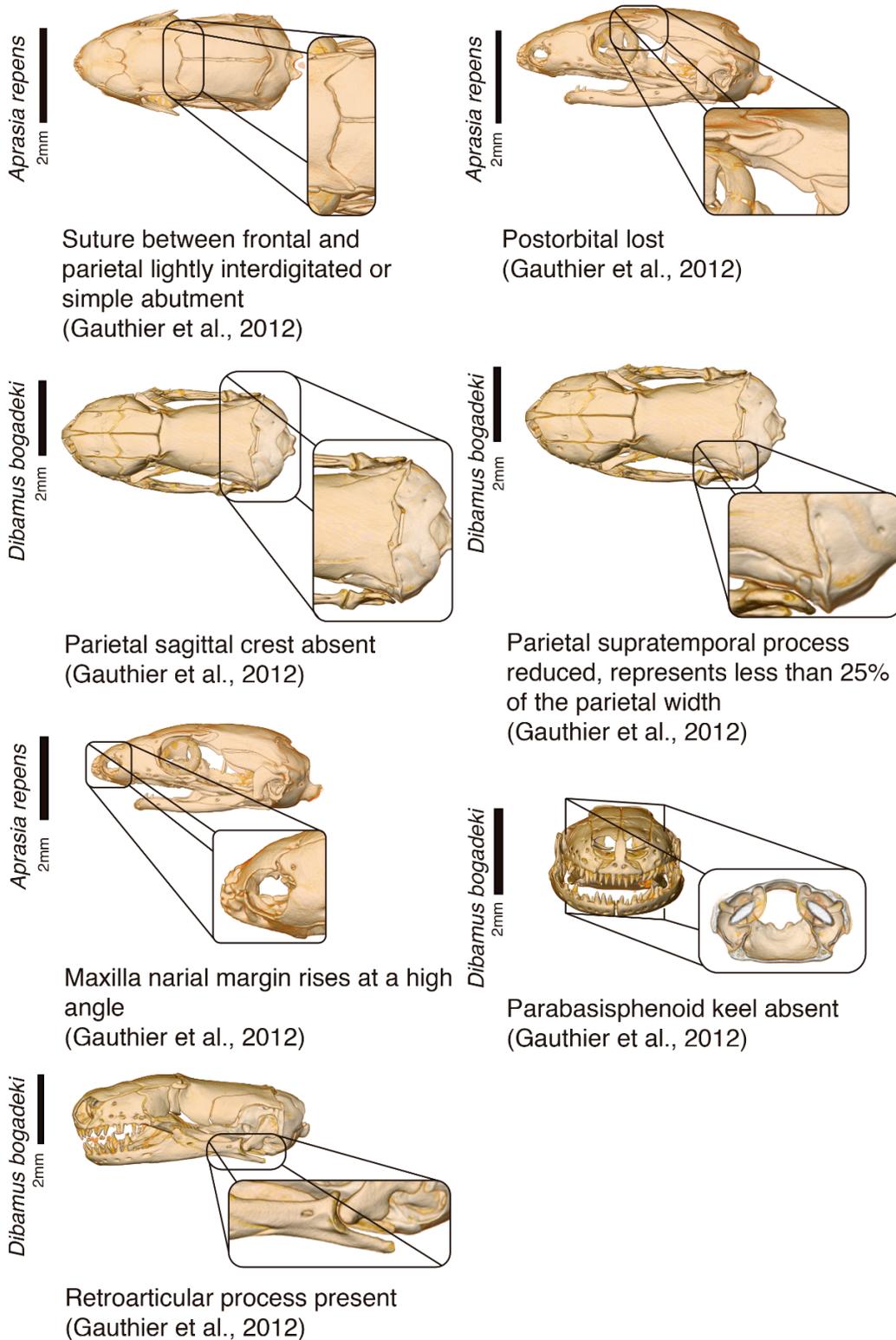


Figure 12. Convergent characteristics of miniaturized head-first burrower squamates obtained from the constrained analysis. Author created.

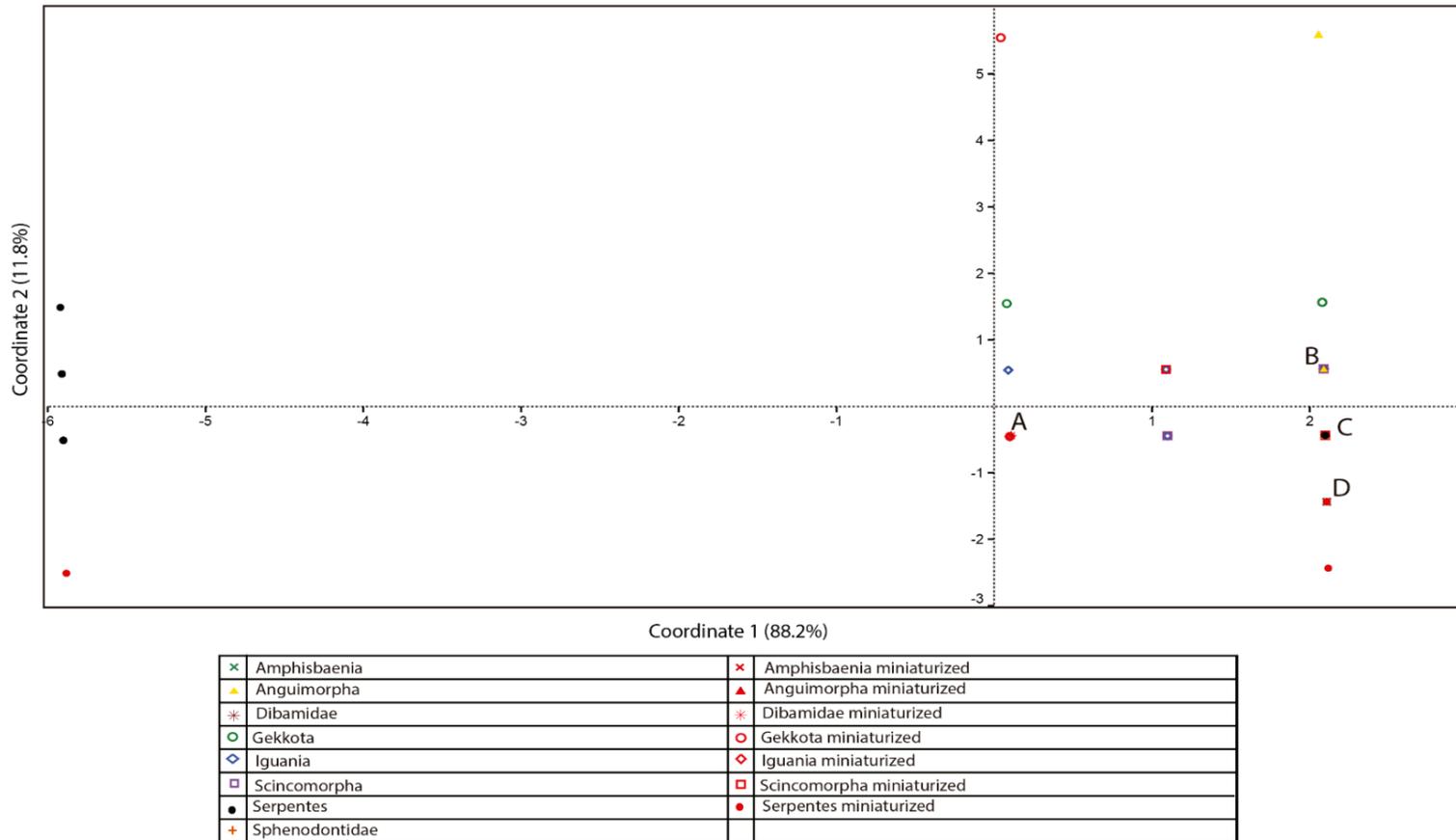


Figure 13. Principal Coordinate Analysis (PCoA) of all miniaturized species. The PCoA of the characteristics of miniaturization obtained from the constrained analysis of all species with 15 mm of skull length or less. Overlap of species of different groups is indicated with capital letters. A= iguanians, dibamids and geckos; B= anguimorphs, skinks, iguanians, geckos; C= snakes, dibamids, anguimorphs, skinks and iguanians; D= snakes, dibamids, amphisbaenians, anguimorphs. Author created.

