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Convergent evolution of body shape in squamate reptiles

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Abstract

Convergent evolution is a common pattern in nature, with many documented examples ranging from molecular and genomic scales to organismal and possibly to ecosystem scales. Although there are many documented examples of convergence, methods for formal testing of convergence are only recently being developed and studies of mechanism are less common still. Here, I construct a phylomorphospace of squamate reptile body shape and use it to test for convergence among clades and taxa that are thought to be under similar selective regimes. I test for convergence by examining the degree of overlap among convergent taxa in the phylomorphospace and by examining the direction of evolution along convergent phylogenetic branches by comparing non-convergent ancestors and convergent descendants. I find strong evidence for convergence in body shape among taxa that have evolved elongation because of fossoriality or because of inhabiting complex environments, gliding, and sand-dwelling. I find some evidence for body shape convergence in taxa that have evolved dry adhesion, but no evidence of convergence among herbivores or bipedal lizards. I also document a near perfect overlap in phylomorphospace between Iguanidae and Agamidae, but find that the analogous clades of Teiidae and Lacertidae inhabit adjacent, non-overlapping portions of the space. I discuss my findings in the context of a theoretical morphospace and make suggestions for future research.

Introduction

The extent of similarity between organisms is often striking and although the concept of homology to describe this similarity was formalised long ago (Owen 1848), it remains a central theme in studying evolution (Bergstrom & Dugatkin 2011). In an evolutionary context, similarity can arise from either homology—the retention of similarity from common ancestry—or homoplasy—the recurrence of similarity (Darwin 1859; Wake 1991; Hall 2007). Homoplasy is used interchangeably with convergent evolution and it encapsulates the phenomena of true convergence, parallelism, and reversal (Wake 1991). The latter can then be differentiated by their developmental mechanism and pattern of evolution, where convergence tends to occur via different developmental mechanisms among unrelated taxa, parallelism involves the same developmental mechanism and often more closely related taxa, and reversal can have the same or different mechanisms and typically involves the regain of a previously lost phenotype (Hall 2007).

Convergent evolution is widely recognised as an interesting biological phenomenon that is widespread and requires explanation (Stayton 2008; Losos 2011; McGhee 2011). Convergent evolution occurs at all possible levels of organisation, including genomic (Castoe *et al.* 2009), developmental (Eckalbar *et al.* 2012; Sanger *et al.* 2012), physiological (Schulte *et al.* 2000), morphological (Wiens *et al.* 2006), functional (Alfaro *et al.* 2005), and even ecological (Losos 1990b; Rosenblum 2006). Hundreds of examples of convergent evolution are now known (reviewed by McGhee 2011), but the pattern of convergence has only been described in some of these and a mechanistic understanding of why convergence happens exists in only rare cases.

Two alternative general explanations of convergent evolution have emerged. On the one hand, convergent evolution might be the product of adaptive evolution of a similar solution to a common selective regime (Losos 2011). From this perspective, not only must there be a convergent phenotype, but that phenotype must evolve in a similar ecological context with similar selective pressures (Wake 1991; Revell *et al.* 2007). A hypothesis of such adaptive convergence can be tested using functional studies or by measuring selective pressures on the convergent phenotype (Losos 2011). On the other hand, convergent evolution might be the product of constraint, where a finite set of possible phenotypes bias the direction of evolution to a few functional but suboptimal designs (Thomas & Reif 1993). This view argues that although historical contingency affects the course of evolution, the outcome is

largely determined by limitations on what can evolve (Thomas & Reif 1993). Indeed, many phenotypic innovations occur repeatedly, suggesting predictability of outcome (Vermeij 2006).

These classical explanations of convergent evolution are not mutually exclusive nor are they the only explanations (Wake 1991; Losos 2011). Recent work has shown that, given a quantitative trait and multiple species evolving through time, convergence is expected simply as a product of random evolution (Stayton 2008), demonstrating that a process like genetic drift can produce a convergent pattern (Losos 2011). Under the simple conditions of random evolution, convergence will increase with the number of taxa considered and decrease as the number of traits involved (i.e., complexity) increases (Stayton 2008). Convergent evolutionary patterns can also arise from traits evolving along genetic lines of least resistance, biogeography, and competitive interactions (Wiens *et al.* 2006; Losos 2011). All these possibilities should be treated as hypotheses to be tested (Losos 2011).

With many examples of convergent evolution having been documented (McGhee 2011), a unified approach to describing convergent patterns has emerged. Whatever its underlying mechanism, convergent evolution can be studied powerfully using a theoretical morphospace on which the convergent taxa and their ancestors are mapped, all in a phylogenetic context (Wake 1991; Thomas & Reif 1993; Stayton 2006; Revell *et al.* 2007; Stayton 2008; Losos 2011; McGhee 2011). Universal constraints in the form of physical laws put bounds on such a morphospace (Thomas & Reif 1993), and the organism's *Bauplan* further constrains the available morphospace (Wake 1991). Factors such as evolution along genetic lines of least resistance (Schluter 1996) and functional constraints can then result in uneven occupation of the morphospace (Losos 2011). Finally, the phylogeny can be mapped onto the space, resulting in a "phylomorphospace" (Sidlauskas 2008) that can readily be used to study convergent evolution.

With a phylomorphospace, patterns of convergent evolution can be identified by comparing ancestors that are not convergent to descendants that are (Stayton 2006; Hall 2007; Revell *et al.* 2007). In this context, convergence can be defined as occurring when two taxa evolve to be more similar to one another than their ancestors were (Stayton 2008). Stayton (2006) uses the phylomorphospace approach to distinguish three patterns of convergence: (1) convergent species evolving to occupy the same area of morphospace; (2) convergent species evolving towards the same area of morphospace, but

occupying different areas; and (3) convergent species evolving in the same direction in morphospace, but not converging toward a common phenotype.

