

Prey processing in lizards: behavioral variation in sit-and-wait and widely foraging taxa

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Abstract: We determined the degree to which lizards process (i.e., chew) and manipulate their prey, using a phylogenetically broad sample of 12 species. Two transport and two chewing behaviors were identified. The transport behaviors included side-to-side movements and lingually mediated posterior movements of the prey. Chewing behaviors included puncture crushing and a previously undescribed behavior we term palatal crushing. Iguanian lizards (sit-and-wait predators) engaged in more palatal-crushing behaviors than autarchoglossans (widely foraging predators) did. However, iguanians also engaged in fewer cycles of chewing and transport behaviors per feeding bout. Autarchoglossan lizards used puncture crushing extensively and exhibited more variability in the sequence of behaviors used within a bout (interspersions of transport behaviors among chewing behaviors). Three behaviors (puncture crushing, interspersions, total) were shown to be coevolving after the effects of phylogeny were removed. The variation in feeding behavior we observed between iguanian and autarchoglossan lizards parallels patterns in tongue morphology and foraging mode in these large groups. Thus, it seems likely that each represents a component of a highly integrated character complex linking feeding morphology, behavior, and ecology.

Résumé : Un échantillon de 12 espèces présentant une bonne diversité phylogénétique a permis de faire une étude quantitative du traitement (i.e., mastication) et de la manipulation des proies chez les lézards. Deux comportements de transport et deux de mastication ont été identifiés. Les comportements de transport incluent des déplacements latéraux des proies et des déplacements vers l'arrière au moyen de la langue. Les comportements de mastication sont un écrasement avec ponctions et un comportement inédit que nous qualifions d'écrasement palatal. Les lézards iguaniens, qui chassent à l'affût, utilisent plus le comportement d'écrasement palatal que les autarchoglosses, qui recherchent activement leurs proies. Cependant, les iguaniens complètent moins de cycles de comportements de mastication et de transport par épisode d'alimentation. Les lézards autarchoglosses utilisent fréquemment l'écrasement avec ponctions et montrent plus de variabilité dans la séquence des comportements au cours d'un même épisode d'alimentation (intercalation de comportements de transport parmi les comportements de mastication). Trois comportements (écrasement avec ponctions, intercalation et total) apparaissent être en coévolution, si on enlève les effets de la phylogénie. La variation observée dans le comportement alimentaire entre les iguaniens et les autarchoglosses correspond à des différences de morphologie de la langue et de quête de nourriture chez ces grands groupes. Il se peut donc que chacun des caractères représente une composante d'un complexe fortement intégré qui relie la morphologie, le comportement et l'écologie de l'alimentation.

[Traduit par la Rédaction]

Introduction

Describing and explaining the functional significance of feeding mechanisms and behaviors within and among taxa has long been a goal of many ecologists and functional morphologists. Often this work seeks to explain differences in diet and (or) morphology in terms of behavioral variation in obtaining or using resources (Pianka 1981; Schwenk and Throckmorton 1989; Illius and Gordon 1993; Lauder and Reilly 1994; Robinson and Wilson 1998; Herrel et al. 1999a; Nakano et al. 1999; Shipley et al. 1999). Rarely, however, is the range of behaviors (behavioral repertoire) that organisms use during the acquisition and processing of food adequately

described and quantified in a comparative context (Reilly et al. 2001).

Mastication and transport cycles have been reviewed for several mammalian taxa processing various types and (or) sizes of food items (Hiiemae and Crompton 1985; Hiiemae 2000). The mammalian feeding repertoire is composed of chewing cycles that prepare the food for swallowing and digestion (e.g., puncture crushing and the tribosphenic chewing strokes) and transport cycles to reposition the food for further chewing (e.g., side-to-side transport) or shift it posteriorly for swallowing (Hiiemae et al. 1979; Hiiemae and Crompton 1985). Thus, a basic understanding of mammalian feeding behavior exists. However, analogous detailed investigations of prey processing and general behavioral patterns of other amniote groups have yet to be fully described. This lack of data leaves the false impression that non-mammalian taxa engage in little prey processing (Schwenk 2000a; Reilly et al. 2001). The focus of this paper is to take the first broadly comparative look at prey processing in lizards.

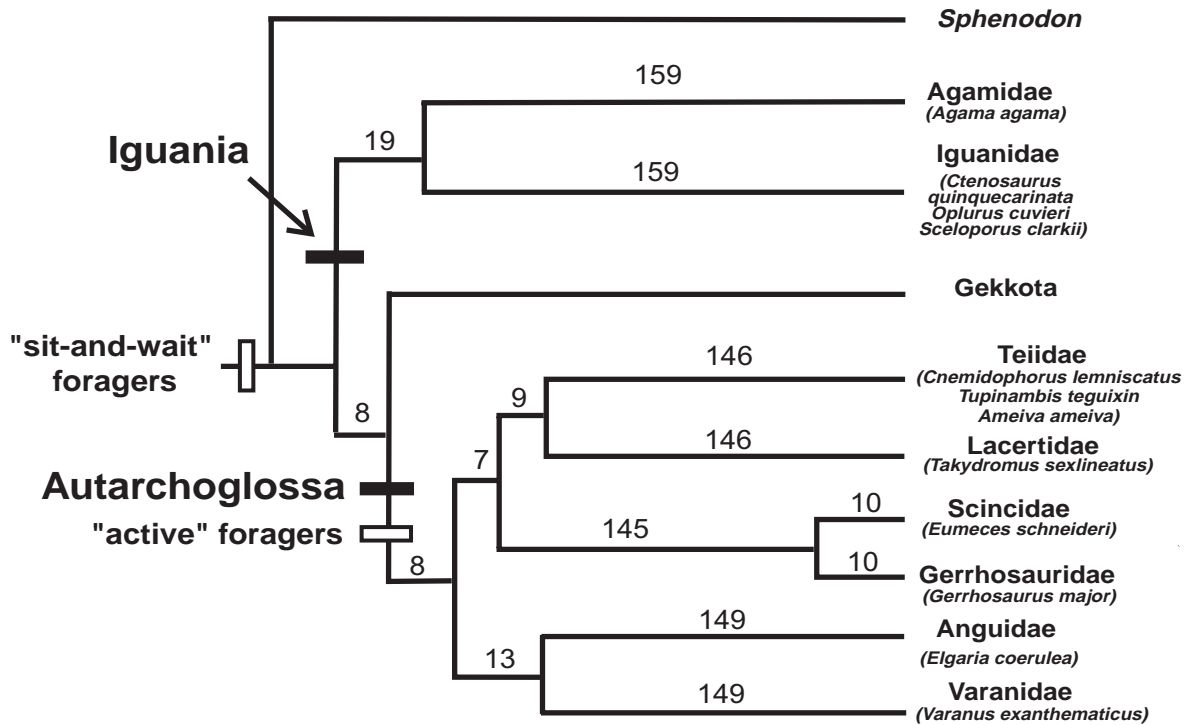
Extant lizards are an ecologically and dietarily diverse group of over 4500 species and are therefore well suited to

