

# Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis

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Although the relationship between dietary and phenotypic specialization has been well documented for many vertebrate groups, it has been stated that few such general trends can be established for lizards. This is often thought to be due to the lack of dietary specialization in many lizards. For example, many species that are reported to be insectivorous may also consume a variety of plant materials, and the reverse is often true as well. In this study, we investigate whether a correlation exists between general cranial form and dietary niche in lizards. Additionally, we test previously proposed hypotheses suggesting that herbivorous lizards should be larger bodied than lizards with other diets. Our data indicate that lizards specializing in food items imposing different mechanical demands on the feeding system show clear patterns of morphological specialization in their cranial morphology. True herbivores (diet of fibrous and tough foliage) are clearly distinguished from omnivorous and carnivorous lizards by having taller skulls and shorter snouts, likely related to the need for high bite forces. This allows herbivores to mechanically reduce relatively less digestible foliage. Carnivores have relatively longer snouts and retroarticular processes, which may result in more efficient capture and processing of elusive prey. When analysed in an explicit phylogenetic context, only snout length and skull mass remained significantly different between dietary groups. The small number of differences in the phylogenetic analyses is likely the result of shared evolutionary history and the relative paucity of independent origins of herbivory and omnivory in our sample. Analyses of the relationship between diet and body size show that on average herbivores have a larger body size than carnivores, with omnivores intermediate between the two other dietary groups. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 86, 433–466.

ADDITIONAL KEYWORDS: body size – feeding system – herbivory – lepidosaur – omnivory – skull.

## INTRODUCTION

Since Darwin addressed the concept of adaptive variation through natural selection (Darwin, 1859), biologists have sought evidence to bolster his theory. To do so, researchers have often used the feeding apparatus as a model system to examine correlations between the design and ecology (i.e. diet, foraging mode) of organisms (Barel *et al.*, 1989; Liem, 1993; Wainwright & Reilly, 1994; Wainwright & Richard, 1995; Grant,

1999; Bouton, Witte & Van Alphen, 2002). Because of the clear link to an animal's fitness, and the mechanical demands imposed by different food items, the design of the feeding system is expected to show strong adaptations to dietary niche (Findley & Black, 1983; Demes & Creel, 1988; Mittelbach, Osenberg & Wainwright, 1992; Aguirre *et al.*, 2002). Indeed, studies on a wide diversity of vertebrates including fish, mammals and birds have revealed strong correlations between the design of the feeding system and the trophic ecology of the organism studied, thus demonstrating how the mechanical and behavioural properties of food items may shape the design of the trophic system (Arendsen de Wolff-Exalto, 1954; Turnbull, 1970; Wainwright, 1988; Grant, 1999).

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Mechanical demands imposed by differences in food properties are expected to be reflected in functional changes of the feeding system. Studies on ungulates (Perez-Barberia & Gordon, 1999), primates (Dumont, 1997), bears (Sacco & Van Valkenburgh, 2004), frogs (Emerson, 1985) and bats (Van Cakenberghe, Herrel & Aguirre, 2002) have found significant correlations between diet/feeding type and cranial morphology, in accordance with a priori biomechanical predictions. Using a phylogenetic simulation analysis, Van Cakenberghe *et al.* (2002) found a highly significant relationship between morphometric variables and dietary groups that were defined on the basis of the functional demands on the feeding system. A similar analysis of ungulates (Perez-Barberia & Gordon, 1999) revealed that species that consumed 'tougher' foods had higher coronoid processes. Although this was one of only a few significant variables after controlling for the effects of phylogeny, coronoid height is thought to be linked to the generation of bite force since it reflects the effective lever arm for the temporalis muscle. Morphological changes that have a direct effect on performance, such as this one, are expected to be most susceptible to selective forces acting on the system.

Consumption of plant material has been often studied because it presents a number of unique challenges to the trophic system. Vertebrates do not produce the enzymes necessary to break down the cellulose that makes up the fibrous cell wall of plants, so animals that consume such foods must find alternative methods to access the energy-rich carbohydrates and proteins contained within (Szarski, 1962; Greene, 1982; King, 1996). Because a herbivorous lifestyle does have several potential benefits associated with it, including lower foraging costs, a higher relative abundance of food and a relatively high nutritional content, physiological adaptations for exploiting plant materials have been highly developed in most vertebrate clades. In many mammalian herbivores, an improved digestive efficiency is often accomplished through a higher degree of mechanical breakdown of foliage. The outcome of this breakdown is a mechanical destruction of parts of the cell wall and an overall reduction in particle size, thus exposing a greater surface area of the food item to digestive processes.

Despite clear general predictions and the trends observed in other vertebrate groups, it has been stated for lizards that 'Despite the widespread assumption to the contrary, there is no necessary relationship between dietary specialization and phenotypic specialization in the lepidosaurian feeding apparatus [referring to craniocervical system].' (Schwenk, 2000: 271; see also King, 1996). Relative to most other vertebrate groups, few species of lizards appear to be dietary specialists, and even fewer exclusively consume plant matter. However, some degree of plant consumption is still

seen in approximately half of the families of lizards, representing many independent origins (Cooper & Vitt, 2002). The majority of studies linking phenotypic specialization with herbivory in lizards have generally focused on digestive anatomy and physiology. Various strategies for potentially increasing nutrient uptake from plants appear to be utilized, including deliberate ingestion of sand and small rocks (Sylber, 1988), presence of cellulolytic bacteria and intestinal nematodes (Dubuis *et al.*, 1971; Sokol, 1971; Nagy, 1977) and partitioning and enlargement of the colon and caecum (Iverson, 1980, 1982; Herrel, Vanhooydonck & Van Damme, 2004). It has also been noted that some herbivorous lizards (e.g. *Amblyrhynchus cristatus*, *Iguana iguana*) show a tendency towards serrate, laterally compressed dentition, presumably to increase processing efficiency when feeding on fibrous food items (Hotton, 1955; Montanucci, 1968; Herrel, in press), but this may not be a universal feature among plant-eaters. Finally, plant consumption in lizards has been linked to increased body size (Pough, 1973; Van Damme, 1999; Cooper & Vitt, 2002; Herrel, in press), but this notion has rarely been quantitatively tested across a broad range lizard families while controlling for phylogeny.

The feeding system in lizards and other vertebrates can be modelled using lever mechanics, thus allowing for clear *a priori* hypotheses concerning the design of the feeding system. Using biomechanical principles, and considering the requirements for processing different food types (Lucas & Pereira, 1990; Lucas *et al.*, 2000; Sibbing & Nagelkerke, 2001), functional hypotheses can be constructed. We predict herbivory to be associated with: (1) increased skull height and width, (2) an increased jaw closing in-lever, and (3) higher skull mass. By both allowing a more mechanically advantageous orientation of adductor muscles when the jaws are closed and increasing the space available for the jaw adductor musculature, increased skull height and width are predicted to lead to higher bite force production (e.g. see Herrel *et al.*, 1999a, b; Herrel, De Grauw & Lemos-Espinal, 2001; Stayton, 2005). Increasing the jaw closing in-lever (distance between the attachment of jaw closing musculature and the jaw joint) is expected to allow for a greater bite force to be applied for a given amount of jaw musculature. Additionally, a relatively short jaw closing out-lever (i.e. shorter snout) is of importance because herbivorous lizards need to crop pieces of plant material at tips of the jaws. Finally, high bite forces should theoretically be better resisted by having a skull with a higher safety factor (ratio between its strength and the maximum stress to which it is normally exposed), and we expect this to correlate with a higher average skull mass in herbivores.

However, not only herbivorous lizards are potentially constrained by the nature of their food. A differ-

ent set of predictions apply to lizards that consume primarily elusive animal prey. We expect species feeding on mobile prey to optimize for speed in the jaw system, potentially coming at the expense of force production. Both of these variables cannot be optimized simultaneously, because of the well-established trade-off between speed and force in simple lever systems (like the lizard jaw apparatus; see also Stern, 1974; Russell & Thomason, 1993; Weishampel, 1993). Specifically, carnivory is predicted to be linked with: (1) increased jaw opening in-lever and (2) increased snout and skull lengths. Increasing the jaw opening in-lever (distance from jaw joint articulation to back of retroarticular process) will result in a more advantageous location of the jaw opening muscle, allowing for faster jaw movements, and potentially resulting in a higher success in capturing elusive prey. Increased snout length is expected to correlate with an increased jaw closing out-lever, and should have a positive effect on jaw closing velocity at the tips of the jaws.

Morphological predictions for omnivorous species are more difficult to establish. Do species that include both plant and animal matter have an intermediate morphology between herbivores and carnivores (jack of all trades, master of none), or is their skull morphology designed for one of the more 'specialized' categories, allowing for either speed or force, but not both? Because of the inherent trade-off between speed and force in the mechanics of the jaw system (both at a mechanical and physiological level), a 'master of all' morphology (high and long skull) is not expected.

## METHODS

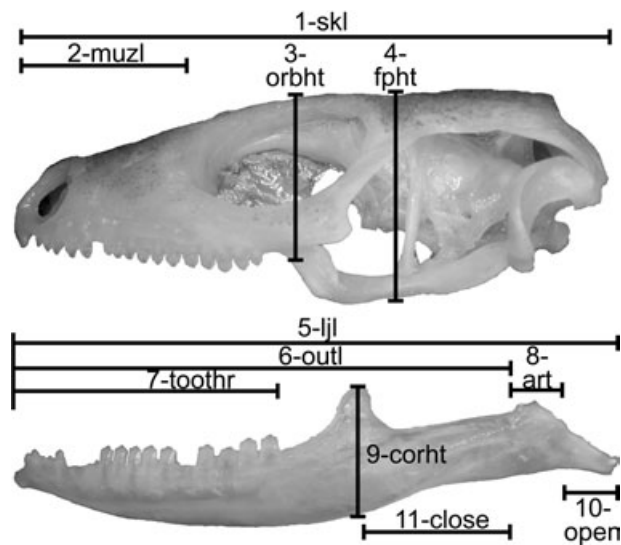
### SPECIMENS

Six hundred and forty specimens, representing 104 genera and 246 species of lepidosaurs were measured (Appendix). Ophidian (snake) and several groups of fossorial lepidosaurs (Amphisbaenia, Dibamidae, Pygopodidae) were excluded from sampling due to extreme modifications in cranial morphology in these groups unrelated to diet (Iordansky, 1984; Kardong *et al.*, 1997; Cundall & Greene, 2000; Schwenk, 2000). All taxonomic designations were taken from specimen records and validity of taxon names was verified using the European Molecular Biology (EMBL) Reptile Database (<http://www.reptile-database.org/>). Specimens were located at a number of institutions, including the American Museum of Natural History (AMNH), National Museum of Natural History (NMNH), The Field Museum, Chicago (FM), Museum of Comparative Zoology, Harvard (MCZ), Northern Arizona University Vertebrate Museum (NAU), South Australian Museum (SAM), as well as two private collections (A. Herrel and J. Meyers).

Specimens were chosen to maximize dietary diversity in the sample. Because several diet types (i.e. herbivory, omnivory) have apparently evolved independently in lepidosaurs (Cooper & Vitt, 2002), a broad taxonomic range was sampled, representing almost all families of lepidosaurs (Appendix). When possible, we attempted to sample species that represented independent radiations of diet type. A number of lizards show an ontogenetic shift from a juvenile diet of insects to a herbivorous adult diet (e.g. *Ctenosaura pectinata*: Durtsche, 2000; *Egernia stokesii*: Duffield & Bull, 1998; Chapple, 2003; *Liolaemus lutzae*: Rocha, 1998; *Tropidurus torquatus*: Fialho, Rocha & Vrcibradic, 2000), so only adult specimens were included in the sample. Specimens were used only if one of two independent variables used for size scaling (postcranial skeletal mass or snout-vent length) were available. Snout-vent length was taken from records accompanying specimens. Because this measure was often not present, resulting in a reduced data set, a second independent measure of body size, postcranial skeletal mass was recorded when possible. This resulted in two partially overlapping data sets, each of which was analysed separately.

