

HISTORICAL PATTERNS IN LIZARD ECOLOGY: WHAT TEIIDS CAN TELL US ABOUT LACERTIDS

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Abstract: Lacertid, teiid, and gymnophthalmid lizards share much of their evolutionary history. We explore ecological traits of these lizards in an attempt to identify similarities that may have a historical origin as well as differences that may reflect the effects of differing ecological settings on the portion of their histories that is independent. Within Teioidea, major divergence in body size occurred producing Gymnophthalmidae (small size) and Teiidae (larger size). Small body size in gymnophthalmids affected their ecology differently than larger body size did in teiids, particularly in respect to thermal ecology. Teiids maintain higher body temperatures and are more successful in open, hot habitats than are gymnophthalmids. Body size varies from small to relatively large in lacertids. A striking difference between lacertids and their sister clade, Teioidea, is the inclusion of many ants in the diets of some species. Differences in data collection make direct comparisons between lacertids, gymnophthalmids, and teiids difficult. We demonstrate, with data on three lizard species, how interpretations based on numerical versus volumetric dietary data varies depending on how specialized a particular lizard species is. We recommend standardization of data collection such

that future comparisons can be more meaningful.

Keywords: Lacertidae, lizard diets, lizard ecology, historical ecology, phylogeny, Teiidae.

Resumen: Patrones históricos en la ecología de lagartos: Qué nos enseñan los teidos acerca de los lacértidos. -Lacertidae, Teiidae y Gymnophthalmidae comparten gran parte de su historia evolutiva. Exploramos los rasgos ecológicos de estos lagartos en un intento para identificar las similitudes que pudieran tener un origen histórico, así como las diferencias que puedan reflejar ambientes ecológicos diferentes durante la porción independiente de sus historias evolutivas. Dentro de Teioidea, la mayor divergencia se produjo en tamaño corporal, dando lugar a Gymnophthalmidae (pequeño tamaño) y Teiidae (gran tamaño). El pequeño tamaño corporal de los gimnofthalmidos afectó a su ecología de modo diferente a como lo hizo el tamaño corporal grande en los teidos, particularmente en relación a la ecología térmica. Los teidos mantienen temperaturas corporales más altas y tienen más éxito en los hábitats abiertos que los gimnofthalmidos. En los lacértidos el tamaño varía desde tamaños corporales pequeños a relativamente grandes. Una diferencia llamativa

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entre los lacértidos y su grupo hermano, los Teioidea, es la inclusión de numerosas hormigas en la dieta de algunas especies. Las diferencias existentes en el modo de obtener los datos hace que las comparaciones entre lacértidos, gimnoftálmidos y teidos sean difíciles. Demostramos con datos de tres especies de lagartos de qué modo las interpretaciones basadas en datos de dieta numéricos o volumétricos varían dependiendo de lo especializada que sea una especie particular de lagarto. Recomendamos una estandarización del modo de obtención de los datos de forma que las futuras comparaciones puedan ser más relevantes.

Palabras clave: Lacertidae, dieta de lagartos, ecología de lagartos, ecología histórica, filogenia, Teiidae.

Resum: Patrons històrics en l'ecologia dels llangardaixos: Què ens ensenyen els Teiidae sobre els lacèrtids.- Lacertidae, Teiidae i Gymnophthalmidae comparteixen gran part de la seva història evolutiva. Hem explorat els trets ecològics d'aquests llangardaixos en un intent d'identificar les similituds que poguessin tenir un origen històric, així com les diferències que poden reflectir ambients ecològics diferents durant la porció independent de les seves històries evolutives. Dins de Teioidea, la divergència més gran es va produir en talla corporal, donant lloc a Gymnophthalmidae (petita mida) y Teiidae (mida gran). La petita talla corporal dels gimnoftálmids afectà la seva ecologia de manera diferent a com ho va fer la talla corporal gran dels teiids, particularment en relació a l'ecologia tèrmica. Els teiids mantenen temperatures corporals més altes i tenen més èxit en hàbitats oberts que els gimnoftálmids. En els lacèrtids la grandària varia des de talles corporals petites a relativament grans. Una diferència aparent entre els lacèrtids i el seu grup germà, els Teioidea, és la inclusió de nombroses formigues en la dieta d'algunes espècies. Les diferències existents en el mode

d'obtenció de dades fa que les comparacions entre lacèrtids, gimnoftálmids i teiids siguin difícils. Demostrem amb dades de tres espècies de llangardaixos de quina manera les interpretacions basades en dades de dieta numèriques o volumètriques varien depenent de com d'especialitzada sigui una espècie particular de llangardaix. Recomanem una estandarització del mode d'obtenció de dades, de manera que les futures comparacions puguin ser més rellevants.

Paraules clau: Lacertidae, dieta dels llangardaixos, ecologia dels llangardaixos, ecologia històrica, filogenia, Teiidae.

