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History and the Global Ecology of Squamate Reptiles

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ABSTRACT: The structure of communities may be largely a result of evolutionary changes that occurred many millions of years ago. We explore the historical ecology of squamates (lizards and snakes), identify historically derived differences among clades, and examine how this history has affected present-day squamate assemblages globally. A dietary shift occurred in the evolutionary history of squamates. Iguanian diets contain large proportions of ants, other hymenopterans, and beetles, whereas these are minor prey in scleroglossan lizards. A preponderance of termites, grasshoppers, spiders, and insect larvae in their diets suggests that scleroglossan lizards harvest higher energy prey or avoid prey containing noxious chemicals. The success of this dietary shift is suggested by dominance of scleroglossans in lizard assemblages throughout the world. One scleroglossan clade, Autarchoglossa, combined an advanced vomeronasal chemosensory system with jaw prehension and increased activity levels. We suggest these traits provided them a competitive advantage during the day in terrestrial habitats. Iguanians and gekkotans shifted to elevated microhabitats historically, and gekkotans shifted activity to nighttime. These historically derived niche differences are apparent in extant lizard assemblages and account for some observed structure. These patterns occur in a variety of habitats at both regional and local levels throughout the world.

Keywords: evolutionary innovations, cladogenesis, community ecology, squamate history, niche, phylogeny.

On-line enhancements: appendix table.

Factors structuring present-day communities are complex and in many instances have been elusive. Competition (Cody 1974; Schoener 1974), predation (Morin 1983; Wilbur and Fauth 1990), and historical contingency (Losos 1992, 1994, 1996) have received the greatest attention as causative agents. Most studies have focused on ongoing ecological interactions among extant taxa (Pianka 1973, 1986; Spiller and Schoener 1988; Winemiller 1991, 1996; Cadle and Greene 1993; Ricklefs and Latham 1993; Cody 1994; Lawton et al. 1994; Diffendorfer et al. 1996; Losos et al. 1997). The suggestion that niche structure in communities may have a phylogenetic basis (Vitt et al. 1999; Webb et al. 2002) challenges ecologists to consider the evolutionary history of organisms to help identify underlying causes of observed structure in communities.

Specifically, what events in the evolutionary history of large and widespread clades contributed to observable disparity in ecological traits among subclades, and how might these differences affect present-day community structure? Here we explore the impact that historically derived differences among squamate clades may have had in structuring present-day communities. This represents the first attempt to evaluate global ecology of any large group of organisms in the context of its evolutionary history. We focus on squamates (lizards and snakes) because they are diverse, they are currently nearly worldwide in distribution, they have undergone numerous adaptive radiations, they exhibit considerable ecological and morphological disparity, and their evolutionary relationships are relatively well known. We briefly comment on each of these to set the stage for our analysis of global ecology.

Squamata is composed of two large clades, Iguania (about 1,230 known species) and Scleroglossa (about 6,000 known species). Since these two clades are of equal age (defined by their common ancestry), scleroglossans have clearly diversified much more (over 4.5 times) than iguanians. About 3,100 scleroglossan species have been traditionally referred to as "lizards," and the remaining 2,900 species have been referred to as "snakes." Squamates are diverse in most natural habitats except at high latitudes and elevations where temperature becomes a limiting fac-

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tor for ectotherms. They occur on all continents except Antarctica. Apparent ecological diversity within numerous clades suggests that adaptive radiations have been frequent. Examples of ecological disparity within subclades of squamates can be found elsewhere (Greene 1997; Pianka and Vitt 2003). Ecological and morphological disparity has been examined in several contexts, ranging from differences among species in habitat use and diet to variation in body size and *Bauplan*. Recognizing which diversification events constitute adaptive radiations is problematic for reasons specified by Losos and Miles (2002).

Major lizard clades first recognized 80 yr ago (Camp 1923; Underwood [1923] 1971) have been supported by morphological studies (Estes et al. 1988; Lee 1998; Schwenk 1988; Rieppel 1994; Wu et al. 1997). Nevertheless, some subclades remain *incertae sedis* (e.g., all amphisbaenian families, Dibamidae) with respect to placement in major clades, and the exact origin of Serpentes within Anguimorpha (or even if they are anguimorphans) remains controversial (Caldwell 1999; Greene and Cundall 2000; Rieppel and Zaher 2000; Harris et al. 2001; Rieppel and Kearney 2001). At lower taxonomic levels, relationships within some sets of subclades (e.g., the 11 subclades of Iguanidae; Frost et al. 2001) remain unresolved.

From the literature, we first identify historically derived differences among major squamate clades. We then show how these differences among clades may have influenced squamate ecology on a global level. Examination of diet data of nonsnake squamates suggests that historically derived differences among subclades affected the kinds of prey eaten. We argue that historically derived attributes of scleroglossans related to food acquisition provided them a competitive advantage over iguanians, not only resulting in greater diversification but consistently greater representation in squamate assemblages worldwide. We also suggest that autarchoglossans historically had competitive advantages in food acquisition and in increased activity levels that may have forced iguanians and gekkotans to diverge along other niche axes.

Methods

Taxa Included

Our discussion is mostly confined to the following taxa: Lepidosauria, *Sphenodon*, Squamata, Iguania, Scleroglossa, Gekkota, Autarchoglossa, and Serpentes. Throughout, we use "lizards" to refer to all non-Serpentes squamates and "snakes" to refer to Serpentes. Serpentes is a monophyletic group exhibiting a number of shared derived traits that set its members off on an evolutionary trajectory considerably different from that of its scleroglossan lizard ancestors. Most relevant to this discussion is the highly kinetic jaw structure that allows most snakes to swallow prey much larger than their heads. We focus on prey differences among clades prior to the evolution of independence of lower jaw movements in prey handling and swallowing (Greene 1997). Nevertheless, we comment on snake evolution as it pertains to global ecology of squamates. References to additional squamate taxa appear throughout the text. Their relationships can be found elsewhere (Pough et al. 1998; Zug et al. 2001; Pianka and Vitt 2003).

Dietary Analyses

Snakes are excluded from our dietary analyses because they are so different. All dietary data included here stem from studies of lizards conducted in African, Australian, and North American deserts by E. R. Pianka and in the New World Tropics by L. J. Vitt. Methods for collection of lizards, species involved, initial identification, and measurements of prey appear elsewhere (e.g., Pianka 1973, 1986; Vitt and Zani 1996; Vitt et al. 1999, 2000). We pooled diet data for all lizard species and localities. Because initial prey categories for desert and Neotropical lizards were nearly identical, we can reanalyze our data at any or all taxonomic levels. The initial desert lizard data set included 20 broad prey types (Pianka 1986) and the initial Neotropical lizard data set included 30 prey types. Relatively few prey categories composed most of the diets of desert and tropical lizards. Consequently, we examined mean percentage utilization of the seven most important prey categories for all lizards: ants (A); beetles (B); grasshoppers and crickets (G); non-ant hymenopterans (H); insect larvae, pupae, and eggs (L); spiders (S); and termites (T). Ants were treated separately from other hymenopterans because they exhibit their own morphotype, are highly diverse and abundant, and because some lizards specialize on them (i.e., lizards discriminate them from other hymenopterans). Because we were most interested in differences between major clades, we pooled data for all species to make comparisons between the sister clades Iguania and Scleroglossa. Diet data for Scleroglossa were further separated by subclades (Gekkota and Autarchoglossa) because fundamental differences exist between these two taxa in their ecologies and mechanisms of chemical discrimination (see below). Our intent was to maximize our ability to identify underlying causes of major dietary differences between clades.

