The sclerotic ring:
Evolutionary trends in squamates

by

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Dedication

This thesis is dedicated to my family, friends, and mentors who helped me get to where I am today. Thank you.

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Abstract

The sclerotic ring: Evolutionary trends in squamates

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Abstract: The sclerotic ring consists of several bones that form in the sclera of many reptiles. This element has not been well studied in squamates. Squamates are a diverse order of reptiles with a rich fossil record, but debated phylogeny. Squamates are particularly interesting because many species have secondarily lost their sclerotic rings. My research investigates the presence of sclerotic rings in squamates and traces the lineage of these bones across evolutionary time. This research shows that three losses of the sclerotic ring in squamates are supported when considering evolutionary and developmental evidence. Species that lack, or have a reduced, sclerotic ring, are united by their headfirst burrowing lifestyle. Additionally, I have shown that size of the sclerotic ring is related to environment and behaviour. This research will help expand our knowledge of these fascinating bones and will be useful for future phylogenetic analyses.

July 30, 2014

List of abbreviations and definitions

BMP – Bone Morphogenetic Protein

Ihh – Indian Hedgehog

Shh – Sonic Hedgehog

SV – Snout-vent length

Arboreal – Species that live on tree trunks or branches (Grizante *et al*., 2010).

Diel activity – Time of day a species is most active (Hall, 2008a).

Fossorial – Species that are burrowing or cryptic and spend a portion, or all, of their time underground (Wiens *et al*., 2006; Hall, 2008a; Maddin and Sherratt, 2014).

Photopic – Species that are active during well-lit times of day (Hall, 2008a)

Scotopic – Species that are active under low-light conditions (Hall, 2008a)

Terrestrial – Surface-dwelling species that do not spend time underground (Wiens *et al*., 2006).

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1.0 Introduction

1.1 The vertebrate ocular skeleton

The vertebrate ocular skeleton is an important part of the craniofacial skeleton that is present in many lineages (Walls, 1942; Franz-Odendaal and Hall, 2006). It is composed of a cartilaginous component, called scleral cartilage and/or a bony component, called the scleral ossicles, that when present in reptiles forms a ring (Walls, 1942). Several lineages have only the cartilaginous component (i.e. chondrichthyans, crocodiles, some basal mammals, and most actinopterygians) while others have both scleral cartilage and scleral ossicles (i.e. testudines, avians, most squamates, and many teleosts and dinosaurs) (Walls, 1942; Franz-Odendaal and Hall, 2006; Franz-Odendaal, 2008a).

Throughout vertebrate evolution the ocular skeleton, or parts thereof, has been lost several times (Franz-Odendaal and Hall, 2006; Franz-Odendaal, 2011). For example, mammals, snakes, and extant amphibians have all lost the bony component (Walls, 1942). The presence of the cartilage and/or bony components of the ocular skeleton, as well as their development and morphology, have been of great interest to our laboratory and others (e.g. Franz-Odendaal, 2006; Franz-Odendaal and Hall, 2006; Franz-Odendaal and Vickaryous, 2006; Franz-Odendaal, 2008a; 2008b; Hall, 2008a; 2008b; 2009; Schmitz and Motani, 2011a; Duench and Franz-Odendaal, 2012; Jabalee *et al*., 2013).

In both teleosts and reptiles, the ocular skeleton has been well described (e.g. Slonaker, 1918; de Beer, 1937; Curtis and Miller, 1938; Nelson, 1942; Walls, 1942; Murray, 1943; Underwood, 1984; de Queiroz and Good, 1988; Franz-Odendaal, 2006; 2008a; 2008b; 2011; Duench and Franz-Odendaal, 2012; Jourdeuil and Franz-Odendaal, 2012). In zebrafish and chickens, both components of the ocular skeleton are derived from the neural crest (Couly *et al*., 1993; Kague *et al*., 2012). The neural crest is a population of cells that is derived from the neuroectoderm and contributes to the skull (Hall, 2005). In reptiles (including birds), scleral ossicles are dermal bones that ossify intramembranously, without a cartilage precursor, and are situated anteriorly with respect to an underlying cup of cartilage that surrounds the retina (Franz-Odendaal, 2006; Franz-Odendaal and Hall, 2006; Franz-Odendaal, 2011). The scleral cartilage and scleral ossicles (up to 18) are separate elements in reptiles (Franz-Odendaal and Hall, 2006). In contrast, teleost scleral ossicles ossify endochondrally, with a cartilage precursor (Franz-Odendaal and Hall, 2006; Franz-Odendaal, 2011). Additionally, in teleosts, there are only ever two scleral ossicles maximum, joined by cartilage to form an integrated ring (Franz-Odendaal and Hall, 2006). These two elements may fuse to form a solid ring of bone in some fish (e.g. *Astyanax mexicanus*) (Franz-Odendaal, 2008a).

Walls (1942) first proposed that the ocular skeleton might not be homologous between teleosts and reptiles. Franz-Odendaal (2011) has since expanded greatly on and confirmed this hypothesis, concluding that the bony components of the ocular skeleton are likely not homologous between teleosts and reptiles while the cartilaginous components are likely homologous.

1.2 The reptilian ocular skeleton

Among extant reptiles (i.e. Curtis and Miller, 1938 (birds); Underwood, 1970; 1984 (lizards); Franz-Odendaal, 2008 (turtles); Hall, 2008a; 2008b; 2009 (birds and lizards)), the scleral cartilage is present as a cup that forms around the posterior portion of the eye while the scleral ossicles are positioned at the corneal-scleral limbus (the anterior portion of the eye) and form the sclerotic ring (Figure 1.1A, de Beer, 1937). The sclerotic ring does not articulate with any skeletal elements in the body, including the scleral cartilage (de Beer, 1937; Walls, 1942). The individual ossicles connect to each other in a way that is reminiscent of the sutures in the calvariae (de Beer, 1937). The concave morphology of the sclerotic ring (Figure 1.1B) depresses the sclero-corneal junction, which causes the formation of a broad annular sulcus (Walls, 1942). Walls (1942) suggested that this sulcus is important for accommodation (i.e. visual acuity) because it places the ciliary body closer to the lens. The sclerotic ring may additionally prevent distortion of the posterior portion of the eye when the cornea changes shape to focus light on the retina (Walls, 1942).

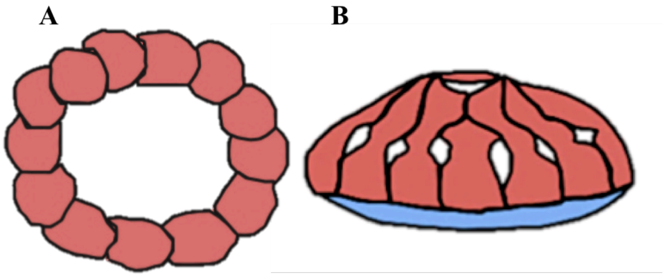

Figure 1.1. The ocular skeletal morphology in reptiles. A) The sclerotic ring (red) showing individual ossicles in the chicken. B) The ocular skeleton in the European green lizard with the sclerotic ring and the scleral cartilage (blue). Figure modified from Franz-Odendaal (2011).

In both birds and squamates (lizards) there is some morphological consistency when it comes to the number of scleral ossicles and how they overlap each other (e.g. Curtis and Miller, 1938; Underwood, 1984; Franz-Odendaal, 2011). Underwood (1970; 1984) described the ocular skeletal morphology in squamates and recognized 19 common overlap patterns that are loosely related to families. For example, in one family the ossicle overlying the ciliary artery may lay on top of its neighbouring ossicles, while in another family this ossicle may lay underneath its neighbours (Underwood, 1970; 1984). These patterns led Underwood (1970; 1984) to suggest that they are loosely phylogenetically correlated; however, he notes that there are several exceptions to this rule. Other research (including the work by Underwood, 1970; 1984), has found that despite this morphological similarity, there is also some degree of variation in scleral ossicle arrangement, size, and shape (Nelson, 1942; Columbre *et al.,* 1962; Franz-Odendaal, 2008b). For example, Coloumbre *et al.* (1962) found that when eye size is reduced in chickens, the sclerotic ring also becomes smaller. Nelson (1942) and Franz-Odendaal (2008b), both working with chickens, found that fluctuating asymmetry is present in the number of ossicles between individuals of the same species, and between eyes of the same individuals. However, Curtis and Miller (1938), working with wild populations of birds, found that fluctuating asymmetry is much lower in wild species. All of these studies show that while the overall shape of the sclerotic ring is consistent amongst reptiles, there is variation when considering the individual elements that make up the sclerotic ring.

1.3 Skeletal morphology: Influenced by environment and/or behaviour

Over the course of evolution, the habitat/environment and behaviour of organisms has an effect on how the skeletal morphology evolves (e.g. Wimberger, 1991; Kimmel *et al.*, 2005; Maddin and Sherratt, 2014). For example, the ultimate shape of the opercle (a bone that is part of the operculum) in threespine sticklebacks (*Gasterosteus aculeatus*) is determined by habitat (Kimmel *et al.*, 2005). Sticklebacks that have moved permanently to lake habitats have smaller and less ventrally elongated opercles than those that only travel to lakes for breeding purposes (Kimmel *et al.*, 2005). Another example is jaw morphology in neotropical cichlids (*Geophagus brasiliensis* and *G. steindachneri*)

(Wimberger, 1991). Cichlids that eat shrimp have a longer oral jaw, but a shorter area behind the jaws than those that feed on chironomid larvae (Wimberger, 1991). As these studies show, bone morphology can be used to predict the environment/habitat and/or behavior of extant species. Not surprisingly, the ocular skeleton has been used in this way by some researchers.

1.3.1 The ocular skeleton: Influenced by environment and/or behaviour

The ocular skeletal morphology is influenced by the environment and/or behaviour of extant and extinct vertebrates (e.g. Caprette *et al.*, 2004; Fernández *et al.*, 2005; Franz-Odendaal, 2008a; Hall, 2008a; 2008b; 2009; Pilgrim and Franz-Odendaal, 2009; Schmitz and Motani, 2011a). For example, presence or absence of scleral ossicles in teleost fish appears to correlate with activity level and environment (Franz-Odendaal, 2008). Relatively inactive teleosts (e.g. Gasterosteiformes and Lophiiformes), as well as those living in deep-sea habitats, tend to lack scleral ossicles, while more active fish (e.g. Salmoniformes and Cypriniformes) have one, or two scleral ossicles per eye (Franz-Odendaal, 2008a). In chondrichthyans, Pilgrim and Franz-Odendaal (2009) found that more active predators have stiffened tesserae in the scleral cartilage, which translates to more skeletal support than found in slow-moving, benthic species. In birds, similar patterns exist, for example, diving birds have more robust (e.g. heavier and more rigid) rings compared to other species, and both diving birds and rapid fliers have a steeper sclerotic ring slope than other species as a consequence of their tubular eye shape (Curtis and Miller, 1938). From the above examples it is clear that scleral ossicle presence and/or robustness may be related to behaviour.

In addition to studies that show a correlation between the ocular skeleton and behaviour, it has also been shown that scleral ossicle morphology is correlated with environment (e.g. Hall, 2008a; 2008b; 2009 in birds and squamates). Hall (2008a; 2008b; 2009) showed that the size of the aperture of the sclerotic ring (the inner diameter) could be used to distinguish between photopic (smaller apertures) and scotopic (larger apertures) birds and squamates. For example, scotopic lizards, those active in low-light conditions such as nocturnal lizards, tend to have larger corneal diameters (which is virtually the same measurement as the aperture of the sclerotic ring) than squamates in photopic habitats (Hall, 2008a). Hall (2008a; 2009) also stresses; however, that the sclerotic ring alone is useless for reliably inferring diel activity in fossils and extant squamates because of the overlap in the corneal diameters of scotopic and photopic squamates. However, other researchers, such as Schmitz and Motani (2011a; 2011b) disagree and claim the sclerotic ring can be used to infer diel activity. Schmitz and Motani (2011a) found using phylogenetic discriminate analysis on several extant amniotes that the sclerotic ring aperture is generally a reliable method of inferring diel activity in extinct archosaurs (e.g. dinosaurs and pterosaurs). Therefore, there is some disagreement in the literature on the reliability of scleral ossicle-mediated interpretations of behaviour (e.g. Hall, 2009; Hall *et al.*, 2011; Schmitz and Motani, 2011a; 2011b).

In summary, there have been numerous studies that show that bone presence and/or morphology can be a good predictor of environment and/or behaviour in fossils. However, one must be careful because while the morphology of the sclerotic ring varies in organisms that inhabit different environments or have different behaviours, these differences may not be pronounced enough to be useful when inferring environment and behavior in fossils.

1.4 Ocular skeletal development in reptiles

In reptiles (chickens, *Gallus gallus*), the development and ossification of the sclerotic ring was first described by Murray (1941; 1943), later by Coulombre *et al*. (1962), and has since been expanded upon by the Franz-Odendaal lab (e.g. Franz-Odendaal, 2006; Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012; Jourdeuil and Franz-Odendaal, 2012; Jabalee *et al*., 2013). Development of the sclerotic ring begins approximately seven days after incubation in chickens (Murray, 1941). After approximately two days, 14 papillae have developed in the conjunctival epithelium (Murray, 1941). These papillae are first seen as flat thickenings of the epithelium, and later they project into the underlying mesenchyme and upwards (Murray 1941; 1943). A condensation of mesenchymal cells is induced below each papilla and it is these condensations that form the scleral ossicles in a one to one ratio with the papillae (Murray, 1943).

The developmental and signaling pathways involved in the formation of the chicken ocular skeleton are still a subject of intense study (e.g. Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). However, some details have been deciphered. For example, Hamburger and Hamilton (1951) found that the papillae always form in a set sequence, with the first papillae forming above the ciliary artery and the last forming over the choroid fissure. Franz-Odendaal (2006; 2008b) later confirmed that this sequence is conserved in both chickens and turtles. Two major gene families, the Hedgehog family of signaling proteins and Bone Morphogenetic Proteins (*BMPs*) have been shown to be involved in scleral ossicle development (Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). Sonic Hedgehog (*shh*), an important signaling protein for segmentation and limb development, is involved in the maintenance of the papillae (Franz-Odendaal, 2008). *Shh* and Indian Hedgehog (*ihh*) are present in large concentrations in the papillae epithelium, but only *ihh* is found in the underlying mesenchyme (Franz-Odendaal, 2008b). Both *shh* and *ihh* are found in the papillae during the later stages of development, acting as long-range and short-range signals (Franz-Odendaal, 2008b; Franz-Odendaal and Duench, 2012). Furthermore, locally inhibiting *shh* prevents the induction of specific scleral ossicles in the ring (Franz-Odendaal, 2008b). *BMPs*, the other hand, may not be crucial for the healthy development of the papillae, but are important for the formation of the skeletal condensations that will form the scleral ossicles (Duench and Franz-Odendaal, 2012). Inhibiting induction via *BMP* results in loss of scleral ossicles. All of this research shows that there is some underlying compensation mechanism that mediates the completion of a sclerotic ring. That is, when individual ossicles are inhibited, their neighbours will expand into the empty space and complete the ring (Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). While these studies have greatly helped our understanding of scleral ossicle development, the continued study of this topic is important to increase our knowledge of the development of intramembranous bone and of the craniofacial skeleton in general.

1.5 Squamata: A diverse order of reptiles

Squamates (i.e. snakes, lizards, and their relatives) are a large clade with over 9000 species (Pyron *et al*., 2013). Squamates have evolved several different body plans, inhabit many environments (e.g. fossorial, terrestrial, arboreal), and display a range of behaviours. For example, it is generally agreed that photopic vision is the ancestral state for squamates, but several groups have secondarily evolved scotopic vision (Hall, 2008a). For these reasons, squamates are a useful group when studying variation. Furthermore, squamates have a rich and long fossil record, extending to the late Permian, approximately 300 million years ago (Gauthier, 1994). Squamata is nested within in Lepidosauromorpha, a lineage that also includes tuatara (e.g. *Sphenodon punctatus*, which has a sclerotic ring). Lepidosauromorphia is the sister group to Archosauromorpha, which also includes dinosaurs (present sclerotic ring), birds (present sclerotic ring) and crocodiles (absent sclerotic ring). Together, these two groups form Sauria.

Squamata has traditionally been divided into two lineages, Iguania and Scleroglossa (Figure 1.2A). Unfortunately, there is still some uncertainty when it comes to the positions of the individual families, and whether or not the traditional divisions of Iguania and Scleroglossa are legitimate (e.g. Figure 1.2B; Weins *et al*., 2010; Gauthier *et al*., 2012; Pyron *et al*., 2013). When morphological data is used, the Iguania-Scleroglossa division is recovered (Figure 1.2A). However, when molecular data is included, Scleroglossa becomes paraphyletic (Figure 1.2B; Weins *et al*., 2010; Pyron *et al*., 2013). Even between morphologically based phylogenetic studies, the families (especially those within Scleroglossa) are recovered in different positions (i.e. Conrad, 2008 versus Gauthier *et al*., 2012). Unfortunately, a single phylogenetic hypothesis for squamates is difficult to recover because, although there are many fossil species, these fossils are fragmented and poorly preserved (Conrad, 2008). This makes it difficult to obtain accurate and complete morphological information and virtually impossible to obtain molecular data from the fossil material.

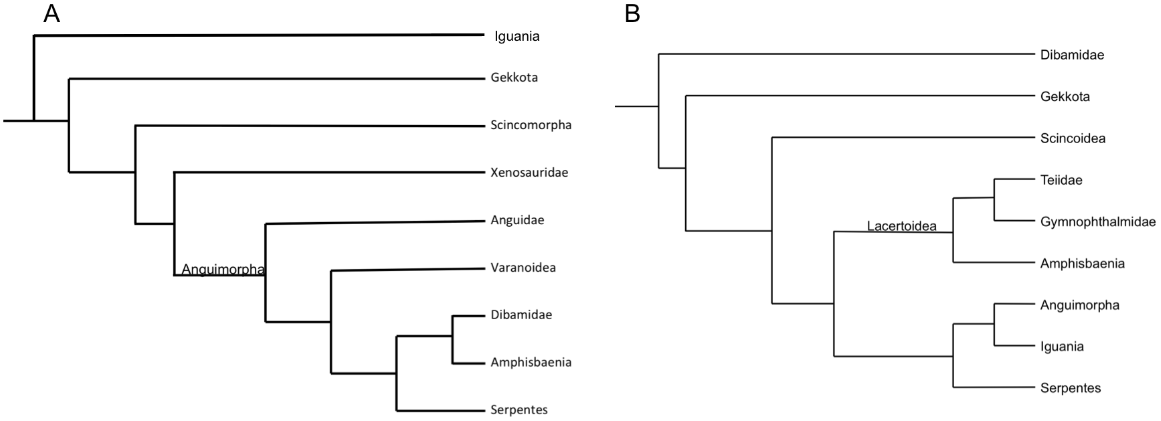

Figure 1.2. The two current phylogenies for Squamata. A) Morphological phylogeny modified from Gauthier *et al*. (2012). B) Molecular phylogeny modified from Pyron *et al*. (2013).

1.6 Limbless squamates pose a problem for phylogenetic analyses

Limbless lineages are particularly problematic when considering the squamate phylogeny (e.g. Conrad, 2008; Weins *et al*., 2010; Gauthier *et al*., 2012) because the absence of limbs and the simplification of the body and cranium have evolved several times in Scleroglossa. Researchers argue that some of these groups are consistently placed near each other on morphological phylogenies because of these shared characters and not because of relatedness (e.g. Lee, 1998; Pyron *et al*., 2013). This view is shared by morphological phylogeneticists, who admit that support for a clade consisting solely of limbless species is poor (e.g. Conrad, 2008; Gauthier *et al*., 2012).

Interestingly, many of these difficult to resolve lineages are also the groups where some or all members are missing scleral ossicles (Walls, 1942). Both Serpentes and Dibamidae lack scleral ossicles in all species, while some species in Amphisbaenia lack scleral ossicles (Walls, 1942; Kearney, 2003). Each of these groups will be discussed separately below.

1.6.1 Serpentes

Snakes comprise a large group of limbless squamates. There are around 1800 species; they exist on every continent (save for Antarctica), and live in most habitats (e.g.

fossorial, arboreal, aquatic; Caprette, 2005). Snakes range in size from mere centimeters to several meters. The phylogenetic position of snakes within squamates has long been an enigma, and their position within the phylogeny has changed several times (e.g. Lee and Scanlon, 2002; Conrad, 2008; Gauthier *et al*, 2012; Pyron *et al*., 2013). Snakes share several morphological traits with other squamate groups, including limblessness and the reduction of bones in the skull (Lee, 1998). They are, however, unique amongst extant squamates with respect to their eye morphology (i.e. they lack a sclerotic ring and diurnal snakes have yellow lens pigments) and in their method of visual accommodation (Caprette, 2005). While other squamates focus by contracting ciliary muscles that are anchored to the sclerotic ring, snakes focus by moving their lens forward by contracting the iris muscle (Walls, 1942). These differences might be relevant for phylogenetic analyses (e.g. Walls, 1942; Caprette *et al*., 2004).

1.6.2 Amphisbaenia

Five (sometimes six) families and several genera represent amphisbaenians, or worm lizards (Kearney, 2003). Nearly all members are entirely limbless, and all are adapted for headfirst burrowing (Kearney, 2003; Müller *et al*., 2011; Folie *et al*., 2013). Many amphisbaenians are also small to medium sized; their sizes range between 10 and 80 cm with most falling between 25 and 40 cm long (Folie *et al*., 2013). In spite of their fossorial lifestyle, amphisbaenians are surprisingly well distributed across the globe and live in many different habitats, including deserts, tropical rainforests, and woodlands (Hembree, 2007; Folie *et al*., 2013). Most species have cone-shaped skulls with blunt snouts, while others have sloping skulls with flattened snouts or bony keels (Kearney, 2003; Kearney and Stuart, 2004; Hembree, 2007). Many amphisbaenians have tiny eyes that are covered with a scale (Foureaux *et al*., 2010). In addition to their cranial morphology, their post-cranial morphology is also adapted to headfirst burrowing. Therefore, amphisbaenians are missing many morphological characters that are useful for phylogenetic analyses.

1.6.3 Dibamids

Dibamidae is represented by two genera, the monotypic *Anelytropis*, which has a small range in northeastern Mexico, and *Dibamus*, which has 20 species and a larger range in Southeast Asia (Rieppel, 1984; Neang *et al*., 2011; Townsend *et al*., 2011). In spite of their large geographic distance, both genera are morphologically similar. Dibamidae species are blind, lacking an optic nerve, but retain a rudimentary eyeball covered by a scale (Rieppel, 1984; Greer, 1985; Hallermann, 1998). Limbs are entirely lost in females; however, males retain two, small, flap-like hind limbs (Neang *et al*., 2011; Townsend *et al*., 2011). Dibamidae have miniaturized skulls associated with headfirst burrowing, and all species are indeed fossorial (Townsend *et al*., 2011). Dibamids are considered small to medium sized, with a range between 5 and 20 cm snout-vent length (Hallermann, 1998). Historically, Dibamidae has been recovered at many different positions on the phylogeny, with various analyses placing them within Gekkota, Scincomorpha, or Anguimorpha (e.g. Rieppel, 1984; Lee, 1998). Phylogenetic placement of Dibamidae is made difficult because this family is considered mosaic; it shares morphological characteristics with many groups, including Scincomorpha, Gekkota, Amphisbaenia, and Serpentes (Rieppel, 1984). Therefore, the phylogenetic position of Dibamidae remains uncertain.

1.7 Using the ocular skeleton to resolve the squamate phylogeny

The scleral ossicles have been used, with other eye traits, to resolve snake phylogeny (Caprette *et al*., 2004; Caprette, 2005). Additionally, the presence and absence of the sclerotic ring has been used as a character in other morphological phylogenies (e.g. Kearney, 2003 in amphisbaenians; Conrad, 2008 in squamates; Gauthier *et al*., 2012 also in squamates). When mapping phylogenies using ocular morphology, snakes (as well as caecilians, an amphibian clade that also lacks scleral ossicles) are placed as more closely related to aquatic reptiles than other clades (Caprette *et al*., 2004). This differs significantly from the commonly accepted idea that snakes are closely related to skinks or anguimorphans (e.g. Conrad, 2008; Gauthier *et al*., 2012; Pyron *et al*., 2013). This deviation from the norm is cause for concern regarding the usefulness of the ocular morphology in phylogenetic studies; however, there is at present no clear relationship between scleral ossicles and other morphological features such as limblessness. For example, there are many species that lack both limbs and scleral ossicles, but there are other species that have partial or full limb reduction and have scleral ossicles (Conrad, 2008; Franz-Odendaal and Hall, 2006), suggesting distinct evolutionary pressures in each region of the body. It is entirely possible that as in teleosts (Franz-Odendaal, 2008a) and chondrichthyans (Pilgrim and Franz-Odendaal, 2009), the presence and absence of scleral ossicles is correlated with the environment.

In order to better understand the patterns of gains and losses of scleral ossicles in the squamate phylogeny, both extinct and extant species require examination.

1.8 Objectives

The overarching goals of this research are twofold. First, this project aims to compile a database on the presence/absence of the sclerotic ring in extinct and extant squamates. Second, this project will expand our knowledge of the evolutionary history of the sclerotic ring and how its presence/absence and morphology is correlated with environment and behaviour. In order to successfully complete these goals, the following objectives were identified:

1. Investigate the presence or absence of scleral ossicles in extinct and extant squamates;
2. Map gains and losses of scleral ossicles on the phylogeny to determine whether trends across evolutionary time can be identified;
3. Research the life history and behaviour of extant Scleroglossa to determine whether there is a relationship between the presence/absence or morphology of scleral ossicles and environment, and/or behaviour.

2.0 Methods

2.1 Investigating sclerotic ring presence/absence in extinct and extant squamates

In order to investigate the presence/absence of the sclerotic ring in Squamata, a database was compiled of extant and extinct squamate species by surveying available literature, online databases, and museum collections. In total, 400 extant species (611 specimens) were examined (see Appendix A1 for my personal observations of extant species, n=93, and Appendix A2 for those extant species I found in the literature, n=307). I also examined 167 fossil species (Appendix A3).

2.1.1 Extant specimen database

While compiling the extant species database, museums with large herpetological collections were selected for site visits. In 2013, I visited the National Museum of Natural History Smithsonian Institute (USNM) and the Museum of National History in the UK (MNHUK) to examine dry skeletons and cleared and stained specimens. Of the 400 extant species in the database, I observed the presence/absence of the sclerotic ring first hand in 93 species, and the other 307 species were obtained from online databases (e.g. Digimorph and the American Museum of Natural History's Online Database) and descriptions in the literature (Table 2.1). A summary of the families assessed for each major squamate lineage (e.g. Iguania, Gekkota, Scincomorpha, Anguimorpha, and Serpentes), the number of species and specimens observed (either first hand, or by other researchers in the literature), and the resources used to obtain presence/absence data can be found in Table 2.1. It should be noted that the total number of specimens listed in Table 2.1 (611 individual specimens) represents the minimum number of specimens. This is because many authors did not include the number of specimens they examined and in the absence of evidence to the contrary I recorded one observed specimen. The species in this database are those that are commonly represented in phylogenetic analyses (i.e. all the major lineages are represented), as well as several, less commonly represented species. In total, these extant 400 species from 233 genera and 66 families are included (Appendix A1 and A2).

Table 2.1. The major squamate extant lineages examined and the data sources. This summary includes the number of families, species, and specimens from which data were obtained for each lineage. See Appendix A1 and A2 for a more detailed list of extant species.

Major taxonomic lineage	Families (n)	Species (n)	Specimens examined (n)	Source of data
Iguania	15	100	163	Lobo and Abdala (2001); Maisano (2001); Kearney (2003); Rodrigues (2005); Conrad (2008); Gauthier *et al*. (2012); American Museum of Natural History Online Database; Digimorph; personal observations (n=3)
Gekkota	5	56	90	Underwood (1957); Stephenson and Stephenson (1956); Stephenson (1960); Underwood (1984); Kearney (2003); Conrad (2008); Gauthier *et al*. (2012); Digimorph; personal observations (n=17)
Lacertoidea (Scincomorpha)	6	67	88	Burt and Burt (1931); Barahona and Barbadillo (1998); Maisano (2001); Kearney (2003); Nance (2007); Rodrigues *et al*. (2007); Conrad (2008); Tarazona and Ramirez-Pinilla (2008); Gauthier *et al*. (2012); Digimorph; personal observations (n=26)

Table 2.1. Continued.