My goal in this study is to test the hypothesis that convergent evolution has occurred in the body shape of squamate reptiles in several situations where convergent evolution has been predicted or assumed but often not tested. I then describe the patterns of convergence that I identify. With >8400 species, a cosmopolitan distribution, and species filling every conceivable niche outside of arctic regions (Pough *et al.* 2004; Uetz *et al.* 2007), squamates are an ideal clade for studying macroevolutionary patterns. Squamates contain a rich collection of examples of hypothesised convergent evolution that I test for here (see Appendix). In so doing, I neglect some examples of convergence in squamates, such as the repeated evolution of viviparity (Dunbrack & Ramsay 1989; Shine 1995; Schulte *et al.* 2000), because I would not expect them to influence body-shape evolution. Other examples of purported convergence in squamates might suggest wider patterns because they also occur in other taxa. For example, a snake-like body shape (i.e., elongate body with reduced limbs) has evolved >25 times in squamates (Wiens *et al.* 2006), but is also seen in fishes (Ward & Brainerd 2007), salamanders (Wake 1991), and mammals (Bejder & Hall 2002). Likewise, gliding has evolved at least four times in lizards (see Appendix), but has also evolved in frogs (McCay 2001), snakes (Socha & LaBarbera 2005), and mammals (Paskins *et al.* 2007). Most of the examples of convergence that I examine are in the context of a selective regime: the evolution of adhesion, bipedalism, sand-dwelling, gliding, herbivory, elongation associated with burrowing, and elongation associated with surface-dwelling (see Appendix). If body-shape convergence is indeed happening in these cases, then I would expect unrelated species that are under the same selective regime to either occupy a common area of morphospace or to be more similar to one another than their ancestors are. I also examine two general examples of clade convergence, where it has been noted that Iguanidae are broadly convergent with Agamidae (Melville *et al.* 2006) and that Teiidae are broadly convergent with Lacertidae (Miles *et al.* 2007). In both these cases, the former clade represents the New World analogue of the latter, Old World clade. Finally, I examine the famous example of *Anolis* ecomorphs and their convergence (e. g., Williams 1982).

Methods

Morphospace of squamate body shape

Before testing for convergence, I produced a morphospace to describe important aspects of squamate body shape using the raw morphometric dataset and supertree phylogeny, both of which were published in Bergmann and Irschick (2012). The dataset was collected from 2D radiographs and included the following measurements: head length (HL), body length (BL), body width (BW), hind limb length (HLL), hind limb width at thigh level (HLW), foot length including the longest toe (Foot), and the number of digits on the front (FD) and hind (HD) limbs (Bergmann & Irschick 2012). I used measurements for 636 species distributed from all clades of squamates, but with only rudimentary sampling of snakes belonging to Typhlopidae. I pruned the supertree, which originally included 1375 species (Bergmann & Irschick 2012) to include only those represented in the morphometric dataset using Mesquite v2.75 (Maddison & Maddison 2011).

To prepare the data for analysis, I natural-log transformed the morphometric variables and added two to the digit number variables (FD and HD) before transformation to avoid having zeros in the dataset. I then removed the effects of body size from the morphometric variables (but not digit number variables) in a phylogenetically informed manner (Blomberg *et al.* 2003) as implemented using the "phytools" package (Revell 2009) in R (R Development Core Team 2012). This was necessary because lizards are extremely variable in body size (three orders of magnitude) and this variation overshadowed shape variation in the analyses. I used HL as the proxy for body size because the standard measure of snout-vent or body length has undergone considerable evolution given that many squamates are elongate (Wiens & Singluff 2001; Wiens *et al.* 2006; Brandley *et al.* 2008; Siler & Brown 2011).

I analysed the size-adjusted morphometric data using an evolutionary principal component analysis (ePCA) that takes phylogeny into account again using the "phytools" package in R (Revell 2009; R Development Core Team 20122012). This approach resulted in qualitatively similar results to a regular PCA (Bergmann & Irschick 2012), but accounts for the evolutionary relatedness (non-independence) of species. I visualised the morphospace created by the first two PCs from the ePCA by plotting those PCs on a scatterplot and superimposing the phylogeny using Mesquite (Maddison & Maddison 2011).

This plotting of data and phylogeny into a common space is termed a phylomorphospace (Sidlauskas 2008).

Testing for convergence

I tested for convergence in two different ways: (1) by determining whether convergent taxa overlapped in morphospace and (2) by comparing the position of non-convergent ancestors to convergent descendants in the morphospace. Together, these approaches enabled me to determine whether convergent taxa occupied a common morphospace, evolved to be more similar than their non-convergent ancestors, or were evolving in a similar direction (Stayton 2006). I accomplished the first approach by simply plotting the phylomorphospace for the convergent taxa on a single plot and determining whether or not there was any overlap. By identifying hypothesised convergent taxa *a priori* from the literature (see Appendix), I avoided some of the circularity associated with simply testing whether or not similar-looking species were convergent (i.e., looked the same). I accomplished the second approach by reconstructing the ancestral character states for every node on the phylogeny for the first two PCs and natural-log transformed HL on the phylogeny using squared-change parsimony as implemented in the "Trace Character History" function in Mesquite (Maddison & Maddison 2011). I then extracted the values for the convergent taxa (these could be tip values or ancestral values depending on whether a species or a clade was convergent) and for their immediate ancestors that were not convergent (the parent node of each convergent taxon). To evaluate convergence using this second approach, I compared ancestor-descendant character-value pairs to elucidate direction and magnitude of evolution along the branches on which convergent evolution is hypothesised to have happened.

Results

Evolution of squamate body shape

A scree plot of variance explained by each PC of the ePCA (not shown) indicated that the first two PCs explained the majority of variation. PC-3 explained <8% of variation in the dataset and so is not considered further. The eigenvector for PC-1 (Table 1) shows that this component represents a trade-off between BL on the one hand and BW, digit numbers, and limb measure-

ments on the other, such that high values of PC-1 indicate short, wide bodies with well-developed limbs. As such, I interpret PC-1 as an index of relative elongation and limb reduction: species with high values are lizard-like and species with low values are snake-like. All body dimensions load most strongly on PC-2, whereas limb variables have much smaller loadings (Table 1). Hence, species with high PC-2 values have robust bodies, whereas those with low values have gracile bodies. I interpret PC-2 as an index of body robustness.

Table 1:
Evolutionary PCA loadings for the first two principal components (PCs), with eigenvalues and the proportion of total variance explained by each PC presented. Bold values indicate loadings that are elevated and interpreted.

