

ADAPTATIONS TO HERBIVORY IN IGUANINE LIZARDS

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Introduction

Totally herbivorous lizards are found in three disjunct regions: (1) the New World tropics northward into the Mojave Desert of the SW United States (all the Iguaninae but two species), (2) the Near and Middle East from North Africa to Southwest Asia (spiny tailed agamids *Uromastyx*); and (3) the tropical Far East in the Fiji Islands (the banded iguanas *Brachylophus*), the Philippines and Indonesia (water lizards *Hydrosaurus*), and the Solomon Islands (giant skinks *Corucia*). They are found on islands as well as continents, in predator-filled to nearly predator-free environments, in xeric (most), mesic, and hydric habitats, and they include both oviparous and viviparous (only *Corucia*) forms.

These lizards are generally considered to be unspecialized in comparison to more obviously specialized lizard groups such as the Teiidae, Chamaeleonidae, Varanidae, Anguinae, and Helodermatidae. However, I believe that these herbivorous lizards, in particular the iguanines, are much more specialized than is generally realized.

Perhaps the most unique characteristic of the lizards of the sub-family Iguaninae is their success at herbivorousness. Unfortunately, complete, reliable data on diet and feeding habits for most of the iguanines are not available; most of the published information is only anecdotal, and, in some cases (see below), clearly misleading. Intrigued by my observations that the ground iguana, *Cyclura carinata*, is almost totally herbivorous from hatching through adulthood (a weight range of 15 to 1900 g), I began examining lizard herbivory in terms of diet, feeding habits, feeding strategies, and adaptational correlates (both morphological and physiological). By looking simultaneously at all of these aspects of her-

bivory, I hoped to better understand the mechanisms involved in its evolution in lizards.

Diet

One of the problems inherent to discussions of herbivory lies with the definition of "herbivorous." Many workers have called lizards herbivorous based only on a few records of plant food in their diets. In reality each species probably lies somewhere along a carnivory-omnivory-herbivory continuum, and may even fluctuate along that continuum depending on such factors as season, size or resource availability. For purposes of this discussion I consider as "truly herbivorous" (i.e., on the far right of the continuum) only those species whose diets include essentially only vegetation (whether fruits, flowers, seeds or foliage) throughout the year.

Many species generally called "herbivorous" are probably facultative herbivores at best, and more likely, simple omnivores. Based on the literature and my own dissections of several hundred lizard species, such forms as *Anolis equestris*, *Basiliscus* spp., *Agama* spp., *Physignathus leseuri*, *Angolosaurus skoogi*, *Gerrhosaurus* spp., *Egernia* spp., *Phymaturus* spp., *Tiliqua* spp., *Macroscincus coctei*, and *Trachydosaurus rugosus*, although often termed herbivorous in the literature, are clearly not true herbivores. In fact, by my definition, the only totally herbivorous extant lizards are the iguanines ± 30 species; but see below) among the Iguanidae; the genera *Uromastyx* and *Hydrosaurus* among the Agamidae (ca 17 species); and *Corucia zebrata* in the Scincidae.

I also found no basis for earlier speculations that the iguanines *Amblyrhynchus cristatus*, *Cyclura nubila*, *Iguana*, and *Dipsosaurus dorsalis*,

and the agamid *Uromastix hardwicki* exhibit an ontogenetic shift from carnivory to herbivory. Most of these suggestions were based: (1) on diet information from captive lizards, or (2) on anecdotal field observations. In fact, of all the true herbivores I have dissected, only the iguane *Ctenosaura similis* showed any indication of an omnivorous juvenile diet. Further field study will be necessary to establish quantitatively the extent of this omnivory by size and season. I thus conclude that an ontogenetic shift from carnivory to herbivory is not usual in lizards truly herbivorous as adults, and further, that the documentation of such a transition (as appears to be the case for *C. similis*) will at best be the very rare exception rather than the rule.