Because prey-type differences between major lizard clades could simply reflect size-specific differences in prey clades (e.g., ants in general are smaller than orthopterans), we compared mean prey size among lizard clades with and without ants, which constituted a common small prey type. This analysis was restricted to Neotropical lizards because individual prey size data were readily available. Because prey sizes were log-normally distributed, data were $\log_{10}$ transformed prior to statistical tests. We then compared prey size among clades with an ANOVA. The above analysis provides a snapshot of the sizes of prey eaten by lizard clades but does not account for differences in sample sizes among species or potential effects of lizard body size on prey size. To test for differences between sister clades in prey size, we calculated mean body size (snout-vent length [SVL]) and mean prey size for all lizard species, $\log_{10}$ transformed the variables, and conducted ANCOVAs with clade as the class variable and SVL as the covariate. Sister clade comparisons we made were Iguania × Scleroglossa and Gekkota × Autarchoglossa.

Effects on Global Ecology

Global consequences of historically derived differences between Iguania and Scleroglossa fall into three categories: diversification, adaptive radiation, and niche characteristics. Because we are comparing sister clades (e.g., Iguania and Scleroglossa), we can assume that the time available for diversification and adaptive radiation within each clade is equal. Thus, differences in numbers of extant species provide one indication of relative success in diversification. However, because we have only two clades of equal age, we cannot determine the degree to which adaptive radiation has occurred within each clade. This issue has recently been addressed by Losos and Miles (2002). Despite the great apparent ecological disparity among species within each clade, a null model for comparison cannot be generated from the two samples. One alternative is to examine clade representation in squamate assemblages in major regions of the world. By doing so, rather than asking the degree to which each clade has diversified or radiated adaptively, we simply ask how well species representing each clade have performed within mixed-species assemblages. We assume that relative representation in multiple assemblages is independent of geography, physiognomy, or climate and provides repeated measures of relative success. If historically derived characteristics of scleroglossans provided them with a competitive advantage during their evolutionary history, then they should dominate most or all squamate assemblages with respect to number of species represented. The data set for this analysis is regional (not locality specific); we included all regions for which we could obtain accurate counts of all squamates (snakes included). Our regions include politically defined areas (countries), ecoregions (e.g., Amazonia), and islands simply because those are the data that exist. They are Amazonia (Cadle and Greene 1993; Avila-Pires 1995), Argentina (Cei 1986), Australia (Cogger 1992), Baja California (Grismer 2002), Belize (Stafford and Meyer 2000), Caatinga (NE Brazil; Vanzolini et al. 1980), Cerrado (Colli et al. 2002), China (Zhao and Adler 1993), Costa Rica (Savage 2002), Cuba (Estrada and Ruibal 1999), East Africa (Spawls et al. 2002), Europe (Hellmich 1962), Guatemala (J. Campbell, personal communication), Hispaniola (Powell et. al 1999), Honduras (Wilson and McCranie 2002), India (Tikader and Sharma 1992), Iran (Anderson 1999), Iraq (Khalaf 1959), Israel (Werner 1995), Jamaica (Crombie 1999), Madagascar (Henkel and Schmidt 2000), Mexico (Flores-Villela 1993), Mongolia (Ananjeva et al. 1997), New Caledonia (Bauer and Sadlier 2000), North Africa (Schleich et al. 1996), Puerto Rico (Rivero 1978), Russia (Ananjeva et al. 1998), South Africa (Branch 1988), South Asia (Das 1996), Southeastern Asia (Manthey and Grossmann 1997), United States (Collins and Taggart 2002), Venezuela (Pefaur and Rivero 2000), and the Yucatán Peninsula (Lee 2000). Some pseudoreplication exists because wide-ranging species may be represented in more than a single region. However, our emphasis for this comparison is on relative proportions of scleroglossans in assemblages, not the species composing those assemblages. We conducted a similar analysis on lizard data (snake data not available) from 68 study sites to test for conformity between regional and site-specific results.

Because we are examining the impact of historical events on present-day squamate assemblages, our expectation is that similar patterns of relative clade representation should be apparent between regions sharing none of their resident species. New and Old Worlds are ideal for this comparison because they share no native squamate species but all three major clades are represented in each. We calculated the proportion of each assemblage contributed by various subclades for comparison. Interpreting differences in clade representation between the New and Old World required examination of relative contributions to squamate assemblages by iguanians, gekkotans, autarchoglossan lizards, and snakes. We separated Serpentes from all other Autarchoglossans because they differ from their ancestors in many biological attributes (e.g., Greene 1997). A few regions, such as New Caledonia, are exceptional in entirely lacking one of the three clades. Other areas, such as Argentina, Cuba, and the deserts of North America, display a paucity of autarchoglossans.

Finally, we examined the impact of autarchoglossan lizards on gekkotans and iguanians by comparing place (microhabitat) and time niche characteristics in many well-studied assemblages. If at least a portion of niche differences among species within lizard assemblages is historically derived, we expect within-clade differences in time and place niche characteristics to be less than between clade differences. For this analysis, we selected 44 well-studied lizard assemblages (snakes could not be included). Our criteria for inclusion were that all species in each lizard assemblage were simultaneously studied; data on place, time, and food niches were collected; data were collected in a similar manner; and the assemblages included representatives from Iguania (73 species), Gekkota (42 species), and Autarchoglossa (123 species). Assemblages in Amazonia (10 sites), Caatinga (one site), Cerrado (three sites), Great Victoria Desert of Australia (10 sites), Kalahari Desert (10 sites), and North American deserts (10 sites) were included. Because many species occurred in two or more assemblages but none varied ecologically independent of assemblage at the level of our comparisons, we deleted all duplicates such that each species was represented only once. Time niche varies among species within lizard assemblages (e.g., Pianka 1986), but at the most basic level, most species can easily be categorized as nocturnal or diurnal. Thus, we scored each studied species as nocturnal, diurnal, or active both at night and during the day. Place niches also vary considerably among lizard species within assemblages (e.g., Pianka 1986; Vitt and Zani 1996), species often being segregated both vertically and horizontally. Examination of data in lizard community studies reveals that nearly all lizards can easily be categorized as using or not using elevated perches. Elevated perches include a diversity of arboreal and saxicolous microhabitats. Species not using elevated perches are most often found on or under the ground. Such broad categorization ignores differences in activity times or microhabitat use that might result from present-day species interactions, but our emphasis is on patterns originating deep in squamate evolutionary history. If historical differences between major clades have had an impact on time and place niche characteristics, we would expect to detect it at the most basic level.

Results and Discussion

History of Clade Differences

Squamate history dates back to early Jurassic or late Triassic (Estes 1983; Evans 1993). Squamata is sister to Rhynchocephalia, the two comprising Lepidosauria (Gauthier et al. 1988; Rieppel 1994). The two extant rhynchocephalians (*Sphenodon*) are superficially lizard-like and, in most phylogenetic analyses of squamates, are used as outgroup even though they are highly derived in some ways (Gans 1983). Presumed ancestral traits shared with squamates include the following: lingual prehension for prey capture; foretongue-hyobranchium coupling; hyolingual transport of prey; pharyngeal packing during swallowing (Schwenk and Throckmorton 1989; Schwenk 2000); a rudimentary vomeronasal chemosensory system (Gabe and Saint Girons 1976); visual hunting; sit-and-wait ambush foraging mode; low activity levels and energy requirements; and an apparent diapsid, akinetic skull (reviewed by Pianka and Vitt 2003).