Variable	PC-1	PC-2
Head width	0.071	**0.312**
Body length	**−0.125**	**0.379**
Body width	**0.142**	**0.817**
Front digits	**0.241**	−0.128
Hind digits	**0.249**	−0.124
Hind limb width	**0.294**	0.219
Hind limb length	**0.681**	−0.084
Foot length	**0.538**	−0.067
Eigenvalue	0.0045	0.0013
% explained	62.05	17.74

An examination of the phylomorphospace (Fig. 1) defined by the first two PCs indicates that most of the included species are lizard-like. Although only about 10% of extant lizards were sampled (and a negligible number of snakes), species sampling included all major lizard clades without bias based on body shape. Thus, this phylomorphospace should be indicative of lizard body-shape diversity in general. The phylomorphospace shows that most species are either lizard-like or snake-like. Although various intermediate forms do exist, they are simply a lot less frequent. In both the lizard-like and snake-like clusters, there is a range of body shapes from gracile to robust (Fig. 1). Typhlopid snakes and *Amphisbaenia* are the most robust snake-like species (Fig. 1), whereas the cordylid *Chamaesaura* is the most gracile (Fig. 1). The limbless anguids (Fig. 2A) and scincids (not shown) are variable and

intermediate in robustness. The scincids have also evolved a snake-like body shape the greatest number of times, accounting for most of the phylogeny branches crossing from left to right of the phylomorphospace (Fig. 1). snakes), species sampling included all major lizard clades without bias based on body shape. Thus, this phylomorphospace should be indicative of lizard body-shape diversity in general. The phylomorphospace shows that most species are either lizard-like or snake-like. Although various intermediate forms do exist, they are simply a lot less frequent. In both the lizard-like and snake-like clusters, there is a range of body shapes from gracile to robust (Fig. 1). Typhlopid snakes and *Amphisbaenia* are the most robust snake-like species (Fig. 1), whereas the cordylid *Chamaesaura* is the most gracile (Fig. 1). The limbless anguids (Fig. 2A) and scincids (not shown) are variable and intermediate in robustness. The scincids have also evolved a snake-like body shape the greatest number of times, accounting for most of the phylogeny branches crossing from left to right of the phylomorphospace (Fig. 1).
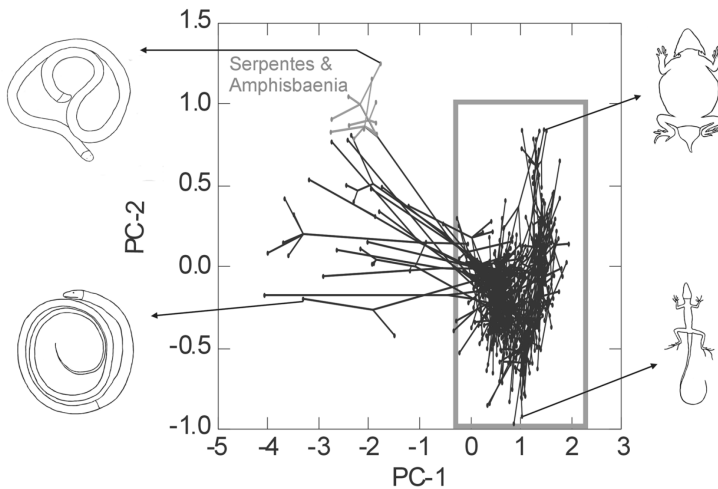

Figure 1:
The phylomorphospace of squamate body shape as defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). The phylomorphospace is shown for all 636 species sampled along with representative body shapes from the edges of the morphospace. The grey rectangle represents the area shown in Figs 3 and 4).
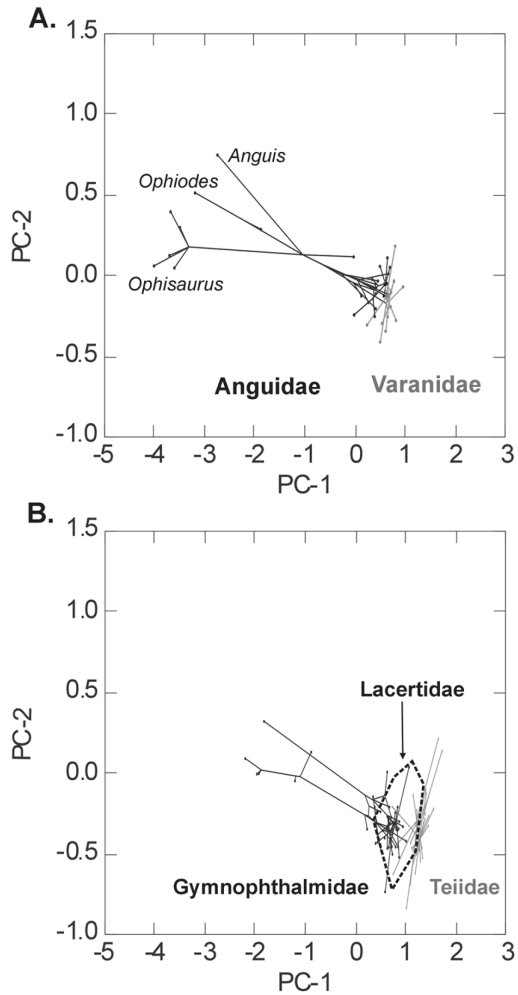
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Figure 2:
A phylomorphospace for (A) Anguidae (black) and Varanidae (grey), and (B) for Gymnophthalmidae (black), Teiidae (grey) and Lacertidae (dashed polygon). The boundaries of these plots are the same as for Fig. 1.

Among clades with only lizard-like body shapes, there is also considerable variation in body shape. Iguanidae in general are highly diversified, with the genus *Phrynosoma* having the most robust body shape of all lizards and *Anolis* being among the most gracile (Fig. 3A). The three clades of Phryno-somatinae (sand, horned, and fence lizards) are well differentiated from one another (Fig. 3B). Agamidae are similarly diverse, with *Uromastyx* and *Draco* being the most robust (the latter is not robust *per se*, but has ribs elongated into patagia; McGuire & Dudley 2005) and *Japalura* the most gracile (Fig. 4A). Finally, both major adhesive pad-bearing clades, Gekkota and *Anolis*, occupy relatively restricted areas of the phylomorphospace, coinciding with a relatively gracile body shape. It is important to note that these latter two clades occupy virtually non-overlapping, but adjacent areas of the phylomorphospace (Fig. 4B).