### MEASUREMENTS

Two general types of measurements, mass and length, were measured and recorded from the skull, mandible and postcranial skeleton. The two mass measurements, cranial (skull + mandible) and postcranial skeletal mass were taken with an electronic scale (Ohaus, Model Scout 201) to the nearest 0.01 g. All skulls and mandibles were inspected for breakage and completeness to ensure accurate measurements. For postcranial skeletal mass, skeletal elements of specimens were inventoried, and this variable was only recorded if the complete postcranial skeleton was present. Twelve linear measurements were taken from the skull and mandible (Fig. 1) to the nearest 0.01 mm using digital calipers (Mitutoyo, Model 500-197). These included skull length (skl), muzzle length (muzl), skull height at mid-orbit (orbht), skull height at frontal-parietal suture (fpht), lower jaw length (ljl), mandibular symphysis to anterior border of quadrate-articular jaw joint (outl), toothrow length (toothr), length of jaw joint articulation (art), height at coronoid (corht), length of retroarticular process (open), coronoid process to anterior border of jaw joint (close) and bimanibular width (bimand). All data were  $\log_{10}$  transformed before analysis. Variables were chosen based on their perceived value in representing both overall skull shape and for their potential biomechanical relevance. For example, increased frontal-parietal height is expected to correlate with increased bite force (Herrel *et al.*, 2001a, b) and lever arm length



**Figure 1.** Lateral view of *Gallotia galloti* skull illustrating craniometric variables used in this study. (1) Skull length (skl); (2) muzzle length (muzl); (3) skull height at mid-orbit (orbht); (4) skull height at frontal–parietal suture (fpht); (5) lower jaw length (ljl); (6) mandibular symphysis to anterior border of jaw joint (outl); (7) toothrow length (toothr); (8) length of jaw joint articulation (art); (9) height at coronoid (corht); (10) length of retroarticular process (open), and (11) coronoid process to anterior border of jaw joint (close). Bimandibular width (bimand), maximum width of the articulated mandibles, is not shown.

of jaw opening muscles (i.e. retroarticular process length) has a well established biomechanical relationship with jaw opening speed (Smith & Savage, 1959; Alexander & Dimery, 1985; Bramble & Wake, 1985).

#### DIETARY DATA

Dietary data for all species were collected from published literature (Appendix). Species were classified as herbivorous, omnivorous or carnivorous. Herbivorous lizards were those that had a diet composed of at least 80% fibrous or tough plant material (i.e. leaves, shoots, roots, seeds, etc. and not soft items like fruit or nectar), omnivores consumed between 10% and 80% plant material (the rest of the diet was composed of both invertebrate and vertebrate prey). This dietary classification scheme differs only slightly from that adopted by Cooper & Vitt (2002) in their study of plant consumption in lizards. Cooper & Vitt (2002) did not consider omnivory as a separate diet group (herbivores and omnivores were grouped together as herbivorous), and many herbivorous species had soft materials (i.e. nectar, fruit) as part or all of their diet.

Although almost all carnivores consumed entirely animal material (insects, spiders, vertebrates, etc.), we used the 10% rule to prevent animals that had incidentally ingested plant material from being included as omnivores. Fruit consumption was not considered in assigning species to a dietary group. Only consumption of fibrous or tough plant materials was considered in the definition of herbivory, because our variables were chosen based on parameters relating to the mechanical challenges required to break down foliage and not necessarily the taxonomic designation of the food item (i.e. a functional notion of dietary specialization; see Schwenk, 2000).

As discussed by Cooper & Vitt (2002), the variety of ways of reporting data in studies of lizard diets makes comparison of studies problematic. When available, quantitative data were used to determine percentage of vegetation present in the diet. If multiple sources of dietary data were present in different studies, percent of stomach contents by volume data was considered to be the most reliable, followed by percent by mass, while the least reliable quantitative data were percentage presence by item number and frequency. Qualitative data were considered to be the least reliable type, but were used when necessary. Due to the large number of species in our data set and the relative lack of dietary data for lepidosaurs as a whole, we were unable to find diet information for several species. In these cases, the diet of the most closely related species in the same genus was used. This technique was used in only a few instances, and all of these were genera where diet was invariant intragenerically. Additionally, dietary accounts were only extrapolated from other species in cases of carnivory in order to avoid inflating the number of independent origins of the less common diet types, which could result in artificially high  $F_{\text{phylo}}$  values in the phylogenetic simulation analyses (see below).

#### ANALYSES

All non-phylogenetic statistical analyses were conducted using SPSS v.11.5 (SPSS, Inc). In order to account for the effect of body size, all variables were regressed against one of two independent measures of size, postcranial skeletal mass (PSM) or snout–vent length (SVL). Because these variables represent different aspects of body size and the data set for each is different, two separate analyses were conducted, one with each of the size-corrections. SVL is traditionally used as a measure of overall body size in lepidosaurs, but because not all specimens had SVL in their record, postcranial skeletal mass was chosen as an additional independent variable. Post-cranial skeletal mass was regressed against SVL for specimens that had both size measures available (141 specimens) to test



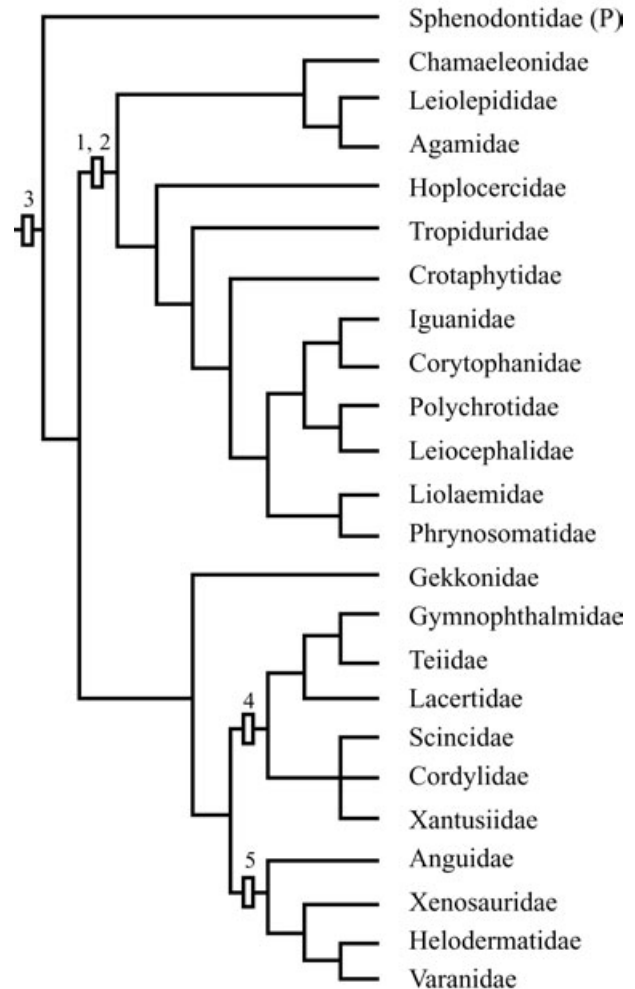
whether there was a correlation between the two independent variables. A highly significant correlation was interpreted as evidence that PSM is also a good indicator of body size.

#### Non-phylogenetic analyses

Log<sub>10</sub> transformed data from all specimens were used in two separate non-phylogenetic analyses (one with each of the size measures as the independent variable). The following statistical procedures were applied for both analyses. First, a univariate analysis of variance (ANOVA) was performed on the independent variable (snout–vent length or postcranial skeletal mass) with diet type as the fixed factor to determine whether there were significant size differences among any diet groups. Since there were significant differences for both size measures, all variables were regressed against either SVL or PSM to explore differences in cranial shape. Unstandardized residuals of dependent variables from this regression were used in a nonrotated, correlation matrix principal components analysis (PCA) that included all variables except bimandibular width, coronoid height, and skull mass. The first two were not included because they were not always represented in the data set, while skull mass was excluded because it was not a shape descriptor. Separate univariate ANOVAs and *post hoc* Tukey HSD tests were conducted for these three variables. The PCA was unrotated, with the number of significant axes determined *post hoc* using the broken stick test (Jackson, 1993). Finally, multivariate ANOVAs and *post hoc* Tukey HSD tests were performed on all significant factors in order to evaluate whether differences between diet types on each PCA axis were significant.

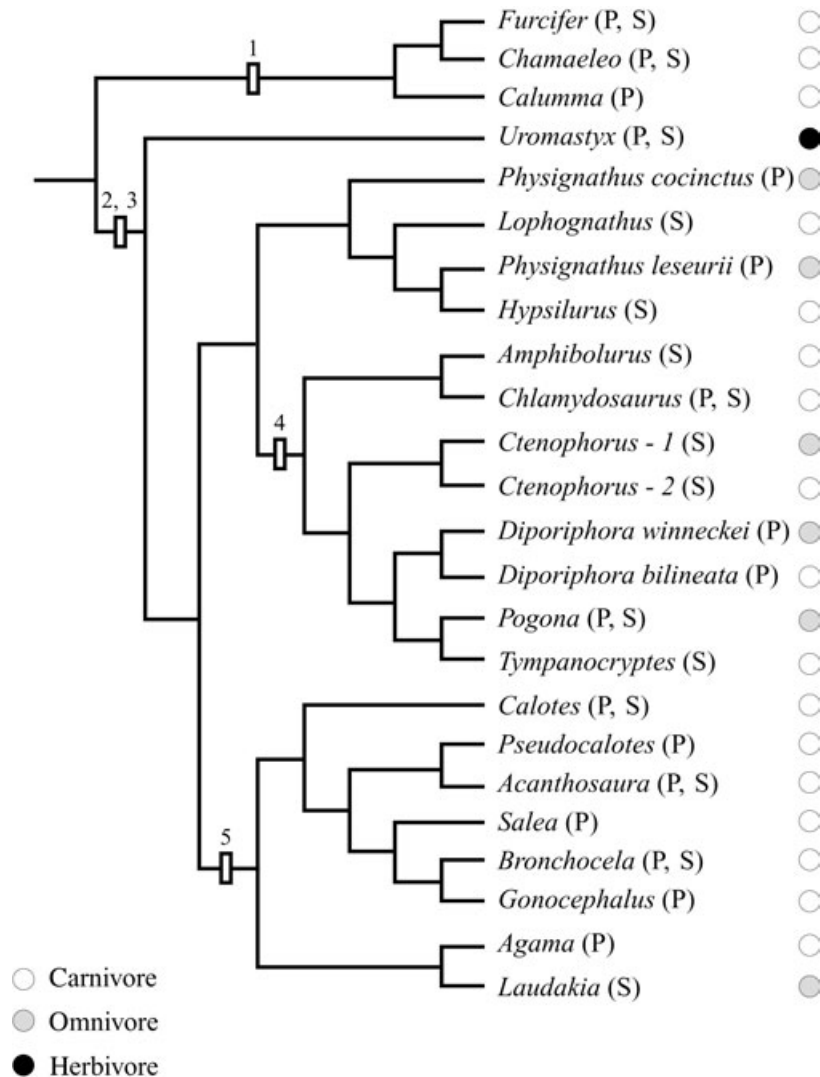
#### Phylogenetic simulation analyses

The shared evolutionary history of organisms requires phylogenetic relationships to be taken into account when examining differences between species or groups of species (the diet groups defined in this study; Felsenstein, 1985; Harvey & Purvis, 1991). This necessitates the construction of a phylogeny of all groups included in the analysis. Because no comprehensive phylogeny was available for the taxa sampled in this study, multiple independent phylogenies were integrated (Figs 2–7). The family level morphology-based phylogenies of Estes, de Queiroz & Gauthier (1988) and Lee (1998) have been generally accepted for lizards. However, several molecular studies using sequences from the nuclear *RAG1*, *c-mos* and mitochondrial *ND2* genes (Harris, 2003; Townsend *et al.*, 2004; Vidal & Hedges, 2004) have produced different phylogenies that vary significantly regarding family level relationships. Despite this development, there has not been sufficient time since these molecular phy-



**Figure 2.** Overview phylogeny of lepidosaurs. In Figs 2–7, P and S indicate that species means were used in postcranial skeletal mass and snout–vent length phylogenetic simulation analyses, respectively. Phylogeny references: (1) Frost & Ethridge (1989); (2) Schulte *et al.* (2003); (3) Lee (1998); (4) Whiting *et al.* (2003); (5) Macey *et al.* (1999)

logenies were presented to allow them to be critically examined. Because of this, a modified version of the Estes *et al.* (1988) and Lee (1998) phylogenies was used to establish family level relationships among scleroglossans. Scleroglossa is considered to be a monophyletic clade, with two monophyletic subgroups, Scincomorpha and Anguinomorpha. The taxonomic status of *Iguania* has been debated, but we have followed the scheme of Frost *et al.* (2001a) (Acrodonta/Pleurodonta dichotomy) and Macey *et al.* (1997) (Pleurodonta interrelationships). We chose to assign family, rather than subfamily level designation to iguanid lizard groups (Crotaphytidae, Corytophanidae, Hoplocercidae, Iguanidae, Leiocephalidae, Liolaemidae, Phrynosomatidae, Polychrotidae and



**Figure 3.** Phylogeny of Acrodonta (Agamidae + Chamaeleonidae + Leiolepididae). Numbers after some genera in Figs 3–7 (e.g. *Ctenophorus* – 1, *Ctenophorus* – 2) indicate that multiple diet categories are represented in a single genus (see text). Phylogeny references: (1) Raxworthy *et al.* (2002); (2) Macey *et al.* (2000a); (3) Macey *et al.* (2000b); (4) Melville *et al.* (2001); Joger (1991). See Fig. 2 legend.

Tropiduridae) *sensu* Frost *et al.* (2001a). This had no effect on the results of this analysis.