Although little is known about the origin of squamates, they are presumed to have been present on Pangaea during the middle Triassic because their sister taxon Sphenodontida existed then (Evans 1995). Recent discovery of a primitive acrodont iguanian from Gondwana dated at early-middle Jurassic provides evidence that iguanians had begun to diversify before the breakup of Pangaea (Evans et al. 2002). Gondwana presumably had primitive iguanians (Estes 1983; Bauer 1993; Evans 1995), gekkotans (Kluge 1987), and amphisbaenians (Cei 1986), whereas Laurasia must have contained ancestral eublepharid geckos (Grismer 1988), scincomorphans, and anguimorphans (Estes 1983). When Gondwana broke apart, its iguanians and gekkotans were isolated on three southern landmasses: South America (iguanids, sphaerodactyline geckos), the Australian region (agamids, diplodactylids) (Estes 1983), and Africa-Madagascar (oplurines, gekkonids). Estes (1983) postulated the following biogeographic scenario: when the Atlantic Ocean opened about 100–120 mya, an ancestral group of pleurodont iguanians was split, giving rise to South American iguanids and Madagascar oplurines. Intervening mainland African forms died out. Then, a northern acrodont group was divided into an African and Madagascar chameleon clade and an Asian (or Asia + India + Australia) agamid clade (Bauer 1993).

Autarchoglossans diversified on Laurasia (Estes 1983). When Laurasia fragmented, Africa remained close to Eurasia and thus had the potential to be invaded by autarchoglossans. However, South American and Australian iguanians were presumably protected for millions of years from autarchoglossans by isolation, although eventually Autarchoglossa colonized the entire world.

Gekkonids and skinks dispersed widely and became virtually cosmopolitan. Both crossed oceans by rafting or moving across land bridges (Taylor 1935; Greer 1974; Gibbon 1985; Grismer 1988; Bauer 1993; Adler et al. 1995; Allison 1996). Other groups either remained confined to their landmass of origin or exhibited a more limited dispersal (Estes 1983; Estes and Pregill 1988; Zug et al. 2001). Snakes are nested within Scleroglossa, probably within Anguimorpha (Schwenk 1988; Rieppel 1994; Lee 1998; but see Wu et al. 1997; Hallermann 1998). Unfortunately, exactly when and how snakes diversified and colonized continents remains poorly known (Bauer 1993; Greene 1997).

The first historically derived trait with ecological implications in ancestral squamates, streptostyly, occurred in the Gondwana part of Pangaea about 200 mya; an additional moveable link (the upper jaw joint bone, the quadrate) rotates freely on the skull (fig. 1). Squamates lost the lower temporal arch, retaining only a single upper fenestra in the skull roof. Loss of the lower arch freed the quadrate

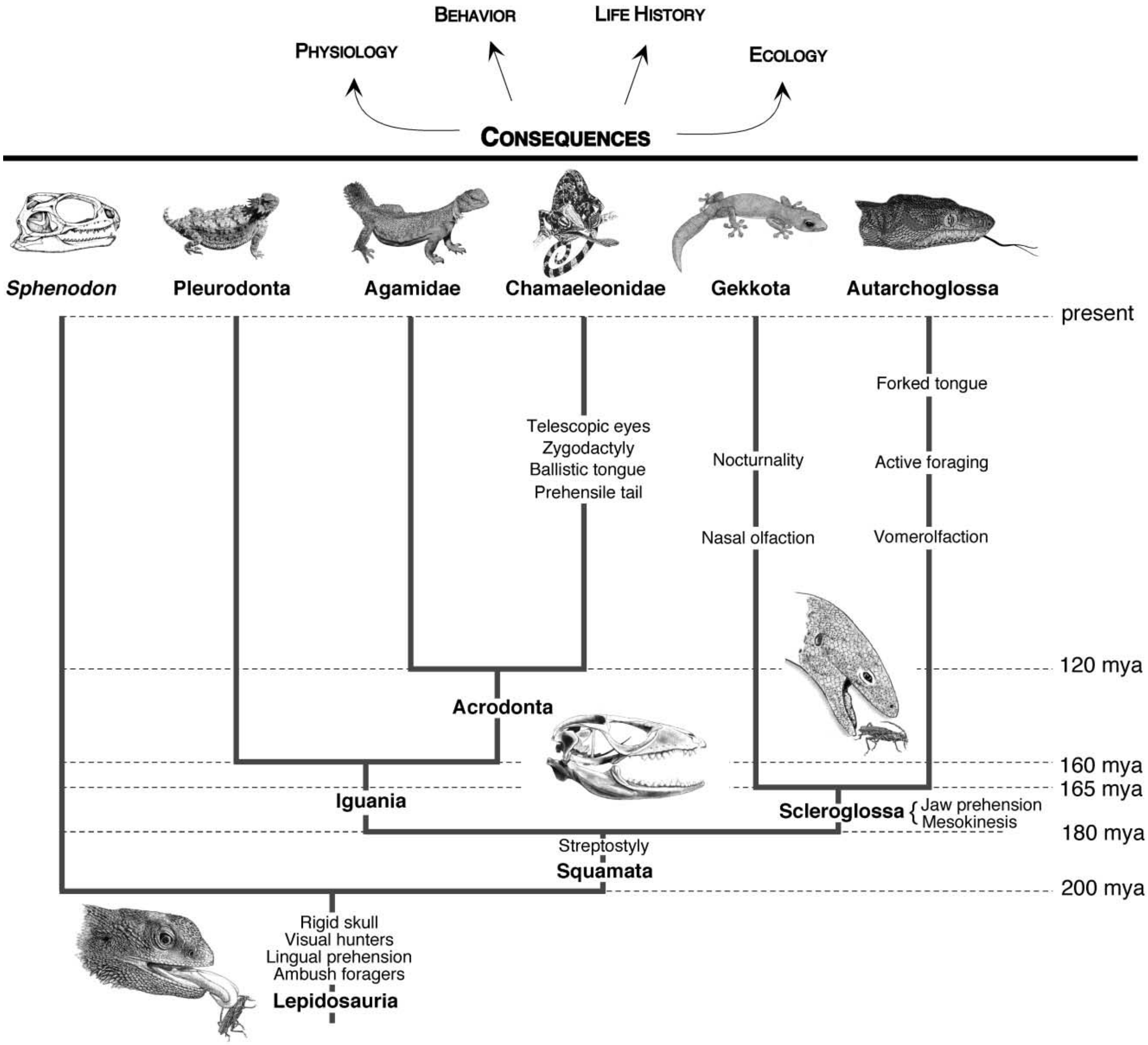

Figure 1: Streptostyly facilitated the first major radiation of lizards, the Iguania, a highly successful clade comprised mostly of visually oriented ambush-foraging species. Iguania retain most ancestral character states. Streptostyly was retained in all descendents, with additional innovations facilitating the explosive diversification of Scleroglossa. The transition from lingual prehension in iguanians to jaw prehension in scleroglossans freed the tongue from involvement in prey acquisition so that it could be used primarily to sample chemicals in the environment. Nocturnality may have enabled gekkotans to escape competition and provided access to resources as yet untapped by other scleroglossans. Similarly, active foraging and increased vomeronasal development gave autarchoglossans access to hidden and sedentary prey and contributed to their diversification. Retained ancestral traits of iguanians and innovations leading to scleroglossans affected most aspects of squamate behavior, physiology, ecology, and life history. Snakes arose from within autarchoglossans.

to move. Streptostyly increased gape and the mechanical advantage of jaw musculature, allowing a faster and more powerful bite (Smith 1980, 1982), facilitating exploitation of novel food resources, development of new feeding strategies, and a wide variety of dietary specializations compared to nonstreptostylic ancestors.