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Fig. 1. Phylogeny and general foraging modes of taxa used in this study. Numbers along branches indicate estimates of branch length (mybp). The phylogeny and branch lengths are based on Estes et al. (1988) and Cooper (1997). Data on branch lengths were obtained from Cooper (1997) and references therein.



an investigation of variation in prey-processing behaviors. Within squamates, numerous morphological studies have revealed major dietary, morphological, and functional differences among lizard groups (Herrel et al. 1999b; reviewed in Schwenk 2000b). Tongue morphology, a factor likely to be important in prey processing, is known to vary substantially across the group as a whole (Schwenk 1988, 2000b). The iguanian clade retains the ancestral condition of a heavily papillose short thick tongue with a round tip and a wide base. Tongue morphology is more variable and derived in various ways in the autarchoglossan clade; however, these lizards typically have a narrower triangular foretongue with distinct tips and a reduced base compared with that of iguanians (Schwenk 2000b).

The iguanian and autarchoglossan clades have also diverged in foraging mode (e.g., Cooper 1994, 1995a; Perry 1999). Foraging mode describes the movement patterns of lizards as they forage and can be split broadly into two major categories. Sit-and-wait foragers are ambushers, while wide foragers tend to move through the habitat in search of food items. These modes expose lizards to different prey types, resulting in different diets. Sit-and-wait foragers tend to eat more mobile prey and wide foragers encounter more sedentary prey (Huey and Pianka 1981). Thus, key components of morphology and ecology covary across lizards, which suggests that feeding behavior might also covary with these characters.

In this study we make the first attempt to quantify and compare the feeding repertoires of lizards, using a phylogenetically diverse sample of species. Basic chewing and transport behaviors are defined and their relative frequencies

across a diversity of taxa are determined. Our results show that particular behaviors are used more frequently by certain taxa and that this parallels a broad dichotomy in foraging mode, tongue morphology, and metabolic rate among lizards.

Methods

The phylogenetic relationships of the 12 species studied are shown in Fig. 1. The genus *Sphenodon* (Rhynchocephalia) is the outgroup to lizards and snakes (Squamates) (Estes et al. 1988). It has been classified as a sit-and-wait predator (Cooper 1995a, 1999) and thus this foraging mode is considered to be primitive for lizards. Squamates are split into the Iguania and Scleroglossa (Gekkota + Autarchoglossa). This study focuses on representatives of the Iguania and Autarchoglossa. The Gekkota, the sister taxon to the Autarchoglossa, was not included in this study because most species are nocturnal (and therefore difficult to film with strobes) and their foraging mode may be sit and wait, wide foraging, or mixed (Perry 1999). With few exceptions, autarchoglossans are widely considered to have evolved a widely foraging feeding mode (Cooper 1995a).

Lizards were purchased from commercial dealers and housed in glass terraria on a 12 h light : 12 h dark cycle. Each terrarium contained a water dish, shelter, and a heat and UV source. Water (supplemented with vitamins) was available ad libitum. Lizards were maintained on a variety of commercially available reptile food (primarily crickets and mealworms).

Lizard feeding bouts were filmed in lateral view with a NAC high-speed video system at 200 frames/s. Because the

body sizes of the lizards under study varied greatly, the smaller lizards were fed crickets standardized to lizard head length. The much larger species, *Tupinambis teguixin* and *Varanus exanthematicus*, were fed mice standardized to lizard head length. During each filmed feeding bout, lizards were fed to satiation. Data collection began immediately following the strike (prey capture) and ended with the first swallowing cycle (i.e., when the prey was no longer seen in the oral cavity but had entered the pharynx). This sequence, from strike to swallowing, defines one feeding bout. Only behaviors involved in prey manipulation and processing once the prey was within the mouth were considered. We defined a transport behavior as any behavior during which the prey item was moved anteroposteriorly within the mouth without any attempt to alter its shape or form. Prey-processing behavior, i.e., chewing (sensu Schwenk 2000b; Reilly et al. 2001), was defined as any behavior during which the size, shape, and (or) structural integrity of the prey item was changed via contact with the tongue, palate, jaws, and (or) teeth. Finally, side-to-side prey movements (SS) were classified as a separate category.

Videotapes were initially reviewed and the types of feeding behaviors that occurred consistently across all species were defined. All videotapes were then reviewed in greater detail and the order and number of each defined feeding behavior were tallied for each feeding bout for each individual. The raw occurrence data for each behavior for each bout were pooled across individuals within species to calculate mean occurrences of each behavior and the mean total number of behaviors per bout (TOT). Percentages were then calculated to yield the relative frequency of each behavior for each lizard family. Variation in the sequence of chewing and transport behaviors used during a bout was quantified by creating another variable, interspersions, which is the mean number of times a lingual transport behavior (T) was followed by a chewing behavior (either puncture crushing (PC) or a behavior we term palatal crushing (PLC)), indicating how often prey items are repositioned for further chewing.

Our sample of lizards included one representative species per family except Iguanidae and Teiidae, for which three species of each were filmed. Thus, for familial comparisons, the means for the three species within each family were pooled to generate a family mean. The iguanian species *Ctenosaurus quinquecarinata*, *Oplurus cuvieri*, and *Sceloporus clarkii* were considered to be monophyletic, based on the analyses of Macey et al. (1997) and Schulte et al. (1998). We recognize that feeding behavior is not a family-level phenomenon; however, this level was used because few phylogenetic hypotheses exist to account for relationships within many autarchoglossan families, teiids in particular. Furthermore, data on branch lengths within lizard families (see below) are scarce. Therefore, the level of family was deemed appropriate for comparison because key aspects of lizard feeding biology (foraging mode (Cooper 1994); tongue morphology (Schwenk 1988)) are highly conserved at this taxonomic level and because phylogenies with branch lengths are available.