INTRODUCTION

The set of evolutionary changes that produced the common ancestor to the Scleroglossa set the stage for a cascade of events giving rise to the highly divergent Gekkota and Autarchoglossa (PIANKA & VITT, 2003; VITT *et al.*, 2003). Although both originated on Gondwana, the primary diversification of Autarchoglossa occurred on Laurasia (ESTES, 1983). Thus, throughout the early evolutionary history of autarchoglossans in the Old World, they coexisted with iguanians and gekkotans. However, the New World experienced early diversification of iguanians prior to the arrival of autarchoglossans that gave rise to teiids and gymnophthalmids (ESTES, 1983). Divergence in prey capture, chemosensory abilities, and activity levels likely provided scleroglossans new evolutionary options. Jaw prehension freed the tongue from involvement in prey capture (SCHWENK, 2000, SCHWENK & WAGNER, 2001), the skull

became more flexible (FRAZZETTA, 1983; ARNOLD, 1998; HERREL *et al.*, 2000), and chemosensory systems were enhanced (SCHWENK, 1993a, b, 1994; COOPER, 1996a, b, 1997a, b): these innovations provided scleroglossans with new opportunities for diversification in a terrestrial environment dominated by sedentary, sit-and-wait foraging lizards in the Iguania. Autarchoglossans in particular, with their relatively high activity levels, appear to have flourished in terrestrial environments (PIANKA & VITT, 2003; VITT *et al.*, 2003). Nocturnality in an ancestor to the Gekkota minimized historical interactions between them and the primarily diurnal iguanians and autarchoglossans. Cladogenesis continued within iguanians, gekkotans, and autarchoglossans, producing lizard families recognized today.

Within autarchoglossans, Teioidea stands out partially because of the relative consistency of body form among species and partly because of the unusually high activity levels, particularly within Teiidae. Although scalation varies considerably, especially in gymnophthalmids, morphological variation is relatively conservative among members of the Teioidea (see below), with the exception of several subterranean lineages within the gymnophthalmidae. Most terrestrial or semi-arboreal species are elongate, fusiform, and have relatively long tails. Morphological evolution centers on elongation of the body and tail, usually associated with an active terrestrial lifestyle. However, extreme elongation along with near limblessness and drastic reduction of the tail has occurred

independently several times within the Gymnophthalmidae and appears associated with subterranean habits (see PELLEGRINO *et al.*, 2001).

Teioidea are often abundant in terrestrial and some subterranean habitats, but rare in vegetation off the ground. Even considering exceptions such as the partially arboreal species of *Kentropyx* in South America (e.g., VITT & CARVALHO, 1992), Teioidea achieve their greatest success in terrestrial environments. High activity levels are supported by high body temperatures while active, indeed, some of the highest activity body temperatures among lizards occur in the Teiidae (e.g., CASAS-ANDREU & CURROLA-HIDALGO, 1993; SCHALL, 1977). Achieving and maintaining high body temperatures at high latitudes and elevations is a major challenge for moderate to large-sized ectothermic vertebrates and may explain the relatively low diversity or absence of teiids in temperate zones and at high elevations. Many gymnophthalmids occur in the Andes (e.g., HILLIS, 1985; HILLIS & SIMMONS, 1986; KIZIRIAN, 1995) and in shaded rainforest (AVILA-PIRES, 1995) and operate at relatively low body temperatures (e.g., VITT *et al.*, 1998a, b).

Because Lacertidae is the sister taxon to the Teioidea, these clades share much of their evolutionary history (Figure 1). Their present day distributions, with Teioidea (Teiidae and Gymnophthalmidae) restricted to the New World and Lacertidae restricted to the Old World, suggests that much of their post-divergence evolutionary histories are independent. Nevertheless,

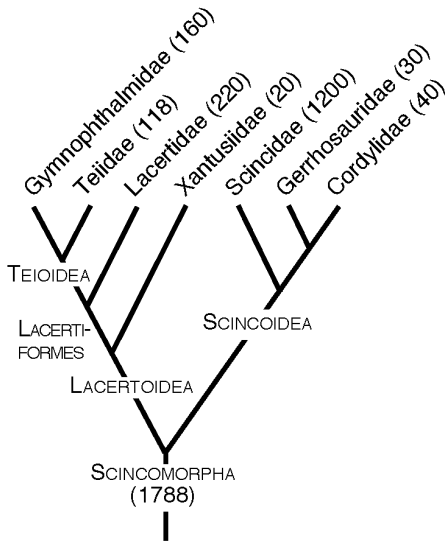


Figure 1. Phylogeny of the Scincomorpha showing approximate number of species in each clade. The phylogeny is based largely on SCHWENK (2001) and numbers of species are taken from ZUG *et al.* (2001) with some modifications. Some relationships remain controversial (e.g., xantusiids, VICARIO *et al.* 2003)

at a superficial level, teiids, and perhaps some gymnophthalmids, appear to be ecological counterparts to lacertids. In this essay, we examine morphological traits and ecology of teiid lizards drawing comparisons with studied lacertids and some other lizard clades. We also examine evolutionary events within teiids and search for similar trends in lacertids. Finally, based on the ecological roles teiids have played in New World lizard assemblages, we consider some historical differences among subclades within the Lacertiformes that might account for present day differences in ecological

attributes. We point out that Lacertiformes only comprises about 7% of known squamates. Teiids comprise 1.7%, lacertids 3.1%, and gymnophthalmids 2.3% of squamates. Among Lacertiformes, about 118 teiids, 220 lacertids, and 160 gymnophthalmids are currently recognized (PIANKA & VITT, 2003).