Surprisingly few data are available on the specific diets of most herbivorous lizards. Most of the attention has been directed to species in the American southwest, the desert iguana (*Dipsosaurus dorsalis*) and the chuckwalla (*Sauromalus obesus*), with some consideration given to the Neotropical *Iguana*. Although some authorities provide significant lists of plant foods (21 plant species for *Dipsosaurus dorsalis*; 22 species for *Sauromalus obesus*), most references refer to but a few of the plant species eaten, and rarely categorize them by plant part. Thus the true diversity of diet in these lizards is generally unappreciated. For example, it has recently been shown that *Cyclura carinata* includes at least 58 plant species in its diet; *Cyclura cornuta stejnegeri*, at least 71 species; *Sauromalus varius*, about 60 genera; and *Uromastix acanthinurus*, at least 45 species. These high diversities imply that foraging strategies in these lizards are probably much more complex than generally realized.

Feeding Ecology

Other than Auffenberg's work, studies of the ecological aspects of feeding in herbivorous lizards have received little attention. However, it is known that herbivorous lizards spend the majority of their activity cycle resting, not feeding or foraging as do most carnivorous lizards or mammalian herbivores. It apparently takes very little time to fill the digestive tract, especially in relation to normal total food passage time (96+

hours). Moberly estimated that *Iguana* spends 90% of its time resting, and Beverly Dugan (personal communication) estimated that the same species spent 96% of the day inactive and only 1% feeding. Auffenberg has calculated that *Cyclura carinata* spends only 18% of its daily activity period on a typical summer day actually involved in feeding and/or foraging behavior; and others have commented on the reduced time spent feeding by *Dipsosaurus dorsalis*, *Sauromalus obesus* and *Uromastix acanthinurus*, respectively. Several herbivorous lizard species also inhabit regions temperate enough to necessitate the suspension of activity for the winter months: *Dipsosaurus dorsalis*, *Sauromalus obesus*, and *Uromastix acanthinurus*. Yet although no feces may be produced and the rest of the gastrointestinal tract may be empty, the proximal colon apparently always contains digesta.

Another neglected aspect of the feeding ecology of herbivorous lizards concerns food limitation. Despite the apparent abundance of plant food, availability of food resources may be the primary limiting factor for populations of many iguane lizard species. For example, in Colombia, Mueller has shown that green iguanas inhabiting strongly seasonal habitats are smaller than those in less seasonal habitats. Similarly, Case has shown that chuckwallas, *Sauromalus obesus*, grow faster and larger in habitats with more diverse and more abundant food resources. Nagy and Case have even documented cessation of reproduction in adult *Sauromalus* in harsh years. *Cyclura carinata* unquestionably grew faster and increased its fecundity in captivity with unlimited food. *Dipsosaurus dorsalis* likewise grew faster with unlimited food in captivity than it did in the field. Insufficient food resources (in quantity and/or quality or availability and/or useability) appear to impose restraints on growth and fecundity in these lizards.

Rand has suggested that food may be limiting to *Iguana iguana* in highly seasonal tropical habitats only during part of the year. During the winter, food resources for *Cyclura carinata* are not only restricted to items more difficult to digest (primarily leaves) and of lower caloric content

than at other times of the year, but environmental temperatures may also physiologically limit the effectiveness (efficiency?) of the lizard's use of those resources which are available. Further, even during times of maximum primary productivity, i.e., times when high quality foods (e.g., fruits) are most abundant, lizards can only eat and assimilate as much as their digestive machinery can process. Because of their low relative metabolic rates and daily fluctuations in body temperatures, this machinery may well limit energy intake even at maximum efficiency. Thus food limitation in individual iguanine lizards (but not populations) may operate via resource useability (or processability) in addition to simple availability. Again we lack the critical ecological and physiological studies to test this hypothesis.

