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Distribution, extent, and evolution of plant consumption by lizards

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Abstract

Animal diets crucially affect fitness, yet many aspects of their ultimate determinants are unknown. The distribution and extent of herbivory in lizards, its evolutionary history, and ecological factors that may favour it are discussed. Most lizards are exclusively or primarily carnivorous, yet many species eat some plants and a few are almost exclusively herbivorous. Based on a literature survey of diets of over 450 lizard species, the distribution and degree of omnivory and herbivory are described. Some plants occur in the diets of slightly over half of lizard species, and plants formed 10% or more of the dietary volume of 12.1% of species, and 90% or more of the diet of 0.8% of species. The greatest percentage of omnivorous species (> 10% plant diet), over 30% in each, and highest mean percentage plant matter in the diet are in Iguanidae, Corytophanidae, Gerrhosauridae, Agamidae, Xantusiidae, and Tropiduridae. Numerous other omnivores occur in Lacertidae and Scincidae and fewer in several additional families. Herbivorous lizards (> 90% plant volume) tend to be folivorous and to possess adaptations for processing leaves, including specialized dentition for cutting or reducing leaves, elongated intestines, colic valves that slow passage of food, and intestinal flora that digest cellulose. Omnivorous lizards lacking such specializations may eat some leaves, but consume much more fruit, flowers, and seeds, plant parts that are easy to digest, likely to be very abundant seasonally, and may be highly nutritious. Some lizards eat nectar and pollen; even sap is eaten by at least one gecko. Ontogenetic increase in plant consumption and decrease in prey consumption is known, but its generality has been controversial. Such ontogeny has been demonstrated in three iguanid species, a skink, a lacertid, two tropidurids, a phrynosomatid, and two corytophanids, but it does not occur in some other species. Thus, the presences of ontogenetic variation must be evaluated for each species. The importance of specific foods may also vary with age. Omnivory and/or herbivory have originated in many lizard families, with at least nine origins in Iguania and 23 in Scleroglossa. Origins have been rare in Gekkonoidea and Anguimorpha and common in Scincomorpha, especially in Lacertidae and Scincidae. Losses of omnivory have been much less frequent than gains. Only a few origins can account for all the herbivory in lizards. Concentrated changes tests show that there is a significant association in Lacertidae, Lacertiformes, Lacertoidea, Scincidae, and Scleroglossa between insularity and omnivory. Insular lizards may broaden their diets to compensate for limited availability of prey. Addition of other factors that reduce availability of prey, i.e. extreme aridity and cave-dwelling, to insularity, strengthened the relationship to omnivory in Lacertidae and Lacertoidea. We were unable to demonstrate a role of aridity independent of insularity, but present anecdotal evidence suggests that it may promote evolution of plant consumption. Large body size in lizards has long been associated with herbivory, and more recently, with omnivory in lacertid lizards. Using a conventional regression approach in which each species is considered to supply an independent data point, this relationship was confirmed for all lizards. Although larger species have diets with more plants, plant consumption accounts for only 9% of the variation in body length, which is not surprising given that other factors such as predation, competition, and sexual selection affect body size. The frequency of transitions body size associated with transitions to ominivory or carnivory was also examined. In Iguania, Scleroglossa, and all lizards, transitions supporting the hypothesis that omnivory favours increase in body size were significantly more frequent than non-supporting transitions. This suggests that substantial plant consumption favours evolution of larger size, probably because of the energetic considerations first presented by Pough (1973). Because actively foraging lizards move widely through the habitat to locate prey and tongue-flick to locate prey by chemical cues, we hypothesized that they may be more likely to evolve omnivory than ambush foragers, which wait motionless for prey and do not tongue-flick to locate or identify prey. The basis of this prediction is that the wider searching of active foragers predisposes them to contact with a greater variety and quantity of plants and that chemosensory tongue-flicking used by omnivores to identify plant food might be easier to evolve in active foragers that already use pre-chemical discrimination. The prediction is supported by a significantly greater per species frequency of origins of omnivory by active foragers than by ambushers. A scenario for the progressive evolution of omnivory and herbivory from ancestrally carnivorous lizards is discussed.

Key words: lizards, herbivory, evolution, foraging mode, insularity, body size, aridity

IINTRODUCTION

Obtaining adequate nutrition is among the most fundamental challenges affecting fitness. Although optimal selection of diet from a set of nutritionally acceptable and available foods has been studied intensely (Stephens & Krebs, 1986), much less is known about the evolutionary history of diets in most taxa and about ecological factors leading to dietary differences among taxa. These issues were examined with respect to plant consumption in lizards, which form an excellent group for such study because there is an extensive literature about their diets, their phylogenetic relationships are reasonably well known, and because most species eat only animal prey or eat small amounts of plant food, facilitating the tracing of evolutionary shifts to omnivory and herbivory. Ecological factors may be particularly important in determining shifts to plant consumption by lizards because omnivory and herbivory occur within several families that consist primarily or exclusively of carnivorous species.

Most lizards are predators of small animals and only rarely consume plant material, but there are many omnivorous species and some that are almost exclusively herbivorous. About 3% of species are estimated to be herbivores (Iverson, 1982), but no survey of lizard diets has been published to allow an assessment of the degree of plant consumption. Reflecting the lack of readily accessible data, a recent review of herbivory in lizards (G. King, 1996) provided only highlights of a few species considered to be herbivorous, but no quantitative information. Another source of difficulty is that definitions of herbivory in lizards vary widely among authors, ranging from exclusive or nearly exclusive plant consumption (Iverson, 1982) to omnivory with plants constituting a very small fraction of the diet (Van Damme, 1999). Disparities among definitions, which have often been implicit and ambiguous, have undoubtedly led to confusion. The difficulty of obtaining quantitative dietary information from a literature widely scattered in prominent and obscure journals and in several languages has impeded investigations of herbivory. Many questions about the importance of plants in lizard diets, its evolution, and about relationships between plant consumption, ecological factors, and phylogeny thus have remained unanswered. Several factors that might lead to the evolution of omnivory and herbivory have been proposed, including large body size (Pough, 1973), occupation of habitats with restricted availability of prey, reduced interspecific competition, and reduced predation (Rand, 1978), but there is little evidence about most of them.

The plant and animal components of lizard diets were reviewed, providing volumetric and other quantitative measures of the contribution of plants to the total diet where possible, for a wide range of lizards. The evolution of plant consumption was traced to ascertain its historical origins and losses as far as possible given current limitations of data and uncertainty about some aspects of lizard phylogeny. More limited data on plant parts consumed were examined and other factors, such as seasonal availability, digestibility, and total degree of plant consumption, that may affect relative amounts of parts such as leaves, fruits, and flowers in the diet was considered. The evidence for ontogenetic changes in degree of plant consumption and types of plant parts consumed is reviewed, and factors, such as nutritional content, availability of fermentative intestinal flora for digestion of cellulose, and variation in energetic needs with age, that might affect them are discussed.

There has been much speculation about factors that influence the herbivory, but few attempts to test hypotheses have been made. Evolution of plant consumption may be favoured by habitat factors that reduce availability of prey, as proposed by Rand (1978) and Pérez-Mellado & Corti (1993). The only such relationship that has been demonstrated by a study using comparative methods based on phylogenetics is that omnivory is more likely to evolve on islands than on the mainland in lacertid lizards (Van Damme, 1999). Rand (1978) believed that low productivity on islands cannot completely explain an association between insularity and plant consumption because interspecific competition and predation are also reduced on islands, favouring evolution of large body size by social selection. Large body size was hypothesized to favour plant consumption. Szarski (1962) suggested that herbivores have less energy to allocate to reproduction than carnivores due to the energy-poor diet and that herbivores having low recruitment rates thus might not be excluded on islands having low predation rates. Ignoring possible influences of interspecific competition and predation, complications remain that make it difficult to isolate the effects of any one variable on plant consumption. For example, many omnivorous species on islands are large, and some of the islands that they occupy are arid.

Another potential factor is intraspecific competition. When predation and interspecific competition are reduced, population densities may increase greatly, reducing the prey supply, thus favouring individuals that eat a diverse diet (Rand, 1978) and leading to incorporation of plants into the diet *de novo* or to increased plant utilization. Insular lizard populations often attain much higher densities than mainland populations (Pérez-Mellado & Corti, 1993), but there is insufficient data on population density or other factors to test their effects. We focus instead on ascertaining whether insularity is associated with increased plant consumption in a broad range of lizard taxa.

Two other factors that may affect plant consumption by lizards are body size and foraging behaviour. Large body size is perhaps the best known correlate of herbivory in lizards (Pough, 1973). Hypotheses that have been proposed to explain this relationship are that small lizards are too weak to reduce vegetation (Sokol, 1967), that large lizards need to supplement scarce large prey with plants (Rand, 1978), and that energetic considerations preclude small lizards from full herbivory, but permit large lizards to obtain sufficient caloric benefit from plants (Pough, 1973).

Foraging mode is correlated with several other important aspects of lizard ecology, behaviour, and morphology, and may be a master factor that strongly influences much of the natural history of lizards (Vitt & Congdon, 1978; Huey & Pianka, 1981; Vitt & Price, 1982; Cooper, 1997). Active foragers use chemical cues sampled lingually to locate and identify prey whereas ambushers do not, and have more deeply notched and elongated tongues and more abundant vomeronasal chemoreceptors than ambushers (Cooper, 1995, 1997). The possibility that foraging mode might affect the likelihood of evolving omnivory or herbivory is examined.

Several factors that are hypothesized to affect plant consumption are interconnected. Because the available data set is not sufficiently large and complete to attempt to remove effects of all but one variable at a time statistically, factors are examined in isolation, recognizing the interpretive limitations imposed, and the available evidence is discussed. An attempt is made to ascertain whether correlated evolution has occurred between plant consumption and habitat features such as insularity and aridity, the relationship between body size and plant consumption is re-examined, and an effect of foraging mode on the difficulty of evolving omnivory is proposed. Finally, a scenario for the progressive evolution of plant consumption by lizards derived from insectivorous ancestors is described.

METHODS

The extensive literature on lizard diets was reviewed selectively to obtain the best data sets possible for well-studied species and some data for species in taxa for which quantitative dietary data are unavailable. Dietary data are sometimes difficult to locate because they are scattered, often in regional or local journals, and may not be apparent from article titles. A sizeable, but far from complete, data set has been amassed that includes information on several hundred species, enough to ascertain the broad patterns of distribution and evolution of omnivory and herbivory. A taxonomically arranged list of the dietary citations, many of which are not listed in this paper because of limitation of space, is available from WEC.

Lack of comparability among the many forms of dietary data has deterred reviews of plant consumption. The best types of data are volumes, masses, and energetic contents of foods in digestive tracts, but these are the least frequently reported in older literature, in anecdotal reports of unusual dietary items, and in descriptions of natural history. It might be possible to use conversion factors among volumetric, mass, and energetic data to make them comparable, but we have not attempted to do so. We have chosen to use volumetric data on contents of the digestive tract for quantitative estimates of plant consumption because such data are much more widely available than mass or energetic data. Faecal volumetric data were omitted from quantitative analyses because of the uncertainty about their comparability with those for gut contents.

Dietary data are often reported as percentages of the total number of plant items in the digestive tract or as percentages of stomachs containing plant material. Item and occurrence data can be quite misleading. For large and small foods, item data underestimate or overestimate the energetic importance to the total diet. Very large items may be infrequent, but constitute a large proportion of energy intake. Small items such as ants and termites may be by far the most frequent items in the digestive tracts, yet account for a small percentage of dietary volume. Occurrence data are even worse because they give no indication of energetic or numerical abundance. In addition to these data from gut content, volumetric, item, and occurrence data are sometimes based on analysis of faeces, especially data on protected lizard species.

Three main considerations were used in deciding upon criteria for omnivory and herbivory: disparities exist among data types; no universally valid conversion factors among data types are available; there is a lack of information on enough taxa using any 1 data type. A lizard was arbitrarily considered omnivorous if at least 10% of the diet was plant material based on any of the above types of data. Two species were considered to be omnivores based on qualitative data.

Selection of 10% as the cut-off is arbitrary, but has the advantage of excluding species that may ingest some plant matter incidentally with animal food. It might exclude some species in which only a small proportion of individuals ingest substantial quantities of plants and others in which plant consumption is ephemeral, which would obscure some interesting aspects of omnivory. Our only other qualm is that some species meeting the

Table 1. Lepidosaurian species for which plants constitute at least 10% of the diet. Plant parts: BD, bud; BE, berry; FL, flower; FR, fruit; FU, fungi; L, leaf; NC, nectar; NT, nut; SH, shoot; ST, stem; TH, thorn. Type data: I, item; O, occurrence; M, mass; Q, qualitative; V, volume

Taxon	Type data	% plant	Parts	Source
Sphenodontidae				
Sphenodon punctatus	I	14	L, FL, S, T	Walls, 1981
Agamidae				
Ctenophorus clayi	V	11.5	–	Pianka, 1986
C. nuchalis	V	25.3	–	Pianka, 1986
C. reticulatus	V	27.3	–	Pianka, 1986
Diporiphora winneckei	V	27.5	–	Pianka, 1986
Pogona barbatus	Q	–	L, FL	Rose, 1974
P. minor	V	19.3	–	Pianka, 1986
Uromastyx acanthinurus	Q	–	H	Dubuis *et al.*, 1971
Uromastyx aegyptius	M	100	L, FR	Foley *et al.*, 1992
Phrynosomatidae				
Sceloporus poinsettii	V	40.1	FL	Barbault *et al.*, 1985
Uma inornata	M	54	L, FL, SD	Durtsche, 1995
U. paraphygas	V	19.3	L, FL, SD	Gadsden & Palacios-Orona, 1997
U. scoparia	V	13.3	–	Pianka, 1986
Tropiduridae				
Homolophus pacificus	M	62.5	FL, FR, L, SD	Schluter, 1984
Leiocephalus carinatus	V	17.8	FR	Schoener *et al.*, 1982
L. inaguae	V	24.9	FL, FR	Schoener *et al.*, 1982
L. punctatus	V	15.0	FL, FR	Schoener *et al.*, 1982
Liolaemus lutzae	V	72	FL, L	Rocha, 1998
L. ruibalii	I	28.47	–	Sage, 1974
Phymaturus palluma	I	100	FL, FR, L, ST	Videla, 1983
Tropidurus hispidus	V	21.91	SD	Vitt, 1995
T. oreadicus	V	27.56	FL, FR, L, SD	Vitt, 1993
T. semitaeniatus	V	22.41	–	Vitt, 1993
T. torquatus	V	45.61	FL, FR	Fialho *et al.*, 2000
Polychrotidae				
Anolis evermanni	M	13.5	FR, SD	Lister, 1981
Polychrus acutirostris	V	25.11	FL, FR, SD	Vitt, 1995, pers. obs.
Iguanidae				
Amblyrhynchus cristatus	M	100	Algae	Nagy & Shoemaker, 1984
Conolophus pallidus	I	> 99	–	Carpenter, 1969
C. subcristatus	I	98	–	Carpenter, 1969
C. pectinata	V	100	FL, FR, L	Durtsche, 2000
Ctenosaura similis	V	98	–	Van Devender, 1982
Cyclura carinata	V	> 95	FL, FR, L, SH, ST	Iverson, 1979
C. pinguis	V	71	FR, L	Carey, 1975
D. dorsalis	V	97.3	–	Pianka, 1986
Iguana iguana	M	100	–	Van Marken Lichtenbelt, 1993
Sauromalus ater	M	> 99	FL, FR, L, BD	Nagy, 1973
S. hispidus	M	100	–	Sylber, 1988
Corytophanidae				
Basiliscus basiliscus	V	22	FL, FR, FU, L, NT	Barden, 1943
B. plumifrons	V	27.64	–	Vitt, unpublished data
Gekkonidae				
Hoplodactylus maculatus	O	57.5	FR	Whitaker, 1987
Rhacodactylus auriculatus	I	21.7	FL, L	Bauer & Sadlier, 1994
Lacertidae				
Acanthodactylus erythrurus	O	65.5	–	Schleich *et al.*, 1996
Lacerta bedriagae	O	50	L	Castilla, Bauwens, Damme *et al.*, 1989
L. dugesii	V	43.7	FR, FL, SD, L	Sadek, 1981
Lacerta lepida	O	80	FL, FR, L, SD	Castilla, Bauwens & Llorente, 1991
Meroles anchietae	V	49.1	SD	Murray & Schramm, 1987
Podarcis filofensis	I	13.8	–	Sorci, 1990
P. hispanica	I	42.8	–	Pérez-Mellado & Corti, 1993
P. lilfordi	V	61.8	FL, FR, L, NC, SD	Pérez-Mellado & Corti, 1993
P. muralis	V	22.1	–	Pérez-Mellado & Corti, 1993
P. pityusensis	V	50	–	Pérez-Mellado & Corti, 1993
Psammodromus algirus	I	23.3	–	Sorci, 1990
Teiidae				
Cnemidophorus arubensis	I	> 50	FL, FR, L, SD	Schall, 1973
C. lemniscatus	V	17.49	FR	Vitt, Zani & Caldwell., 1997
C. murinus	V	76	FL, FR, L, SD, NC, FU	Dearing, 1988; Dearing & Schall, 1992
C. sp.	M	75.2	FL, FR, SD	Markezich *et al.*, 1997
Tupinambis rufescens	V	36.7	FR	Williams, Donadio & Re, 1993