Despite the lack of consensus regarding the relationships between lizard families, all the previously mentioned studies confirm the monophyly of individual lizard families, at least for the genera present in our data set (monophyly of Tropiduridae and Polychrotidae is still unclear, but groups causing controversy are not included here). Individual family phylogenies were compiled from multiple sources:

Agamidae (Joger, 1991; Macey *et al.*, 2000a, b; Melville, Schulte & Larson, 2001)

Anguidae (Macey *et al.*, 1999)

Chamaeleonidae (Raxworthy, Forstner & Nussbaum, 2002)

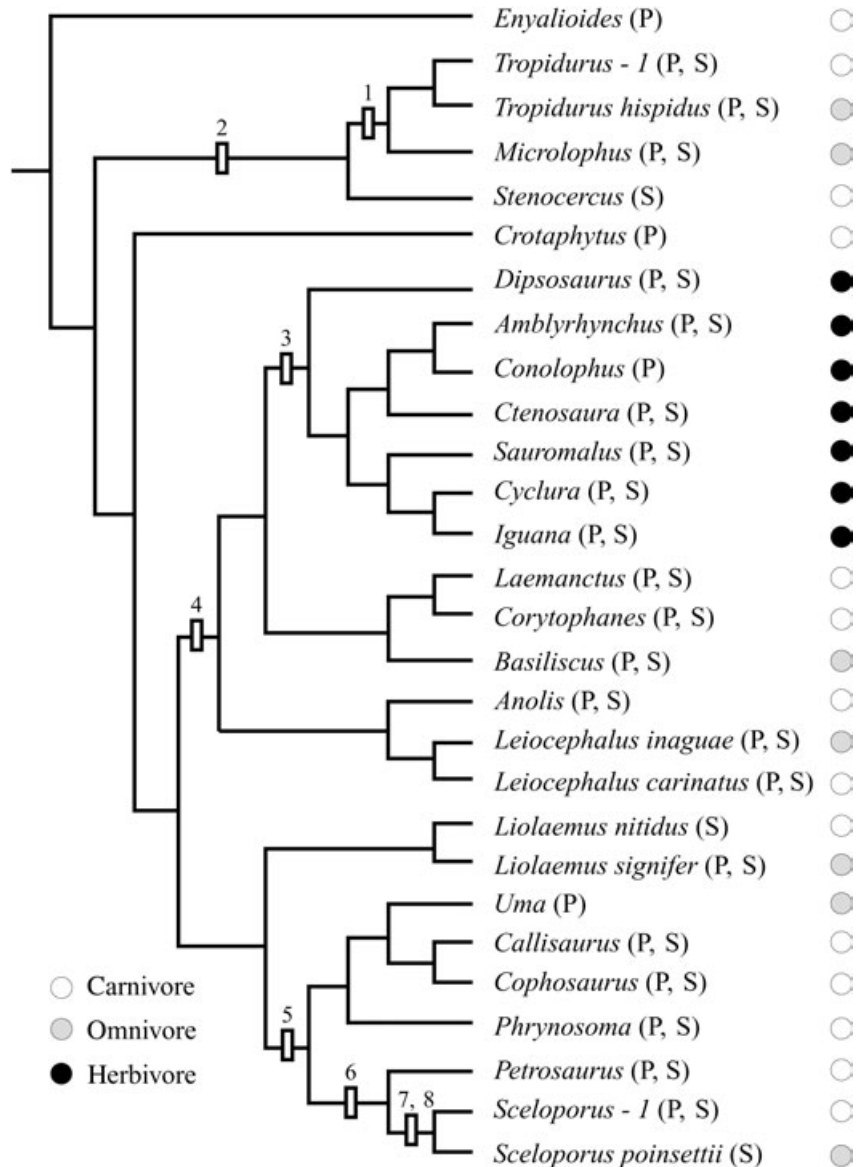
Cordylidae (Lang, 1991; Frost *et al.*, 2001b; Odierna *et al.*, 2002; Lamb *et al.*, 2003)

Corytophanidae (Frost *et al.*, 2001a; Schulte, Valladares & Larson, 2003)

Gekkonidae (Underwood, 1954; Mitchell, 1965; Kluge, 1967; Kluge, 1987; Kluge & Nussbaum, 1995; Donnellan, Hutchinson & Saint, 1999; Zaaf & Van Damme, 2001)

Gerrhosauridae (Lang, 1991; Frost *et al.*, 2001b; Odierna *et al.*, 2002; Lamb *et al.*, 2003)

Iguanidae *sensu stricto* (Wiens & Hollingsworth, 2000)



**Figure 4.** Phylogeny of Iguanidae *sensu lato* (Corytophanidae + Crotaphytidae + Hoplocercidae + Iguanidae + Leiocephalidae + Liolaemidae + Phrynosomatidae + Polychrotidae + Tropiduridae). Phylogeny references: (1) Harvey & Gutberlet (2000); (2) Frost *et al.* (2001c); (3) Wiens & Hollingsworth (2000); (4) Frost *et al.* (2001a); (5) Reeder & Wiens (1996); (6) Flores-Villela *et al.* (2000); (7) Mink & Sites (1996); (8) Wiens & Reeder (1997). See Figs 2, 3 legends.

Lacertidae (Arnold, 1989; Harris, Arnold & Thomas, 1998; Harris & Arnold, 1999)

Phrynosomatidae (Mink & Sites, 1996; Reeder & Wiens, 1996; Wiens & Reeder, 1997; Flores-Villela *et al.*, 2000)

Polychrotidae (Frost *et al.*, 2001a)

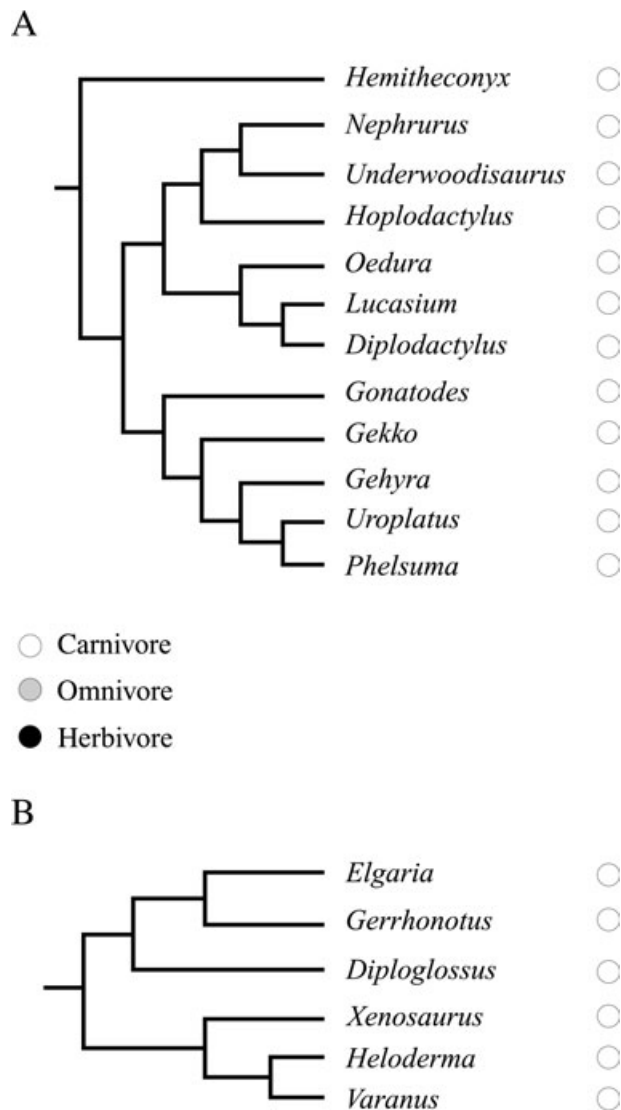
Scincidae (Hutchinson *et al.*, 1990; Honda *et al.*, 2000; Donnellan *et al.*, 2002; Reeder, 2003; Whiting, Bauer & Sites, 2003)

Teiidae (Fitzgerald, Cook & Aquino, 1999; Reeder, Cole & Dessauer, 2002; Whiting *et al.*, 2003)

Tropiduridae (Harvey & Gutberlet, 2000; Frost *et al.*, 2001c)

Xantusiidae (Hedges & Bezy, 1993)

Because our phylogenetic simulation analysis was conducted on morphological characters, we chose to use molecular based phylogenies with the highest bootstrap supports when possible. Molecular phylogenies were preferred in order to avoid the possible confounding effects of using morphology-based phylogenies, which might reflect morphological character



**Figure 5.** Phylogeny of (A) Gekkonidae and (B) Anguimorpha (Anguidae + Helodermatidae + Varanidae + Xenosauridae). Phylogeny references: (1) Donnellan *et al.* (1999); (2) Zaaf & Van Damme (2001); (3) Underwood (1954); (4) Kluge (1987); (5) Kluge (1967); (6) Mitchell (1965); (7) Kluge & Nussbaum (1995); (8) Macey *et al.* (1999). See Figs 2, 3 legends.

evolution (the very feature being examined in this study).

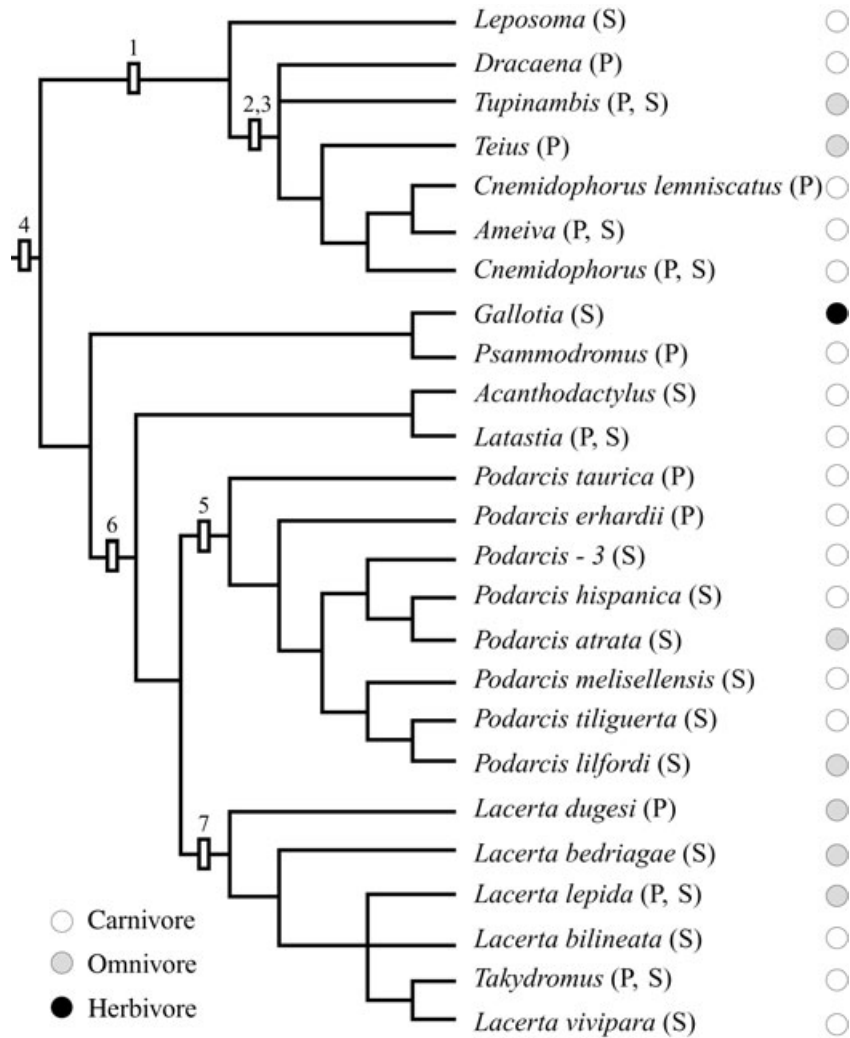
Owing to the large number of different species present in our data set, and the lack of species-level phylogenetic resolution for many groups, species were grouped by genus and trait values averaged for the phylogenetic simulation analysis. If the dietary classification of all species sampled in a particular genus was the same (e.g. all species sampled from the genus *Varanus* are carnivorous), the genus was

considered as a single datapoint. If there were multiple diet types represented within a genus, the genus was divided into the minimum number of monophyletic groups necessary to properly represent the dietary diversity of that group (e.g. for the genus *Egernia*, herbivorous group 1, omnivorous group 1, carnivorous group 1, herbivorous *Egernia kinkorei* group; *Egernia* – 1, *Egernia* – 2, *Egernia* – 3, and *Egernia kinkorei* in Fig. 7). This was only the case for a few genera, because most genera that were represented in our data set had a common intrageneric diet type. Whenever this technique was necessary, the minimum number of possible groups was constructed. A subset of the data that was analysed using only one representative species from each genus (the one with the highest sample size) confirmed that averaging all species in a genus did not give artificially significant results. We consider species averaging across a genus to be a conservative approach that would, if it had any effects, only decrease the significance of differences between dietary groups. Several genera present in the non-phylogenetic analysis were not included in the phylogenetic one (Gekkonidae: *Cyrtodactylus*, *Gymnodactylus*, *Thecadactylus*; Scincidae: *Cryptoblepharis*) because of uncertain phylogenetic positions.