MATERIAL AND METHODS

Most, but not all data summarized here stems from published studies on teiids, lacertids, and gymnophthalmids. We include some data on other lizard taxa for comparison. Data included herein were collected in a similar way making comparisons possible. Because this of course limits generality of any comparisons, we also comment on specific information from other lacertid studies that are directly relevant to our conclusions. We assembled a morphology data set containing the following variables: lizard snout-vent length (SVL) in mm, total mass in g, head width, head length, head height, body width, body height, hind leg length and foreleg length, all in mm for 11,726 individuals of 112 lizard species in 46 genera distributed among the families Amphisbaenidae, Anguidae, Corytophanidae, Gekkonidae, Gymnophthalmidae, Hoplocercidae, Iguanidae, Lacertidae, Leisiosauridae, Polychrotidae, Scincidae, Teiidae, Tropiduridae and Xantusiidae. We restrict the morphological analyses herein to 6935 individuals representing 41 species of Lacertoidea (23 gymnophthalmids, 12

teiids, and 6 lacertids), but we comment on how they compare with lizards in general. We also assembled a data set on lizard body temperatures from our studies. Because we were only interested in comparisons at higher taxonomic levels, we did not examine potential differences among taxa in relationships of body temperatures to substrate or air temperatures. For perspective, we included data on gekkonoid and iguanian lizards. Thus, data for this analysis include 3889 individual body temperature measurements on 67 lizard species.

Dietary comparisons present problems due to variation among studies in data reported. Thus we restrict our dietary analysis to our own data because they were collected similarly. We combined data on desert and rainforest lizards (see VITT *et al.*, 2003 for details) and restrict the analysis to the seven most important prey categories by volume. We examine differences among the three major lizard clades, Iguania, Gekkota, and Autarchoglossa.

Finally, to demonstrate limitations of basing conclusions on numerical versus volumetric dietary data, we provide analysis of a data set on 448 *Ameiva ameiva*, containing 27 prey categories, 165 *Anolis fuscoauratus* containing 22 prey categories, and 58 *Plica umbra* containing 16 prey categories. These species were chosen because they represent different diet strategies. One (*A. ameiva*) is a generalist that eats a lot of termites numerically, another (*A. fuscoauratus*) is a dietary generalist that eats a lot of ants and small beetles numerically, and the third

(*P. umbra*), is an ant specialist. Methods for dietary analysis can be found elsewhere (e.g., VITT & ZANI, 1996).

RESULTS AND DISCUSSION

Setting the evolutionary stage

High activity levels, jaw prehension of prey, a tongue designed to transmit chemical information from the external environment to the lizard's sensory system, and an active foraging mode must have given ancestors to autarchoglossans a competitive advantage over all small diurnal vertebrates with a sit-and-wait foraging mode in a world rich in invertebrates and small vertebrates (PIANKA & VITT, 2003; VITT *et al.*, 2003). Jaw prehension dates back to the ancestor of scleroglossans and provided two primary advantages: 1) the tongue could be freed up for other functions and 2) larger prey could be manipulated. In autarchoglossans, the tongue is used to transmit chemicals from the external environment to the lizard's vomeronasal sensory system. Even though scleroglossans, and autarchoglossans in particular, are capable of eating large prey, many continue to eat small prey (VITT *et al.*, 2003). Sit-and-wait foraging lizards in the Iguania depend upon vision for prey detection and pursue moving insects (HUEY & PIANKA, 1981) and prey are captured by lingual prehension (SCHWENK, 2000). Consequently, most nonmobile or hidden invertebrates and vertebrates are likely undetected by iguanian lizards, and large-sized prey,

particularly vertebrates, would be difficult to manipulate with the tongue. Poorly developed chemosensory systems in iguanians did not allow the sophisticated prey discrimination exhibited by most scleroglossans, and autarchoglossans in particular (COOPER, 1994a, b, 1995a, b; SCHWENK, 1993a, b; 1994). Nevertheless, several clades within Iguania developed chemosensory prey discrimination in response to a switch to herbivory (COOPER & ALBERTS, 1990, 1991).

Teiids, gymnophthalmids, and lacertids comprise the Lacertoidea (Figure 1), a group of lizards generally characterized as elongate and fusiform. The conservative morphology of these three taxa is apparent in SVL to mass regressions (Figure 2). Although significant differences in the SVL-mass relationships exist between clades

(ANCOVA slope test, $F_{1, 4308} = 22.1$, $P < 0.0001$), species, and in some cases sexes, the all-species relationship is relatively tight. Some exceptions exist, but a vast majority of lizards in the Lacertoidea are terrestrial active foragers. Teiids and Gymnophthalmids are restricted to the new World and, with the exception of a handful of species, they are terrestrial. The striking exceptions are at opposite ends of a size gradient. A few small gymnophthalmids like *Bachia* (AVILA-PIRES, 1995; COLLI *et al.*, 1998), *Psilophthalmus*, and *Procellosaurinus* (RODRIGUES, 1991a, b) are nearly limbless and live underground, and two of the largest teiid genera, *Dracaena* and *Crocodilurus* bask from elevated perches in trees over water and forage in swamps, streams, and rivers (AVILA-PIRES, 1995; PIANKA & VITT, 2003).