Table 1 (*cont.*)

Taxon	Type data	% plant	Parts	Source
Xantusiidae				
Xantusia riversiana	V	18.7	FL, FR, L, SD, ST	Fellers & Drost, 1991
Lepidophyma smithii	M	91	Fig FR	Mautz & López-Forment, 1978
Scincidae				
Corucia zebrata	V	100	–	M. McCoy, 1980
Ctenotus grandis	M	23.1	BE, SD	Twigg *et al.*, 1996
C. leae	V	40.2	–	Pianka, 1986
C. leonhardi	V	10.8	–	Pianka, 1986
C. regius	O	26.7	–	Read, 1998
Egernia cunninghami	V	93.9	FL, FR	Brown, 1991
E. kintorei	V	82.5	–	Pianka, 1986
E. saxatalis	V	28.6	FL, FR, FU	Brown, 1991
E. stokesii	V	96.15	–	Duffield & Bull, 1998
Lamprolepis smaragdina	I	11.65	–	Auffenberg & Auffenberg, 1988
Oligosoma inconspicuum	V	16	BE	Patterson, 1992
O. lineoocellatum	O	15.5	FR, SD	Spencer *et al.*, 1998
O. maccanni	V	18	BE	Patterson, 1992
Tiliqua multifasciata	V	74.7	–	Pianka, 1986
T. rugosa	V	93.7	FL, FR, FU	Brown, 1991
Gerrhosauridae				
Angolosaurus skoogi	V	82.6	FL, L, SD, TH	Pietruszka *et al.*, 1986
Gerrhosaurus bulsi	O	25	–	D. G. Broadley, pers.comm.
G. major	O	11	–	D. G. Broadley, pers.comm.
G. nigrolineatus	O	10	–	D. G. Broadley, pers.comm.
G. validus	O	72	FL, L, SD, BE	D. G. Broadley, pers.comm.
Cordylidae				
Platysaurus guttatus	O	78	–	Broadley, 1978
P. imperator	O	10	FL, L, SD	Broadley, 1978
P. intermedius	O	17.2	–	Broadley, 1978
P. mitchelli	O	30	–	Broadley, 1978
P. ocellatus	O	33	–	Broadley, 1978
Varanidae				
Varanus olivaceus	I	55.0	FR	Auffenberg, 1988

[a] See text.

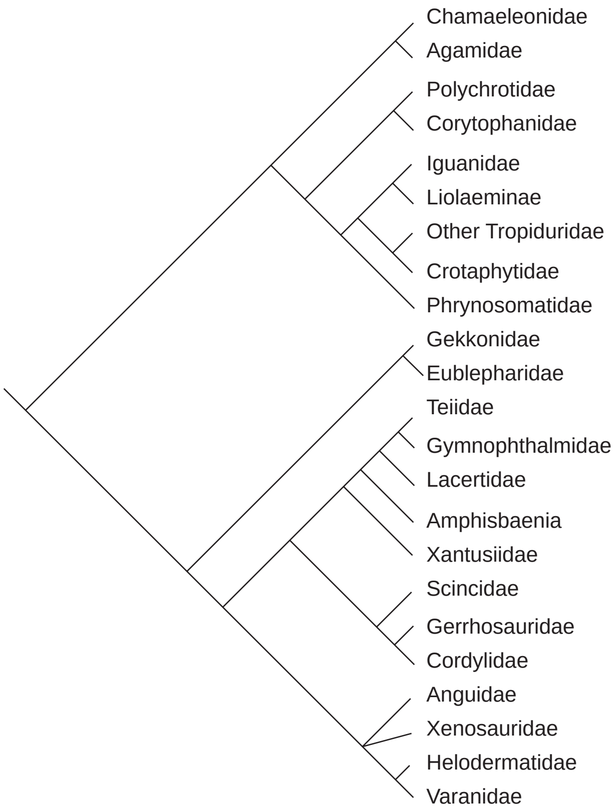

Fig. 1. The phylogeny of lizards, primarily at the familial level. Higher taxa are defined in the text.

criterion based on occurrence data might consume a substantially smaller percentage volume of plants, being essentially consumers of animal prey. Little opportunity for such an effect existed because only 15 species were considered omnivorous based on occurrence data, and of these only 5 had occurrence values $<25\%$. Of those 5, 2 were gerrhosaurids, 2 cordylids, and 1 was a skink (Table 1). The skink was a member of a genus containing both omnivorous and carnivorous species, *Ctenotus*. Gerrhosaurids and cordylids were excluded from analyses of the evolution of omnivory because of the paucity of data and lack of phylogenetic information. In the absence of information on intrageneric relationships, the skink's genus was considered to have a single origin of omnivory, giving a minimal estimate. Thus, the occurrence data had no effect on our analyses of shifts in character state or of correlated evolution.

The term carnivory is used to denote a diet containing $>90\%$ animals by any of the types of data except occurrence. Occurrence data were excluded because an omnivore or herbivore by the 10% and 90% criteria could otherwise simultaneously be considered a carnivore and have up to 100% occurrence of animal food. Our definition of carnivory here differs from that of authors who use it to indicate consumption of vertebrates (e.g. Greene, 1982).

In discussing the distribution and evolution of plant consumption and in analysing correlated evolution, the best available information about lizard phylogeny has been used. Our basic phylogeny (Fig. 1) is that of Estes, De Queiroz & Gauthier (1988) modified for Iguania to include some families described by Frost & Etheridge (1989). Relationships of families within Iguania are poorly known, but are treated as described by Macey *et al.* (1997) and Schulte *et al.* (1998). On the basis of lingual features, Amphisbaenia is treated as a member of Lacertoidea (Schwenk, 1994).

In Fig. 1, Iguania is represented by the left main branch and Scleroglossa by the right. Acrodonta consists of Chamaeleonidae and Agamidae. The remaining iguanians have traditionally been placed in a single large family, Iguanidae *sensu lato*. We follow Frost & Etheridge (1989) in dividing this group into multiple families and restricting Iguanidae to a small monophyletic group of large herbivores. All taxa shown in Fig. 1 are families with the exceptions of Liolaeminae and other tropidurids. Although these groups are formally placed in Tropiduridae (Frost & Etheridge, 1989), this family has recently been shown to be paraphyletic (Schulte *et al.*, 1998). The relationships among iguanian families are poorly resolved. Here we use the best available estimates of interfamilial relationships (Fig. 1 based on Macey *et al.*, 1997; Schulte *et al.*, 1998).

In Scleroglossa, the 2 leftmost families in Fig. 1, Gekkonidae and Eublepharidae, represent Gekkonoidea and the other taxa Autarchoglossa. Within Autarchoglossa, the left main branch is Scinomorpha and the right is Anguimorpha. The 2 main divisions of Scincomorpha are Lacertoidea on the left and Scincoidea on the right. Lacertiformes includes Lacertidae, Teiidae, and Gymnophthalmidae, and Cordyliformes includes Cordylidae and Gerrhosauridae.

Within iguanian families the sources of relationships were: Agamidae – Moody (1980), Honda *et al.* (2000*a*); Chamaeleonidae – Hillenius (1986); Polychrotidae – Guyer & Savage (1986), Cannatella & De Queiroz (1989), Jackman *et al.* (1999); Phrynosomatidae – Adest (1977), Reeder & Wiens (1996), Wiens & Reeder (1997); Tropiduridae – Frost (1992), Pregill (1992), Etheridge (1995, 2000), Halloy, Etheridge & Burghardt (1998), Schulte *et al.* (1998). Within Scleroglossa the sources were: Gekkonoidea – King & Mengden (1987), Kluge (1987), Grismer (1988), Bauer (1990), Donnellen, Hutchison & Saint (1999); Lacertidae – Arnold (1989), Fu (1998), Harris, Arnold & Thomas (1998), Harris & Arnold (1999); Scincidae – Greer (1970, 1974, 1979), Horton (1972), Arnold & Leviton (1977), Hutchinson (1981), Caputo, Odierna & Aprea (1994), Honda *et al.* (1999, 2000*b*); Teiidae – Presch (1974), Wright (1993); Xantusiidae – Hedges, Bezy & Maxson (1991).

The TRACE routine of MacClade 3.01 (Maddison & Maddison, 1992) was used to reconstruct the evolutionary history of omnivory and herbivory. To test relationships between plant consumption and other factors, concentrated changes tests (Maddison, 1990) were conducted. This test allows the detection of correlated evolution between 2 binary variables, taking into account the phylogenetic relationships among species. It examines whether 1 state of a binary dependent variable occurs significantly more often than by chance on branches of a phylogenetic tree of the independent variable having specified character states. This test performs well in simulations (Lorch & Eadie,1999), yielding appropriate levels of significance.

Variables examined that might be related to plant consumption were insularity, prey availability, body size, and foraging mode. For concentrated changes tests, plant consumption was coded as omnivory–herbivory or carnivory. In the tests of prey availability, lizards were considered to have reduced availability if they lived on islands, in very arid habitats, or in caves. Habitat data were taken from the papers cited for diets and from regional field guides. The hypotheses that insularity and reduced prey availability favour evolution of plant consumption were examined. Because a fully resolved tree is needed for tests, transformations in insularity, aridity, and omnivory were treated as delayed (occurring at the later of the possible times) when the character states were equivocal. These cases are noted with the results.

Previous tests of the hypothesis that plant consumption is associated with large body size did not use modern comparative methods that account for phylogenetic relationships. A phylogenetic approach was used to avoid spuriously high correlation that might result from considering closely related species or populations to provide independent data points (Harvey & Pagel, 1991). Comparative tests such as Maddison's test (1990) and correlation using phylogenetically independent contrasts (Felsenstein, 1985) are desirable, but appropriate data are very difficult to obtain in this case. Because body size is labile even among populations within species, the critical information needed to conduct meaningful correlated changes tests was often lacking.

The relationship between plant consumption and body size was examined by conducting a conventional regression analysis that treated each species as providing an independent data point, using our volumetric data set for plant consumption and maximum snout–vent length (SVL) as the measure of body size. For an evolutionary approach, we focused on changes in body size that occurred during transitions to omnivory or herbivory or from omnivory to carnivory. For those species where it could be ascertained whether changes in body size had occurred in comparison with the carnivorous or omnivorous populations of the same species or sister groups, binomial tests were conducted of the hypothesis that body size would increase with acquisition of omnivory and decrease with its loss. Increases in size with gains of omnivory and decreases in size with its loss were scored as supporting the hypothesis, and no change in body size when food consumption changed, decrease in body size in conjunction with a gain of omnivory, and increase in size with loss of omnivory were scored as not supporting the hypothesis. The hypotheses are 1-tailed, but results of the tests are presented conservatively as 2-tailed.

Too few changes in foraging mode occurred for a meaningful concentrated changes test of the relationship between foraging mode and omnivory. Instead, the relationship between foraging mode and acquisition of plant consumption was examined by conducting a χ^2 test of the relative frequencies of independent origins of omnivory and herbivory in active foragers and ambush foragers. For all tests $\alpha = 0.05$.

Data on the occupation of mainland *vs* island habitats, aridity, and cave dwelling were obtained from the dietary papers or sources of SVL data. SVLs were taken from Bogert & Mártin del Campo (1956), Schall (1974), Carey (1975), Fitch (1975), Medica & Arndt (1976), Andrews (1979), Crisp, Cook & Hereward (1979), Vanzolini, Ramos-Costa & Vitt (1980), Barbault & Maury (1981), Fitch & Seigel (1984), Stebbins (1985), Pianka (1986), Conant & Collins (1991), Cusumano & Powell (1991), Schwartz & Henderson (1991), Jenssen & Feely (1991), Vitt (1991, 1995, 2000), Cogger (1992), Cei (1993), Cree (1994), Avila-Pires (1995), Losos (1995), Vitt & De Carvalho (1995), Rocha (1996), Vitt & Zani (1996*a,b,c*), Gadsden & Palacios-Orona (1997), Branch (1998), Campbell (1998), Van Sluys (1998), Barbadillo *et al.* (1999), Colli & Zamboni (1999), Durtsche (1999), Van Damme (1999), G. Smith, Ballinger & Lemos-Espinal (2000), and papers cited for dietary data.

DISTRIBUTION OF HERBIVORY

By taxon

Tuataras, members of the sister group of Squamata (Rhynchocephalia), have long been considered carnivores, but field data show that 14% of items in the stomach were plant material (Table 1). Despite this rather high percentage, Walls (1981) and Ussher (1999) thought ingestion of plants was incidental, not intentional. It is unclear whether *Sphenodon* is a useful outgroup.

Among lizards all members of some families are strict carnivores or eat only small quantities of plant material, but substantial plant consumption occurs in many families in both Iguania and Scleroglossa. In Iguania, it occurs in all families for which data are available except Chamaeleontidae and Crotaphytidae, being universal in Iguanidae and fairly frequent in Tropiduridae, Agamidae, and Corytophanidae. In Scleroglossa, it is absent in Pygopodidae, Eublepharidae, Gymnophthalmidae, Cordylidae, and most families of Anguimorpha – Anguidae, Xenosauridae, and Helodermatidae.

The most herbivorous family of lizards is Iguanidae (Table 1). Iguanids are one of a few lizard groups in which the digestive tract is specialized for plant digestion. Morphologically, the intestine contains colic valves that may slow the passage of food to permit more time for digestion by the intestinal flora needed to degrade cellulose (Iverson, 1982; McBee & McBee, 1982). These features permit iguanids to be folivorous. Several species are strict herbivores throughout life and plants form most of the diet in adults of all species (13 species from seven genera in the data). In other species there is a pronounced ontogenetic change in diet (Van Devender, 1982; Nagy & Shoemaker, 1984; Durtsche, 1999).

Frequent plant consumption is fairly widespread in Tropiduridae. Representatives of five of eight genera are omnivorous or herbivorous (Table 1). An additional species, *Leiocephalus punctatus*, ate 9% plant by volume. Strict herbivory is reported only for *Phymaturus palluma* (Videla, 1983), which is considered omnivorous by Donoso-Barros (1966). Omnivory occurs in all three subfamilies of Tropiduridae – Leiocephalinae (*Leiocephalus*), Liolaeminae (including *Phymaturus* and *Liolaemus*), and Tropidurinae (*Homolophus* (now *Tropidurus*) and *Tropidurus*).

The degree of plant consumption by tropidurids differs considerably among congeners and within species. Of six species of *Leiocephalus* studied by Schoener, Slade & Stinson (1982), plants constituted 0–24.9% of dietary volume, with two species eating only 5% or less plants. In *Liolaemus* only one of 13 species studied is omnivorous. In *Tropidurus*, four of the seven species studied are omnivorous. Substantial intraspecific variation in omnivory has been observed in *Liolaemus lutzae*, in which the variation is ontogenetic, and in *T. hispidus* (Vitt, 1995; Vitt & de Carvalho, 1995; Vitt, Zani & Caldwell, 1996), *T. oreadicus* (Colli, De Araujo *et al.*, 1992; Vitt, 1993), and *T. torquatus* (Rocha & Bergallo, 1994; Teixeira & Giovanelli, 1999; Fialho, Rocha & Vrcibradic, 2000). In these three species of *Tropidurus*, some studies indicate carnivory and others omnivory, suggesting the possibility that diets vary geographically within species or that plant consumption varies temporally. These lizards may eat substantial quantities of readily digestible parts of plants such as fruits and flowers when they are available and eat proportionally more animals at other times. The lack of a large plant component in the diet in a particular study may thus be misleading.