When Gondwana and Laurasia split about 180 mya, the Iguania-Scleroglossa divergence occurred. Iguania mostly retained ancestral traits, diversifying into about 1,230 species in two subclades, Acrodonta and Pleurodonta. Most surviving iguanians are ambush predators, use visual cues to capture mobile prey (which they ingest using their tongue), have low activity levels, and have poorly developed vomeronasal chemosensory systems (Pianka and Vitt 2003). About 100–120 mya on the Africa-Madagascar plate, a unique set of historically derived traits evolved in one iguanian subclade, the Chamaeleonidae, setting a new direction in iguanian evolution. Zygodactyly combined with turret-like telescopic eyes, ballistic tongues, and prehensile tails allowed chameleons to balance on narrow perches to exploit arboreal habitats (Peterson 1984; Wainwright et al. 1991), look around without moving their heads (Ott and Schaeffel 1995; Necas 1999), and capture prey more than a body length away. Their highly sophisticated lingual feeding tactics and extreme sit-and-wait ambush foraging eliminated the riskiest aspect of sit-and-wait foraging—pursuit movements. Chameleons diverged from other iguanians and occupy their own completely disjunct niche space.

On the Laurasian plate from 180 to 165 mya, Scleroglossa diverged dramatically from the putative ancestral condition retained by Iguania. Its ancestor switched from tongue to jaw prehension of prey (Schwenk 2000; Schwenk and Wagner 2001; fig. 1). This freed the tongue from its role in prey capture. The foretongue and hyobranchial skeleton uncoupled (Schwenk 2000). Scleroglossan skulls became less robust and more kinetic than those of iguanians (Schwenk 2000). Additional points of potential flexibility arose in scleroglossan skulls, a condition known as cranial kinesis, in particular mesokinesis. This allows the muzzle and upper jaw to flex upward and downward, making the jaws still more efficient in capture and manipulation of agile prey (Frazzetta 1983; Arnold 1998; Herrel et al. 2000; Schwenk 2000). Such jaws also bend and better conform to prey (e.g., Savitzky 1981; Patchell and Shine 1986), additionally enhancing feeding success. Iguanians appear to be anatomically precluded from flexing the snout and lack mesokinetic movements (Schwenk 2000). Scleroglossan adaptations appear to improve the performance of prey capture and manipulation compared to the lingual feeding iguanians, possibly facilitating use of new food resources.

At the Gekkota-Autarchoglossa divergence about 165 mya, tongues took on different roles, chemosensory systems diverged and developed (Gabe and Saint Girons 1976; Schwenk and Throckmorton 1989; Schwenk 1993*a*, 1993*b*, 2000; Cooper 1997*a*), and ancestral gekkotans became nocturnal whereas ancestral autarchoglossans remained diurnal like their ancestors (fig. 1). These sister clades differ in degree of diversification: about 1,000 species of gekkotans exist compared to some 5,000 species of autarchoglossans. The dominant chemosensory system of ancestral scleroglossans remains undetermined. Within its two subclades, Gekkota has emphasized nasal olfaction and Autarchoglossa has enhanced vomerolfaction. Both discriminate prey based on chemoreception (Schwenk 1993*a*; Cooper 1995, 1996*a*, 1997*a*, 1997*b*; Dial and Schwenk 1996). Geckos may have become olfactory specialists to compensate for limited ability to detect distant objects visually while active at night. In Gekkota, tongues are used to clean lips and spectacles (in those with spectacles). Nasal olfaction detects small, volatile molecules from potentially large distances and also triggers tongue flicking and the vomeronasal system for further analysis of chemical cues. In contrast, vomerolfaction detects primarily larger, nonvolatile molecules sampled by lingual contact. It provides superior discrimination and tracking ability but is more limited in the distance over which it can operate (Cowles and Phelan 1958; Halpern 1992; Schwenk 1995). In autarchoglossans, the foretongue became specialized for protrusion and for picking up and transporting chemical signals into the mouth to be received and deciphered by the vomeronasal system (Schwenk 1993*b*, 1994, 2000; Cooper 1996*b*). The vomeronasal system was present in squamate ancestors but, with few exceptions, remained weakly developed in iguanians (Gabe and Saint Girons 1976; Schwenk 1993*b*; Cooper 1996*b*). We hypothesize that higher activity levels in autarchoglossans and possibly basal gekkotans were initially coupled to increased foraging movements. An ability to detect and discriminate among prey chemically could allow access to visually undetectable prey types, including highly cryptic invertebrates and vertebrates living in crevices, in the ground, and in some cases in water—prey that lizards had to search for to find (e.g., Huey and Pianka 1981; Vitt and Cooper 1986; Cooper 1994, 1995, 1997*a*). Morphological and ecological diversity within Autarchoglossa is impressive (Greene 1997; Pianka and Vitt 2003).

Ecological Consequences of Historically Derived Traits

Numerous hypotheses are suggested by positioning historically derived traits on the squamate phylogeny (fig. 1). We examine three in detail here.

The first hypothesis, discussed above, is that historically derived traits in the ancestor to scleroglossans facilitated use of new food resources. This hypothesis predicts that a detectable prey shift should occur at the Iguania-Scleroglossa transition. Three nonexclusive mechanisms exist: (1) the shift to jaw prehension and mesokinesis could translate into the ability to handle prey that cannot be manipulated effectively with lingual prehension; (2) chemical prey discrimination in scleroglossan ancestors could facilitate prey choice based on characteristics other than prey mobility; and (3) enhanced vomerolfactory ability could facilitate locating sedentary and cryptic prey. The second, related, hypothesis is that scleroglossans should have been better competitors with respect to prey acqui-