Because tongue morphology is conserved phylogenetically (Schwenk 1988) and is likely to be an important factor in determining variation in feeding behavior, phylogenetic effects within the data were also assessed. The effects of phylogeny (i.e., the statistical non-independence of comparative

data) were removed by computing phylogenetically independent contrasts (ICs) on family means for five of the behavioral variables (Felsenstein 1985). Assuming a Brownian-motion model of evolution, ICs were calculated for numbers of T, PC, PLC, INT, and TOT. Correlation coefficients between these variables were then computed for the raw family means and for the ICs. The phylogeny used in these analyses is based on Estes et al. (1988). Data on branch lengths (in millions of years before present (mybp)) were obtained from Cooper (1997 and references therein), except for the lengths between the Scincidae and the Gerrhosauridae. The time since divergence of these families is not known, therefore this branch length was arbitrarily set at 10 mybp.

ICs were calculated in COMPARE 4.4 (Martins 2001). The absolute value of each IC was plotted against its standard deviation to check for appropriate branch-length standardization (Garland et al. 1992). No significant trends were observed for any variable.

To visualize how feeding behaviors might have evolved across the squamate clade, ancestral character states were reconstructed along the phylogeny with branch lengths shown in Fig. 1 for TOT, INT, T, PC, and PLC. The SS variable was of low and relatively uniform occurrence and therefore was not included in this analysis. Our calculations of ancestral states follow the generalized least squares (GLS) approach described in Martins and Hansen (1997) and were performed in COMPARE 4.4. The GLS approach calculates ancestral state values as a weighted average of the other taxa on the phylogeny. A Brownian-motion model of evolution was assumed. The within-family variation was assumed to be zero, therefore the values reported are the sum-of-squared-changes parsimony estimates of ancestral state values.

Results

Prey manipulation and transport behaviors

We analyzed a total of 337 feeding bouts from a sample of 12 lizard species (sample sizes per species are given in Table 1). Two transport behaviors were found to be highly repeated and easily observable from the video records. These were SS and posteriorly directed T behaviors of the prey item. The SS movements were manipulative movements whereby the prey item was transferred, either lingually or inertially, to the opposite side of the jaws (e.g., right → left, left → right). Processing and (or) transport behaviors may follow SS movements. SS behavior was highly variable and no patterns were detected in its use or frequency in any species studied. The use of this behavior likely depends on properties of the prey, particularly position, size, and degree of struggling.

The T behaviors were transport movements during which the prey item was moved posteriorly within the mouth by the tongue in preparation for further processing or swallowing. They were usually carried out in series at the end of each feeding bout, but were occasionally interspersed between chewing behaviors. Three autarchoglossan taxa also used inertial transport movements (I). During this behavior, the head was thrust forward over the prey item, with no associated movement of the tongue (Gans 1969). These simple I movements were observed only in the autarchoglossan families Teiidae (*Ameiva ameiva*, *T. teguixin*) and Varanidae (*V. exanthematicus*). *Tupinambis teguixin* and

Table 1. Numbers of individual behaviors, total numbers of behaviors per bout, and interspersions data for prey-processing behaviors in lizards feeding on prey of the same relative size.