Variables that had high principal component axis loadings ( $> 0.700$  or  $< -0.700$ ) in the non-phylogenetic analysis (except skull mass) and were expected to differ between dietary groups because biomechanical reasons were used for the phylogenetic simulation analysis. These included skull mass (sklmass), skull length (skl), muzzle length (muzl), height at frontal-parietal joint (fpht) and length of retroarticular process (open). Genus means (or genus subgroup diet means, see above) were calculated for all variables and then  $\log_{10}$  transformed. Body size differences between diet groups were also tested in a phylogenetic simulation analysis.

The phylogenetic simulation analysis was conducted using the PDTREE, PDSIMUL and PDANOVA modules of the PDAP program created by Garland *et al.* (1993). The PDTREE module was used to construct separate phylogenies for both the SVL and PSM data sets. All branches in the tree were set to unity, as there are no branch lengths available for the vast majority of the trees (see also Diaz-Urriarte & Garland, 1998). Then, a gradual Brownian motion model of evolution in the PDSIMUL module produced 1000 unbounded evolutionary simulations. Finally, we used PDANOVA to generate an  $F$ -value statistic ( $F_{\text{phylo}}$ ) value for all variables/data sets, which takes into account the phylogenetic relationships of the species involved. If the  $F$ -value (from a traditional non-phylogenetic analysis) is greater than  $F_{\text{phylo}}$ , the difference between dietary groups is considered to be





**Figure 6.** Phylogeny of Teiidae, Gymnophthalmidae and Lacertidae. Phylogeny references: (1) Whiting *et al.* (2003); (2) Reeder *et al.* (2002); (3) Fitzgerald *et al.* (1999); (4) Harris *et al.* (1998); (5) Harris & Arnold (1999); (6) Arnold (1989); (7) Harris *et al.* (1998). See Figs 2, 3 legends.

significant in a phylogenetic context. Unlike in the non-phylogenetic analysis, *post hoc* testing to determine which of the three dietary groups differ from each other cannot be conducted in PDAP, and  $F_{\text{phylo}}$  only indicates if all three groups differ significantly from each other. In some cases, results from the non-phylogenetic analysis indicated that two diet groups sometimes did not differ from each other (e.g. coronoid height), so we conducted not only an overall analysis for both data sets, but also performed three additional two-way diet comparisons for all variables in each simulation analysis (herbivore–carnivore, omnivore–herbivore, omnivore–carnivore), resulting in a total of eight phylogenetic simulation analyses for each variable.

## RESULTS

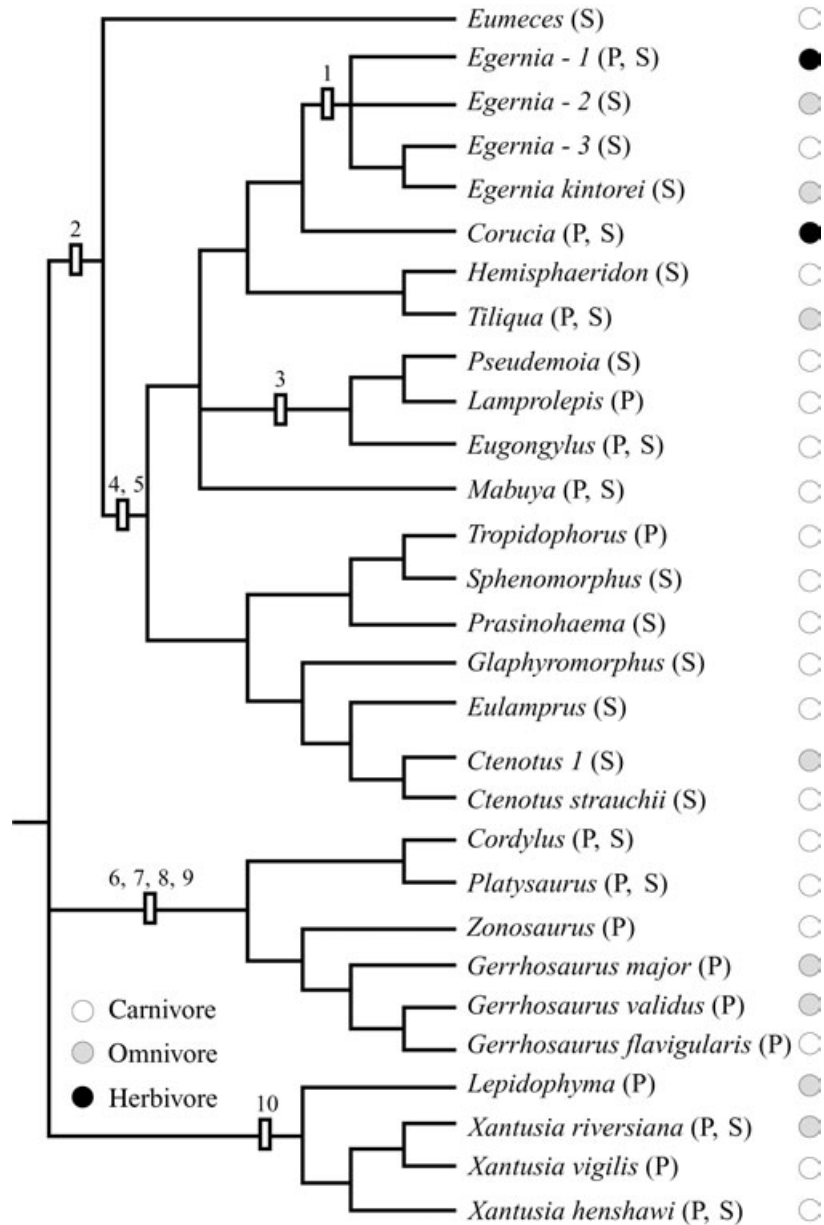
### EVALUATION OF INDEPENDENT VARIABLES

There was a high correlation between SVL (traditionally used as a measure of size) and PSM ( $r^2 = 0.935$ ,  $P < 0.001$ ), indicating that PSM was as appropriate an estimate of body size as SVL.

### NON-PHYLOGENETIC ANALYSES

#### *Post-cranial skeletal mass analysis*

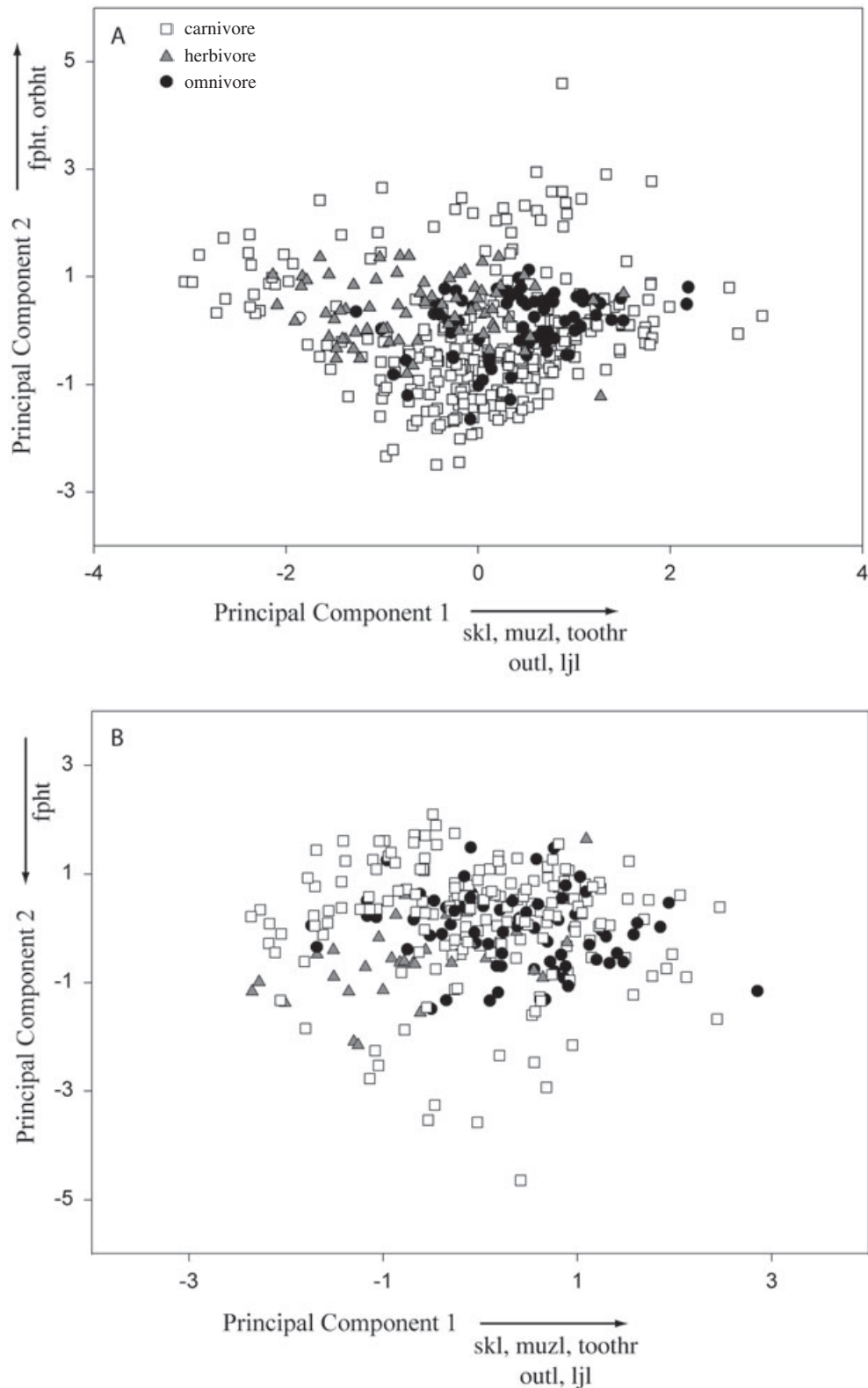
This principal components analysis included 429 specimens (73 herbivores, 73 omnivores, 283 carnivores; Appendix, Fig. 8A). The first two principal components (PCs) were used, cumulatively explaining over 72% of



**Figure 7.** Phylogeny of Scincidae and Cordyliformes (Cordylidae + Gerrhosauridae + Xantusiidae). Phylogeny references: (1) Donnellan *et al.* (2002); (2) Whiting *et al.* (2003); (3) Hutchinson *et al.* (1990); (4) Honda *et al.* (2000); (5) Reeder (2003); (6) Odierna *et al.* (2002); (7) Lamb *et al.* (2003); (8) Frost *et al.* (2001b); (9) Lang (1991); (10) Hedges & Bezy (1993). See Figs 2, 3 legends.

the variance in the data (PC1: 53.1%, PC2: 19.8%, Table 1, left side). Multivariate analysis of variance (MANOVA) conducted with the PC1 and PC2 scores indicated that significant differences existed between diet types (Wilks' Lambda:  $F = 17.112$ ,  $P < 0.001$ ). Univariate ANOVAs indicated differences among diet groups on both PC axes (Tables 2A and 2B). On the first PC axis, length residuals (skull length, muzzle length, lower jaw length, jaw outlever length, too-

throw length) were all heavily loaded ( $> 0.700$ ). *Post hoc* tests showed that herbivorous species had significantly lower PC1 means (generally shorter skulls) than either of the other diet groups on this axis ( $P < 0.001$ ), and omnivores had significantly higher PC1 means than carnivores ( $P = 0.023$ ). The most heavily loaded variables on the second PC axis were height at mid-orbit and height at the frontal-parietal joint. Carnivores had significantly lower PC2 group



**Figure 8.** Plots of principal components analyses on (A) postcranial skeletal mass data set and (B) snout-vent length data set. In both analyses, the first principal component axis is a 'length' axis, and the second is a 'skull height' axis. Herbivores tend to have relatively shorter (in the negative x direction on PC1) and taller (in the positive y direction on PC2 in 2A and the negative y direction on PC2 in 2B) skulls than omnivores or carnivores.