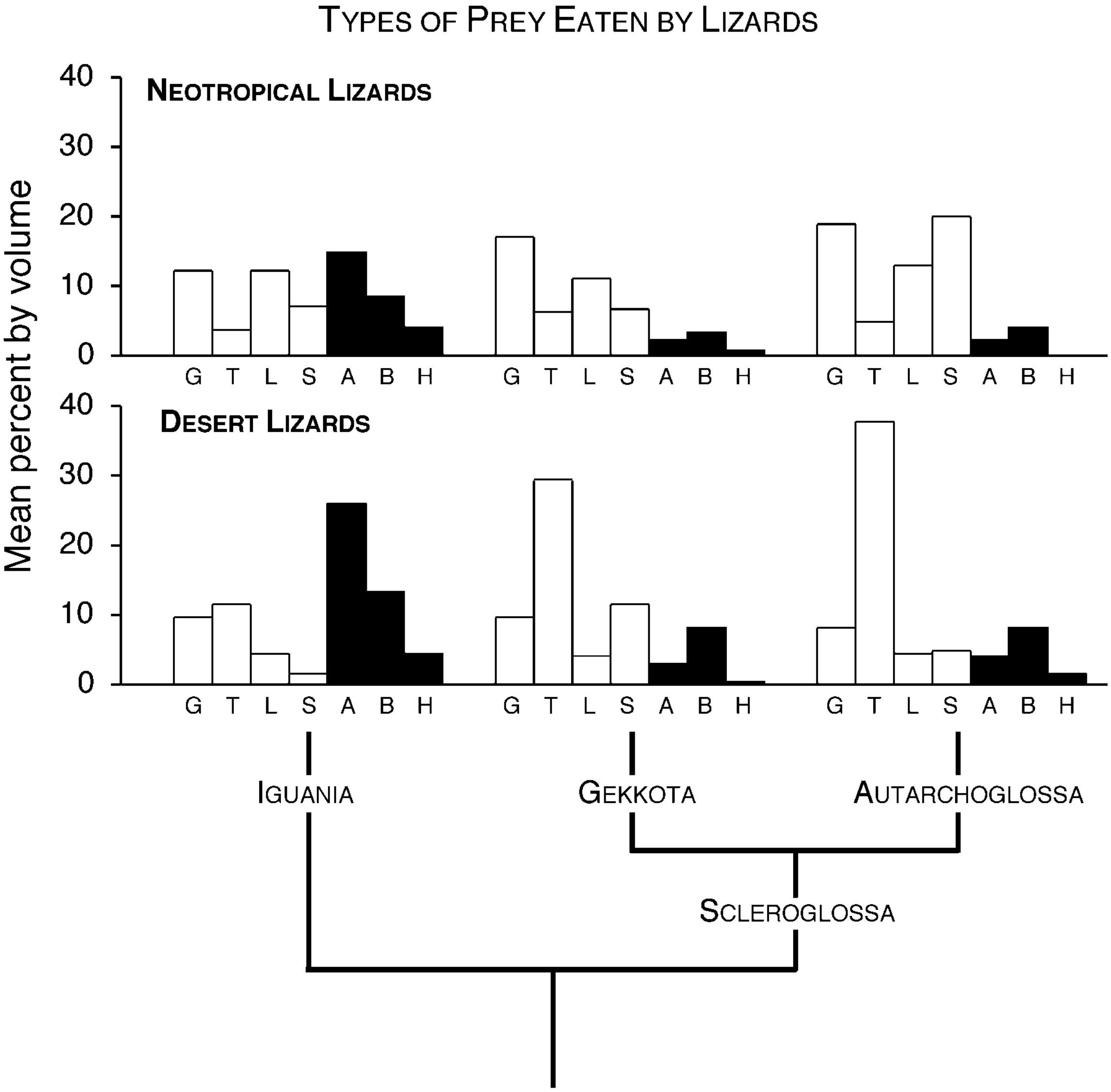

Figure 2: Mean percentage utilization of the most important seven prey categories by Neotropical lizards (*upper*) and desert lizards (*lower*). Proportions of ants and other noxious insects decrease from high values in Iguania to low values in Scleroglossa (*black bars*). In both regions, ants are replaced by a combination of grasshoppers, insect larvae, and spiders in Neotropical lizards and by termites and spiders in desert lizards. Prey types are as follows: grasshoppers and crickets (*G*); termites (*T*); insect larvae, pupae, and eggs (*L*); spiders (*S*); ants (*A*); beetles (*B*); and non-ant hymenopterans (*H*). Ants, some beetles, and other hymenopterans are known to contain numerous toxic defensive chemicals.

sition historically than iguanians because they added enhanced prey handling (mesokinesis) and chemosensory-mediated prey discrimination to the arsenal of historically derived traits shared with iguanians. This hypothesis predicts that scleroglossans should dominate squamate assemblages in terms of relative representation on a global level. Our third hypothesis is that, if autarchoglossans were better competitors for food as a result of the combination of jaw prehension, mesokinesis, vomeronasal chemoreception, and high activity levels, gekkotans and iguanians should have diverged historically from autarchoglossans and from each other along niche axes other than food (time and place) to use microhabitats and habitats unoccupied by autarchoglossans.

Hypothesis 1. A Detectable Shift in Prey Should Occur at the Iguania-Scleroglossa Transition. A summary of dietary data on Neotropical and desert lizards (fig. 2) is consistent with this hypothesis. We assume that Iguania retained the ancestral squamate diet. Dramatic dietary shifts occur at the Scleroglossa transition in both Neotropical and desert lizards, the most striking of which is a reduction in occurrence of ants, other hymenopterans, and beetles in diets of species in both scleroglossan subclades. Whether ants, other hymenopterans, or beetles are more difficult to manipulate with jaw prehension remains unstudied. One hypothesis is that jaw prehension simply enhances the capture of larger prey, thus reducing the need for small prey, such as ants. Close examination of prey size for Neotropical lizards fails to support this hypothesis, however. First, prey size did not shift radically when jaw prehension replaced lingual prehension of prey (fig. 3). Adjusting for body size did not change this result. Only marginal differences exist in slopes ($F = 3.9$, $\mathrm{df} = 1, 82$, $P = .052$) or intercepts ($F = 3.5$, $\mathrm{df} = 1, 82$, $P = .065$) of the regressions of mean prey size on mean body size between iguanians and scleroglossans. Within Scleroglossa, gekkotans eat smaller prey and autarchoglossans eat slightly larger prey than iguanians (fig. 3). The relationships between body and prey size differ between gekkotans and autarchoglossans (slope test, $F = 5.4$, $\mathrm{df} = 1, 44$, $P = .024$).

Linking the dietary shift to changes in jaw structure appears weakly supported. Enhancement of chemical sensing abilities in gekkotans (nasal olfaction) and autarchoglossans (vomerolfaction) suggests the hypothesis that prey shifts resulted from the ability to discriminate prey based on chemical cues, which has been repeatedly demonstrated experimentally in both taxa (Cooper 1994, 1995, 1996*a*, 1997*a*, 1997*b*). Two nonexclusive hypotheses might account for reductions of ants, beetles, and non-ant hymenopterans in scleroglossan diets: lizards that can discriminate prey chemically either (1) select prey based on

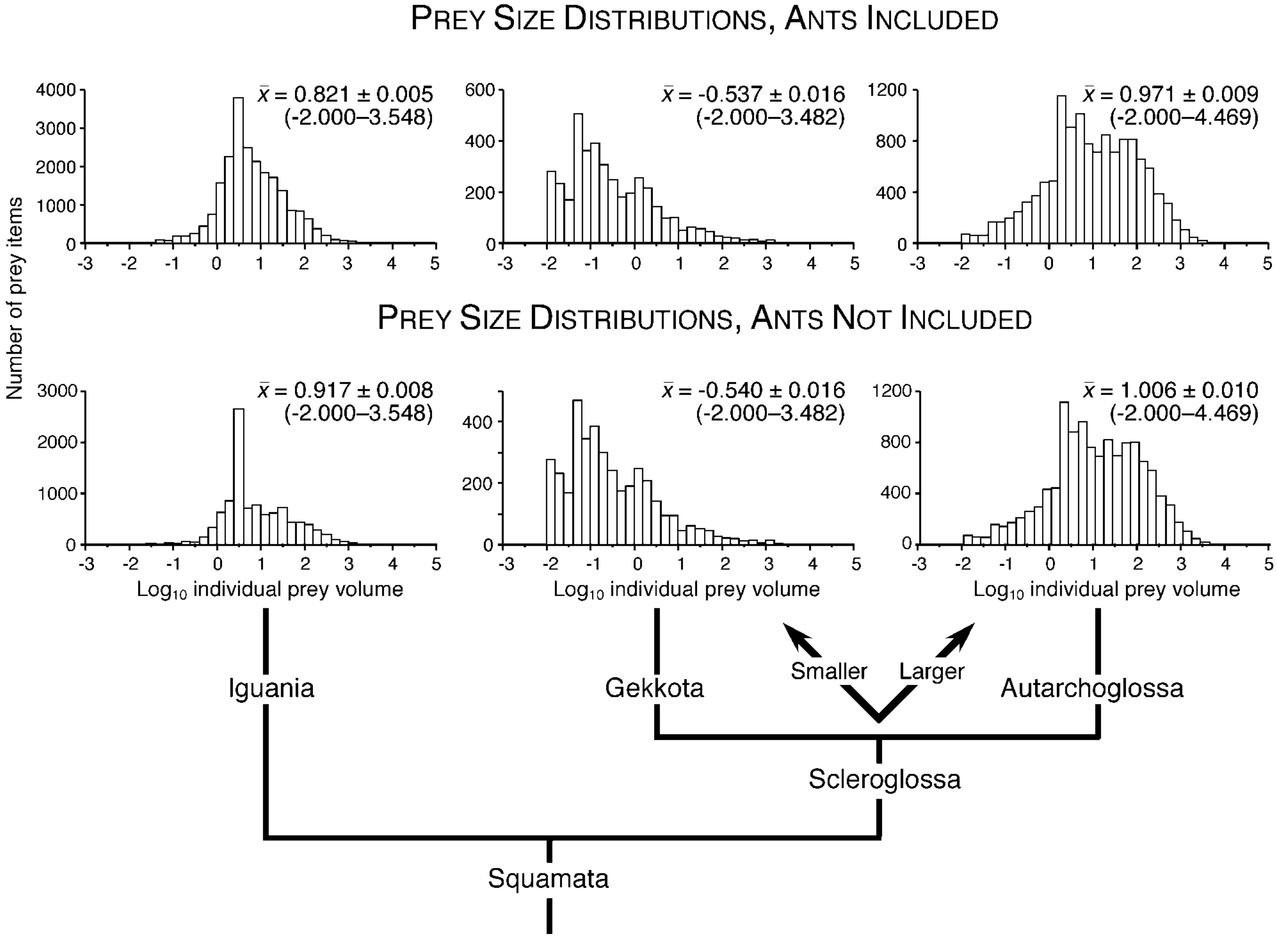

Figure 3: Distributions of individual prey volumes (millimeters cubed) for 83 Neotropical lizard species. Eliminating ants increases mean prey size substantially in iguanians but has relatively little effect on prey size of gekkotans and autarchoglossans (partly because they eat few ants). A relationship exists between lizard body size and prey size both within and among lizard species (not shown here). Adjusting for effects of lizard body size does not change this result qualitatively but does reveal no significant differences among clades (see text).