Digestive Physiology

Other physiological aspects of lizard herbivory have received some attention. For example, digestive efficiencies of carnivorous lizards are known to vary typically from 70 to 90% and to exceed significantly those of herbivorous lizards, which normally range from 30 to 70%. But Throckmorton and Hansen, and Sylber, have reported efficiencies high in the carnivore range for the herbivores *Ctenosaura pectinata* fed sweet potato tubers and *Sauromalus varius* fed dandelion flowers, shredded carrot roots and "chick starter." However, those two species, like most herbivorous lizards, probably don't have such easily digestible foods available in nature for most of the year. For example, during at least parts of the year, the herbivorous iguanines *Dipsosaurus dorsalis*, *Cyclura carinata*, and *Iguana iguana* each primarily rely on leaves which are fibrous and presumably difficult to digest. Ingested leaves often pass through the entire gastrointestinal tract of *Cyclura carinata* and *Cyclura cornuta* nearly intact. We badly need data on the relationship of digestive efficiencies to variables such as diet (and age and colon anatomy).

Freeland and Janzen have suggested that the detoxification of plant secondary compounds by herbivores may be metabolically very expensive. Thus herbivorous lizards must either avoid toxic vegetation or expend energy detoxifying plant

compounds. It is therefore not surprising that *Dipsosaurus dorsalis* apparently eats only the flowers of the creosote bush, *Larrea divaricata*, leaving the fruits and leaves. It is noteworthy that *Cyclura cornuta* and *C. carinata* both feed commonly on the fruits and leaves of the manchineel, *Hippomane mancinella*, and the fruits of the poisonwood tree, *Metopium toxiferum*, species which contain strong alkaloids. Specific feeding strategies of herbivorous lizards have not been studied well enough to shed light on the relative importance of plants such as these to lizard nutrition and energetics, but evidence indicates that secondary plant compounds may be among the most important factors determining food preferences in herbivores.

Many aspects of the diet, feeding behavior, and digestive physiology of herbivorous lizards obviously remain to be investigated. The information is especially critical to our understanding of the functional and evolutionary significance of their morphological specializations. Because they number so few among extant lizard species and because their numbers are so rapidly declining it is important that attention be focused on them without delay.

Trophic Adaptations

All true herbivorous lizards, regardless of family, are specialized in that they all share one significant morphological adaptation (and a suite of associated physiological and ecological ones) found in no other living lizards: all have a distinctly enlarged, partitioned colon. All iguanine lizards but *Amblyrhynchus cristatus* possess from one (*Dipsosaurus dorsalis*; Figure 1) to eleven (some *Cyclura cornuta*) transverse valves in the proximal colon (Table 1). Valves are of two kinds, circular (sometimes with sphincter) or semilunar, (Figures 1 and 2) and circular valves (if present) always occur proximally to semilunar valves. Intraspecific variation in the number and type of valves is small, but greater in species with higher modal numbers of valves. There is no significant ontogenetic change in the number or the kind of valves.

The colon of *Amblyrhynchus cristatus* differs from that of other iguanines only in the height of