Scincoidea (Scincomorpha)	5	62	79	Rieppel (1984); Underwood (1984); Greer (1985); Kearney (2003); Conrad (2008); Gauthier *et al*. (2012); Digimorph; personal observations (n=46)
Anguimorpha (excluding Amphisbaenia, Dibamidae and Serpentes)	7	33	87	Conrad (2008); Gauthier *et al*. (2012); American Museum of Natural History Online Database; Digimorph
Amphisbaenia and Dibamidae	8	40	62	Gans (1978); Rieppel (1984); Greer (1985); Kearney (2003); Conrad (2008); Digimorph; personal observations (n=1)
Serpentes	19	41	41	Kearney (2003); Conrad (2008); Gauthier *et al*. (2012); Polschowskia and Werenberg (2013); Digimorph
Rhynchocephalia (Squamate outgroup)	1	1	1	Gauthier *et al*. (2012); Digimorph
Total:	**66**	**400**	**611**	**---**

2.1.2. Fossil specimen database

Data for fossil specimens were obtained exclusively from the literature. The literature was surveyed to identify well-preserved specimens with reasonably complete skeletons, or at least reasonably complete skulls. In total, 161 fossil specimens were found in the literature; however, only 20 fossils were complete enough to assess presence/absence. These fossils were described in: Berman (1973; 1976; 1977), Sullivan (1987), Gao and Norell (1997), de Queiroz *et al*. (1998), Bardet *et al*. (2003), Rieppel *et al*. (2003), Evans *et al*. (2005), Conrad (2008), Conrad and Norell (2008), Evans and

Barbadillo (2010), Nydam *et al*. (2010), Konishi *et al*. (2011), Wang and Evans (2011), Bolet and Evans (2012), Daza *et al*. (2012), Evans and Wang (2012), Gauthier *et al*. (2012), and Yi and Norell (2013). See Appendix A3 for a complete list of fossil specimens that were assessed. Since many of these fossils are fragmented and often only contain portions of the skull, in many cases it was impossible to determine whether a sclerotic ring was present or not. To further complicate analyses, many authors refer to scleral ossicles as "unidentifiable bone fragments" (e.g. Sullivan, 1987) in their descriptions or fail to mention them altogether. Fossils were only considered to have a sclerotic ring if authors coded this character as positive in their phylogenic studies, or if the authors described a partial or complete sclerotic ring. Fossils that were relatively complete, and had complete skulls, were coded as absent for a sclerotic ring if I could not identify a sclerotic ring in the images, and if the author did not mention the presence of this structure. These absences could also have been coded as unknown; however, it is reasonable to code them as absent because the skulls were complete and well preserved, with no signs of predation or decay.

2.2 Phylogenetic mapping of the sclerotic ring

In order to map the gains and losses of sclerotic rings on the squamate phylogeny, the literature was surveyed for well-cited and supported phylogenies. Unfortunately, a single, well-supported phylogenetic hypothesis for Squamata does not exist. Therefore, I had to work with several phylogenies, both morphological and molecular. Conrad (2008) published a widely accepted morphological analyses in 2008, and this phylogeny was the standard until recently and is still widely cited. The most recent morphological phylogenetic analysis was conducted by Gauthier *et al*. (2012), who assessed 192 species for 610 morphological characters. This more recent phylogenetic study was used instead of other, older morphological analysis (i.e. Conrad (2008)), because Gauthier and colleagues assessed more characters (610 versus 363). However, while Gauthier *et al.* (2012) will be the main morphological phylogeny for this project, analyses will also be made using Conrad's (2008) work since it is frequently cited in the literature (see Discussion). The most recent molecular phylogenetic study was conducted by Pyron *et al.* (2013). This research group assessed 4161 species using 12 genes (seven nuclear loci and five mitochondrial genes), building on their previously published work. Overall, using both morphological and molecular phylogenies will give this project a broader perspective because both methods of analyses have their strengths and weaknesses (see Discussion) and will allow me to conduct a more comprehensive analysis of the evolution of the sclerotic ring in Squamata.

Of particular interest are the groups that have an unresolved position on the squamate phylogeny (Amphisbaenia, Dibamidae, and Serpentes and their closest relatives, other Scleroglossan lizards) since many of these species are known to lack the sclerotic ring. Of additional interest is the phylogeny of Amphisbaenia, the only squamate clade where the sclerotic ring is present in all families except for one. Kearney (2003) conducted a large-scale morphological analysis of Amphisbaenia where she assessed members of all 23 extant genera as well as several fossils. In total, she assessed 163 morphological characters. Therefore, Kearney's (2003) phylogeny will be used in addition to Gauthier *et al.* (2012) and Pyron *et al.* (2013) in order to assess the evolution of the sclerotic ring in squamates.

Three character states are represented on these phylogenies (found in the Results sections): presence (1), absence (0), and unknown, which is indicated by a question mark (?).

2.3 Life history and behaviour of squamates

In order to determine if there is a relationship between the presence/absence or morphology of the sclerotic ring and environment (fossorial versus non-fossorial lifestyles) or behaviour (e.g. photopic or scotopic), I conducted a large scale literature review into the behaviour and environment of squamates (Table 2.2). Specifically, I researched which lineages are photopic or scotopic, and which lineages have fossorial and limbless members, as all of these behaviours are known to be correlated with eye and/or sclerotic ring morphology (e.g. Hall, 2008a; 2009; Schmitz and Motani, 2011).

Table 2.2. Summary of literature consulted for squamate behaviour and lifestyle.

Trait	Source of data
Diel activity	Underwood (1957); Busack (1978); Ballinger *et al*. (1995); Rodrigues (1996); Lopez *et al*. (2002); Lemos-Espinal *et al*. (2003); Kearney (2003); Llewelyn *et al*. (2005); Hall (2008); Rodrigues and dos Santos (2008); Sites *et al*. (2011)
Fossorial lifestyle	Lee (1998); Wiens *et al*. (2006); Roscito and Rodrigues (2010)
Limbless morphology	Lee (1998); Wiens *et al*. (2006)

Since sclerotic ring measurements have been used to assess diel activity (extant and fossil species) in previous studies (e.g. Hall, 2008a; 2009; Schmitz and Motani, 2011) similar measurements were included here. Specifically, these measurements include the inner and outer maximum diameter of the sclerotic ring (Figure 2.1). For most specimens, these measurements were taken using a dissecting microscope fitted with an ocular micrometer and rounded to the nearest micrometer. Some larger specimens (e.g. some geckos) required the use of digital calipers for measurements. In these instances three decimal places were recorded and were later rounded to one decimal place for consistency. Studies in teleosts have shown that preservation methods can change the size of a specimen; however, these differences are only significant in specimens smaller than five millimeters (Hjorleifsson and Klein-MacPhee, 1992). Counting individual scleral ossicles was attempted, but it was found that getting an accurate number on the smaller sclerotic rings was too costly for the amount of time I had in the museums. For each specimen that was articulated, the snout-vent length was noted from the specimen label or measured using digital calipers. The sex of the specimen, and the location of the collection site were also recorded for possible later use in statistical analyses and for later research into habitat. These data are collected in Appendix B.

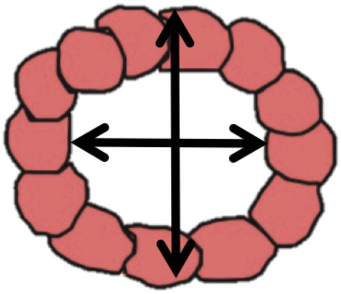

Figure 2.1. Schematic of a sclerotic ring showing the measurements used for analyses. Both the inner and outer diameters (arrows) were recorded on species with an intact sclerotic ring.

In total, I measured the inner and outer diameters of the sclerotic ring in 100 dry skeletal and alcohol preserved specimens that had a complete, preserved ring in order to determine whether there is any statistical significance in the inner and outer diameters exists between families and/or between species with different behaviours and life styles. These specimens are from seven families and 31 genera in Gekkota and Scincomorpha. Statistical analyses on these specimens were performed using Minitab 16. As the data was not normally distributed, Mann-Whitney tests (to compare between families) and Kruskal-Wallis tests (to compare species with different behaviours/habitats) were used with a 95% confidence interval (Appendix C, Tables C1-C4). I performed analyses between species that were scotopic versus photopic, and fossorial versus non-fossorial, for both the inner and outer sclerotic ring diameters (see Appendix C, Tables C5-C12). In order to account for body size, I divided my data set into groups that were smaller than the median snout-vent length (59 mm) and larger than the median snout-vent length. I then further divided these size groups into scotopic versus photopic and fossorial versus non-fossorial and performed the same statistical tests as described above (Appendix C, Tables C13-C20). Finally, I performed a Spearman correlation between the two measurements (inner and outer diameter) using Microsoft Excel and Minitab 16 (Appendix C, Figure C1).

3.0 Results

3.1 Overview of the presence and absence of the sclerotic ring in squamates

In order to investigate the presence and absence of the sclerotic ring in squamates, I assessed this character in 400 extant species and 20 fossil species. The extant species are from five lineages: Iguania, Gekkota, Scincomorpha, Anguimorpha, and Serpentes (Appendices A1 and A2). Within these lineages, only Anguimorpha and Serpentes have families that lack a sclerotic ring. All families (n=31) and species (n=285) examined in Iguania, Gekkota, and Scincomorpha had a sclerotic ring (Figure 3.1), while all the Serpentes families (n=19) and species (n=41) lacked a sclerotic ring. Within Anguimorpha families (n=15), 13 families (37 species) had a sclerotic ring and in Dibamidae (six species from two genera) and Rhineuridae (one species from one genera) all members lacked a sclerotic ring (Figure 3.1). The sclerotic ring is therefore present in the majority of squamate families (45 out of 66 sampled, or two-thirds), while one third of families sampled were absent for this character. All of the families and species that lacked a sclerotic ring can be found in "Krypteia" (a term used by Gauthier *et al*. (2012) to refer to Serpentes, Amphisbaenians, and Dibamids; Figure 3.1).

In order to better understand sclerotic ring evolution, I also assessed this trait in fossil squamates (n=20, Appendix A3). Thirteen fossil species have a sclerotic ring in Iguanidae (n=1), Mosasauria (an extinct group of marine reptiles, n=6), Gekkota (n=1), Lacertoidea (n=1) and Anguimorpha (n=4) (Figure 3.2). An additional three species that are considered basal Scleroglossans also have remnant sclerotic rings (Figure 3.2). Four species lack a sclerotic ring, one of those species is in Varanoidea, two are in Amphisbaenia (in Rhineuridae) and one is a fossil snake (Figure 3.2). Despite the low numbers of fossil specimens in each lineage, overall these results are in agreement with extant data and indicate that the loss of the sclerotic ring is a derived trait that only occurs in Anguimorpha.

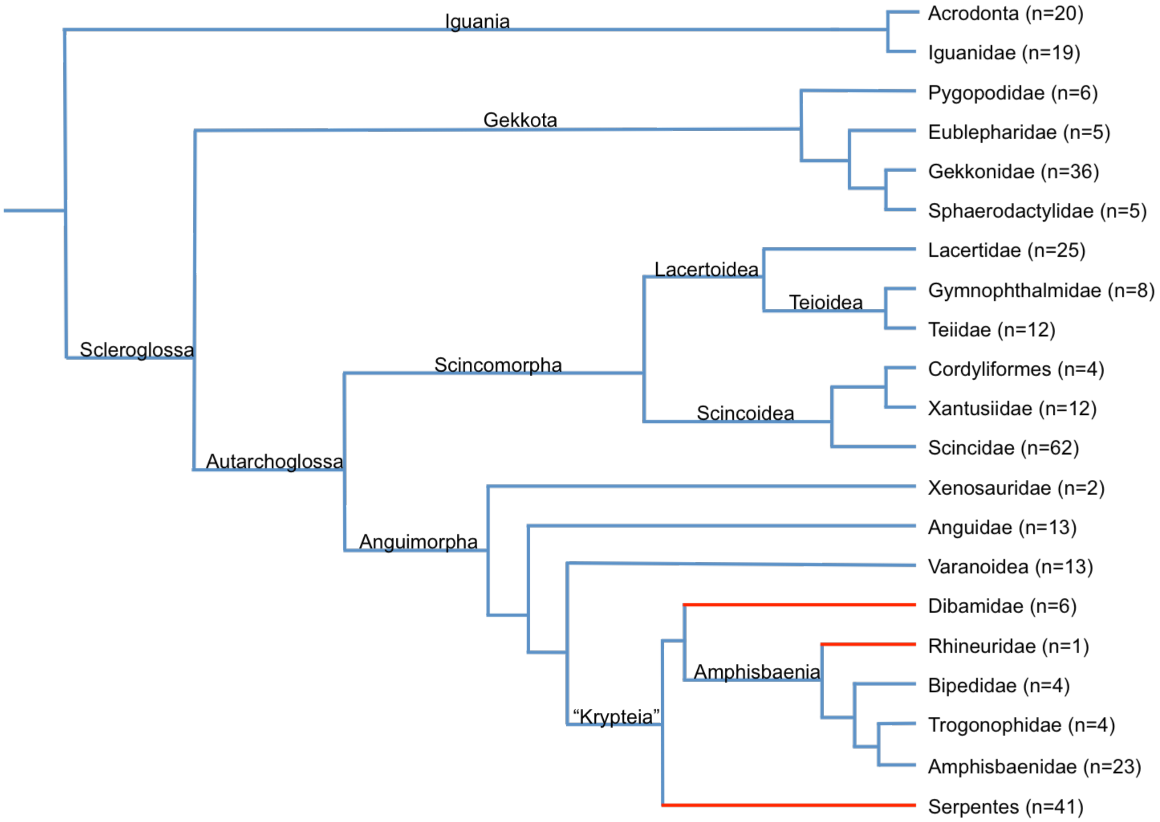

Figure 3.1. Family level phylogeny of extant squamates modified from Gauthier *et al*. (2012). Red lines indicates branches where the sclerotic ring has been lost, while blue lines includes present sclerotic rings. Numbers after the families indicate the number of species assessed.

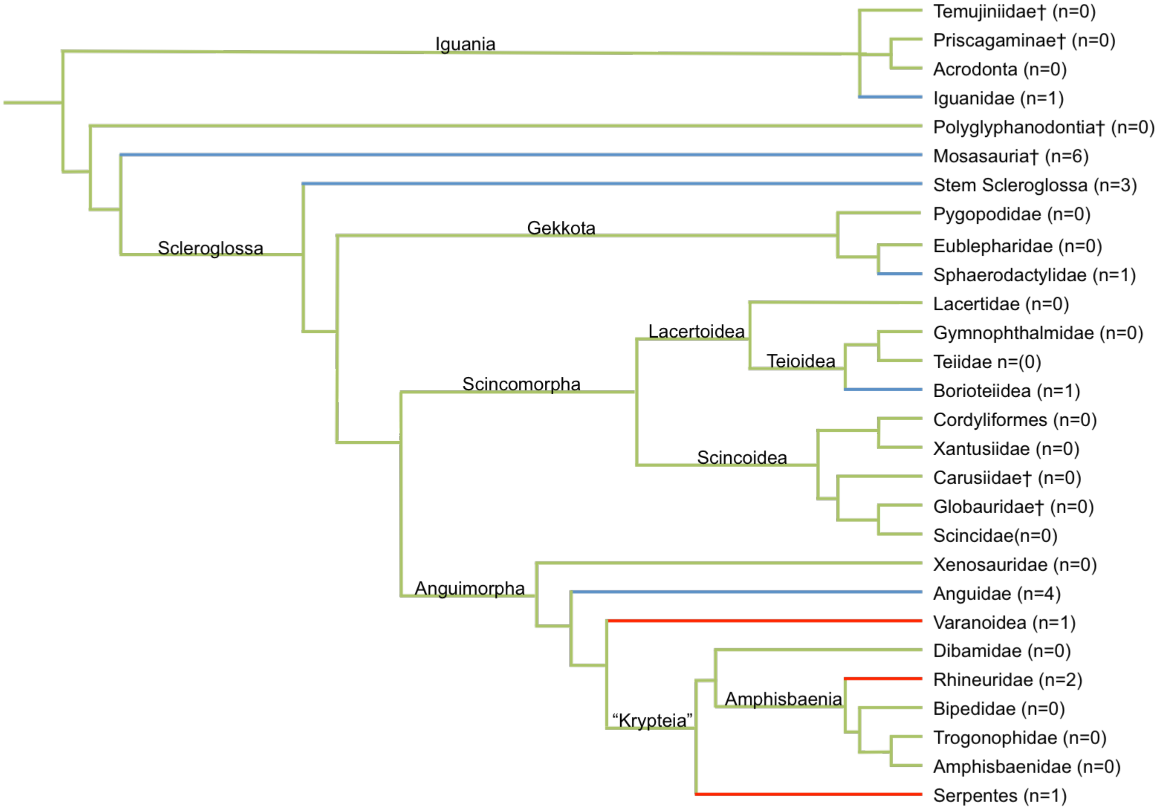

Figure 3.2. Family and higher-level phylogeny showing presence/absence of a sclerotic ring in fossil taxa modified from Gauthier *et al*. (2012), and Mo *et al*. (2010). Blue indicates lineages where a sclerotic ring is present, red indicates branches where the sclerotic ring has been lost and green lineages represent an unknown character state. Daggers indicate lineages that do not have extant members. Numbers after the families indicate the number of specimens assessed.

3.2 Phylogenetic mapping of the sclerotic ring character trait

In order to better visualize the evolution of the sclerotic ring, these data were mapped onto four phylogenies. Two morphological phylogenies from Gauthier *et al*. (2012) represent a comprehensive phylogeny for the whole of Squamata, while a morphological phylogeny from Kearney (2003) was used to examine more closely the relationships within Amphisbaenia. Finally, a molecular phylogeny from Pyron *et al*. (2013) was used as another comprehensive phylogeny for Squamata. The other phylogeny from Conrad (2008) was also used for comparisons (see Discussion). The other phylogenies are discussed separately, below.

3.2.1. Gauthier *et al*. (2012) morphological phylogeny using fossil data

To understand the evolution of the sclerotic ring, the fossil data were mapped on a family level phylogeny from Gauthier *et al*. (2012) with additional information on Borioteiidea from Mo *et al*. (2010; Figure 3.2). Due to the fragmented nature of many of these fossils, it is unknown if most fossil lineages had a sclerotic ring (Figure 3.2, Appendix A3). Of the 167 fossil specimens examined, only 20 were complete enough to assess presence/absence. For example, only one fossil represents the whole of Iguania (one species in Iguanidae, sclerotic ring is present). Unsurprisingly, members of the extinct marine group, Mosasauria, are best represented (n=6, all found with an intact sclerotic ring). Historically, marine species are well preserved because they are quickly covered by sediment, protecting them from predators and weathering. All of the well-preserved fossils with sclerotic rings are located in positions that are basal to “Kypteia”, which has a poor fossil record due to their small size (Figure 3.2). In addition to the fossils in Iguania and Mosasauria, there are also three fossil taxa at the stem of Scleroglossa, one genus in Scincomorpha, and four in Anguidae (an Anguimorphan family) that are all known to have a sclerotic ring. Consistent with the results of extant studies, fossils that lack a sclerotic ring (two in Rhineuridae, and one in Serpentes) are, for the most part, found in the highly derived “Krypteia” lineages (Figure 3.2). The other lineages in “Krypteia” consist of fragmented fossils (i.e. the other families in Amphisbaenia) or completely lack fossils (i.e. Dibamidae). A fossil (*Estesia mongoliensis*) in Varanoidea (the sister group to “Krypteia”) also lacks a sclerotic ring, which is in contrast to the extant species in this group, which all have a sclerotic ring (Figures 3.1 and 3.2). For this reason, I predict that the lack of sclerotic ring in this particular specimen is the result of a decay loss (i.e. predator removal or damage to the fossil) and not a true phylogenetic loss (see Discussion).

In summary, based on morphological evidence, the presence of a sclerotic ring is an ancestral trait for squamates. These data support both the literature, and the extant data. Furthermore, in spite of the limited fossil evidence, this trait is ancestral in Squamata, and the loss of this character occurred relatively recently in squamate history (Figures 3.1 and 3.2).

3.2.2 Gauthier *et al*. (2012) morphological phylogenies using extant data

In order to illustrate the losses of the sclerotic ring in extant squamates, I narrowed my focus to Anguimorpha (specifically "Krypteia" and its sister taxa in Varanoidea), which contains the groups that lack the sclerotic ring (i.e. Dibamidae, Amphisbaenia, and Serpentes).

In the maximum parsimonious phylogeny modified from Gauthier *et al*. (2012), the sclerotic ring is lost at the stem of "Krypteia" (Figure 3.3). Serpentes branched first from the other members of "Krypteia", and all basal members of these groups (e.g., all of Serpentes, Dibamidae, and Rhineuridae) do not have a sclerotic ring (Figure 3.3). The more derived families in Amphisbaenia (e.g. all the families excluding Rhineuridae) have a sclerotic ring (Figure 3.3)

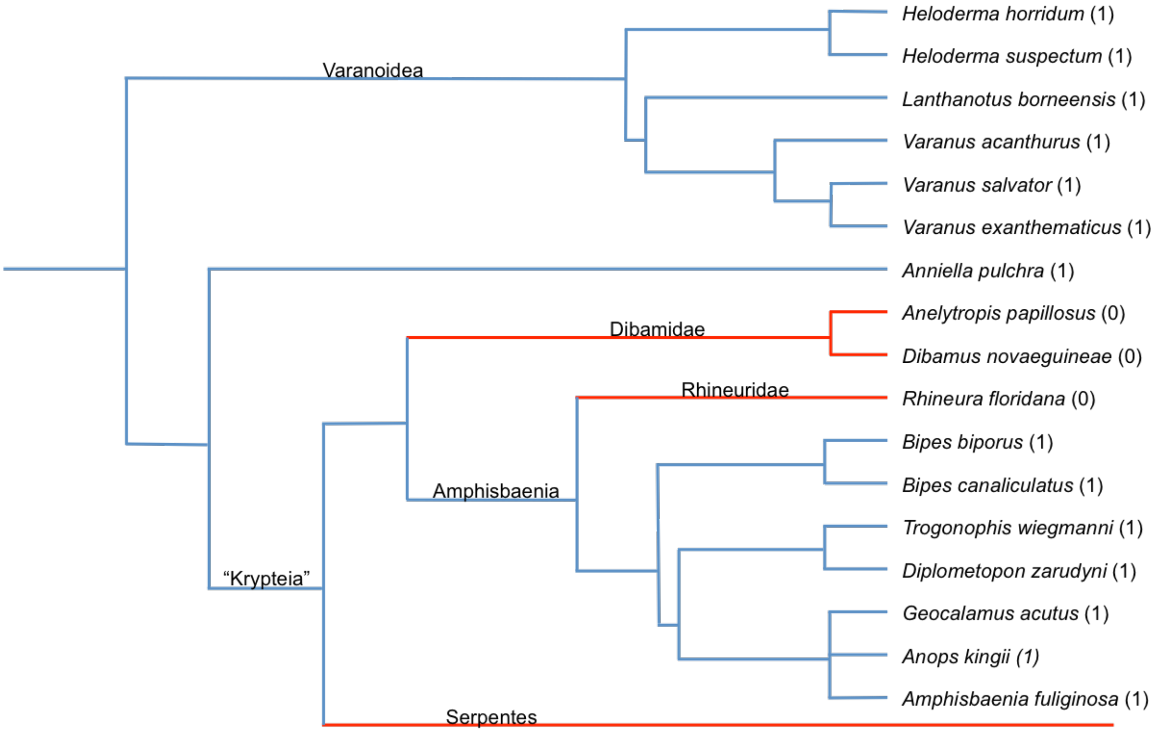

Figure 3.3. Maximum parsimony (strict consensus) phylogeny of more derived extant squamate relationships, modified from Gauthier *et al*. (2012). Zero (red) indicates branches where the sclerotic ring has been lost, while one (blue) indicates a present sclerotic ring.

When examining the data mapped on the Bayesian phylogeny modified from Gauthier *et al*. (2012), the relationships between members of "Krypteia" and their close relatives in Varanoidea change (Figure 3.4). In the Bayesian phylogeny, Serpentes and Amphisbaenia are sister groups, and are closely related to Dibamidae, which diverged from Serpentes and Amphisbaenia first (Figure 3.4). This is in contrast to the maximum parsimonious phylogeny, where Dibamidae and Amphisbaenia are more closely related and form a sister group to Serpentes (Figure 3.3). Another difference is that *Anniella pulchra* is the sister taxon to the Dibamidae + Amphisbaenia + Serpentes clade in the maximum parsimonious phylogeny (Figure 3.3), while this species diverged at a more basal position outside of Varanoidea in the Bayesian phylogeny (data not shown).

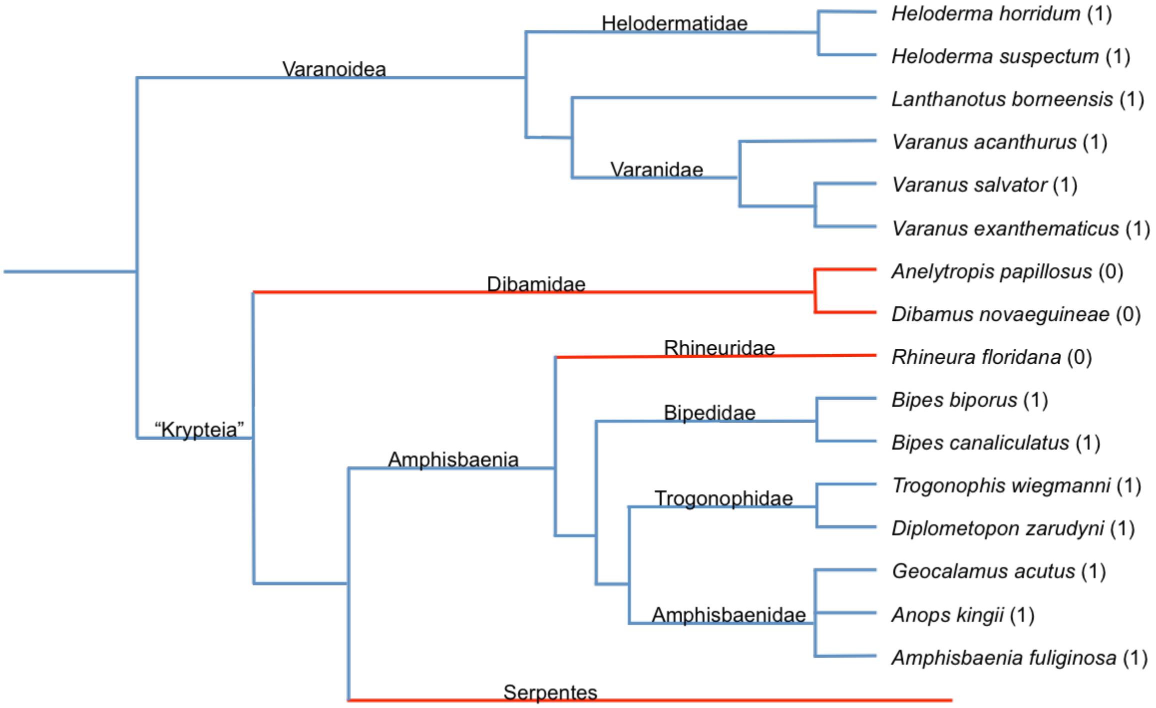

Figure 3.4. Bayesian phylogeny of more derived extant squamate relationships, modified from Gauthier *et al*. (2012). Zero (red) indicates branches where the sclerotic ring has been lost, while one (blue) indicates a present sclerotic ring.

In summary, the maximum parsimonious and Bayesian phylogenies (Gauthier *et al*. 2012) both indicate losses in three lineages within "Krypteia". The loss may have occurred at the base of "Krypteia", with a secondary gain occurring in more derived Amphisbaenians after the divergence of Rhineuridae (Figures 3.3 and 3.4). Alternatively, each lineage may have lost the sclerotic ring independently (Figures 3.3 and 3.4).