cues indicating relatively high energy content or (2) avoid prey containing chemical defense systems, especially those that might be toxic or negatively affect metabolism. Support exists for both hypotheses. Neotropical and desert scleroglossan lizards differ in what they eat, but striking similarities also exist in what they do not eat. To a large extent, ants, beetles, and non-ant hymenopterans in iguanian diets were replaced in scleroglossan diets by a combination of termites, grasshoppers, and spiders, which, in itself, varies between deserts and Neotropics (fig. 2). Termites (clumped prey), grasshoppers, and spiders may constitute relatively higher-energy prey. Alternatively, ants, beetles, and other hymenopterans often contain noxious chemicals, particularly alkaloids (Blum 1981; Evans and Schmidt 1990; Daly et al. 1994, 2000) that may be avoided by lizards using chemical senses to detect them. This issue has not yet been directly addressed. Nevertheless, some evidence from herbivorous lizards suggests that alkaloids could be used to discriminate prey. The only iguanians known to discriminate food types based on chemicals are in the subclade Iguaninae, all of which are herbivorous. Avoidance of plant defensive toxins is one hypothesis to explain evolution of enhanced vomerolfaction by these lizards (Cooper and Alberts 1990, 1991). At least one herbivorous autarchoglossan also avoids plants containing alkaloids (Schall 1990). Although alkaloids may be detected by taste in scleroglossans and iguanians (Schall 1990; Stanger-Hall et al. 2001; Cooper et al. 2002), the sensory basis for detection of other metabolic toxins has not been determined. Because scleroglossans can detect several categories of metabolic toxins (Cooper et al. 2002), avoiding them may have opened up new metabolic opportunities, allowing higher activity levels as well as prolonged activity at high body temperatures, a hypothesis yet untested. A phylogenetically corrected analysis of relative liver size comparing lizards that do and do not eat noxious insects could shed some light on this issue (e.g., Jacksic et al. 1979). Finally, scleroglossan lizards not only have diverged in important aspects of their diets from iguanians, they have continued to include large proportions of some of what appear to be among the most energetically profitable prey used by iguanians: grasshoppers, termites, insect larvae, and spiders (see Slobodkin 1962 for examples of relative energy content in arthropods).

Dramatic differences in diets between major lizard clades suggest that a portion of structuring with respect to food niches in lizard assemblages is historical (see also Vitt et al. 1999). If historically derived characteristics in species of a particular clade provide enhanced ability to find and capture prey, then historically derived shifts on other niche axes (place or time) might also be expected (examined below under hypothesis 3).

Hypothesis 2. Historically, Scleroglossans Were Competitively Superior to Iguanians. A simple comparison of total number of species between two clades of equal age is not sufficient to address this hypothesis because such a comparison does not necessarily reflect consequences of species interactions even though species numbers differ impressively (4.5 times as many scleroglossans worldwide). Rather, the ability of scleroglossans to repeatedly dominate squamate assemblages containing iguanians should reflect relative competitive ability of scleroglossan species to at least some degree (but see niche comparisons below). The possibility (although remote) exists, for example, that all scleroglossan diversity might occur in a few regions rather than worldwide, and iguanians might dominate squamate assemblages in most other regions. However, scleroglossans, especially autarchoglossans, dominate nearly all squamate faunas at a regional level independent of geography or habitat type (fig. 4*A*). The same is true when data from specific sites are compared: 65.3% ± 2.8% (SE) are scleroglossans (69.3% ± 0.017% of these are autarchoglossans), whereas 34.7% ± 2.8% are iguanians. Thus, on average, autarchoglossans comprise 44.5% ± 1.9% of lizard assemblages at individual sites.

Historical differences in the timing of colonization by iguanians and scleroglossans suggest that differences in lizard faunas might exist between the Old and New World. Scleroglossans are better represented in the Old World (fig. 4*B*). Confounding the issue is that one scleroglossan subclade, Serpentes, evolved a nonlizard-like feeding apparatus, sending snake evolution off in a different direction from other autarchoglossans; most snakes are predators of other vertebrates (Greene 1997) and may not compete with

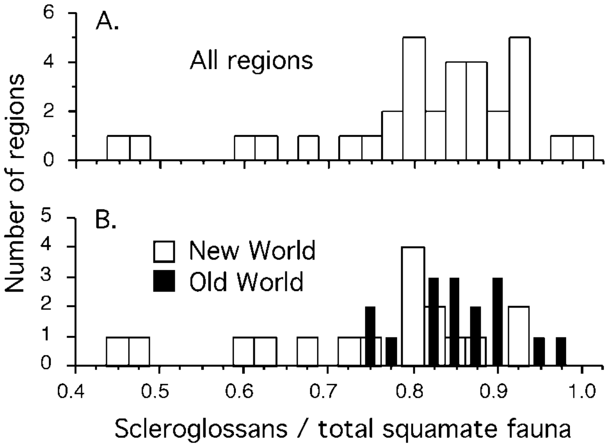

Figure 4: *A*, Scleroglossans as proportions of squamate faunas in 34 regions of the world. *B*, Differences in proportions of scleroglossans between the New and Old World ($t = -3.609$, df = 34, $P = .0011$ on arcsine-transformed ratios).

lizards (but many prey on lizards). Removing snakes produces similar results but with lower proportions of scleroglossans (fig. 5*A*). The most striking result is that scleroglossan lizards are much better represented in regions of the Old World than in the New World (fig. 5*B*). This results primarily from a high diversity of iguanians and low diversity of skinks in New World squamate assemblages and a higher representation of snakes among New World autarchoglossans than in the Old World. The antiquity and isolation of New World iguanians may have given them such a competitive advantage in elevated microhabitats that by the time autarchoglossan lizards arrived, they were unable to move into these microhabitats. The observation that nearly all teiids and gymnophthalmids are terrestrial supports this hypothesis. Old World iguanians experienced interactions with autarchoglossan lizards during their entire evolutionary history. Similar trends are apparent in all New versus Old World comparisons (table 1). Data on regional squamate assemblages (see appendix in the online edition of *The American Naturalist*) reveal that such trends are widespread within local assemblages.

Snakes and autarchoglossan lizards exhibit complementary patterns of species richness, with more New World snake species and relatively more Old World autarchoglossan lizards. This apparent complementarity requires further comment. Scincidae is the largest subclade of autarchoglossan lizards, with more than 1,200 described species (Greer 2001). A vast majority occur in the Old World, and they have undergone a massive adaptive radiation in Australia (about 325 species, 47% of Australian squamates; Cogger 1992). In spite of the fact that skinks are good dispersers, only a few lineages have managed to reach the New World. *Eumeces*, *Scincella*, and *Sphenomorphus* probably dispersed from the Laurasian plate across Beringia, whereas *Mabuya* is thought to have rafted across the Atlantic from east Africa to northern South America (Bauer 1993). *Neoseps* is a New World derivative of *Eumeces* (T. Reeder, personal communication). Colubrids represent 73% of all South American snakes compared to 55% of the snake fauna of Africa (Bauer 1993). Although colubrids are well represented in Southeast Asia (83% of all snakes; Manthey and Grossman 1997), few have reached Australia (9%; Cogger 1992), where skink diversity is high.