**Table 1.** Results of the principal components (PC) analysis on the two non-phylogenetic data sets. Using a broken stick test, only the first two axes were found to be significant. Bold values indicate high loadings on a particular axis ( $> 0.700$  or  $< -0.700$ ). Results using the two data sets, postcranial skeletal mass (PSM) and snout–vent length (SVL), are extremely similar to each other

Variable	PSM PC1	PSM PC2	SVL PC1	SVL PC2
% variance	53.11	19.75	50.46	15.61
Eigenvalue	5.31	1.98	5.05	1.56
Skull length (skl)	<b>0.915</b>	-0.197	<b>0.829</b>	0.225
Muzzle length (muzl)	<b>0.814</b>	-0.326	<b>0.747</b>	0.416
Height at mid-orbit (orbht)	0.376	<b>0.846</b>	0.640	-0.678
Height at frontal-parietal (fpht)	0.405	<b>0.850</b>	0.627	<b>-0.716</b>
Lower jaw length (ljl)	<b>0.976</b>	-0.109	<b>0.953</b>	0.154
Jaw outlever (outl)	<b>0.975</b>	-0.056	<b>0.956</b>	0.111
Toothrow length (toothr)	<b>0.913</b>	0.156	<b>0.796</b>	-0.107
Joint articulation length (art)	0.341	0.206	0.414	-0.075
Retroarticular process length (open)	0.357	-0.548	0.266	0.520
Adductor lever arm (close)	0.692	-0.094	0.548	0.201

**Table 2.** A, results of univariate ANOVAs of first two PCA factors and of variables not included in principal components analyses, including skull mass (sklmass), mandible height at coronoid (corht), and bimandibular width (bimand). All diet group means are residual means, and significant differences between all groups ( $P < 0.05$ ) are indicated in bold. B, results of Tukey HSD *post hoc* tests for significant variables from the above table for each dietary comparison (herbivore/omnivore, omnivore/carnivore, herbivore/carnivore). Significant differences ( $P < 0.05$ ) are indicated in bold

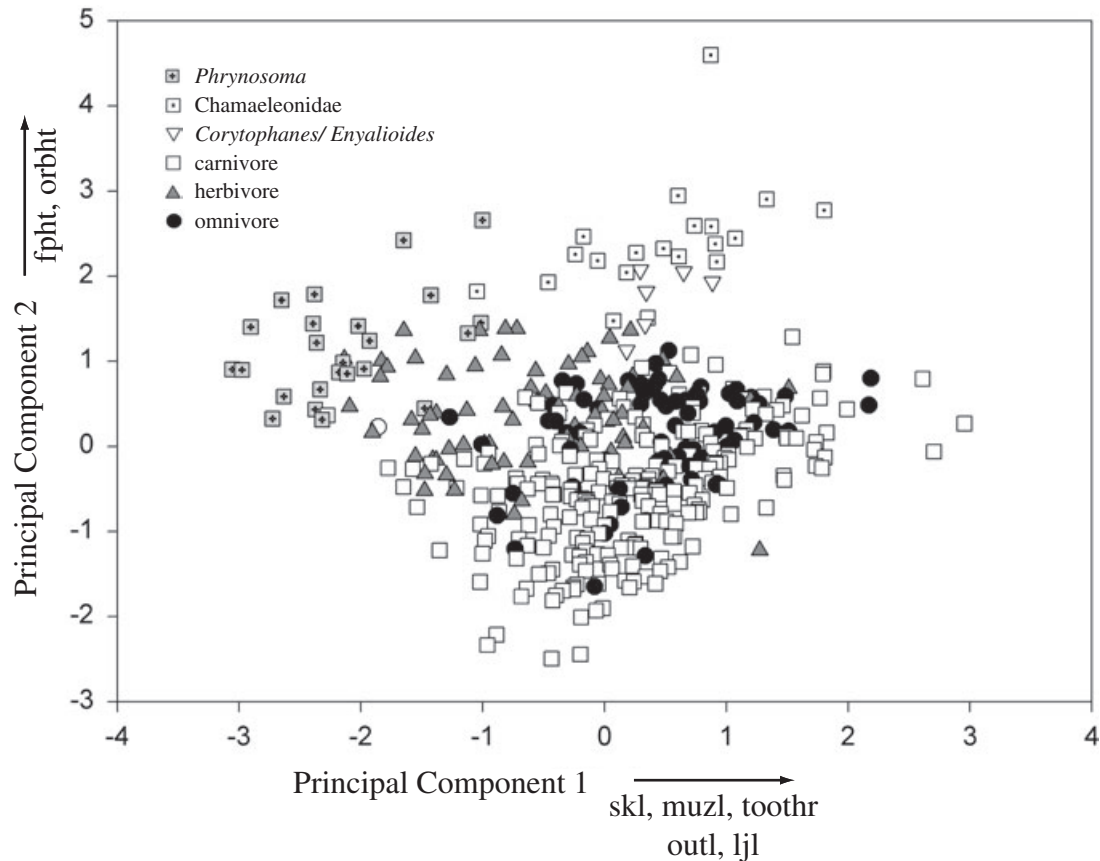
A

Variable	<i>F</i>	<i>P</i>	Herbivore mean	Omnivore mean	Carnivore mean
PSM					
PC1	21.187	<b>&lt; 0.001</b>	-0.606	0.389	0.057
PC2	8.083	<b>&lt; 0.001</b>	0.378	0.105	-0.125
sklmass	10.808	<b>&lt; 0.001</b>	-0.077	0.071	0.001
corht	5.764	<b>0.004</b>	0.006	0.038	-0.012
bimand	1.489	0.227	0.012	0.012	-0.007
SVL					
PC1	11.642	<b>&lt; 0.001</b>	-0.683	0.291	0.019
PC2	5.698	<b>0.004</b>	-0.519	-0.011	0.101
sklmass	6.620	<b>0.002</b>	-0.099	0.063	-0.005
corht	7.348	<b>0.001</b>	-0.005	0.047	-0.016
bimand	5.476	0.005	0.013	0.031	-0.014

B

Variable	Herbivore–omnivore comparison		Omnivore–carnivore comparison		Herbivore–carnivore comparison	
	<i>P</i>	Direction	<i>P</i>	Direction	<i>P</i>	Direction
PSM						
sklmass	<b>&lt; 0.001</b>	<b>H &lt; O</b>	<b>0.016</b>	<b>O &gt; C</b>	<b>0.006</b>	<b>H &lt; C</b>
corht	0.203	ns	<b>0.003</b>	<b>O &gt; C</b>	0.404	ns
SVL						
sklmass	<b>0.001</b>	<b>H &lt; O</b>	0.068	ns	0.05	ns
corht	0.084	ns	<b>&lt; 0.001</b>	<b>O &gt; C</b>	0.858	ns
bimand	0.640	ns	<b>0.004</b>	<b>O &gt; C</b>	0.316	ns





**Figure 9.** Plot of principal component analysis of postcranial skeletal mass data set. Symbols are the same as in Fig. 8, but carnivores have been further divided into chamaeleonids (dotted squares), *Phrynosoma* (cross-hatched shaded squares), *Corytophanes/Enyalioides* (down-pointing open triangles), and all other carnivores (open squares). See text for further discussion.

means (lower skulls) than herbivores ( $P < 0.001$ ). There were no other significant differences between diet groups on this axis.

Univariate ANOVA revealed no significant differences in bimandibular width between diet types ( $F = 1.489$ ,  $P = 0.227$ ). For coronoid height, all comparisons were statistically insignificant except between omnivores and carnivores (omnivores  $>$  carnivores;  $P = 0.003$ ). For skull mass, all diet groups differed significantly from each other. On average, omnivores had the heaviest skulls, followed by carnivores, and then herbivores with the lightest skulls (Table 2A, B).

A plot of the two significant principal component factors (Fig. 9, from the PSM data set) indicates that the majority of the carnivorous species that have PC2 (height axis) scores higher than the herbivore and omnivore means are either chamaeleonids or belong to the genera *Phrynosoma*, *Corytophanes*, or *Enyalioides*. All of these species are carnivores with a relatively high degree of dorsal cranial ornamentation, explaining their location on this axis. Despite their

overlap with the herbivorous lizards, elimination of these species does not result in more highly significant results in either of the MANOVAs.

There were significant differences in PSM between all diet groups ( $F = 32.855$ ,  $P < 0.001$ ). *Post hoc* tests indicated that all groups were significantly different from each other, except for herbivores and omnivores ( $P = 0.072$ ). On average, herbivores had the heaviest PSM, followed by omnivores and then carnivores with the lightest average PSM (Table 3).

#### *Snout-vent length analysis*

This PCA included 285 specimens (34 herbivores, 68 omnivores, 183 carnivores; Appendix, Fig. 8B). In general, the results were similar to the PSM analysis. The first two PCs were significant, cumulatively explaining over 66% of the variance in the data (PC1: 50.5%, PC2: 15.6%, Table 1, right side). MANOVA conducted with the PC1 and PC2 scores indicated that significant differences existed between diet types (Wilks' Lambda:  $F = 9.991$ ,  $P < 0.001$ ). Univariate ANOVAs

**Table 3.** Results of analyses examining differences in body size among diet groups. For the non-phylogenetically corrected data set, *post hoc* testing indicates that herbivores do not have a significantly different postcranial skeletal mass than omnivores ( $P = 0.072$ ) and omnivores do not have a significantly different snout–vent length than carnivores ( $P = 0.062$ ). All other two group comparisons are different from each other ( $P < 0.001$ ). For a result from the phylogenetic simulation analysis to be significant (at  $P < 0.05$ ), the  $F$ -statistic ( $F$ ) must be greater than the phylogenetic  $F$ -statistic ( $F_{\text{phylo}}$ ). In both phylogenetic simulation analyses, all groups are significantly different from each other ( $P < 0.001$ ) with the same body size trend (herbivore > omnivore > carnivore)

Variable	$F$	$F_{\text{phylo}}$	$P$	Herbivore mean	Omnivore mean	Carnivore mean
PSM	32.85	11.19	< 0.001	1.077	0.785	0.295
SVL	29.13	7.09	< 0.001	2.243	2.006	1.936

and *post hoc* tests indicated differences among diet groups on both PC axes (Table 2A, B). On the first PC axis, length residuals (skull length, muzzle length, lower jaw length, jaw outlever length, and toothrow length) were all heavily loaded ( $> 0.700$ ). As before, all diet groups were significantly different from each other ( $P < 0.001$ ) with herbivores scoring lowest and omnivores scoring highest. On the second PC axis, the most significantly loaded variables were again the two height measures. Herbivores had significantly lower PC2 group means than omnivores and carnivores ( $P < 0.001$ ; in this analysis, the two height measures had high negative loading), indicating a trend towards higher skulls in herbivores. Omnivore and carnivore PC2 group means did not differ significantly from each other ( $P = 0.703$ ).

Univariate ANOVA of bimandibular width showed that all comparisons were statistically insignificant except between omnivores and carnivores (omnivores > carnivores;  $P = 0.004$ ). Similarly, for coronoid height, the only significant difference was between omnivores and carnivores (omnivores > carnivores;  $P < 0.001$ , Table 2A). For skull mass, the same trend existed as in the PSM analysis (omnivores > carnivores > herbivores, Table 2B), but only omnivores and herbivores were significantly different from each other ( $P < 0.001$ ; the carnivore/herbivore comparison approached significance,  $P = 0.05$ ).

As for PSM, there were also significant differences in SVL between all diet groups ( $F = 29.130$ ,  $P < 0.001$ ). *Post hoc* testing indicated that all groups were significantly different from each other, except for omnivores and carnivores ( $P = 0.062$ ). On average, herbivores had the longest SVL, followed by omnivores and then carnivores with the shortest average SVL (Table 3).

#### PHYLOGENETIC SIMULATION ANALYSIS

Fewer differences between dietary groups could be demonstrated in the phylogenetic simulation analysis than in the non-phylogenetic one. For the postcranial

mass data set, all  $F_{\text{phylo}}$  values were larger than their respective traditional  $F$ -values (Table 4, left side). However, several comparisons approached significance. The phylogenetic skull length comparison with all three diet groups was significant at  $P = 0.089$ , and the omnivore–herbivore contrast showed that omnivores tended towards having longer muzzles than herbivores ( $P = 0.095$ ). The SVL data set analysis showed significant differences between groups (Table 4, right side). Muzzle length differed significantly among all diet groups (herbivores less than carnivores and omnivores,  $F_{\text{phylo}} = 6.832$ ,  $P = 0.042$ ), and skull mass in herbivores was significantly less than omnivore skull mass ( $F_{\text{phylo}} = 10.432$ ,  $P = 0.025$ ). Similar to the principal components analysis, a separate phylogenetic simulation analysis that excluded the carnivorous outliers (Chamaeleonidae, *Phrynosoma*, *Corytophanes*, *Enyalioides*) did not result in significantly lower  $F_{\text{phylo}}$  values. For both data sets, there were significant differences in body size (PSM and SVL) between groups ( $P < 0.001$ ; Table 3).