Convergence in squamate body shape

I use the direction of evolution in the phylomorphospace along the phylogenetic branches along which convergence is hypothesised to have occurred as the primary evidence of convergence, with convergent clade overlap being secondary, but also important (Stayton 2006). I address each example in the context of its selective regime in turn.

Dry adhesion has evolved four times independently in the taxa that I sampled: in the gekkotans Diplodactylidae and Gekkonidae, in *Anolis*, and in the skink *Prasinohaema virens* (see Appendix). None of these taxa have converged on a similar body shape as defined by my indices of elongation and robustness, but the two gekkotan clades have evolved in parallel to be more lizard-like than their ancestors (Fig. 5A). The skink and *Anolis* have also evolved in parallel to become more gracile than their ancestors (Fig. 5A). Gekkota and *Anolis* also occupy adjacent, but almost mutually exclusive areas of morphospace (Fig. 4B). The restricted areas of morphospace that these taxa occupy could instead suggest a constraint on body-shape evolution, perhaps resulting from their adhesive abilities (Bergmann & Irschick 2012). It should be noted that other examples of convergence occur within these clades (e. g. Russell 1977) such that it would be interesting to test for convergence within each.
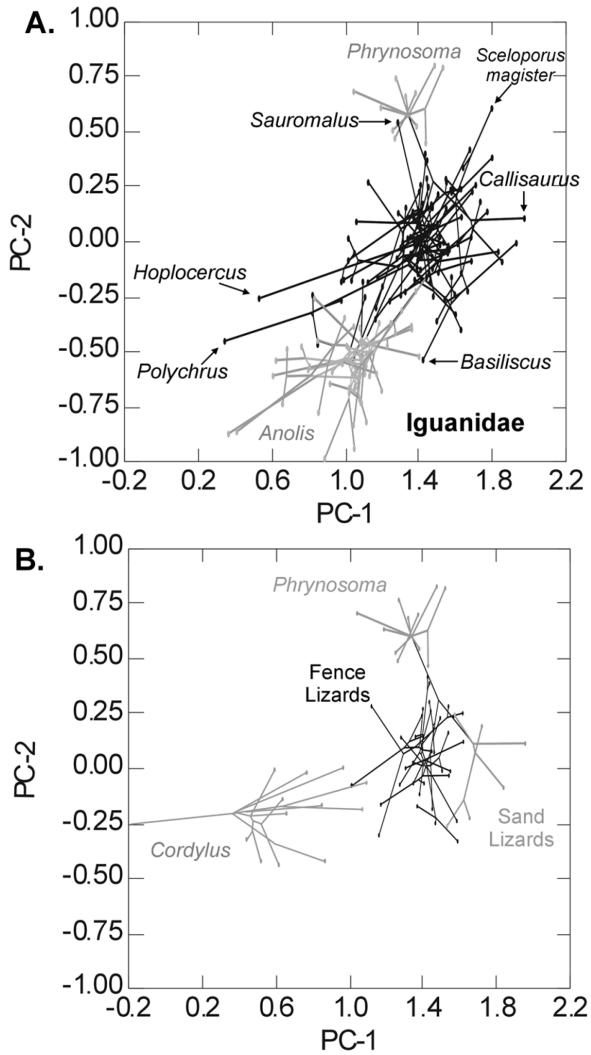
Figure 3:
A phylomorphospace for (A) Iguanidae, and for (B) Phrynosomatidae and Cordylidae, with representative species and major clades labelled. The boundaries of these plots are the same as for Fig. 1.
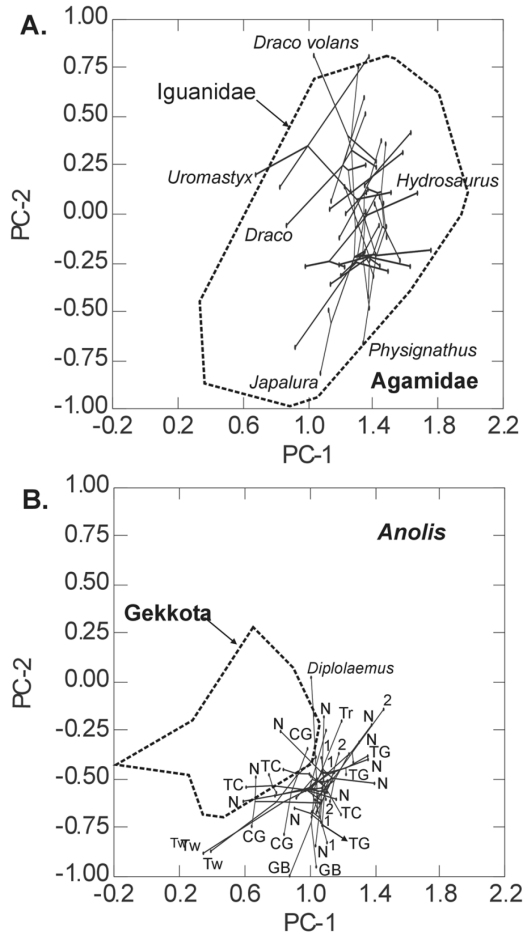
Figure 4:
A phylomorphospace for (A) Agamidae with a polygon showing the morphospace occupied by Iguanidae (Fig. 3A); representative agamid species are labelled. A phylomorphospace for (B) *Anolis* with a polygon representing the morphospace occupied by Gekkota. In (B), *Anolis* ecomorphs are labelled as follows: CG, crown giant; GB, grass-bush; TC, trunk-crown; TG, trunkground; Tr, trunk; Tw, twig; N, none (either mainland species or ones for which ecomorph classification has not been determined); 1, from Lesser Antillean islands with a single species; and 2, from Lesser Antillean islands with two species. The boundaries of these plots are shown by the grey rectangle in Fig. 1.
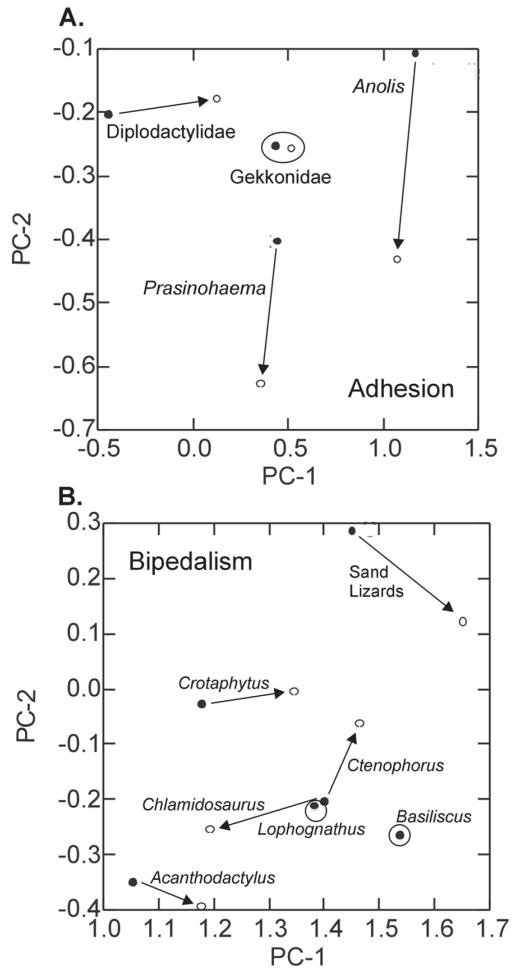
Figure 5:
Plots of of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). Large ovals indicate no evolution between the ancestor and descendent. Convergence plots are shown for (A) dry adhesion and (B) bipedalism, with putatively convergent taxa labelled.