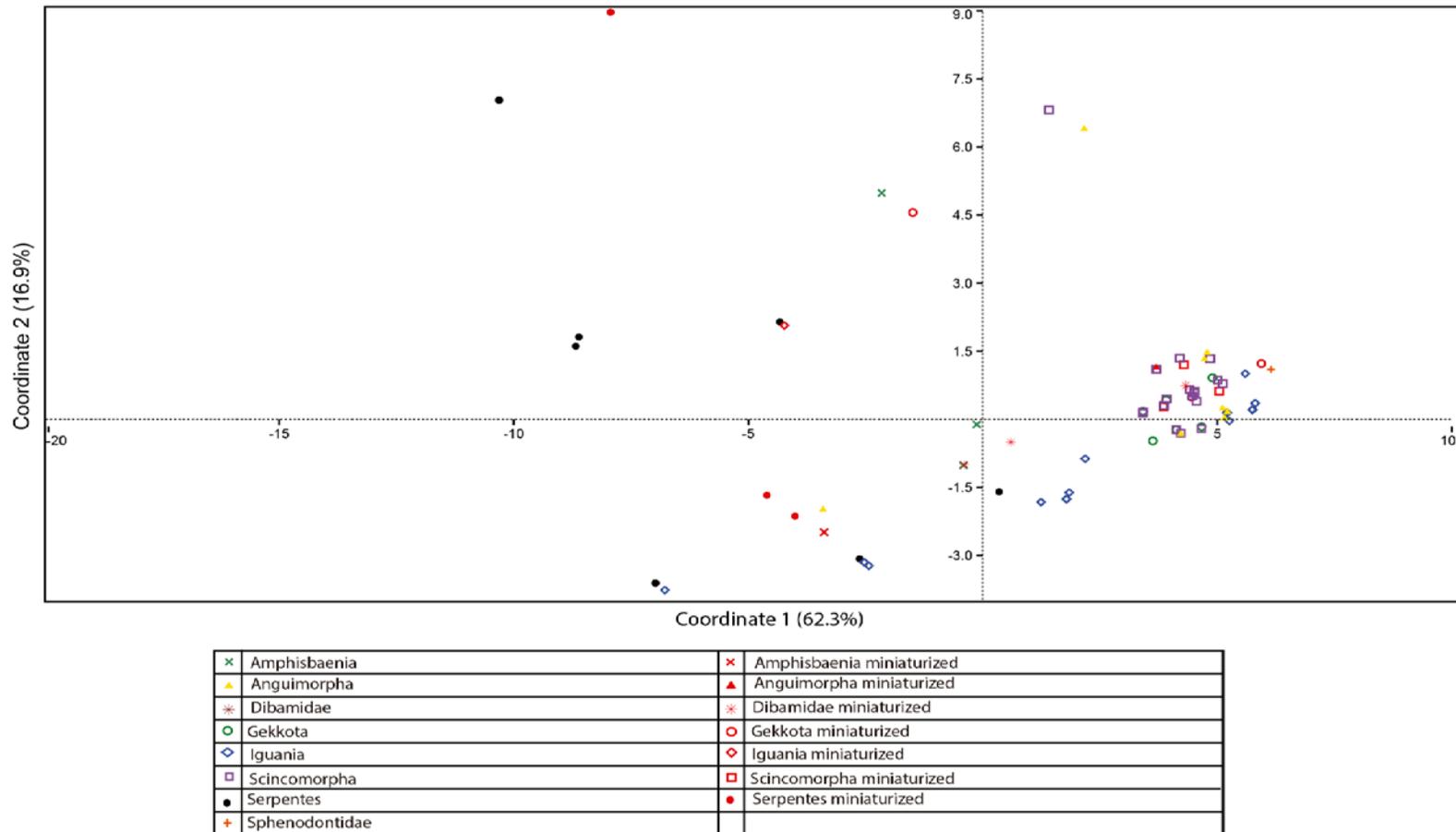


Figure 14. Principal Coordinate Analysis (PCoA) of intermediate miniaturized species. The PCoA of the characteristics of miniaturization obtained from the constrained analysis of all species with 10 mm of skull length or less. Author created.

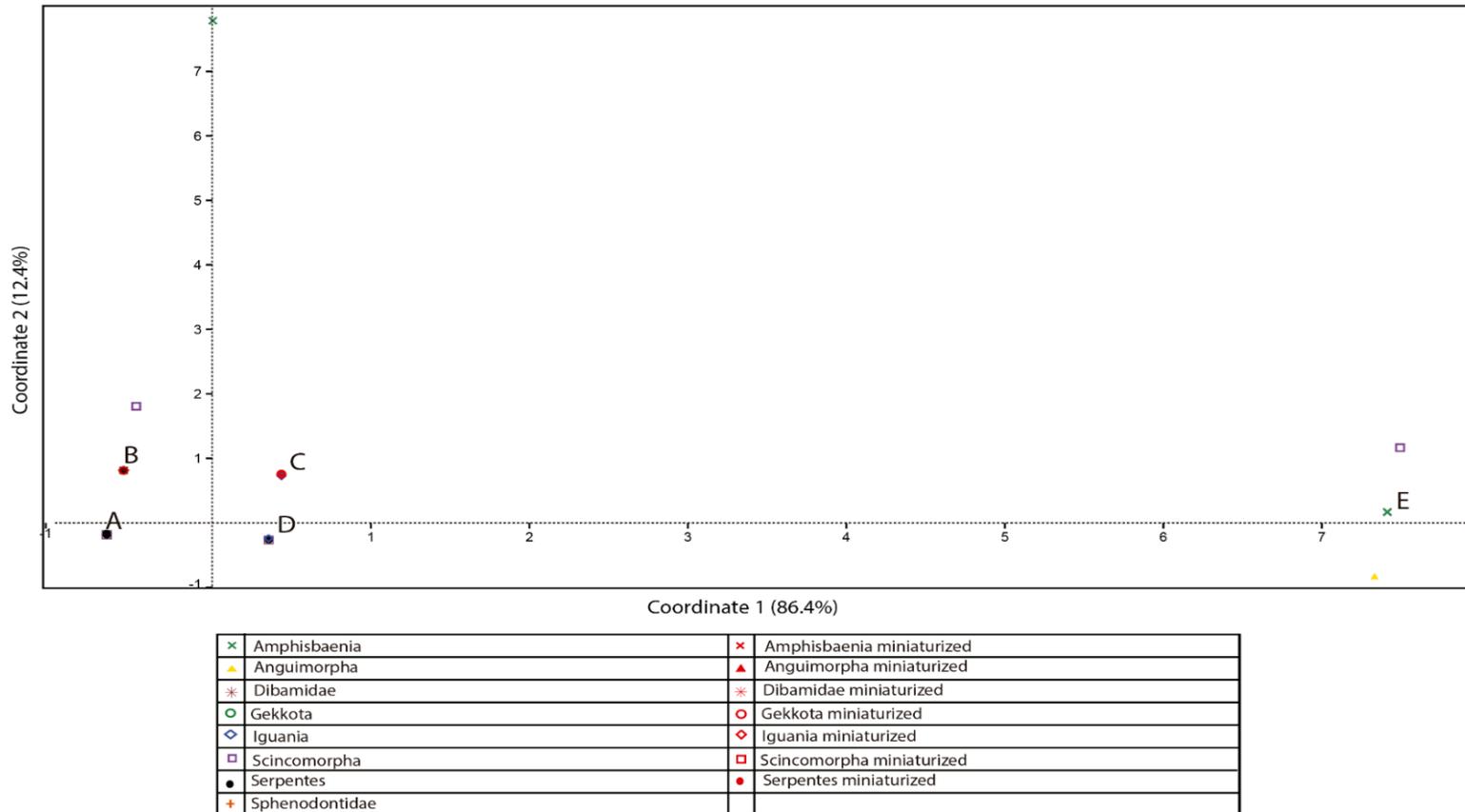


Figure 15. Principal Coordinate Analysis (PCoA) of extreme miniaturized species. The PCoA of the characteristics of miniaturization obtained from the constrained analysis of all species with 5 mm of skull length or less. Overlap of species of different groups is indicated with capital letters. A= iguanians, skinks, anguimorphs, snakes and geckos; B= dibamids, snakes, amphisbaenians, iguanians, and geckos; C= snakes, geckos, and iguanians; D= snakes, iguanians, skinks, anguimorphs and geckos; E= amphisbaenians. Author created.