In Agamidae, the closest relatives of chameleons, both omnivory and herbivory occur. Of 14 genera sampled, omnivory occurs in four genera and herbivory occurs in two other genera (Table 1). *Hydrosaurus pustulosus* is exclusively folivorous (Taylor, 1922), and *Uromastyx acanthinurus* (Dubuis *et al.*, 1971) and *U. aegyptius* (Foley *et al.*, 1992) are almost exclusively herbivorous, eating leaves and fruit. Most omnivores consume a variety of plant parts, most of them easily digestible parts such as fruits and berries that do not require specialized anatomy or intestinal flora for digestion. However, *Pogona barbatus* ingests some leaves. Omnivory is fairly widely distributed among Australian agamines (Moody's (1980) groups II and III), occurring in some species of the genera *Physignathus*, *Ctenophorus*, *Diporiphora*, and *Pogona* (Table 1). In addition, plants form 7.3% of dietary volume in *Caimanops amphiboluroides* (Pianka, 1986). Omnivory was not observed in other agamines, but data are available for only two genera, *Draco* and *Agama*. Agamas consume some plant matter, but the papers reviewed reported plant consumption by only one of three species.

In Corytophanidae, omnivory is present in all *Basi-*

liscus species (Hirth, 1963 for *B. vittatus*) studied. *Corytophanes cristatus* seem not to ingest plant material other than incidentally (Andrews, 1979). No plants were observed in the stomachs of a small sample of *C. cristatus* (L. J. Vitt, pers. data). The lack of plants in the field diet of *C. cristatus* agrees with their refusal to eat anything other than relatively large prey in captivity (Rogner, 1997*a*).

Omnivory is much less common in other iguanian families, but might be present in groups not yet studied. Quantitative data are lacking for Hoplocercidae or Opluridae, but an oplurid species that eats insects and some flowers and leaves is probably omnivorous (Randriamahazo & Mori, 1999). Data for Chamaeleontidae show no plant consumption in two species and < 1.5% of plant items are eaten in two others. It is probable that the small amounts of plant matter in the digestive tracts were ingested incidentally within prey or after adhering to the tongue when it was projected beyond the mouth during attempts to capture animal prey.

In Polychrotidae, omnivory is known for only one species each in two of five genera. Using the 10% criterion, one of 28 species of *Anolis* may be omnivorous, but numerous species consume some plants (e.g. Schoener, 1968; Lister, 1981; Fobes *et al.*, 1992; Cullen & Powell, 1994; Lazell & Perry, 1997; Pérez-Higareda, Smith & Chiszar, 1997). Although plants form only a small part of the total diet of anoles, easily digestible plant parts may be consumed when available. The percentage of plants consumed by *A. evermanni* was greater than reported for other species and reflects consistent omnivory observed through both the wet and dry seasons (Lister, 1981). In *Polychrus acutirostris* plants seem to form about one-fifth to a quarter of the diet (Table 1), but may be taken inadvertently while ambushing insects.

In Phrynosomatidae, all but a few species are carnivorous, omnivory occurring in only two of eight genera sampled. Omnivory is typical only in the genus *Uma*, in which it was observed in three of the four species studied, accounting for < 15% of dietary volume in two species, but for over half of dietary mass in *Uma inornata* (Durtsche, 1995). Although *Sceloporus* are primarily insectivorous, four of nine species had > 5% plant dietary volume, indicating that plants are sometimes utilized. Data from three studies each of *S. jarrovi* and *S. undulatus* (Table 1) revealed consistent insectivory. By far the greatest intraspecific variability in plant consumption was observed in *S. poinsettii* (Table 1). In a single study the diets of *S. poinsettii* differed greatly in two different years, being insectivorous in a year with normal rainfall and omnivorous in an exceptionally dry year (Barbault, Ortega & Maury, 1985). The very high percentage of plant volume in the diet during the dry year (Table 1) may reflect a scarcity of prey during the dry year, the great availability of flowers during the sampling period in the dry year, or both.

Among other phrynosomatids, *c.* 5% of dietary volume consisted of plant material in two of three studies of *Callisaurus draconoides*, and one of two studies each for *Cophosaurus texanus* and *Urosaurus graciosus* (Table 1), the other studies showing almost no plant consumption. In phrynosomatids and other families that exhibit such intraspecific variability, plant consumption is likely to vary seasonally. Numerous primarily carnivorous species eat some fruit, berries, and flowers when available. Dietary samples taken during brief intervals when plant foods are abundant may give a misleadingly high indication of the importance of plants in the diet throughout the year. Nevertheless, such data hint that plants may form a more important part of the long-term diet than is suggested by studies conducted during periods when flowers and fruits are not abundant. Seasonal variation in dietary importance of plants may occur in omnivores from several families, and is a potential source of bias in reviews sampling diverse studies.

In Scleroglossa, plant consumption differs greatly among the three major subtaxa. It is uncommon in Gekkonoidea. In Autarchoglossa it is rare in Anguimorpha, but fairly common in Scincomorpha. In Gekkonoidea omnivory is unknown in Eublepharidae and Pygopodidae. Although many species in Gekkonidae consume small quantities of plant material, quantitative data revealed omnivory in only one species each in two of 31 genera, *Rhacodactylus auriculatus* (Bauer & Sadlier, 1994) and *Hoplodactylus maculatus*. Other species in *Rhacodactylus* are omnivorous in captivity (Mertens, 1964), but there are no quantitative field data. Some geckos from New Zealand may be omnivorous, including several species of *Hoplodactylus* that regularly feed on plants, and *Naultinus grayi*, which drinks nectar (Whitaker, 1968, 1987).

Omnivory occurs in numerous groups within Scincomorpha, most notably in Lacertidae, Xantusiidae, Scincidae, and Gerrhosauridae. Its importance varies considerably among the families of Lacertoidea. Among the 13 genera of lacertids sampled, some species in three genera are omnivorous (Table 1). One other species, *Podarcis sicula* had diets with 7.5% plant volume and 6.2% plant items in island populations (Sorci, 1990; Pérez-Mellado & Corti, 1993). In addition, the entire genus *Gallotia* is omnivorous (Barbadillo *et al.*, 1999), with a high, but undetermined plant dietary percentage (e.g. Font & Ferrer, 1995; Pérez-Mellado *et al.*, 1999).

Where multiple studies of the same lacertid species are available, major differences in the percentage plant volumes exist in *Psammodromus algirus* and two species of *Podarcis* and smaller differences in two others (Table 1). The extent of lacertid plant consumption varies intraspecifically among populations and seasons. Omnivory is more frequent in insular than in mainland populations (Pérez-Mellado & Corti, 1993; Van Damme, 1999), presumably accounting for the much greater plant consumption by an island population of *P. algirus* than by two mainland populations and possibly for some smaller differences observed among populations of *Acanthodactylus erythrurus* and *Podarcis muralis* (Table 1). However, only a coastal population of *A. erythrurus* from southern Spain seems to be omnivorous. Data for several lacertids suggest that these lizards demonstrate greater plant consumption on islands during summer than spring (Pérez-Mellado & Corti, 1993). This is the source of large differences among studies of *P. lilfordi* (Table 1).

Most teiid lizards are carnivorous, omnivory occurring in a few species in only two of six genera sampled. Although omnivory is limited to *Cnemidophorus* and *Tupinambis* using our criterion (Table 1), several more species eat some plant matter, notably in *Ameiva* (Magnusson & Da Silva, 1993; Vitt & De Carvalho, 1995) and *Kentropyx* (Vitt & De Carvalho, 1995).

With one exception the dietary data for teiids are remarkably consistent within species. Six studies of *Ameiva ameiva* (Hirth, 1963; Magnusson & Da Silva, 1993; Vitt & Colli, 1994; Vitt, 1995; Vitt & De Carvalho, 1995; L. J. Vitt, pers. data), five of *Cnemidophorus sexlineatus* (Fitch, 1958; Hamilton & Pollack, 1961; Hardy, 1962; Paulissen, 1987; Paulissen, Walker & Cordes *et al*., 1997), and four of *C. tigris* (C. J. McCoy, 1965; Pianka, 1970; Mitchell, 1979; Whitaker & Maser, 1981) show *A. ameiva* to consume 1–3.5% plants by volume and *C. sexlineatus* and *C. tigris* to be almost entirely carnivorous. Only in *C. lemniscatus* has the plant contribution to the diet been found to be highly variable, being under 5% in two studies (Magnusson & Da Silva, 1993; Markezich, Cole & Dessauer, 1997 for the blue morph) and 13–17% in two others (Vitt & De Carvalho, 1995; Vitt *et al*., 1997). It is unclear whether this intraspecific variation is the result of dietary differences among populations or of differences among studies in availability of easily digested plant food.

Omnivory is absent in Gymnophthalmidae. Of 17 species and 11 genera surveyed, no plant material whatsoever was reported except in *Bachia bresslaui*, for which plant material was reported as present but unimportant (Colli, Zatz & Da Cunha, 1998).

In Xantusiidae, plant material has been reported in diets of four of five species and both genera studied, and its importance varies greatly among species. No plants were observed in digestive tracts of *Xantusia henshawi* (Brattstrom, 1952) or *Lepidophyma flavimaculatum* (L. J. Vitt, pers. obs., small sample). In *X. vigilis*, plants were *c*. 2% of dietary items in one population (Brattstrom, 1952), but were absent in another population (Pianka, 1986). In contrast, plants form 51.6% of items (Brattstrom, 1952) and 18.7% of volume (Fellers & Drost, 1991) in *X. riversiana*, the cavernicolous *L. smithii* specializes in fig fruits, which are much more abundant than prey in its restricted habitat (Mautz & López-Forment, 1978).

Amphisbaenia has uncertain phylogenetic affinities (Estes *et al*., 1988), but may be part of or closely allied with Lacertoidea (Schwenk, 1994). Little is known about the diets of these fossorial lizards, but plants seem to be unimportant in their diets. None of the three species in the two genera sampled is omnivorous, but some plant material was recorded in the diets of all of them. Plants constituted 3% of the dietary volume of *Amphisbaenia alba* (Colli & Zamboni, 1999) and < 1% for *A. gonavensis* (Cusumano & Powell, 1991; White *et al*., 1992). In *Blanus cinereus* no plants were recorded in one population (Gil, Guerrero & Pérez -Mallado, 1993), but vegetation, including fruit and fungi, made up 5.6% dietary volume in another population (López, Martin & Salvador, 1991).

Diets in Scincidae, the largest lizard family, span the entire range from strict carnivory to omnivory with emphasis on animal prey, omnivory with a minor animal component, to herbivory. Omnivores or herbivores occurred in only eight of 34 scincid genera sampled (23.5%; Table 1), and were restricted to Lygosominae. In addition to the species listed in Table 1, several other skinks eat plants to some extent. Plants formed 6.7%, 5%, and 5.6% of the dietary volumes of *Ctenotus brooksi*, *C. dux*, and *C. pantherinus* (Pianka, 1986), and 6.4% of the diet for *C. robustus* (Brown, 1991). Plants were 9.9% and 8.4% of dietary volumes of *Egernia inornata* (Pianka, 1986) and *E. whitii (*Brown, 1991). The degree of omnivory is quite variable in *Ctenotus* and *Egernia*. It is widespread in both genera, but both include carnivores (e.g. *Ctenotus ariadne*, *C. atlas*, *C. colleti*, *C. schomburgki*, *Egernia depressa* and *E. kintorei* and others; Pianka, 1986).

Mabuya is largely carnivorous, 15 species consuming few or no plants (Barbault, 1975; Pianka, 1986; Auffenberg & Auffenberg, 1988; Castanzo, 1991; Vitt & Blackburn, 1991; Castanzo & Bauer, 1993; Vitt, 1995; Vrcibradic & Rocha, 1996; Heideman & Bates, 1999; L. J. Vitt, pers. data for *M. nigropunctata*). However, plants were 8.1% and 5.4% of dietary volume for *Mabuya agilis* (Vrcibradic & Rocha, 1996) and *M. variegata* (Castanzo, 1991). In other studies of the latter two species, *M. agilis* ate no plants (Vrcibradic & Rocha, 1995) and plants were only 1.6% of dietary volume in *M. variegata* (Pianka, 1986).

Omnivory likely occurs in some lygosomines for which there are no quantitative data. *Macroscincus coctei*, which may be extinct, was omnivorous, consuming leaves, fruits, and seeds, but also eggs and birds (Greer, 1976). This species had tooth morphology similar to that of *Iguana*, laterally compressed with multiple cusps adapted for herbivory (Greer, 1976). Several lygosomine species from New Zealand may be omnivorous, including three species of *Cyclodina* and five of *Oligosoma* (formerly *Leiolopisma*) that eat fruit (Whitaker, 1987).

Although all scincid species in Table 1 are lygosomines, some scincines excluded from Table 1 because of lack of quantitative data live in arid areas and are highly dependent on plants during seasons of prey scarcity. In deserts of northern Africa and Saudi Arabia, *Eumeces schneideri* (Kuchling, 1970; Rogner, 1997*b*), *Scincus mitranus* (A. Al-Johany, pers. obs.) and *S. scincus* (Schleich *et al*., 1996) are omnivorous, and some species of *Chalcides* consume plants (Barbadillo *et al*., 1999). Minor plant consumption may be widely distributed among scincines. For example, *E. laticeps* sometimes eat grapes and berries in the field (W. E. Cooper &

L. J. Vitt, pers. obs.), but no plants were detected in the digestive tracts (Vitt & Cooper, 1986).

Species for which two or more studies of diet are available for the most part show minor variation in plant consumption, as noted above for two species of *Mabuya*. The major exception is *Ctenotus grandis*, which had a plant dietary volume of 2.9% (Pianka, 1986), but a plant mass of 23.1% (Twigg *et al*., 1996). In *C. pantherinus*, plant dietary volumes were 0% (Twigg *et al*., 1996) and 5.6% (Pianka, 1986). In *Eumeces obsoletus*, no plants occurred in the diet in one study (Fitch, 1955), but small amounts of plant material considered to be accidentally ingested were found in 9.6% of stomachs in another study (Hall & Fitch, 1972). No or nearly no plants were detected in the diet of *Eremiascincus richardsoni* in two studies (Pianka, 1986; James & Losos, 1991), *Pseudemoia spenceri* (Brown, 1986, 1991), and *Scincella lateralis (*Lewis, 1951; Hamilton & Pollack, 1961; Brooks, 1963). Although the dietary importance of plants typically varies only slightly among studies, a single study limited to times when digestible plant parts are abundant or prey scarce may fail to detect omnivory. Additional species, especially in *Ctenotus* and *Egernia*, will probably be found to be omnivorous some of the time.

Dietary data are limited for Cordyliformes (Gerrhosauridae and Cordylidae), almost all reports being either anecdotal, based on small samples, and/or consisting only of occurrence data. Quantitative comparative study of cordyliform diets would be valuable. In Gerrhosauridae, volumetric data are available only for the omnivorous *Angolosaurus skoogi* (Table 1). In the only other published study, no plants were found in the diet of *Gerrhosaurus flavigularis* (De Waal, 1978). D. G. Broadley's (pers. obs.) occurrence data for six species of *Gerrhosaurus* show that all species consume some plants, but to a quite variable degree. The greatest plant consumption occurs in *G. validus*, which eats a variety of plant parts, but several species consume plants with some frequency (Table 1). It seems probable that of the species of *Gerrhosaurus* in Table 1, only *G. validus* and perhaps *G. bolsi* would be considered omnivorous using volumetric data.

Some data are available for three cordylid genera. In *Cordylus*, *C. giganteus* contained flowers in one study (Jacobsen *et al*., 1990), but no plants in another (De Waal, 1978), and no plants were recorded in *C. cordylus* or *C. polyzonus* (De Waal, 1978). Quantitative data on cordylids are available only for the insectivorous *C. giganteus*, in which dirt and grass were 2.78% of dietary mass (Van Wyk, 2000). In *Platysaurus*, plants were present in eight of nine species, being absent only in *Platysaurus torquatus* (Broadley, 1978; De Waal, 1978; Greef & Whiting, 1999; Whiting & Greef, 1999). In *P. maculatus* and *P. pungweensis* (Broadley, 1978), plants occurred in only 1% of stomachs. *Platysaurus broadleyi* consumes substantial, but unquantified, amounts of fig fruits (Greef & Whiting, 1999; Whiting & Greef, 1999). The other species seem to be omnivorous (Table 1), but the importance of plants in the diet is difficult to assess based on occurrence data. Based on limited data for two species of *Pseudocordylus*, *P. langi* consumes some flowers leaves, but *P. spinosus* and *P. subviridis* ate no plants (Broadley, 1964). Limiting consideration to the 14 species and three genera for which some quantitative data are available, omnivory is probable in only four of seven species of *Platysaurus*. This is somewhat surprising because cordylids have been regarded as insectivores.

Almost all anguimorphans are carnivorous, and many are strict carnivores. For seven anguid species, no plants were reported in the diets of five species in the genera *Anguis* (Capizzi *et al*., 1998), *Diploglossus* (Vitt, 1985), *Elgaria* (Fitch, 1935), and *Ophisaurus* (Hamilton & Pollack, 1961; Fitch, 1989), and only small amounts of plant material were reported in the diets of *Sauresia agasepsoides* (White *et al*., 1992) and *Wetmorena haitiana* (Cisek *et al*., 1990). For the sole xenosaurid sampled, *Xenosaurus grandis*, plants constituted 2.2% of dietary volume.