3.2.3 Kearney *et al*. (2003) morphological phylogeny using extant and fossil data

In order to determine losses in Amphisbaenia, I mapped the extant and fossil data onto a comprehensive phylogeny for this group modified from Kearney (2003) (Figure 3.5). In Kearney's phylogeny, Rhineuridae is deeply nestled within Amphisbaenia, while in Gauthier *et al*. (2012) Rhineuridae is the most basal family. Rhineuridae is considered to be a monotypic genus (only one extant species remaining), which indicates that no matter where Rhineuridae is placed on the phylogeny, one loss of the sclerotic ring has occurred in extant Amphisbaenia (Figure 3.5). Two fossil specimens in Rhineuridae that are generally accepted to be sister taxa (*Spathorhynchus* and *Dyticonastis*) also lack a sclerotic ring. With one loss occurring in extant *Rhineura* and one loss at the base of *Spathorhynchus* and *Dyticonastis*, two losses in total have occurred in Rhineuridae (Figure 3.5).

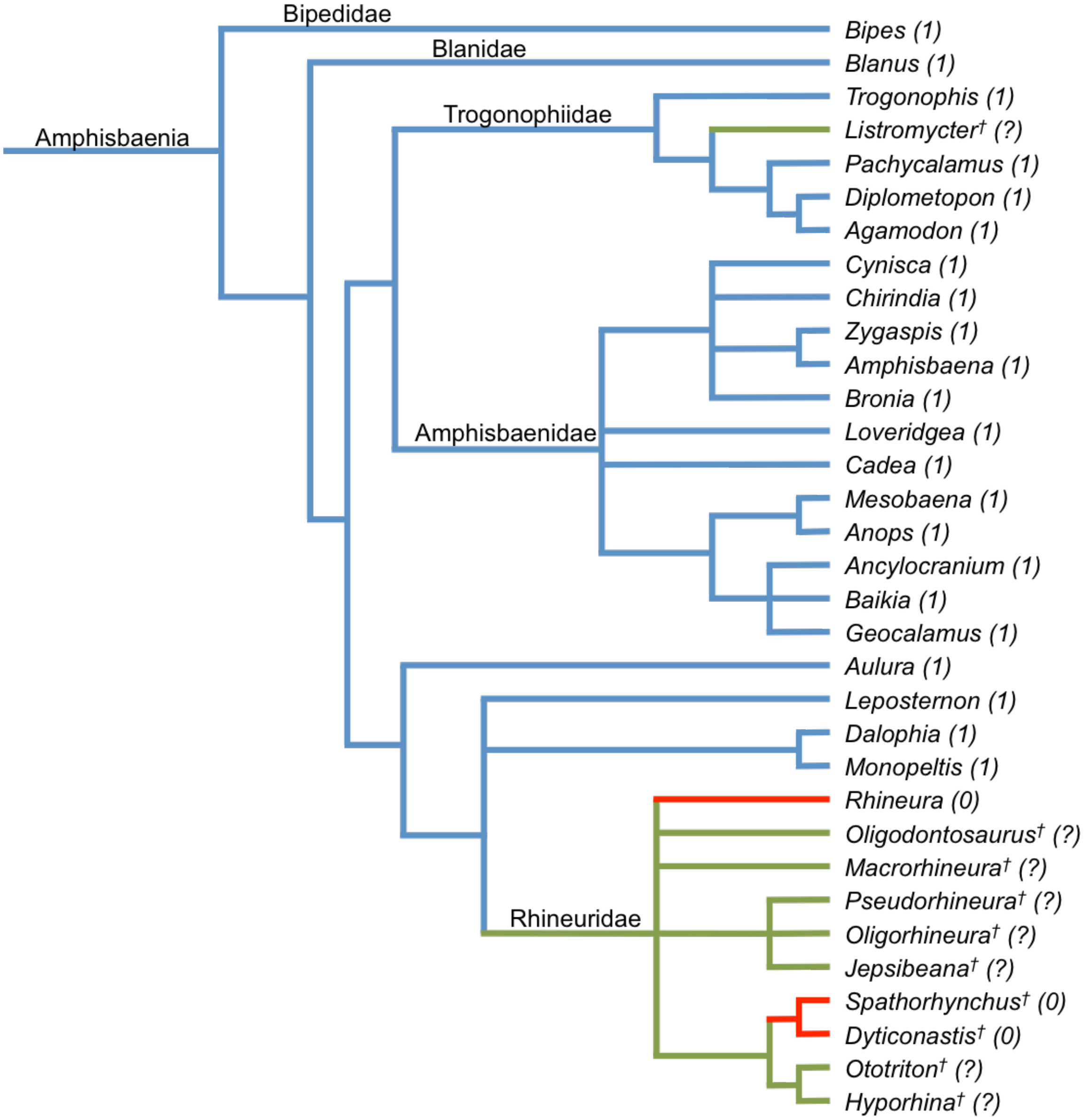

Figure 3.5. Phylogeny of extant and fossil amphisbaenian relationships, modified from Kearney (2003). Zero (red) indicates branches where the sclerotic ring has been lost, while one (blue) indicates a present sclerotic ring. Question marks (green lineages) indicate fossils too fragmented to assess. Daggers indicate fossil species.

While both the Gauthier *et al*. (2012) phylogenies (maximum parsimonious and Bayesian) and the Kearney phylogeny (2003) indicate one loss in extant Amphisbaenians, the phylogenies differ in where this loss has occurred. When considering the extant amphisbaenian phylogeny within the greater picture (i.e. the phylogeny for the whole of Squamata), this could mean two losses in squamates (one at the base of "Krypteia" and a second loss that is dependent on Rhineuridae being a derived family) and one secondary gain (Figures 3.3 and 3.4). When adding the fossil data for Amphisbaenia, another loss would have occurred in *Spathorhynchus* and *Dyticonastis*, representing a third loss (Figure 3.5). However, it is possible that one loss has occurred at the base of Rhineuridae and encompasses all members of this family (see Discussion). Therefore, two losses have occurred (one at the base of "Krypteia" and one at the base of Rhineuridae). If Rhineuridae is the basal amphisbaenian family, as is the case in the Gauthier *et al*. (2012) phylogenies, then the most parsimonious hypothesis (least number of steps) is one loss has occurred at the base of "Krypteia" and a secondary gain occurs before the remaining Amphisbaenian families diverge (Figures 3.3 and 3.4). Alternatively, as mentioned above, individual losses (one each in Rhineuridae, Dibamidae, and Serpentes) of this character could have occurred (Figures 3.3-3.5).

3.2.4 Pyron *et al.* (2013) molecular phylogeny using extant data

I also mapped my presence/absence data on a family level molecular phylogeny modified from Pyron *et al*. (2013) (Figure 3.6). The molecular phylogeny does differ significantly in its relationships when compared to the morphological phylogeny, in spite of both using *Sphenodon* as their out group taxon. (e.g. Iguania is the most basal squamate lineage in the morphological phylogeny and Scleroglossa is paraphyletic). Additionally, the families without a sclerotic ring are no longer closely related in the molecular phylogeny; therefore, this molecular phylogeny (Pyron *et al*., 2013) clearly indicates three separate losses. First, Dibamidae branches from Squamata near the base of the clade and this family has since lost the sclerotic ring (Figure 3.6). A second loss has occurred within Amphisbaenia, where Rhineuridae is located (Figure 3.6). Finally, Serpentes, still the most derived lineage in this molecular phylogeny, represents the third loss of the sclerotic ring (Figure 3.6). These three losses are in contrast to the morphological phylogenies, in which one of three hypotheses can be made: three individual losses, a single loss and a secondary gain, or two losses and a secondary gain (Figures 3.3-3.5). The most parsimonious (the least number of steps) hypothesis would be one loss and a secondary gain (two steps).

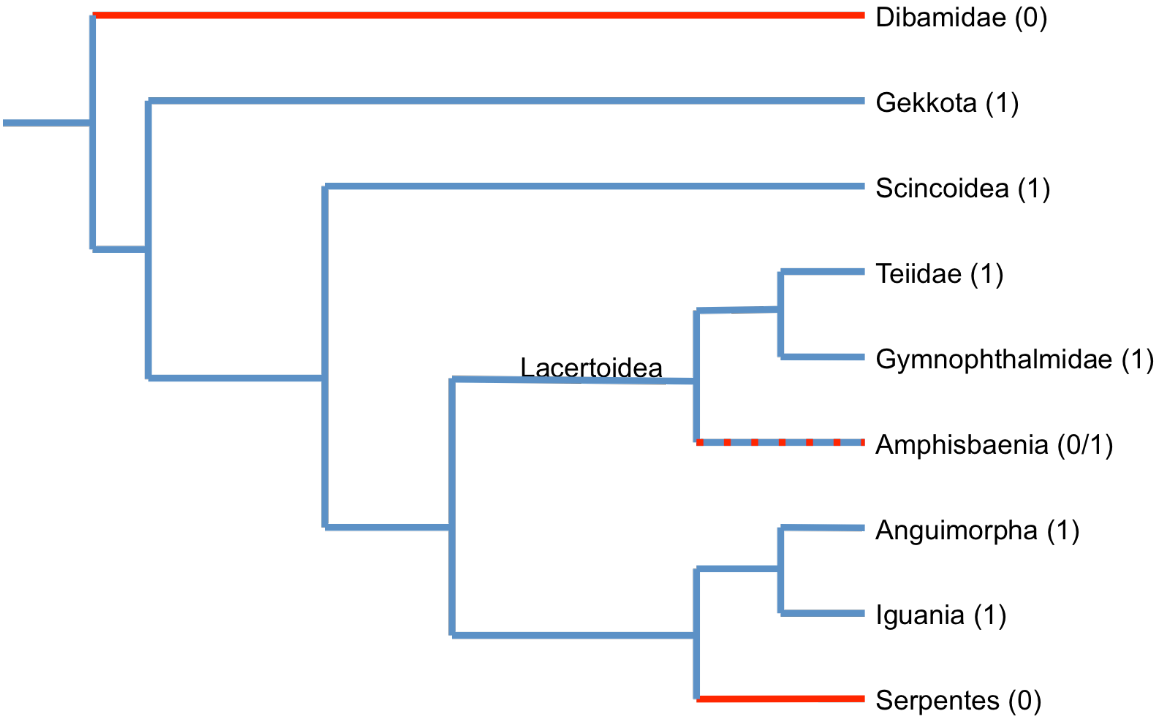

Figure 3.6. Family and higher-level molecular phylogeny modified from Pyron *et al*. (2013). Zero (red) indicates branches where the sclerotic ring has been lost, while one (blue) indicates a present sclerotic ring. The red-blue line indicates lineages in which some species have scleral ossicles and others do not.

3.3 Environment, behaviour, and limb morphology of extant squamates

In order to assess whether the loss of the sclerotic ring is correlated with environment and/or behaviour in squamates, aspects of squamate behaviour that are known to be correlated with eye morphology were researched (e.g. diel activity, fossorial lifestyle). Additionally, since the species that lack a sclerotic ring and/or have a fossorial lifestyle are known to have reduced limbs, I also researched where limbs are reduced or lost in squamates.

3.3.1 Squamate behaviour

Diel activity (time of day a species is most active) is known to be correlated with eye morphology (e.g. Hall, 2008a; 2008b; 2009; Schmitz and Motani, 2011a). In order see where photopic and scotopic species are located relative to each other; I mapped known diel activity on the family level phylogeny from Gauthier *et al*. (2012) (Table 2.2; Figure 3.7). Most squamate lineages are photopic (e.g. Iguania, Anguidae, Amphisbaenidae and others shown on Figure 3.7). Scotopic vision occurs in Gekkota (e.g. Pygopodidae and Eublepharidae are entirely scotopic, and some species in Gekkonidae are also scotopic), and some species in Scincomorpha (e.g. species in Gymnophthalmidae, Xantusiidae, Scincidae). Additionally, Serpentes can be scotopic or photopic. The sources for this data set can be found on Table 2.2.

In lineages that have lost the sclerotic ring (namely Dibamidae, Rhineuridae, and Serpentes), only the diel activity of Serpentes is certain. Dibamidae and Rhineuridae are so secretive that there is much uncertainty surrounding their behaviour and lifestyle, although their burrowing lifestyle suggests that they likely spend much of their life in lowlight environments. Still, at least in Serpentes, both scotopic and photopic species lack a sclerotic ring. It is important to note; however, that snake eyes are fundamentally different from other squamates (e.g. Walls, 1942; Caprette *et al.*, 2004).

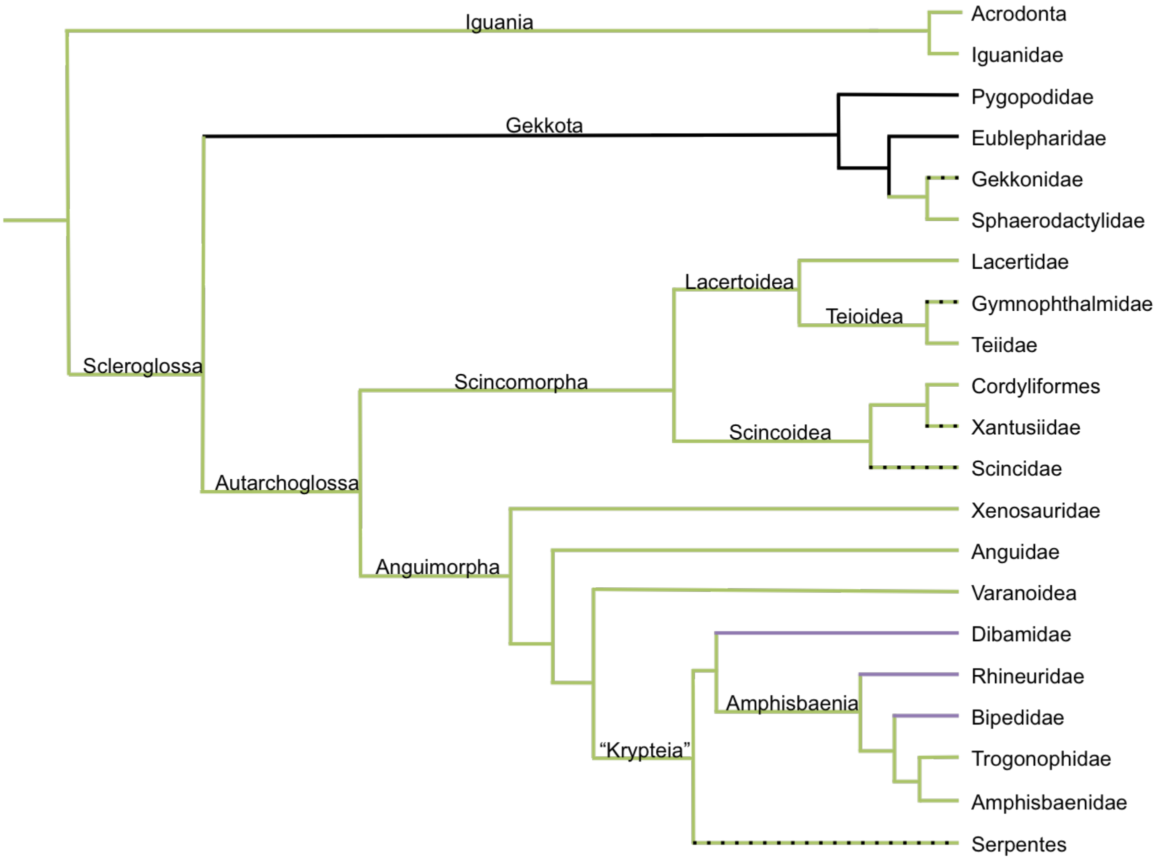

Figure 3.7. Phylogeny modified from Gauthier *et al.* (2012) showing families that are scotopic (black lines) and photopic (green lines). Purple indicates lineages where diel activity is unknown; however, these burrowing species generally occupy low-light environments. Dashed lines indicate lineages with scotopic and photopic species.

A fossorial (burrowing) lifestyle has also been correlated with a simplification of the body plan, including the loss of limbs. A fossorial lifestyle is relatively common in Squamata (9 out of 21 families), and has evolved several times and in several lineages (Figure 3.8). In addition to the fossorial species of "Krypteia", Pygopodidae (in Gekkota) and some species in Gymnophthalmidae and Scincidae (both in Scincomorpha) are also fossorial (Figure 3.8). Species in these families are highly derived (Wiens *et al.*, 2006) and have evolved a simplified body plan that is common to burrowing species. For example, all fossorial species are either entirely limbless or have reduced limbs; however, many limbless species (e.g. most snakes) are not, at least presently, fossorial. Thus, limb reduction is more common in squamates than a fossorial lifestyle; the limbless body plan has evolved in snakes, amphisbaenians, rhineurids, dibamids, skinks (Scincidae), cordyliformes, teiids, and pygopods (11 out of 21 families; Figure 3.9). To sum, both a fossorial lifestyle and limb reduction have evolved several times in Squamata and this has occurred in every lineage within Scleroglossa (e.g. Gekkota, Scincomorpha, Anguimorpha, Serpentes; Figures 3.8 and 3.9).

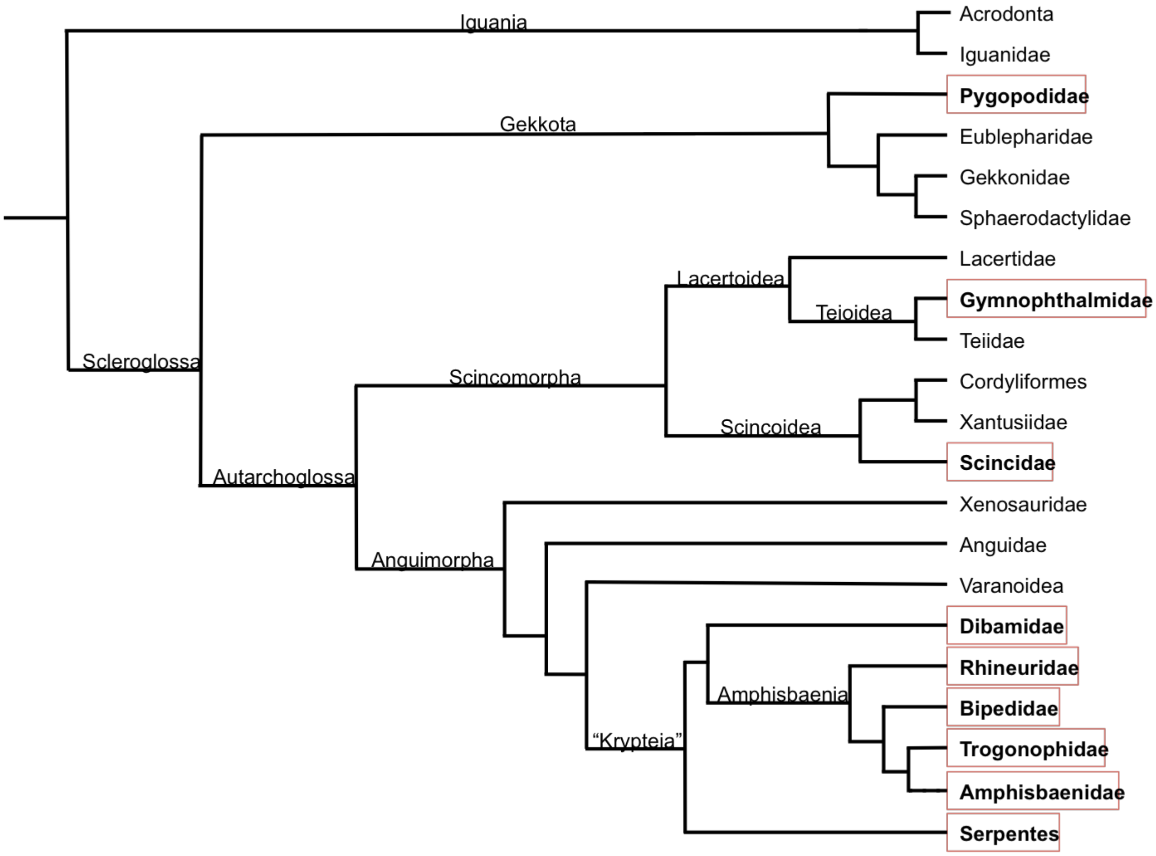

Figure 3.8. Phylogeny modified from Gauthier *et al*. (2012) showing families where a fossorial lifestyle has evolved in some or all species (red boxes, bold lettering).

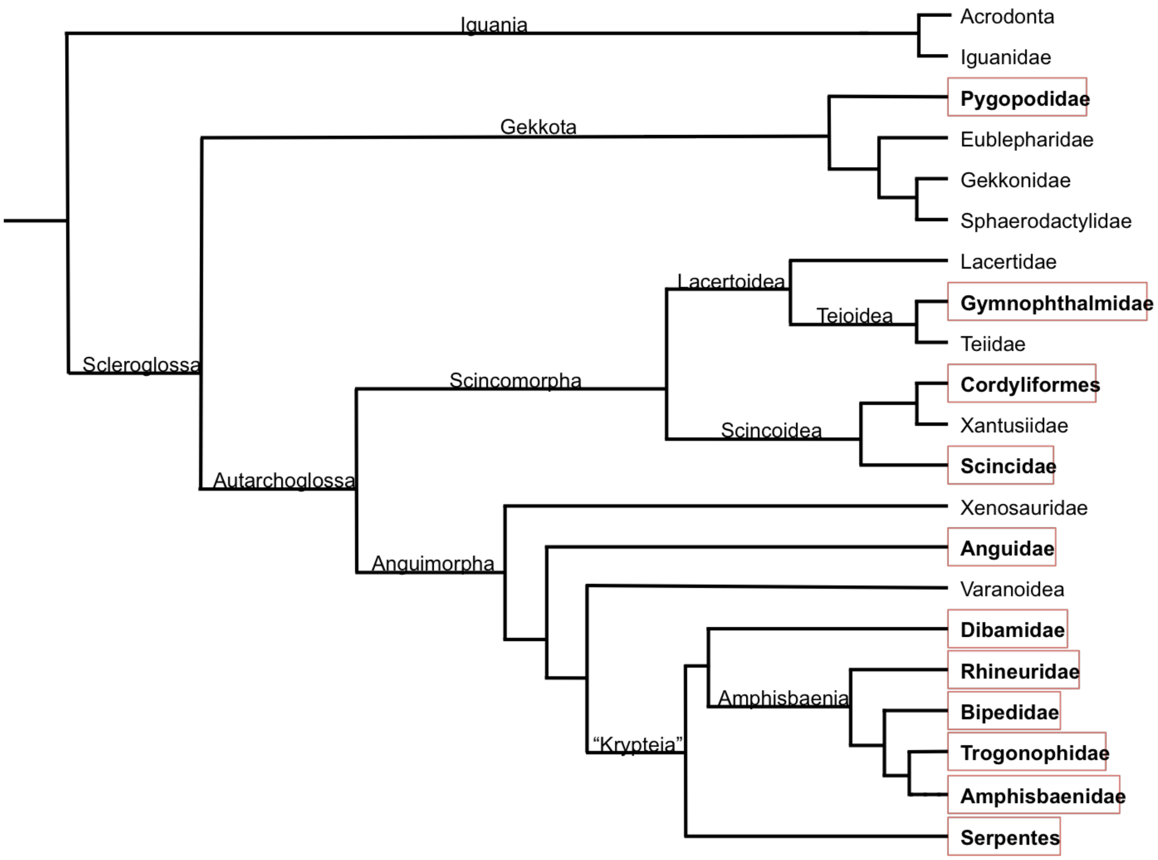

Figure 3.9. Phylogeny modified from Gauthier *et al*. (2012) showing families where reduced limbs or complete limblessness has evolved in some or all species (red boxes, bold lettering).

In summary, although sclerotic ring size has been found to be correlated with diel activity (e.g. Schmitz and Motani, 2011; Hall, 2008a), two of the families under scrutiny here (e.g. Dibamidae, Rhineuridae) both do not have sclerotic rings and are too rare and reclusive for their diel activity to be known (Figure 3.7). Additionally, although all the groups that lack a sclerotic ring (Dibamidae, Rhineuridae, and Serpentes) are also united in their fossorial lifestyle and reduction or loss of limbs, many other squamate groups are also fossorial and/or lack limbs, but have a sclerotic ring. These include other families in Amphisbaenia, and species in Pygopodidae, Scincidae, and Gymnophthalmidae (Figures 3.1, 3.8, and 3.9). Therefore, neither diel activity, nor limblessness nor fossorial lifestyles are strongly related to the presence or absence of the sclerotic ring.

3.3.2 Sclerotic ring measurements

In order to better understand the morphological differences between different families and genera with different ecological niches, statistical analyses were performed on measurements of the maximum inner and outer diameters of the sclerotic ring obtained from 100 specimens that had complete, articulated sclerotic rings (see Appendix B). These specimens represent seven families and 31 genera (Figure 3.10). The sample population also contains scotopic and photopic species, as well as fossorial and non-fossorial species (Table 3.1).

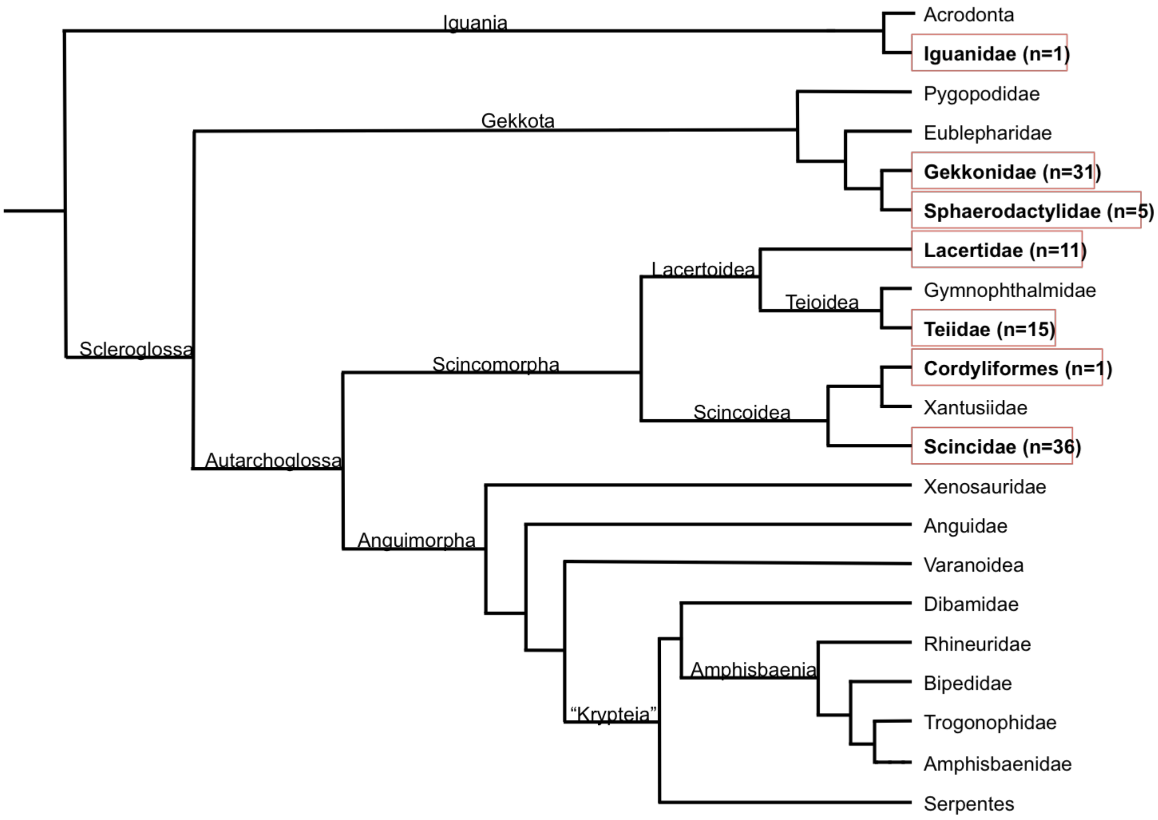

Figure 3.10. Phylogeny modified from Gauthier *et al.* (2012) showing the families where inner and outer sclerotic ring diameters were measured (bold lettering, red boxes). Numbers of specimens measured are in brackets after the family name.