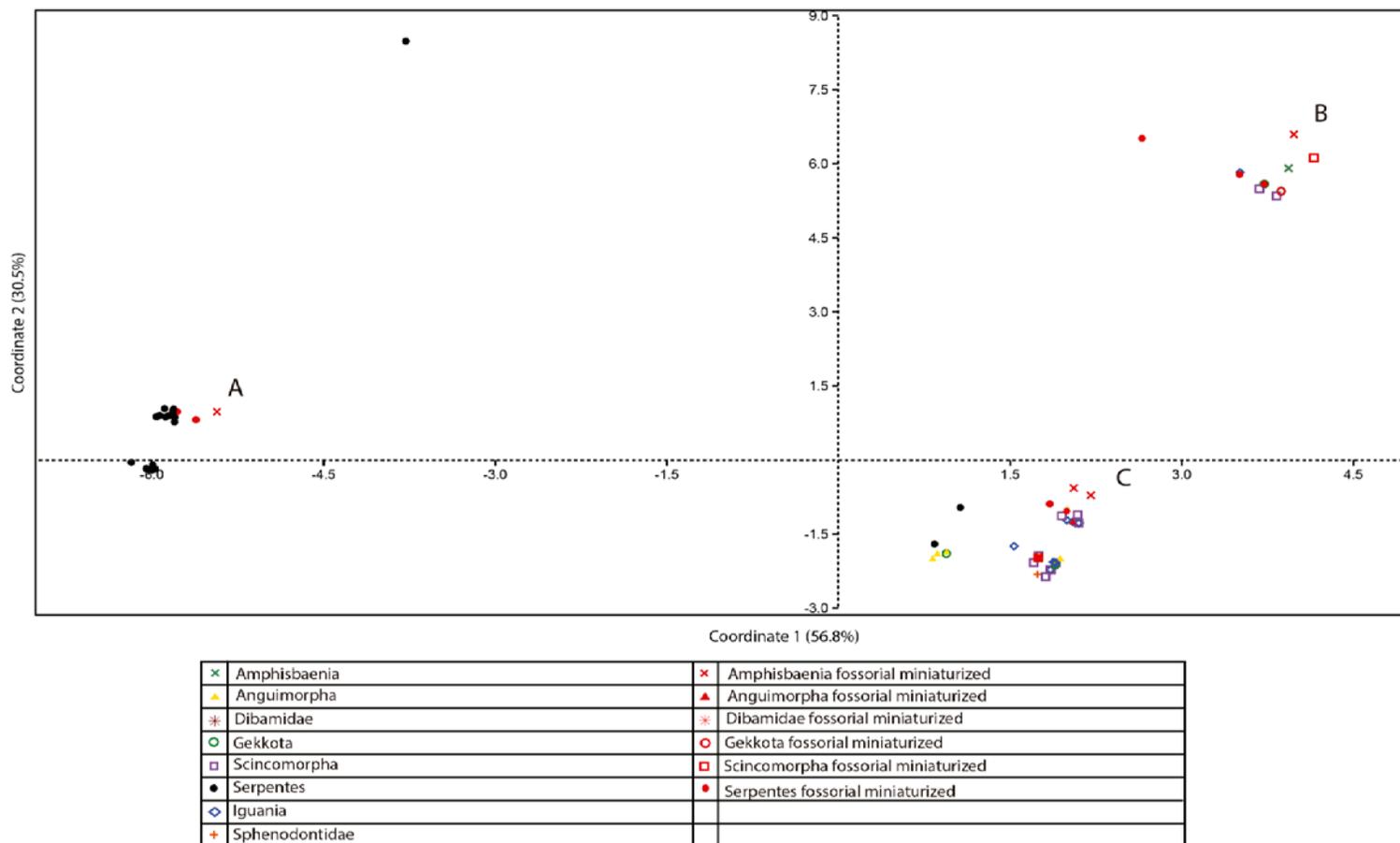


Figure 16. Principal Coordinate Analysis (PCoA) of head-first burrower miniaturized species. The PCoA of the characteristics of miniaturization obtained from the constrained analysis of all head-first burrowing species with 15 mm of skull length or less. Overlap of species of different groups is indicated with capital letters. A= snakes and amphisbaenians; B= snakes, amphisbaenians, skinks and iguanians; C= geckos, iguanians; skinks, anguimorphs, dibamids, snakes. Author created.

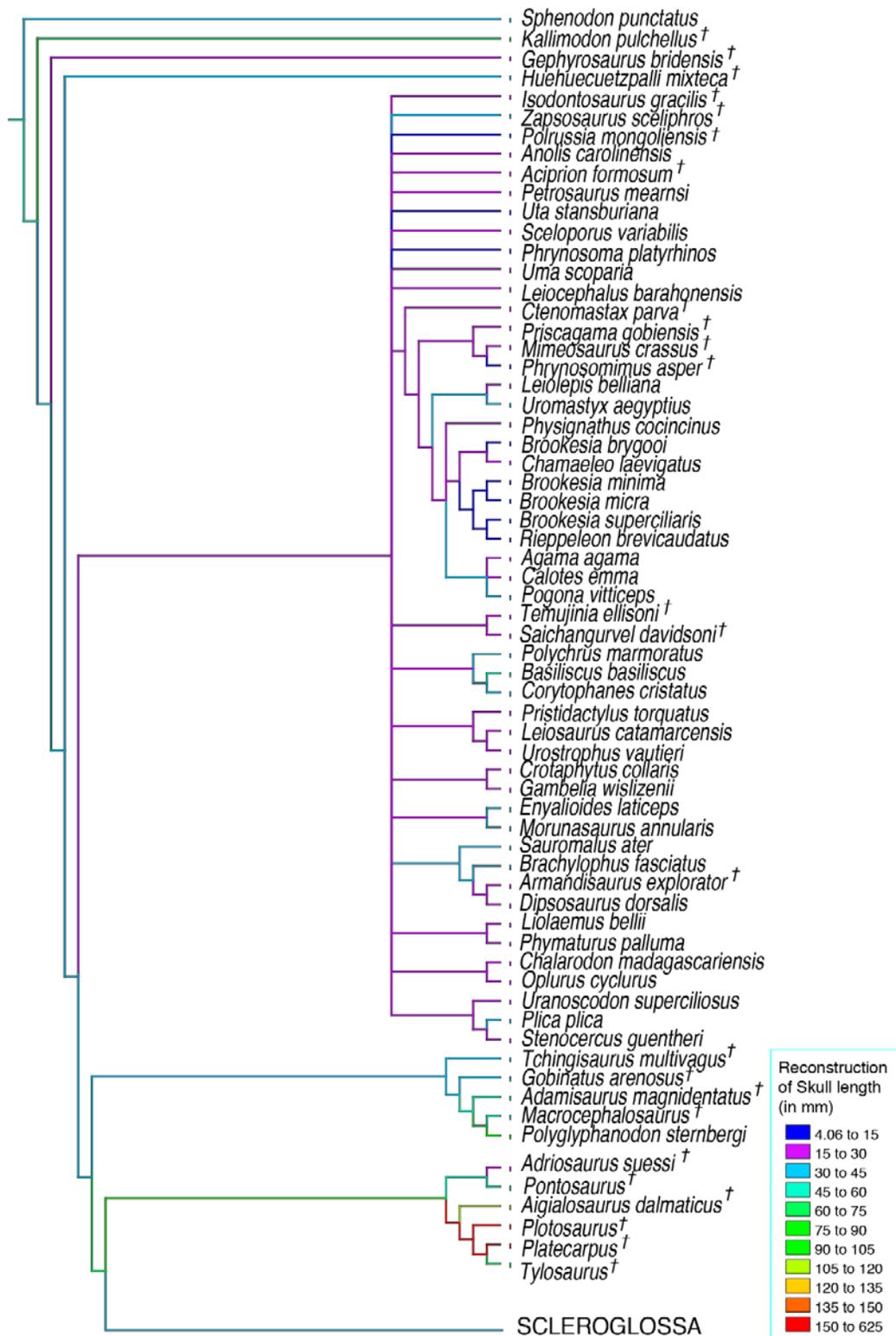


Figure 17. Ancestral state reconstruction of skull length in Squamata, part one. Author created.

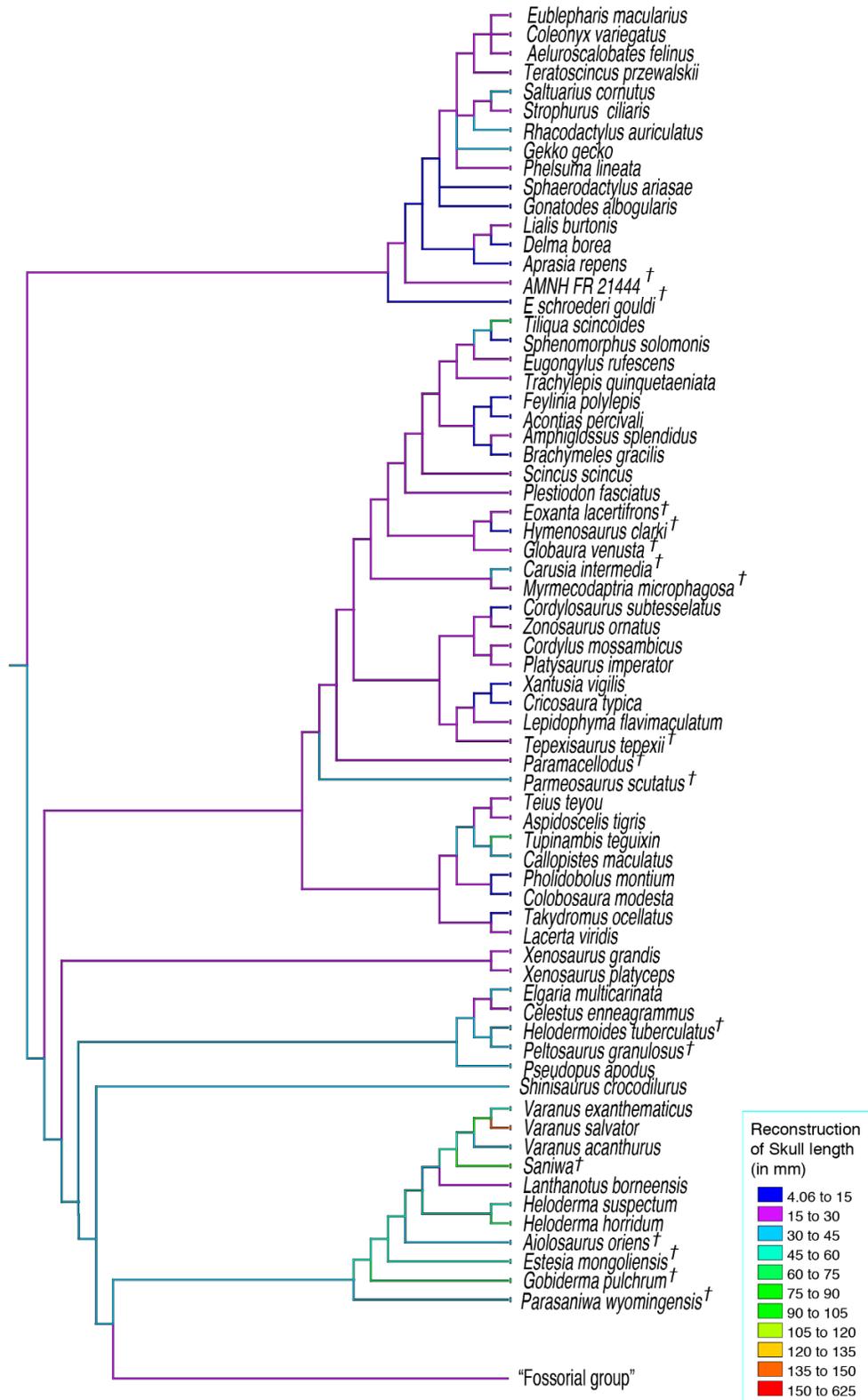


Figure 18. Ancestral state reconstruction of skull length in the Squamata, part two Scleroglossa. Author created.