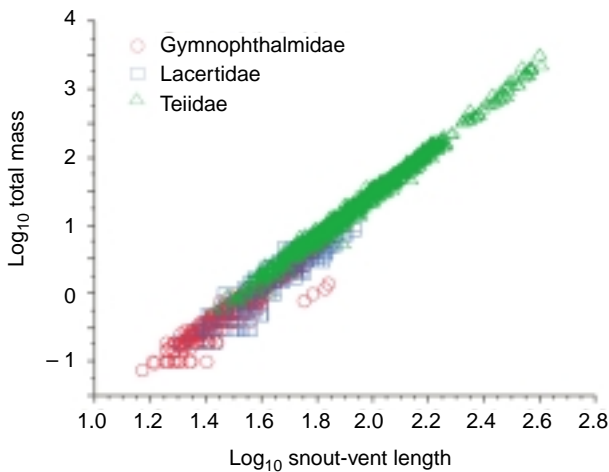


Figure 2. Relationship between total body mass and snout-vent length in teiid, gymnophthalmid, and lacertid lizards. The outlier points falling below the regression are nearly limbless gymnophthalmid lizards in the genus *Bachia*

Teiid morphology and its consequences

We first comment on lizard morphology in general because a broad perspective is necessary to interpret patterns within the Lacertoidea. We concentrate on the SVL to total mass relationship even though some interesting differences occur in other morphological variables. Among those species for which we had both SVL and mass data, a significant difference in slopes (ANCOVA with clade as the class variable and \log_{10} SVL as the covariate, $F_{2,9353} = 148.6$, $P < 0.0001$) exists among Iguania, Gekkota, and Autarchoglossa. These clades do not fall on the same regression line. Slopes of the log-log relationships are: Iguania 3.22, Gekkota 2.93, and Autarchoglossa 3.22. Comparison of autarchoglossans and iguanians yields no difference in slopes or intercepts ($F_{1,7754} = 0.07$, $P = 0.7858$; $F_{1,7754} = 1.09$, $P = 0.2972$) but the power in both tests (0.058 and 0.171, respectively) is low. Thus autarchoglossans and iguanians fall on a similar but highly variable regression. Most of that variation is among iguanians. An important, but not obvious point in the Iguania - Autarchoglossa (lizards only) comparison is that SVL-specific mass in iguanians is attained primarily by a robust body whereas similar SVL-specific mass in many autarchoglossans is attained by a combination of body and tail elongation with mass of the tail contributing greatly to overall mass. We only point that out here, but this raises several interesting questions. For example, are physiological processes of

4-legged squamates so restrictive that larger deviations in length-mass relationships simply do not occur? If so, did a major physiological shift in the ancestor of snakes open up new physiological and ecological options?

Even though the SVL - mass relationship in 4-legged squamates is conservative, interesting and in some cases surprising variation exists. Comparison of Teioidea with Iguania reveals a significant difference in slopes of the SVL - mass relationship with Teioidea increasing in mass more as SVL increases ($F_{1,7152} = 0.07$, $P = 0.0142$). Power of the slope test is high (0.69). To briefly summarize, gekkotans have shifted away from an overall lizard *Bauplan* by becoming relatively light in mass and Teioidea have shifted the opposite direction becoming slightly heavier. This result may seem surprising, because one is immediately struck by the apparent streamlined nature of Teioidea morphology. Coupled with streamlined morphology in Teioidea is elongation and in many instances apparent thickening and lengthening of the tail, which can be important in locomotion (e.g., BALLINGER *et al.*, 1979). This probably contributes to the added size-specific mass. Higher size-specific mass in Teioidea may partially account for the nearly clade-wide restriction to terrestrial microhabitats. Cost of locomotion combined with an active lifestyle may limit abilities of Teioidea to climb, a hypothesis that remains to be tested.

Conservatism in morphology within Teioidea is reflected both in comparisons among subclades (Figure 2) and in comparisons among genera of

teiid lizards (Figure 3). Whether one is examining ecologically distinct gymnophthalmids (Figure 4) or teiids of drastically different body sizes (Figure 5), the overall *Bauplan* is similar. One conclusion that can be drawn from this is that the Teioidea *Bauplan* has proven

successful in terrestrial microhabitats. The *Bauplan* of many lacertids is similar to that of Teioidea (e.g., Figure 6), likely reflecting success of the ancestral *Bauplan* of lizards in the Lacertoidea. The most striking difference between Lacertids as a group and Teioidea is that