Table 3.1. Family and genus for each specimen measured and the diel activity and fossorial versus non-fossorial lifestyle information, including resources consulted. N=100

Taxon	Genus	Diel activity	Lifestyle	Resources consulted
Iguanidae	*Cyclura*	Photopic	Non-fossorial	Carey (1966)
Gekkonidae	*Cosymbotus*	Scotopic	Non-fossorial	Feder & Feder (1981)
	Gehyra	Scotopic	Non-fossorial	Fisher (1997); Hall (2008)
	Gekko	Scotopic	Non-fossorial	Gao *et al*. (2005); Hall (2008)
	Hemidactylus	Scotopic	Non-fossorial	IUCN Red List
	Lepidodactylus	Scotopic	Non-fossorial	Hall (2008); IUCN Red List
	Perochirus	Photopic	Non-fossorial	IUCN Red List
Sphaerodactylidae	*Pseudogekko*	Photopic	Non-fossorial	Taylor (1922); IUCN Red List
	Gonatodes	Photopic	Non-fossorial	IUCN Red List
Lacertidae	*Lacerta*	Photopic	Non-fossorial	Hall (2008); IUCN Red List
	Meroles	Photopic	Non-fossorial	Pianka (1971); Hall (2008)
	Mesalina	Photopic	Non-fossorial	Hall (2008); IUCN Red List
	Ophisops	Photopic	Non-fossorial	Hettige *et al.* (2000); Hall (2008)
	Podarcis	Photopic	Non-fossorial	Hall (2008); IUCN Red List
	Zootoca	Photopic	Non-fossorial	Gvoždík & Castilla (2001); IUCN Red List
Teiidae	*Ameiva*	Photopic	Non-fossorial	Vitt & Colli (1994); Hall (2008)
	Cnemidophorus	Photopic	Non-fossorial	Paulissen (1987)
	Kentropyx	Photopic	Non-fossorial	Vitt (1991)
	Neustricurus	Photopic	Non-fossorial	Vitt *et al*. (1998)

Table 3.1. Continued

Family	**Genus**	**Diel activity**	**Lifestyle**	**Resources consulted**
Gerrhosauridae	*Gerrhosaurus*	Photopic	Non-fossorial	Battersby (1954)
Scincidae	*Ablepharus*	Photopic	Non-fossorial	Kolbintzev *et al.* (1999) IUCN Red List
	Brachymeles	Photopic	Fossorial	Alcala *et al.* (2004); IUCN Red List
	Carlia	Photopic	Non-fossorial	Buden (2009); IUCN Red List
	Cryptoblepharus	Photopic	Non-fossorial	IUCN Red List
	Emoia	Photopic	Non-fossorial	Wiles & Geurreo (1996) IUCN Red List
	Eumeces	Photopic	Non-fossorial	Hall (2008); IUCN Red List
	Lamprolepis	Photopic	Non-fossorial	Perry & Buden (1999)
	Lampropholis	Photopic	Non-fossorial	Forsman & Shine (1995)
	Mabuya	Photopic	Non-fossorial	Diesmos *et al.* (2004); Hall (2008)
	Scincella	Photopic	Fossorial	Nicoletto (1985); IUCN Red List

As the inner and outer measurements were not normally distributed, all the statistical analyses performed on these data were non-parametric tests. First, a Spearman correlation test was performed and determined that the inner and outer diameter measurements are highly related (r_s=0.896, p<0.001), which indicates that there is a strong positive relationship between the two diameters (e.g. larger inner diameters also mean larger outer diameters; Figure 3.11). This indicates that species with a large inner diameter also tend to have a larger outer diameter, and species with smaller outer diameters also have smaller inner diameters. Additionally, analyses show that both the inner and outer diameters differ significantly between families (p<0.001; Table 3.2, rows 1 and 2).

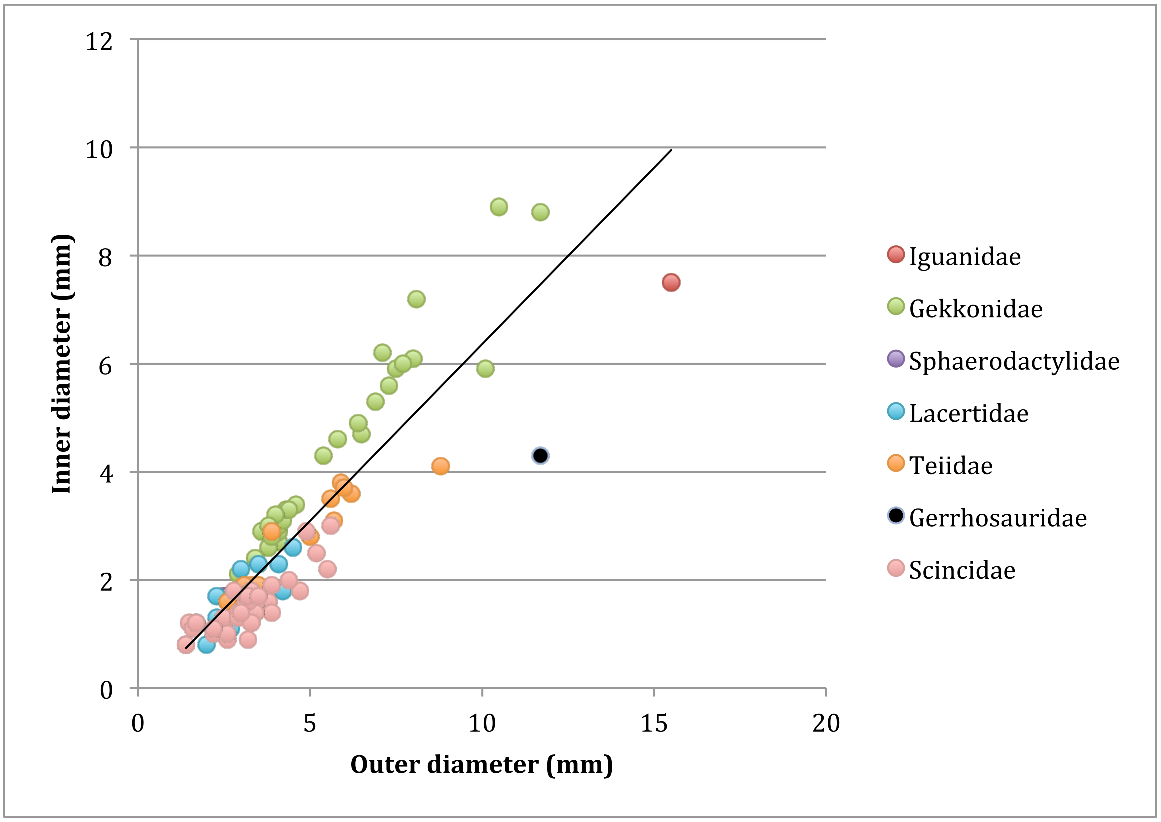

Figure 3.11. Scatterplot showing the relationship between the outer diameter (mm) of the sclerotic ring and the inner diameter (mm) and a line of best fit. A Spearman correlation test indicated a positive relationship between the two measurements (n=100; r_s=0.896). This indicates that species with larger apertures also have larger outer diameters; and therefore, a wider sclerotic ring.

Table 3.2. Summary of statistically analyses run on the inner and outer sclerotic ring diameters (mm). See Appendix C for these statistical analyses in detail.

Test	Measurement	Groups compared (n)	P-value	Appendix C Table
Kruskal-Wallis	Max. outer diameter (mm)	Gekkonidae (n=31) Sphaerodactylidae (n=5) Lacertidae (n=11) Teiidae (n=15) Scincidae (n-36)	P<0.001	C.2
Kruskal-Wallis	Max. inner diameter (mm)	Gekkonidae (n=31) Sphaerodactylidae (n=5) Lacertidae (n=11) Teiidae (n=15) Scincidae (n=36)	P<0.001	C.4

Table 3.2. Continued.

Test	Measurement	Groups compared (n)		P-value	Appendix C Table
Mann-Whitney	Max. outer diameter (mm)	Scotopic (n=25)	Photopic (n=34)	P<0.001	C.6
Mann-Whitney	Max. inner diameter (mm)	Scotopic (n=25)	Photopic (n=34)	P<0.001	C.8
Mann-Whitney	Max. outer diameter (mm)	Fossorial (n=7)	Non-fossorial (n=92)	P<0.001	C.10
Mann-Whitney	Max. inner diameter (mm)	Fossorial (n=7)	Non-fossorial (n=92)	P<0.001	C.12
Kruskal-Wallis	SV length (mm)	Gekkonidae (n=28) Sphaerodactylidae (n=5) Lacertidae (n=9) Teiidae (n=15) Scincidae (n=32)		P<0.001	N/A
Mann-Whitney	SV length below median (≤59 mm); max. outer diameter	Photopic (n=32)	Scotopic (n=14)	P<0.001	C.13
Mann-Whitney	SV length above median (>59 mm); max. outer diameter	Photopic (n=32)	Scotopic (n=14)	P<0.001	C.14
Mann-Whitney	SV length below median (≤59 mm); max. inner diameter	Photopic (n=32)	Scotopic (n=14)	P<0.001	C.15
Mann-Whitney	SV length above median (≤59 mm); max. inner diameter	Photopic (n=32)	Scotopic (n=14)	P<0.001	C.16
Mann-Whitney	SV length below median (≤59 mm); max. outer diameter	Fossorial (n=3)	Non-fossorial (n=42)	P<0.001	C.17
Mann-Whitney	SV length above median (≤59 mm); max. outer diameter	Fossorial (n=3)	Non-fossorial (n=42)	P<0.001	C.18
Mann-Whitney	SV length below median (≤59 mm); max. inner diameter	Fossorial (n=4)	Non-fossorial (n=40)	P<0.001	C.19
Mann-Whitney	SV length above median (≤59 mm); max. inner diameter	Fossorial (n=4)	Non-fossorial (n=40)	P<0.001	C.20

The measurements for the inner and outer diameters were then split into scotopic versus photopic specimens, and fossorial versus non-fossorial (see Appendix B for each species analyses and its diel activity and lifestyle). Mann-Whitney tests on both groups showed that there was a significant difference in both the inner and outer diameter of the sclerotic ring between scotopic and photopic species, and between fossorial and non-fossorial species ($p<0.001$; Tables 3.1 and 3.2, rows 3 to 6). Therefore, scotopic species have significantly larger sclerotic rings than photopic species, and non-fossorial species have significantly larger sclerotic rings than fossorial species.

In order to be certain that body size was not a factor in my results, I accounted for body size by analyzing the snout vent (SV) length between the five families (Gekkonidae, Sphaerodactylidae, Lacertidae, Teiidae, and Scincidae) and found that these families did differ significantly in size ($p<0.001$; Table 3.2, row 7). The median SV length was 59 mm. In order to take these differing body sizes into consideration, I divided my specimens into individuals that fell below the median SV length, and above the median SV length, ignoring their family. Median SV length was used because the data are not normally distributed. I further subdivided these categories into scotopic versus photopic species, and fossorial versus non-fossorial species. I then performed the same statistical analyses as above. When accounting for body size, scotopic versus photopic and fossorial versus non-fossorial were still statistically significant ($p<0.001$; Table 3.2, rows 8 to 15).

In summary, the inner and outer diameters were significantly different between families ($p<0.001$), and also between scotopic and photopic species ($p<0.001$), and fossorial and non-fossorial species ($p<0.001$), even when taking into account body size. Under conservative testing procedures using a Bonferroni correction ($\alpha=0.003$) all tests were still statistically significant. Interestingly, photopic species tend to have smaller sclerotic rings (both aperture, or inner diameter, and maximum diameter of the ring) than scotopic species, and fossorial species have smaller sclerotic rings than non-fossorial species. Following this, it indicates that photopic or fossorial species have smaller eyes than scotopic or non-fossorial species (see Discussion).

4.0 Discussion

One of the major goals of this project was to create a database of species that would be useful for future phylogenetic analyses that have the presence/absence of the sclerotic ring as a character. I believe that this goal has been met with my database, which contains 400 extant species and 167 fossil species. Presence and absence of this character is commonly used in morphological phylogenetic analyses (e.g. Estes *et al*., 1988; Kearney, 2003; Conrad, 2008; Gauthier *et al*., 2012; and numerous fossil assessments); however, these studies have not assessed this character in as many taxa as my study. For example, Conrad (2008) assessed the most taxa with 222 species. Gauthier *et al*. (2012) assessed 192 taxa, and Wiens *et al*. (2010) assessed 64. Others, (e.g. de Queiroz, 1982; Caprette *et al*., 2004) only considered specific families and out-group taxa in their analyses. While Squamata has over 9000 extant species (Pyron *et al*., 2013), analyzing 400 extant species and 167 fossil species represents a greater proportion of taxa analyzed compared to previous studies and additionally I assessed species that are not commonly considered in phylogenetic analyses.

This research also continues the scleral ossicle lineage work by the Franz-Odendaal lab. This comprehensive database, along with the data set developed by Franz-Odendaal (2008a; 2011) for teleosts (547 species) and major vertebrate lineages, will be valuable to future phylogenetic studies that both incorporate a wide range of vertebrate taxa and wish to include the sclerotic ring as a character. Overall, this database will be useful not only for phylogenetic analyses but also when tracing the lineage of the sclerotic ring in vertebrates.

4.1 On the fossil specimens and the loss of the sclerotic ring in evolutionary history

In this study, I assembled a database that included presence/absence data for both extant and extinct squamates. In assessing extinct species, I found that it is quite difficult to trace the evolution of the sclerotic ring within Squamata because of the lack of compelling fossil evidence. For example, Dibamidae does not have a fossil record (Townsend *et al*., 2011), and most known amphisbaenian fossils are in one family, Rhineuridae (Kearney, 2003). For snakes, the competing theories on their evolution have caused fossils to continually move between basal and derived positions (Lee and Scanlon, 2002; Caprette *et al*., 2004). These findings make it difficult to narrow down a time when the sclerotic ring could have been lost in these lineages. However, while the fossil record is fragmented for Squamata, it is known that most species in related tetrapod lineages (e.g. see Franz-Odendaal and Hall, 2006) have a sclerotic ring, which indicates that the default state for squamates is to have a sclerotic ring.

For this project, I assessed 167 fossils; many of them in lineages known to have sclerotic rings based on previous studies, but found only 16 fossils had a sclerotic ring (Appendix A3). It is even more difficult to assess absence in fossils, as most squamates are represented by fragmentary, poorly preserved fossils. Sclerotic rings are fragile and subject to loss during the fossilization process (Conrad, 2008; Gauthier *et al*., 2012). Sclerotic rings can be lost in many ways. For example, eyes are common targets of scavenging predators. Furthermore, these elements do not articulate with the rest of the skeleton and are therefore easily lost during decomposition. These facts further complicate attempts to determine where in the lineage losses occurred. Assessing the presence of a sclerotic ring in fossils is difficult; however, it is assessing absence that is the primary issue because of the difficulty in determining if the absence of a sclerotic ring is a true loss, or a loss that resulted from the fossilization process.

In order to account for the above challenges, I only assessed fossils as absent for the sclerotic ring if they had a well-preserved head region, especially around the orbits. In total, four species fall into this category (Appendix A3). While these fossils could have been coded as unknown, it is reasonable to code them as absent because of the reasons above and because I took into consideration the traits shared by extant species lacking a sclerotic ring when assessing their character state. Below, I discuss each and comment on whether or not I consider my assessment valid.

One of the species I assessed as lacking a sclerotic ring is a snake (*Haasiophis terrasanctus*) that has a mixture of traits considered to be lizard and snake in origin and, therefore, has been positioned on the phylogeny as both a basal (more lizard-like) and derived snake (Palci *et al*., 2013). Extant lizards have scleral ossicles and, without exception, extant snakes do not. The most recent assessment by Palci *et al*. (2013) placed *H. terrasanctus* in a basal position on the snake clade rather than on the lizard phylogeny. Since extant snakes do not have a sclerotic ring, I am confident in my assessment that *H. terrasanctus* truly lacks a sclerotic ring.

I also assessed two fossils as lacking sclerotic rings in Rhineuridae. There is a high degree of skull morphological similarity between all species within Rhineuridae (Hembree, 2007). *Rhineura floridana*, the extant species in Rhineuridae, lacks a sclerotic ring, and is morphologically similar to the fossils lacking the sclerotic ring. This high degree of morphological similarity between extinct and extant species in this family suggests high pressures and constraints on these Rhineurid species, possibly relating to their restricted range and environment (something I will expand on later; see section

4.6.3). Therefore, I am also confident in my assessment for absence of the sclerotic ring in the two species in Rhineuridae.

The fourth and final species I assessed as lacking a sclerotic ring is an anguimorphan lizard (*Estesia mongoliensis*). *E. mongoliensis* is a monstersaur that has a well-preserved skull found without a sclerotic ring. Interestingly, *Estesia* does not fit into the typical morphology that I would expect of a species that lacks a sclerotic ring, based on my assessment of other species that lack a sclerotic ring. That is, it has limbs and is quite a bit bigger than dibamids, rhineurids, and basal snakes (Yi and Norell, 2013). Its skull alone is 15 cm (Yi and Norell, 2013), larger than the snout-vent lengths of dibamids and rhineurids. Additionally, although the taxa that bracket *E. mongoliensis* are all extinct monstersaurs, their close extant relatives all have robust limbs and sclerotic rings. Therefore, I think it is likely that *E. mongoliensis* had a sclerotic ring and my assessment of "absent" is not a phylogenetic loss. For these above reasons I have decided to code *E. mongoliensis* as unknown (?) on the phylogenies I use here in the discussion instead of absent.

4.2 One loss and one secondary gain of the sclerotic ring in Squamata lineages is supported by morphological phylogenetic evidence

Squamata does not have one widely accepted phylogeny. Therefore, I have chosen to conduct my analyses using several phylogenies. In this section, I discuss the two main morphological phylogenies I used (Kearney, 2003 and Gauthier *et al.*, 2012). When mapping my data on these morphological phylogenies, I found that the most parsimonious explanation for the evolution of the sclerotic ring in squamates is one loss at the base of the Dibamidae-Amphisbaenia-Serpentes clade followed by a secondary gain in more derived amphisbaenians. However, as I will discuss below (section 4.5) the most parsimonious solution may not stand when evolutionary and developmental evidence are considered.

4.2.1 One loss of the sclerotic ring occurred within Amphisbaenia

Using the Kearney (2003) phylogeny, I found that one loss of the sclerotic ring in Rhineuridae is the most parsimonious. Although the current fossil data supports two losses of the sclerotic ring in Amphisbaenia (Figure 4.1, red, vertical lines), I argue that one loss is actually the most likely and parsimonious scenario (Figure 4.1, red star). Only one family within Amphisbaenia lacks a sclerotic ring: Rhineuridae. This family consists of one extant genus, *Rhineura floridana*, and several fossil species. I was able to assess extant *Rhineura*, as well as two sister fossil taxa, *Spathorhynchus natronicus* and *Dyticonastis rensbergeri*. The remaining fossils were too fragmented to assess. Therefore, the current data supports two losses within Rhineuridae (Figure 4.1, red, vertical lines). However, Hembree (2007) has shown that there is a high degree of morphological conservation in Rhineuridae. Rhineurids are united by a strong craniofacial angle, a flattened face, and a shovel-like snout, to name a few traits (see Hembree, 2007). In fact, Hembree (2007) has condensed the number of genera within this family, moving several fossil species into the genus *Rhineura*. Furthermore, there is additional evidence that Rhineuridae's united appearance is the result of phylogenetic niche conservation (Hipsley and Müller, 2014). Their nearly identical skulls and historically small range in North America also supports this theory (Hipsley and Müller, 2014). For all of these reasons, I think it is very likely that one loss of the sclerotic ring in Amphisbaenia, rather than two independent losses, occurred at the base of Rhineuridae (Figure 4.1, red star). However, the fossil evidence is too fragmented to claim one loss with absolutely certainty. Therefore, while I am predicting that all the taxa within Rhineuridae (including the incomplete, fossil taxa) lack a sclerotic ring, I recognize that this cannot be proven until the fossil evidence is found, if ever.

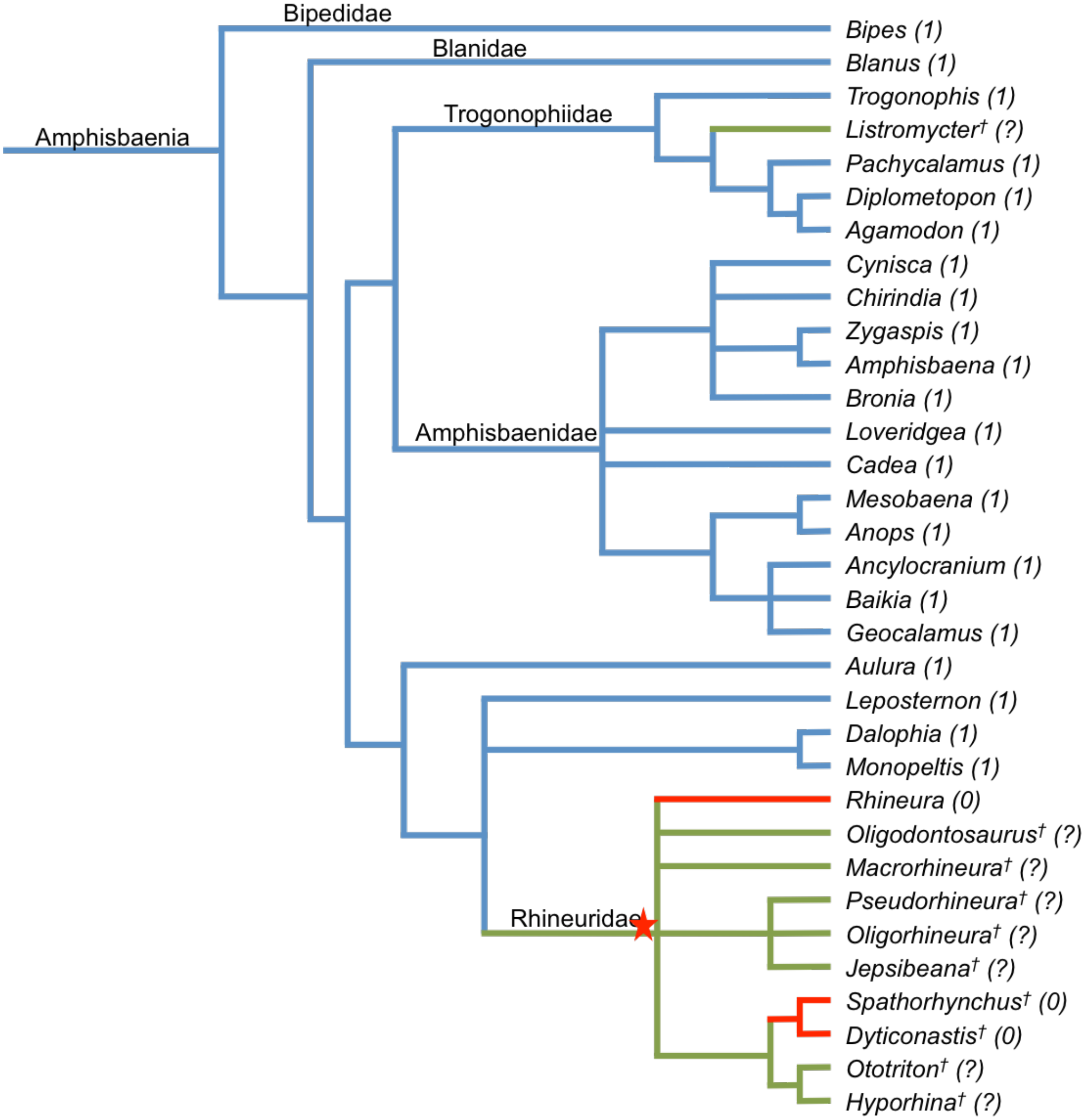

Figure 4.1. Phylogeny modified from Kearney (2003) showing two loss scenarios in extant and fossil (indicated with a dagger) amphisbaenians.. Blue (1) lineages indicate genera where the sclerotic ring is present, red (0) indicate that this character is absent, and green (?) are fossil lineages where this character could not be assessed. Red, vertical lines indicate one hypothesis, the red star indicates the other hypothesis.

4.2.2 One loss and one secondary gain of the sclerotic ring occurred in Squamata

Both the maximum parsimonious and Bayesian phylogenies from Gauthier *et al*. (2012) support one loss and one secondary gain of the sclerotic ring in Squamata. The basal position of Rhineuridae in Gauthier *et al*. (2012) supports one loss at the base of the "Krypteia" clade, which encompasses Serpentes, Amphisbaenia, and Dibamidae, in both the maximum parsimonious and Bayesian phylogenies (Figure 4.2, vertical lines). In both, a secondary gain of the sclerotic ring occurs later in Amphisbaenia, after the other families have split from Rhineuridae (Figure 4.2, vertical lines). Of course, this scenario depends on the basal position of Rhineuridae, which was recovered in both Gauthier *et al*. (2012) and Pyron *et al*. (2013) analyses. Gauthier *et al*. (2012) used the most morphological characters, while Pyron *et al*. (2013) assessed the most species, which is in contrast to Kearney (2003), who recovered Rhineuridae in a derived position using only Amphisbaenians and their close relatives, as well as morphological characters. Therefore, the most parsimonious scenario is one loss and one secondary gain, or two steps.

Another possible hypothesis, that is less parsimonious, is that each lineage may have lost the sclerotic ring in their individual lineages, which would be a total of three losses (one loss in Dibamidae, one in Serpentes, and one in Amphisbaenia; Figure 4.2, stars). Therefore, the possible hypotheses are three losses, or one loss and a secondary gain. However, three steps, is less parsimonious than one loss and one secondary gain (two steps). Therefore, the Gauthier *et al*. (2012) phylogenies support one loss and one secondary gain.

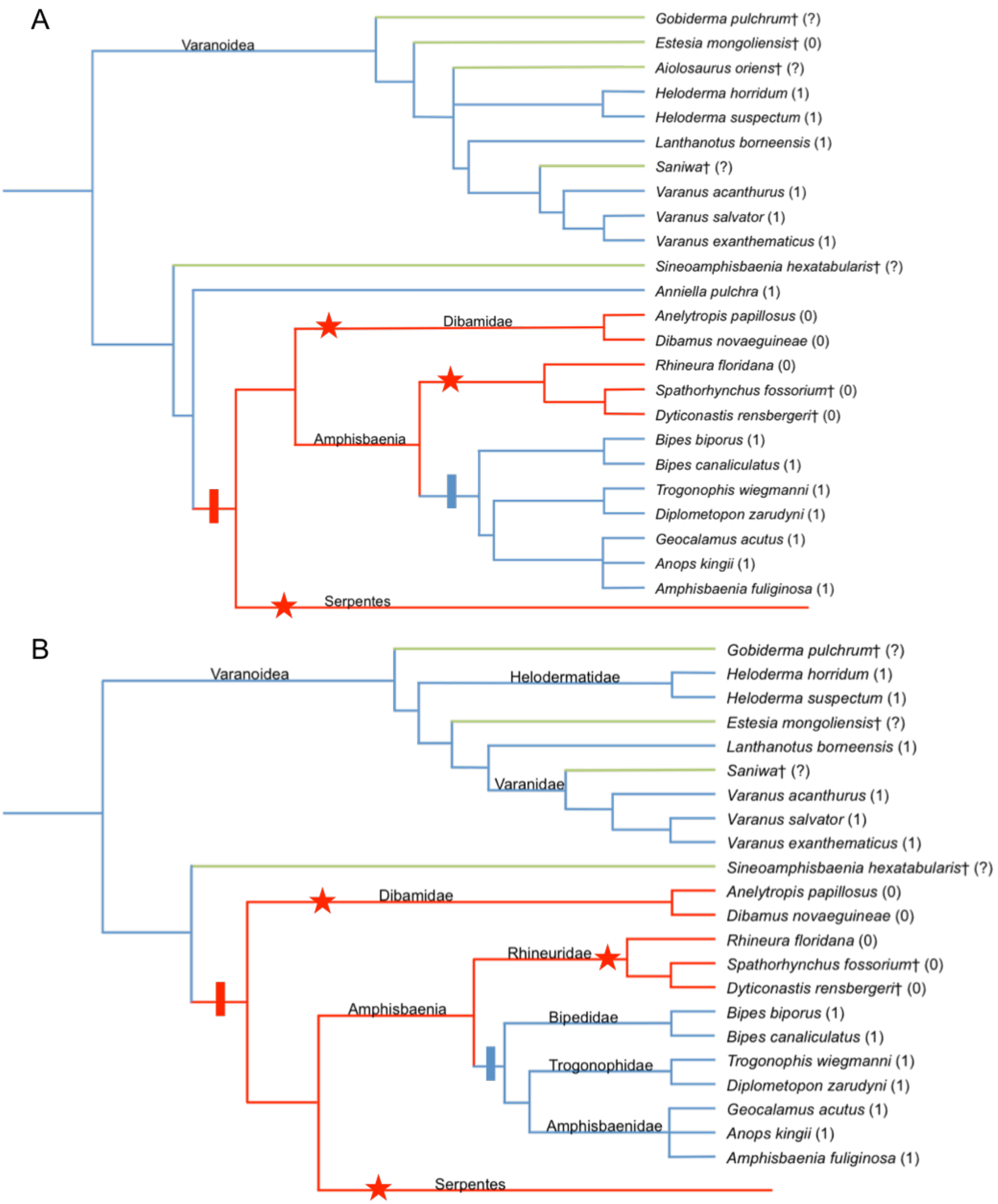

Figure 4.2. Phylogenies from Gauthier et al. (2012) showing scenarios of possible sclerotic ring loss in squamates. A) Maximum parsimonious, strict consensus phylogeny. B) Bayesian phylogeny. This phylogeny includes both extant and fossil (indicated with a dagger) species. Blue (1) lineages indicate genera where the sclerotic ring is present, red (0) indicates that this character is absent, and green (?) are fossil lineages where this character could not be assessed. Vertical lines indicate one hypothesis, stars the other.