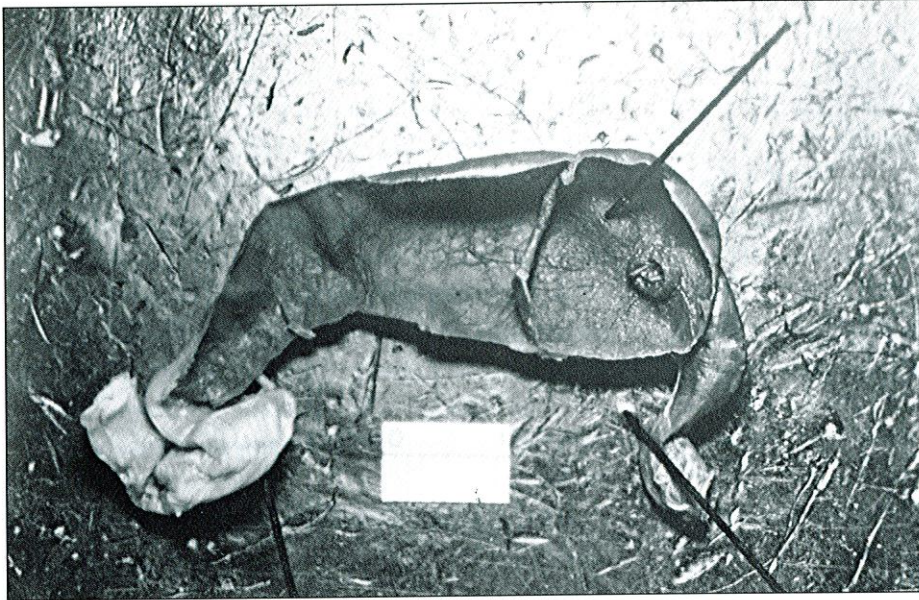


Figure 1. Ventral view of frontal section through the colon of *Dipsosaurus dorsalis* (UF 40726). Note ileocecal valve and singular circular valve. Anterior to right.

Table 1. Modal Number of Colic Valves in Iguanine Lizards with Sample Sizes Greater than Five

Species	% of Total Sample with Modal Condition	Modal Number CV's	Modal Number SLV's	Species Range
<i>Dipsosaurus dorsalis</i>	100	1	0	SW US/NW Mexico
<i>Ctenosaura clarki</i>	88	1 (0-2)	1 (1-2)	Southern Mexico
<i>Ctenosaura quinquecarinatas</i>	100	1	2	SE Mexico to Nicaragua
<i>Ctenosaura palearis</i>	86	1	2 (1-2)	Guatemala
<i>Ctenosaura similis</i>	95	1 (2-4)	2 or 3	Mexico to Panama
<i>Ctenosaura acanthura</i> and <i>C. pectinata</i>	100	1	3	Mexico
<i>Brachylophus fasciatus</i>	100	0	4	Fiji Islands
<i>Cyclura carinata</i>	93	1	4 (4-5)	Turks & Caicos Islands
<i>Iguana iguana</i>	48	1	6 (3-6)	Mexico to South America West Indies
<i>Cyclura cyclura figginsi</i>	43	4 (2-6)	3 (2-6)	Bahamas
<i>Cyclura cornuta</i>	38	3 (3-4)	6 (5-7)	Hispaniola

Ranges appear in parentheses below modes.

CV = circular valves

SLV = semilunar valves

the valves; the infolded tissue layers involved in them are the same. The valves in all iguanines are formed by the infolding of the mucous membrane, the submucosa, and at least the circular (internal) muscular component of the muscularis externa. The serosa is not involved in the valvular structure. The valves may have evolved as simple infoldings (or creases) along with the medial colic all due to the increased bulk of digesta commensurate with an increasingly herbivorous diet and limited abdominal space. I visualize this process as functionally similar to crease formation when rigid tubing is bent.

The variation in colon valve morphology in the iguanines seems to be of little value in phylogenetic comparisons. For example, modal number of valves varies within the genus *Cyclura* from 5 to 9. In addition, as mentioned above, the colon of *Amblyrhynchus* (with only folds, not complete valves) differs internally from all other iguanines, including *Conolophus* (with 1 circular and 4 semilunar valves) to which it is supposedly most closely related. However, because the number, type and size of valves is so constant within a given iguanine species, colon structure is an important taxonomic adjunct. Colons of unknown species can nearly always be allocated at least to genus, based solely on morphology of that organ. In fact, this level of constancy suggests the existence of an undescribed

iguanine taxon in the West Indies. The colon of *Iguana iguana* from the northern Lesser Antilles differs radically from that of the remainder of the species' range. Four total valves were present in each of three individuals from Montserrat and St. Croix, whereas all other specimens examined by me bore five, six (modal), or seven valves. No other iguanine species exhibits such extensive geographic variation. In light of Lazell's comments on the slightly different pattern and scalation characteristics in the same northern Antilles population, a systematic reappraisal seems warranted.