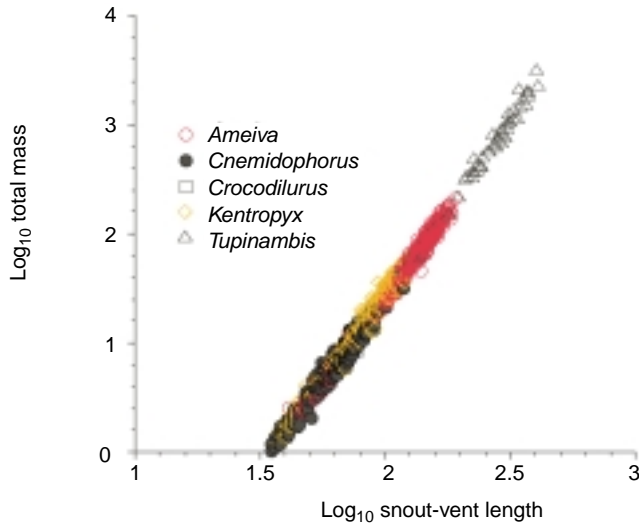


Figure 3. Relationship between total body mass and snout-vent length in 5 genera of teiid lizards representing both subclades (Teiinae and Tupinambinae)



Figure 4. A. *Vanzosaura rubricauda*, a gymnophthalmid that lives in open habitats in central and southern South America. B. *Cercosaura ocellata*, a gymnophthalmid that lives in leaf litter of the southern Amazon rainforest and northern Cerrado of Brazil



Figure 5. A. The large-bodied teiid *Tupinambis longilineus*. B. The relatively small-bodied teiid *Kentropyx altamazonica*. Both are from the Rio Ituxi in Amazonas, Brazil. Note the overall similarities in *Bauplan* even though each is in a different subclade (Tupinambinae versus Teiinae) and mass differs by an order of magnitude

no extant giant species of lacertids exist and no diminutive species of Teiidae exist. The smallest is *Cnemidophorus inornatus*, which, at a maximum SVL of about 69 mm, is still larger than most gymnophthalmids. A few island lacertids are large compared to others (e.g., *Gallotia*), but no morphological or ecological equivalents of *Tupinambis*, *Dracaena*, or *Crocodylurus* exist in the Lacertidae. The most likely explanation for this may be the presence of varanids throughout much of the evolutionary history of lacertids in the Old World and their absence throughout recent history of New World lizards. Varanids are highly active and voracious predators



Figure 6. Male and female of the lacertid *Podarcis sicula* from Menorca, Spain

(e.g., PIANKA, 1994), resembling in many ways, some of the larger teiids like *Ameiva*, *Tupinambis*, *Crocodylurus*, and *Dracaena*. The only Varanoidea that have survived in the New World are in the genus *Heloderma* (Helodermatidae) and their lifestyle is quite different from that of varanids, and their distribution is limited. Absence of small-bodied teiids may result from historical interactions with the sister clade Gymnophthalmidae, most of which are small. Within Lacertidae, some species have evolved small body size (e.g., *Takydromus*) but in terms of the number of small species, lacertids have not been nearly as successful at generating small-bodied species in the Old World as gymnophthalmids have been in the New World. One hypothesis for this difference is that gymnophthalmids did not encounter a diverse skink fauna during their early evolutionary history whereas lacertids did. Small-bodied skinks have been very successful throughout the Old World and on Pacific islands. Considering that gymnophthalmids have done well in some relatively cool environments, one

has to wonder why they did not colonize North America. One possible reason is that the only potential distribution corridor, Central America, is longitudinally small and has only periodically provided a connection to North America.

Several other aspects of morphology provide insight into potential similarities and differences in ecology of lacertids and teiids. We consider one here. Relative length of hindlimbs varies among subclades within Lacertoidea (Figure 7). Slopes differ in the relationships between hindlimb length and SVL ($F_{2,5159} = 57.8$, $P < 0.0001$) among subclades with gymnophthalmids having the shortest hindlimbs, lacertids intermediate, and teiids the longest. Even though relative hindlimb lengths of teiids and lacertids appear superficially similar in Figure 7, the regressions have different slopes

(1.006 and 0.904, respectively; $F_{1,4333} = 145.8$, $P < 0.0001$). Teiids have relatively longer hindlimbs and the disparity appears to increase with increasing body size. Reasons for this remain unknown, but several hypotheses can be proposed. Diversification of teiids in the absence of varanids may have released them from evolutionary constraints on limb length allowing them to diverge considerably from the Teioidea ancestor. Alternatively, lacertid hindlegs may have shortened in response to a lack of iguanian diversity providing opportunities to use microhabitats that did not contain competitors historically.