4.3 Three individual losses of the sclerotic ring in Squamata lineages is supported by molecular phylogenetic evidence

I have chosen to include a molecular phylogeny because the literature is currently divided into those researchers that support morphological phylogenies, and those that support molecular phylogenies. In the phylogeny by Pyron *et al.* (2013), which only considers extant squamates, Dibamidae diverged from the other squamate lineages very early on its history (Figure 4.3). Amphisbaenia and Serpentes are similarly no longer closely related, and only Serpentes retain their position as the most derived squamate group and Amphisbaenians are positioned in Lacertoidea (Figure 4.3). Therefore, the molecular phylogeny conducted by Pyron *et al.* (2013) supports three individual losses of the sclerotic ring, one in Dibamidae, one in Serpentes, and one in the Rhineurid lineage within Amphisbaenia (Figure 4.3, stars).

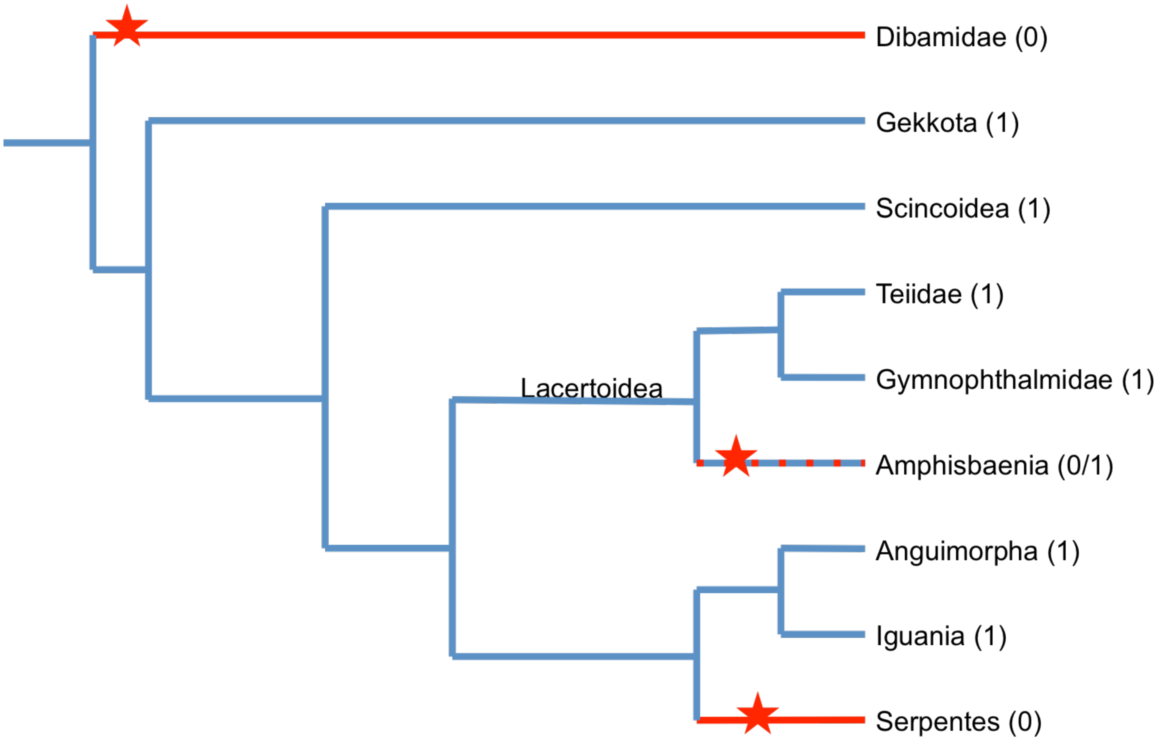

Figure 4.3. Family and higher-level molecular phylogeny modified from Pyron *et al.* (2013) showing where the sclerotic ring has been lost (red stars). Blue (1) lineages indicate genera where the sclerotic ring is present and red (0) indicates that this character is absent. Dashed line indicates a lineage where some members have a sclerotic ring and others do not.

4.4 Comparison of the Gauthier *et al.* (2012) and Pyron *et al.* (2013) phylogenies with the Conrad (2008) phylogeny

I include the Conrad (2008) phylogeny in my analyses because this phylogeny gives another morphological perspective. Conrad (2008) conducted morphological phylogenetic analyses on Squamata that was the standard until the publication of the phylogenies by Gauthier *et al*. (2012). Furthermore, Gauthier *et al*. (2012) used most of the same characters as Conrad (2008) and many others. In Conrad (2008), Dibamidae, Amphisbaenia, and Serpentes, are closely related; however, these groups are nestled in Scincoidea (Figure 4.4) as opposed to i) their location in Anguimorpha, as is the situation in Gauthier *et al*. (2012) (Figure 4.2) and ii) the position of Dibamidae as the sister group to all other squamates, Amphisbaenia in Lacertoidea, and Serpentes as the sister group to Iguania and Anguimorpha as described in Pyron *et al*. (2013) (Figure 4.3). Conrad (2008) supports the one loss in Amphisbaenia that I found using the other three phylogenies. However, on Conrad (2008)'s phylogeny, Rhineuridae is positioned in a slightly more derived position, but is still considered basal, along with Trogonophiidae, which has a sclerotic ring (Figure 4.4). Given that Amphisbaenia and Serpentes are closely related, and Serpentes lacks a sclerotic ring, the Conrad (2008) phylogeny would support three individual losses of this trait: once in snakes, once in rhineurids, and once in dibamids (Figure 4.4, stars). Another possible explanation is one loss at the base of Dibamidae, Amphisbaenia, and Serpentes, a secondary gain later in Amphisbaenia, and another loss in Rhineuridae (Figure 4.4, vertical lines). These two explanations are equally parsimonious; however, as will be discussed in a later section it may be easier developmentally to lose scleral ossicles than gain them. Therefore, three individual losses are the most parsimonious in this case.

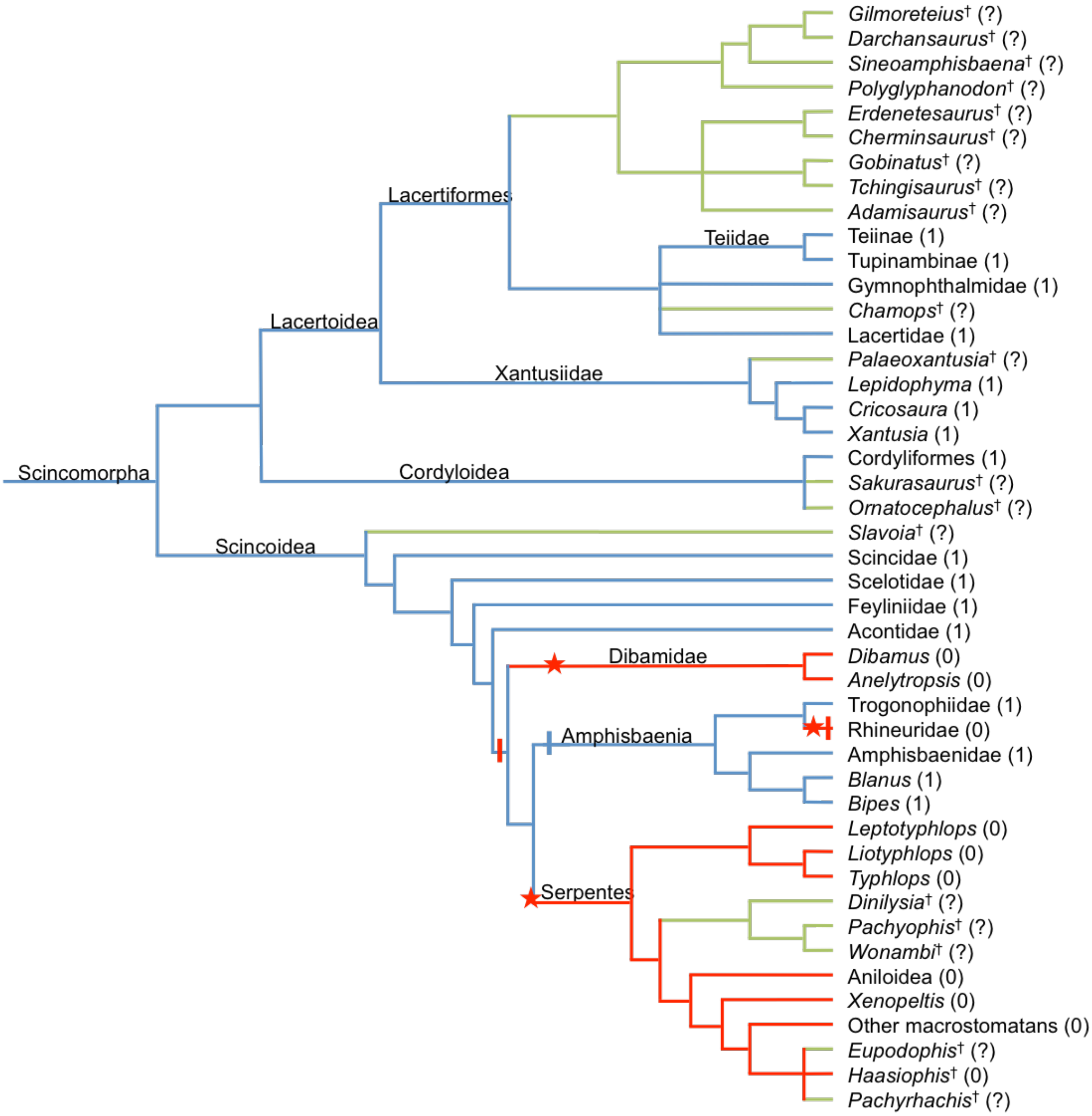

Figure 4.4. Scincomorpha strict consensus phylogeny modified from Conrad (2008) showing Serpentes, Amphisbaenia, and Dibamidae and their closest relatives in Scincidae. Vertical lines indicate one hypothesis for sclerotic ring losses and stars indicate the other hypothesis. 0 (red) indicates species where scleral ossicles are absent, 1 (blue) indicates presence and a question mark (green) indicates fossil specimens where presence/absence could not be assessed. Daggers indicate extinct lineages.

In summary, in all three squamate phylogenies described here (Conrad, 2008; Gauthier *et al*., 2012; Pyron *et al*., 2013) three individual losses of the sclerotic ring is a possible scenario. For Conrad (2008) and Pyron *et al*. (2013), three individual losses is the most parsimonious scenario, while in Gauthier *et al*. (2012), three losses is not the most parsimonious scenario (see sections 4.2 and 4.3).

4.5 Together, developmental and evolutionary evidence supports three individual sclerotic ring losses

4.5.1 Developmental evidence

Studies have shown that the number of scleral ossicles that make up the sclerotic ring is variable and that loss of individual ossicles can be induced after manipulation (e.g. Curtis and Miller, 1938; Coulombre *et al*., 1962; Underwood, 1984; Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). To date, no one has been able to "force" a ring to develop in a species without a sclerotic ring, yet it is relatively easy to "force" the loss of a scleral ossicle in a species with a sclerotic a ring (Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). Furthermore, the variation in the number of individual ossicles not only differs between species, but between individuals in the same species, as well as between eyes in the same individual (e.g. Curtis and Miller, 1938; Underwood, 1984; Franz-Odendaal, 2008b). This variation in nature indicates that individual losses are not uncommon.

Research using chickens shows that there is strong selection pressure to maintain an intact ring. If an individual ossicle is lost, the neighbouring ossicles will increase their size to fill the empty space (Franz-Odendaal, 2008b; Duench and Franz-Odendaal, 2012). This compensation mechanism is due, in part, to the sequential induction of the scleral papillae and the prolonged scleral ossicle induction phase of two days. In some cases (e.g. in the mutant *scaleless*) this compensation is so extreme that the sclerotic ring is made up of a few, very large scleral ossicles (Palmoski and Goetinck, 1970), once again demonstrating that losses of ossicles can occur developmentally.

Snakes are an excellent example of the developmental pressures resulting in the loss of the sclerotic ring. Snakes lost the entire sclerotic ring early in their evolutionary history and this loss has been attributed to their hypothesized ancestral scotopic and fossorial lifestyle (Walls, 1942). However, snakes have since recolonized land and arboreal environments; yet have not regained sclerotic rings. This may be because snakes have evolved an entirely different mode of accommodation over their evolutionary history (e.g. Walls, 1942; Caprette *et al*., 2004). Walls (1942) has suggested that the eyes in snakes may have, in the past, simplified to such a degree that they cannot form a sclerotic ring, nor can they accommodate in the same way as other squamates.,. For example, all snakes are united in having a reduced ciliary artery. Interestingly, it has been shown in other reptiles (e.g. chickens) that the first papilla forms above the ciliary artery (Hamburger and Hamilton, 1951). . Although highly speculative, it is possible that a similar reduction has occurred in other lineages that lack a sclerotic ring (e.g. dibamids, rhineurids), and it may be similarly difficult for these lineages to regain sclerotic rings.

In summary, current developmental evidence shows that losses of individual ossicles (and possibly the entire ring) occurs more readily than the gain of ossicles. The current data may be an indication that three separate losses of the sclerotic ring, as supported by Conrad (2008) and Pyron *et al*., (2013), is the more accurate hypothesis, instead of the one loss and a secondary gain as supported by Gauthier et al. (2012).

4.5.2 Evolutionary evidence

Evolutionary evidence (i.e. fossil and morphological evidence) supports three individual losses of the sclerotic ring. Müller *et al*. (2011) suggested, based on the fossil specimen *Cryptolacerta hassiaca*, that in amphisbaenians, skull modification preceded body elongation and limb reduction. This hypothesis differs from that which is commonly accepted for snakes, where limbs were lost before cranial modifications evolved (e.g. Gans, 1975; Greer, 1991; Wiens *et al.*, 2001). Müller *et al.* (2011) suggests that amphisbaenians and snakes may have independently evolved reduced limbs and skull modifications associated with a fossorial lifestyle, and that their shared ecological characters may be hiding different character evolutionary histories. This theory has also been suggested by Lee (1998). This is not surprising, as independent evolution of limblessness and fossorial lifestyles has occurred as least 25 times in Squamata in every lineage except for Iguania (Wiens *et al.*, 2006; Urben *et al.*, 2014). Therefore, it is possible that the sclerotic ring has been lost several times and in different lineages (e.g. individual losses in snakes, dibamids, and rhineurids), as has been shown for other traits associated with a fossorial lifestyle. Limblessness and fossorial lifestyles as the precursor to losing the sclerotic ring may be supported by Iguanids, which all have sclerotic rings, and limblessness and fossorial lifestyles are not traits found in this clade.

Individual losses of sclerotic rings is further supported by the competing theories on snake evolution. Snakes have a unique mode of accommodation among extant squamates, and there are two theories on how this mode of accommodation evolved. One theory is that snakes are derived from fossorial and scotopic ancestors (Caprette, 2005). This is corroborated by the many extant species that have similar body morphology to snakes (e.g. dibamids, amphisbaenians) and are burrowers that live in low light conditions (Caprette *et al.*, 2004). Therefore, it has been hypothesized that basal snakes were burrowers living in low light environments (Caprette *et al.*, 2004). However, there is also compelling evidence that snakes may be closely related to aquatic squamates (e.g. mosasaurs) as both these groups have very similar eyes (Caprette, 2005). For example, both snakes and basal aquatic vertebrates have rigid lenses (Caprette *et al.*, 2004). They also share their mode of accommodation (along with some secondary aquatic mammals, like whales) by a forward lens movement (Caprette *et al*., 2004). When solely considering the sclerotic ring, an aquatic ancestry does not hold as much weight as a burrowing ancestry. Mosasaurs, for example, had robust sclerotic rings, while burrowing species have reduced eyes, and in the case of dibamids and rhineurids, lack sclerotic rings.

To sum, there is evolutionary evidence that supports a fossorial body plan (including the loss or reduction of the sclerotic ring) resulting from convergent evolution in dibamids, amphisbaenians, and snakes. The environmental pressures that occur during the evolution of headfirst burrowing may account for the loss and reduction of the sclerotic ring in these lineages.

4.6 The squamate species that lack a sclerotic ring are united by their headfirst burrowing ancestry, reduced limbs, and other shared traits

Dibamidae, Serpentes, and Amphisbaenia have long presented a problem for squamate phylogeny as attempts so far to resolve their position have been unsuccessful (e.g. Greer, 1985; Lee, 1998; Conrad, 2008; Gauthier *et al*., 2012). These groups share many derived morphological traits that are thought to be the result of a head-first burrowing lifestyle, such as the reduction or loss of limbs, elongation of the body, reinforcement and simplification of the skull bones, and miniaturization (Lee, 1998; Coates and Ruta, 2000; Gauthier *et al*., 2012). They are also united by either having lost the sclerotic ring (e.g. snakes, dibamids, rhineurids), or having a reduced ring (e.g. amphisbaenians excluding rhineurids). All of these characters represent a loss or reduction of traits, which may be obscuring the data and resulting in false-close relationships between these groups (e.g. Lee, 1998; Gauthier *et al*., 2012). However, these characters (with the exception of the lost sclerotic ring) are not unique to dibamids, snakes, or amphisbaenians. Many other lineages have reduced limbs and burrowing lifestyles (Figures 3.7 and 3.8; Wiens *et al.*, 2006), but these other lineages are more easily placed within the squamate phylogeny (and also have robust sclerotic rings) (e.g. Conrad, 2008; Gauthier *et al.*, 2012). The main difference between dibamids, snakes, amphisbaenians and these other lineages, such as pygopods or limbless and burrowing skinks, is that these other lineages have close relatives with limbs, while dibamids, snakes, and amphisbaenians do not (Figures 3.7 and 3.8; Gauthier *et al.*, 2012). Furthermore, most species in these groups are relatively small, all have reduced eyes, and many are missing key, informative morphological characters because their skull bones are streamlined, consolidated and reinforced (Gauthier *et al.*, 2012). These are all traits associated with headfirst burrowing. Again, these traits are not found in the Iguania, where no species lacking limbs or inhabiting a fossorial habitat exist. Therefore, it is likely that the loss of the sclerotic ring is related to an ancestral headfirst burrowing lifestyle.

To further support the theory that a lost sclerotic ring is associated with headfirst burrowing, it is important to note that some other limbless and fossorial species that have a sclerotic ring do not construct their own burrows. For example, pygopods are limbless and fossorial; however, they have robust sclerotic rings and live in natural cracks and spider burrows (Kluge, 1976). Gymnophthalmids, conversely, are adapted to a fossorial lifestyle (in sand), but share skull morphological traits with both dibamids and pygopods (Roscito and Rodrigues, 2010). Therefore, while head burrowing may have resulted in the loss or reduction of the sclerotic ring, there must be other selective pressures at work. It is likely that the combination of all these cranial traits associated with fossorial habitats (i.e. reinforcement and simplification of the skull, miniaturization), have resulted in the loss of the sclerotic ring in dibamids, snakes, and rhineurids. Perhaps, other fossorial lineages (e.g. those in Gymnophthalmidae) are in a transition phase, where they are becoming adapted to headfirst burrowing, but their sclerotic ring has not yet been lost or reduced. This hypothesis would be supported if transitional fossil species for snakes, dibamids, or rhineurids were found. Indeed, there may be evidence of this hypothesis since amphisbaenians (excluding rhineurids) are adapted to headfirst burrowing and have reduced, but present, sclerotic rings. Thus, amphisbaenians may represent a transitional group between presence and absence of sclerotic rings.

4.6.1 Morphological variation between limbless lineages may account for the loss of the sclerotic ring

Research conducted by Wiens *et al*. (2006) showed that even limbless groups differ significantly in their morphology. For example, members of the family Bipedidae have forelimbs, while all other amphisbaenians do not. Wiens *et al*. (2006) found two morphologies, limb-reduced species with long tails that are commonly surface dwellers, and limb-reduced species with short tails that tend to be burrowers. Snakes are, of course, a common exception in studies on limblessness as basal snakes were most likely short tailed and burrowers (Wiens *et al*., 2006). However, snakes have since reinvaded surface habitats and are now found on every continent except Antarctica, and include arboreal, aquatic, and terrestrial forms (Caprette, 2005; Wiens *et al.*, 2006). Interestingly, amphisbaenians, dibamids, and snakes all fall into the short-tailed burrower group, along with several species that have a sclerotic ring (Wiens *et al*., 2006). There is, of course, variation in the limblessness morphologies (Kearney, 2003; Urben *et al*., 2014). For example, the amphisbaenian family Bipedidae has functioning forelimbs, while in other amphisbaenian families the degree to which the hind limbs and pelvic girdle is reduced varies (Kearney, 2003; Urben *et al*, 2014). Unfortunately, more research into the various limbless lineages and their exact degree of limb reduction is required before any comparisons can be made between the groups that do not have sclerotic rings, and those that do. At present, I conclude that short-tailed burrowers are more likely to be lacking or have reduced sclerotic rings; further research into the eyes of members of this group that are not snakes, dibamids, or amphisbaenians is required.

4.6.2. A scotopic past?

It was first suggested by Walls (1942) that scotopic vision might be correlated with the loss of the sclerotic ring and it is certainly true that fossorial species inhabit low-light environments. Walls (1942) based his theory on the correlation between species that live in scotopic environments, and their lack of sclerotic rings (e.g. crocodiles and mammals). In reptiles that have sclerotic rings,, they may be important for visual acuity; therefore, lineages that have lost the sclerotic ring must have, at some point in their past, gone through a stage where visual acuity was not essential. A fossorial lifestyle meets these requirements, as lateral eyes are not particularly useful for seeing in tunnels (Walls, 1942). Dibamids and rhineurids are examples of lineages that are fossorial and have reduced visual acuity, and Walls (1942) suggested that snakes, crocodiles, and early mammals went through a similar transition phase. Basal synapsids, for example, have sclerotic rings, while mammals, which are a derived group within Synapsida, do not (Rowe, 1988; Castanhinha *et al*., 2013). There is still much support for this theory in the literature (see the review from Gerkema *et al*., 2013), and perhaps low-light environments for dibamids, amphisbaenians, and possibly snakes, contributed to their loss of their sclerotic rings. This study has shown that scotopic species tend to have both a larger inner and outer diameter (Figure 3.11). This trend may have become more extreme in lineages that have lost the sclerotic ring; resulting in a morphology where the sclerotic ring (max outer diameter) grew larger as the scleral ossicles themselves became narrower (as a result of the larger inner diameter). This narrow sclerotic ring morphology would not be particularly supportive, and bone is metabolically expensive to make. These reasons may have resulted in the eventual loss of the sclerotic ring in lineages. Therefore, a transition to a scotopic or low light environment and subsequent relaxed pressures on sight and the ring itself may be the reason the sclerotic ring has been lost in these squamate lineages. A large-scale study on scotopic squamates, comparing their sclerotic rings to photopic species would provide insight on the role of scotopic vision in the loss of the sclerotic ring.

4.6.3 Rhineuridae is an example of extreme habitat and speciation events

Rhineuridae is interesting because it is the only Amphisbaenian family that lacks a sclerotic ring. In addition, rhineurids are also unique amongst amphisbaenians because they have had a historically small range in North America, which is known from their rich fossil record, and the one extant species is restricted to the Florida peninsula (Kearney, 2003; Hipsley and Müller, 2014). It is theorized that rhineurids have had strong evolutionary constraints because there is a high degree of morphological similarity between the extant and extinct forms (Hembree, 2007; Hipsley and Müller, 2014). There is also environmental evidence for this, as rhineurids nearly disappeared during the middle Miocene (approximately 14 million years ago) after the onset of long-term freezing temperatures (Hipsley and Müller, 2014). While it is possible there is a preservation bias in the fossil record, it is also possible that the extreme temperature and restricted environment during the Miocene resulted in lack of gene flow and lack of or gain of adaptations that are unique to Rhineuridae. These adaptations may include the loss of the sclerotic ring.

4.7 The morphology of the sclerotic ring is a good indicator of environment and behaviour

In order to determine if the sclerotic ring morphology or presence is correlated with environment and behaviour, I measured the sclerotic ring's aperture and maximum outer diameter in extant squamates (n=100). Even after accounting for body size, scotopic species have significantly larger sclerotic rings than photopic species, and non-fossorial species have significantly larger sclerotic rings than fossorial species. This result was not unexpected, as both Hall (2008a; 2008b; 2009) Schmitz and Motani (2011a) have shown that scotopic birds, lizards, and archosaurs have comparatively larger apertures than photopic species. This is probably because, as Hall (2009) has shown, the aperture measurement is associated with the corneal diameter, and the cornea is larger in scotopic species. Hall (2008a; 2009) measured the corneal diameter and did not measure the sclerotic ring aperture (because it is difficult to separate the sclerotic ring from the rest of the eye). In this project, I specifically measured the sclerotic ring aperture and found that my results agree with both Hall (2008a; 2008b; 2009) and Schmitz and Motani (2011a). Although there has been some argument in the literature on whether or not the sclerotic ring is a valid measurement for discerning diel activity (e.g. Hall, 2009; Hall *et al.*, 2011; Schmitz and Motani, 2011a; 2011b), my results clearly show that the size of the ring is significantly different between scotopic and photopic species, and fossorial and non-fossorial species. However, these data alone may not be useful for inferring information on fossil specimens or those with unknown diel or habitat data because there can be considerable overlap between scotopic and photopic, and fossorial and non-fossorial measurements. I was restricted by available specimens (extant and fossil) and time constraints, and a larger-scale study that includes more specific data on diel activity (i.e. active during the day, night, dawn or twilight) and those living in low-light environments (i.e. more fossorial species) would provide a more comprehensive view of the spread of sclerotic ring measurements as related to diel activity. A much larger study would also be more useful for inferring diel activity or fossorial lifestyle in extinct squamates with intact sclerotic rings. Finally, a larger study with a wider spread of diel activity would allow me to perform the statistical analyses (phylogenetic discriminate analysis) used by Schmitz and Motani (2011a).