#### DISCUSSION

By creating two partially overlapping data sets (postcranial skeletal mass and snout–vent length), we were able to get an indication of the robustness of our results. Approximately 11% of the specimens sampled were included in both analyses, giving us relatively independent datasets with a different assemblage of species represented in each. Despite this, the results from both of the PCAs were extremely similar, with almost the exact same variables loading highly on each axis (with the exception of height at mid-orbit, Table 1). Univariate ANOVAs of variables not included in the PCA were also similar, and the directionality of the two-way dietary comparisons was always the same between both data sets (Table 2A, B). For the phylogenetic simulation analysis there were differences in the significance of the results between the two analyses (i.e. no results from the PSM analysis were

**Table 4.** Results of phylogenetic simulation analyses using the postcranial skeletal mass (PSM) and snout–vent length (SVL) data sets. Abbreviations for variables found in text are displayed in Fig. 1. For a result from the phylogenetic simulation analysis to be significant (at  $P < 0.05$ ), the  $F$ -statistic ( $F$ ) must be greater than the phylogenetic  $F$ -statistic ( $F_{\text{phylo}}$ ). Significant results from the 3-group analysis, as well as the three 2-group comparisons (herbivore–omnivore, omnivore–carnivore, herbivore–carnivore) are indicated in bold. Results approaching significance ( $0.10 < P < 0.05$ ) are indicated in italics

Variable	PSM			SVL			
	$F$	$F_{\text{phylo}}$	$P$	$F$	$F_{\text{phylo}}$	$P$	$P$
3-GROUP							
skl <sub>mass</sub>	4.24	11.52	0.254	5.89	7.93		<i>0.074</i>
skl	7.63	10.23	<i>0.089</i>	4.24	6.42		0.124
muzl	6.80	8.97	0.118	<b>7.12</b>	<b>6.83</b>		<b>0.042</b>
fpht	2.05	9.30	0.444	1.76	7.06		0.398
open	1.05	9.03	0.640	1.29	6.65		0.502
HERBIVORE–OMNIVORE							
skl <sub>mass</sub>	5.14	13.23	0.254	<b>13.43</b>	<b>10.44</b>		<b>0.025</b>
skl	6.07	12.96	0.201	3.96	9.75		0.207
muzl	10.92	13.98	<i>0.095</i>	5.84	10.82		0.140
fpht	7.33	12.61	0.148	2.30	9.49		0.378
open	0.30	14.74	0.784	0.19	9.48		0.800
OMNIVORE–CARNIVORE							
skl <sub>mass</sub>	0.54	3.73	0.470	0.38	3.12		0.514
skl	1.74	3.95	0.205	0.10	3.37		0.749
muzl	1.91	3.92	0.180	1.68	3.02		0.173
fpht	0.84	3.66	0.344	0.65	3.47		0.400
open	1.81	3.82	0.186	2.41	3.14		<i>0.089</i>
HERBIVORE–CARNIVORE							
skl <sub>mass</sub>	8.02	17.81	0.214	7.29	14.27		0.155
skl	13.91	17.89	0.109	6.73	12.26		0.157
muzl	10.54	18.77	0.158	11.99	12.71		<i>0.054</i>
fpht	2.59	19.41	0.526	2.63	11.34		0.389
open	0.51	17.95	0.750	0.07	13.29		0.886

significant), but we believe that this is most likely due to the differences in the phylogeny that was used (see below). The general similarity of results from the two data sets, especially considering the lack of specimen overlap, is additional confirmation of the validity of these results.

Our assessment of diet was based upon published accounts that often varied greatly in the degree of detail presented. Additionally, for several species, we were unable to obtain any data, so diet had to be extrapolated based on that of the most closely related species. Despite the relative ambiguity for a few groups, we still see clear patterns associating diet with skull morphology. Quantitative reviews of diet in lizards would help to establish whether gradation in diet (e.g. amount of plant material consumed) is reflected with a corresponding morphological gradient both within and between diet categories. Additionally, material testing of various food items would test the

validity of dietary categories as mechanically similar units (but see Herrel *et al.*, 1999b), which is highly relevant considering that our mechanical predictions are based on the assumption that herbivores are faced with the challenge of processing tough and fibrous food items (see also Schwenk, 2000).

As there was little overlap between our two data sets, there were differences between the phylogenies in our two simulation analyses (~43% of genera/subgeneric diet groups were present in both). Two characteristics of these phylogenies, the presence of polytomies and ‘clustering’ of dietary groups in portions of the tree may affect the utility of variables in distinguishing between diet types (Garland *et al.*, 1993; Vanhooydonck & Van Damme, 1999). In both of the integrated phylogenies that we used (for the PSM and SVL data sets), there were few hard or soft polytomies. Regardless, it is not expected that lack of phylogenetic resolution should have a significant adverse

effect on  $F_{\text{phylo}}$  values, especially at the levels seen in our phylogeny. Trait clustering, on the other hand, has been demonstrated to raise  $F_{\text{phylo}}$  values, negatively affecting the significance of these results (Garland *et al.*, 1993; Vanhooydonck & Van Damme, 1999).

The distribution of diet groups across our phylogeny may explain why we have significant results from our simulation analysis of the SVL data set but not the PSM data set. Carnivorous genera/subgeneric diet groups are common in all families, but the number of independent occurrences of omnivory and herbivory differs between the two data sets. In the PSM phylogeny, there are 17 independent origins of omnivory and only four of herbivory, while in the SVL data set there are 19 origins of omnivory and six of herbivory. Omnivory is relatively widespread in both data sets, but the relative paucity of herbivores may have led to decreased significance of results in the SVL analysis. These results could potentially be strengthened by the inclusion of herbivorous species for which we were unable to obtain data (e.g. *Phymaturus palluma* [Tropiduridae], *Angolosaurus skoogi* [Gerrhosauridae]).

For lepidosaurs, SVL is a convenient and easily measured proxy for body size, especially in nonskeletonized specimens. Results from this study indicate that PSM is highly correlated with SVL, and therefore can be accurately used in order to remove size from morphometric analyses. Pough (1973) was the first to suggest that herbivorous lizards have a higher average body mass than carnivorous ones, but until now, this has not been quantitatively tested across a wide range of lizards (but see Schluter, 1984; Van Damme, 1999; Herrel, in press). Our results strongly confirm Pough's hypothesis when framed in a phylogenetic context across a large diversity of lizard families, although there are some obvious exceptions (i.e. large-bodied carnivorous varanids). The explanation for this correlation is still unclear, and our results can not address this issue (see Van Damme, 1999 for further discussion).

In contrast to previously published statements (Greene, 1982; King, 1996; Schwenk, 2000), there does appear to be a clear relationship between dietary and phenotypic specialization in lepidosaurs. As indicated in the non-phylogenetic analyses, herbivores show a tendency towards having skulls, muzzles, retroarticular processes and tooththrows with a relatively reduced length and relatively taller skulls than those of both carnivores and omnivores. These results were highly significant and confirmed our predictions that herbivory is associated with increased skull height and carnivory with increased muzzle, skull, tooththrow, and retroarticular process lengths. There are clear mechanical implications for each of these differences, but they cannot be viewed as mechanical adaptations

*per se*. While the results of the non-phylogenetic analyses indicate strong correlations between diet type and morphology across a wide taxonomic range of lepidosaurs, only the significant results from the phylogenetic simulation analysis are suggestive of possible phenotypic adaptations for a specific diet.

As noted above, the phylogenetic simulation analysis yielded fewer significant results, but there is still a trend towards carnivorous and omnivorous species having longer muzzles than herbivorous ones. We suggest that this may be a possible adaptation for prey capture. A longer snout (and presumably longer tooththrow, although we did not examine this variable in the simulation analysis) increases the likelihood of successful captures of elusive insect or vertebrate prey items because the jaw opening and closing velocities are higher. For lepidosaurs that use jaw prehension as their prey capture technique (as opposed to lingual prehension) this advantage might be especially large. This result is relevant to a recent study (Vitt *et al.*, 2003), which related various aspects of the feeding system in squamates (including the shift to jaw prehension) to the group's historical diversification and current geographical distribution. Although Vitt *et al.* (2003) examine evolution of this system in the context of dietary transitions within carnivorous species only, it is possible that the morphological differences found in our analysis are relevant to their hypothesis that the evolution of scleroglossans and jaw prehension is linked to a detectable shift in prey type. A more detailed examination of the components of a carnivorous diet (rather than grouping all carnivores together in a single diet group as we have done here) and the relationship to cranial morphology, would be a logical next step to explore these issues.

The skulls of herbivorous species were relatively lighter than those of carnivorous ones. This was contrary to our original prediction, which stated that herbivores would have heavy skulls to resist high bite forces. It is possible that safety factors in the skulls of herbivorous species are high relative to the bite forces that they generate, but this does still not explain the relative lightness in their skulls, seen in both the non-phylogenetic and phylogenetic simulation analyses. A modelling study by Herrel, Aerts & De Vree (1998) may address our finding here. The results of that study indicate that, for a given bite force, herbivorous lizards have lower joint reaction forces. This suggests that because of the shape and design of the skull, equal magnitude forces transmitted through the jaw joint may have less impact on the skull of a herbivorous lizard than a carnivorous lizard, decreasing the need for a massively built skull. Additionally, altering the orientation of the food reaction force away from being perpendicular to the tooththrow drastically increases joint reaction forces. Herbivorous lizards feeding on nonmo-



bile prey might be expected to have more predictable food reaction force orientations, reducing this need for a heavy skull even further. More detailed morphometric shape-based analyses (see Stayton, 2005) and examination of bone density and safety factors in lizard crania may help to resolve fine differences in skull morphology between herbivores, omnivores and carnivores to address this question.

An omnivorous lifestyle increases prey availability in habitats with seasonal floral and faunal variation (Cooper & Vitt, 2002), and omnivory may often originate in this type of ecological context. Considering the correlations between diet and phenotype seen in this study, it is reasonable to ask whether, for a given morphological feature, omnivorous lizards group together with herbivores or carnivores. Are omnivores phenotypically 'specialized' for consumption of both plant and animal materials? The results presented here provide no clear answer to this question. The PCA indicates that omnivores have a significantly higher group mean on the length axis than either herbivores or carnivores, and have a significantly lower mean than herbivores on the skull height axis. Additionally, the phylogenetic simulation results give few indications of the presence of an adaptive morphology in omnivorous species.

Our examination of omnivores does not suggest that they are morphologically 'intermediate' in skull form, and they appear to have a morphology unique from that of both herbivores and carnivores. Results from the non-phylogenetic univariate ANOVAs show that omnivores, while not differing from herbivores, do have wider mandibles (similar to head width) and higher coronoid processes. This may indicate specializations for hard biting (potentially increasing jaw closing muscle mass and attachment area), and is further evidence of their skull morphology that is distinct from both other diet groups. Studies including more detailed dietary and morphological information may shed further light on this issue.

This study has established that there is indeed a relationship between diet and cranial morphology in lepidosaurs, and that there is a biomechanically relevant basis for many of the patterns that are seen. The evidence for adaptive morphology is less strong, but in some cases still exists. A logical next step would be to investigate whether the morphological differences seen between dietary groups are linked to any differences in feeding performance, data that would reveal more about potential adaptations to diet in the lepidosaur trophic apparatus. Maximal bite force is a good measure of feeding performance from a mechanical standpoint (Herrel, Van Damme & De Vree, 1996, 2001a, b), although alternative measures of feeding performance (e.g. processing speed, foraging efficiency) are also important.

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## APPENDIX

Dietary data for species included in this study. Species are grouped alphabetically by family, with the number of specimens measured after each species name. Mark in PSM or SVL column indicates that the species was included in the postcranial skeletal mass and/or snout–vent length principal components analysis. Diet types include herbivorous (H), omnivorous (O) and carnivorous (C). Criteria for diet determination included in the main text. Type of data used to assess diet also indicated. M/V: percentage by mass/volume; N, percentage by number; F, frequency present; Q, qualitative data. For some species (e.g. some gekkonids), diet type determined based on closely related species. \*based on carnivory in . . . ; \*\*based on omnivory in . . .