Perhaps the most intriguing thing about iguanine colic variation is the significant linear relationship between number of valves and mean body size for interspecific comparisons (Figure 3). The larger the species, the more complex is the colon (i.e., the more colic compartments present).

Although not as complexly modified, the colon of *Uromastyx* and *Hydrosaurus* is also partitioned: *Uromastyx* proximally and *Hydrosaurus* distally. In being partitioned, the colon of *Corucia* differs radically from all other skinks I have examined (Figure 4), including species of the closely related genera *Egernia* and *Tiliqua*. Thus a partitioned colon has apparently evolved independently at least three times (once in each of the three families) in the Lacertilia. At least in regard to their gastrointestinal tract anatomy, these

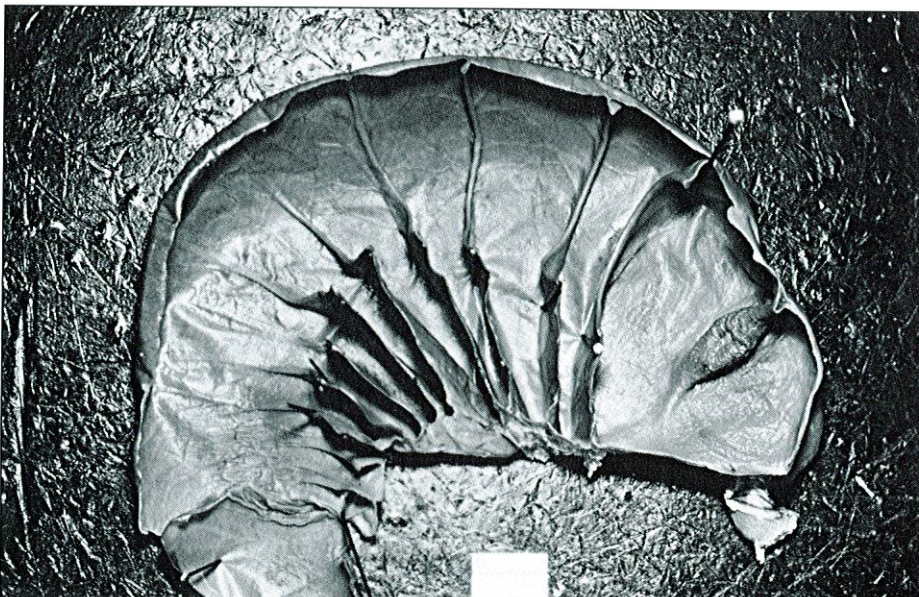


Figure 2.

Ventral view of frontal section through the proximal colon of *Cyclura cornuta* (UF 33554). Note four circular valves (CV's) and seven semilunar valves (SLV's). Anterior to right.