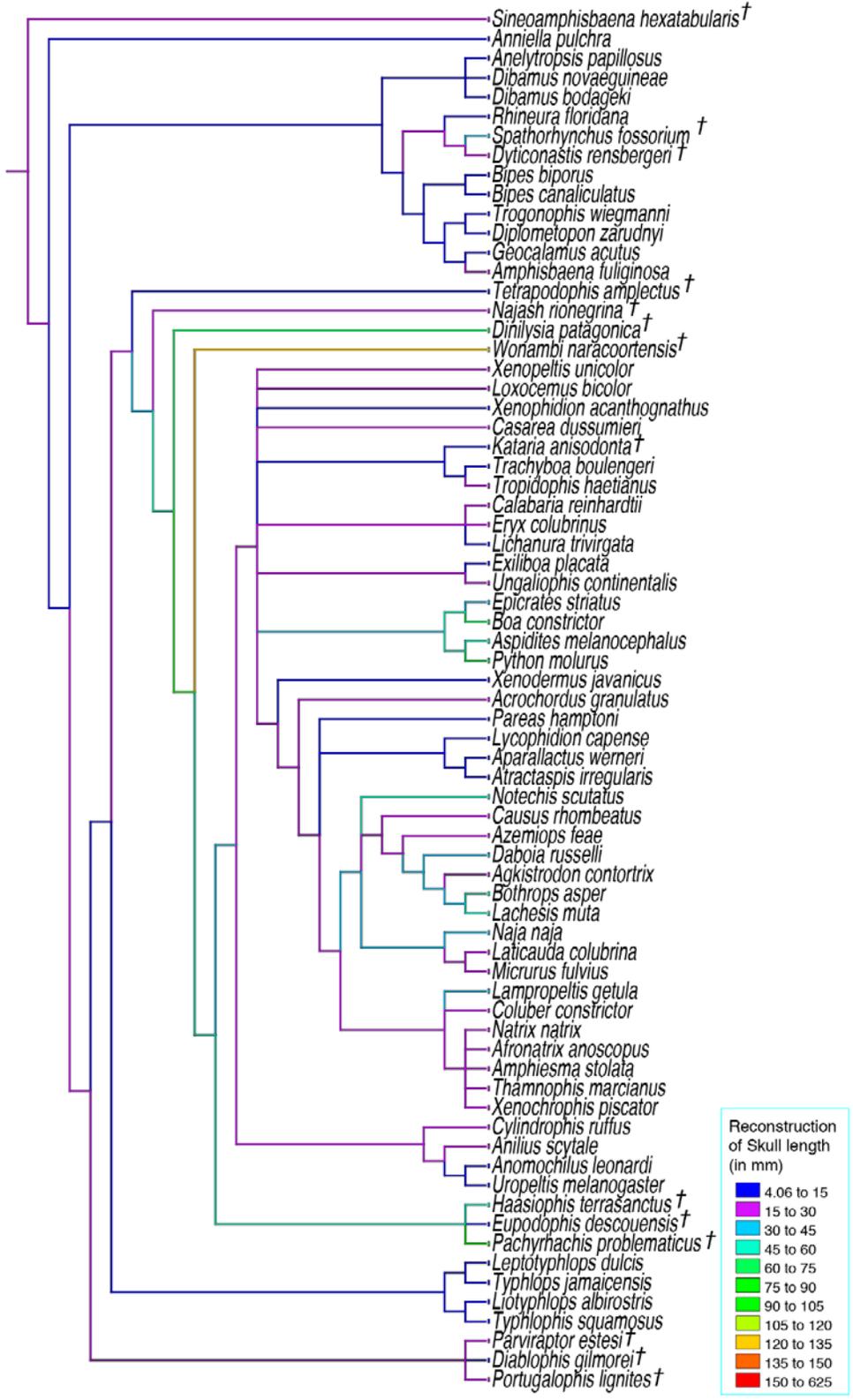


Figure 19. Ancestral state reconstruction of skull length in the Squamata, part three Fossorial group. Author created.

CHAPTER V

Discussion

Miniaturization is a common evolutionary process in Squamata (Rieppel, 1996). The review presented in chapter two allowed the compilation of a set of common cranial traits associated with miniaturization in squamates. Because these characteristics apply only to some miniaturized species, it is difficult to produce a generalized process of morphological change that applies to all miniaturized species. One example is the closure of the post-temporal fenestra (Rieppel, 1984a), which occurs in the vast majority of miniaturized squamates, but remains open in miniaturized chameleons (*Brookesia minima* or *Brookesia micra*). Another example is the occipital condyle, which in most miniaturized taxa is located in the posterior-most part of the skull (Daza et al., 2011), with the exception of miniaturized chameleons.

The exploration of a large squamate data set using different skull size categories identified 11 traits that are convergent in miniaturized species. The most inclusive category included all miniaturized species that have a skull length equal to or smaller than 15 mm, and two traits were found with this analysis. These two traits (posterior termination of the dentary coronoid process below the level of the coronoid apex and the number of dentary teeth between 10 – 20) were present in all miniaturized species, but were not exclusive to miniaturized taxa. The same is true for six convergent traits for the intermediate miniaturized species and three for the extreme miniaturized species. Other factors may be affecting the presence or absence of these traits, such as phylogenetic history and the skull design specific to each major group of squamates (Herrel et al., 2007).

An additional factors affecting the presence of the convergent traits is missing data that are more frequent in fossil taxa given the nature of the fossil record. For instance, a determination regarding the fusion of the nasal bones, a condition proposed to be convergent between extreme miniaturized species, is not available for *Hymenosaurus clarki*, a stem scincomorph from the Cretaceous of Mongolia of which only a partial skull with incomplete nasals is preserved (Kequin and Norell, 2000). The same occurs with the posterior termination of the dentary coronoid process below the coronoid apex that is a characteristic undetermined for fossil species with specimens that do not preserve the lower jaw or are where the jaw is not preserved well enough to observe the character (e.g., *Tetrapodophis amplexus*, Martill et al., 2015); or the unknown number of dentary teeth in *Eichstaettisaurus schroederi* (Evans et al., 2004).

Inapplicable data also have an important effect on the results. For instance, one of the traits found for the constrained group of 10 mm or less is the resting position of the epipterygoid. In this case, many of the species were scored as not applicable because they lack an epipterygoid bone (e.g., chameleons; Evans, 2008), dibamids (except for *Anelytropsis*, Greer, 1985), amphisbaenians (Gans and Montero, 2008) and snakes (Cundall and Irish, 2008).

Not all the miniaturized species have 10 to 20 teeth, but most of them (except for species of the Scincomorpha and Serpentes) do, which could indicate one of the tendencies miniaturization is results in reduction of tooth number, and is perhaps linked to an increase on the relative size of these structures.

The only category in which most of the miniaturized species have the convergent traits is the category of extreme miniaturization that contains 5 species and found three

convergent traits. Of these traits, a reduced premaxilla nasal process and paired nasals are present in all species except in *Sphaerodactylus ariasae*. Daza et al. (2008) recognized that one of the common characteristics of miniaturization in sphaerodactylids is the elongation of the ascending nasal process of the premaxilla. The evaluation of the characteristics of miniaturization in other miniaturized species (Table 3) suggests miniaturized gymnophthalmids or skinks, as in sphaerodactyls, do have a long ascending nasal process (see also Guerra and Montero, 2009; Roscito and Rodrigues, 2010). The shortened ascending nasal process is more common in head-first burrowers and some chameleons that have a shortened snout.

The characteristic that is present in all the extremely miniaturized species and in some of the species with an intermediate degree of miniaturization is the absence of the splenial bone. Gauthier et al. (2012) proposed that this character held three different states: presence, absence, or fusion to the dentary. However, in some miniaturized squamates, such as *Rieppeleon brevicaudatus* or other chameleons, the splenial is so reduced that it is very difficult to determine if it is absent, reduced, or has become fused to the dentary or other post-dentary bones (Rieppel, 1987). Therefore, the differentiation between these two states is dependent on literature and researcher interpretation. In sphaerodactyl geckos, the splenial has been considered absent (Daza et al., 2008), but it may be also fused to the coronoid anteromedial foot (Bauer et al., 2018). Simplification of the jaw elements seems to be a generalized trend in miniaturized taxa that can be accomplished in multiple ways (i.e., different fusion patterns). This reduction in the number of postdentary bones has also been proposed for miniaturized head-first burrowers (Lee, 1998).