All but one species of Varanoidea, including Helodermatidae, Varanidae, and Serpentes are carnivorous. No plants were found in the diets of the two extant species of Helodermatidae (Beck, 1990; Beck & Lowe, 1991). In Varanidae, little information is available about the diet of *Lanthanotus*, but known dietary items in captivity are animal prey (Pianka & Vitt, in press). Of 21 species of *Varanus*, plants were recorded in the diets of only five species, forming < 1% of the diet in *Varanus caudolineatus* (Thompson & King, 1995), *V. gouldii* (D. King & Green, 1979) and *V. tristis* (Pianka, 1986), and being present as incidental fragments in *V. timorensis* (D. King, 1993). In contrast to its congeners, *V. olivaceus* eats nearly equal numbers of plant and animal items (Table 1). The closely related snakes are all strict carnivores (Greene, 1997).

Frequency among lizard species and higher taxa

The survey shows that plant consumption is widely distributed among lizard families, but does not indicate quantitative differences among families in proportional plant consumption or proportions of species that are

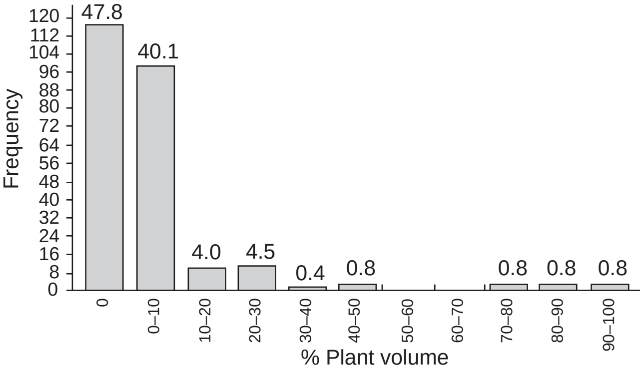

Fig. 2. Frequency distribution for lizard species of the percentage contribution of plant matter to total diet volume.

Table 2. Plants as percentage volume of total diets of lizard families and percentage of each family that are omnivores or herbivores (based on all types of data)

	Plant volume				Proportion of species that are omnivorous or herbivorous	
Family	*n*	X	SE	Range	*n*	Proportion
Chamaeleontidae	2	0.00	0.00	–	4	0.00
Agamidae	12	16.88	8.05	0.80–100.00	24	41.67
Phrynosomatidae	24	3.70	1.21	0.00–20.05	25	16.00
Tropiduridae	17	11.30	3.41	0.00–49.95	33	35.48
Polychrotidae	25	1.86	1.05	0.00–25.1	33	6.06
Iguanidae	2	85.50	14.50	71.00–100.00	13	100.00
Corytophanidae	2	13.82	13.82	0.00–27.64	4	75.00
Crotaphytidae	3	2.87	1.02	0.90–4.30	3	0.00
Gekkonidae	35	0.36	0.14	0.00–4.30	54	3.70
Pygopodidae	3	0.00	0.00	–	14	0.00
Eublepharidae	1	0.00	0.00	–	1	0.00
Lacertidae	11	2.80	2.02	0.00–21.89	48	22.92[a]
Teiidae	22	2.08	1.66	0.00–36.70	35	14.29
Gymnophthalmidae	16	0.00	0.00	–	17	0.00
Xantusiidae	3	6.23	6.23	0.00–18.70	5	40.00
Amphisbaenidae	3	2.92	1.58	0.14–5.61	3	0.00
Scincidae	51	7.89	2.88	0.00–96.15	99	15.15
Gerrhosauridae	1	82.58	0.00	–	7	42.86
Cordylidae	–	–	–	–	14	28.57
Anguidae	4	0.68	0.47	0.00–2.00	7	0.00
Xenosauridae	1	2.24	0.00	–	1	0.00
Helodermatidae	2	0.00	0.00	–	2	0.00
Varanidae	7	0.07	0.06	0.00–0.40	22	4.55
Total	246	5.07	0.94	0.00–100.00	463	17.89

[a] Excludes *Gallotia*.

omnivorous or herbivorous. The volumetric data, although they omit many known omnivores and herbivores, provide the best quantitative summary of plant consumption (Fig. 2). For all lizards combined, the dietary plant volume was slightly over 5%, with a standard error of slightly under 1% (Table 2). Because most species consumed little or no plant material, the median was only 0.01% and the mode was 0.00% (Fig. 2).

Plant consumption in lizards had long been considered atypical and restricted to a small proportion of species, but it has been increasingly recognized that many lizards eat some plants (e.g. Greene, 1982). Still, it is surprising that slightly over half of all species for which volumetric data are available eat plants (Fig. 2). Some of these ingest plants infrequently and possibly unintentionally, but the proportion of species that eat enough to be considered herbivores or omnivores is also surprisingly high. Over one-sixth of species sampled are omnivores or herbivores (Table 2), and slightly < one-eighth of species (12.1%) if only volumetric data are considered. The fraction based on the comprehensive, but not the volumetric, data set may be an overestimate because we attempted to obtain information about species that eat substantial amounts of plants.

Herbivory is much rarer than minor plant consumption and omnivory. Using the 90% criterion, only 20 species are herbivorous in the comprehensive data set, constituting only 4.32% of species, very close to prior estimates of about 2% (Pough, 1973) or 3% (Iverson, 1982). These data are subject to the same overestimation as the omnivory data. Using only the volumetric data, the estimates are lower, with only 0.8% of species herbivorous. Herbivores include the 29 species of Iguanidae (Zug, Vitt & Caldwell, 2001), a few species each of agamids and skinks, and probably some tropidurids. Given a current estimate of about 4080 lizard species (Zug *et al.*, 2001), we estimate that *c.* 1% of lizard species are herbivorous, close to the estimate from the volumetric data. Even using the comprehensive data set, there are no herbivores in most families. Among herbivores, 65% in our comprehensive data set are iguanids, 20% skinks, 10% agamids, and 5% a xantusiid. Herbivores might occur additionally in Lacertidae (*Gallotia*) and possibly in Gerrhosauridae.

Families differed substantially in mean per cent plant volume and its variability. The highest mean per cent plant volumes were in Agamidae, Tropiduridae, Iguanidae, Corytophanidae and Gerrhosauridae, all > 10%, and in Xantusiidae and Scincidae, which were both slightly over 6% (Table 2). The very high percentage for Iguanidae is an underestimate for two reasons: (1) most species not included are almost entirely herbivorous; (2) one of the two species included in Table 2, *Cyclura pinguis*, seems to consume far more insects than is known for adults of any other iguanid species, but the sample size was small (Carey, 1975). The percentage for Gerrhosauridae is an overestimate because volumetric data are available only for *Angolosaurus skoogi*, probably the most herbivorous species in the family. Occurrence data for several other gerrhosaurid species indicate omnivory with much smaller plant consumption or insectivory. The familial estimate is slightly too low for Varanidae because there are no volumetric data for the omnivorous *V. olivaceus*.

Despite these limitations, it is clear that plant consumption is absent or constitutes a small percentage of the total diet of most lizards. The mean data in Table 2 also correctly identify those families in which omnivory or herbivory are present in a substantial fraction of species. Substantial plant consumption is conspicuously infrequent in Gekkonoidea, the exceptions being species from New Zealand (Whitaker, 1987) and New Caledonia (Bauer & Sadlier, 1994).

The greatest variability in percentage plant volume as indicated by standard errors was in Agamidae, Iguanidae, Corytophanidae, and Xantusiidae. The variability for Iguanidae is misleadingly high for the same reasons given above. For Agamidae, Corytophanidae, and Xantusiidae, the large standard errors correspond to the presence of substantial fractions of both carnivores and omnivores or herbivores in those families. Somewhat smaller standard errors occur in Tropiduridae, Lacertidae, Teiidae, and Scincidae because most species in these families are insectivorous despite the presence of a few species with substantial plant consumption. The standard error and range for Lacertidae may be artificially low as a result of the lack of volumetric data on intestinal contents for *Gallotia* and some insular species of *Podarcis*.

PARTS OF PLANTS EATEN

Most lizards that eat plants occasionally or in small quantities eat only easily digestible parts or products that require neither morphological specialization nor intestinal flora for digestion of cellulose. Insectivores may occasionally ingest flowers or fruit intentionally when they are abundant and/or prey are scarce. Occasional ingestion may be undetected in short-term dietary studies (e.g. Barbault *et al.*, 1985; Vitt & Cooper, 1986). Carnivorous lizards sometimes ingest leaves, blades of grass, or fragments of them in very small quantities, but such ingestion seems to be accidental or incidental to ingestion of prey, as is ingestion of sand, dirt, wood, and other objects in small amounts (e.g. Dixon & Medica, 1966; Medica & Arndt, 1976; Van Wyk, 2000).

Omnivores that lack the ability to digest cellulose may preferentially eat plant parts rich in nutrients having low cellulose content (e.g. Pérez-Mellado & Corti, 1993; Durtsche, 1995). Among 42 species of omnivores for which plant parts consumed were recorded (Table 1), fruits were eaten by 71.4% of species, flowers by 64.3%, seeds by 52.4%, and leaves by 47.6%. Seeds in the digestive tracts of five species not noted to have eaten fruit may have been ingested in fruits that were no longer detectable. However, *Meroles anchietae* regularly ingests seeds as separate items (Murray & Schramm, 1987), and *Gallotia simonyi* probably does so (Pérez-Mellado *et al.*, 1999). For several omnivorous species that ingest some leaves, leaves formed a smaller portion of the plant diet than other plant parts (e.g. Murray & Schramm, 1987; Dearing, 1988; Fellers & Drost, 1991; Bauer & Sadlier, 1994; Pérez-Mellado *et al.*, 1999).

Table 3. Percentages of dietary volume (V) or mass (M) constituted by leaves, fruit, and flowers for adults of several species of iguanid lizards

Species	Type of data	Leaf	Fruit	Flower	Source
Conolophus pallidus	V	58.2	7.4	19.4	Christian *et al.*, 1984
Ctenosaura pectinata	V	52	2	35	Durtsche, 1999
Ctenosaura similis	V	25	73	0	Van Devender, 1982
Iguana iguana	M	52.1	7.7	35.2	Van Marken Lichtenbelt, 1993
Sauromalus	M	35.5	32	11.4	Nagy & Shoemaker, 1975

Herbivorous lizards, especially folivores, have adaptations for processing plants, especially leaves. They have specialized blade-like teeth for shearing plant food (Hotton, 1955; Montanucci, 1968) or massive teeth for crushing (Throckmorton, 1976). Their colons are enlarged (Henke, 1975; Iverson, 1980) and contain intestinal flora that digest cellulose and intestinal structures, that presumably slow the passage of food, are present in some herbivorous lizards (Iverson, 1982; McBee & McBee, 1982). They are present in those species that rely heavily on leaves as food, such as iguanids and *Hydrosaurus pustulosus* (Taylor, 1922; Iverson, 1982).

Valves partitioning the colon occur in iguanids, *Hydrosaurus*, *Uromastyx*, and *Corucia*, all of which consume large quantities of leaves. They have not been studied in *Phymaturus*, and are absent in *Tiliqua* and *Egernia* despite heavy plant consumption (Iverson, 1982). Thus, colic valves are absent in species for which plants form the bulk of the diet, but animals continue to be eaten frequently. Colic valves are limited to fairly strict herbivores, but even omnivorous lizards lacking them may have digestive tracts modified to process the larger volumes of food that they require because of the lower energy value per mass of plant than animal food. The omnivorous teiids *Cnemidophorus murinus* and *Tupinambis teguixin* have much greater intestinal capacities and longer intestines than do closely related insectivores (Dearing, 1993).

Although *H. pustulosus* is a folivore (Taylor, 1922), most herbivores continue to use other plant parts (Table 1). Nevertheless, data for adults of several iguanid species show that leaves form an important part of the diet for all of them (Table 3). For the species in

Table 3, leaves made up nearly half of the diet and were the largest item except in *Ctenosaura similis*. Specialization by *Amblyrhynchus cristatus* on aquatic algae (Nagy & Shoemaker, 1984) is unique.

Herbivores, as well as omnivores, may select the most nutritious plants and plant parts. The diet of *Conolophus pallidus* includes the most nutritious plant parts (Christian, Tracy & Porter, 1984) and *I. iguana* selects the more nutritious immature leaves and does not eat mature leaves, which have a lower digestible protein content and are more difficult to digest (Troyer, 1984*a*). *Ctenosaura pectinata* also prefers new leaves (Durtsche, 2000).

The relative importance of fruit and flowers may be strongly affected by availability when data are collected. For example, *C. pectinata* eats leaves primarily in the wet season when new leaves and herbaceous plants are most abundant (Durtsche, 2000). More generally, the seasonal availability of plant parts strongly affects the degree of plant consumption by omnivores and the types of plant parts consumed by omnivores and herbivores. In the omnivorous *Uma inornata*, plants are the bulk of the diet in May, with mainly flowers being eaten, but arthropods are predominant in July, with leaves and seeds being the main plant parts consumed (Durtsche, 1995). Plant consumption was greatest during the time of greatest prey availability, suggesting that the availability of readily digestible flowers richer in nutrient content than leaves is the primary reason for greater plant consumption in May (Durtsche, 1995). *Sauromalus ater* eats primarily leaves in spring, but eats fruits and flowers when available (Nagy, 1973). In *I. iguana*, leaf consumption is greatest when young leaves appear (Van Marken Lichtenbelt, 1993).

The importance of leaves in the diet seems to increase with the proportional volume of plants in the diet. Leaves are scarce in the diets of carnivores, but are included in diets of several omnivores that have strong plant components (e.g. *Angolosaurus skoogi* – Pietruszka *et al.* (1986); *Gerrhosaurus validus* – D. G. Broadley (pers. comm.); *Cnemidophorus murinus* – Dearing (1988), Dearing & Schall (1992)), and are important in diets of many herbivores, including iguanids (Table 3), *Hydrosaurus pustulosus* (Taylor, 1922), and *Corucia zebrata* (Rogner, 1997*b*). *Varanus olivaceus* is exceptional among omnivores in that more than half of its diet is plant material, but only fruit is eaten (Auffenberg, 1988).

Some lizards select specific plant materials, such as nectar, pollen, or sap, which may have concentrated nutrients. Nectar consumption occurs in several geckos and lacertids, the teiid *Cnemidophorus murinus* (Dearing, 1988), and the polychrotid *Anolis stratulus* (Perry & Lazell, 1997). The geckos *Hoplodactylus duvauceli*, *H. maculatus*, and *H. pacificus* consume nectar (Whitaker, 1968, 1987; Eifler, 1995), as do the lacertids *Gallotia galloti* (Font & Ferrer, 1995); *G. simonyi* (Pérez-Mellado *et al.*, 1999), *Lacerta dugesii* (Elvers, 1977), *Podarcis lilfordi* (Sáez & Traveset, 1995; Pérez-Mellado & Casas, 1997), *P. muralis* (Pérez-Mellado & Corti, 1993), and *P. pityusensis* (Pérez-Mellado & Corti, 1993). *Gallotia caesaris* and *Podarcis lilfordi* lick sugar solutions, which may be an adaptation to feeding on nectar (Cooper & Pérez-Mellado, in press). The lacertids *G. simonyi* (Pérez-Mellado *et al.*, 1999), *P. lilfordi* and *P. pityusensis* (Pérez-Mellado & Corti, 1993) and the gecko *Rhacodactylus auriculatus* (Bauer & Sadlier, 1994) eat pollen. The gecko *Gehyra australis* consumes sap (Letnic & Madden, 1998).

ONTOGENY

The degree of ontogenetic variation in plant consumption by lizards that are herbivorous as adults varies greatly among species. Most studies are of iguanids. Both adults and hatchlings of *Iguana iguana* are strictly herbivorous (Van Devender, 1982; Troyer, 1984*a*; Van Marken Lichtenbelt, 1993). In *Dipsosaurus dorsalis* adults and hatchlings ate few animal prey, with hatchlings eating 1.8% and adults 0.9% of animal food by mass (Mautz & Nagy, 1987). The percentage of prey in the diet is greater for hatchlings than adults in the iguanids *Amblyrhynchus cristatus* (Nagy & Shoemaker, 1984), *Ctenosaura pectinata* (Durtsche, 1999, 2000), and *C. similis* (Van Devender, 1982). In *C. pectinata* there is a further ontogenetic change, with a higher proportion of the diet consisting of leaves in adults than hatchlings (Durtsche, 2000). Increased plant consumption by older lizards has also been reported in the skink *Egernia stokesii* (Duffield & Bull, 1998). Even the juvenile diet is 87.85% plants, but the percentage of animal food is significantly higher and the percentage of plants significantly lower than in adults (Table 1).