5.0 Summary and conclusions

In summary, this study aimed to compile a database of the presence/absence of the sclerotic ring in squamates. This study also then used this database, along with recent phylogenetic analyses from the literature, to assess gains and losses of the sclerotic ring across evolutionary time. The final goal of this thesis was to assess the correlation between the presence/absence and morphology of the sclerotic ring with environment and/or behaviour. All three of these goals were successfully completed. My database containing 573 extinct and extant species will undoubtedly be useful for future phylogenetic studies. Furthermore, I was able to map the gains and losses of the sclerotic ring on several phylogenies (both morphological and molecular) from the literature. Using these phylogenies and additional developmental and evolutionary data, I hypothesize that there has been three individual losses of the sclerotic ring in squamates. One loss in the family Rhineuridae, nested in Amphisbaenia, is well supported in all the phylogenies considered here. This loss in Amphisbaenia, along with one loss each in Dibamidae and Serpentes, is supported by the Conrad (2008) morphological phylogeny and the Pyron *et al*. (2013) molecular phylogeny. Finally, I found a correlation between diel activity and sclerotic ring size, and habitat and sclerotic ring size. Specifically, scotopic species have larger sclerotic rings than photopic species, and non-fossorial species have larger rings than fossorial species. Additionally, those groups that lack or have a reduced sclerotic ring are united by their headfirst burrowing ancestry. Their reduced eye is likely the result of the lateral position of the eye in the skull, as lateral eyes are not particularly useful at photoreception in low-light environments. These groups are all perfectly adapted to a life of constructing burrows using their heads, and I propose that the loss of the sclerotic ring is a direct result of subsequent relaxed selective pressures on vision.

In the future, I think this research can be taken even further. For example, a broader sample size of sclerotic ring measurements and counts of ossicles in the rings would be helpful in continuing to tease out the relationship between sclerotic ring size and diel activity and lifestyle. Furthermore, larger sample sizes from a greater range of species would allow individuals within lineages to be compared. For example, a comparison between scotopic and photopic species in each family or lineage would be interesting. A more interesting study, in my opinion, would involve the measurement of sclerotic rings in other limbless groups (e.g. in Gymnophthalmidae and Pygopodiae) and their close relatives, to see if these groups have similarly reduced sclerotic rings as seen in amphisbaenians. Unfortunately, these groups are cryptic and the specimens may not be available for such a widespread study. As this study has shown, the sclerotic ring is a useful tool for studying behaviour and environment. This, along with its usefulness in developmental studies, makes the sclerotic ring an interesting system for studying bone development, evolution, and morphology.

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Appendix A1: Extant specimens assessed for this project (personal observations)

Table A1.1. Summary of all species assessed personally during my visits to the Smithsonian Museum of Natural History (USNM) and the Museum of Natural History in London, UK (MNHUK), including specimen museum codes. N=93

Genus	Species	Family	Code	Specimen Location
IGUANIA				
Anolis	*valencienni*	Dactyloidea	Present (1)	MNHUK 1964.1845
Cyclura	*nubile caymanensis*	Iguanidae	Present (1)	MNHUK N/A
Holbrookia	*maculata*	Phyrnsomatidae	Present (1)	MNHUK 89.9.25.5
GEKKOTA				
Aristelliger	*lar*	Gekkonidae	Present (1)	USNM 221823/221821
Cosymbotus	*platyurus*	Gekkonidae	Present (1)	USNM 305919
Gehyra	*multilata* *oceanica*	Gekkonidae	Present (1)	USNM 507617/512277
Gonatodes	*ceciliae* *hasemani* *humeralis*	Sphaerodactylidae	Present (1)	USNM 306178/292399/290883
Hemidactylus	*brookii* *frenatus*	Gekkonidae	Present (1)	USNM 507619/509339
Lepidodactylus	*christiani* *lugubris* *herrei* *moestus*	Gekkonidae	Present (1)	USNM 305929/323685/305932/559794
Perochirus	*scutellatus*	Gekkonidae	Present (1)	USNM 518823
Phelsuma	*laticauda*	Gekkonidae	Present (1)	USNM 536543
Pseudogekko	*smaragdinus*	Gekkonidae	Present (1)	USNM 497586
Spaerodactylus	*argivus lewisi*	Sphaerodactylidae	Present (1)	USNM 217297
LACERTOIDEA				
Adolfus	*alleni*	Lacertidae	Present (1)	MNHUK 1934.5.26.45
Ameiva	*ameiva* *exsul* *griswoldi* *ameiva aquilina*	Teiidae	Present (1)	USNM 292427/192658/192654/192651
Cnemidophorus	*sexlineatus*	Teiidae	Present (1)	USNM 541695
Gallotia	*galloti*	Lacertidae	Present (1)	MNHUK 1969.19
Gymnophthalmus	*underwoodi*	Gymnophthalmidae	Present (1)	USNM 163059
Kentropyx	*calcarata*	Teiidae	Present (1)	USNM 292411
Lacerta	*dugesii* *agilis*	Lacertidae	Present (1)	MNHUK 1969.17/1969.15
Latastia	*longicaudata*	Lacertidae	Present (1)	MNHUK 97.10.28.234
Meroles	*squamulosa*	Lacertidae	Present (1)	MNHUK 1970.1712
Mesalina	*brevirostris*	Lacertidae	Present (1)	MNHUK 1969.8
Ophisops	*minor* *leschenaulti*	Lacertidae	Present (1)	MNHUK 1969.5/1969.6
Philochortus	*spinalis*	Lacertidae	Present (1)	MNHUK 95.5.19.24
Podarcis	*muralis liolepis* *muralis* *bocagei* *tauricus* *sicula*	Lacertidae	Present (1)	USNM 220260/284454 MNHUK 1969.20-21/1969.42-43/1969.40-41

Table A1.1. Continued

Genus	Species	Family	Code	Specimen Location
LACERTOIDEA (continued)				
Pseuderemias	*brenneri* *smithii*	Lacertidae	Present (1)	MNHUK 1937.12.5.524 1937.12.5.411-422
Takydromus	*spetentrionalis*	Lacertidae	Present (1)	MNHUK 1969.58-62
Zootoca	*vivpari*	Lacertidae	Present (1)	MNHUK 1969.5
SCINCOIDEA				
Ablepharus	*deserti*	Scincidae	Present (1)	MNHUK 79.11.14.215
Brachymeles	*bicolor* *tridactylus* *boulengeri* *boulengeri taylori*	Scincidae	Present (1)	USNM 498997/229623/509414/305968
Carlia	*ailanpalai* *tutela* *bicarinata* *nigrigulare* *fusca*	Scincidae	Present (1)	USNM 323690/507539/231916/232188/232106
Chamaesaura	*anguina*	Cordylidae	Present (1)	USNM 49037
Corucia	*zebrata*	Scincidae	Present (1)	USNM 306212
Cryptoblepharus	*poecilopleurus*	Scincidae	Present (1)	USNM 306215
Emoia	*impar* *caeruleocauda* *boettgeri* *cyanura* *pallidiceps*	Scincidae	Present (1)	USNM 509542/323701/507565/249752/567197
Eumeces	*laticeps* *inexpectatus* *lynxe* *tunganus* *sumichrasti* *schwartzei* *latiscutatus* *chinesis* *elegans* *egregious* *copei* *marginatus*	Scincidae	Present (1)	USNM 525729/332754/113599/107447/113610/113604/034121/065349/060574/032098/113541/036522
Gerrhosaurus	*flavigularis* *major*	Gerrhosauridae	Present (1)	USNM kdQ134/279863
Lamprolepis	*smaragdina*	Scincidae	Present (1)	USNM 507551
Lampropholis	*delicata*	Scincidae	Present (1)	USNM 279295
Lepininia	*noctua*	Scincidae	Present (1)	USNM 512290
Lepinia	*noctua*	Scincidae	Present (1)	USNM 230253
Mabuya	*elegans* *multrcarinata* *cumingi* *gravenhorsti* *affinis*	Scincidae	Present (1)	USNM 336438/509420/499004/336441/248841
Ristella	*travancorics*	Scincidae	Present (1)	BMNH 1946.8.2.61

Table A1.1. Continued

Genus	Species	Family	Code	Specimen Location
SCINCOIDEA (continued)				
Scincella	*lateralis* *potanini*	Scincidae	Present (1)	USNM 332758/292040
Sphenomorphus	*scutatus* *steerei*	Scincidae	Present (1)	USNM 536537/305978
AMPHISBAENIA + DIBAMIDAE				
Dibamus	*argenteus*	Dibamidae	Absent (0)	USNM 229591/287289/ 287351

Appendix A2: Extant specimens assessed for this project (literature review)

Table A2.1. Summary of all species assessed through literature reviews, including specimen museum codes. N=307

Genus	Species	Family	Code	Specimen Location	Source
RHYNCHOCEPHALIA (Squamata out group)					
Sphenodon	*punctatus*	Sphenodontidae	Present (1)	YPM 9194	Digimorph; Gauthier *et al.* (2012)
IGUANIA					
Acanthocercus	*cyanogaster*	Agamidae	Present (1)	AMNH R50797	AMNH Online Database
Agama	*agama* *agama lionotus*	Agamidae	Present (1)	FMNH 47531 CAS 199024/199003/199001/154502/103649/198910	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Kearney (2003); Maisano (2001)
Anisolepis	*undulatus*	Iguanidae	Present (1)	MCZ R5927 AMNH R120468	AMNH Online Database; Rodrigues (2005)
Anolis	*occultus* *vermiculatus* *carolinesensis* *ortonii* *luteogularis* *sagrei*	Polychrotidae	Present (1)	AMNH 115547/70092/R56886/R46157 FMNH 242298 CM 64126 KU 248656 MVZ 215192	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008); Maisano (2001)
Basiliscus	*bascilicus* *vittatus*	Corytophanidae	Present (1)	FMNH165622 KU 184174/157296/59591/67208	Digimorph; Gauthier *et al.* (2012); Maisano (2001)
Brachylophus	*fasciatus*	Iguanidae	Present (1)	FMNH 210158	Digimorph; Gauthier *et al.* (2012)
Brookesia	*brygooi*	Chamaeleonidae	Present (1)	FMNH 260015	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Callisaurus	*draconoidea*	Phyronsomatidae	Present (1)	CAS 91239 MVZ 205090 KU 72121	Maisano (2001)
Calotes	*emma*	Agamidae	Present (1)	FMNH 252264	Digimorph; Gauthier *et al.* (2012)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
IGUANIA (continued)					
Chalarodon	*madagascariensis*	Opluridae	Present (1)	YPM 12866	Digimorph; Gauthier *et al.* (2012)
Chamaeleo	*calyptratus* *laevigatus* *cristatus* *ituriensis* *quilensis*	Chamaeleonidae	Present (1)	FMNH 47572 AMNH R1801/R47624/R47506 TNHC 62768	AMNH Online Database; Digimorph; Gauthier *et al.* (2012)
Cophosaurus	*texanus*	Iguanidae	Present (1)	AMNH R20369	AMNH Online Database
Corytophanes	*cristatus*	Corytophanidae	Present (1)	FMNH 69227	Digimorph; Gauthier *et al.* (2012)
Crotaphytus	*collaris*	Crotaphytidae	Present (1)	FMNH 48667	Digimorph; Gauthier *et al.* (2012)
Dipsosaurus	*dorsalis*	Iguanidae	Present (1)	YPM 14376	Digimorph; Gauthier *et al.* (2012)
Draco	*quinquefascuiatus*	Agamidae	Present (1)	FMNH 221322	Digimorph
Enyalioidea	*laticeps*	Hoplocercidae	Present (1)	FMNH 40008/31354/206132	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Gambelia	*wislizenii*	Crotaphytidae	Present (1)	YPM 14380 AMNH R22854	AMNH Online Database; Digimorph; Gauthier *et al.* (2012)
Hoplocercus	*spinosus*	Hoplocercidae	Present (1)	AMNH 89398/90384/90658/93807	Conrad (2008)
Leiocephalus	*carinatus* *barahonensus* *lunatus* *melanochlorus* *barahonensis*	Iguanidae Leicephalidae	Present (1)	FMNH 22754 AMNH R51195/R49792/R22656/R51195 USNM 260564	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Leiolepis	*belliana* *reevesii revesii* *triploida*	Agamidae	Present (1)	USNM 205722 AMNH R30728/R30714 YPM 12864	AMNH Online Database; Digimorph; Gauthier *et al.* (2012)
Leiosaurus	*catamarcensis*	Leiosauridae	Present (1)	CM 65003	Digimorph; Gauthier *et al.* (2012)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
IGUANIA (continued)					
Liolaemus	*bellii* *signifier* *zapallarensis* *nitidus* *kingii* *chiliensis* *bibronii* *burger* *lemniscatus* *neuquensis* *nigroviridis* *grosseorum*	Lioleamidae Tropiduridae	Present (1)	AMNH 77610/R65194/R90459/77625/R37733/R38044/R37733/R37534 MVZ 125659 MCN 506/565-658/490-491/501-502/514-517/519-520/569-572/508-509	AMNH Online Database; Gauthier *et al.* (2012); Conrad (2008); Lobo & Abdala (2001)
Moloch	*horridus*	Agamidae	Present (1)	Dr. Eric Planka	Digimorph
Morunasaurus	*annularis*	Hoplocercidae	Present (1)	AMNH R57178	Gauthier *et al.* (2012); Conrad (2008)
Oplurus	*cyclurus* *quadrimaculatus*	Opluridae	Present (1)	AMNH 138120/R71462/R47944/R71452 YPM 12861	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Petrosaurus	*mearnsi* *thalassinus*	Iguanidae Phrynosomatidae	Present (1)	FMNH 8431 AMNH R5651	AMNH Online Database; Digimorph; Gauthier *et al.* (2012)
Phrynosoma	*asio* *btaconnieri* *cornutum* *cornatum* *ditmarsi* *douglassii* *hermandesi* *mcallii* *modestum* *orbiculare* *platyrhinos* *solare* *taurus*	Phrynosomatidae	Present (1)	WLH 1093 AMNH R46279 TNHC 1930/11839/062316/48520/18496 MVZ 80250 LACM 138354/126543/123351	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Kearney (2003)
Phymaturus	*palluma*	Liolaemidae	Present (1)	FMNH 209123	Digimorph; Gauthier *et al.* (2012)
Physignathus	*cocincinus*	Agamidae	Present (1)	YPM 14378	Digimorph; Gauthier *et al.* (2012); Conrad (2008)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
IGUANIA (continued)					
Plica	*plica*	Tropiduridae	Present (1)	FMNH 81451	Digimorph; Gauthier *et al.* (2012)
Pogona	*vitticeps*	Agamidae	Present (1)	ROM 22699	Digimorph; Gauthier *et al.* (2012)
Polychrus	*marmoratus* *femoralis* *gutturosus*	Polychrotidae	Present (1)	AMNH R141130 R32675 R32676 FMNH 42501 81405	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Pristidactylus	*torquatus*	Leiosauridae	Present (1)	FMNH 206964	Digimorph; Gauthier *et al.* (2012)
Rhampholeon	*boulengeri*	Chamaeleonidae	Present (1)	AMNH R39399	AMNH Online Database; Conrad (2008)
Sauromalus	*ater*	Iguanidae	Present (1)	CAS 174700 TMM M8950 M0922 FMNH 31015 TNH 18483 YPM HERR010327/011067/011194/011623-25/013407/013786/015372/017083	Gauthier *et al.* (2012)
Sceloporus	*variabilis* *mucronatus* *pyrocephalus*	Iguanidae Phrynosomatidae	Present (1)	FMNH 122866 AMNH R18816 R15624	AMNH Online Database; Digimorph; Gauthier *et al.* (2012)
Stenocercus	*guentheri* *scapularis* *huancabambae* *iridescens*	Iguanidae Tropiduridae	Present (1)	FMNH 98440/40612/27674 AMNH R56777/R56770/R28636/R21993	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Tropidurus	*peruvianus* *hygomi* *koepckeorum* *occipitalis*	Iguanidae	Present (1)	AMNH R38023/R37892/R28582/R37542/R37538/R22038/R21999	AMNH Online Database
Uma	*scopario*	Phrynosomatidae	Present (1)	FMNH 1203	Digimorph; Gauthier *et al.* (2012)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
IGUANIA (continued)					
Uranoscodon	*superciliosus*	Tropiduridae	Present (1)	YPM 12871	Digimorph; Gauthier *et al.* (2012)
Uromastyx	*aegyptius*	Agamidae	Present (1)	AMNH R73357 FMNH 78661	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Urostrophus	*vautieri*	Leiosauridae	Present (1)	FMNH 83576	Digimorph; Gauthier *et al.* (2012)
Uta	*stansburiana*	Phrynosomatidae	Present (1)	FMNH 213914	Digimorph; Gauthier *et al.* (2012)
GEKKOTA					
Aeluroscalabotes	*felinus*	Eublepharidae	Present (1)	FMNH 188235	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Underwood (1957)
Aprasia	*pulchella*	Pygopodidae	Present (1)	N/A	Conrad (2008); Stephenson (1960); Underwood (1957)
Carphodactylus	*laevis*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Christinus	*marmoratus*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Coleonyx	*mitratus* *variegatus*	Eublepharidae	Present (1)	FMNH 5053 YPM 14383	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Underwood (1957)
Delma	*borea* *fraseri*	Pygopodidae	Present (1)	USNM 128679 Australia	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Stephenson (1960)
Diplodactylus	*ciliaris* *tessellatus*	Diplodactylidae	Present (1)	FMN 215488 Australia	Digimorph; Stephenson (1960)
Dravidogekko	*sp.*	Gekkonidae	Present (1)	N/A	Underwood (1984)
Ebenavia	*horni*	Diplodactylidae	Present (1)	Australia	Stephenson (1960)
Eublepharis	*macularius*	Eublepharidae	Present (1)	CM 67524	Digimorph; Gauthier *et al.* (2012)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
GEKKOTA (continued)					
Gekko	*gekko*	Gekkonidae	Present (1)	AMNH R141109 R130786 FMNH 14448/31013 /14417/18681 8/55929	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Kearney (2003)
Gonatodes	*albogularis*	Sphaerodactylidae	Present (1)	FMNH 209439 209440	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Hemitheconyx	*caudcinctus*	Eublepharidae	Present (1)	AMNH R104409 FMNH209441 YPM 14381	Digimorph; Conrad (2008)
Heteronota	*binoei*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Hoplodactylus	*duvaucelii* *pacificus*	Gekkonidae	Present (1)	N/A	Stephenson & Stephenson (1956)
Lialis	*burtonis*	Pygopodidae	Present (1)	FMNH 166958	Digimorph; Gauthier *et al.* (2012); Stephenson (1960)
Lucasius	*damaeus*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Naultinus	*elegans*	Gekkonidae	Present (1)	N/A	Stephenson & Stephenson (1956)
Nephrurus	*levis*	Diplodactylidae	Present (1)	YPM 12868	Digimorph; Stephenson (1960)
Oedura	*leseurii*	Gekkonidae	Present (1)	N/A	Underwood (1954)
Pachydactylus	*bibroni*	Gekkonidae	Present (1)	FMNH 209449	Conrad (2008)
Peropus	*oceanicus* *variegatus*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Phelsuma	*lineata*	Gekkonidae	Present (1)	FMNH 260100	Digimorph; Gauthier *et al.* (2012)
Phyllurus	*cornutus* *platurus* *milii*	Gekkonidae	Present (1)	FMNH 57503 Australia	Digimorph; Stephenson (1960); Stephenson & Stephenson (1956)
Pletholax	*sp.*	Pygopodidae	Present (1)	N/A	Conrad (2008)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
GEKKOTA (continued)					
Pygopus	*lepidopus*	Pygopodidae	Present (1)	N/A	Conrad (2008); Kearney (2003); Stephenson (1960); Underwood (1957)
Rhacodactylus	*auriculatus*	Gekkonidae	Present (1)	CAS 205486	Digimorph; Gauthier *et al.* (2012)
Rhynchoedura	*ornata*	Gekkonidae	Present (1)	Australia	Stephenson (1960)
Saltuarius	*cornutus*	Gekkonidae	Present (1)	FMNH 57498/57500/ 57501/57503 UMMZ 127590	Gauthier *et al.* (2012)
Strophurus	*ciliaris*	Gekkonidae	Present (1)	FMNH 215488 LACM 56800/56822/ 56857 YPM HERR010211	Gauthier *et al.* (2012)
Teratoscincus	*microleptis* *przewalskii*	Gekkonidae	Present (1)	AMNH R88252 CAS 17101/167390 /167393/ 167394	Gauthier *et al.* (2012); Conrad (2008)
LACERTOIDEA					
Acanthodactylus	*boskianus* *erythruus*	Lacertidae	Present (1)	CAS 134176 YPM R5629 R5203 UAM unknown	Maisano (2001); Barahona & Barbadillo (1998)
Alexandrasaurus	*camacan*	Gymnophthalmidae	Present (1)	MZUSP 94252 94253	Rodrigues *et al.* (2007)
Aspidoscelis	*tigris*	Teiidae	Present (1)	FMNH 161622	Digimorph; Gauthier *et al.* (2012)
Bachia	*heteropa* *bicolor* *barbouri*	Gymnophthalmidae Teiidae	Present (1)	USNM 227718 248783 AMNH 28437	Tarazona & Ramirez-Pinilla (2008); Kearney (2003); Burt & Burt (1931)
Callipistes	*maculatus*	Teiidae	Present (1)	FMNH 53726	Digimorph; Gauthier *et al.* (2012)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
LACERTOIDEA (continued)					
Callipistes	*maculatus*	Teiidae	Present (1)	FMNH 53726	Digimorph; Gauthier *et al.* (2012)
Cnemidophorus	*tigris*	Teiidae	Present (1)	MVZ 176756/176759/206245 KU 7887637 72357 CAS 189033	Maisano (2001)
Colobosaura	*modesta*	Gymnophthalmidae	Present (1)	USNM 341978	Digimorph; Gauthier *et al.* (2012)
Cricosaura	*typica*	Xantusiidae	Present (1)	USNM 547842 LACM 196770	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Holaspis	*guentheri*	Lacertidae	Present (1)	YPM 12860	Digimorph
Lacerta	*viridis*	Lacertidae	Present (1)	YPM 12858	Digimorph; Gauthier *et al.* (2012)
Lepidophyma	*flavimaculatum* *smithii* *gaigeae*	Xantusiidae	Present (1)	FMNH 98560 LACM 128570/136359	Digimorph; Conrad (2008)
Neusticurcus	*ecpleopus*	Gymnophthalmidae	Present (1)	KU 109803/148251/109781	Maisano (2001)
Pholidobolus	*montium*	Gymnophthalmidae	Present (1)	FMNH 197865	Digimorph; Gauthier *et al.* (2012)
Psammodromus	*algirus*	Lacertidae	Present (1)	UAM 1969.53	Barahona & Barbadillo (1998)
Tachydromus	*ocellatus*	Lacertidae	Present (1)	FMNH 255513	Digimorph; Gauthier *et al.* (2012)
Teius	*teyou*	Teiidae	Present (1)	FMNH 10873	Digimorph; Gauthier *et al.* (2012); Kearney (2003)
Tupinambis	*teguixin* *nigropunctatus*	Teiidae	Present (1)	FMNH 22416	Digimorph; Gauthier *et al* (2012); Kearney (2003)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
LACERTOIDEA (continued)					
Xantusia	*extorris* *henshawi* *magdalena* *riversiana* *sonora* *vigilis* *arizonae*	Xantusiidae	Present (1)	FMNH 22101/22329 LACM 2014/100716 /108770/ 123671 UAZ 17386 17345 YPM R9216 9218/9217	Digimorph; Gauthier *et al*. (2012); Conrad (2008); Maisano (2001)
SCINCOIDEA					
N/A	N/A	Acontidae	Present (1)	N/A	Conrad (2008)
N/A	N/A	Feylinidae	Present (1)	N/A	Conrad (2008)
N/A	N/A	Scelotidae	Present (1)	N/A	Conrad (2008)
Ablepharus	*sp.*	Scincidae	Present (1)	N/A	Underwood (1984)
Acontias	*percivali* *meleagris*	Scincidae	Present (1)	USNM 63567	Gauthier *et al*. (2012); Kearney (2001)
Amphiglossus	*splendidus*	Scincidae	Present (1)	FMNH 75807	Digimorph; Gauthier *et al*. (2012)
Angolosaurus	*skoogi*	Gerrhosauridae	Present (1)	CAS 206978	Digimorph; Nance (2007)
Brachymeles	*gracilis*	Scincidae	Present (1)	FMNH 52642	Digimorph; Gauthier *et al*. (2012)
Chalcides	*ocellatus* *chalcides*	Scincidae	Present (1)	ZMB 29768 YPM 12690	Digimorph; Kearney (2003)
Cordylosaurus	*subtessallatus*	Gerrhosauridae	Present (1)	FMNH 74082	Digimorph; Gauthier *et al*. (2012)
Cordylus	*mossambicus*	Cordylidae	Present (1)	YPM 12670	Digimorph; Gauthier *et al*. (2012)
Egernia	*striolata*	Scincidae	Present (1)	YPM 12865	Digimorph
Eugongylus	*rufescens*	Scincidae	Present (1)	FMNH 142306	Digimorph; Gauthier *et al*. (2012)
Eumeces	*schneideri* *fasciatus* *obsoletus*	Scincidae	Present (1)	YPM 12668 126689 USNM 62113	Digimorph; Kearney (2003)

Table A2.1. Continued

Genus	**Species**	**Family**	**Code**	**Specimen Location**	**Source**
SCINCOIDEA (continued)					
Feylinia	*grandisquamis*	Scincidae	Present (1)	USNM 62113	Kearney (2003)
Gerrhosaurus	*nigrolineatus*	Gerrhosauridae	Present (1)	YPM 14382	Digimorph
Platysaurus	*imperator*	Cordylidae	Present (1)	N/A	Gauthier *et al*. (2012)
Plestiodon	*fasciatus*	Scincidae	Present (1)	N/A	Gauthier *et al*. (2012)
Scincus	*scincus*	Scincidae	Present (1)	YPM 12686	Digimorph; Gauthier *et al*. (2012)
Sphenomorphus	*solomonis*	Scincidae	Present (1)	CAS 110021	Digimorph; Gauthier *et al*. (2012)
Sphenomorphus	*solomonis*	Scincidae	Present (1)	CAS 110021	Digimorph; Gauthier *et al*. (2012)
Tiliqua	*scincoidea*	Scincidae	Present (1)	FMNH 57518	Digimorph; Gauthier *et al*. (2012); Underwood (1982)
Tracheloptychus	*petersi*	Gerrhosauridae	Present (1)	YPM 12691	Digimorph
Trachylepis	*quinquetaentiata*	Scincidae	Present (1)	N/A	Gauthier *et al*. (2012)
Typhlosaurus	*bicolor*	Scincidae	Present (1)	N/A	Kearney (2003)
Zonosaurus	*ornatus*	Gerrhosauridae	Present (1)	YPM 12671	Digimorph; Gauthier *et al*. (2012)
ANGUIMORPHA					
Abronia	*sp.*	Anguidae	Present (1)	FMNH 38523	Conrad (2008)
Anguis	*sp.*	Anguidae	Present (1)	AMNH R56193	Conrad (2008)
Anniella	*pulchra*	Anneillidae	Present (1)	FMNH 213666	Digimorph; Gauthier *et al*. (2012); Conrad (2008); Kearney (2003)
Barisia	*sp.*	Anguidae	Present (1)	FMNH 6526/6528	Conrad (2008)
Celestus	*enneagramus*	Anguidae	Present (1)	FMNH 13254/ 108860	Digimorph; Gauthier *et al*. (2012); Conrad (2008)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
ANGUIMORPHA (continued)					
Diploglossus	*costatus*	Anguidae	Present (1)	FMNH 19248 AMNH R51163	AMNH Online Database; Conrad (2008)
Dopasia	*sp.*	Anguidae	Present (1)	FMNH 24298	Conrad (2008)
Elgaria	*multicarinata*	Anguidae	Present (1)	FMNH 23235/213397/23601	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Gerrhonotus	*infernalis*	Anguidae	Present (1)	FMNH 22452 YPM 14379	Digimorph; Conrad (2008)
Heloderma	*horridum* *suspectum*	Helodermatidae	Present (1)	AMNHR74778/R142627 FMNH 22038/250611/31366/98468/98776/218077/22232/22249/98774 TMM 64380/62766	Digimorph; Gauthier *et al.* (2012); Conrad (2008); Kearney (2003)
Lanthanotus	*borneensis*	Lanthanotidae	Present (1)	FMNH 13098/134711/148589 YPM 6057	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Ophiodes	*sp.*	Anguidae	Present (1)	FMNH 9270	Conrad (2008)
Ophisaurus	*ventralis* *attenuates* *apodus*	Anguidae	Present (1)	AMNH 98466 FMNH 98467/207671 YPM 12870	Digimorph; Conrad (2008)
Pseudopus	*apodus*	Anguidae	Present (1)	FMNH 216745/22088/22359	Gauthier *et al.* (2012); Conrad (2008)
Shinisaurus	*crocodiliurus*	Shinisauridae	Present (1)	FMNH 233120/134242/215541 UofF 57112/61149/61685/62315/62316/62497/62536/62578/69203 AMNH R44928	AMNH Online Database; Digimorph; Gauthier *et al.* (2012); Conrad (2008)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
ANGUIMORPHA (continued)					
Varanus	*olivaceus* *eremius* *tristis* *prasinus* *salvadorii* *komodoensis* *varius* *griseus* *niloticus* *exanthematicus* *acanthurus* *gouldii* *salvatar*	Varanidae	Present (1)	FMNH 223181/229907/31380/212985/58299/35144/12300/17144-46/22084/22496/45807/22199/22200 AMNH R59873/R10524/R74603 UTA 13015 TMM M1295	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
Xenosaurus	*grandis* *platyceps*	Xenosauridae	Present (1)	FMNH 211833/123702 UofF 43396/43397/45590/53691/56122	Digimorph; Gauthier *et al.* (2012); Conrad (2008)
AMPHISBAENIA + DIBAMIDAE					
Agamodon	*anguliceps*	Trogonophidae	Present (1)	AMNH 134243	Kearney (2003); Gans (1978)
Amphisbaena	*alba* *caeca* *cubana* *darwini* *fenestrata* *fugliginosa* *gonavensis* *innocens* *vermicularis*	Amphisbaenidae	Present (1)	FMNH 195924 USNM 025540/026459/129269/192810/065526/221816/118906/059068 MVZ 204284 204285 AMNH R137640	Digimorph; Kearney (2003)
Ancylocranium	*ionidesi*	Amphisbaenidae	Present (1)	CG 1129	Kearney (2003)
Anelytropsis	*papillosus*	Dibamidae	Absent (0)	AMNH 64023 TCWC 45503	Conrad (2008); Greer (1985)
Anops	*kingi*	Amphisbaenidae	Present (1)	FMNH 80100	Digimorph; Kearney (2003)
Aulura	*anomala*	Amphisbaenidae	Present (1)	CG 2766	Kearney (2003)
Baikia	*africana*	Amphisbaenidae	Present (1)	BMNH 1966.344	Kearney (2003)