Bipedalism has evolved six times in the taxa sampled (see Appendix). Although bipedal lizards often have long, gracile hind limbs, short front limbs, narrow pelvic girdles, short trunks, and long tails (Snyder 1962), my data show no evidence of convergence (Fig. 5B). Instead, each convergent taxon evolves in a different direction and not toward any common area in the phylomorphospace.

Sand-dwelling has evolved four times in my dataset (see Appendix) and, although the taxa have not converged morphologically, *Phrynosoma*, *Uma*, and *Lerista* have evolved in a similar direction, whereas the lacertid *Meroles* has not (Fig. 6A). The limited level of convergence in this example is unsurprising because many of these taxa use sand in different ways as exemplified by their different burying behaviours (Arnold 1995).

Gliding has evolved three times independently in the taxa that I sampled (see Appendix). The gekkonid *Ptychozoon* and the agamid *Leiolepis* have evolved in parallel to be more robust and lizard-like than their non-gliding ancestors, whereas *Draco* has evolved along a different trajectory (Fig. 6D). This might be because gliding is highly developed in *Draco*, which has a highly specialised and extreme morphology (McGuire 2003), whereas the other two taxa have relatively rudimentary patagia.

My dataset contains taxa representing eight independent instances of the evolution of herbivory. In addition to examining the first two PCs (Fig. 7A), I also considered body size (Fig. 7B) as represented by ln(HL) because it has long been thought that herbivory coincides with large body size in lizards (see references in Stayton 2006). Exceptions to this "rule" exist, particularly in small, cold-climate *Liolaemus* species (Espinoza *et al.* 2004) and I find little evidence of body shape and size convergence in these taxa (Fig. 7). This result differs from those of Stayton (2006), most likely because he was studying skull shape, which is more directly functionally relevant to herbivory than body shape. In my dataset, only the Giant Prehensile-Tailed Skink, *Corucia zebrata*, has evolved a larger body size relative to its ancestor (Fig. 7B).

Body elongation and limb reduction, or the evolution of a snake-like body shape, has evolved more than 25 times in squamates (see Appendix), but not all snake-like squamates are alike. Elongate body shapes have evolved either as long-tailed surface dwellers that often specialise in moving through dense
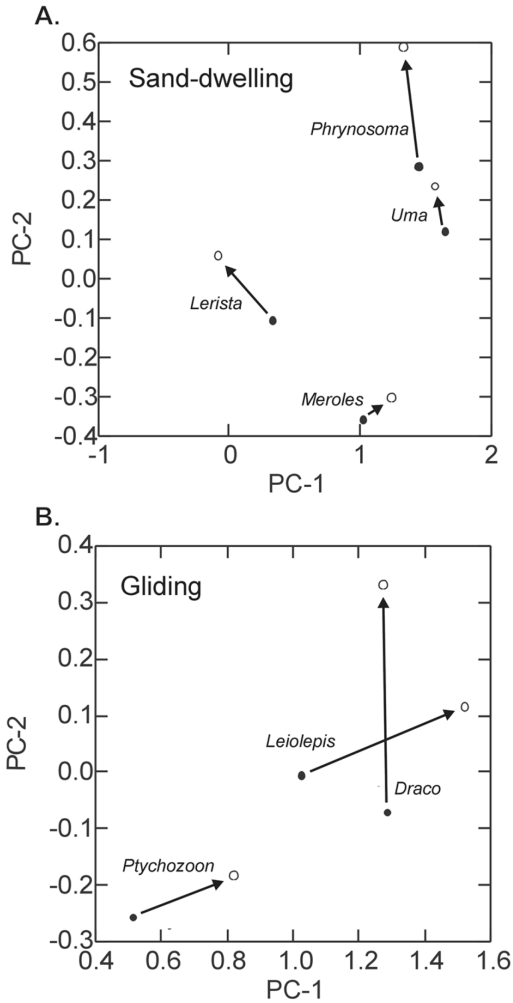
Figure 6:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). Convergence plots are shown for (A) sand-dwelling and (B) gliding, with taxa putatively convergent labelled.
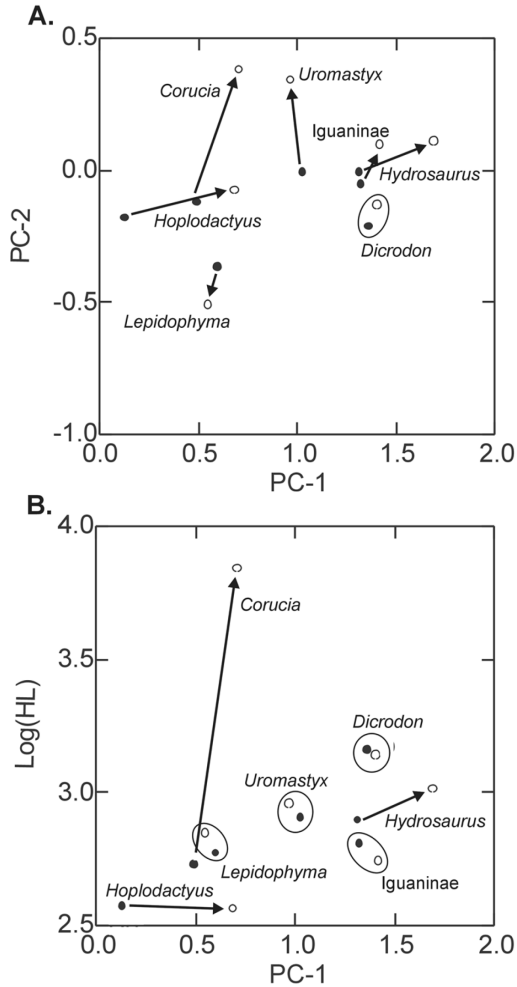
Figure 7:
Plots of pairs of herbivorous non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by (A) PC-1 (an index of elongation) and PC-2 (an index of robustness) and (B) PC-1 and log(head length). Putatively convergent taxa are labelled.