Plants also assume increased importance in the diet of some omnivores. Greater consumption of prey by hatchlings than by adults has been reported in *Lacerta lepida* (Valverde, 1967), the tropidurids *Liolaemus lutzae* (Rocha, 1998) and *Tropidurus torquatus* (Fialho *et al.*, 2000), the phrynosomatid *Sceloporus poinsettii* (Ballinger, Newlin & Newlin, 1977), and the corytophanids *Basiliscus basiliscus* (Fleet & Fitch, 1974) and *B. vittatus* (Hirth, 1963). No statistical evidence for an ontogenetic change was presented for *B. basiliscus*, but plant material was present in all six adults (SVL > 120 mm), two of three juveniles (91–103 mm SVL) and none of seven juveniles (SVL < 91 mm). Pooling the two older groups, there is a clear increase with age in proportion of lizards that ate plants ($P < 0.0018$, two-tailed Fisher exact test).

Views about the ontogeny of plant consumption by herbivores have themselves undergone marked change. Hatchling diets containing greater prey and lesser plant components were once considered typical for herbivores on the basis of limited evidence. Later, ontogenetic changes were generally considered unproven and unimportant. It is now clear that large changes in plant consumption occur in several species, but are absent in others. Dietary ontogeny must be evaluated on a case by case basis.

Factors affecting ontogenetic shifts toward greater plant consumption have not been established, but there are several candidates, including ontogenetic change in ability to digest cellulose, avoidance of plant toxins, ability to capture prey, and energetic requirements. Hatchling iguanids lack the intestinal flora needed to digest cellulose, and must obtain it by eating faeces of adult conspecifics (Troyer, 1982, 1984*b*). Thus, hatchlings of some iguanid species may delay or reduce plant consumption until they have a functional fermentative intestinal flora. Other iguanids consume almost exclusively plants at all ages (Troyer, 1984*a*; Mautz & Nagy, 1987).

Age- or size-related changes in ability to capture mobile prey might affect percentage of plants in the diets of some herbivores. Small, abundant prey available to hatchlings might be difficult for adults to capture, which seems to be true for adult *Uromastyx aegyptius* (W. E. Cooper, pers. obs.). Because hatchlings and juveniles have higher mass-specific metabolic rates than adults (Troyer, 1984*a*), the greater mass-specific caloric value of animal prey than plant food might favour greater utilization of prey by hatchlings, but there is no evidence on this point.

Little is known about ontogenetic changes in the proportions of different plant parts eaten by herbivores, but hatchlings lacking the intestinal flora to digest cellulose efficiently (Troyer, 1982, 1984*b*) might be expected initially to prefer fruits and flowers over leaves. However, most iguanids studied show no ontogenetic increase in leaf consumption. Exceptions are *Ctenosaura pectinata* (Durtsche, 2000) and *C. similis*. In *C. similis*, leaf consumption increases ontogenetically, but so does consumption of fruits and flowers (Van Devender, 1982), so that no consistent increase in ingestion of leaves relative to fruit and flowers occurs. In *I. iguana* leaves are the bulk and a constant proportion of the diet at all ages (Van Devender, 1982). The diets of adult and juvenile *Cyclura stejnegeri* are very similar (Wiewandt, 1977).

Some herbivores lack obvious ontogenetic dietary changes, but may undergo more subtle ones. Hatchling and juvenile *I. iguana* have twice and 1.4 times the daily energetic requirement relative to body mass as adults, respectively, and their growth requires a greater intake of protein (Troyer, 1984*a*). Consequently, they select leaves having greater digestible protein content than do adults, i.e. they eat more immature leaves (Troyer, 1984*a*).

Only in *Dipsosaurus dorsalis* has the prediction of increasing importance of leaves with age been verified. The autumnal diet of adults contains a much higher proportion of leaves and a much lower proportion of flowers than that of hatchlings (Mautz & Nagy, 1987). Because the digestive tract of *D. dorsalis* is less specialized than that of other iguanids (Mautz & Nagy, 1987) and these lizards are smaller than most iguanids, the ability to digest leaves might be less developed in hatchlings than in other iguanids. However, there is a more likely explanation. Juveniles of both *I. iguana* and *Dipsosaurus dorsalis* digest plant foods more rapidly than adults (Troyer, 1984*a*; Mautz & Nagy, 1987). Rapid processing and selection of highly nutritious plant parts may enable these two species to be nearly entirely herbivorous even as hatchlings.

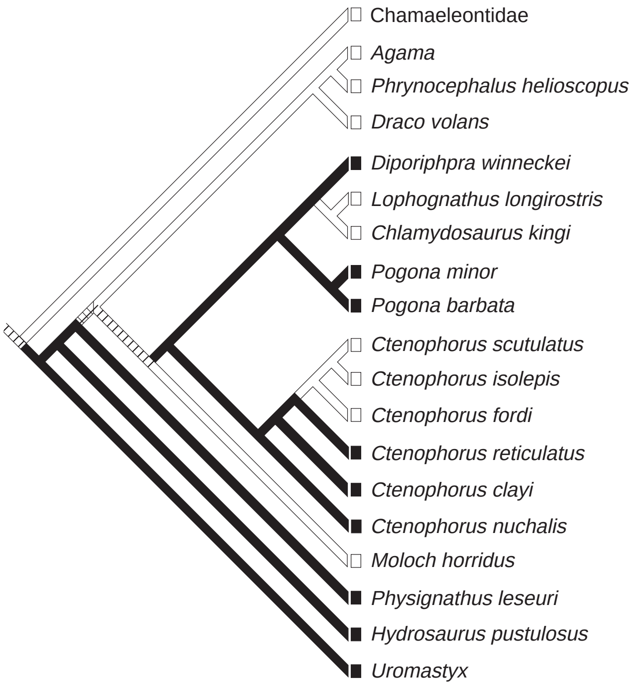

Fig. 3. Evolution of plant consumption by acrodont lizards. Diet: white branches, carnivory; black branches, omnivory or herbivory.

Data on ontogenetic changes in proportional contributions of plants and plant parts to the diet, selection of food for nutritional content, digestive efficiency of plant parts, food intake, and speed of digestive processing in additional herbivores would help to ascertain the frequency of ontogenetic changes and the reasons for interspecific differences. Do species such as *C. similis* and *C. pectinata* that consume more insects as hatchlings than as adults lack rapid passage rates or selection of more nutritious plant parts?

EVOLUTION OF PLANT CONSUMPTION

By family

Omnivory has evolved numerous times in lizards. Herbivory has evolved several times, but much less frequently than omnivory. Our estimates of numbers of losses may not be accurate because of incompleteness of sampling and efforts to obtain data on omnivores and herbivores. As a result of the lack of information for most species and some families, and the uncertainties of phylogenetic relationships, it is impossible to trace accurately all changes that occurred during the evolution of plant consumption by lizards. Enough information is available to trace broad patterns, to detect numerous independent evolutionary changes, and to suggest areas in need of investigation.

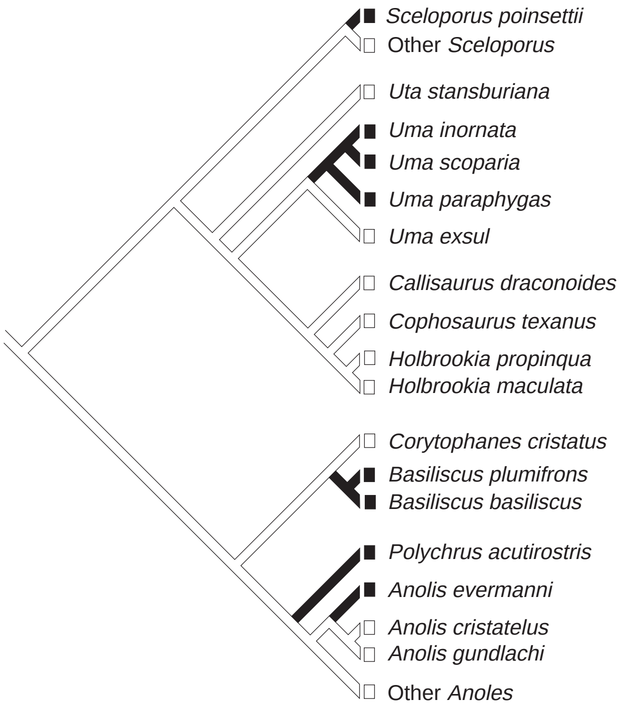

Fig. 4. Evolution of plant consumption by phrynosomatid, polychrotid, and corytophanid lizards. Diet: white branches, carnivory; black branches, omnivory or herbivory.

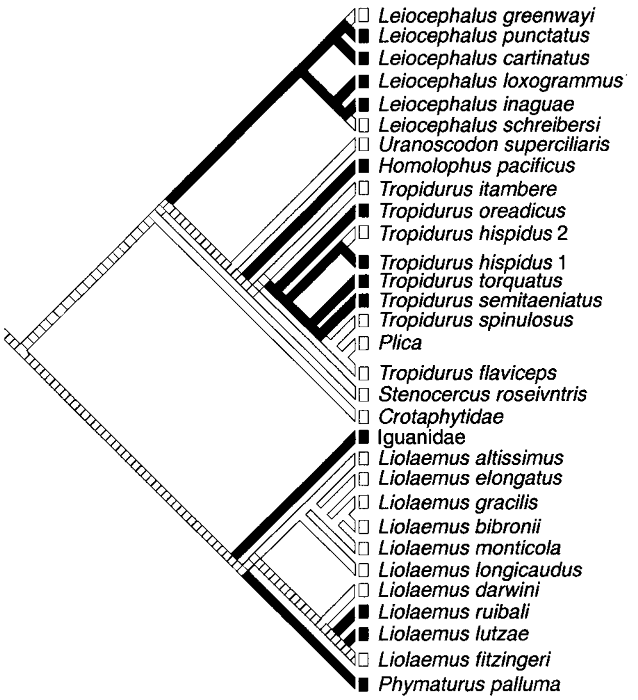

Fig. 5. Evolution of plant consumption using the preferred phylogeny for tropidurid, iguanid, and crotaphytid lizards. Diet: white branches, carnivory; black branches, omnivory or herbivory.

Tracing the evolution of plant consumption is particularly difficult in Iguania because the relationships among families are uncertain (Macey *et al*., 1997; Schulte *et al*., 1998). In Acrodonta, omnivory is absent in Chamaeleontidae, but is widely distributed in Agamidae. Because it is present in *Uromastyx*, *Hydrosaurus*, *Physignathus*, and *Liolepis*, omnivory may have evolved in the common ancestor of Agamidae in Moody's (1980) phylogeny (Fig. 3). One or two independent origins account for herbivory in Agamidae, depending on the uncertain character states in Fig. 3. The data for Moody's (1980) group III suggest that omnivory might have been lost in *Moloch* and in the ancestor of *Lophognathus* (formerly *Gemmatophora*) and *Chlamydosaurus*. The presence of omnivory in three of six species of *Ctenophorus* suggests that it has been gained or lost at least once in the genus, but intrageneric relationships are uncertain. Figure 3 presents one of several possible relationships. Based on limited data, omnivory may have been lost in the common ancestor of Moody's (1980) groups V and VI, represented here by *Agama*, *Phrynocephalus*, and *Draco* (Fig. 3), or in the common ancestor of them and their sister group. Honda *et al*. (2000*a*) recently revised relationships of some agamid genera, but insufficient genera were included to permit tracing the evolution of plant consumption. However, the maximum likelihood dendrogram of Honda *et al*. (2000*a*), implies that the group represented by *Agama*, *Phrynocephalus* and *Draco* in Fig. 3 is the sister group of all other agamids. If so, a single origin may have occurred in the common ancestor of all other agamids. The diet of the common ancestor of acrodonts is uncertain in Fig. 3, but carnivory in the common ancestor of Scleroglossa (see below) makes it clear that the ancestral acrodont was carnivorous.

Agamids have undergone large changes in the importance of plants in the diet and in the types of plants eaten. Prominent use of leaves seems to have had one or two independent origins in Agamidae. The folivorous genera are in different subfamilies, Leiolepedinae (*Uromastyx*) and Agaminae (*Hydrosaurus*). Herbivory with prominent folivory might have been gained separately in *Hydrosaurus* and *Uromastyx* or it might have appeared in the common ancestor of Agamidae and been lost in *Leiolepis*, in which some species eat few plants (Rogner, 1997*a*).

In the large family Polychrotidae, omnivory is known only in *Polychrus acutirostris* and a single species in the speciose *Anolis* (Table 1), both of which acquired omnivory independently (Fig. 4). In its sister family, Corytophanidae, all species of *Basiliscus* sampled are omnivores (Table 1 and Hirth, 1963), whereas *Corytophanes cristatus* may eat small amounts of plant matter incidentally (Andrews, 1979) and a small sample had no plants in the diet (L. J. Vitt, pers. obs.). Thus, omnivory is most likely to have originated separately once in Corytophanidae (Fig. 4).

In Phrynosomatidae, omnivory evolved independently once in *Uma* and at least once in *Sceloporus*, being present in *S. poinsettii* (Fig. 4) and *S. torquatus*

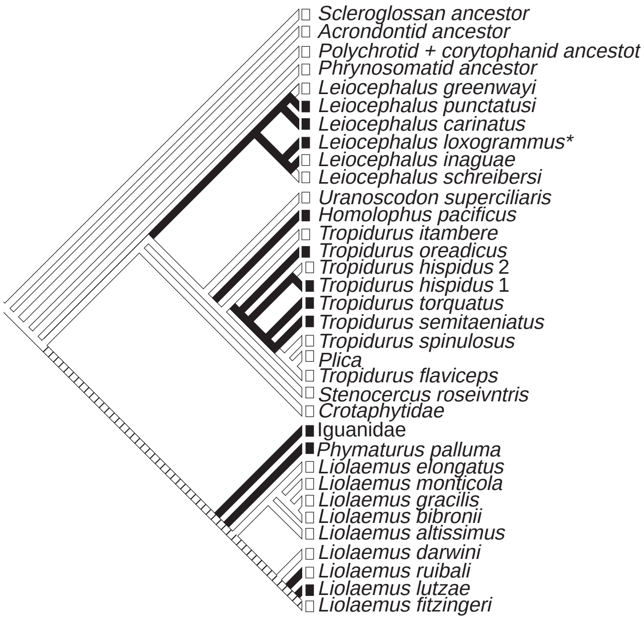

Fig. 6. Evolution of plant consumption using the preferred phylogeny for tropidurid, iguanid, and crotaphytid lizards. Addition of successive outgroups on the left to the phylogeny shown in Fig. 5 restricts uncertainty to the rightmost branch. Diet: white branches, carnivory; black branches, omnivory or herbivory.

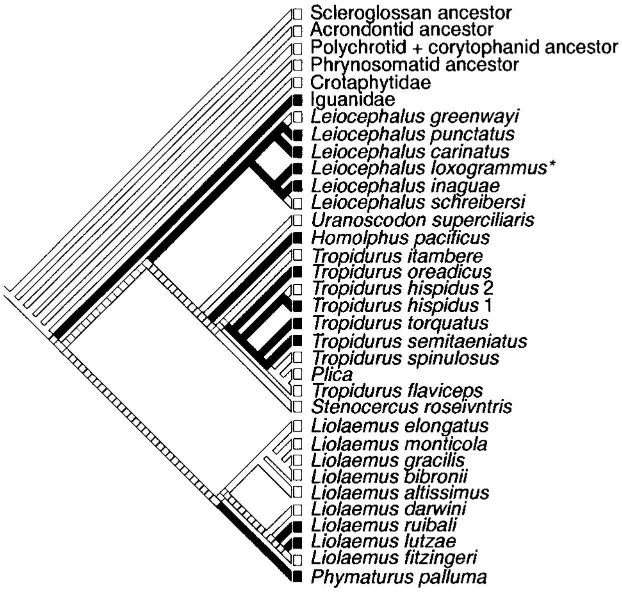

Fig. 7. Evolution of plant consumption for tropidurid, iguanid, and crotaphytid lizards using an alternative phylogeny in which Tropiduridae is monophyletic and Iguanidae is its sister group. Diet: white branches, carnivory; black branches, omnivory or herbivory.

(Búrquez, Flores-Villela & Hernandez, 1986) (both in the *torquatus* species group) (Wiens & Reeder, 1997). More cases are likely in *Sceloporus*, but may be limited to times of prey scarcity and/or abundance of easily digested plant parts.