The effect of phylogeny on each of the characteristics and in each of the categories of miniaturization is clearly illustrated in the PCoA analyses where there is not a clear pattern that separates miniaturized species from non-miniaturized species. This indicates that the differences among the miniaturized and non-miniaturized species include more traits than the ones used for the PCoA analyses. This also can indicate that these traits are highly variable among Squamata, and as a result no patterns are recovered.

If the traits do not indicate differences between miniaturized and non-miniaturized species, then it would be expected for species to be grouped with their relatives; however, clusters of representatives of major clades were not often recovered either. For example, in the PCoA analyses that uses the characteristics obtained from the constrained analysis of all miniaturized species and for the intermediate miniaturization (Figures 13 and 14), snakes are separated from the rest of Squamata but a few species cluster with some species of lizards (e.g., geckos, skinks or dibamids).

These results reaffirms that differences between clades and between miniaturized and non-miniaturized species are shown by the combination of multiple morphological traits.

Miniaturization and fossoriality, and particularly head-first burrowing, have been linked, and in some cases miniaturization has been considered a consequence of head-first burrowing (Rieppel, 1984b; Lee, 1998). Some of the reasons for this association include the need to obtain a more compact skull, which is reinforced and with reduced mobility (Rieppel, 1984a, 1984b, 1996). Another reason is the relationship that exists between the diameter of the tunnel and the body size of the organism (Gans and Montero, 2008). According to this study the body size increases quadratically in relation to the

diameter of the tunnel because the body mass of the organism is distributed along the body allowing muscles to grow and maintain the digging capabilities. Therefore, a smaller body size reduces the tunnel size and the energy required for burrowing (Rieppel, 1996).

The morphological convergence of miniaturized head-first burrowers has been previously studied (Rieppel, 1996; Lee 1998), and herein I explored other morphological characteristics. The analysis with a constrained group of 23 miniaturized head-first burrowers provided eight possible convergent traits. The traits are not present in all of the species, however, two species have all the characteristics: the dibamid *Dibamus novaeguineae* and the scolecophidian *Typhlops jamaicensis*.

Differences among amphisbaenians and species that belong to different taxonomic groups are clear with regard to some of the characteristics, and these differences may be related to phylogenetic history. One characteristic is the interdigitation of the suture between the parietal and the frontal. According to the analysis, head-first burrowers have a light interdigitation, but in some amphisbaenians these are deeply interdigitated, which is a synapomorphy of the Ambisbaenidae (Gans and Montero, 2008). Another characteristic of amphisbaenians is the presence of a sagittal crest in many species of *Amphisbaena* and *Diplometopon* (Maisano et al., 2007), but a reduction in size of this crest has been reported in species with smaller skulls (Gans and Montero, 2008).

Snakes also include many miniaturized head-first burrower species (e.g., Scolecophidia), but these fossorial animals also exhibit large morphological variation and considerably different skull patterns as those of lizards (Cundall and Irish, 2008). In the

dataset used for the analysis, there are 19 miniaturized snakes of which 10 are strictly head-first burrowers (see Appendix 1). In this set of snakes, only *Anomochilus leonardi* has all the characteristics of miniaturization.

All species of the clade Scolecophidia (blind and thread snakes) are small and head-first burrowers (Cundall and Irish, 2008). This group is deeply nested within snakes and is the sister taxa to the Alethinophidia. Members of this group have many of the characteristics of miniaturization, although they retain a well-developed supratemporal process of the parietal, which is shared with dibamids and amphisbaenians.

Convergent morphologies among head-first burrowers described previously (see review chapter) show how different species respond to different evolutionary pressures (Rieppel, 1996), but the results found here also show that some characteristics are associated with the phylogenetic history of the groups. It is evident that fossoriality and miniaturization have evolved several times in the Squamata.

Previous studies have shown that one of the origins of fossoriality is in snakes, and have shown a marked morphological transition into a cylindrical skull shape (Da Silva et al., 2018). According to Da Silva et al. (2018), the ancestor of snakes was mainly terrestrial and underwent a transition into fossoriality that was accompanied by the development of a more cylindrical skull with lateral and posterior expansion of the parietal region and a curved quadrate, the same pattern for head-first burrowing species described by Rieppel (1996) and Lee (1998). Scolecophidians went through additional body size reduction as compared to Alethinophidian snakes (Da Silva et al., 2018). The ancestral state reconstruction done in this study recovers the same pattern of reduction of skull length in scolecophidians compare to that of other snakes.

The analysis of skull size distribution indicates that groups within Squamata other than scolecophidians have become miniaturized (e.g., the chameleon genera *Brookesia* and *Rieppeleon*, the gekkotans from the family Sphaerodactylidae, skinks of the family Scincidae and night lizards of the Xantusiidae). A large skull is plesiomorphic in all of these groups, necessary for miniaturization as defined of Hanken and Wake (1993).

Is there a unique formula for miniaturization in squamates?

During this project, I compiled a list of 21 characters (Table 3), 10 from the literature (see Chapter 1) and 11 from the constrained phylogenetic analyses (see Chapter 4). After the evaluation of these traits in 20 miniaturized species, none of the traits analyzed were present in all miniaturized species.

However, it is clear here that phylogenetic history and skull design, which is determined by additional selective pressures (Herrel et al., 2007), plays an important role in determining the presence or absence of these features. For example, iguanians (Chamaleonidae and Dactyloidae) lack several of the characteristics of miniaturization including the neurocranium and the dermatocranium positioned at the same level, the closure of the post-temporal fenestra, and the elongation of the skull (not for Dactyloidea or anoles). These conditions resemble the ones in non-miniaturized species of the same families (especially Chamaeleonidae; Evans, 2008), but when comparing the size or degree of development of some of these traits between related species it is evident that they are modified. For example, the alignment between the neurocranium and the dermatocranium when determined by the distance between the supraoccipital and the parietal in dwarf chameleons: it decreases towards the smallest skull lengths from *B. micra*, to *B. superciliaris* with an intermediate state in *B. minima*. The size of the post-

temporal fossa or the supratemporal fenestra is smaller in *B. micra*, intermediate in *B. minima* and larger in *B. superciliaris*.

Finally, the morphological variation in the jaw of squamates has not been studied in detail. Previously only one characteristic, the reduction of the postdentary bones, was identified by Lee (1998) as a character associated with miniaturization and fossoriality. Constrained phylogenetic analyses identified two additional characteristics: the reduction of dentary teeth and the absence of the splenial. These characters of the jaw and other possible characters such as the coronoid height in the gekkota (Daza et al., 2008), and its relation to miniaturization are poorly study and are in need of further exploration. These traits might be may be important for developing a better understanding of miniaturization in Squamata. The observation of developmental series of different miniaturized species, like those of Tarazona et al. (2008) or Bell et al., (2003) are fundamental for determining if bones in the lower jaw are lost or fused.

From total analysis of all characters previously described, and those newly identified by this study, it is clear that miniaturization occurs in different ways among squamates is there are not one single trait that applies to all taxonomic groups.

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APPENDIX A

Table A1

Skull length of squamate species

<i>Species</i>	Skull Length (mm)	Source
<i>Sphenodon punctatus</i>	43.8	DigiMorph.org
<i>Kallimodon pulchellus</i> [†]	67.0	Rauhut and Lopez-Arbarello, 2016
<i>Gephyrosaurus bridensis</i> [†]	30.0	Evans, 1980
<i>Huehucuetzpalli mixteca</i> [†]	32.2	Reynoso, 1998
<i>Ctenomastax parva</i> [†]	16.7	DigiMorph.org
<i>Priscagama gobiensis</i> [†]	27.0	Borsuk-Bialynicka and Moody, 1984
<i>Mimeosaurus crassus</i> [†]	27.5	Keqin and Norell, 2000
<i>Phrynosomimus asper</i> [†]	12.5	Keqin and Norell, 2000
<i>Leiolepis belliana</i>	29.7	DigiMorph.org
<i>Uromastix aegyptius</i>	44.3	DigiMorph.org
<i>Brookesia brygooi</i>	12.0	DigiMorph.org
<i>Chamaeleo laevigatus</i>	21.4	DigiMorph.org
<i>Physignathus cocincinus</i>	25.9	DigiMorph.org
<i>Agama agama</i>	25.3	DigiMorph.org
<i>Calotes emma</i>	29.7	DigiMorph.org
<i>Pogona vitticeps</i>	42.8	DigiMorph.org
<i>Temujinia ellisoni</i> [†]	22.5	DigiMorph.org
<i>Saichangurvel davidsoni</i> [†]	23.0	Conrad and Norell, 2007
<i>Isodontosaurus gracilis</i> [†]	15.8	DigiMorph.org
<i>Zapsosaurus s celiphros</i> [†]	30.8	DigiMorph.org
<i>Polrussia mongoliensis</i> [†]	10.8	DigiMorph.org
<i>Basiliscus basiliscus</i>	46.6	DigiMorph.org
<i>Corytophanes cristatus</i>	30.7	DigiMorph.org
<i>Polychrus marmoratus</i>	31.3	DigiMorph.org
<i>Anolis carolinensis</i>	20.5	DigiMorph.org
<i>Leiosaurus catamarcensis</i>	25.5	DigiMorph.org
<i>Pristidactylus torquatus</i>	26.1	DigiMorph.org
<i>Urostrophus vautieri</i>	22.6	DigiMorph.org
<i>Aciprion formosum</i> [†]	24.9	DigiMorph.org
<i>Crotaphytus collaris</i>	27.6	DigiMorph.org
<i>Gambelia wislizenii</i>	22.7	DigiMorph.org
<i>Enyalioides laticeps</i>	32.6	DigiMorph.org
<i>Morunasaurus annularis</i>	32.9	DigiMorph.org
<i>Brachylophus fasciatus</i>	34.0	DigiMorph.org