vegetation or as short-tailed burrowers (Wiens *et al.* 2006; Brandley *et al.* 2008). These are likely different selective regimes and so I treat each separately. My dataset includes fifteen (of ~22) instances of the evolution of the elongate burrowing ecotype and the vast majority of these have evolved along parallel trajectories toward a different area of morphospace than that occupied by their ancestors (Fig. 8A). The wide area of morphospace occupied by the descendent burrowers (Fig. 8A) indicates that despite snake-like body shapes appearing simple, there is still considerable variation in the degree of robustness. The results for the surface-dwelling ecomorph are less striking, but three of four examples have also evolved in largely the same direction (Fig 8B). The exceptions are the anguid clades *Ophisaurus + Anguis* and *Ophiodes*, which appear to have actually decreased in the degree of elongation over evolutionary time (Fig. 4B), although this result might arise from poor resolution at the base of the anguid clade on the supertree.

Anolis lizards have repeatedly evolved multiple ecomorphs that differ in microhabitat, often defined by the perch diameter that they inhabit (Losos 2009). Despite being one of the best documented examples of convergent evolution, the ecomorphs have only sometimes come to occupy a common morphospace as defined by my body-shape dataset (Fig. 4B). It is likely that the current dataset is not sufficiently detailed to identify the convergence documented by others. For example, limb morphology is a key component of *Anolis* convergence, yet my dataset contains relatively few limb measurements.

Finally, I examined whether Agamidae and Iguanidae as well as Teiidae and Lacertidae represent convergent clades in general (see Appendix). Agamid and iguanid ancestors did not evolve toward a common area of morphospace or in a similar direction (not shown), but their radiations have come to occupy largely the same area of the morphospace (Fig. 4A). By contrast, although the ancestors of teiids and lacertids have evolved in a similar direction to be increasingly lizard-like and gracile (Fig. 9), they occupy close, but adjacent areas of morphospace (Fig. 2B). From a comparison of morphospace occupation, lacertids instead appear to be more convergent with the limbed gymnophthalmids, the sister group to teiids (Fig. 2B).
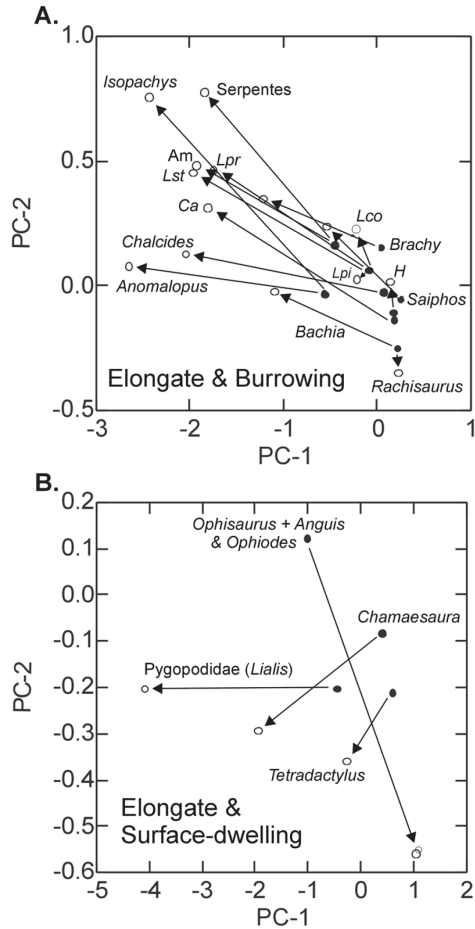
Figure 8:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness) for elongate taxa that are (A)burrowers and those that are (B) surface-dwellers. Abbreviations: Am, *Amphisbaenia*; Brachy, *Brachymeles*; Ca, *Calyptomatus*; H, *Hemiergis peronii*; Lco, *Lerista connivens*; Lpi, *L. picturata*; Lpr, *L. praepedita*; and Lst, *L. stylis*.
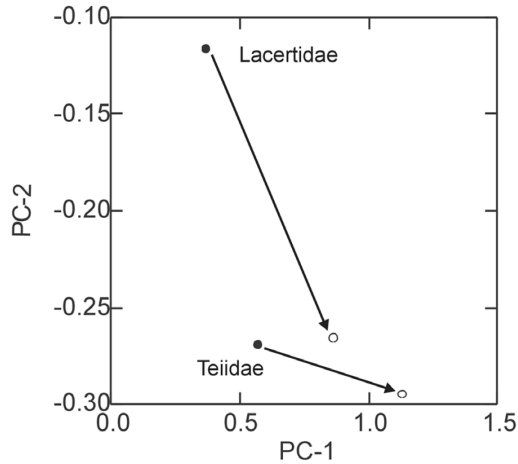
Figure 9:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness) for Lacertidae and Teiidae.