Teiid activity and body temperatures

All known lizard species in the Lacertoidea are diurnal. Compared with other clades, teiids and lacertids tend to have slightly higher body temperatures

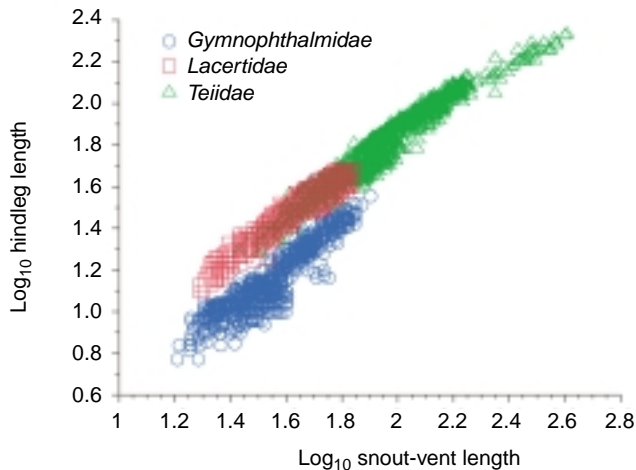


Figure 7. Relationship between SVL and HLL in families of the Lacertoidea

and gymnophthalmids tend to have slightly lower body temperatures (Figure 8). Teiids in general and lizards in the genus *Cnemidophorus* in particular, tend to have among the highest active body temperatures known in lizards, with some exceeding 40°C (e.g., ASPLUND, 1970; CASAS-ANDREU & CURROLA-HIDALGO, 1993; PIANKA, 1970; SCHALL, 1977). Nevertheless, some desert lacertids appear to have equally high body temperatures while active. For example body temperature of *Nucras tessellata* averages $39.2 \pm 2.8^\circ\text{C}$ (PIANKA, 1986). In some environments (particularly deserts), lacertids are very

teiid-like in their thermal biology and activities. In other environments, particularly high elevation environments, lacertid thermoregulation appears similar to that of high elevation iguanians (e.g., CARRASCAL *et al.*, 1992; MARTIN & SALVADOR, 1993; VAN DAMME *et al.*, 1987, 1990; BAUWENS *et al.*, 1990, 1996). They maintain relatively low body temperatures and bask considerably to gain heat. Thus, some lacertids have diverged from their ancestors in thermal physiology allowing them to persist in Old World habitats similar to those dominated by iguanians in the New World.

Diets and foraging mode

The shift from lingual to jaw prehension in scleroglossans with concomitant enhancement of chemical sensing (olfactory in Gekkota and vomeronasal in Autarchoglossa) set the stage for a major dietary shift (see VITT *et al.*, 2003) that ultimately led to the evolution of extreme modifications of the jaw allowing ingestion of huge prey as seen in many varanoids (in particular, most snakes; GREENE, 1997). Chemical discrimination of prey (e.g., COOPER, 1990; 1994a, b; 1995a, b; 1997a, b) allowed 1) identification of highly profitable prey and 2) identification of potentially toxic prey. The obvious prediction is that scleroglossans should include less biomass of noxious insects such as ants in their diets and replace those with insects of higher energy content or those not producing noxious chemicals. In general, this appears to be the case (Figure 9). We were unable to