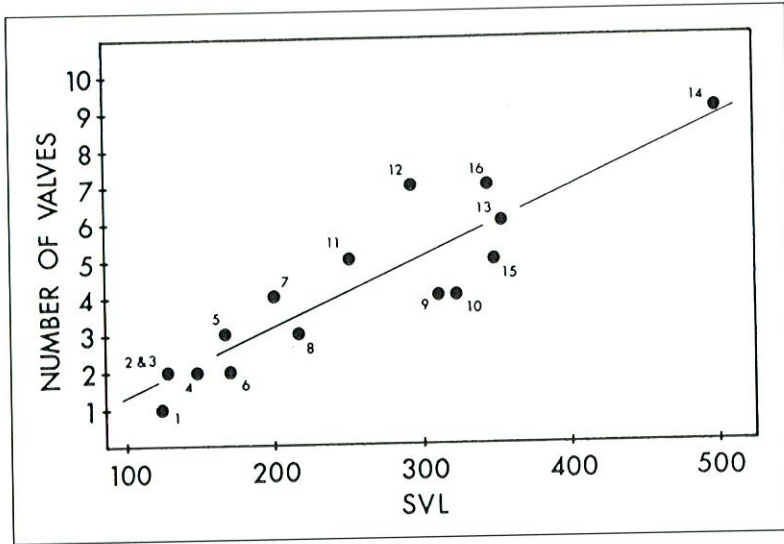


Figure 3. Relationship between modal number of colic valves and body size (mm snout-vent length) for the following iguanine species: *Dipsosaurus dorsalis* (1), *Ctenosaura defensor* (2), *C. quinquecarinatas* (3), *C. clarki* (4), *C. palearis* (5), *Sauromalus obesus* (6), *Brachylophus fasciatus* (7), *Ctenosaura hemilopha* (8), *C. similis* (9), *C. acanthura* (=pectinata) (10), *Cyclura carinata* (11), *C. cyclura* (12), *C. ricordi* (13), *C. cornuta* (14), *Conolophus subscristatus* (15), and *Iguana iguana* (16).

lizards can hardly be considered unspecialized.

Though I have established that all truly herbivorous lizards possess a partitioned colon, I am still uncertain about its functional significance. The partitioned colon surely slows the passage of digesta through the gut, and relative absorptive surface area (for water and nutrients) is certainly increased. But the presence of tremendously dense nematode faunas (and presumably bacterial and protozoan populations) in the normal cecum of all these herbivorous lizards suggests that they provide important microhabitats for colic (cellulytic?) symbionts. For example, McBee and McBee have documented an excess

of 10^{10} bacterial cells or clumps per gram of colic material, and I estimated the population of nematodes in the colon of a single healthy adult *Cyclura carinata* to be in excess of 15,000. Juveniles of *C. carinata* begin accumulating colic nematodes soon after hatching, and worm populations are usually about 100 by age 3 months, continuing to increase with age. These nematodes (families Atractidae and Oxyuridae) have direct life cycles, and eggs are likely ingested during substrate licking, geophagy, or coprophagy—behaviors frequently observed in these lizards. Significantly, these heavy worm burdens are typical of herbiv-

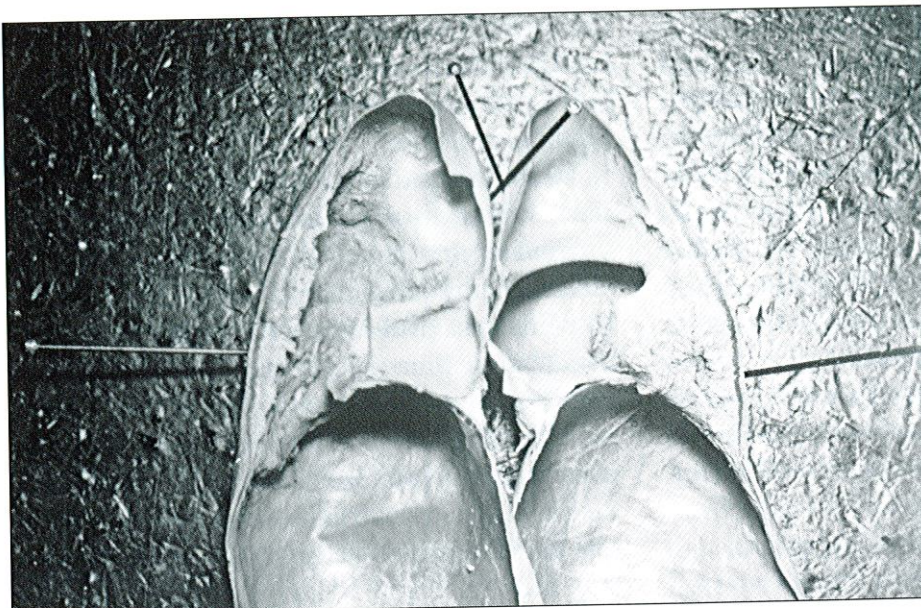


Figure 4. Ventral (right) and dorsal halves of the proximal colon of *Corucia zebrata* (UF 41309). Anterior to top.

orous lizards, whereas such burdens are not found in omnivorous or carnivorous lizards.