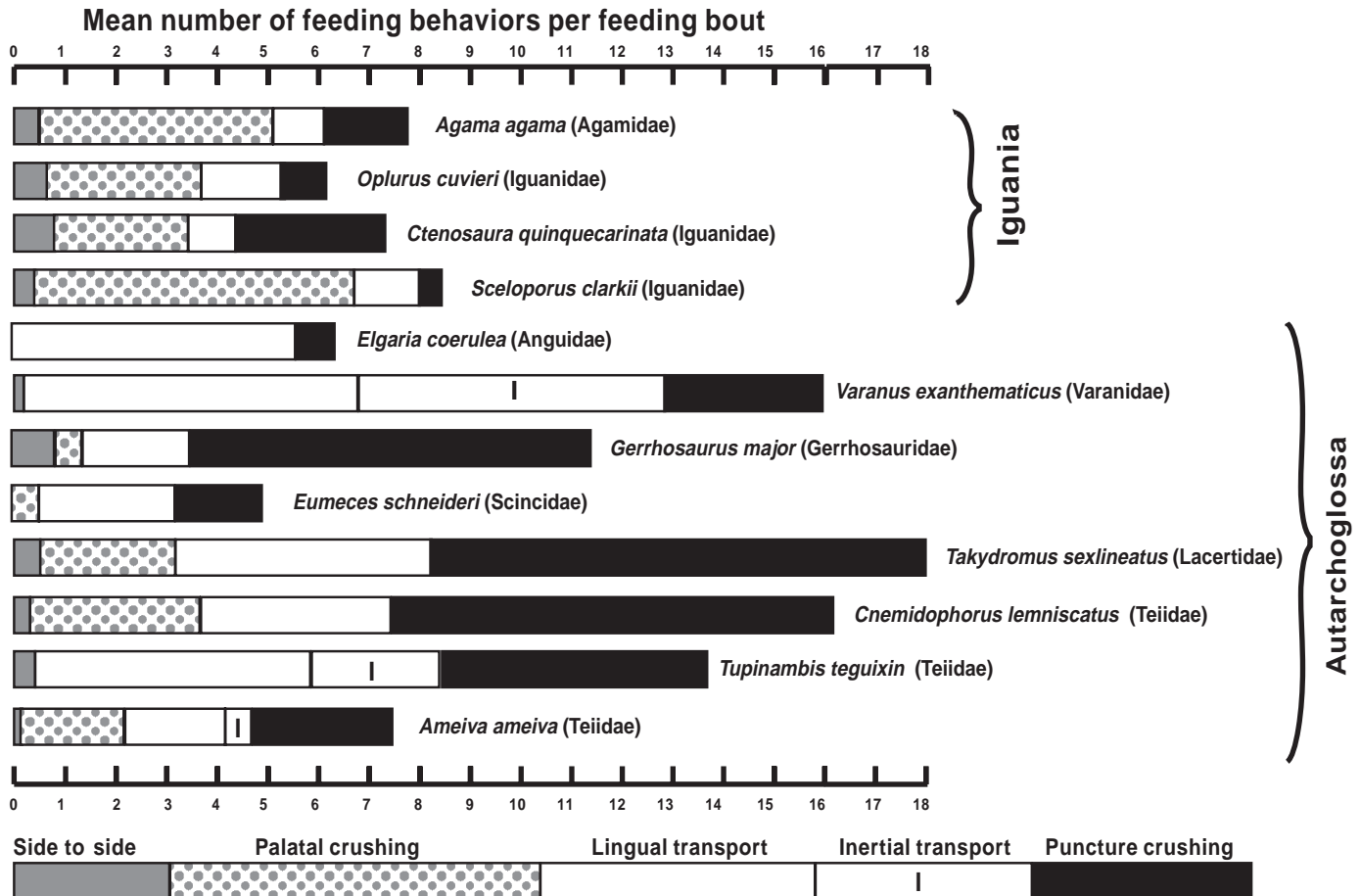
Species ^a	Side-to-side movement	Palatal crushing	Transport	Inertial transport	Puncture crushing	Total	Interspersion ^b
<i>Agama agama</i> (7, 5, 6)	0.56 ± 0.15 (7)	4.50 ± 0.44 (57)	1.00 ± 0.00 (13)	0.00 ± 0.00 (0)	1.72 ± 0.29 (23)	7.78 ± 0.30	0.56 ± 0.15
<i>Oplurus cuvieri</i> (23, 12, 20)	0.07 ± 0.04 (1)	3.65 ± 0.25 (59)	1.55 ± 0.14 (25)	0.00 ± 0.00 (0)	0.84 ± 0.13 (14)	6.11 ± 0.18	0.18 ± 0.05
<i>Ctenosaurus quinquecarinata</i> (5, 5)	0.80 ± 0.20 (10)	2.60 ± 0.64 (36)	1.00 ± 0.00 (14)	0.00 ± 0.00 (0)	2.90 ± 0.57 (39)	7.30 ± 0.42	0.80 ± 0.20
<i>Sceloporus clarkii</i> (5, 5)	0.40 ± 0.24 (4)	6.40 ± 0.40 (77)	1.20 ± 0.20 (14)	0.00 ± 0.00 (0)	0.40 ± 0.24 (4)	8.40 ± 0.24	0.40 ± 0.25
<i>Elgaria coenleia</i> (6, 6, 5, 7)	0.00 ± 0.00 (0)	0.00 ± 0.00 (0)	5.63 ± 0.22 (91)	0.00 ± 0.00 (0)	0.63 ± 0.17 (9)	6.25 ± 0.31	0.17 ± 0.08
<i>Varanus exanthematicus</i> (5, 5, 5)	0.20 ± 0.11 (1)	0.00 ± 0.00 (0)	6.67 ± 0.67 (41)	6.07 ± 0.61 (38)	3.07 ± 0.33 (19)	16.00 ± 0.89	1.73 ± 0.15
<i>Gerrhosaurus major</i> (5, 11, 9, 5)	0.77 ± 0.18 (7)	0.53 ± 0.16 (5)	2.17 ± 0.26 (19)	0.00 ± 0.00 (0)	7.90 ± 0.37 (70)	11.37 ± 0.35	1.30 ± 0.16
<i>Eumeces schneideri</i> (14, 18, 16, 13, 16)	0.00 ± 0.00 (0)	0.69 ± 0.12 (15)	2.49 ± 0.18 (52)	0.00 ± 0.00 (0)	1.71 ± 0.18 (33)	4.90 ± 0.21	0.39 ± 0.06
<i>Takydromus sexlineatus</i> (6, 12)	0.61 ± 0.16 (4)	2.61 ± 0.68 (14)	5.22 ± 0.87 (27)	0.00 ± 0.00 (0)	9.56 ± 0.71 (55)	18.00 ± 1.15	1.78 ± 0.21
<i>Chenidophorus lemniscatus</i> (7, 6, 7, 17)	0.25 ± 0.09 (2)	3.44 ± 0.58 (21)	3.97 ± 0.44 (25)	0.00 ± 0.00 (0)	8.47 ± 0.67 (53)	16.13 ± 0.75	1.70 ± 0.19
<i>Tupinambis teguixin</i> (7, 4, 8, 8)	0.52 ± 0.16 (4)	0.00 ± 0.00 (0)	5.41 ± 0.57 (40)	2.48 ± 0.79 (18)	5.37 ± 0.72 (38)	13.78 ± 0.82	1.59 ± 0.17
<i>Ameiva ameiva</i> (7, 10, 9)	0.15 ± 0.09 (2)	1.96 ± 0.34 (29)	2.08 ± 0.23 (29)	0.31 ± 0.14 (3)	3.00 ± 0.46 (37)	7.50 ± 0.47	1.65 ± 0.14
Pooled family mean							
Iguanidae	0.42 ± 0.16 (3)	4.22 ± 0.43 (55)	1.25 ± 0.11 (24)	0.00 ± 0.00 (0)	1.38 ± 0.31 (18)	7.27 ± 0.28	0.46 ± 0.17
Teiidae	0.31 ± 0.07 (3)	1.89 ± 0.29 (16)	3.85 ± 0.29 (31)	0.88 ± 0.28 (7)	5.81 ± 0.44 (43)	12.74 ± 0.57	1.65 ± 0.17

Note: Values are given as the mean ± standard error, with percent occurrence of a behavior for that species in parentheses.

^aNumbers in parentheses show the number of bouts per individual.

^bThe mean number of times transport movements (side-to-side, transport behaviors, or inertial transport behaviors) were followed by prey-crushing behaviors (palatal crushing or puncture crushing), *Oplurus cuvieri*, *C. quinquecarinata*, and *S. clarkii* belong to the family Iguanidae; *T. teguixin*, *C. lemniscatus*, and *A. ameiva* belong to the family Teiidae.

Fig. 2. Mean occurrences of prey-processing behaviors of lizards, obtained from high-speed video recordings of individual feeding bouts by lizards feeding on prey of sizes adjusted to the same relative head length ($N = 337$). Note the relative increase in puncture crushing and total numbers of prey-processing cycles for the autarchoglossans.



V. exanthematicus also used inertial feeding behaviors that involved the protraction and retraction of the tongue in tandem with inertial movements of the head, and these behaviors have been described in detail elsewhere (Elias et al. 2000). In this analysis the inertial transport with tongue behaviors were pooled with normal T behavior because each behavior involved the use of the tongue.

Chewing behaviors

The chewing behaviors observed were PC and PLC. The PC behavior involves piercing and (or) crushing the prey by the jaws and marginal teeth in such a way that the structural integrity of the prey is changed. The teeth frequently penetrated the prey and its shape was obviously changed by the forces imposed on it by the jaws and teeth. This behavior is essentially the same as the puncture crushing observed in mammals because the jaws of lizards approach each other vertically and the upper and lower teeth do not come into contact because the prey prevents them from doing so (Reilly et al. 2001). In the PLC behavior the prey item was compressed or crushed between the tongue and palate (i.e., inside the marginal tooth rows) so that it was fractured and (or) its shape was changed. This behavior is further defined by a lack of anterior–posterior or side-to-side movement of the prey. Several PLCs were often observed in sequence.