<i>Armandisaurus explorator</i> [†]	30.0	Norell and De Queiroz, 1991
<i>Dipsosaurus dorsalis</i>	23.1	DigiMorph.org
<i>Sauromalus ater</i>	39.0	DigiMorph.org
<i>Liolaemus bellii</i>	16.9	DigiMorph.org
<i>Phymaturus palluma</i>	18.1	DigiMorph.org
<i>Chalarodon madagascariensis</i>	16.5	DigiMorph.org
<i>Oplurus cyclurus</i>	24.6	DigiMorph.org
<i>Petrosaurus mearnsi</i>	21.4	DigiMorph.org
<i>Uta stansburiana</i>	13.1	DigiMorph.org
<i>Sceloporus variabilis</i>	18.4	DigiMorph.org
<i>Phrynosoma platyrhinos</i>	13.7	DigiMorph.org
<i>Uma scoparia</i>	17.9	DigiMorph.org
<i>Leiocephalus barahonensis</i>	16.8	DigiMorph.org
<i>Plica plica</i>	33.4	DigiMorph.org
<i>Stenocercus guentheri</i>	20.6	DigiMorph.org
<i>Uranoscodon superciliosus</i>	28.3	DigiMorph.org
<i>Tchingisaurus multivagus</i> [†]	30.4	Keqin and Norell, 2000
<i>Gobinatus arenosus</i> [†]	35.0	Keqin and Norell, 2000
<i>Adamisaurus magnidentatus</i> [†]	48.0	Keqin and Norell, 2000
<i>Macrocephalosaurus</i> [†]	50.0	Keqin and Norell, 2000
<i>Polyglyphanodon sternbergi</i> [†]	81.5	Gilmore, 1942
<i>Sineoamphisbaena hexatabularis</i> [†]	24.0	Wu et al., 1996
<i>Adriosaurus suessi</i> [†]	25.0	Lee and Caldwell, 2000
<i>Pontosaurus</i> [†]	55.0	Pierce and Caldwell, 2004
<i>Aigialosaurus dalmaticus</i> [†]	120.0	Dutchak and Caldwell, 2006
<i>Clidastes</i> [†]	Not available	
<i>Platecarpus</i> [†]	625.0	Konishi et al., 2012
<i>Plotosaurus</i> [†]	427.1	DigiMorph.org
<i>Tylosaurus</i> [†]	71.7	Everhart, 2002
<i>Eichstaettisaurus schroederi & gouldi</i> [†]	14.0	Evans et al., 2004
AMNH FR 21444 [†]	16.4	DigiMorph.org
<i>Delma borea</i>	9.0	DigiMorph.org
<i>Lialis burtonis</i>	29.1	DigiMorph.org
<i>Strophurus ciliaris</i>	22.5	DigiMorph.org
<i>Rhacodactylus auriculatus</i>	31.5	DigiMorph.org
<i>Saltuarius (Phyllurus) cornutus</i>	38.1	DigiMorph.org
<i>Aeluroscalobates felinus</i>	27.4	DigiMorph.org
<i>Coleonyx variegatus</i>	15.2	DigiMorph.org
<i>Eublepharis macularius</i>	26.8	DigiMorph.org
<i>Teratoscincus przewalskii</i>	22.7	CAS 140562 CT scan

<i>Gonatodes albogularis</i>	12.3	DigiMorph.org
<i>Phelsuma lineata</i>	16.0	DigiMorph.org
<i>Gekko gecko</i>	43.9	DigiMorph.org
<i>Lacerta viridis</i>	21.7	DigiMorph.org
<i>Takydromus ocellatus</i>	12.3	DigiMorph.org
<i>Colobosaura modesta</i>	10.9	DigiMorph.org
<i>Pholidobolus montium</i>	12.2	DigiMorph.org
<i>Callopiastes maculatus</i>	33.0	DigiMorph.org
<i>Tupinambis teguixin</i>	67.1	DigiMorph.org
<i>Aspidoscelis tigris</i>	25.5	DigiMorph.org
<i>Teius teyou</i>	27.7	DigiMorph.org
<i>Paramacellodus</i> [†]	18.3	Evans and Chure, 1998
<i>Parmeosaurus scutatus</i> [†]	30.2	DigiMorph.org
<i>Tepexisaurus tepexii</i> [†]	23.3	Reynoso and Callison, 2000
<i>Cricosaura typica</i>	8.0	DigiMorph.org
<i>Lepidophyma flavimaculatum</i>	24.0	DigiMorph.org
<i>Palaeoxantusia "Wyoming"</i> ^{††}	Not available	
<i>Xantusia vigilis</i>	9.6	DigiMorph.org
<i>Platysaurus imperator</i>	26.9	DigiMorph.org
<i>Cordylus mossambicus</i>	28.2	DigiMorph.org
<i>Zonosaurus ornatus</i>	24.7	DigiMorph.org
<i>Cordylosaurus subtesselatus</i>	9.3	DigiMorph.org
<i>Myrmecodaptria microphagosa</i> [†]	25.9	Keqin and Norell, 2000
<i>Carusia intermedia</i> [†]	33.8	Keqin and Norell, 2000
<i>Globaura venusta</i> [†]	18.8	Keqin and Norell, 2000
<i>Hymenosaurus clarki</i> [†]	11.9	Keqin and Norell, 2000
<i>Eoxanta lacertifrons</i> [†]	18.0	Borsuk-Bialynicka, 1988
<i>Plestiodon (Eumeces) fasciatus</i> [']	16.3	DigiMorph.org
<i>Scincus scincus</i>	18.1	DigiMorph.org
<i>Brachymeles gracilis</i>	11.5	DigiMorph.org
<i>Acontias percivali</i>	9.1	Maisano, pers. comm, 2018
<i>Amphiglossus splendidus</i>	17.8	DigiMorph.org
<i>Feylinia polylepis</i>	10.7	DigiMorph.org
<i>Trachylepis (Mabuya) quinquetaeniata</i> [']	20.7	Maisano, pers. comm, 2018
<i>Sphenomorphus solomonis</i>	14.6	DigiMorph.org
<i>Eugongylus rufescens</i>	26.7	DigiMorph.org
<i>Tiliqua scincoides</i>	68.0	DigiMorph.org
<i>Shinisaurus crocodilurus</i>	32.0	DigiMorph.org
<i>Xenosaurus platyceps</i>	22.0	Herrel et al., 2001
<i>Xenosaurus grandis</i>	28.4	DigiMorph.org
<i>Pseudopus (Ophisaurus) apodus</i> [']	41.2	DigiMorph.org

<i>Peltosaurus granulatus</i> [†] (AMNH 8138)	35.2	DigiMorph.org
<i>Helodermoides tuberculatus</i>	45.0	DigiMorph.org
<i>Anniella pulchra</i>	9.6	DigiMorph.org
<i>Celestus enneagrammus</i>	16.0	DigiMorph.org
<i>Elgaria multicastrata</i>	34.0	DigiMorph.org
<i>Gobiderma pulchrum</i> [†]	62.0	Keqin and Norell, 2000
<i>Estesia mongoliensis</i> [†]	57.0	Norell et al., 1992
<i>Aiolosaurus oriens</i> [†]	39.8	Keqin and Norell, 2000
<i>Heloderma horridum</i>	65.0	DigiMorph.org
<i>Heloderma suspectum</i>	55.7	DigiMorph.org
<i>Lanthanotus borneensis</i> (FMNH 148589)	24.5	DigiMorph.org
<i>Saniwa</i> [†]	75.5	Conrad et al., 2008
<i>Varanus salvator</i>	140.1	DigiMorph.org
<i>Varanus acanthurus</i>	32.1	DigiMorph.org
<i>Varanus exanthematicus</i>	57.3	DigiMorph.org
<i>Anelytropsis papillosus</i>	8.6	DigiMorph.org
<i>Dibamus novaeguineae</i>	8.2	DigiMorph.org
<i>Spathorhynchus fossorium</i> [†]	33.3	DigiMorph.org
<i>Dyticonastis rensbergeri</i> [†]	26.7	DigiMorph.org
<i>Rhineura floridana</i>	11.8	DigiMorph.org
<i>Bipes biporus</i>	7.0	DigiMorph.org
<i>Bipes canaliculatus</i>	8.9	DigiMorph.org
<i>Trogonophis wiegmanni</i>	13.2	DigiMorph.org
<i>Diplometopon zarudnyi</i>	8.0	DigiMorph.org
<i>Geocalamus acutus</i>	9.3	DigiMorph.org
<i>Amphisbaena fuliginosa</i>	17.5	DigiMorph.org
<i>Tetrapodophis amplexus</i> [†]	10.0	Martill et al., 2015 supp
<i>Coniophis praecedens</i>	Not available	
<i>Najash rionegrina</i> [†]	17.8	Apesteguia and Zaher, 2006
<i>Leptotyphlops dulcis</i>	5.7	DigiMorph.org
<i>Typhlops jamaicensis</i>	7.5	DigiMorph.org
<i>Liotyphlops albirostris</i>	4.1	DigiMorph.org
<i>Typhlophis squamosus</i>	4.1	DigiMorph.org
<i>Dinilysia patagonica</i> [†]	62.0	Caldwell and Calvo, 2008
<i>Wonambi naracoortensis</i> [†]	121.8	Scanlon and Lee, 2000
<i>Kataria anisodonta</i> [†]	7.2	Scanfero et al., 2013
<i>Haasiophis terrasanctus</i> [†]	45.6	Tchernov et al., 2000
<i>Eupodophis descouensis</i> [†]	13.9	Palci et al., 2013
<i>Pachyrhachis problematicus</i> [†]	77.8	Palci et al., 2013
<i>Anilius scytale</i>	25.0	DigiMorph.org