Table 1: Proportions of major lizard clades in Old and New World and combined ("World")

	Region			
Variable	New World	Old World	*P* value	World
IG/LZ	.474 ± .037	.193 ± .026	<.0001*	.334 ± .033
SL/LZ	.526 ± .037	.806 ± .026	<.0001*	.666 ± .033
GEK/LZ	.193 ± .025	.274 ± .022	.0132*	.233 ± .018
AL/LZ	.333 ± .037	.532 ± .037	.0020*	.433 ± .032
IG/SQ	.265 ± .034	.118 ± .015	.0009*	.194 ± .023
GEK/SQ	.113 ± .021	.175 ± .018	.0194*	.143 ± .015
SL/SQ	.277 ± .025	.496 ± .025	<.0001*	.383 ± .030
AL/SQ	.165 ± .015	.321 ± .033	.0001*	.241 ± .022
SCL/SQ	.735 ± .034	.870 ± .016	.0016*	.801 ± .022
SN/AUT	.726 ± .025	.544 ± .043	.0007*	.638 ± .029
SN/SQ	.458 ± .040	.385 ± .035	.1213	.423 ± .027
AUT/SQ	.622 ± .045	.705 ± .025	.2281	.663 ± .027

Note: IG = Iguania, LZ = lizards, SL = scleroglossan lizards, GEK = Gekkota, AL = autarchoglossan lizards, SQ = all squamates, SCL = Scleroglossa, SN = snakes, AUT = Autarchoglossa. *P* values are based on two-tailed *t*-tests of arcsine-transformed data. The *t*-test probability values appear only to show that proportions are considerably different in most cases. Considerable phylogenetic pseudoreplication exists in this data set.

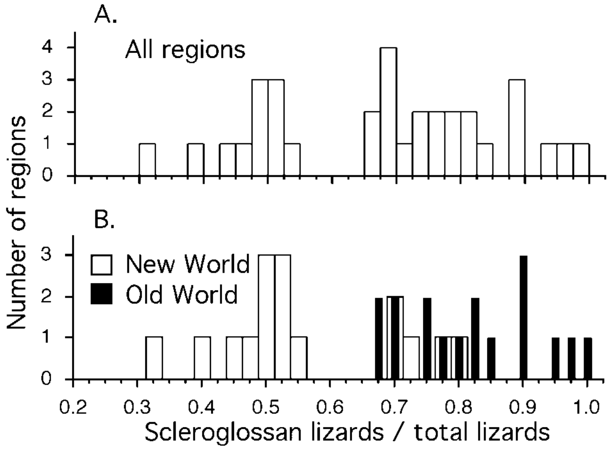

Figure 5: *A*, Scleroglossan lizards as proportions of lizard faunas in 34 regions of the world. *B*, Differences in proportions of scleroglossan lizards between the New and Old World ($t = -6.114$, df = 34, $P \leq .0001$ on arcsine-transformed ratios).

Site-specific comparisons might clarify these relationships. However, data for snakes are lacking for most sites where lizards have been sufficiently studied, and, because many lizard study sites are in the same ecoregion (e.g., either Amazonia or Australian deserts), the large degree of pseudoreplication precludes such comparisons. Limited evidence suggests that scleroglossan lizards dominated fossil lizard assemblages as well. Six Late Cretaceous (70–80 mya) Mongolian sites, containing from nine to 22 lizard species, averaged 68.6% ± 6.0% scleroglossans (Kequin and Norell 2000). Only one site contained a gekkotan. Modern-day Mongolia has only three extant iguanians, three gekkotans, six autarchoglossan lizards, and seven snakes (Ananjeva et al. 1997).

Hypothesis 3. Iguanians and Gekkotans Historically Shifted to Microhabitats or Times Not Used by Most Autarchoglossans to Offset Competition for Food. Historically derived characteristics in the ancestor to autarchoglossans contributing to a competitive advantage in prey acquisition include enhanced higher activity levels and vomerolfaction for prey search and discrimination (fig. 1). If niche shifts are historically based, we expect (1) gekkotans and iguanians to use different place and/or time niches than autarchoglossans, (2) similar niche shifts in independently derived assemblages, and (3) iguanians or gekkotans to fill autarchoglossan niches where the latter are absent. We test the first two predictions by examining data on niche relationships among members of each of the three clades from our study sites. In Neotropical lowland forest, semiarid caatinga, cerrado, and deserts of the world, many gekkotans are active at night, and many of those that are active during the day use elevated perches or live in enclosed spaces (fig. 6). Iguanians in these same habitats are all diurnal, and most tend to use elevated perches. Most autarchoglossans are terrestrial, using relatively open spaces, or are subterranean. We conclude that the most basic niche characteristics of species composing major lizard clades have a historical origin. Some evidence from localities with few or no scleroglossans supports the third prediction. South American autarchoglossan lizards that achieve body sizes similar to or larger than those of iguanians (teiids and anguids) are absent from high elevations in the southern Andes, most likely as the result of their inability to thermoregulate sufficiently to maintain high activity levels. In this region, iguanian lizards in the genus *Liolaemus* have diversified greatly and occupy many niches often associated with teiid lizards (e.g., Cei 1986). Likewise, *Anolis* (Iguanidae) lizard faunas have diversified and dominate squamate assemblages of many Caribbean islands where diurnal scleroglossan lizards (Teiidae, Gymnophthalmidae, Scincidae, and Anguidae, in particular) have been relatively unsuccessful or are absent. In contrast, *Anolis* lizards do not dominate most mainland squamate faunas.

We argue that historically derived differences among major squamate clades caused ecological shifts that have been carried forward to extant species on a worldwide basis. Such innovations include mesokinesis and acquisition of chemical discrimination of prey, leading to a dietary shift in Scleroglossa; nocturnality in basal gekkotans, resulting in divergence in temporal niche; and use of elevated perches in iguanians and gekkotans, resulting in divergence of spatial niches. Because iguanians, gekkotans, and autarchoglossans are fundamentally different enough historically, all can achieve some degree of success in mixed assemblages. Unless one of the major clades simply never reached a place (or major habitat features necessary for its success do not exist), each is better at performing its own clade-specific behaviors (iguanians on vertically structured habitats, gekkotans in the night, autarchoglossans in open terrestrial microhabitats). Thus, all three compete successfully in mixed assemblages. The repeated presence of all three clades in most regions supports this argument.

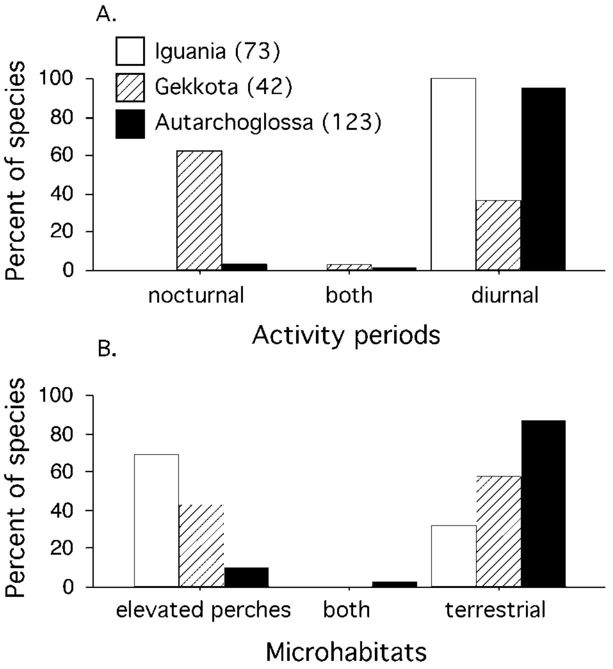

Figure 6: *A*, Comparison of percentage of lizard species (snakes excluded) in three major clades active at night, during the day, or both nocturnal and diurnal. *B*, Percentage of species in each clade active on elevated perches, the ground, or both (sample sizes given in the text).