Tropiduridae is a metataxon (Schulte *et al*., 1998). Molecular data suggest that the subfamilies Leiocephalinae and Tropidurinae are the sister taxon of Crotaphytidae and the subfamily Liolaeminae plus Opluridae (not shown) is the sister of Iguanidae (Figs 1 & 5; Schulte *et al*., 1998). Combined molecular and morphological data suggest that Liolaeminae is the sister of Opluridae, and that Leiocephalinae plus Tropidurinae form a taxon of equal rank with them, Crotaphytidae, and Iguanidae, the four larger taxa forming a polytomy (Schulte *et al*., 1998).

The greatest uncertainty about evolution of omnivory among iguanians occurs in Tropiduridae and its relatives. In the morphological phylogeny (Fig. 5), the diet of the common ancestor of Iguanidae, Crotaphytidae, and Tropiduridae is uncertain; several patterns of gain and loss are possible (Fig. 5). Based on outgroup analysis, the common ancestor of the iguanid–crotaphytid–tropidurid clade was insectivorous (Fig. 6). Omnivory evolved in the common ancestor of *Leiocephalus*, and seems to have been lost twice within the genus. Omnivory has evolved independently and been lost at least twice each in *Tropidurus* (Fig. 6). We lack data for *T. thoracicus*, which is omnivorous or perhaps even herbivorous (Dixon & Wright, 1975).

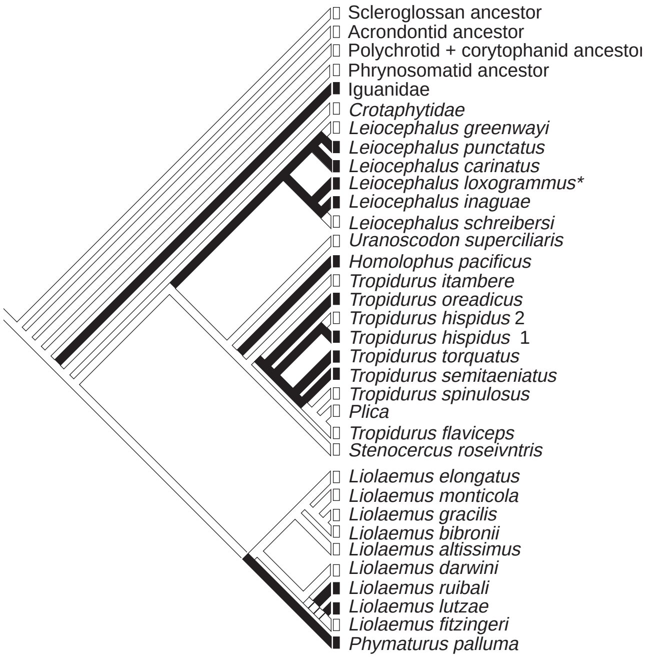

Fig. 8. Evolution of plant consumption for tropidurid, iguanid, and crotaphytid lizards using an alternative phylogeny in which Tropiduridae is monophyletic and Crotaphytidae is its sister group. Diet: white branches, carnivory; black branches, omnivory or herbivory.

The common ancestor of Iguanidae and Liolaemines might been a heavy consumer of plants, but its character state is uncertain (Fig. 6). There have been multiple gains or losses in the genus *Liolaemus* (Fig. 6). The universality of herbivory in Iguanidae implies that it

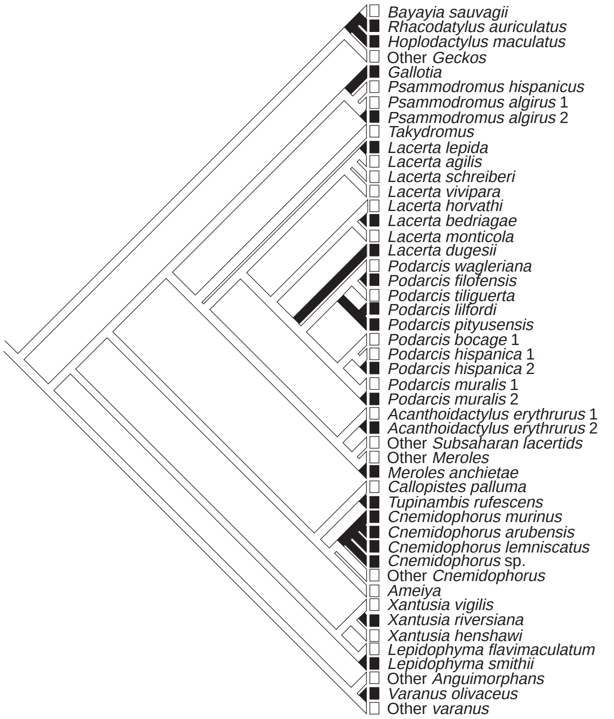

Fig. 9. Evolution of plant consumption for scleroglossan lizards excluding Scincoidea. Diet: white branches, carnivory; black branches, omnivory or herbivory.

was present in the family's common ancestor and that no losses have occurred within the family. Dietary specialization on plants is present in *Phymaturus* and some species of *Liolaemus*, notably *L. lutzae*, have a much higher plant intake than others.

Alternative phylogenies for the iguanid–crotaphytid-tropidurid clade resolve the polytomy by considering Tropiduridae to be monophyletic (Figs 7 & 8). If Iguanidae is the sister group of Tropiduridae (Fig. 7), there is greater uncertainty than in the resolution favoured by Macey *et al*. (1997) and Schulte *et al*. (1998). If Crotaphytidae is the sister group of Tropiduridae, the character states are much better resolved (Fig. 8), with uncertainty remaining only in the *boulengeri* species group (Etheridge, 1995). The number of independent origins and losses of omnivory varies from four to five gains and four or more losses in Fig. 6, to as few as one gain and four losses in Fig. 7, to six or seven gains and at least five losses in Fig. 8.

Despite the ambiguity resulting from poor phylogenetic resolution, it is clear that the degree of plant consumption is labile in Leiocephalinae and Tropiduridae. The number of independent origins and losses represented in Tropiduridae cannot be confidently estimated, but the estimate based on Fig. 6 is favoured because of the probable paraphyly of Tropiduridae. It is possible that a high proportion of tropidurids consume plants in certain circumstances.

The history of plant consumption is clearer in some scleroglossan groups than in Iguania because the phylogeny of Scleroglossa is better resolved and few species eat plants in appreciable amounts in two major scleroglossan taxa, Gekkonoidea and Anguimorpha. There are many omnivores in Scincomorpha. In Gekkonoidea at least one independent origin is needed to account for the presence of omnivory in *Rhacodactylus* and *Hoplodactylus*, closely related carphodactylines (Bauer, 1990; Fig. 9). Limited data suggest that *Bavayia sauvagii* is insectivorous. Because *Bavayia* is more closely related to *Rhacodactylus* than is *Hoplodactylus*, two independent origins or a single origin and a loss are required (accelerated or delayed transformation options in TRACE). In Anguimorpha a single origin of omnivory occurred in *Varanus olivaceus*, all other species being carnivorous (Fig. 9). This shows that a high percentage of plant matter can be incorporated into the diet directly by species having carnivorous ancestors without the necessity of predecessor species eating some, but few, plants.

In Lacertoidea, omnivory has arisen multiply in Lacertidae, Teiidae, and Xantusiidae, but is absent in other taxa. Two independent origins occurred in Xantusiidae, in *X. riversiana* and *Lepidophyma smithii* (Fig. 9). In Lacertidae seven independent origins occurred in the species sampled (Fig. 9). One was in *Meroles anchietae*, one of only two omnivores in Eremiainae, a primarily African clade (Harris *et al*., 1998) The other is *Acanthodactylus erythrurus*, which was omnivorous in two of five studies. Another independent origin occurred within *Psammodromus algirus*, which is omnivorous on an island and insectivorous elsewhere (Seva, 1984; Pollo & Pérez-Mellado, 1988; Sorci, 1990). One origin accounts for omnivory in all species of *Gallotia. Lacerta lepida* independently derived omnivory (Castilla, Bauwens & Llorente, 1991; Van Damme, 1999). Using the phylogeny of Harris & Arnold (1999) for *Podarcis*, omnivory in the sister species *P. lilfordi* and *P. pityusensis* presumably had one origin. A distinct origin occurred in the closely related *P. filofensis*. Omnivory in *P. hispanica* occurs on an island (Pérez-Mellado & Corti, 1993), but not the mainland (Pérez-Mellado, 1983; Van Damme, 1999). *Psammodromus hispanicus* also ate more plants on an island (Pérez-Mellado, 1982) than on the mainland (Pollo & Pérez-Mellado, 1988). Using a 5% criterion for herbivory (Van Damme, 1999), more independent origins have occurred in Lacertidae (e.g. *P. sicula*, Ouboter, 1981; *Lacerta bedriagae*, Castilla, Bauwens, Damme *et al*., 1989).

In Teiidae, separate origins of omnivory occurred in *Tupinambis* and *Cnemidophorus* (Fig. 9), which belong to the two major branches of Teiidae (Presch, 1974). Within *Cnemidophorus* one origin might account for all omnivory because *C. arubensis* and *C. murinus* are insular forms located off the coast of Venezuela, where the species called *Cnemidophorus* sp. (green) (Markezich *et al*., 1997) occurs, and all are in the *lemniscatus* species group (Markezich *et al*., 1997). The green *Cnemidophorus* sp. is possibly an unusual variant of *C. lemniscatus* (Markezich *et al*., 1997).

Our poorest information about omnivory for scleroglossans is in Scincoidea (Estes *et al*., 1988), which

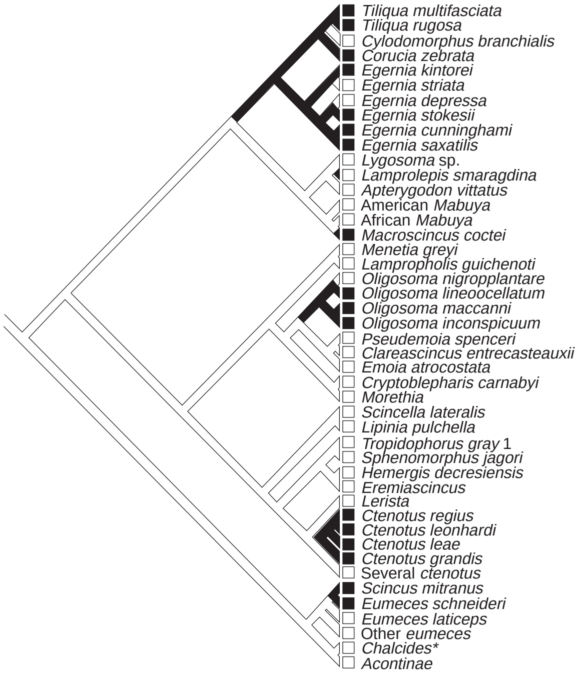

Fig. 10. Evolution of plant consumption for Scincidae using the phylogeny taken from multiple sources and based on various types of characters. Diet: white branches, carnivory; black branches, omnivory or herbivory.

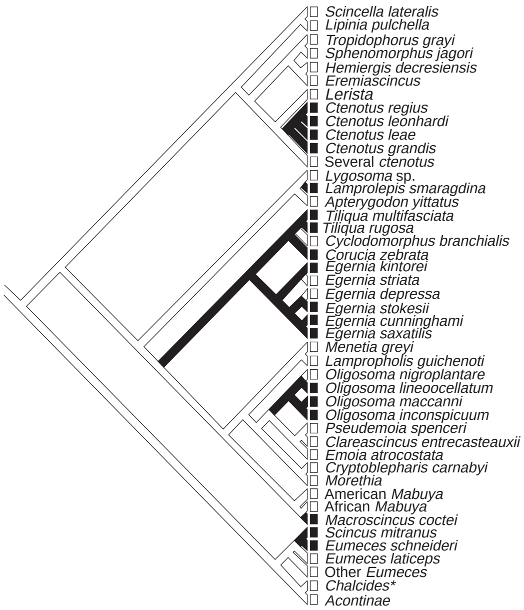

Fig. 11. Evolution of plant consumption for Scincidae using the phylogeny of Honda *et al.* (2000*b*) for Lygosominae based on mitochondrial DNA sequences. Diet: white branches, carnivory; black branches, omnivory or herbivory.

consists of Scincidae and the cordyliform families Cordylidae and Gerrhosauridae (Lang, 1991). Some phylogenetic relationships within Scincidae are too poorly known and diet data are too limited to permit a highly reliable reconstruction of the evolution of plant consumption. The situation is much worse for Cordyliformes. Several independent origins of omnivory have occurred in Scincidae, at least five in Lygosominae and one in Scincinae. This is so for both of the alternative phylogenies in Figs 10 & 11, which differ greatly in relationships of major groups of the subfamily Lygosominae, but not in the placement of genera within these groups. The phylogeny of Fig. 9 can be expanded to include Fig. 10 or 11 to show all of the available information for Scleroglossa. The tree in Fig. 10 or 11 is the sister of Lacertoidea.

Omnivory may be more widespread in Lygosominae than in other subfamilies and requires at least five independent origins. Because *Macroscincus coctei* is nested within *Mabuya* (Greer, 1976), in which the remaining species are insectivorous, its omnivory originated independently. Other omnivorous lygosomines in Table 1 all occur in Australia, New Zealand, or New Caledonia. Because *Corucia*, *Egernia*, and *Tiliqua* form the Egernia group (Hutchinson, 1981), one origin of or increase in omnivory may account for the high plant consumption in *C. zebrata*, *T. rugosus*, and *T. multifasciata*, with herbivory originating in *C. zebrata*. Evolution of omnivory within *Egernia* is unclear because of the lack of data for some species, the uncertainty of intrageneric relationships, and intraspecific variability. Multiple origins, losses, or changes in the degree of omnivory are possible because the three species known to be omnivorous belong to different lineages containing other species that are carnivorous or eat less plant material (Figs 10 & 11). In *Ctenotus*, which belongs to the *Sphenomorphus* group, and *Oligosoma*, which is part of the *Eugongylus* group (Greer, 1979), at least one independent origin or loss has occurred in each genus, and multiple origins and losses are possible. Because intrageneric relationships for *Ctenotus* are unknown, Figs 10 & 11 show all insectivores on one branch to minimize the number of origins of omnivory.

Among scincines, one origin accounts for omnivory in the very closely related *Eumeces schneideri* and *Scincus mitranus* (Caputo *et al.*, 1994). Because we have data for few scincine species and know that some of them occasionally eat fruit or flowers (Rogner, 1997*b*; Barbadillo *et al.*, 1999 for *Chalcides* sp.; Vitt & Cooper, 1986 for *Eumeces laticeps*), undocumented origins of omnivory are likely to have occurred in extremely arid regions of northern Africa and Saudi Arabia or on islands such as the Canaries. Data are lacking for eastern Asian scincines.

Data for cordyliform lizards are too scarce to permit many firm conclusions. For Gerrhosauridae there are no data on the Madagascan genera and some African genera and the data for several *Gerrhosaurus* are scanty. Omnivory might have evolved separately in *Angolosaurus* and within *Gerrhosaurus*, but was possibly present in the common ancestor of *Gerrhosaurus* and lost in some of its species, and might even have been present in the common ancestor of Gerrhosauridae. In Cordylidae omnivory seems to have evolved at least once, possibly in *Platysaurus* or even in the common ancestor of *Platysaurus* and *Pseudocordylus* (Lang, 1991). Variability within *Platysaurus* hints at possible multiple gains and/or losses.

Gains, losses and higher taxa

Plant consumption has evolved numerous times in lizards, but the exact pattern of gains and losses cannot be traced in all groups because of insufficient data and equivocal phylogenies. Nevertheless, present data are adequate to show that omnivory has evolved independently numerous times in both Scleroglossa (Figs 9–11) and Iguania (Figs 3–6). The greatest number of origins is in Scincomorpha (Lacertoidea plus Scincoidea). Of these, 15 are in Lacertoidea, with 11 in Lacertidae and two each in Teiidae and Xantusiidae, and an additional six origins are in Scincidae, bringing the total in Scincomorpha to 21. The single origins in Gekkonoidea and Anguimorpha bring the scleroglossan total to 23. Adding the minimum of nine origins in Iguania, there have been at least 32 origins of omnivory, and probably many more.

About 2.33 times as many origins have occurred in Scleroglossa as in Iguania. Using the estimated numbers of species from Zug *et al.* (2001), there are 2.36 times as many scleroglossans as iguanian species. Omnivory is equally likely to evolve on a per species basis in the two major lizard clades. Its evolution has been rare in Gekkota, the single origin of omnivory being only 3.1% of all origins and 3.7% of omnivorous species, whereas 23.8% of all lizard species are geckos. In Autarchoglossa, comprising 46% of all species, 68.8% of origins of omnivory occurred.