<i>Trachyboa boulengeri</i>	11.3	Maisano, pers. comm, 2018
<i>Tropidophis haetianus</i>	16.2	DigiMorph.org
<i>Calabaria reinhardtii</i>	22.8	DigiMorph.org
<i>Anomochilus leonardi</i>	6.9	DigiMorph.org
<i>Cylindrophis ruffus</i>	23.3	DigiMorph.org
<i>Uropeltis melanogaster</i>	14.2	Maisano, pers. comm, 2018
<i>Xenopeltis unicolor</i>	29.1	DigiMorph.org
<i>Loxocemus bicolor</i>	27.8	DigiMorph.org
<i>Xenophidion acanthognathus</i>	9.9	Maisano, pers. comm, 2018
<i>Casarea dussumieri</i>	16.0	DigiMorph.org
<i>Exiliboa placata</i>	13.0	DigiMorph.org
<i>Ungaliophis continentalis</i>	17.8	DigiMorph.org
<i>Eryx colubrinus</i>	19.1	DigiMorph.org
<i>Lichanura trivirgata</i>	14.7	DigiMorph.org
<i>Epicrates striatus</i>	40.0	DigiMorph.org
<i>Boa constrictor</i>	70.1	DigiMorph.org
<i>Aspidites melanocephalus</i>	48.4	DigiMorph.org
<i>Python molurus</i>	68.2	DigiMorph.org
<i>Xenodermus javanicus</i>	11.9	Maisano, pers. comm, 2018
<i>Acrochordus granulatus</i>	16.3	Rieppel, 2007
<i>Pareas hamptoni</i>	11.8	DigiMorph.org
<i>Lycophidion capense</i>	14.1	DigiMorph.org
<i>Aparallactus werneri</i>	9.9	Maisano, pers. comm, 2018
<i>Atractaspis irregularis</i>	15.0	DigiMorph.org
<i>Causus rhombeatus</i>	19.2	DigiMorph.org
<i>Azemiops feae</i>	18.4	Maisano, pers. comm, 2018
<i>Daboia russelli</i>	35.4	Maisano, pers. comm, 2018
<i>Agkistrodon contortrix</i>	22.8	DigiMorph.org
<i>Bothrops asper</i>	49.4	DigiMorph.org
<i>Lachesis muta</i>	49.6	DigiMorph.org
<i>Naja naja</i>	32.8	DigiMorph.org
<i>Notechis scutatus</i>	46.7	Cundall and Irish, 2008
<i>Laticauda colubrina</i>	28.0	DigiMorph.org
<i>Micrurus fulvius</i>	20.8	DigiMorph.org
<i>Natrix natrix</i>	25.0	DigiMorph.org
<i>Afronatrix anoscopus</i>	16.5	DigiMorph.org
<i>Amphiesma stolata</i>	17.0	DigiMorph.org
<i>Thamnophis marcianus</i>	25.5	DigiMorph.org
<i>Xenochrophis piscator</i>	26.7	DigiMorph.org
<i>Lampropeltis getula</i>	30.7	DigiMorph.org
<i>Coluber constrictor</i>	27.4	DigiMorph.org
<i>Parviraptor estesi</i> [†]	20.4	Caldwell et al., 2015

<i>Diablophis gilmorei</i> [†]	11.3	Caldwell et al., 2015
<i>Portugalophis lignites</i> [†]	22.8	Caldwell et al., 2015
<i>Eophis underwoodi</i> [†]	Not available	
<i>Chamops segnis</i> [†]	Not available	
<i>Parasaniwa wyomingensis</i> [†]	36.5	Conrad, 2008
<i>Exostinus lancensis</i> [†]	Not available	
<i>Odaxosaurus piger</i> [†]	Not available	
<i>Leptochamops denticulatus</i> [†]	Not available	
<i>Sphaerodactylus ariasae</i>	4.2	Ctscan USMN 541810
<i>Brookesia minima</i>	5.5	Ctscan YPM HERR.010232
<i>Brookesia superciliaris</i>	11.1	Ctscan YPM HERR.010233
<i>Rieppeleon brevicaudatus</i>	11.5	Ctscan YPM HERR.011665
<i>Brookesia micra</i>	4.1	Ctscan ZSM uncatalogued
<i>Dibamus bodageki</i>	7.1	Ctscan YPM HERR 612715
<i>Aprasia repens</i>	5.0	Ctscan YPM HERR 014702

Brookesia_superciliaris102000200011000010010001000000000--11000000-0-

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Aprasia_repens100100000000010011001020000000000--1013000000-1--

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VITA

Maria Camila Vallejo-Pareja

Department of Biological Sciences
Sam Houston State University
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Education:

BSc. Biology 2005 – 2011: Department of Biology, Universidad Nacional de Colombia – Bogotá, 2005 - 2011. Advisor: PhD. Joao Muñoz-Duran

Professional experience:

Smithsonian Tropical Research Institute, Center for Tropical Paleocology and Archaeology, Panama 2010-2014. Research Assistant. Advisor: PhD. Carlos Jaramillo.

Publications:

Scientific Publication in Peer reviewed Journals

Bauer, A.M., Beach-Mehrotra, M., Bermudez, Y., Clark, G.E., Daza, J.D., Glynne, E., Hagyari, D., Harnden, J., Holovacs, N., Kanasiro, A., Lofthus A.J., Pierce, Z., Ryan, A., Syed, S., **Vallejo-Pareja, M.C.**, Walker, B. and J. Willet. 2018. The tiny skull of the Peruvian gecko *Pseudogonatodes barbouri* (Gekkota: Sphaerodactylidae) obtained via a divide-and-conquer approach to morphological data acquisition. *South American Journal of Herpetology* 13:102–116.

Perez, M.E., **Vallejo-Pareja, M.C.**, Carrillo, J.D, and C. Jaramillo. Pliocene capybaras (Rodentia, Caviidae) from northern South America (Guajira, Colombia), and its implications in the Great American Biotic Interchange. *Journal of Mammalian Evolution*, DOI 10.1007/s10914-016-9356-7

Bacon, C.D., Molnar, P., Antonelli, A., Crawford, A.J., Montes, C. and **M.C. Vallejo-Pareja**. 2016. Quaternary glaciations and the Great American Biotic Interchange. *Geology*, DOI 10.1130/G37624.1

Vallejo-Pareja, M.C., Carrillo. J.D., Moreno-Bernal, J.W., Pardo-Jaramillo, M., Rodríguez-Gonzales, D.F., and J. Muñoz-Durán. 2015. *Hilarcotherium castanedaii* a new Miocene Astrapothere (Mammalia, Astrapotheria) from the Upper Magdalena Valley, Colombia. *Journal of Vertebrate Paleontology*, DOI 10.1080/02724634.2014.903960.

Ramirez-Chaves, H.E., Suarez-Castro, A.F., Morales-Martinez, D.M., and **M.C. Vallejo-Pareja**. 2015. Richness and distribution of porcupines (Erethizontidae: Coendou) from Colombia. *Mammalia*, DOI 10.1515/mammalia-2014-0158.

Moreno, J.F., Hendy, A.J.W., Quiroz, L., Hoyos, N., Jones, D.S., Zapata, V., Zapata, S., Ballen, G., Cadena, E., Cárdenas, A.L., Carrillo-Briceño, J.D., Carrillo, J.D., Delgado-Sierra, D., Escobar, J., Martinez, J.I., Martinez, C., Montes, C., Moreno, J., Perez, N., Sanchez, R., Suarez, C., **Vallejo-Pareja, M.C.**, and Jaramillo, C. 2015. An Overview and Revised Stratigraphy of Early Miocene-Pliocene Deposits in Cocinetas Basin, La Guajira, Colombia. *Swiss Journal of Paleontology*, DOI 10.1007/s13358-015-0071-4.