General behavior patterns

Behavior-occurrence data are presented in Table 1. Figure 2 summarizes the frequencies of each behavior across all feeding bouts for each species. All species exhibited T and PC behaviors. The number of T behaviors (open bars in Fig. 2) per bout was greater in autarchoglossans than in iguanians except in three species, *Eumeces schneideri*, *Gerrhosaurus major*, *A. ameiva*. Only three species, *V. exanthematicus*, *T. teguixin*, and *A. ameiva*, were observed to use simple I behaviors (open bar I in Fig. 2). SS behavior (shaded bars in Fig. 2) was used infrequently and was not observed in *Elgaria coerulea* or *E. schneideri*.

Among iguanian taxa, PLC (stippled bars in Fig. 2) clearly dominated prey-crushing behaviors, while PC (solid bars in Fig. 2) dominated in autarchoglossans. PLC behavior was not observed in *E. coerulea*, *V. exanthematicus*, or *T. teguixin*. TOT (i.e., transport and chewing behaviors combined) in iguanians ranged from 6 to 8.4 per bout (Table 1). In five of the autarchoglossan species the total number of behaviors was much greater than in iguanians, ranging from 14 to 18 per bout. However, three autarchoglossan species, *E. coerulea*, *E. schneideri*, and *A. ameiva*, had values similar to those of iguanians, with *E. schneideri* having the lowest total of any species in the study. The autarchoglossan taxa showed high INT values (>1.3 vs. <0.9) compared with

Fig. 3. The “interspersion” of prey-processing behaviors. Interspersion is the mean number of times a transport behavior is followed by a chewing behavior (puncture crushing, palatal crushing), indicating the greater degree of prey handling involved in repositioning the prey item for chewing in autarchoglossans.

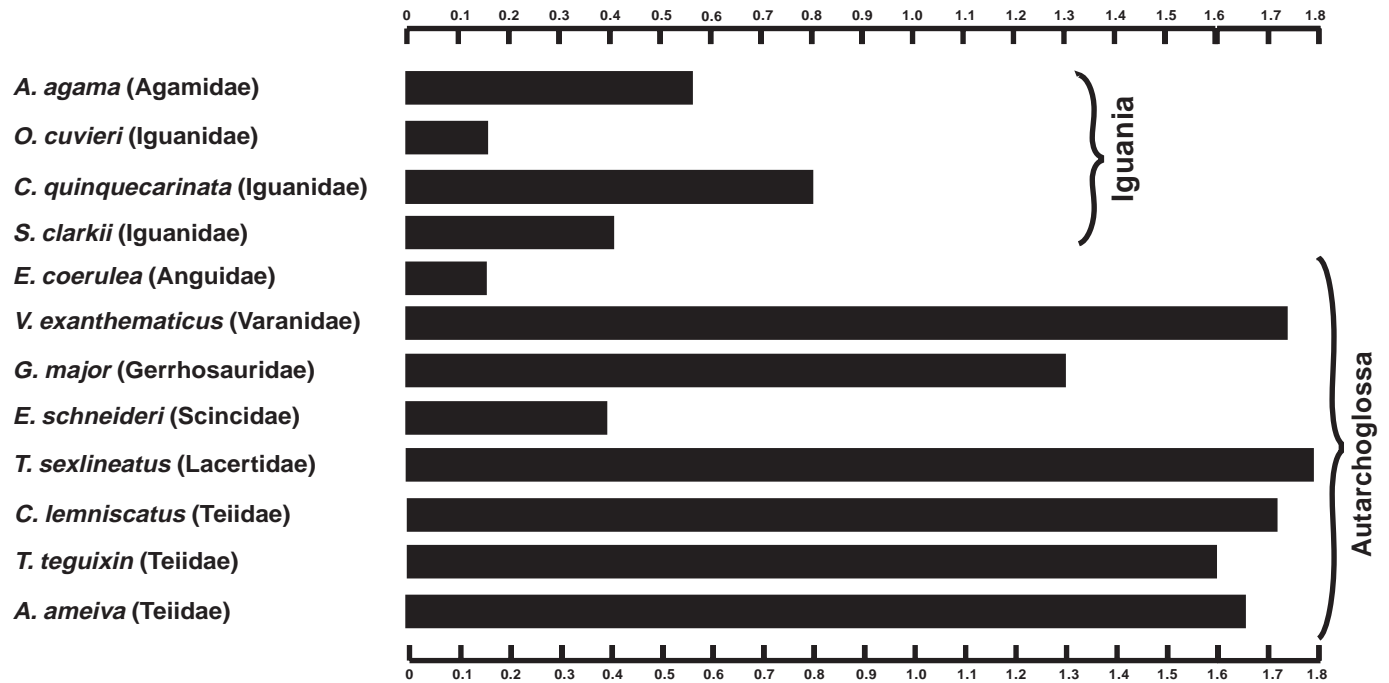
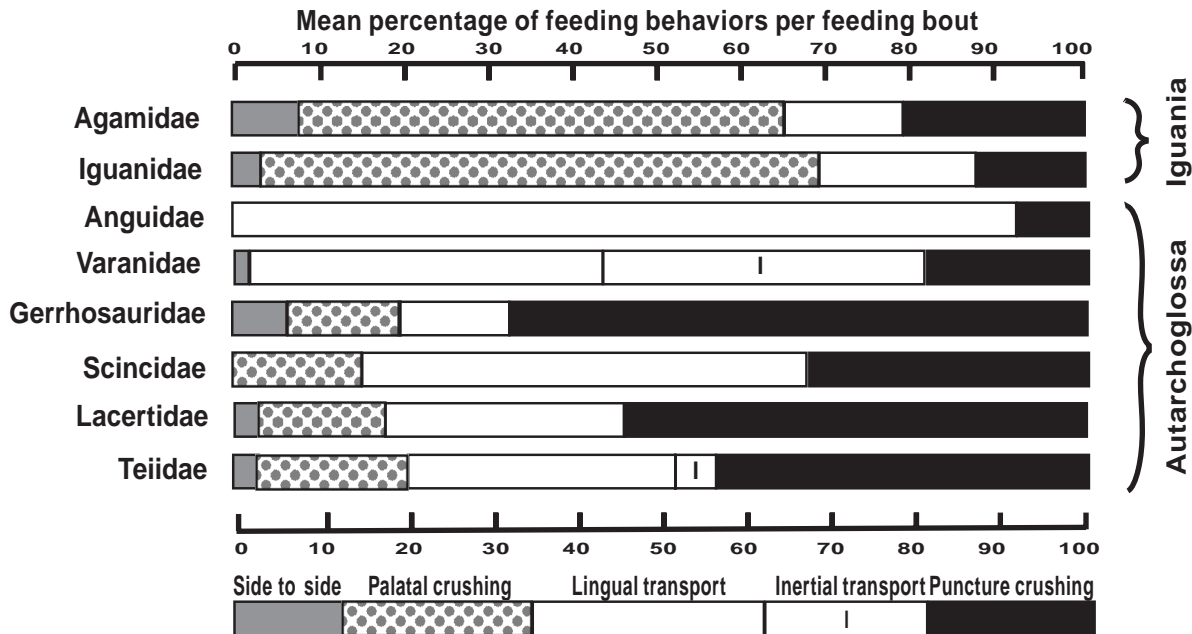