Numerous studies have attributed morphological (Vitt and Price 1982), physiological (Anderson and Karasov 1981), life-history (Vitt and Congdon 1978; Vitt and Price 1982), behavioral (Cooper 1995, 1997*a*), and ecological (Huey and Pianka 1981; Pianka 1986) characteristics of squamates to differences among species in foraging mode. Our analysis suggests that although foraging mode has had profound ecological and evolutionary effects on squamates, it is just one among many features that evolved deep in squamate history rather than the cause of all other differences.

Caveat

Our analysis of the effects of historically derived differences among squamate clades suggests that a major determinant of squamate species composition and community structure is historical. This should not be taken to imply that ongoing or recent species interactions do not contribute to community structure. Rather, historical differences predispose members of different clades to perform relatively better with respect to some niche axes than species in other clades. These differences are nested deep within squamate phylogeny. Scleroglossan lizards appear to be superior to iguanians at harvesting high energy and nonnoxious prey. Likewise, autarchoglossans, because of their relatively higher activity levels and advanced vomeronasal chemoreception systems, appear to be better competitors for food in terrestrial environments than iguanians or gekkotans. The most advanced autarchoglossans, snakes, became major predators on vertebrates, including all squamate clades. Iguanians and gekkotans historically shifted to elevated microhabitats, and gekkotans shifted to nocturnal activity. These historically derived differences in very basic niche characteristics most likely contribute to highly structured and diverse extant squamate assemblages. Nevertheless, many exceptions exist. For example, several gekkotan lineages have reverted to diurnality. Examples include day geckos (*Phelsuma*) on islands in the Indian Ocean and on Madagascar, African *Rhoptropus*, *Lygodactylus* in Africa and South America, and viviparous geckos in New Zealand. Iguanian diversity in these areas is zero, low, or represented primarily by the highly divergent chameleons. Other examples of reversions to ancestral states include territorial sit-and-wait cordylid lizards in South Africa, also a region with low iguanian diversity. Such evolutionary reversals illustrate the ecological utility of the ancestral *Bauplan* and lifestyle and should occur under circumstances in which members of the competing clade are absent or constrained for some other reason.

Finally, our analysis also suggests that effects of ongoing species interactions should be most observable in squamate assemblages in which species differences do not have a deep history (see Webb et al. 2002). This may account for the utility of *Anolis* lizards in evolutionary studies of ecological processes (e.g., Losos 1992, 1994; Losos et al. 1997) because their diversification is relatively recent. Observing morphological responses of squamates to ecological change in mixed-clade lizard assemblages in complex faunas is difficult, except under extreme conditions (e.g., rapid morphological change in morphology of *Tropidurus* isolated on rock outcrops; Vitt et al. 1997). Thus, the comparative approach we have employed here offers the best hope for revealing the important role of historical contingency in shaping current ecological patterns.

Acknowledgments

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APPENDIX

Table A1: Representation of various clades in squamate faunas of the world

Region	No. species	IG/LZ	GEK/LZ	AL/LZ	IG/SQ	GEK/SQ	SL/LZ	AL/SQ	SCL/SQ	SN/SQ	AUT/SQ	SN/AUT
New World:												
Amazonia	203	.322	.144	.533	.143	.064	.678	.236	.857	.557	.793	.702
Argentina	114	.778	.086	.136	.553	.061	.222	.096	.447	.289	.386	.750
Baja	139	.571	.119	.310	.345	.072	.429	.187	.655	.396	.583	.679
Belize	107	.500	.205	.295	.206	.084	.500	.121	.794	.589	.710	.829
Caatinga	43	.211	.368	.421	.093	.163	.789	.186	.907	.558	.744	.750
Cerrado	171	.250	.094	.656	.094	.035	.750	.246	.906	.626	.871	.718
Costa Rica	202	.522	.130	.348	.178	.045	.478	.119	.822	.658	.777	.847
Cuba	114	.697	.247	.056	.544	.193	.303	.044	.456	.219	.263	.833
Guatemala	216	.506	.115	.379	.204	.046	.494	.153	.796	.597	.750	.796
Hispaniola	138	.491	.345	.164	.391	.275	.509	.130	.609	.203	.333	.609
Honduras	201	.602	.182	.216	.264	.080	.398	.095	.736	.562	.657	.856
Jamaica	36	.296	.370	.333	.222	.278	.704	.250	.778	.250	.500	.500
Mexico	658	.539	.101	.360	.275	.052	.461	.184	.725	.489	.673	.727
Puerto Rico	41	.515	.303	.182	.415	.244	.485	.146	.585	.195	.341	.571
U.S.A.	255	.487	.052	.461	.220	.024	.513	.208	.780	.549	.757	.725
Venezuela	207	.304	.214	.482	.164	.116	.696	.261	.836	.459	.720	.638
Yucatán	125	.471	.196	.333	.192	.080	.529	.136	.808	.592	.728	.813
Mean		.474	.193	.333	.265	.113	.526	.165	.735	.458	.622	.726
SE		.037	.025	.037	.034	.021	.037	.015	.034	.040	.045	.025
Old World:												
Australia	696	.110	.265	.625	.091	.218	.890	.514	.909	.181	.695	.260
China	352	.349	.197	.454	.151	.085	.651	.196	.849	.568	.764	.743
East Africa	359	.317	.342	.342	.142	.153	.683	.153	.858	.552	.705	.783
Europe	85	.055	.091	.855	.035	.059	.945	.553	.965	.353	.882	.400
India	214	.267	.339	.388	.206	.262	.727	.299	.790	.229	.528	.434
Iran	180	.184	.336	.480	.128	.233	.816	.333	.872	.306	.639	.478
Iraq	72	.262	.286	.452	.153	.167	.738	.264	.847	.417	.681	.612
Israel	85	.175	.300	.525	.082	.141	.825	.247	.918	.529	.776	.682
Madagascar	309	.329	.369	.302	.239	.269	.671	.220	.761	.272	.492	.553
Mongolia	19	.250	.250	.500	.158	.158	.750	.316	.842	.368	.684	.538
New Caledonia	83	.000	.382	.618	.000	.313	1.000	.506	1.000	.181	.687	.263
North Africa	257	.110	.205	.685	.054	.101	.890	.339	.767	.506	.844	.599
Russia	141	.200	.153	.647	.121	.092	.800	.390	.879	.397	.787	.505
Southeast Asia	430	.316	.280	.404	.142	.126	.684	.181	.858	.551	.733	.752
South Africa	321	.108	.278	.610	.081	.209	.888	.458	.919	.249	.707	.352
South Asia	626	.220	.430	.350	.109	.212	.780	.173	.891	.506	.679	.746
Mean		.203	.281	.515	.118	.175	.796	.321	.870	.385	.705	.544
SE		.026	.022	.037	.015	.018	.026	.033	.016	.035	.025	.043

Note: IG = Iguania, LZ = lizards, GEK = Gekkota, AL = autarchoglossan lizards, SQ = all squamates, SQ = Squamata, SL = scleroglossan lizards, SCL = Scleroglossa, SN = snakes, AUT = Autarchoglossa.