Outreach Publications

Perez-Consuegra, N., Moreno, F., and **Vallejo-Pareja, M.C.** 2014. Gliptodontes : mamíferos gigantes en el pasado de la Guajira Colombiana. *Hipotesis, Apuntes Científicos Uniandinos*, 17, 52–57. [Translated title: Gliptodonts: extinct giant mammals from La Guajira, Colombia]

Teaching experience:

Department of Biological Sciences, Sam Houston State University. Zoology Graduate Teaching Assistant (Fall and Spring 2016, 2017)

Universidad de Los Andes, Geological field camp. Teaching assistant Geological field Camp - Deciphering the Geology of the Azuero Peninsula, Panamá. (Summer 2014)

Biology Department, Universidad Nacional de Colombia

Cátedra José Celestino Mutis “Biodiversidad en Colombia: Amenazas, desafíos y acciones diversas” (Spring 2010)

Cátedra José Celestino Mutis “Darwin 200 Años” (Spring 2009)

Introducción a la Sistemática Animal [Translated title: Introduction to animal systematics] (Spring 2008)

Fundación UNIMUSICA, Middle school biology teacher (2009-2010)

Scholarships and awards:

2017. James D. Long Biology Endowed Scholarship. Sam Houston State University, Texas.
2017. Dr. Everett Wilson Biology Endowed Scholarship. Sam Houston State University, Texas.
2017. Department of Biology Scholarship Fund. Sam Houston State University, Texas.
2017. Gans Collections and Charitable Fund Travel Grant for participating in the Joint Meeting of Ichthyologists and Herpetologists, Austin, TX (July 12-16, 2017)
2017. ToScA Travel Bursary, Tomography for Scientific Advancement for participating in the ToScA North America Meeting, Austin, TX (June 6-8)
- 2016 - 2017. Graduate leadership Scholarship. Sam Houston State University, Huntsville, Texas.
2016. Graduate Student Scholarship. Sam Houston State University, Huntsville, Texas.
2014. NESCent Travel Award for the course "Paleobiological and phylogenetic approaches to macroevolution", Durham, NC (July 22 to 29).
- 2005-2011. Undergraduate Scholarship "Mejores Bachilleres del País", Universidad de Nacional de Colombia

Selected presentations at professional meetings:

- Vallejo-Pareja, MC.**, Daza, JD., Maisano, JA., Thies, ML. 2017. Consequences of Miniaturization in the Skull of Lizards and Snakes. Joint Meeting of Ichthyologists and Herpetologists, Austin, TX.
- Vallejo-Pareja, MC.**, Daza, JD., Maisano, JA., Thies, ML. 2017. Consequences of Miniaturization in the Skull of Squamates. ToScA North America Meeting, Austin, TX.
- Carrillo, J.D., **Vallejo-Pareja, M.C.**, Cárdenas, A.L., Moreno, J., Jaramillo, C.,

Jimenez, L., Hendy, A., Jones, D. 2012. The Neotropical fossil record and the Great American Biotic Interchange. Geological Society of America Annual Meeting GSA. Charlotte. USA.

Moreno-Bernal, J.W., Moreno, F., Carrillo, J.D., **Vallejo-Pareja, M.C.**, Hendy, A. Zapata, V., Montes, C., Jaramillo, C. 2012. Neotropical late Miocene- early Pliocene vertebrates from the Castilletes formation, Northern Colombia. Society Vertebrate Paleontology Annual Meeting SVP. Raleigh. USA.

Vallejo-Pareja, M.C., Moreno J.W., Moreno J.F., Carillo, J.D., Jimenez, L. 2011. Histricognath Rodents form Castilletes Formation. PCP-PIRE-All hands meeting. Panama 2011.

Vallejo-Pareja, M.C., Schwartzmann, A., Moreno J.F. 2011. Vertebrate Microfossils from late Oligocene-early Miocene Las Cascadas Formation. Fellows and interns symposium – Smithsonian Tropical Research Institute. March 18, 2011

Pardo-Jaramillo, M. Rodriguez-Gonzalez, D.F. **Vallejo-Pareja, M. C.** Carrillo-Sánchez, J. D. Muñoz-Durán, J. Moreno-Bernal, J. W. 2010. Un Nuevo Género y Especie de Astrapotheriidae del Mioceno del Valle Superior del Magdalena, Colombia. X Congreso Argentino de Paleontología y Bioestratigrafía – VII Congreso Latinoamericano de Paleontología. La Plata. Argentina. September 20 - 24 de 2010. [Translated title: **A new genus and species of Miocene Astrapotheriidae from the Upper Magdalena Valley, Colombia. X Argentinean meeting of Paleontology and Biostratigraphy – VII Latin American meeting of Paleontology**]

Muñoz-Saba, Y, D. Casallas-Pabón, N. Calvo-Roa, J.D. Carrillo, **M.C. Vallejo-Pareja.** 2010. Caracterización de la diversidad de mamíferos de selvas Amazónicas conservadas: estudio de caso Estación Ecológica OME (Colombia). IX Congreso Internacional de Manejo de Fauna Silvestre en la Amazonía y Latinoamérica. Santa Cruz, Bolivia. [Translated title: **Mammalian characterization of a pristine Amazon rainforest, OME field station (Colombia). IX International meeting of wildlife management in the Amazon and Latin America**].

Fieldwork experience:

Geological field Camp - Deciphering the Geology of the Azuero Peninsula, Panamá. Azuero Peninsula, Panama. March and June, 2014. Universidad de Los Andes. Responsible: PhD. Camilo Montes

Castilletes Paleontology Project, January-February 2014, La Guajira Department - Colombia. Universidad del Norte, Smithsonian Tropical Research Institute and University of Zurich. Responsible: PhD. Jaime H. Escobar and PhD. Carlos Jaramillo.

Paleontological exploration of Sucre- Colombia, October 2013, Sucre Department - Colombia. Smithsonian Tropical Research Institute. Responsible: PhD. Carlos Jaramillo.

Paleosogamoso, July 2013, Santander - Colombia. Smithsonian Tropical Research Institute. Responsible: PhD. Carlos Jaramillo.

Castilletes Paleontology Project, January 2013, La Guajira Department - Colombia. Smithsonian Tropical Research Institute. Responsible: PhD. Carlos Jaramillo.

Panama Geology and Paleontology Project, 2010 - 2012, Panama - Smithsonian Tropical Research Institute. Responsibilities: PhD. Carlos Jaramillo and PhD. Camilo Montes.

Estación Ecológica OME, May 2009, Amazonas - Colombia. Universidad Nacional de Colombia. Responsible: PhD. Thomas Defler and PhD. Yaneth Muñoz Saba

Service to profession:

I Simposio de Paleontología Tropical 2013 [Translated title: I Symposium of Tropical Paleontology]: Organization committee. Bucaramanga, Escuela de Geología Universidad Industrial de Santander. June 14, 2013

The Paleobiology Database: contributor since July 2012. Upload of South American Cenozoic mammals data. Authorizer: Carlos Jaramillo. <http://paleobiodb.org/cgi-bin/bridge.pl>

II Congreso Nacional de Estudiantes de Biología 2009 [Translated title: II National Meeting of Biology Students]: Manager of Evaluation Committee. Manager Committee II Congreso Nacional de Estudiantes de Biología. Bogotá September 28 - October 2

Service to Department and University:

Biological Sciences Graduate Student Organization (BSGSO) Officer: Secretary. Fall 2016 - Spring 2018.

9th Undergraduate Research Symposium Moderator, Honors College, Sam Houston State University, April 23, 2016.

10th Undergraduate Research Symposium Moderator, Honors College, Sam Houston State University, April 29, 2017.

Workshops and courses:

Cladistics workshop in TNT, 2016. Sam Houston State University. Huntsville, Texas. December 12 – 14. **Instructor:** J. Salvador Arias.

Paleobiological and Phylogenetic Approaches to Macroevolution, 2014. NESCent course. Durham, North Carolina. July 22 to July 29, 2014. **Instructors:** Samantha Price, Graham Slater and Lars Schmitz

Anatomía Comparada de Vertebrados I: Sistema esquelético y dientes, 2012. [Translated title: Vertebrate Comparative Anatomy I: Skeleton and Dentition]. Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. Argentina. December 3rd - December 14, 2012. **Instructors:** Alfredo Carlini and Laura Lopez

Arc-GIS Desktop – Tools and Functionalities, 2011. Smithsonian Tropical Research Institute. Panamá. February 15th- February 25th, 2011. **Instructor:** Milton Solano.

Curso de Campo de Mamíferos Neotropicales, Estación Ecológica OME, Amazonas, 2009. [Translated title: Neotropical Mammals field Course, OME Field Station, Amazonas]. Universidad Nacional de Colombia. Bogotá D.C. Colombia. May 1st- May 30th, 2009. **Instructors:** Thomas Defler and Yaneth Muñoz Saba.

Languages:

Spanish: Native language

English: 97 TOEFL iBT score (2013-September -27)

Languages:

Juan Diego Daza, Ph.D. Assistant Professor, Department of Biological Sciences. Sam Houston State University. E-mail: jdd054@shsu.edu

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Camilo Montes, Ph.D. Professor Department of Geosciences. Universidad de los Andes.
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Environmental Sciences. University of Gothenburg, Sweden. E-mail:
christinedbacon@gmail.com