Discussion

The theoretical morphospace

The construction of morphospaces is a powerful approach to studying phenotypic evolution in general and convergence in particular because it enables one to consider not only the phenotypes that have evolved, but also those that have not (which is why this is sometimes called a theoretical morphospace; Thomas & Reif 1993; McGhee 2011). A morphospace approach implicitly incorporates the concept of constraints, which are thought to play an important role in convergent evolution (Wake 1991; Thomas & Reif 1993). Specifically, physical laws and organismal *Baupläne* set limits on which areas of the morphospace can be inhabited and developmental constraints and genetic correlations can then further curtail the options available to evolution, resulting in the uneven occupation of the morphospace (Thomas & Reif 1993; Losos 2011). When evolved phenotypes are considered in the context of their function and ecological context, the morphospace can also be a tool

to help address questions about the role of adaptation in the convergent process (Stayton 2006; Revell *et al.* 2007; Losos 2011).

Similar to other authors (Stayton 2006; Revell *et al.* 2007; Siler & Brown 2011), I generated a continuous morphospace using a PCA approach. My ePCA results and resulting morphospace are largely concordant with those of Bergmann and Irschick (2012), who used the same dataset but did not account for phylogeny with their PCA, and with those of Wiens *et al.* (2006), who used different variables and biased their sampling to include a disproportionate number of elongate species. This suggests that the phylomorphospace is robust to variation in procedure and species sampling.

The phylomorphospace presented here (Fig. 1) is interesting in and of itself because it reveals certain patterns about the variation in snake-like, intermediate, and lizard-like squamates. One might hypothesise that the evolution of a snake-like morphology involves a gross simplification of the body plan on account of the loss of limbs such that one snake-like species looks like all the others. If this were the case, then one would expect snake-like morphologies to occur in a very restricted area of the morphospace, one that is much smaller than the area occupied by lizard-like species. Instead, what is seen is that snake-like species occupy a large area of the morphospace, ranging from robust to gracile across an area that is only slightly smaller than that occupied by lizard-like species. This suggests that not all snake-like morphologies are equivalent. Indeed, the space occupied by elongate burrowers is completely separate from the space occupied by elongate surface-dwellers (Figs. 8A, B; compare the locations of the open circles). This suggests similar, convergent morphologies can arise because of different selective pressures, challenging the view of what convergence is. For example, if convergence is viewed as similar solutions evolving because of similar selective pressures (e. g., Losos 2011), what does it mean when different selective pressures produce the same phenotype? It will be fruitful to examine this question from a functional perspective because it suggests that convergent phenotypes can be multifunctional.

Another important observation from the complete phylomorphospace is that intermediate species are restricted in their morphology. The narrow band of branches crossing from the lizard-like cluster to the snake-like cluster (Fig. 1) is restricted to intermediate robustness; no intermediate species are very robust or very gracile. This is suggestive of a constraint as to how a snake-like shape can evolve, although the constraint is relaxed once it has evolved. In-

deed, different selective pressures might be working on species with intermediate body shapes than on snake-like or lizard-like species (Brandley *et al.* 2008), but what these pressures are remains unknown.

Other approaches to creating a morphospace have taken a character-based approach, where multiple characters are coded discretely (Thomas & Reif 1993; McGhee 2011). This is appealing as a thought experiment because the bounds of the morphospace are clearly defined. However, this approach introduces bias arising both from obtaining a complete set of characters and character states, and because many discretely coded-characters actually represent simplifications of continuous variables (Wiens 2001). Although a continuous morphospace, as produced by a PCA, is smooth as opposed to stepped and treats variation in a more organic way, it is still limited by the characters included (although not their states). However, because PCA simplifies patterns of variation to a few axes that explain the majority of this variation, this approach can overinflate apparent convergence because the latter tends to increase as the number of variables (or phenotype complexity) decreases (Stayton 2008). Nevertheless, the greater the number of variables or morphospace axes, the harder they are to visualise and interpret.

Detecting convergence

With the growing availability of robust phylogenies and the mainstream use of ancestral reconstruction techniques, researchers have focused on identifying convergence by studying the evolution of the phenotype along the branches of the phylogeny on which convergence is thought to have occurred (Stayton 2006; Revell *et al.* 2007). This is the primary approach taken here (Figs. 5–9). However, comparing ancestor-descendant pairs failed to detect convergence in Agamidae and Iguanidae (not shown), whereas examining the morphospace occupied by each clade gave compelling evidence for convergence (Fig. 4A). In this example, the premise for convergence was not predicated on both clades being subjected to similar selective pressures because both clades contain extremely diverse species both morphologically and ecologically (Melville *et al.* 2006). The common occupation of morphospace by these two clades might be more suggestive of shared constraints arising from their evolutionary history and body plan. For example, neither clade has ever evolved elongate, limb-reduced forms and every species has five digits on each limb (Greer 1991). Instead, Agamidae and Iguanidae appear to be parallel radiations, likely with many examples of adaptive convergence

(Losos 2011) within them. Because these two clades occur in mutually exclusive geographic areas, this suggests that ecological opportunity and biogeography have played a large role in their evolution, similar to what has been hypothesised for snake-like morphologies (Wiens *et al.* 2006). The findings presented here argue that a diversity of approaches to detecting and studying convergent evolution is important because it represents a complex evolutionary pattern that can arise from a diversity of processes.

Although hundreds of examples of convergence have been documented (McGhee 2011) and specific patterns of evolution have been described for some of these (e. g., Wiens & Singluff 2001; Herrel *et al.* 2004; Stayton 2006; Wiens *et al.* 2006; Revell *et al.* 2007; this study), research into why convergence happens is lagging (but see Irschick *et al.* 1996; Herrel *et al.* 2008; Eckalbar *et al.* 2012). The mechanisms behind convergence can be studied in a variety of ways, including functional studies and measurement of selective pressures (Losos 2011). Studies of genetic covariance structure underlying traits that have converged in multiple taxa would also be compelling because constraints on genetic covariance and integration might then constrain the evolutionary options available to respond to a particular selective pressure (Kolbe *et al.* 2011). Macroevolutionary modelling is another appealing approach that might be able to differentiate random evolution from common selective regimes resulting in convergent evolution (Hansen 1997; Butler & King 2004). There are now a variety of powerful tools available that can be brought to bear on the underlying reasons for convergent evolution and, in applying them, it is important to keep in mind that these underlying reasons might not be mutually exclusive.

Acknowledgements

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Appendix

Examples of convergent evolution possibly related to body shape in Squamates. Times refers to the number of times a feature has evolved independently in each clade.