Fig. 4. Feeding repertoires of lizard families expressed as percent use of each behavior. Note the dominance of palatal crushing in iguanian feeding bouts and the dominance of puncture crushing and increase in lingual transport in autarchoglossan taxa.



iguanians (Table 1, Fig. 3). Note, however, that again, *E. coerulea* (Anguidae) and *E. schneideri* (Scincidae) were more similar to iguanians in the degree to which Ts were interspersed between chewing behaviors.

The iguanian families Agamidae and Iguanidae used the PLC behavior more than any other behavior (Fig. 4). These iguanians used PC infrequently and T to an even lesser extent. Conversely, the autarchoglossan families employed a

higher frequency of T and PC behaviors. The anguid *E. coerulea* used a very high percentage of Ts, few PCs, and no other behaviors while feeding.

Evolution of behaviors

Significant correlations were observed before and after phylogenetic effects were accounted for in three pairs of variables (TOT vs. PC, TOT vs. INT, PC vs. INT) (Table 2).

Fig. 5. Evolutionary patterns of feeding behavior in lizards for total (TOT), interspersions (INT), lingual transport (T), puncture crushing (PC), and palatal crushing (PLC). Numbers at the tips of the branches are familial means. Ancestral nodal values were estimated by the GLS method of Martins and Hansen (1997). Changes in the shading of the branches represent general trends (darker shading denotes higher values) in the evolution of trait values. Taxa shown in boldface type have values that are more similar to the iguanian condition than to the autarchoglossan condition.

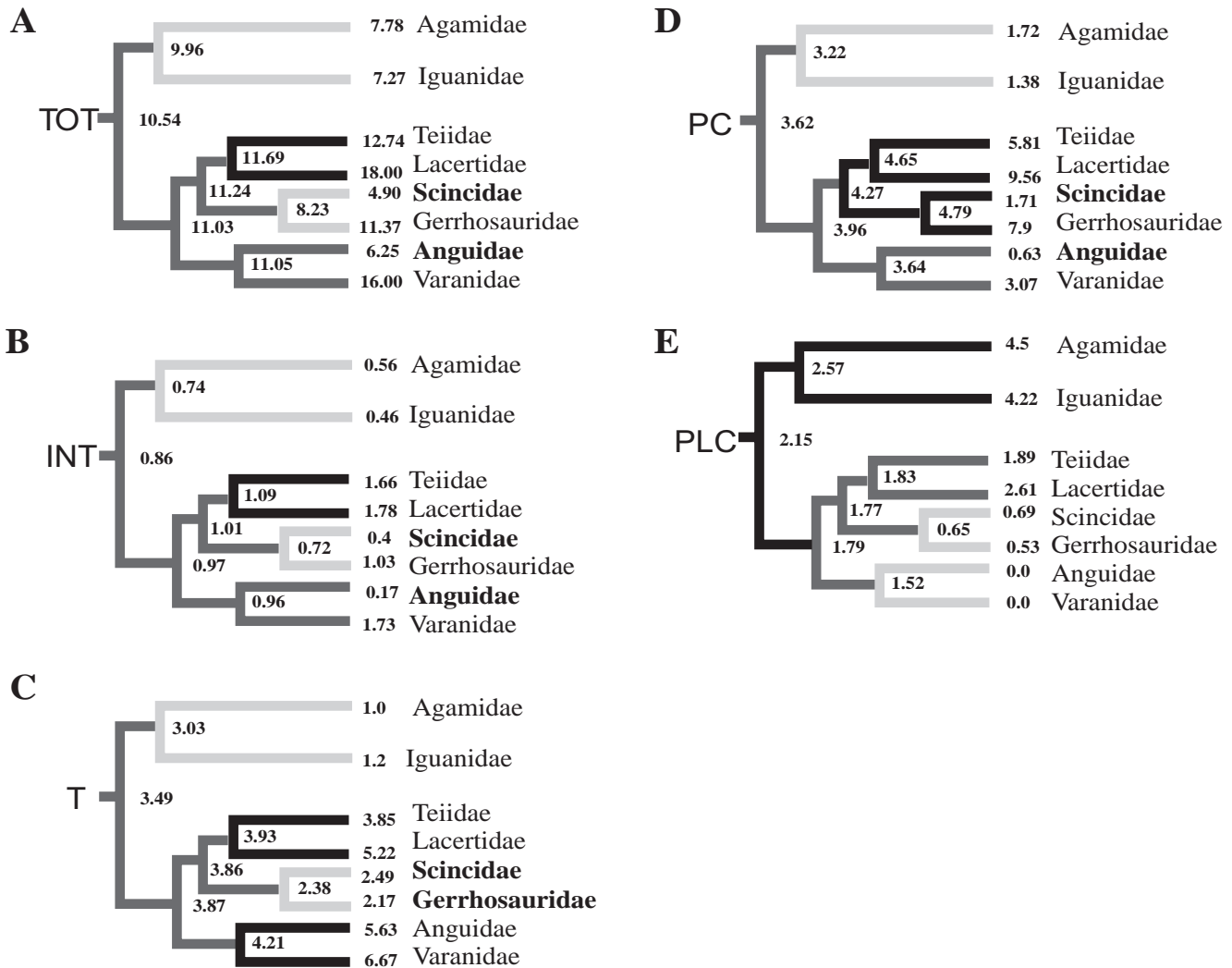


Table 2. Matrix of correlation coefficients of raw data (above the diagonal) and of independent contrasts (below the diagonal).