The question remains as to just what the relationship is between these organisms and their hosts. Hypothesizing that colic compartmentalization permits the proliferation of nematodes, bacteria, and perhaps protozoa (if by no other means than by reducing the likelihood of egestion due to peristaltic flow of digest), I compared the number of colic nematode species described from each lizard species with the number of colic valves for the 11 best-studied iguanine lizard species (Figure 5). Clearly, increased colic partitioning allows an increase in diversity (and surely abundance) of at least nematodes, and probably bacteria and protozoa as well.

A positive linear correlation is also suggested by a comparison of nematode species richness and mean body length for the ten iguanine species for which data are available. No such relationship for cecal nematodes is identifiable in carnivorous lizards. In fact, larger, carnivorous lizard species often harbor fewer nematode species than smaller lizard species. I would be surprised if colic bacteria and perhaps protozoa did not exhibit these same relationships.

The tremendous nematode densities in healthy lizards suggest they are not parasitic, but rather commensalistic, or perhaps even mutualistic. Potential roles for these nematodes include (1) the simple mixing and mechanical breakdown of vegetation, effectively increasing the surface area of digesta particles; (2) the production of useable waste products (vitamins, cellulase, volatile fatty acids?); and/or (3) the regulation of the composition and/or abundance of colonic microbes (on which some nematodes are known to feed). However, in a study of digestion in the yellow chuckwalla (*Sauromalus varius*), Hansen and Sylber treated their lizards for intestinal worms, assumed none were present, and yet found very high digestibility coefficients for low to mid-fiber diets. This seems to indicate a reduced importance of colonic nematodes, but only if it can be certainly established that the worms were, in fact, eliminated.

The importance of bacteria and protozoa to digestion in other herbivorous organisms (pri-

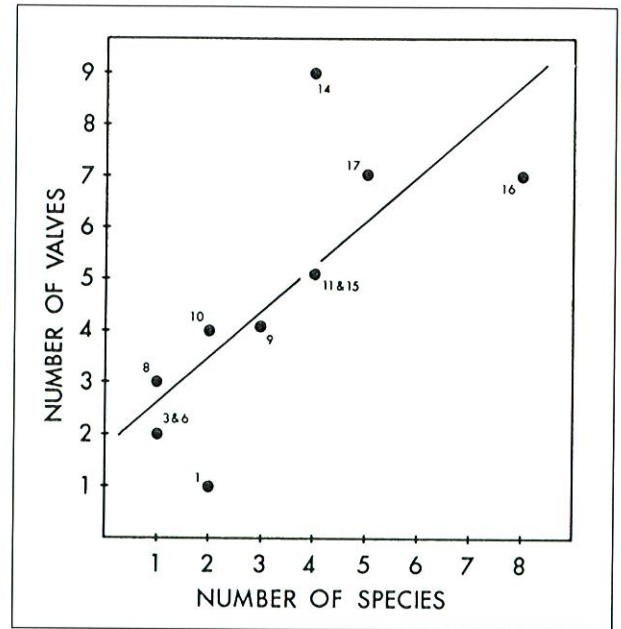


Figure 5. Intestinal nematode species richness versus colic modification (modal number of colic valves) for the 11 best-studied iguanine species. Species are coded as in Figure 3, except *Cyclura nubila* (17).

marily higher vertebrates and insects) is well-established. Their significance in herbivorous reptile digestion should be intuitive, especially since it has recently been established that there is considerable cellulolytic activity in the colon of herbivorous lizards, and also that colic fermentation products (volatile fatty acids) are assimilated by the green iguana, *Iguana iguana* and yellow chuckwalla, *Sauromalus varius* (and even provide at least 15.2% of the daily energy budget in the herbivorous green turtle, *Chelonia mydas*). Thus, hindgut fermentation appears to be very important to the digestive physiology of herbivorous reptiles.