In Scleroglossa (excluding Scincoidea), losses of omnivory have occurred less frequently than gains. Only one possible loss was detected in Gekkonidae (Fig. 9) and four in Scincidae (Figs 10 & 11). Van Damme (1999) found some reversion in Lacertidae, but gains were far more frequent. The absence of lacertid reversions in our data reflects our smaller lacertid sample and our criterion of double the plant consumption for omnivory. For iguanians, only in Agamidae (at least twice) and Tropiduridae (at least four times in the favoured phylogeny) is there evidence for reversion to carnivory. Thus, there have been 10 or 11 losses of omnivory, about one-third as many as origins. Because there are far more insectivorous than omnivorous species, the frequency of loss is rather high relative to gain. This might be a consequence of unreliable detection of plants in the diet of species that consume them intermittently rather than a true indication of a high loss rate.

Herbivory

Herbivory has evolved much less frequently than omnivory. It was present in the common ancestor of Iguanidae and evolved once in the common ancestor of Iguanidae + Liolaeminae or in the common ancestor of Iguanidae and separately in *Phymaturus*. A single origin can account for its presence in the agamids *Uromastyx* and *Hydrosaurus*. Only two to three independent origins of herbivory have occurred in Iguania. Herbivory may have been lost in *Liolepis* and the common ancestor of *Physignathus* and sister taxon in Fig. 3. Herbivory is also rare in Scleroglossa. The skinks *Corucia zebrata*, *Tiliqua rugosa*, *Egernia cunninghami* and *E. stokesii* are herbivorous and *Tiliqua multifasciatus* and *E. kintorei* approach the 90% criterion for herbivory. A single origin might account for herbivory in these lizards, but multiple origins are possible. In addition to these cases, independent origins might have occurred in some *Rhacodactylus* or *Gallotia*, but the data are inadequate to determine whether they are omnivores or herbivores by the 90% criterion.

FACTORS THAT MIGHT AFFECT THE EVOLUTION OF PLANT CONSUMPTION

Insularity

Insularity is the only ecological variable proven to be related to plant consumption using phylogenetic methods. Van Damme (1999) found that insular lacertids eat more plant matter than those on the mainland, confirming the hypothesis of Rand (1978) and Pérez-Mellado & Corti (1993). Lower prey availability on islands might be a major impetus for broadening of the diet to include plants (Pérez-Mellado & Corti, 1993). Low predation pressure might allow prolonged digestion of plants (Janzen, 1973; Van Damme, 1999). These ideas remain untested.

The effects of insularity were not tested for Iguania because of phylogenetic uncertainty, but there is no obvious association, most iguanian origins having occurred on the mainland. Insular taxa in Scleroglossa (Figs 9–11) were three leftmost geckos, *Gallotia*, *Psammodromus algirus* 2, *Lacerta bedriagae, L. dugesii*, *Podarcis filofensis*, *P. tiliguerta*, *P. lilfordi*, *P. pityusensis*, *P. hispanica* 2, *P. muralis* 2, *Cnemidophorus murinus*, *C. arubensis*, *Xantusia riversiana*, and *Varanus olivaceus* from Fig. 9. Insular taxa in Scincidae in Figs 10 & 11 are *Corucia zebrata*, *Lamprolepis smaragdina*, *Apterygodon vittatus*, *Macroscincus coctei*, all four species of *Oligosoma*, *Emoia atrocostata*, *Lipinia pulchella*, *Tropidophorus grayi*, and *Sphenomorphus jagori*.

Our data strongly confirm the hypothesis that insularity increases the likelihood of evolving omnivory in scleroglossa. As did Van Damme (1999), a significant association ($P < 0.001$) was found between insularity and omnivory in Lacertidae (Fig. 9), for which eight of 11 gains occurred on islands. Using alternative phylogenies, the relationship remained significant at similar P values if *Takydromus* is the sister taxon of Eremiainae (*Acanthodactylus* + *Meroles* + other sub-Saharan genera) or of *Podarcis* + *Lacerta*. In additional phylogenies examined to account for uncertainties in relationships within *Podarcis*, correlated evolution between insularity and omnivory was significant at slightly lower *P* values. Alternatives tested were: *P. filofensis* as the sister species of *P. lilfordi*–*P. pityusensis* and *P. wagleriana* as the sister of *P. tiliguerta*; *P. wagleriana* as the sister group of the other four species; *P. tiliguerta* as the sister of the others.

In Lacertiformes (Lacertidae + Teiidae; Fig. 9) there are 13 gains of omnivory, nine of which occur on islands, giving highly significant correlated evolution ($P < 1 \times 10^{-6}$). In Lacertoidea (Lacertiformes + Xantusiidae; Fig. 9), too, omnivory is associated with insularity ($P < 1 \times 10^{-6}$), with 12 of 19 gains of omnivory occurring on islands.

For Scincidae (Figs 10 & 11) three gains and one loss of omnivory occurred on islands from the total of six gains and four losses, plus an increase of plant consumption in the insular *Corucia zebrata*. The tree of insular *vs* mainland location was fully resolved using the delayed transformation option of TRACE. For the phylogeny in Fig. 10, omnivory is significantly associated with islands: $P = 0.035$ for three gains and one loss or $P = 0.003$ for four gains and one loss. For the phylogeny in Fig. 11, the corresponding probabilities are $P = 0.039$ and $P = 0.008$.

For all of Scincomorpha (Fig. 9 less the four leftmost and three rightmost branches joined with Fig. 10 or Fig. 11 as the sister taxon Lacertoidea) 15 of 21 gains and one of four losses, for Autarchoglossa (Scincomorpha + Anguimorpha) 16 of 22 gains and one of four losses, and for all of Scleroglossa (Figs 9 & 10 or Fig. 11 inserted as the sister group of Lacertoidea) 17 of 23 gains and only one of five losses occurred on islands. For each of these groups the evolution of omnivory or herbivory is strongly associated with insularity ($P < 1 \times 10^{-6}$). Because data for skinks are sparse in some groups containing both omnivores and carnivores (e.g. *Ctenotus*, *Egernia*), the relationship between omnivory and insularity in Scleroglossa minus Scincoidea (14 of 17 gains and no losses of omnivory occurred on islands) was examined. The evidence for correlated evolution between insularity and plant diet in this group remains strong ($P < 1 \times 10^{-6}$).

Hypotheses explaining the association between plant consumption and insularity in lizards remain untested, but there is some empirical evidence consistent with a role of reduced prey availability. On islets in the Balearic Islands, the omnivorous *Podarcis lilfordi* increases plant consumption during times of prey scarcity (Pérez-Mellado & Corti, 1993). Increased plant consumption during prey scarcity is by no means restricted to islands (Fuentes & Di Castri, 1975; Schluter, 1984). Data on the relative frequencies of seasonal prey scarcity in insular and mainland habitats would be useful for evaluating the prey availability hypothesis.

Aridity

Numerous carnivorous lizards live in arid environments. We suspect that aridity may promote plant consumption because of chronic, seasonal, or unpredictable, yet frequent, scarcity of animal foods, but are unable to demonstrate an effect of aridity independent of insularity. Some of the origins that we counted as being on islands occurred on arid islands, confounding effects of aridity and insularity. Another complication is that availability of plants may differ among deserts. Lack of quantitative data on the degree of aridity would make an analysis subjective.

Circumstantial evidence suggests the importance of aridity. Some island habitats occupied by omnivorous lizards are arid, e.g. *Gallotia simonyi* on El Hierro; iguanids and *Homolophus pacificus* in the Galapagos. Beach habitats occupied by some *Leiocephalus* and *Acanthodactylus erythrurus* are more arid than nearby mainland areas. Omnivory is common in skinks of the genera *Ctenotus*, *Egernia*, and *Tiliqua* and the agamids *Diporiphora winneckei*, *Pogona barbatus*, and *P. minor* that occupy arid regions of Australia. The iguanid genera *Dipsosaurus*, *Ctenosaura*, and *Sauromalus* also occupy arid habitats. Most iguanids other than *Iguana* occupy islands or arid mainland habitats. In North America the only phrynosomatid omnivores are several species of dune-dwelling *Uma* and two species of *Sceloporus* in arid North America (Ballinger *et al*., 1977; Barbault *et al*., 1985; Búrquez *et al*., 1986). Extreme aridity is may account for high plant consumption by *Meroles anchietae* (Robinson & Cunningham, 1978; Murray & Schramm, 1987) and *Angolosaurus skoogi* (Pietruszka *et al*., 1986) in deserts of southern Africa. The skinks *Eumeces schneideri* and *Scincus* sp. are omnivores that occupy very arid regions of North Africa and the Arabian Peninsula, as does the herbivorous *Uromastyx*.

There are many counter-examples of omnivory in species that occupy mesic habitats, such as some tropidurids, basilisks, *Polychrus acutirostris*, *Tupinambis rufescens*, and *Varanus olivaceus*. A likely explanation for occurrence of some tropical omnivores in mesic settings is that flowers, fruits, and other digestible plant parts may be abundant through most of the year, making them a reliable food source.

Prey availability

If reduced prey availability is a major factor, omnivory should be associated with several factors that lead to chronic, seasonal, or otherwise frequent low prey density. Three such factors are insularity, aridity, and occupation of cave habitats containing few prey. Their combined effects were examined in Lacertidae and Lacertoidea by conducting concentrated changes tests for correlated evolution between omnivory and presecence of any combination of insularity, aridity, and cave-dwelling. Besides the insular taxa above, *Lepidophyma smithii* is cavernicolous and *Meroles anchietae* and *Acanthodactylus erythrurus* 2 occupy very arid habitats. The relationship in other groups was not tested because of the lack of good data on aridity.

In Lacertidae, nine transitions occurred from mainland to islands or to increased aridity and one transition from an island to mainland. Ten of the 11 gains in omnivory occurred on islands (eight) or in arid circumstances (two – *Meroles anchietae* and *Acanthodactylus erythrurus*). There was significant correlated evolution between omnivory and the occupation of insular or arid habitats ($P < 1 \times 10^{-6}$). In Lacertoidea, 11 transitions occurred to either insular or arid habitats, one to a cave habitat, and one from island to mainland. Of 15 gains of omnivory, nine were on islands (10 if the increased plant consumption in the presumed *Cnemidophorus murinus–C. arubensis* clade had been counted as an origin), two were in arid habitats, and one was in a cave (*Lepidophyma smithii*). Thus, 12 and possibly 13 of 15 gains occurred in circumstances in which prey availability is probably reduced. There has been significant convergent evolution of omnivory and the conditions associated with prey scarcity ($P < 1 \times 10^{-6}$).

Because most origins of omnivory occurred on islands, tests regarding prey availability do not establish the independent importance of aridity or cave-dwelling. Aridity may be important because the island habitats occupied by several of the omnivores are arid or semiarid. Evidence for the importance of limited prey availability is suggestive rather than conclusive because the findings are not independent of insularity or aridity. Nevertheless, factors associated with limited prey availability account for at least 80% of origins of omnivory in Lacertoidea. Omnivory has arisen on the mainland only three times in all Lacertoidea outside caves or arid habitats.

Body size

Plant consumption in lizards was once thought to be closely linked to body size, being found mainly in species with body mass > 300 g, nearly all species < 50–100 g being strict carnivores (Pough, 1973). More extensive data on lizard diets now available include many reports of smaller species eating plants. Nevertheless, a relationship between herbivory and large body size was detected in a sample of lacertid species that included numerous small omnivores (Van Damme, 1999). Van Damme's analysis was not comparable to Pough's (1973) for several other reasons. The range of body sizes was much smaller in the recent study, which might have obscured a size effect, suggesting that effect of body size is robust. Since Van Damme's (1999) study was limited to a single family, size might have a different relationship to plant consumption in other families. Many of the lacertid species considered by Van Damme (1999) to be herbivorous based on a 5% criterion would probably not have been considered so by Pough (1973).

Using our 10% criterion, many of the omnivorous and herbivorous species over a wide taxonomic range are large. For example, the herbivorous iguanids and agamids, the gerrhosaurs, skinks in the genera *Macroscincus*, *Tiliqua*, *Corucia*, and *Egernia*, lacertids in *Gallotia*, and *Varanus olivaceus* are all large. Of the three origins in Lacertoidea not readily attributable to prey scarcity, two occurred in quite large species: *Lacerta lepida* and *Tupinambis rufescens* are up to 260 mm and over 400 mm snout–vent length, respectively (Avila-Pires, 1995; Barbadillo *et al*., 1999). Nevertheless, many omnivores are small, and some carnivores are large.

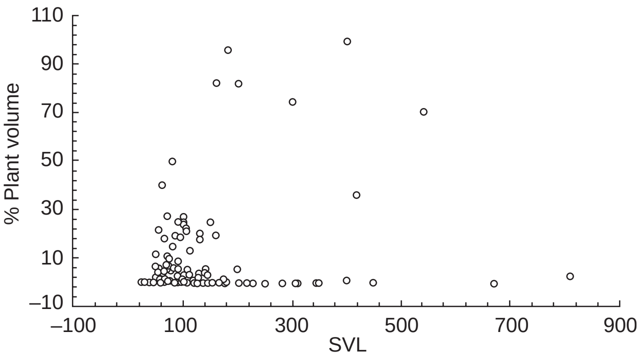

Fig. 12. Relationships between body size and percentage volume of plant material in the diet for lizard species.

The percentage plant volume in the diet increases significantly with SVL (% plant volume = 0.301 SVL + 0.054, $r = 0.30$; F = 23.75; d.f. = 1, 238; $P = 2 \times 10^{-6}$; Fig. 12). The intercept was not significantly different from zero ($t = 0.05$, d.f. = 238, $P > 0.10$). The correlation is not very high, indicating that the degree of plant intake is not a strong determinant of body size (or vice versa) for lizards as a whole. This is hardly surprising as there is considerable variation in the degree of plant consumption throughout much of the size range of lizards (Fig. 12) and among lizards of similar size within families. Another factor that lessens that correlation is inclusion of a number of large carnivorous lizards (e.g. numerous anguimorphans) and several legless elongated carnivores such as the huge *Amphisbaena alba* (810 mm) and pygopodids, and the absence of data on the omnivorous *Varanus olivaceus*, gerrhosaurs, and several other large omnivores, and inclusion of data on only two iguanid species. Plant consumption should not be expected to account for a high proportion of variation in body size among lizards because the evolution of body size is complex, undoubtedly being affected by multiple factors, including phylogeny, sexual selection, fecundity selection, competition, and predation.