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
AGAMIDAE								
<i>Acanthosaura crucigera</i> (1)	X	X	C				X	Manthey & Grossman (1997)
<i>Agama agama</i> (2)	X		C				X	Spawls <i>et al.</i> (2002)
<i>Amphibolurus nobbi</i> (1)		X	C				X	Witten & Heatwole (1978)
<i>Bronchocela cristatella</i> (6)	X		C	* <i>Gonocephalus</i>				Manning (1992) in Greer (2003)
<i>Bronchocela jubata</i> (2)	X		C	* <i>Gonocephalus</i>				Manning (1992) in Greer (2003)
<i>Bronchocela marmorata</i> (2)	X		C	* <i>Gonocephalus</i>				Manning (1992) in Greer (2003)
<i>Calotes calotes</i> (1)	X		C	* <i>C. versicolor</i>				Manthey & Grossman (1997)
<i>Calotes nigrilabris</i> (1)	X		C	* <i>C. versicolor</i>				Manthey & Grossman (1997)
<i>Calotes versicolor</i> (3)	X		C				X	Manthey & Grossman (1997)
<i>Chlamydosaurus kingii</i> (2)	X	X	C	X	X	X	X	Greer (1989); Shine & Lambeck (1989); Griffiths & Christian (1996)
<i>Ctenophorus decresii</i> (1)		X	C				X	Gibbons & Lillywhite (1981)
<i>Ctenophorus fionni</i> (4)		X	C				X	Gibbons & Lillywhite (1981)
<i>Ctenophorus fordi</i> (1)		X	C	X				Pianka (1986)
<i>Ctenophorus isolepis</i> (2)		X	C	X				Pianka (1986)
<i>Ctenophorus nuchalis</i> (2)		X	O	X				Pianka (1986)
<i>Ctenophorus reticulatus</i> (3)		X	O	X				Pianka (1986)
<i>Diporiphora bilineata</i> (1)	X		C				X	Gow & Swanson (1977)
<i>Diporiphora winneckeii</i> (1)	X		O				X	Houston (1998)
<i>Gonocephalus liogaster</i> (2)	X		C	* <i>G. spinipes</i>				Manning (1992) in Greer (2003)
<i>Hypsilurus dilophus</i> (1)		X	C	* <i>H. boydii</i>			X	Torr (1993)
<i>Laudakia stellio</i> (1)		X	O		X		X	Disi <i>et al.</i> (2001); Dusen & Oz (2001)
<i>Lophognathus longirostris</i> (1)		X	C	* <i>L. temporalis</i>			X	Christian <i>et al.</i> (1989)
<i>Physignathus cocinctus</i> (2)	X		O				X	Greer (1989)
<i>Physignathus lesueurii</i> (2)	X		O				X	Greer (1989)
<i>Pogona barbata</i> (6)	X		O				X	Houston (1998)
<i>Pogona vitticeps</i> (3)	X	X	O	X	X		X	Kennerson & Cochrane (1981); MacMillen <i>et al.</i> (1989)
<i>Pseudocalotes tympanistriga</i> (3)	X		C	* <i>Acanthosaura</i>				Manthey & Grossman (1997)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Salea kahkhiensis</i> (2)	X		C	* <i>Gonocephalus</i>				Manning (1992) in Greer (2003)
<i>Tympanocryptis lineata</i> (2)		X	C	X	X			MacMillen <i>et al.</i> (1989)
<i>Tympanocryptis tetraporphora</i> (1)		X	C	*other <i>Tympanocryptis</i> (2 spp.)				Pough (1973); MacMillen <i>et al.</i> (1989)
ANGUIDAE								
<i>Anguis fragilis</i> (1)		X	C			X	X	Capizzi <i>et al.</i> (1998)
<i>Diploglossus fasciatus</i> (1)		X	C	X	* <i>D. lessonae</i>			Vitt (1995)
<i>Diploglossus millepunctatus</i> (1)	X		C	X	* <i>D. lessonae</i>			Vitt (1995)
<i>Elgaria multicarinata</i> (2)	X	X	C				X	Grismer (2002); Stebbins (2003)
<i>Gerrhonotus liocephalus</i> (2)	X	X	C				X	Conant & Collins (1998)
CHAMAELEONIDAE								
<i>Calumma parsonii</i> (2)	X		C				X	Henkel & Schmidt (2000)
<i>Chamaeleo calypttratus</i> (2)	X	X	C				X	Schmidt (2001)
<i>Chamaeleo chamaeleon</i> (5)	X	X	C				X	Schleich <i>et al.</i> (1996); Disi <i>et al.</i> (2001)
<i>Chamaeleo dilepis</i> (3)	X	X	C				X	Branch (1998); Spawls <i>et al.</i> (2002)
<i>Chamaeleo gracilis</i> (2)	X		C				X	Spawls <i>et al.</i> (2002)
<i>Chamaeleo jacksonii</i> (3)	X		C				X	Spawls <i>et al.</i> (2002)
<i>Chamaeleo namaquensis</i> (1)	X	X	C				X	Branch (1998)
<i>Chamaeleo oweni</i> (1)	X		C	*all other Chamaeleonidae				
<i>Furcifer oustaleti</i> (2)	X	X	C				X	Spawls <i>et al.</i> (2002)
<i>Furcifer pardalis</i> (1)	X	X	C	*all other Chamaeleonidae				
CORDYLIDAE								
<i>Cordylus cordylus</i> (8)	X		C				X	Branch (1998); M. Whiting, pers. comm.
<i>Cordylus giganteus</i> (4)	X	X	C	X	X		X	Branch (1998); van Wyk (2000); M. Whiting, pers. comm.
<i>Cordylus microlepidotus</i> (2)	X		C				X	M. Whiting, pers. comm.
<i>Cordylus niger</i> (2)	X		C				X	M. Whiting, pers. comm.
<i>Cordylus tropidosternum</i> (1)	X	X	C				X	Branch (1998); Spawls <i>et al.</i> (2002)
<i>Cordylus vittifer</i> (2)	X	X	C				X	M. Whiting, pers. comm.
<i>Cordylus warreni</i> (1)	X		C				X	M. Whiting, pers. comm.
<i>Platysaurus guttatus</i> (5)	X	X	C				X	M. Whiting, pers. comm.
<i>Platysaurus imperator</i> (2)	X	X	C				X	Branch (1998); M. Whiting, pers. comm.
<i>Platysaurus mitchelli</i> (1)	X	X	C				X	M. Whiting, pers. comm.
CORYTOPHANIDAE								
<i>Basiliscus basiliscus</i> (2)	X	X	O	X			X	Barden (1943); Savage (2002)
<i>Basiliscus galeterius</i> (2)	X	X	O	**all other <i>Basiliscus</i>				

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Basiliscus plumifrons</i> (3)	X	X	O	X	X		X	Vitt & Zani (1998); Cooper & Vitt (2002); Savage (2002)
<i>Basiliscus vittatus</i> (9)	X	X	O	X			X	Hirth (1963); Lee (1996); Savage (2002)
<i>Corytophanes cristatus</i> (5)	X	X	C	X		X	X	Andrews (1979); Lee (1996); Vitt & Zani (1998); Savage (2002)
<i>Corytophanes hernandesii</i> (1)	X	X	C				X	Lee (1996)
<i>Laemanctus serratus</i> (1)		X	C				X	Lee (1996)
CROTAPHYTIDAE								
<i>Crotaphytus collaris</i> (5)	X		C	X	X		X	Hotton (1955); Whitaker & Maser (1981); Best & Pfaffenberger (1987)
GEKKONIDAE								
<i>Cyrtodactylus phillipinicus</i> (1)	X		C	* <i>C. louisiadensis</i>			X	Greer (2003)
<i>Diplodactylus stenodactylus</i> (1)		X	C				X	Greer (1989)
<i>Diplodactylus tessallatus</i> (1)		X	C				X	Greer (1989)
<i>Diplodactylus vittatus</i> (1)		X	C				X	Greer (1989)
<i>Gehyra purparescens</i> (1)		X	C	based on other <i>Gehyra</i> species (2 spp.)				Greer (2003)
<i>Gekko gekko</i> (14)	X	X	C				X	Manthey & Grossman (1997)
<i>Gonatodes humeralis</i> (1)		X	C	X	X	X	X	Avila-Pires (1995); Miranda & Andrade (2003); Vitt <i>et al.</i> (2000)
<i>Gymnodactylus darwinii</i> (1)		X	C	X	X	X		Colli <i>et al.</i> (2003)
<i>Hemitheconyx caudicinctus</i> (2)	X	X	C	*all other Gekkonidae				
<i>Hoplodactylus pacificus</i> (4)	X	X	C				X	Whitaker (1987)
<i>Lucasium damaeum</i> (1)		X	C	*all other Gekkonidae				
<i>Nephurus asper</i> (1)	X		C	*all other Gekkonidae, <i>N. levis</i>				
<i>Nephurus levis</i> (1)		X	C	X				Pianka (1986)
<i>Nephurus stellatus</i> (1)		X	C	*all other Gekkonidae				
<i>Oedura tryoni</i> (1)		X	C				X	Greer (1989)
<i>Phelsuma dubia</i> (1)	X		C				X	Spawls <i>et al.</i> (2002)
<i>Phelsuma madagascariensis</i> (1)		X	C				X	Garcia & Vences (2002)
<i>Thecadactylus rapicauda</i> (7)	X	X	C				X	Avila-Pires (1995); Lee (1996)
<i>Underwoodisaurus milii</i> (2)		X	C				X	How <i>et al.</i> (1990) in Greer (2003)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Uroplatus fimbriatus</i> (2)	X		C	*all other Gekkonidae				
GERRHOSAURIDAE								
<i>Gerrhosaurus flavigularis</i> (2)	X		C				X	Spawls <i>et al.</i> (2002)
<i>Gerrhosaurus major</i> (1)	X		O				X	Cooper & Vitt (2002)
<i>Gerrhosaurus validus</i> (2)	X		O				X	Cooper & Vitt (2002)
<i>Zonosaurus trilineatus</i> (1)	X		C				X	Henkel & Schmidt (2000)
GYMNOPHTALMIDAE								
<i>Leposoma percarinatum</i> (1)		X	C		X		X	Avila-Pires (1995); Texeira & Fonseca (2003)
HELODERMATIDAE								
<i>Heloderma horridum</i> (2)	X		C				X	Stebbins (2003); Herrel <i>et al.</i> (1997); Beck & Lowe (1991)
<i>Heloderma suspectum</i> (4)	X		C				X	Beck (1990); Stebbins (2003)
HOPLOCERCIDAE								
<i>Enyalioides palpebralis</i> (1)	X		C				X	Avila-Pires (1995)
IGUANIDAE								
<i>Amblyrhynchus cristatus</i> (9)	X	X	H	X			X	Wikelski <i>et al.</i> (1993); Wikelski <i>et al.</i> (1997); Durtsche (2000); Rubenstein & Wikelski (2003)
<i>Conolophus pallidus</i> (3)	X		H				X	Christian <i>et al.</i> (1984)
<i>Conolophus subcristatus</i> (4)	X		H				X	Christian <i>et al.</i> (1984)
<i>Ctenosaura acanthura</i> (1)	X		H				X	Christian <i>et al.</i> (1984)
<i>Ctenosaura hemilopha</i> (5)	X	X	H				X	Grismer (2002)
<i>Ctenosaura pectinata</i> (2)	X		H	X			X	Durtsche (2000); Benitez- Malvido <i>et al.</i> (2003)
<i>Ctenosaura similis</i> (3)	X	X	H				X	Hotton (1955); Savage (2002)
<i>Cyclura carinata</i> (1)	X		H				X	Gonzalez-Rossell <i>et al.</i> (2001)
<i>Cyclura cornuta</i> (2)	X	X	H				X	Rivero (1998)
<i>Dipsosaurus dorsalis</i> (13)	X	X	H	X			X	Hotton (1955); Minnich & Shoemaker (1970); Mautz & Nagy (1987)
<i>Iguana iguana</i> (11)	X	X	H				X	Montanucci (1968); Troyer (1984); Savage (2002); Benitez- Malvido <i>et al.</i> (2003)
<i>Sauromalus ater</i> (2)	X	X	H	X				Nagy (1973); Nagy & Shoemaker (1975)
<i>Sauromalus hispidus</i> (1)	X	X	H	X			X	Sylber (1988); Grismer (2002)
LACERTIDAE								
<i>Acanthodactylus boskianus</i> (2)		X	C	X			X	Schleich <i>et al.</i> (1996); Disi <i>et al.</i> (2001)



APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Acanthodactylus pardalis</i> (3)		X	C		X		X	Schleich <i>et al.</i> (1996)
<i>Gallotia galloti</i> (1)		X	H			X	X	Valido & Nogales (2003)
<i>Lacerta bedriagae</i> (3)		X	O				X	Castilla <i>et al.</i> (1989)
<i>Lacerta bilineata</i> (1)		X	C	X			X	Nettmann & Rykena (1984)
<i>Lacerta dugesii</i> (2)	X		O	X	X	X	X	Sadek (1981)
<i>Lacerta lepida</i> (7)	X	X	O				X	Castilla <i>et al.</i> (1991)
<i>Lacerta vivipara</i> (3)		X	C	X	X		X	Pilorge (1982); Heulin (1986); Koponen & Hietakangas (1972)
<i>Latastia longicaudata</i> (6)	X	X	C				X	Spawls <i>et al.</i> (2002)
<i>Podarcis atrata</i> (1)		X	O	X			X	Castilla & Bauwens (1991)
<i>Podarcis erhardii</i> (1)	X	X	C	X			X	Quayle (1983); Vallakos (1986)
<i>Podarcis hispanica</i> (3)		X	C				X	Schleich <i>et al.</i> (1996)
<i>Podarcis lilfordi</i> (2)		X	O	X			X	Brown & Perez-Mellado (1994); Castilla (1999)
<i>Podarcis melisellensis</i> (1)		X	C	X			X	Tiedemann & Henle (1986)
<i>Podarcis muralis</i> (3)		X	C		X	X		Mou & Barbault (1986); Bombi & Bologna (2002)
<i>Podarcis sicula</i> (3)		X	C		X	X		Bombi & Bologna (2002); Burke & Mercurio (2002);
<i>Podarcis taurica</i> (1)	X		C			X		Chondropoulos <i>et al.</i> (1993)
<i>Podarcis tiliguerta</i> (3)		X	C		X	X		Capula & Luiselli (1994)
<i>Psammotromus algirus</i> (6)	X		C	X	X	X	X	Diaz & Carrascal (1990); Carretero & Llorente (1993); Schleich <i>et al.</i> (1996)
<i>Takydromus sexlineatus</i> (1)		X	C	X			X	Manthey & Grossmann (1997); Cooper <i>et al.</i> (2000);
<i>Takydromus septentrionalis</i> (4)	X	X	C	X			X	Xiang <i>et al.</i> (1993); Xiang <i>et al.</i> (1996)
LEIOCEPHALIDAE								
<i>Leiocephalus carinatus</i> (2)	X	X	C	X				Schoener <i>et al.</i> (1982)
<i>Leiocephalus inaguae</i> (2)	X	X	O	X				Schoener <i>et al.</i> (1982)
LEIOLEPIDIDAE								
<i>Uromastix acanthinura</i> (7)	X	X	H	X			X	Dubuis <i>et al.</i> (1971); Schleich <i>et al.</i> (1996)
<i>Uromastix aegyptia</i> (3)	X	X	H	X			X	Foley <i>et al.</i> (1992); Disi <i>et al.</i> (2001)
<i>Uromastix hardwickii</i> (6)	X	X	H				X	Wilms (1995)
<i>Uromastix ocellata</i> (1)	X	X	H				X	Wilms (1995)
<i>Uromastix princeps</i> (3)	X		H				X	Wilms (1995)
LIOLAEMIDAE								
<i>Liolaemus nitidus</i> (1)		X	C				X	Donoso-Barros (1966)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Liolaemus signifer</i> (4)	X	X	O				X	Donoso-Barros (1966)
PHRYNOSOMATIDAE								
<i>Callisaurus draconoides</i> (4)	X	X	C				X	Hotton (1955); Grismer (2002); Stebbins (2003)
<i>Cophosaurus texanus</i> (1)	X	X	C	X	X			Maury (1995); Durtsche <i>et al.</i> (1997)
<i>Petrosaurus thalassinus</i> (2)	X	X	C				X	Grismer (2002)
<i>Phrynosoma cornutum</i> (13)	X	X	C				X	Hotton (1955); Sherbrooke (2003)
<i>Phrynosoma douglassii</i> (5)	X	X	C	X	X		X	Hotton (1955); Montanucci (1981); Powell & Russell (1984); Stebbins (2003)
<i>Phrynosoma mcallii</i> (1)	X		C				X	Sherbrooke (2003)
<i>Phrynosoma modestum</i> (2)	X		C				X	Sherbrooke (2003)
<i>Phrynosoma platyrhinos</i> (12)	X	X	C	X	X		X	Hotton (1955); Pianka & Parker (1975); Sherbrooke (2003)
<i>Phrynosoma solare</i> (4)	X		C				X	Sherbrooke (2003); Stebbins (2003)
<i>Sceloporus aeneus</i> (1)	X		C	X				Gutiérrez-Mayén & Sánchez-Trejo (1986)
<i>Sceloporus clarkii</i> (3)	X		C				X	Grismer (2002)
<i>Sceloporus couchii</i> (2)	X		C	*other <i>Sceloporus</i>				
<i>Sceloporus gadovae</i> (2)	X		C	*other <i>Sceloporus</i>				
<i>Sceloporus grammicus</i> (2)	X		C	X			X	Barbault <i>et al.</i> (1985); Gutiérrez-Mayén & Sánchez-Trejo (1986)
<i>Sceloporus magister</i> (1)	X	X	C	X	X		X	Hotton (1955); Johnson (1966); Vitt <i>et al.</i> (1981); Grismer (2002)
<i>Sceloporus malachiticus</i> (2)	X		C				X	Savage (2002)
<i>Sceloporus poinsettii</i> (3)		X	O				X	Barbault <i>et al.</i> (1985); Stebbins (2003)
<i>Sceloporus undulatus</i> (1)		X	C	X	X		X	Hotton (1955); Johnson (1966); DeMarco (1985); Lemos-Espinal <i>et al.</i> (2003b); Stebbins (2003)
<i>Uma inornata</i> (1)	X		O	X	X		X	Durtsche (1995); Turner & Schwalbe (1998)
POLYCHROTIDAE								
<i>Anolis equestris</i> (2)	X		C	X			X	Dalrymple (1980); Lister (1981)
<i>Anolis evermanni</i> (4)	X	X	C	X			X	Herrel, unpub. data
<i>Anolis meridionalis</i> (1)		X	C				X	Vitt (1991)
SCINCIDAE								
<i>Corucia zebrata</i> (7)	X	X	H				X	Parker (1983); Hauschild & Gassner (1999)
<i>Cryptoblepharus carnabyi</i> (1)		X	C	X				Brown (1991)
<i>Ctenotus leae</i> (1)		X	O	X	X		X	Pianka (1969)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Ctenotus leonhardii</i> (1)		X	C	X	X	X		Pianka (1969); Read (1998)
<i>Ctenotus strauchii</i> (1)		X	C			X		Read (1998)
<i>Egernia coventryi</i> (1)			O				X	Chapple (2003)
<i>Egernia cunninghami</i> (1)	X		H				X	Chapple (2003)
<i>Egernia inornata</i> (1)		X	C				X	Chapple (2003)
<i>Egernia kintorei</i> (1)		X	O				X	Chapple (2003)
<i>Egernia multiscutata</i> (2)		X	O				X	D. Chapple, pers. comm.
<i>Egernia pulchra</i> (1)		X	C				X	D. Chapple, pers. comm.
<i>Egernia saxatilis</i> (1)		X	O				X	Chapple (2003)
<i>Egernia stokesii</i> (5)	X	X	H				X	Chapple (2003)
<i>Egernia striata</i> (1)		X	C				X	Chapple (2003)
<i>Egernia striolata</i> (2)		X	O				X	Chapple (2003)
<i>Egernia whitii</i> (3)		X	C				X	Chapple (2003)
<i>Eugongylus rufescens</i> (2)	X	X	C				X	McCoy (1980)
<i>Eulamprus heatwolei</i> (2)		X	C				X	Webb (1995) in Greer (2003)
<i>Eulamprus quoyii</i> (3)		X	C				X	Greer (2003)
<i>Eulamprus tenius</i> (1)		X	C				X	Greer (2003)
<i>Eumeces fasciata</i> (1)		X	C		X		X	Breckenridge (1943); Hall (1972); Jiang & Chen (2002)
<i>Glaphyromorphus isolepis</i> (1)		X	C				X	Shea <i>et al.</i> (1988) in Greer (2003)
<i>Glaphyromorphus nigricaudis</i> (1)		X	C	*other				Wilson & Knowles (1988)
<i>Glaphyromorphus pardalis</i> (1)		X	C	*other				Wilson & Knowles (1988)
<i>Hemisphaeriodon gerrardii</i> (1)		X	C				X	Hauschild <i>et al.</i> (2000)
<i>Lampropholis guichenoti</i> (1)		X	C				X	Greer (1989, 2003)
<i>Lamprolepis smaragdina</i> (5)	X		C		X			Reyes (1957); Auffenberg & Auffenberg (1988); Wiles & Conry (1990); Perry & Buden (1990)
<i>Mabuya multifasciata</i> (3)	X		C	X	X	X		Vrcibradic & Rocha (1996)
<i>Mabuya rudis</i> (1)	X		C	X	X	X		Inger (1959); Avila-Pires (1995)
<i>Mabuya striata</i> (1)		X	C	X	X	X	X	Branch (1998); Spawls <i>et al.</i> (2002)
<i>Prasinohaema flavipes</i> (2)		X	C				X	C. Austin, pers. comm.
<i>Pseudemoia pagenstercheri</i> (1)		X	C				X	Brown (1991)
<i>Sphenomorphus bruneus</i> (1)		X	C	*3 other	X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus concinnatus</i> (1)		X	C	<i>Sphenomorphus</i> spp. (all <i>Sphenomorphus</i> )	X	X	X	Inger (1959); Daniels (1987); Savage (2002)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Sphenomorphus jobiensis</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus leptofasciatus</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus maindroni</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus pratti</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus schultzei</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus solomonis</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Sphenomorphus stickeli</i> (1)		X	C		X	X	X	Inger (1959); Daniels (1987); Savage (2002)
<i>Tiliqua gigas</i> (1)		X	O				X	Greer (1989); Hauschild <i>et al.</i> (2000)
<i>Tiliqua nigrolutea</i> (2)	X		O				X	Greer (1989); Hauschild <i>et al.</i> (2000)
<i>Tiliqua rugosa</i> (2)	X		O	X			X	Greer (1989); MacMillen <i>et al.</i> (1989); Dubas & Bull (1991); Hauschild <i>et al.</i> (2000)
<i>Tiliqua scincoides</i> (7)	X	X	O				X	Greer (1989); Hauschild <i>et al.</i> (2000)
<i>Tropidophorus brookei</i> (1)	X		C	* <i>T. grayi</i> (all <i>Tropidophorus</i> )	X			Auffenberg & Auffenberg (1988)
<i>Tropidophorus misaminius</i> (1)	X		C		X			Auffenberg & Auffenberg (1988)
<i>Tropidophorus perplexus</i> (1)	X		C		X			Auffenberg & Auffenberg (1988)
SPHENODONTIDAE								
<i>Sphenodon punctatus</i> (2)	X		C				X	Walls (1981)
TEIIDAE								
<i>Ameiva ameiva</i> (14)	X	X	C		X	X	X	Magnusson & Da Silva (1993); Avila-Pires (1995); Magnusson <i>et al.</i> (1985); Savage (2002)
<i>Cnemidophorus deppii</i> (2)	X		C	X	X	X	X	Vitt <i>et al.</i> (1993); Lee (1996); Savage (2002)
<i>Cnemidophorus exsanguis</i> (1)	X		C				X	Stebbins (2003)
<i>Cnemidophorus gularis</i> (4)	X		C				X	Stebbins (2003)
<i>Cnemidophorus lemniscatus</i> (4)	X		C	X	X	X	X	Magnusson & Da Silva (1993); Avila-Pires (1995); Vitt <i>et al.</i> (1997); Savage (2002); Mesquita & Colli (2003)
<i>Cnemidophorus montaguae</i> (1)	X		C	*other <i>Cnemidophorus</i> species (17 spp.)				
<i>Cnemidophorus neomexicanus</i> (1)	X		C				X	Stebbins (2003)



APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Cnemidophorus sexlineatus</i> (1)	X		C		X			Paulissen (1987)
<i>Cnemidophorus tigris</i> (6)	X	X	C	X				Essghaier & Johnson (1975); Whitaker & Maser (1981); Grismer (2002)
<i>Dracaena guianensis</i> (2)	X		C			X		Avila-Pires (1995)
<i>Teius teyou</i> (1)	X		O		X			Varela & Bucher (2002)
<i>Tupinambis teguixin</i> (19)	X		O			X		Dessem (1985); Avila-Pires (1995)
TROPIDURIDAE								
<i>Microlophus peruvianus</i> (7)	X	X	O			X		Donoso-Barros (1966)
<i>Stenocercus trachycephalus</i> (3)		X	C			X		O. Torres-Carvajal, pers. comm.
<i>Tropidurus hispidus</i> (4)	X	X	O	X	X	X	X	Vitt (1995); Vitt & de Carvalho (1995)
<i>Tropidurus oreadicus</i> (1)		X	C	X	X	X	X	Colli <i>et al.</i> (1992); Avila-Pires (1995)
<i>Tropidurus semitaeniatus</i> (1)		X	C	X		X		Vitt (1993)
<i>Tropidurus torquatus</i> (3)	X	X	C			X		Bergallo & Rocha (1994); Juliano <i>et al.</i> (2002)
VARANIDAE								
<i>Varanus acanthurus</i> (1)	X		C			X		Greer (1989)
<i>Varanus beccarii</i> (1)	X	X	C					*other <i>Varanus</i> species (13 spp.)
<i>Varanus bengalensis</i> (9)	X	X	C					*other <i>Varanus</i> species (13 spp.)
<i>Varanus dumerilii</i> (2)	X		C			X		Manthey & Grossman (1997)
<i>Varanus eremius</i> (1)		X	C	X	X	X	X	Pianka (1994); Houston (1998)
<i>Varanus exanthematicus</i> (4)	X	X	C			X		Spawls <i>et al.</i> (2002)
<i>Varanus gilleni</i> (2)		X	C			X		Greer (1989)
<i>Varanus gouldii</i> (2)	X		C	X	X	X	X	Pianka (1994); Houston (1998)
<i>Varanus griseus</i> (1)	X		C			X		Disi <i>et al.</i> (2001)
<i>Varanus indicus</i> (3)	X	X	C			X		Greer (1989)
<i>Varanus niloticus</i> (7)	X	X	C		X	X		Luiselli <i>et al.</i> (1999); Bennett (2002); Spawls <i>et al.</i> (2002)
<i>Varanus prasinus</i> (3)	X	X	C		X	X		Greene (1986); Greer (1989)
<i>Varanus rudicollis</i> (1)	X	X	C			X		Manthey & Grossmann (1997)
<i>Varanus salvator</i> (11)	X	X	C			X		Manthey & Grossmann (1997)
<i>Varanus tristis</i> (1)		X	C	X	X	X	X	Pianka (1994); Houston (1998)
XANTUSIIDAE								
<i>Lepidophyma gageae</i> (1)	X		O			X		Varela & Bucher (2002)
<i>Xantusia henshawi</i> (1)	X		C			X		Grismer (2002)

APPENDIX *Continued*

Taxon (number sampled)	PSM	SVL	Diet type	M/V	N	F	Q	Reference
<i>Xantusia riversiana</i> (3)	X	X	O		X	X	X	Johnson & Lillywhite (1979); Fellers & Drost (1991); Stebbins (2003)
<i>Xantusia vigilis</i> (1)	X		C				X	Grismer (2002); Stebbins (2003)
<i>XENOSAURUS</i>								
<i>Xenosaurus grandis</i> (4)	X	X	C	X	X	X		Ballinger <i>et al.</i> (1995); Lemos-Espinal <i>et al.</i> (2003a)