	Palatal crushing	Transport	Interspersions	Puncture crushing	Total
Palatal crushing	—	-0.645	-0.264	-0.058	-0.099
Transport	-0.559	—	0.582	0.176	0.571
Interspersions	0.073	0.108	—	0.736*	0.920**
Puncture crushing	0.190	-0.260	0.828*	—	0.765*
Total	0.211	-0.035	0.928**	0.934**	—

Note: Total, interspersions, and puncture crushing are significantly correlated ($df = 5$; *, $P < 0.05$; **, $P < 0.01$).

This indicates that increases in the total number of behaviors used in consuming prey were achieved by adding more PCs and INTs and that both of them increase together. T was negatively correlated with PLC, showing that these variables are inversely related.

Ancestral character state reconstructions for TOT, INT, T, PC, and PLC are presented in Fig. 5. The mean value of each variable for each family is given at the tips of the

phylogenies and the estimated ancestral character state values are given at the corresponding nodes. Changes in the degree of shading along the branches indicate trends in trait values between nodes. From the Iguania–Autarchoglossa node, values for TOT, INT, T, and PC increase within the Autarchoglossa and decrease within the Iguania (Figs. 5A–5D). For PLC, the reverse is true (Fig. 5E), with the Iguania acquiring higher values and the Autarchoglossa lower val-

ues. Note that for the familial means of TOT, INT, and PC, the Scincidae and Anguinae are more similar to iguanian family means than they are to those of other autarchoglossans. Values for transport (T) behaviors in the Scincidae and Gerrhosauridae are also more similar to the iguanian pattern.

Discussion

Historically, lizards have been portrayed as swallowing prey items whole with little or no processing (i.e., chewing). Chewing, in the functional sense, is the reduction of material to render it suitable for swallowing and (or) facilitate the penetration of digestive enzymes to expedite chemical breakdown (Hiemae and Crompton 1985; Schwenk 2000a; Reilly et al. 2001). This study is the first to quantify chewing and transport behaviors and their relative frequencies across a diverse sample of lizards. Our data confirm that lizards do in fact chew; they use their teeth (and jaws, tongue, and palate) to puncture, compress, and (or) reduce food items within the oral cavity. The shape, size, and structural integrity of the prey item are changed by this behavior, which prepares it for swallowing and digestion. Thus, these behaviors meet the functional definition of chewing.

Our analysis revealed an interesting and widely used lizard feeding behavior, PLC. Although palatal crushing has been noted for lizards feeding on eggs (Herrel et al. 1997), it has not previously been thought to be so common. During PLC behavior, the prey was stationary. Had the prey moved laterally or posteriorly, this behavior would have been interpreted as repositioning (SS) or transport (T). However, during PLC the prey did not move, as it was visibly crushed and frequently parts of it broke off, falling out of the mouth. Depending on the position of the prey (how far back in the oral cavity it was positioned during PLC), it could often be seen clearing the palate between sequential PLC cycles. The presence of pterygoid teeth in *C. quinquecarinata* and *O. cuvieri* (and many other iguanians) further suggests that the palatal region serves a chewing function (Etheridge and de Queiroz 1988). Finally, like PCs, many PLCs were used in succession prior to the onset of final transport movements. Thus, PLCs and PCs are undoubtedly chewing behaviors. If each PLC was followed by a T behavior, this could have been interpreted as some sort of “pretransport” behavior whereby prey adhesion to the tongue is facilitated by pressing the tongue up against the prey item (hypothesized as a function of T behavior by Bramble and Wake 1985). But PLCs preceded PCs far more frequently than they preceded Ts. Furthermore if PLC is a prey-adhesion behavior, then INT values would have been higher in the iguanian taxa, in which PLC is the dominant chewing behavior. Although PLC is clearly a chewing behavior, it is possible that tongue adhesion could be facilitated in those few PLCs that directly precede Ts prior to swallowing.

Comparisons of iguanians and autarchoglossans

The most striking finding in this study is the degree to which the lizard feeding repertoire appears to have evolved in concert with tongue morphology and foraging mode. The robust fleshy tongues of iguanians are covered with long papillae and are very important for prey capture and trans-

port of food (Schwenk 2000b), and in some species for pheromone detection (Cooper 1994). Autarchoglossans have more elongate, often forked tongues that are not used at all during prey capture (Schwenk and Throckmorton 1989; Schwenk 2000b) but are used extensively for chemoreception (Schwenk 1993; Cooper 1994, 1997; Schwenk and Wagner 2001). Behaviorally, iguanians and autarchoglossans differ in their mode of foraging as well. With few exceptions, foraging mode follows phylogenetic lines, with iguanian taxa being ambush or sit-and-wait foragers, while autarchoglossan taxa are more active or widely foraging (Perry 1999). Morphological and physiological correlates of these foraging modes include tongue morphology (Copper 1994; Schwenk 1994), body and tail sizes (Huey and Pianka 1981; Perry et al. 1990), locomotor performance (Huey et al. 1984), diet (Huey and Pianka 1981; Gasnier et al. 1994), habitat use (Belluire and Carrascal 1996), metabolic rate (Anderson and Karasov 1981; Nagy et al. 1999), reproduction (Vitt and Price 1982; Vitt 1990), and learning ability (Day et al. 1999). Assuming that sit-and-wait foraging is the primitive condition for squamates (because the outgroup *Sphenodon* is a sit-and-wait forager (Cooper 1995a, 1999)), the Iguania can be interpreted as retaining the primitive mode and the Autarchoglossa appear to have evolved a different mode.

Autarchoglossan (widely foraging) species in our study differed substantially from iguanian (sit-and-wait) species in TOT, INT, and PC (Figs. 2, 5). In contrast, iguanian species showed much higher numbers and percentages of PLCs (Figs. 2, 4). Thus, the widely foraging autarchoglossan taxa seem to have evolved a longer and more complex feeding repertoire than the sit-and-wait iguanians, exhibiting higher values for TOT, INT, and PC. On the other hand, the sit-and-wait iguanians have evolved a repertoire that focuses primarily on PLC and T. The significant correlation of TOT, INT, and PC in the IC analysis suggests that these behaviors are evolving together.