Degree of plant consumption is correlated with body size when each species is considered to provide an independent data point, but this correlation does not establish an evolutionary relationship. From our full dietary data set, we were able to determine body size changes associated with 32 or possibly 33 transitions in plant consumption (Table 4). In Iguania there were six or seven increases in body size associated with gains of omnivory, one in Iguanidae, two in Phrynosomatidae, one each in Polychrotidae and Corytophanidae, and one or two in Agamidae using Moody's (1980) or Honda *et al*.'s (2000*a*) phylogeny, respectively. Igua-

Table 4. Body size changes in relation to transitions of plant consumption. Transitions in diet: P, gains of omnivory or herbivory; L, losses of plant diet. Transitions in body size: +, increase in size; –, decrease in size. SVL, snout–vent length (mm); NC, no change in size. Sources are given for phylogenetic relationships and size

Taxon	Transition		SVL	Comparison taxon	SVL	Sources
	Diet	Size				
Iguania						
Agamidae						
Uromastyx and	P	+	250,	Chamaeleonidae	< 200^{a}	Moody, 1980; Hillenius, 1986; Glaw & Vences, 1994 Schleich *et al*., 1996; Rogner, 1997*a*
Hydrosaurus			> 300			
or *Uromastyx*	P	+	250	*Leiolepis*	200	Smith, 1935; Schleich *et al*., 1996; Honda *et al*., 2000*a*
Hydrosaurus	P	+	> 300	*Physignathus*	200	Cogger, 1992; Schleich *et al*., 1996; Honda *et al*., 2000*a*
Lophognathus longirostris	L	–	100	*Pogona*, *Chlamydosaurus*	250 220	Moody, 1980; Cogger, 1992
Iguanidae	P	+	> 140	Liolaeminae	< 121	Stebbins, 1985; Cei, 1986, 1993; Macey *et al*., 1997
Phrynosomatidae						
Sceloporus poinsettii	P	+	130	Related congeners	< 125^{b}	Stebbins, 1985; Conant & Collins, 1991; Wiens & Reeder, 1997
Uma inornata and *U. scoparia*	P	+	> 100	Other sand lizards	< 100	Stebbins, 1985; Conant & Collins, 1991
Polychrotidae						
Polychrus acutirostris	P	+	150	*Anolis* (several possible)	< 130	Schwartz & Henderson, 1991; Avila-Pires, 1995; Losos, 1995; Jackman *et al*., 2000
Corytophanidae						
Basiliscus vittatus	P	+	170	*Corytophanes cristatus*	125	Campbell, 1998
Leiocephalinae						
Leiocephalus greenwayi	L	–	75	*L. punctatus*, *L. carinatus*	80 130	Schwartz & Henderson, 1991; Pregill, 1992
L. schreibersi	L	+	107	*L. loxogrammus*, *L. inaguae*	90 90	Schwartz & Henderson, 1991; Pregill, 1992
Scleroglossa						
Gekkonidae						
Rhacodactylus sp.	P	+	120–220	*Naultinus grayi*	87^{MD}	Mertens, 1964; Bauer, 1985, 1990; Whitaker, 1987; Cree, 1994
Bavayia sauvagei	L	–	59^{c}	*Rhacodactylus auriculatus*	120^{c}	Bauer & Devaney, 1987; Bauer, 1990
Lacertidae						
Acanthodactylus erythrurus	P	+	56	Conspecific insectovires	56	Van Damme, 1999
Gallotia simonyi	P	+	> 240	*Psammodromus algirus*	93	Barbadillo *et al*., 1999
Lacerta bedriagae	P	NC?	80	*L. horvathi*, *L. monticola*	65 80	Van Damme, 1999
L. dugesii	P	+	> 60	*L. perspicillata*	60	Crisp *et al*., 1979; Sadek, 1981; Van Damme, 1999
L. lepida	P	+	260	Congeners	< 120	Barbadillo *et al*., 1999; Van Damme, 1999
Podarcis filofensis	P	+	65	*P. tiliguerta*	*c*. 60	Arnold & Burton, 1978; Van Damme, 1999
P. hispanica (*atrata*)	P	+	74	Conspecific insectivores	70	Van Damme, 1999
P. muralis	P	+	62	Conspecific insectivores	59	Van Damme, 1999
P. lilfordi–*P. pityusensis*	P	+	80–96	*P. tiliguerta*	65	Arnold & Burton, 1978; Van Damme, 1999

Meroles anchietae	P	– or NC	55	*M. reticulatus*,	55	Branch, 1998; Harris *et al*., 1998
				Other congeners	> 55	
Teiidae						
Tupinambis rufescens	P	+	402	*Crocodilurus lacertinus*	218	Presch, 1974; Avila-Pires, 1995
Cnemidophorus murinus	P	+		*C. lemniscatus* –	87–85	Schall, 1974; Wright, 1993; Markezich *et al*., 1997
and *C. arubensis*			103	*C.* sp. (green)		
Scincidae						
Macroscincus coctei	P	+	320	*Mabuya*	< 180	Greer, 1976
Egernia group (ancestor)	P	+	> 150	*Lygosoma*,	< 100	Smith, 1935;
				Mabuya	< 135	Branch, 1998
Cyclodmorphus branchialis	L	–	100	*Corucia*,	350	M. McCoy, 1980; Cogger, 1992
				Tiliqua	> 250	
Egernia striata	L	–	100	Other *Egernia*	115–200	Horton, 1972; Cogger, 1992
E. depressa	L	–	100	Other *Egernia*	115–200	Horton, 1972; Cogger, 1992
Varanidae						
Varanus olivaceus	P	–	454	*V. bengalensis*	750	Auffenberg, 1984, 1988

[a] All but one larger species. The common ancestor was undoubtedly much smaller than 200 mm SVL.

[b] *S. magister* is larger than *S. poinsettii* and eats plants (5.6% of diet).

[c] Mean + 2 SD.

MD, median.

nians decreased in body size when omnivory was lost twice, once each in Tropiduridae (Leiocephalinae) and Agamidae. In one iguanian species, the tropidurid *Leiocephalus schreibersi* body size increased in association with a loss of omnivory. Another possible case, the polychrotid *Anolis evermanni* was not included in the analysis because a size comparison could be made only based on the assumption that Puerto Rican anoles are monophyletic, which recently has been disproven (Jackman *et al*., 1999). For Iguania there are eight or nine transitions that support an evolutionary association between large body size and plant diet and only one transition that does not support it.

In Scleroglossa, 13 increases in body size occurred in conjunction with transitions to omnivory, eight in Lacertidae, two each in Teiidae and Scincidae, and one in Gekkonidae. Body size decreased with loss of omnivory three times in Scincidae and once in Gekkonidae. One lacertid may not have changed size upon acquiring omnivory, and one lacertid and a varanid seem to have decreased in size upon acquiring omnivory. The loss in size by *Varanus olivaceus* is based on its assumed derivation from *V. bengalensis* (Auffenberg, 1994). In summary, for Scleroglossa, 17 changes in body size associated with transitions in degree of plant consumption support an association between large body size and omnivory and two or three transitions do not.

For all lizards, 25 or 26 joint transitions support the hypothesis that increased body size is a consequence of plant consumption and only three or four contradict it. Evolutionary change in plant consumption in Iguania is significantly associated with change in body size as predicted ($P < 0.018$ or $P < 0.010$, depending on whether there were six or seven joint gains in body size and omnivory). In Scleroglossa, the hypothesis is strongly supported. For 17 supporting transitions and three contradictory ones, $P < 0.0011$. If there are only two contradictory transitions, $P = 0.00033$. For all lizards there is a strong tendency for body size to increase upon adoption of omnivory and to decrease when omnivory is lost. The probabilities for corresponding numbers of supporting and contradicting cases are $P < 5.2 \times 10^{-5}$ for 25 supporting and four contradicting cases, $P < 1.4 \times 10^{-5}$ for 25 and three, $P < 3.0 \times 10^{-5}$ for 26 and four, and $P < 7.7 \times 10^{-6}$ for 26 and three cases. Several hypotheses attempt to explain the association of large body size and plant consumption. The weakness hypothesis (Sokol, 1967) can be dismissed for all but the toughest plant parts: even leaves are eaten by small omnivores such as *Uma* (Durtsche, 1995). The idea that large lizards might need to supplement their diets with plants because large prey are scarce (Rand, 1978) seems unlikely to account for the apparent general relationship between size and plant consumption. First, the significant relationships found in our study apply to a wide range of lizard sizes, including many small lizard omnivores. Second, within lizard species, larger individuals continue to eat small prey, but the maximum prey size increases, so that large individuals have a wider range of available prey (e.g. Vitt & Zani, 1996*d*, 1998; Vitt, 2000). Numerous large lizards are fairly strict carnivores, including helodermatids and several varanids (Auffenberg, 1981; Beck, 1990; Beck & Lowe, 1991) that rely in part or entirely on large vertebrate prey, plus large anguids, and the agamid *Chlamydosaurus kingi*. It might be argued instead that large body size is a possible way to expand the diet to energetically rich vertebrate prey. Both animal and plant consumption might contribute to evolution of large body size on islands and other areas in which small animal prey are scarce.

Energetic considerations may be most important. Pough (1973) argued that because the mass-specific metabolic rate is inversely proportional to body mass, small lizards cannot meet their energy requirements by eating plants alone. Because of their much lower energetic requirements per unit body weight, lizards larger than 50–100 g body weight can meet their greater total caloric needs by consuming plants in quantity (Pough, 1973). They also save energy by grazing as opposed to chasing prey (Pough, 1973), and by devoting a shorter time each day to foraging by eating abundant plants than by feeding on scarcer prey (Nagy & Shoemaker, 1984). Similar benefits apply to smaller, omnivorous lizards that increase body size.

The energetic hypothesis may explain further aspects of plant consumption by lizards, as well as apparent exceptions to the size–diet relationship. Pough (1973) suggested that large lizard species may undergo ontogenetic increase in plant consumption because hatchlings are too small to be fully herbivorous. Such ontogenetic changes do not occur in all herbivores, but the greater energetic efficiency of larger individuals may be an important factor for species in which they do.

Two of the transitions that run counter to the size-diet relationship in our study may be explained by energetics. Large lizards may be big enough when omnivory is acquired to receive the full energetic benefit of large size immediately, or even larger. If so, other factors might be more important in determining any changes in body size. That may explain the apparent decrease in body size of *Varanus olivaceus* relative to its ancestor. The energetic efficiency hypothesis (Pough, 1973) may also account for the apparently contradictory *Meroles anchietae*, which is unusual among lizard omnivores in that its primary plant food is seeds. The high energy content of seeds may obviate any energetic advantage of large size for omnivores.

Foraging mode

Most lizards are active foragers that move through the habitat searching for food or ambush foragers that hunt by remaining immobile while waiting for prey to approach them (Huey & Pianka, 1981; Perry, 1995; Cooper & Whiting, 2000). Because actively foraging lizards may search a wide area for prey and closely search certain plants, their foraging for prey might preadapt them for location of plant food in circumstances favouring plant consumption. Plants typically do not come to ambushing lizards. Thus, omnivory would be expected to evolve more frequently in active foragers than in ambushers.

In our data set, all iguanians, all gekkotans except one species of eublepharid gecko, and all cordylids are ambush foragers, of which there were 221 species. Excluding uncertain taxa (Amphisbaenia, Xantusiidae and Xenosauridae), there are 231 species of active foragers. Ten origins of omnivory occurred in ambush foragers and 19 in active foragers. Using the estimated numbers of species in these groups (Zug *et al.*, 2001) and discounting the very low frequencies of ambush foragers in Lacertidae and Scincidae, there are 2204 species of ambush foragers (54.02%) and 1876 of active foragers (45.98%). Active foragers have a significantly greater rate of independent origins of omnivory than ambush foragers ($\chi^2 = 5.92$, d.f. = 1, $P < 0.02$, one-tailed).

A concentrated changes test would be desirable, but rarity of changes in foraging mode and low frequency of dietary changes make joint changes nearly non-existent, and the distribution of the close association between foraging mode and taxon preclude its effective use.

The greater frequency of origins of omnivory in active than ambush foragers supports the hypothesis of preadaptation of active foragers as wide searches that bring them into contact with many plants. Another factor that might favour the evolution of omnivory in active foragers is that they, but not ambushers, use their chemical senses to identify and locate animal prey (Cooper, 1995, 1997, 2000*a*). The chemosensory sensitivity needed for identification of palatable plants might already exist in active foragers upon adoption of omnivory because of the genetic correlation with chemical discrimination of prey. Frequent tongue-flicking during active foraging would entail contact with plants, facilitating chemical discriminations. To use lingual chemical senses to evaluate potential plant food before seizing it, ambush foragers would have to evolve both frequent tongue-flicking of food before ingestion and perhaps greater discriminatory capacities.

Nevertheless, ambush foraging is not a great obstacle to the evolution of omnivory. When conditions, whether related to food density, competition, predation, or other factors, favour omnivory, movements of ambush foragers in contexts other than foraging, such as patrolling territories, could bring them into enough contact with plants to permit their initial incorporation into the diet. Movement of falling fruits, flowers, or leaves might elicit feeding responses by ambushing lizards. Once ambush foragers incorporate plants into the diet, they evolve use of plant chemical discriminations to identify plant food and perhaps assess its nutritional quality (Cooper & Alberts, 1990; Cooper, 2000*b*,*c*). An untested corollary of the pre-adaptation hypothesis is that omnivores derived from ambush foragers either evolve increased rates of foraging movements to move them between food plants or feed on such concentrated food sources that they can move little once a source has been located. *Dipsosaurus dorsalis* may move long distances between plants to find food, but then graze for a time with little movement on individual plants of species such as *Dalea emoryi* in full bloom (W. E. Cooper, pers. obs.).

SCENARIO FOR THE EVOLUTION OF HERBIVORY

Some degree of plant consumption must frequently evolve from strict carnivory in lizards given that no plants were detected in the diets of nearly half of lizard species. Many carnivores may occasionally supplement their diet by eating easily digested, nutritious plant products such as fruit, flowers, and nectar. During periods of flowering and ripening of fruits, these foods may be abundant, although often only briefly. Insectivorous lizards might be attracted to insects that are in turn attracted by flowers and fruits. If prey are so scarce that lizards are in negative energy balance, eating plants might allow them to reduce net energetic loss or even attain positive energetic balance. Plants might also be consumed for the specific nutrients that they contain or for their high concentrations of broader types of nutrients, such as sugars in fruits and nectar.

In strict carnivores or those that infrequently eat plants, frequent prey scarcity might lead to greater reliance on plants. Omnivory may evolve if prey are usually scarce, are abundant at times, but are reliably scarce seasonally, or if prey are frequently, but unpredictably, scarce when food plants are abundant. The percentage of total dietary volume that is plant material presumably depends jointly on the degree of prey scarcity and the abundance and quality of local plants.

Most herbivorous lizards are folivores, eating large amounts of mature leaves, but most also consume other plant parts. Even some small omnivores such as *Uma* sp. (Durtsche, 1995; Gadsden & Palacios-Orona, 1997) eat many small leaves that are more nutritious and digestible than the large, tough, mature leaves eaten by folivorous herbivores. By selecting small and immature leaves, many such omnivores might obtain some nutritional benefits from leaves, but not enough from mature leaves for them to be the primary or even a major dietary item.

Consumption of some leaves, even immature ones, could be a necessary precursor to the evolution of herbivory dominated by folivory. Among individuals that eat some leaves, natural selection would favour those best able to consume and digest them. Eating immature leaves may favour the acquisition of intestinal flora and a morphology for the digestion of cellulose, and dentition for biting or crushing leaves, making possible inclusion of mature leaves in the diet. Transitions to folivory probably occur only in species that already rely mainly on plants, and especially leaves, for nourishment. The major benefit of folivory is presumably access to a stable, abundant food source. Folivores are much less dependent on flowers and fruit that in most habitats vary greatly in abundance seasonally. Algivory in *Amblyrhynchus cristatus* (Nagy & Shoemaker, 1984) presumably was derived after and made possible by the typical iguanid adaptations for folivory, allowing herbivores to escape a food limitation in a terrestrial setting with scarce vegetation by using an abundant marine food resource.

Morphological and physiological traits related to processing plants show evolutionary changes related to the degree of plant consumption and the types of plants eaten. Certain features of tooth structure are associated with herbivory (Hotton, 1955; Montanucci, 1968; Throckmorton, 1976). Comparative study of dental morphology in relation to the amounts and types of plants eaten would be valuable in reconstructing the evolution of omnivory and herbivory. Some herbivores have exceptionally great bite strength, which may aid in biting pieces from leaves or other plant parts (Herrel, Aerts & De Vree, 1998). Comparative studies of the functional morphology of ingestion in relation to degree of omnivory might also be revealing.

The intestines of folivores are enlarged, their colons containing valves not found in other lizards (Henke, 1975; Iverson, 1980). Iverson (1982) found no colic valves in omnivores, which may be a specific adaptation for folivory. The relationship between plant consumption and intestinal length relative to body size has not been studied comparatively, but omnivorous teiids have longer intestines than carnivorous teiids (Dearing, 1993), suggesting that intestinal length may increase with an increased percentage of plant consumption. A detailed examination of regional digestive morphology and histology might uncover variation related to the degree of omnivory.

Intestinal flora permitting cellulose digestion have been studied primarily in iguanids (McBee & McBee, 1982), but also have been demonstrated in the agamid herbivore *Uromastyx aegyptius*, in which microbial fermentation contributes much of the energy budget (Foley *et al*., 1992). They are likely to be present in other herbivores such as *Hydrosaurus*, *Corucia*, and other species of *Uromastyx*, but this has not been studied. Our scenario suggests that such flora might occur in smaller omnivores or herbivores such as *Uma* and *Phymaturus* that eat substantial amounts of leaves. Colic valves and intestinal flora to aid cellulose digestion may have allowed lizards that were omnivorous to become strict herbivores by adding leaves to the diet.

Our knowledge of plant consumption by lizards remains rudimentary in some respects, but this review has been beneficial. It has yielded reasonably accurate summaries of the frequency and degree of plant consumption and major aspects of its historical evolution, while identifying taxonomic groups that have been inadequately studied and implying key taxa that should be studied to improve our estimates of independent origins and losses. It has also enabled us to give more informed assessments of the types of plant parts eaten in relation to proportional importance of dietary plants and of the occurrence of ontogenetic change in plant consumption. Confirmation of the relationships of plant consumption to large body size and insularity, and support for the hypothesis that prey scarcity favours the evolution of plant consumption, extend our previous knowledge. The effect of foraging mode on the frequency of evolution of omnivory is a new finding. It is our hope that the availability of this dietary information will stimulate research on omnivory and herbivory in lizards.

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