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
AMPHISBAENIA + DIBAMIDAE (continued)					
Bipes	*biporus* *canaliculatus* *tridactylus*	Bipedidae	Present (1)	CAS 150525/150526/ 150529/126478/ 134753	Digimorph; Conrad (2008); Kearney (2003); Gans (1978)
Blanus	*cinereus*	Blanidae	Present (1)	N/A	Conrad (2008); Kearney (2003)
Bronia	*brasiliana*	Amphisbaenidae	Present (1)	N/A	Kearney (2003)
Cadea	*blanoides*	Cadeidae	Present (1)	USNM 036811	Kearney (2003)
Chirindia	*rodoensis*	Amphisbaenidae	Present (1)	BMNH 1964.746	Kearney (2003)
Cynisca	*leucura*	Amphisbaenidae	Present (1)	BMNH 19541.4.9	Kearney (2003)
Dalophia	*longicauda*	Amphisbaenidae	Present (1)	AMNH R112962	Kearney (2003)
Dibamus	*novaeguineae* *taylori*	Dibamidae	Absent (0)	AMNH 8671/32234 CAS 26675/26678 MBS 14776	Conrad (2008); Greer (1985); Rieppel (1984)
Diplometopon	*zarudyni*	Trogonophidae	Present (1)	FMNH 64429	Digimorph; Kearney (2003); Gans (1978)
Geocalamus	*acutus*	Amphisbaenidae	Present (1)	FMNH 262014	Digimorph; Kearney (2003)
Leposternon	*microcephalum*	Amphisbaenidae	Present (1)	FMNH 69954	Digimorph; Kearney (2003)
Loveridgea	*ionidesii*	Amphisbaenidae	Present (1)	CG 1831	Digimorph; Kearney (2003)
Mesobaena	*huebneri*	Amphisbaenidae	Present (1)	UTA 6880	Kearney (2003)
Monopeltis	*capensis*	Amphisbaenidae	Present (1)	CG 4458/3564/3565	Kearney (2003); Gans (1978)
Pachycalamus	*brevis*	Trogonophidae	Present (1)	AMNH 73424	Kearney (2003)
Rhineura	*floridana*	Rhineuridae	Absent (0)	FMNH 31774	Digimorph; Kearney (2003)
Trogonophis	*wiegmanni*	Trogonophidae	Present (1)	FMNH 109462	Digimorph; Kearney (2003); Gans (1978)
Zygaspis	*quadriformes*	Amphisbaenidae	Present (1)	MNHN 431/2074	Kearney (2003)
SERPENTES					
N/A	N/A	Neomacrostomata	Absent (0)	N/A	Conrad (2008)
Agkistrodon	*contortrix*	Viperidae	Absent (0)	FMNH 166644	Digimorph
Amphiesma	*stolate*	Colubridae	Absent	FMNH 169627	Digimorph

Table A2.1. Continued

Genus	Species	Family	Code	Specimen Location	Source
SERPENTES (continued)					
Anilius	*scytale*	Aniliidea	Absent (0)	USNM 20478	Digimorph
Anomoschilus	*leonardi*	Anomochilidae	Absent (0)	FRIM 0026	Digimorph
Aspidites	*melanocephalus*	Pythonidae	Absent (0)	FMNH 97055	Digimorph
Boa	*constrictor*	Boidae	Absent (0)	FMNH 31182	Digimorph; Kearney (2003)
Bothropoides	*jararca*	Viperidae	Absent (0)	N/A	Polachowskia & Werenberg (2013)
Bothrops	*asper*	Viperidae	Absent (0)	FMNH 31162	Digimorph
Calabaria	*reinhardtii*	Viperidae	Absent (0)	FMNH 117833	Digimorph
Casarea	*dussumieri*	Bolyeriidae	Absent (0)	UMMZ 190285	Digimorph
Causus	*rhombeatus*	Viperidae	Absent (0)	FMNH 74241	Digimorph
Coluber	*constrictor*	Colubridae	Absent (0)	FMNH 135284	Digimorph
Cylindrophis	*rufus*	Cylindeophiidae	Absent (0)	FMNH 60958	Digimorph; Kearney (2003)
Diadophis	*punctatus*	Colubridae	Absent (0)	FMNH 244371	Digimorph
Eryx	*colubrinus*	Boidae	Absent (0)	FMNH 63117	Digimorph
Heterodon	*platirhinos*	Colubridae	Absent (0)	FMNH 194529	Digimorph
Homalopsis	*buccata*	Colubridae	Absent (0)	FMNH 259340	Digimorph
Lachesis	*muta*	Viperidae	Absent (0)	FMNH 31178	Digimorph
Laticauda	*colubrina*	Elapidae	Absent (0)	FMNH 202810	Digimorph
Leptotyphlops	*dulcis humilis*	Leptyphlopidae	Absent (0)	TNHC 60638	Digimorph; Conrad (2008); Kearney (2003)
Lichanura	*trivirgata*	Boidae	Absent (0)	YPM 12869	Digimorph
Liotyphlops	*albirostris*	Anomalepididae	Absent (0)	FMNH 21625	Digimorph; Conrad (2008)
Loxocemus	*bicolor*	Loxocemidae	Absent (0)	FMNH 104800	Digimorph
Lycophidion	*capense*	Colubridae	Absent (0)	FMNH 58322	Digimorph
Micrurus	*fulvius*	Elapidae	Absent (0)	FMNH 39479	Digimorph
Naja	*naja*	Elapidae	Absent (0)	FMNH 22468	Digimorph

Table A2.1. Continued

Genus	**Species**	**Family**	**Code**	**Specimen Location**	**Source**
SERPENTES (continued)					
Natrix	*natrix*	Colubridae	Absent (0)	FMNH 30522	Digimorph
Python	*molurua* *regius*	Pythonidae	Absent (0)	TNHC 62769	Digimorph; Kearney (2003)
Sonora	*semiannulata*	Colubridae	Absent (0)	FMNH 26876	Digimorph
Thamnophis	*marcianus*	Colubridae	Absent (0)	FMNH 26290	Digimorph
Trimorphodon	*biscutatus*	Colubridae	Absent (0)	FMNH 42171	Digimorph
Tropidophis	*haetianus*	Tropidophiidae	Absent (0)	TNHC 64040	Digimorph
Typhlophis	*squamosus*	Anomalephididae	Absent (0)	USNM 289090	Digimorph
Typhlops	*jamaicensis*	Typhlopidae	Absent (0)	USNM 12378	Digimorph; Conrad (2008)
Ungaliophis	*continentalis*	Tropidophiidae	Absent (0)	UTA 50569	Digimorph
Uropeltis	*woodmasoni*	Uropeltidae	Absent (0)	TNHC M10006	Digimorph
Xenochrophis	*piscator*	Colubridae	Absent (0)	FMNH 179132	Digimorph
Xenopeltis	*unicolor*	Xenopeltidae	Absent (0)	FMNH 148900	Digimorph; Conrad (2008)

Appendix A3: Fossil specimens assessed for this project (literature review)

Table A3.1. Summary of all fossil species assessed through literature reviews. Museum codes are included. A question mark indicates the presence/absence of a sclerotic ring is unknown; "1" indicates presence, while "0" is absence. Blue highlighted entries indicate fossils with sclerotic rings; red indicates absence of this trait. N=167

Genus	Species	Family	Condition	Age	Code	Location	Source
DIAPSIDA							
Langobardisaurus	*rossii*	Unresolved	Nearly complete, poorly preserved (skull especially)	Late Triassic	(?)	MFSN 19235	Renesto & Vecchia (2007)
Macronemus	*fuyuanensis*	Prolacertidae	Nearly complete skeleton	Middle Triassic	(?)	IVPP V15001	Chun *et al.* (2007)
Marmoretta	*oxoniensis*	Unresolved	Anterior region of right maxilla	Middle Jurassic	(?)	BMNH R12020/R12025/ R12146	Evans (1991)
Sophineta	*cracoviensis*	Unresolved	Incomplete right maxilla	Early Triassic	(?)	ZPAL RV/175	Evans & Borsuk-Bialynicka (2009)
RHYNCHOCEPHALIA (squamate out group)							
Ankylosphenodon	*pachyostosus*	Sphenodontidae	3 skulls; 1 split, 1 damaged, 1 crystallized	Early Cretaceous	(?)	Museum de Histoire Naturelle, Paris	Reynoso (2000)
Gephyrosaurus	*bridensis*	Gephyrosauridae	Dissociated and fragmentary bones	Early Jurassic	(?)	ULC T.1503	Evans (1980)
IGUANIA							
Anolis	*sp.*	Polychrotidae Iguanidae (Gauthier *et al*. 2012)	Almost complete skeleton with soft tissue preserved in amber	Oligocene to early Miocene	(1)	AMNH	de Queiroz *et al.* (1998)
Barbaturex	*morrisoni*	Crown Acrodonta	Partial right dentary	Late to middle Eocene	(?)	UCMP 142227 (holotype)	Head *et al.* (2013)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
IGUANIA (continued)							
Bharatagama	*rebbanensis*	Chamaeleonidae	Partial right dentary	Jurassic	(?)	U of Jammu VPL/JU/KR 66	Evans *et al.* (2002)
Brasiliguana	*prudentis*	Unresolved	Isolated left maxilla and teeth	Late Cretaceous	(?)	MN 7230-V	Nava & Martinelli (2011)
Crotaphytus	*sp.*	Crotaphytidae	Incomplete dentaries	Pleistocene	(?)	NAU 8155 8156	Czaplewski *et al.* (1999)
Ctenomastax	*parva*	Iguanidae	Incomplete skull with partial right mandible	Late Cretaceous	(?)	MAS IGM 3/61	Keqin & Norell (2000)
Desertiguana	*gobiensis*	Phrynosomatidae	Left lower jaw ramus	Late Cretaceous	(?)	PIN 4487/9	Alifanov (2013)
Geiseltaliellus	*pradiguensis*	Iguanidae	Partial dentarties and maxilla	Eocene	(?)	IPS 56093	Bolet & Evans (2013); Auge & Pouit (2012)
Isodontosaurus	*gracilis*	Unresolved	Incomplete mandibles with teeth	Late Cretaceous	(?)	AMNH 6647	Keqin & Norell (2000)
Mimeosaurus	*crassus*	Acrodonta	Left maxilla with jugal	Late Cretaceous	(?)	AMNH 6655	Keqin & Norell (2000)
Phrynosoma	*douglasi* *sp.*	Phrynosomatidae	Incomplete dentary; frontal bone	Pleistocene	(?)	NAU 8160/8174 8159	Czaplewski *et al.* (1999)
Phyrnosomimus	*asper*	Acrodonta	Incomplete skull with mandibles	Late Cretaceous	(?)	PIN 3142/318	Keqin & Norell (2000)
Polrussia	*mongoliensis*	Iguanidae	Incomplete skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-I/119	Keqin & Norell (2000)
Priscagama	*gobiensis*	Acrodonta	Incomplete skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-III/32	Keqin & Norell (2000)
Sceloporus	*magister*	Phrynosomatidae	Maxilla	Pleistocene	(?)	NAU 8161	Czaplewski *et al.* (1999)
Temujinia	*ellisoni*	Iguanidae	Incomplete skull with mandibles	Late Cretaceous	(?)	IGM 3/63	Keqin & Norell (2000)
Tinosaurus	*indicus*	Agamidae	Left dentary	Early Eocene	(?)	iiTr/SB/VLM/ 904	Prasad & Bajpai (2008)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
IGUANIA (continued)							
Tropidurus	*sp.*	Tropididae	Complete right dentary	Quaternary	(?)	MDJ R-005	Hsiou *et al.* (2012); Rodrigues (1996)
Uquiasaurus	*heptanodonta*	Unresolved	Premaxilla	Late Pliocene	(?)	PVL 6388	Daza *et al.* (2012)
Vastanagama	*susani*	Agamidae	Small dentary and teeth	Early Eocene	(?)	IITR/SB/VLM/1050	Prasad & Bajpai (2008)
Zapososaurus	*sceliphros*	Iguanidae	Incomplete skull with mandibles	Late Cretaceous	(?)	IGM 3/71	Keqin & Norell (2000)
MOSASAURIA†							
Clidastes	*sp.*	Mosasauridae	N/A	N/A	(1)	Unknown	Gauthier *et al.* (2012)
Platecarpus	*sp.*	Mososauridae	N/A	N/A	(1)	Unknown	Gauthier *et al.* (2012); Conrad (2008)
Prognathodon	*solvayi overtone*	Mososauridae	Well articulated skull with mandibles	Late Campanian (Cretaceous)	(1)	Royal Tyrrell Museum	Konishi *et al.* (2011); Conrad (2008)
Tethysaurus	*nopcsai*	Mososauridae	Isolated ScO elements	Late Cretaceous	(1)	MNHN Paris	Bardet *et al.* (2003)
Tylosaurus	*sp.*	Mososauridae	N/A	N/A	(1)	Unknown	Gauthier *et al.* (2012); Conrad (2008)
STEM SCLEROGLOSSA							
Jucaraseps	*grandipes*	Unresolved	Small block with impressions and fragments of skull and neck	Early Cretaceous	(1)	Museo de Cuenca, Spain	Bolet & Evans (2012)
Liushusaurus	*acanthocaudata*	Unresolved	Partial skeleton of young adult; partial skull and post cranium	Early Cretaceous	(?)	IVPP V15587A/B V14715A/B	Evans & Wang (2010)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
STEM SCLEROGLOSSA (continued)							
Pedrerasaurus	*latifrontalis*	Unresolved	Fully articulated skeleton, ScO coded as (?) by authors	Early Cretaceous	(?)	Spain	Bolet & Evans (2010)
Sakurasurus	*shokawensis*	Unresolved	Left mandible, miscellaneous bones	Early Cretaceous	(?)	IBEV VP 17	Evans & Manabe (2009)
Scandensia	*cievensis*	Unresolved	Small skeleton, poorly preserved, ScO indicated as present by authors	Early Cretaceous	(1)	Spain	Evans & Barbadillo (1998)
Tijubina	*pontei*	Evansauria	Few skull elements, pectoral girdle and forelimbs	Early Cretaceous	(?)	MPSC-V 010 (holotype)	Simoes (2012)
Yabeninosaurus	*tenuous*	Unresolved	Essentially complete; ScO recorded as (?) by authors	Early Cretaceous	(1)	Beijing	Evans & Wang (2012); Evans *et al*. (2005)
GEKKOTA							
Gobekko	*cretacicus*	Unresolved	Sandstone obscured structures	Cretaceous	(?)	Unknown	Daza *et al*. (2013)
Hoburogekko	*suchanovi*	Unresolved	Preserved muzzle unit	Early Cretaceous	(?)	Paleontological Institute, Moscow	Daza *et al*. (2012)
Myrmecodaptria	*microphagosa*	Unresolved	Incomplete skull with mandibles	Late Cretaceous	(?)	IGM 3/95	Keqin & Norell (2000)
Sphaerodactylus	*dommeli*	Sphaerodactylidae	Preserved in amber, most of skeleton present	Miocene	(1)	Germany	Daza *et al*. (2012)
SCINCOMORPHA							
Chamops	*segnis*	"Teiid-like"	Partial maxilla and jaw fragments	Late Cretaceous	(?)	OMNH 23605 33852 23201	Nydam & Voci (2007)
Eoxanta	*lacertifrons*	Unresolved	Incomplete left skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-III/37	Keqin & Norell (2000)
Gilmoreteius	*sp.*	Gilmoreteiidae	Skull, mandible only	N/A	(?)	Unknown	Langer (1998)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
SCINCOMORPHA (continued)							
Globarua	*venusta*	Unresolved	Incomplete skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-III/40	Keqin & Norell (2000)
Mensicognathus	*molybrochoros*	"Teiid-like"	Partial dentary and teeth	Late Cretaceous	(?)	OMNH 23743	Nydam & Voci (2007)
Polyglyphanodon	*sp.*	Polyglyphanodontidae	Nearly complete skull; left maxilla; nearly complete but disarticulated skull	Late Cretaceous	(?)	Smithsonian	Gilmore (1942)
Savoia	*darevskii*	Unresolved	Skull with mandibles, post cranial skeleton	Late Cretaceous	(?)	ZPAL MgR-I/8	Keqin & Norell (2000); Sulimski (1984)
Tripennaculus	*eatoni*	"Teiid-like"	Partial dentaries and teeth	Late Cretaceous	(?)	OMNH 23146/63128	Nydam & Voci (2007)
LACERTOIDEA							
Adamisaurus	*madnidentatus*	Teiidae	Incomplete skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-11/80	Keqin & Norell (2000)
Ameiva	*sp.*	Teiidae	Incomplete right dentary	Quaternary	(?)	Museu Dom Jose	Hsiou *et al.* (2012)
Cherminsaurus	*kazlowskii*	Teiidae	Skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-III/24	Keqin & Norell (2000)
Cnemidophorus	*sexlineatus*	Teiidae	Left dentary	Late Pleistocene	(?)	CMS 676	Holman (1974)
Dormaalisaurus	*rossmanni*	Lacertidae	Partial dentaries, teeth	Eocene	(?)	IPS 59524	Bolet & Evans (2013)
Erdenetesaurus	*robinsonae*	Teiidae	Incomplete skull with mandibles	Late Cretaceous	(?)	ZPAL MgR-III/19	Keqin & Norell (2000)
Gobinatus	*arenosus*	Teiidae	Incomplete skull with mandibles	Late Cretaceous	(?)	PIN 3142/308	Keqin & Norell (2000)
Gracilicerta	*sindexi*	Lacertidae	Partial dentaries and teeth	Eocene	(?)	IPS 49854	Bolet & Evans (2013)
Kleskunsaurus	*grandeprairensis*	Chamopsidae (Borioteiidea)	Incomplete skull, ScO fragments	Late Campanian (Cretaceous)	(1)	UALVP	Nydam *et al.* (2010)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
LACERTOIDEA (continued)							
Kuwajimalla	*kagaensis*	Unresolved (Borioteiidea)	Incomplete right maxilla	Early Cretaceous	(?)	SBEI 1550	Evans & Manabe (2008)
Lacerta	*fiholi* *viridis*	Lacertidae	Incomplete left dentary, left maxilla; maxilla, premaxillae and dentary	Oligocene Late Miocene	(?)	IRSNB R242 MAFI V.06.1668.1	Auge & Smith (2009); Venczel (2006)
Macrocephalosaurus	*chulsanensis*	Teiidae	Incomplete skull with mandibles and postcranial skeleton	Late Cretaceous	(?)	ZPAL MgR-I/14	Keqin & Norell (2000)
Paradracaena	*sp.*	Teiidae	Incomplete right dentary, 1 dorsal vertebrae	Miocene	(?)	Brazil	Hsiou *et al.* (2009); Pujos *et al.* (2009)
Plesiolacerta	*eratosthenesi*	Lacertidae	Frontal, left dentary and maxilla	Late Oligocene	(?)	Germany	Cernansky & Auge (2013)
Pseudoeumeces	*cadurcensis*	Lacertidae	Incomplete dentaries and maxilla	Oligocene	(?)	MNHN	Auge & Hervet (2009)
Purbicella	*ragei*	Lacertidae	Incomplete skull	Early Cretaceous	(?)	MNHUK	Evans *et al.* (2012)
Tarrotosaurus	*anoualensis*	Unresolved	Incomplete left dentary with 10 teeth	Early Cretaceous	(?)	MNHM MCM 140	Broschinski & Sigogneau-Russell (1996)
Tchingisaurus	*multivagus*	Teiidae	Incomplete mandible with teeth	Late Cretaceous	(?)	PIN 3142/309	Keqin & Norell (2000)
Tianyusarus	*zhengi*	Unresolved (Borioteiidea)	Skull and mandible in articulation with cervical vertebrae	Late Cretaceous	(?)	Shandong Tianyu Natural Museum 05-f702	Mo *et al.* (2010); Lu *et al.* (2008)
SCINCOIDEA							
Aethesia	*frangens*	Scincidae	Mandible only	Early Pliocene to early Pleistocene	(?)	South Australian Museum	Hutchinson & Scanlon (2009)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
SCINCOIDEA (continued)							
Catactegenys	*solaster*	Xantusiidae	Partial right speniodentary	Late Campanian (Cretaceous)	(?)	TMM 43057-287	Nydam *et al.* (2013)
Contogenys	*sloani*	Scincidae	Partial dentaries	Middle Paleocene	(?)	PU 27035 17036a 17036b	Estes (1976)
Dimekodontosaurus	*madseni*	Unresolved	Left mandible, 3D	Cretaceous	(?)	OMMH	Nydam (2002)
Foliesaurus	*boutersemensis*	Unresolved	Incomplete right dentary	Early Oligocene	(?)	IRSNB R245	Auge & Smith (2009)
Hymenosautus	*clarki*	Unresolved	Incomplete skull with mandibles	Late Cretaceous	(?)	IGM 3/53	Keqin & Norell (2000)
Palaeoxantusia	*fera*	Xantusiidae	Broken left splenio-dentary; dentaries	Eocene	(?)	PU 16775/16776	Schatzinger (1980); Estes (1976)
Parmeosaurus	*scutatus*	Unresolved	Well preserved, articulared post cranial skeleton	Late Cretaceous	(?)	IGM 3/138	Keqin & Norell (2000)
Sauriscus	*sp.*	Scincidae	Right dentary	Late Cretaceous	(?)	TMM43057-286	Rowe (1992)
ANGUIMORPHA							
Chianghsia	*nankangensis*	Unresolved (Monstersauria)	Partial skull and lower jaws	Late Cretaceous	(?)	NHMG 009318	Mo *et al*. (2012)
Chometokadmon	*fitzingeri*	Unresolved	Whole skeleton, very fragmented	Early Cretaceous	(?)	MPN 539	Evans *et al.* (2006)
Dalinghosaurus	*longidigitus*	Unresolved (Carusioidea)	Several partial skeletons	Early Cretaceous	(?)	IVPP	Evans & Wang (2005)
Estesia	*mongoliensis*	Unresolved (Monstersauria) (Varanoidea)	3D skull with mandible	Late Cretaceous	(0)	IGM 1/14;3/196;3/760	Yi & Norell (2013); Norell & Keqin (1997)
Exostinus	*lacensis*	Xenosauridae	Partial maxilla	Middle Paleocene	(?)	PU 16780	Estes (1976)
Gobiderma	*pulchrum*	Unresolved (Monstersauria)	Incomplete skulls	Late Cretaceous	(?)	ZPAL MgR III/64/65/66	Conrad *et al.* (2011)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
ANGUIMORPHA (continued)							
Headonhillia	*parva*	Anguidae	Incomplete parietal	Late Eocene	(?)	BMNH R13533	Klembara & Green (2010)
Melanosaurus	*maximus*	Anguidae	N/A	N/A	(1)	AMNH	Conad (2008); Conrad & Norell (2008)
Merkurosaurus	*ornatus*	Unresolved	Skull roof bones, dentary, osteoderms	Early Miocene	(?)	National Museum, Prague PB02018	Klembara (2008)
Ophisauriscus	*sp.*	Anguidae	N/A	N/A	(1)	Unknown	Conrad (2008)
Pancelosaurus	*piger*	Anguidae	Partial dentaries, maxilla, teeth	Middle Paleocene	(?)	PU 17034	Estes (1976)
Parophisaurus	*pawneesis*	Anguidae	Nearly complete skull, "osteoderms" in orbit; coded as present by Conrad	Middle Oligocene	(1)	UMMP 27179	Conrad (2008); Sullivan (1987)
Peltosaurus	*granulosus*	Anguidae	N/A	N/A	(1)	AMNH FR1710/8138/ 42913 FMNH 27072 USNM 13870 YPM VP 001060/001061/ 011393	Gauthier *et al.* (2012)
Placosaurus	*ragei*	Anguidae	Incomplete left dentary	Early to late Eocene	(?)	Belgium	Sullivan *et al.* (2012)
Proglyptosaurus	*heurfanensis*	Anguidae	Distorted skull	Early Eocene	(?)	AMNH 7431	Sullivan (1989)
Pseudopus	*laurillardi*	Anguidae	Parietal, maxilla, pterygoid, lower jaw, 2 vertebraw	Miocene	(?)	NMA 2009/1/2060	Klembara *et al.* (2010)
Saniwa	*ensidens*	Unresolved (Varanoidea)	Complete, articulated, dorsal view	Middle Eocene	(?)	FMNH PR 2378	Rieppel & Grande (2007)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
ANGUIMORPHA (continued)							
Varanus	*amnhophili*	Varanidae	Partial brain case, skull roof fragments, partial right mandible, partial clavicle	6.9 to 7.6 MYO	(?)	AMNH FR 30630	Conrad *et al*. (2012)
AMPHISBAENIA + DIBAMIDAE							
Cryptolacerta	*hassiaca*	Unresolved (sister taxa to Amphisbaenia)	Nearly complete, missing distal tail, reduced orbits, crushed head region	Eocene	(?)	Germany	Müller *et al*. (2011)
Dyticonastis	*rensbergeri*	Rhineuridae	Complete skull	Eocene	(0)	UCMP 76881	Berman (1976)
Hyporhina	*sp.*	Rhineuridae	Skull missing quadrate and part of squamosal; orbit region complete	Oligocene	(?)	Unknown	Taylor (1951)
Jepsibaenia	*sp.*	Rhineuridae	Poorly preserved and distorted skull	Early Eocene	(?)	Unknown	Vanzolini (1951); Gilmore & Jepson (1945)
Leiosaurus	*marelli*	Amphisbaenidae	14 vertebrae	Middle Pleistocene	(?)	PVL 906	Torres & Montero (1998)
Listromyceter	*leakeyi*	Amphisbaenidae	Skull lacking occiput and lower jaw	Lower Miocene	(?)	Natural History Museum of Palaeontology R8292	Charig & Gans (1990)
Lophocranion	*rusingense*	Amphisbaenidae	Two incomplete skulls, portion of braincase	Lower Miocene	(?)	BMNH R8293 R8294	Charig & Gans (1990)
Macrorhineura	*sp.*	Rhineuridae	Partial skull (missing orbital area) and skeleton	Miocene	(?)	Unknown	Macdonald (1970)
Oligodontosaurus	*wyomingensis*	Rhineuridae	Left ramus with complete dentition	Paleocene	(?)	Princeton 14246	Gilmore (1942)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
AMPHISBAENIA + DIBAMIDAE (continued)							
Oligorhineura	*sternbergii*	Rhineuridae	Partial skull and articulated lower jaw	Oligocene	(?)	SMM; HMNS 1191	Dickson (1997)
Ototriton	*sp.*	Rhineuridae	Well preserved skull, missing quadrate region	Eocene	(?)	Unknown	Loomis (1919)
Pseudorhineura	*sp.*	Rhineuridae	Skull, lower jaws, incomplete ribs, 23 vertebrae; fossil extremely weathered	Oligocene	(?)	Unknown	Vanzolini (1951); Gilmore (1938)
Sineoamphisbaena	*hexatabularis*	Unresolved; may be sister taxon to Amphisbaenia	Skull, missing mandible, 19 vertebrae, ribs	Late Cretaceous	(?)	IVPP V10593 (holotype)	Wu *et al*. (1996)
Spathorrhynchus	*natronicus*	Rhineuridae	Complete skull with mandibles and articulated trunk vertebrae (19)	Early Oligocene	(0)	AMNH 8677	Berman (1977, 1973)
Tamaulipasaurus	*morenoi*	Unresolved	Nearly complete skull, missing tip of rostrum	Early or middle Jurassic	(?)	IGM 6620	Clark (1994)
SERPENTES							
Acrochordus	*dehmi*	Acrochordidae	Vertebrae and partial ribs	Miocene	(?)	UCMP 129585	West *et al*. (1991)
Ameiseophis	*robinsoni*	Colubridae	Trunk vertebrae	Middle Miocene	(?)	UCM 30222	Holman (1976)
Barvioboa	*hermi*	Boidae	4 trunk vertebrae	Miocene	(?)	SGDB 7408/MI-1-4	Ivanov & Bohme (2011); Ivanov (2002)
Calamagreas	*weigeli*	Boidae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)
Charina	*prebottae*	Boidae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
SERPENTES (continued)							
Colombophis	*portai*	Anilldae	Pre-cloacal vertebrae	Neogene	(?)	AMU-CURS 154	Head *et al.* (2006)
Coluber	*dolnicensis* *constrictor* *hungaricus*	Colubridae	1 left dentary; vertebrae	Miocene	(?)	SGDB 7408/MI-9 BSPG 1997 XIII 519, 520 BSPG 1997 XIII 541, 542-550	Ivanov & Bohme (2011); Ivanov (2002); Venczel (1994)
Crotalus	*horridus*	Crotalidae	Vertebrae	Late Pleistocene	(?)	CMS-680	Holman (1974)
Dakotaephis	*greeni*	Colubridae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)
Dinilysia	*patagonica*	Unresolved (basal Serpentes)	Poorly preserved skull fragments	Late Cretaceous	(?)	MLP 26-410	Zaher & Scanferla (2012); Caldwell & Albino (2003)
Elaphe	*kohfidschi* *vulpine* *parreyssii*	Colubridae	Mid-trunk vertebrae; lumbar vertebrae; left dentary	Miocene to Late Pleistocene	(?)	NHS 1984/96 CMS-679 SDGB Ah-198	Ivanov (2002); Bechmayer & Szyndlar (1984); Holman (1974)
Eoanilius	*oligocenicus*	Aniliidae	Mid-trunk vertebra	Oligocene	(?)	SMNS 58196/2	Szyndlar (1994)
Epicrates	*sp.*	Unresolved (Macrostomata)	Incomplete mid-trunk vertebrae	Quaternary	(?)	Museu Dom Jose	Hsiou *et al.* (2012)
Haaiophis	*terrascantus*	Unresolved	Complete and well preserved skull with some dorsoventral compression	Middle Cretaceous	(0)	Unknown	Rieppel *et al.* (2003)
Helagras	*orellanensis*	Unresolved	Trunk vertebrae	Middle Oligocene	(?)	UKNHVP 49128	Holman (1983)
Liasis	*dubudingala*	Boidae	Vertebrae	Early Pliocene	(?)	Queensland Museum	Scanlon & Mackness (2002)
Micrurus	*gallicus*	Elapidae	Precaudal vertebrae	Miocene	(?)	BSPG 1997 XIII 642	Ivanov & Bohme (2011)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
SERPENTES (continued)							
Naja	*austriaca*	Elapidae	Basiparasphenoid	Pontian (Miocene)	(?)	NHM 1984/98	Bachmayer & Szyndlar (1985)
Najash	*rionegrina*	Unresolved (Ophidia)	Left dentary, nearly complete and articulated postcranial skeleton	Late Cretaceous	(?)	Argentina	Palci *et al*. (2013); Apesteguia & Zaher (2006)
Nanus	*planicarinatus*	Colubridae	6 trunk vertebrae	Pontian (Miocene)	(?)	NHM 1984/97	Bachmayer & Szyndlar (1985)
Natrix	*longivertebrata* *sipedon* *sansaniensis* *merkurensis*	Colubridae	Vertebrae; compound bones	Late Pliocene; Late Pleistocene; Miocene	(?)	CMS0677 SGDB Ah-291-295 AGDB Ah-313	Ivanov (2002); Bechmayer & Szyndlar (1984); Holman (1974)
Nidophis	*insularis*	Madtsoiidae	Mid-trunk vertebrae		(?)	LPB v.547/1	Vasile *et al*. (2013)
Ogmophis	*miocompactus*	Boiidae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)
Pachyophis	*woodwardi*	Pachyophiidae (Ophidia)	Disarticulated skull, articulated post-cranium skeleton	Cretaceous	(?)	Vienna A3919	Lee *et al*. (1999)
Palaeophis	*virginianus* *sp.*	Palaeophiidae	Vertebrae	Early Eocene	(?)	MSUVP 1191 VAS 1001-1005	Rage *et al*. (2008); Holman & Case (1988)
Paracoluber	*storei*	Colubridae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)
Procerophis	*shanii*	Unresolved	Vertebrae	Eocene	(?)	VAS 1014	Rage *et al*. (2008)
Pterosphenus	*schucherti*	Palaeophiidae	Vertebrae	Early Eocene	(?)	VAS 1009	Rage *et al*. (2008)
Python	*molurus*	Pythonidae	Vertebrae	Miocene	(?)	BSPG 1997 XIII 507, 508	Ivanov & Bohme (2011)
Russellophis	*tenuis*	Russellophiidae	Vertebrae	Eocene	(?)	VAS 1013/1043	Rage *et al*. (2008)