Evolutionary reversals in the Autarchoglossa

Three autarchoglossan species clearly did not follow the patterns of behavioral evolution that are seen in the group in general. First, *A. ameiva*, a medium-sized teiid, showed a reduction in the total number of behaviors used (Fig. 2). However, this reduction in TOT per feeding was driven by a decreased use of transport behaviors. Like other teiid species, this lizard has a very elongate, protrusible tongue and is a known wide forager (Magnusson et al. 1985). Its decreased use of T is hard to explain given its morphological and ecological similarity to the other teiids and suggests that its feeding biology deserves more detailed analysis. Furthermore, behavioral variation within the family Teiidae is clearly evident. We chose the taxonomic level “family” for our comparisons because of its relevance to foraging mode and tongue morphology; however, it is likely that a comparison of feeding behavior within particular clades or dietary groupings (e.g., herbivores) would be equally informative.

Second, *E. schneideri* (Scincidae) trended toward lower values for PC, INT, and TOT (Figs. 2, 5). The patterns observed in skink feeding behavior may be explained by evidence that some skink species have reverted to the iguanian condition. In terms of foraging mode, some skinks have secondarily evolved the sit-and-wait foraging mode from

widely foraging ancestors (Cooper 2000). *Eumeces schneideri* is known to tongue-flick plant and insect material extensively and on this basis is believed to be a wide forager (Cooper et al. 2000). However, no data on foraging patterns in *E. schneideri* are available to evaluate if it has changed its foraging mode. Variation in tongue morphology may also explain the apparent behavioral reversals of *E. schneideri*. It is well known that iguanians engage in lingual prehension of small prey and so do some skink species (Smith et al. 1999), including *E. schneideri* (personal observation). Skinks have a rather broad hind tongue compared with many other autarchoglossans (Schwenk 1995, 2000b), which may contribute to shaping feeding behavior in that prey items can be manipulated differently, owing to the increased surface area and adhesive abilities (Schwenk 2000b).

Finally, *E. coerulea* (Anguinae) also trended toward the iguanian patterns of lower values for PC, INT, and TOT (Figs. 2, 5). As in some skink species (*Eumeces laticeps*, *Eumeces fasciatus*), the tongue of *E. coerulea* is more generalized than that of most autarchoglossans in its relative surface area (relative to its tip width) (Cooper 1995b; Schwenk 2000b). Although *E. coerulea* has been classified as widely foraging on the basis of its chemoreceptive abilities (Cooper 1990, 1994, 1995b), it has also been classified as a sit-and-wait forager, based on other characteristics (Vitt and Price 1982). Even more compelling is the fact that it has been suggested that its sister taxon, *Elgaria multicarinata*, is a sit-and-wait forager because most of its diet consists of freely moving prey, it relies primarily on crypsis for predator avoidance, and it has a low field metabolic rate (Kingsbury 1994, 1995). The sit-and-wait strategy is often coupled with lower metabolic costs, and lizards that are sit-and-wait foragers tend to have lower field and resting metabolic rates than wide foragers because of decreased locomotor costs (Anderson and Karasov 1981; Nagy et al. 1999). Although no movement data are available for *E. coerulea*, the best available reproductive, behavioral, and metabolic evidence suggests that it may have secondarily evolved the sit-and-wait foraging mode.

Conclusions

The data for PC, PLC, and INT show clearly different evolutionary patterns of change in the iguanian and autarchoglossan lizard lineages (Fig. 5) that parallel known contrasting patterns of foraging mode (Perry 1999), tongue morphology (Schwenk 1988, 2000b), and chemosensory behavior (Schwenk 1993; Cooper 1994). Thus, feeding behavior seems to be diverging in concert with changes in these other aspects of the lizards' feeding biology. In addition, two species (*E. coerulea* and *E. schneideri*) appear to have reverted to more iguanian patterns in these systems and also may have reverted to the iguanian feeding repertoire. Thus, tongue morphology and foraging mode appear to play a role in shaping how various feeding behaviors evolve. Indeed, if *E. coerulea* and *E. schneideri* do represent secondarily derived sit-and-wait foragers, then the apparent covariation between foraging mode, tongue morphology, and feeding behavior is truly remarkable. However, explicit tests of the relationships among these variables need to be conducted to verify these general patterns.

This study has shown that lizards do chew and exhibit some processing behaviors similar to, but not as extensive as, those seen in mammals. Mammals and birds have very different and highly efficient chewing behaviors (Reilly et al. 2001). A potential benefit of increased oral processing is that digestive efficiency may be increased and thereby may allow an increase in metabolic rate. Our data show that compared with the iguanians, autarchoglossans have evolved a more complex feeding repertoire with more emphasis on puncturing the prey (PC), more interspersed, and about twice as many prey-processing cycles involved per feeding bout. Is this increase in prey processing related to an increase in the metabolic demands of an active foraging strategy? Interestingly, it has been shown that the resting and field metabolic rates of widely foraging autarchoglossan lizards are higher (Anderson and Karasov 1981; Nagy et al. 1999). Future work must quantify the relationship between foraging mode, metabolic rate, and prey processing. However, it appears that the more extensive prey-processing behavior of autarchoglossans may be correlated with a higher metabolic rate, just as in mammals and birds (Reilly et al. 2001). Although our data do not unequivocally support this hypothesis, lizards may provide a glimpse into how feeding function evolves in response to the demands represented by an increasing metabolic rate.

The results of our study suggest that tongue morphology, foraging mode, diet, and feeding behavior may be coevolving as a highly integrated character complex. Autarchoglossans, with their elongate chemosensory tongues, have evolved a feeding repertoire which is more complex than that of their iguanian relatives. This increased complexity may be related to changes in foraging mode and metabolic rate. Thus, tongue morphology, chemoreception, feeding behavior, and metabolic rate may all be fundamentally linked (this paper; Schwenk 2000b; Wagner and Schwenk 2000; Schwenk and Wagner 2001). Although we studied lizard feeding behavior across a diverse sample of taxa, these behaviors should be quantified in more species and with different types of prey to verify the general patterns we have described and to assess the relationships between the different components of lizard ecology. In particular, the feeding behavior of gekkotans, chamaeleonids, and snakes must be explored. These taxa, although strikingly different from most lizards, will provide important information about the evolution of feeding behavior across squamates. Given that the gekkotan clade is positioned "between" the iguanian and autarchoglossan clades, data from representatives of this group are of particular importance for understanding the evolution of these behaviors and their relevance to foraging mode and metabolic rate. Equally interesting will be further study focusing on taxa such as *Elgaria* in which there appear to be reversals in foraging mode or tongue morphology. Such data would elucidate in greater detail the covariation among and between these behavioral characters and foraging mode, tongue morphology, and metabolic rate.

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