Agamidae and Iguanidae in general

Clade (Taxa)	Times	References
Agamidae (all), Iguanidae (all)	1	Melville *et al.* (2006)

Teiidae and Lacertidae in general

Clade (Taxa)	Times	References
Teiidae (all), Lacertidae (all)	1	Miles *et al.* (2007)

Anolis ecomorphs

Clade (Taxa)	Times	References
Polychrotinae (*Anolis* spp.)	many	Williams (1982); Losos (1990a, b); Jackman *et al.* (1997)

Bipedalism

Clade (Taxa)	Times	References
Agamidae (*Chlamidosaurus kingii*, *Ctenophorus* spp., *Lophognathus* spp.)	3	Clemente *et al.* (2008)
Iguanidae (*Basiliscus* spp., *Crotaphytus* spp.)	2	Snyder (1949); Urban (1965)
Lacertidae (*Acanthodactylus erythrurus*)	1	Aerts *et al.* (2003)
Phrynosomatinae (sand lizards)	1	Irschick & Jayne (1999)

Body flattening in rock dwellers

Clade (Taxa)	Times	References
Cordylidae (*Platysaurus capensis*, *Pseudo-cordylus capensis*)	2	Revell *et al.* (2007)
Phrynosomatinae (*Petrosaurus* spp.)	1	Revell *et al.* (2007)
Polychrotinae (*Anolis bartschi*)	1	Revell *et al.* (2007)
Scincidae (*Carlia mundivensis*, *Carlia rococo*, *Carlia scirtetis*, *Cryptoblepharis litoralis*, *Eulamprus brachysoma*, *Lampropholis mirabilis*, *Techmarscincus jigurru*)	6	Goodman & Isaac (2008)
Tropidurinae (*Tropidurus semitaeniatus*)	1	Revell *et al.* (2007)

Dry adhesion

Clade (Taxa)	Times	References
Gekkota (Diplodactylidae, Gekkonidae)	2	Russell (1979); Irschick *et al.* (1996)
Polychrotinae (*Anolis* spp.)	1	Russell (1979); Irschick *et al.* (1996)
Scincidae (*Prasinohaema virens*)	1	Russell (1979); Irschick *et al.* (1996)

Herbivory

Clade (Taxa)	Times	References
Agamidae (*Hydrosaurus* spp., *Uromastyx* spp.)	2	Stayton (2006)
Diplodactylidae (*Hoplodactylus* spp.)	1	Stayton (2006)
Iguaninae (Iguaninae)	1	Stayton (2006)
Lacertidae (*Lacerta lepida*)	1	Stayton (2006)
Scincidae (*Corucia zebrata*)	1	Stayton (2006)
Teiidae (*Dicrodon guttulatum*)	1	Stayton (2006)
Tropidurinae (*Liolaemus buergeri*, *Liolaemus fitzingeri*, *Liolaemus lineomaculatus*, *Phymaturus* spp.)	2[+]	Espinoza *et al.* (2004)
Varanidae (*Varanus olivaceus*)	1	Stayton (2006)
Xantusiidae (*Lepidophyma smithi*)	1	Stayton (2006)

Gliding

Clade (Taxa)	Times	References
Agamidae (*Draco* spp., *Leiolepis* spp.)	2	Losos *et al.* (1989); McGuire & Dudley (2005)
Gekkota (*Ptychozoon* spp.)	1	Vanhooydonck *et al.* (2009)
Lacertidae (*Holaspis gunteri*)	1	Vanhooydonck *et al.* (2009)

Sand-diving/burying

Clade (Taxa)	Times	References
Agamidae (*Agama etoshae*, *Phrynocephalus* spp.)	2	Arnold (1995); Lamb *et al.* (2003)
Gerrhosauridae (*Angolosaurus skoogi*)	1	Arnold (1995); Lamb *et al.* (2003)
Lacertidae (*Meroles* spp.)	1	Arnold (1995); Lamb *et al.* (2003)
Phrynosomatinae (*Phrynosoma* spp., *Uma* spp.)	2	Arnold (1995); Lamb *et al.* (2003)
Scincidae (*Lerista* spp., *Scincus* spp., *Mabuya acutilabris*)	3	Kendrick (1991); Arnold (1995); Lamb *et al.* (2003)

Elongate burrowers

Clade (Taxa)	Times	References
Amphisbaenia (all)	1	Kearney & Stuart (2004); Wiens *et al.* (2006)
Anguidae (*Anniella* spp., *Sauresia* spp.)	2	Wiens & Singluff (2001)
Dibamidae (all)	1	Lee (1998)
Gymnophthalmidae (*Bachia* spp., *Calyptommatus* spp., *Nothobachia ablephara*, *Rachisaurus* spp.)	3[+]	Pellegrino *et al.* (2001); Kohlsdorf & Wagner (2006)
Scincidae (*Acontias* spp., *Acontophiops* spp., *Anomalopus* spp., *Brachymeles* spp., *Chalcides* spp., *Feylinia polylepis*, *Hemiergis polylepis*, *Isopachys* spp., *Opiomorus* spp., *Lerista* spp., *Paracontias* spp., *Plestiodon reynoldsi*, *Sygomeles* spp., *Saiphos* spp., *Sepsina* spp., *Sphenops* spp., *Typhlacontias* spp., *Voeltzkowia* spp., *Typhlosaurus* spp.)	14[+]	Greer & Cogger (1985); Greer (1991); Kendrick (1991); Greer *et al.* (1998); Whiting *et al.* (2003); Daniels *et al.* (2005); Schmitz *et al.* (2005); Wiens *et al.* (2006); Skinner *et al.* (2008); Heideman *et al.* (2011); Siler & Brown (2011)
Serpentes (all)	1	Townsend *et al.* (2004)

Elongate surface-dwellers

Clade (Taxa)	Times	References
Anguidae (*Ophiodes* spp., *Ophisaurus* spp.)	2	Wiens & Singluff (2001)
Cordylidae (*Chamaesaura* spp.)	1	Wiens *et al.* (2006)
Gekkota (most Pygopodidae)	1	Wiens *et al.* (2006)
Gerrhosauridae (*Tetradactylus* spp.)	1	Wiens *et al.* (2006)