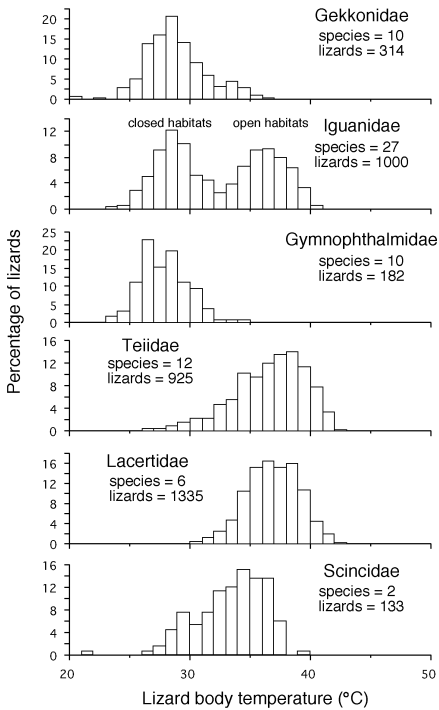


Figure 8. Body temperatures of lizards in 6 clades

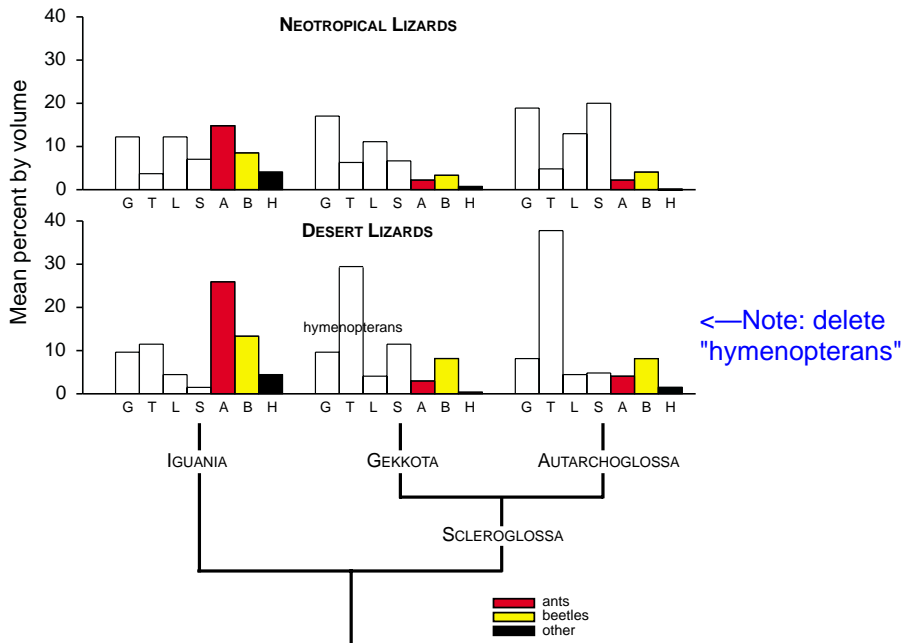


Figure 9. Diets of Neotropical lizards (upper) and desert lizards (lower). Only the seven most important prey categories are shown. A dietary shift occurs in Scleroglossa with a reduction in proportions of ants and other noxious insects. Ants are replaced by a combination of grasshoppers, insect larvae, and spiders in Neotropical lizards and termites and spiders in desert lizards. Prey types are: (G) grasshoppers and crickets, (T) termites, (L) insect larvae, pupae, and eggs, (S) spiders, (A) ants, (B) beetles, and (H) non-ant hymenopterans. Many beetles, ants, and other hymenopterans produce noxious chemicals for defense (e.g., BLUM, 1981; EVANS & SCHMIDT, 1990). Modified and reprinted with permission from the *American Naturalist*

test this hypothesis for lacertids in general because, aside from ERP's desert lizard studies, a vast majority of data on diets of lacertids does not include volumetric data. Most such studies provide counts of prey, and ants (and other hymenopterans) do constitute a significant portion of the diet for many lacertids based on counts (e.g., CASTILLA *et al.*, 1991; PILORGE, 1982; PÉREZ-MELLADO *et al.*, 1991; PÉREZ-MELLADO, 1998). One study that contained numeric and volumetric data

(ROBINSON & CUNNINGHAM, 1978) revealed that two Namib lacertids had diets in which ants and other hymenopterans were not dominant. In one, *Meroles* (formerly *Aporosaura*) *anchietae*, ants comprised 0.42% of the diet by volume and all hymenopterans comprised only 5.19%. In the other, *Meroles cuneirostris*, ants comprised 6.9% of the diet by volume and all hymenopterans comprised 16.5%. The possibility exists that ants eaten by many European lacertids do not contain

noxious chemicals and this would be worth looking into further.

We now diverge slightly to provide an example of how important volumetric data are in lizard studies. We selected data on three lizard species that differ ecologically and in their use of prey; the large-bodied teiid *Ameiva ameiva*, the small-bodied polychrotid *Anolis fuscoauratus*, and the medium-sized tropidurid *Plica umbra* (Figure 10). In *A. fuscoauratus*, large numbers of ants and small beetles contribute very little to the diet volumetrically and, consequently reliability of numeric data as a predictor of volumetric data is poor (52.3%). In *A. ameiva*, high numbers of termites contribute to lack of concordance between numerical and volumetric data, and reliability of numerical data as a predictor of volumetric data is also low (17.6%). In a true ant specialist, *P. umbra*, numeric and volumetric data are nearly identical and reliability of numerical data as a predictor of volumetric data is high (99.3%). Use of numerical data only is unlikely to allow discrimination between lizard species that eat a lot of ants contributing little to their diet volumetrically, and true ant specialists. Use of volumetric data alone is likely to reveal little about specific foraging behaviors. To exemplify the latter, consider *A. ameiva*, a species that eats a lot of termites, which are not very important volumetrically. It is highly unlikely that *A. ameiva* pick up individual dispersed termites. Rather, individuals find clusters of termites and eat a lot at one time similar to many *Cnemidophorus*. Finally, ants, likely due to a relatively high proportion of