Table A3.1. Continued

Genus	Species	Family	Condition	Age	Code	Location	Source
SERPENTES (continued)							
Salvadora	*paleolineata*	Colubridae	Trunk vertebrae	Middle Miocene	(?)	Unknown	Holman (1976)
Simoliophis	*libycus*	Simoliopheidae	Mid-trunk vertebrae	Late Cretaceous	(?)	ZIN PC 2/31	Nessov *et al.* (1998)
Tallahattaophis	*dunni*	Boidae	Trunk vertebrae	Early-middle Eocene	(?)	MSUVP 1189	Holman & Case (1988)
Taxasophis	*galbreathi*	Colubridae	Trunk vertebrae	Middle Oligocene	(?)	MSUP 1038	Holman (1984)
Texasophis	*meini* *bohemiacus*	Colubridae	Trunk vertebrae	Miocene Oligocene	(?)	BSPG 1997 XIII 554 SMNS 57723/1-3,5	Ivanov & Bohme (2011); Szyndlar (1994)
Vipera	*sp.* *sp.* *aspis*	Viperidae	Vertebrae, 1 basioccipital	Early Pliocene Miocene	(?)	IMEDEA 90113/90116 SGDB Ah-610-612	Bailon *et al.* (2010); Ivanov (2002); Bechmayer & Szyndlar (1984)
Wonambi	*sp.*	Madtsoniidae	Vertebrae, partial skulls from several specimens	Pleistocene	(?)	Unknown	Scanlon & Lee (2000)
Yurlunggur	*sp.*	Madtsoniidae	Dentary, right maxilla, frontal, articulated but partial brain case	Late Oligocene	(?)	QMF 45217/45073/45388/45111	Scanlon (2006)

Appendix B: Raw data for sclerotic ring measurements (inner and outer diameters)

Table B.1. Genus and species for each specimen measured at the Smithsonian Museum of Natural History (USNM) and the Museum of National History UK (NMHUK). The maximum inner (ID) and outer (OD) diameters were measured using either an ocular micrometer or digital calipers. Whenever possible the collection location and number, sex, and body length (snout-vent, SV) were additionally recorded. N=100

Genus	**Species**	**Location**	**Sex**	**Body length (mm SV)**	**Max. OD (mm)**	**Max. ID (mm)**	**Collection number**
IGUANIDAE							
Cyclura	*nubila caymanensis*	Cayman Islands	Unknown	Disarticulated	15.5	7.5	None
GEKKONIDAE							
Cosymbotus	*platyurus*	Negros Island Polillo Island (Philippines)	Male (4)	51.0 54.0 59.0 56.0	3.5 4.1 4.1 3.8	2.3 2.7 2.9 2.6	USNM 305917 USNM 509371 USNM 509370 USNM 507614
Gehyra	*multilata* *oceanica*	Mindora Island Negros Island (Philippines) Ngeaur Island Babeldaob Island Ngkesill Island (Palau Islands) Pohnpei Island	Male (4) Female (2)	Male: 56.0 55.0 92.0 Disarticulated Female: 77.0 96.0	Male: 4.1 4.2 5.8 4.6 Female: 5.4 6.5	Male: 3.0 3.1 4.6 3.4 Female: 4.3 4.7	USNM 507617 USNM 305921 USNM 512277 USNM 507564 USNM 498348 USNM 559790
Gekko	*sp.* *gecko*	Babeldaob Island Beliliou Island (Palau Islands) Palawan Island (Philippines)	Male (4) Female (1) Unknown (1)	Male: 117.0 Disarticulated 170.0 140.0 Female: 113.0 Unknown: 142.0	Male: 8.0 7.5 11.7 10.1 Female: 8.1 Unknown: 10.5	Male: 6.1 5.9 8.8 5.9 Female: 7.2 Unknown: 8.9	USNM 498340 USNM 559791 USNM 498341 USNM 287349 USNM 287350 USNM 287351

Table B.1. Continued

Genus	Species	Location	Sex	Body length (mm SV)	Max. OD (mm)	Max. ID (mm)	Collection number
GEKKONIDAE (continued)							
Hemidactylus	*brookii* *frenatus*	Luzon Island Polillo Island (Philippines) Oreor Island (Palau Islands)	Male (2) Female (4)	Male: 54.0 51.0 Female: 57.0 50.0 49.0 44.0	Male: 4.3 4.4 Female: 3.8 3.6 4.0 3.4	Male: 3.3 3.3 Female: 2.9 2.9 3.2 2.4	USNM 507635 USNM 509339 USNM 509405 USNM 507646 USNM 499251 USNM 499257
Lepidodactylus	*christiani* *moestus*	Negros Island (Philippines) Ngemelachel Island (Palau Islands)	Female (3)	48.0 Disarticulated 39.0	3.8 2.6 2.9	3.0 1.6 2.1	USNM 305929 USNM 559794 USNM 498355
Perochirus	*scutellatus*	Kapingmarangi Atoll	Male (5)	112.0 122.0 117.0 115.0 116.0	7.1 6.9 7.7 7.3 6.4	6.2 5.3 6.0 5.6 4.9	USNM 518823 USNM 518824 USNM 518825 USNM 518828 USNM 518829
Pseudogekko	*smaragdinus*	Polillo Island (Philippines)	Male (1)	61.0	3.9	2.8	USNM 497607
SPHAERODACTYLIDAE							
Gonatodes	*hasemani* *albogularis fuscus* *humeralis*	Brazil Panama	Male (2) Female (3)	Male: 42.0 37.0 Female: 45.0 41.0 36.5	Male: 2.6 2.5 Female: 2.7 2.6 2.6	Male: 1.7 1.7 Female: 1.4 1.7 1.6	USNM 292400 USNM 313830 USNM 319194 USNM 290889 USNM 290891
LACERTIDAE							
Lacerta	*viridis*	France	Male (1) Female (1)	Male: 105.0 Female: 125.0	Male: 4.1 Female: 4.5	Male: 2.3 Female: 2.6	USNM 284453 USNM 284452

Table B.1. Continued

Genus	Species	Location	Sex	Body length (mm SV)	Max. OD (mm)	Max. ID (mm)	Collection number
LACERTIDAE (continued)							
Meroles	*squamulosa*	Unknown	Unknown	56.4	3.5	2.3	MNHUK 1970.1712
Mesalina	*brevirostris*	Unknown	Unknown	Unknown	2.0	0.8	MNHUK 1969.8
Ophisops	*leschenaultii*	Unknown	Unknown	32.9	2.3	1.7	MNHUK 1969.6
Podarcis	*muralis* *tauricus* *sicula*	France Unknown	Female (1) Unknown (4)	Female: 42.0 Unknown: 39.0 54.0 37.0 46.0	Female: 2.7 Unknown: 2.3 3.3 3.0 4.2	Female: 1.1 Unknown: 1.3 1.5 2.2 1.8	USNM 284454 MNHUK1969.42 MNHUK1969.43 MNHUK1969.33 MNHUK1969.40-41
Zootoca	*vivipara*	Purchased from dealer	Unknown	Unknown	1.7	1.2	MNHUK 1969.5
TEIIDAE							
Ameiva	*ameiva*	Brazil	Male (1) Female (5)	Male: 143.0 Female: 124.0 116.0 118.0 116.0 131.0	Male: 8.8 Female: 6.2 5.7 5.6 5.9 6.0	Male: 4.1 Female: 3.6 3.1 3.5 3.8 3.7	USNM 292427 USNM 292428 USNM 292429 USNM 292425 USNM 292422 USNM 292421
Cnemidophorus	*sexlineatus*	Walt Disney World, Florida	Male (4) Female (2)	Male: 66.0 65.0 56.0 56.0 Female: 58.0 63.0	Male: 3.3 2.9 3.2 2.6 Female: 3.5 3.1	Male: 1.9 1.7 1.8 1.6 Female: 1.9 1.9	USNM 541681 USNM 541693 USNM 541686 USNM 541695 USNM 541698 USNM 541699

Table B.1. Continued

Genus	Species	Location	Sex	Body length (mm SV)	Max. OD (mm)	Max. ID (mm)	Collection number
TEIIDAE (continued)							
Kentropyx	*calcarata*	Brazil	Male (1) Female (1)	Male: 96.0 Female: 82.0	Male: 5.0 Female: 3.9	Male: 2.8 Female: 2.9	USNM 292411 USNM 292412
Neustricurus	*sp.*	Peru	Male (1)	75.0	3.3	1.6	USNM 346413
GERRHOSAURIDAE							
Gerrhosaurus	*major*	Unknown	Unknown	Unknown	11.7	4.3	USNM 279863
SCINCIDAE							
Ablepharus	*deserti*	Tschimas	Unknown	Unknown	1.5	1.2	MNHUK 79.11.14.215
Brachymeles	*boulengeri* *boulengeri taylori*	Polillo Island Negros Island (Philippines)	Male (3) Female (1)	Male: 82.0 91.0 69.0 Female: 73.0	Male: 2.2 2.5 1.6 Female: 1.4	Male: 1.0 1.1 1.1 Female: 0.8	USNM 509414 USNM 305967 USNM 305968 USNM 305969
Carlia	*ailanpalai* *tutela*	Mariana Islands Palau Islands	Male (4) Female (2)	Male: 59.0 69.0 54.0 51.0 Female: 62.0 44.0	Male: 3.8 2.8 3.4 3.1 Female: 3.3 2.5	Male: 1.6 1.8 1.5 1.5 Female: 1.5 1.3	USNM 323690 USNM 323691 USNM 323679 USNM 507535 USNM 507539 USNM 507540
Cryptoblepharus	*poecilopleurus*	Phoenix Islands	Female (1)	40.0	2.9	1.4	USNM 306215
Emoia	*caeruleocauda* *boettgeri* *cyanura*	Mariana Islands Cook Islands Caroline Islands	Male (5) Female (1)	Male: 53.0 52.0 49.0 45.0 52.0 Female: 53.0	Male: 3.9 3.4 3.2 2.9 3.4 Female: 3.3	Male: 1.4 1.4 1.5 1.3 1.4 Female: 1.2	USNM 323701 USNM 323700 USNM 507565 USNM 512282 USNM 249752 USNM 249754

Table B.1. Continued

Genus	Species	Location	Sex	Body length (mm SV)	Max. OD (mm)	Max. ID (mm)	Collection number
SCINCIDAE (continued)							
Eumeces	*inexpectatus*	Florida North Carolina South Carolina	Male (3) Female (1) Unknown (1)	Male: 74.0 67.0 71.0 Female: 76.0 Unknown: 72.0	Male: 3.3 3.2 3.9 Female: 3.2 Unknown: 3.5	Male: 1.8 1.6 1.9 Female: 1.7 Unknown: 1.7	USNM 332754 USNM 541647 USNM 313904 USNM 541663 USNM 541650
Lamprolepis	*smaragdina*	Babeldaod Island Ngeaur Island (Palau Islands) Ngemelachel Island	Male (2) Female (2)	Male: 98.0 99.0 Female: 94.0 Unknown	Male: 5.6 4.9 Female: 5.2 5.5	Male: 3.0 2.9 Female: 2.5 2.2	USNM 507551 USNM 507549 USNM 507553 USNM 559804
Lampropholis	*delicata*	Hawaii	Male (1)	39.0	2.6	0.9	USNM 279295
Mabuya	*cumingi* *gravenhorsti*	Luzon Island (Philippines) Madagascar	Male (2) Female (2) Unknown (1)	Male: 81.0 79.0 Female: 51.0 50.0 Unknown: Unknown	Male: 4.7 4.4 Female: 2.6 3.2 Unknown: 3.0	Male: 1.8 2.0 Female: 1.0 0.9 Unknown: 1.4	USNM 499004 USNM 498999 USNM 336441 USNM 336440 USNM 499011
Scincella	*lateralis*	Walt Disney World, Florida	Female (3)	46.0 46.0 39.0	1.7 1.4 2.2	1.2 0.8 1.1	USNM 541672 USNM 541669 USNM 541668

Appendix C: Statistical analyses

Table C.1. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum outer diameter of the sclerotic ring in the following families assessed: Gekkonidae (n=31), Sphaerodactylidae (n=5), Lacertidae (n=11), Teiidae (n=15), and Scincidae (n=36).

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Gekkonidae	0.215	31	0.001	0.866	31	0.003
Sphaerodactylidae	0.300	5	0.161	0.883	5	0.325
Lacertidae	0.151	11	0.200	0.950	11	0.638
Teiidae	0.203	15	0.097	0.880	15	0.047
Scincidae	0.149	36	0.041	0.952	36	0.120

Table C.2. Kruskal-Wallis test for statistical differences in the maximum outer diameter for the five families analyzed here: Gekkonidae, Sphaerodactylidae, Lacertidae, Teiidae, and Scincidae.

Family	**N**	**Median**	**Average rank**	**Z**
Gekkonidae	31	4.400	71.0	5.09
Sphaerodactylidae	5	2.600	17.9	-1.89
Lacertidae	11	3.000	34.2	-3.54
Teiidae	15	3.900	58.8	-2.55
Scincidae	36	3.200	36.2	1.38
Overall:	98		49	
H=36.62 | DF=4 | P<0.001				

Table C.3. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum inner diameter of the sclerotic ring in the following families assessed: Gekkonidae (n=31), Sphaerodactylidae (n=5), Lacertidae (n=11), Teiidae (n=15), and Scincidae (n=36).

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Gekkonidae	0.221	31	0.001	0.897	31	0.006
Sphaerodactylidae	0.330	5	0.079	0.877	5	0.294
Lacertidae	0.163	11	0.200	0.955	11	0.708
Teiidae	0.261	15	0.007	0.866	15	0.029
Scincidae	0.147	36	0.046	0.903	36	0.004

Table C.4. Kruskal-Wallis test for statistical differences in the maximum inner diameter for the five families analyzed here: Gekkonidae, Sphaerodactylidae, Lacertidae, Teiidae, and Scincidae.

Family	N	Median	Average rank	Z
Gekkonidae	31	3.300	77.5	6.64
Sphaerodactylidae	5	1.700	34.2	-1.24
Lacertidae	11	1.700	34.8	-1.82
Teiidae	15	2.800	61.0	1.70
Scincidae	36	1.400	27.2	-5.92
Overall:	98		49.5	
H=59.17 | DF=4 | P<0.001				

Table C.5. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum outer diameter of the sclerotic ring in photopic (n=34) and scotopic (n=25) species.

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Scotopic	0.264	25	0.000	0.823	25	P<0.001
Photopic	0.206	74	0.000	0.768	74	P<0.001

Table C.6. Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in photopic (n=34) versus scotopic (n=25) species.

	N	**Median**	
Scotopic	25	4.200	P<0.001
Photopic	34	3.300	

Table C.7. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum inner diameter of the sclerotic ring in photopic (n=34) and scotopic (n=25) species.

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Scotopic	0.266	25	0.000	0.840	25	0.001
Photopic	0.245	74	0.000	0.783	74	0.000

Table C.8. Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in photopic (n=34) versus scotopic (n=25) species.

	N	**Median**	
Scotopic	25	3.200	P<0.001
Photopic	34	1.700	

Table C.9. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum outer diameter of the sclerotic ring in fossorial (n=7) and non-fossorial (n=92) species.

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Fossorial	0.211	7	0.200	0.886	7	0.254
Non-fossorial	0.196	92	0.000	0.796	92	0.000

Table C.10. Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in fossorial (n=7) and non-fossorial (n=92) species.

	N	**Median**	
Fossorial	7	1.700	P<0.001
Non-fossorial	92	3.800	

Table C.11. Kolmogorav-Smirnov and Shapiro-Wilk tests for normality for the maximum inner diameter of the sclerotic ring in fossorial (n=7) and non-fossorial (n=92) species.

	Kolmogorav-Smirnov			**Shapiro-Wilk**		
	Statistic	**df**	**Sig.**	**Statistic**	**df**	**Sig.**
Fossorial	0.278	7	0.108	0.845	7	0.110
Non-fossorial	0.160	92	0.000	0.827	92	0.000

Table C.12. Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in fossorial (n=7) and non-fossorial (n=92) species.

	N	**Median**	
Fossorial	7	1.100	P<0.001
Non-fossorial	92	2.200	

Table C.13. Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in species that are below the median SV length and scotopic (n=14), and below the median SV length and photopic (n=32).

	N	**Median**	
Below median and scotopic	14	3.9000	P<0.001
Below median and photopic	32	2.9500	

Table C.14. Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in species that are above the median SV length and scotopic (n=14), and above the median SV length and photopic (n=32).

	N	**Median**	
Above median and scotopic	8	8.050	P<0.001
Above median and photopic	36	4.250	

Table C.15. Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in species that are below the median SV length and scotopic (n=14), and below the median SV length and photopic (n=32).

	N	**Median**	
Below median and scotopic	14	2.9000	P<0.001
Below median and photopic	32	1.4500	

Table C.16. Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in species that are above the median SV length and scotopic (n=14), and above the median SV length and photopic (n=32).

	N	**Median**	
Above median and scotopic	8	6.000	P<0.001
Above median and photopic	36	2.400	

Table C.17. Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in species that are below the median SV length and non-fossorial (n=42), and below the median SV length and fossorial (n=3).

	N	**Median**	
Below median and non-fossorial	42	3.3500	P<0.001
Below median and fossorial	3	1.7000	

Table C.18 Mann-Whitney test for significant differences between the maximum outer diameter of the sclerotic ring in species that are above the median SV length and non-fossorial (n=42), and above the median SV length and fossorial (n=3).

	N	**Median**	
Above median and non-fossorial	40	5.300	P<0.001
Above median and fossorial	4	1.900	

Table C.19. Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in species that are below the median SV length and non-fossorial (n=42), and below the median SV length and fossorial (n=3).

	N	**Median**	
Below median and non-fossorial	42	1.7000	P<0.001
Below median and fossorial	3	1.1000	

Table C.20 Mann-Whitney test for significant differences between the maximum inner diameter of the sclerotic ring in species that are above the median SV length and non-fossorial (n=42), and above the median SV length and fossorial (n=3).

	N	**Median**	
Above median and non-fossorial	40	2.950	P<0.001
Above median and fossorial	4	1.050	

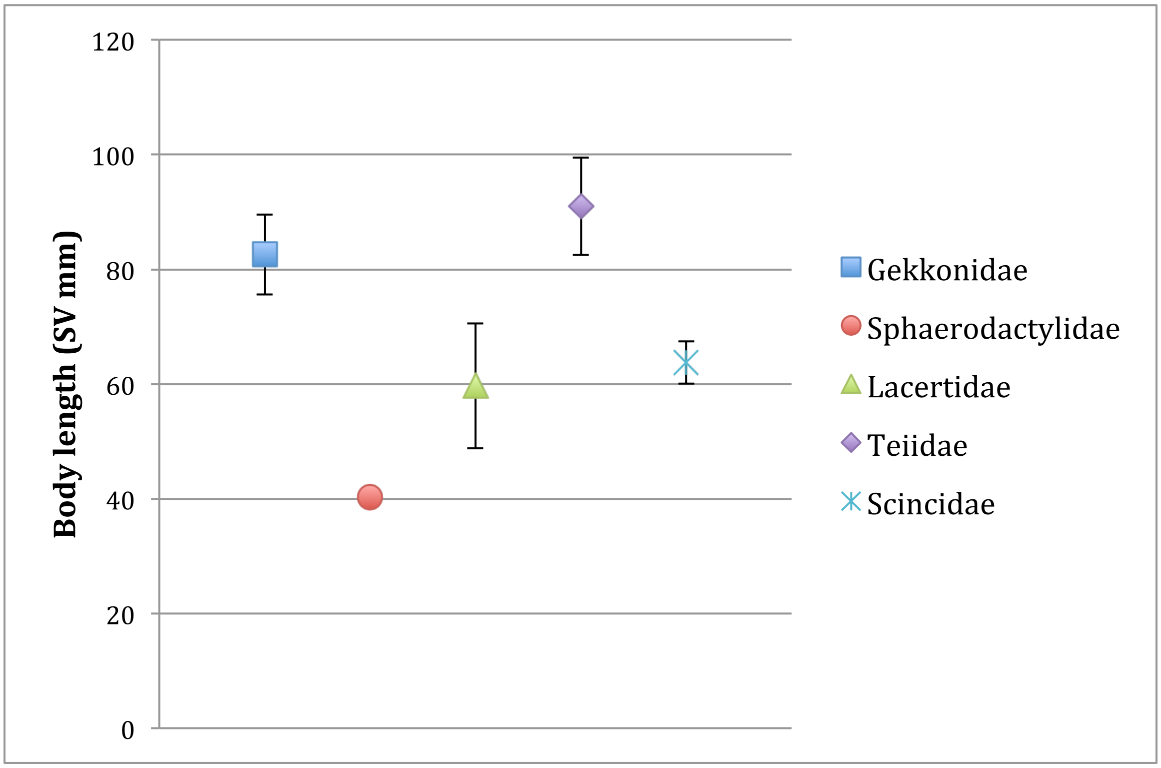

Figure C.1. Mean body length and standard error of the mean for each of the families examined here (n=100).