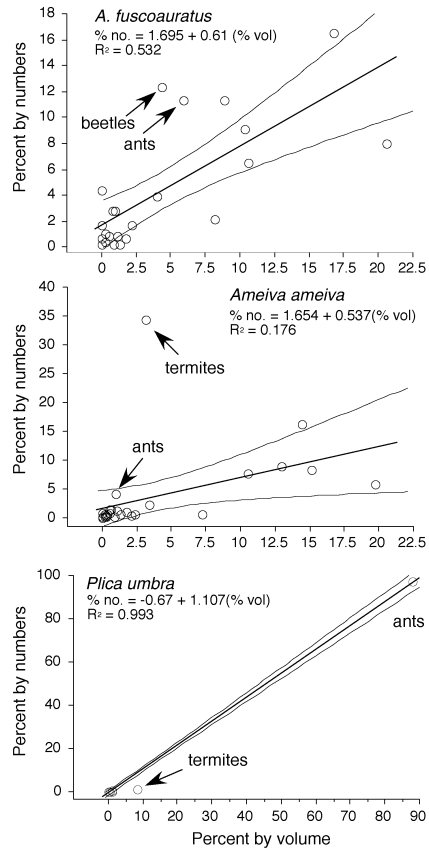


Figure 10. Dietary data on three lizard species selected to demonstrate problems comparing numerical dietary data to volumetric dietary data. In all three examples, regressions are highly significant (all P values < 0.0001). A. *Anolis fuscoauratus* eats a lot of individual ants and small beetles but they contribute very little to the diet volumetrically. Moreover, largely because of the disparity between numerical and volumetric data in generalist lizards, only 53.2% of the variation in percent prey use volumetrically is explained by numerical data. B. The dietary generalist *Ameiva ameiva* eats few ants but large numbers of termites. Termites contribute little to the diet of *A. ameiva* based on volume. In this case, largely due to the disparity in numerical and volumetric data from a single taxon, only 17.6% of the variation in percent prey use volumetrically is explained by numerical data. C. The ant specialist *Plica umbra* serves as an example of correspondence between numerical and volumetric data. In this case, 99.3% of the variation in percent prey use volumetrically is explained by numerical data

exoskeleton, are lower in energy content on a per gram basis (e.g., SLOBODKIN, 1962). Our recommendation is that, if dietary data on lizards are to be useful in macroecology or phylogenetic reconstructions, both types of data should be collected.

CONCLUSIONS

We would like to now return to the question, "What can teiids tell us about the ecology of lacertids?" The great success of teiids in terrestrial habitats of the new World, particularly in arid, semiarid, and tropical regions, suggests that their *Bauplan*, increased activity levels, and foraging behavior (active foraging) has provided them a competitive advantage in these microhabitats historically. However, the same is likely true for all autarchoglossans (PIANKA & VITT, 2003; VITT *et al.*, 2003). The two clades within Teioidea diverged in two important ways. First, they diverged in body size. Nearly all gymnophthalmids are smaller than nearly all teiids. Small body size no doubt gave gymnophthalmids an advantage in environments in which heat sources for rapid and sustained heat gain were not available (rainforest, high elevations, subterranean microhabitats) resulting in their diversification at a continental level in the presence of teiids. Lacertids appear to have diversified considerably in respect to thermal physiology with some species mimicking teiids and others adapting to thermal niches similar to those of many small

iguanians. This resulted in invasion of high elevations and high latitudes by lacertids. Teiids on the other hand, have not invaded high elevations and occur in high latitudes only in arid regions where summer temperatures are high.

The most striking difference between lacertids, gymnophthalmids, and teiids in diet is the inclusion of large numbers of hymenopterans, particularly ants, in the diets of some lacertids. Unfortunately, volumetric data necessary to distinguish relative energetic importance of ants are not available. Nevertheless, based both on impressive percentages of ants numerically (e.g., PÉREZ-MELLADO, 1998) and LJV's own observations on ant-eating in some lacertids, ants are some clearly more important in diets of lacertids than they are in diets of teiids or gymnophthalmids. Whether this reflects lack of chemical defenses in some Old World ants or a shift to tolerance of chemicals produced by Old World ants by lacertids remains to be determined. Nevertheless, some lacertids have shifted to iguanian-like diets as well as to activity at lower body temperatures.

As a final comment, we point to the importance of standardizing data collection and maximizing opportunities while collecting field and laboratory data from specimens. We believe that the greatest advances in our understanding of the ecology of lizards on a global scale will result from comparative studies in a phylogenetic framework, regardless of whether we search for ongoing processes via field experiments (recent history) (e.g.,

LOSOS *et al.*, 1997) or broad patterns via comparisons within and between major clades (deep history) (e.g., CADLE & GREENE, 1993; VITT *et al.*, 1999; WEBB *et al.*, 2002). Many patterns detected by comparative studies, such as the origin of ecomorphs in anoles (WILLIAMS, 1983) have been confirmed with combinations of experimental and phylogenetic studies (e.g., LOSOS, 1992, 1994, 1996; LOSOS *et al.*, 1997). Similarly, phylogenetic approaches to ecological studies on lizard assemblages can provide new insights into the development of present day community structure (e.g., CADLE & GREENE, 1993; LOSOS, 1996; VITT *et al.*, 1999; WEBB *et al.*, 2002).

ACKNOWLEDGMENTS

First, LJV thanks the organizing committee, Valentín Pérez-Mellado, Gloria Cortázar, Eva María Martín, Anna Perera Leg, and Neftalí Sillero Pablo for providing the opportunity to speculate on lacertid ecology based on experience with teiids and gymnophthalmids. Portions of this synthesis results from many long discussions with William E. Cooper, Jr. and we thank him for his insights. LJV also thanks Valentín Pérez-Mellado for the opportunity to visit several lacertid species in their respective microhabitats. The Brazilian portion of this research was conducted under a research convenio between the Sam Noble Oklahoma Museum of Natural History and the Museu Paraense E. Goeldi. Permits were issued by the Conselho

Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Portaria MCT no. 170, de 28/09/94) and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, permit no. 073/94-DIFAS). All animals were treated in accordance with federal, state, and university regulations (Animal Care Assurance 73-R-100, approved 8 November 1994). NSF grants DEB-9200779 and DEB-9505518 to LJV and J. P. Caldwell supported part of the work.

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