Gastrointestinal tract modification for symbiont culture is also the norm in herbivorous organisms that have previously been studied. Colonic partitioning in herbivorous lizards is thus by no means novel. What is surprising is the lack of attention it has received, especially since it appears to be the one adaptation essential for a lizard's completely herbivorous existence. However, numerous studies now in progress by several investigators are addressing the physiology and biochemistry of herbivory in reptiles.

Body Size

True herbivorous lizards share another obvious character. Excluding the varanids (which are very specialized carnivores), they are the largest extant lizards. This relationship has been frequently mentioned in the literature, and several hypotheses offered to explain the adaptive significance of the correlation between large body size and herbivory. These include the advantage of greater mechanical strength for reducing vegetation for consumption (although there is no mastication); the advantage of reduced predation and competition; the advantage of eating easily obtainable foods of medium to poor quality (i.e., plants) rather than higher quality items (e.g., insects) more energetically costly to obtain (since metabolic rates are relatively lower in large lizards); and the advantage of greater thermal inertia, allowing the maintenance of elevated body temperatures and facilitating the digestion of vegetation. Each of these theories relates selective advantages which no doubt accrue to large, herbivorous lizards, but none appears to fully explain the body size-herbivory relationship in these lizards. I here extend another hypothesis which I think more adequately explains the body size-herbivory correlation and permits speculation on the evolution of these characters in lizards. I believe that the anatomical, physiological, and ecological characteristics of the gastrointestinal tract are the most important determinants, not only of herbivorous capabilities, but also of body size in these lizards.

I have already mentioned here the positive relationship of colic complexity to body size in these lizards, and the presumed benefit of that modified colon to digestion. Previous studies on both lizards and turtles have shown that body size may be significantly related to resource availability. Analogously, I believe that the evolutionary increase in colon complexity has increased resource useability (not necessarily availability!), and thereby energetically permitted increased body size. Thus colon modification (and the diversification and increase in the intestinal flora and fauna), these herbivores have been able to grow to larger sizes, and thus more fully gain other selective advantages, such as reduced predation, metabolic and thermoregulatory benefits.

Discussion

I believe that the iguanines, *Uromastyx*, *Hydrosaurus*, and *Corucia* are much more specialized than generally realized. Each has a relatively large body size and a modified colon with large nematode and microbe populations—a combination of characters unique among the lizards. In addition, although I have not mentioned them, these lizards all possess dentition modified for herbivory and (apparently) nasal salt glands for extrarenal salt secretion. These last two characters are shared by lizards which are not entirely herbivorous, however they nevertheless facilitate an herbivorous existence: teeth for efficient cropping and salt glands for dealing with the increased potassium load.

In summary, the evolution of lizard herbivory probably had its roots in xeric habitats (evidenced by the significant inverse correlation between percentage of lizards exhibiting at least some herbivory and annual rainfall in North American communities). In order to inhabit those areas, lizards would have been faced with: (1) problems of ionic balance (regardless of their diets), and (2) seasonal difficulties in obtaining adequate animal food (probably insects). The evolution of extrarenal nasal salt glands in these lizards would presumably have reduced the osmotic problems, and simultaneously may also have allowed the lizards to utilize small amounts of plant resources during seasonal animal food shortages without being susceptible to additional ionic problems from ingesting potassium rich plant parts. The acquisition by these proto-herbivores of small populations of symbiotic (cellulytic) nematodes and/or bacteria would have even further facilitated the efficient use of ingested vegetation. As the diet of these lizards became more omnivorous, the bulk of the digesta in the gastrointestinal tract would presumably have increased. Among other things, this presumably would have resulted in increased gastrointestinal tract capacity, cramped abdominal space and even medial crimping of intestinal loops where they folded back on themselves. If, as I believe, these crimps (1) slowed the movement of digesta (permitting more time for digestion or absorption), or (2) reduced the likelihood of egestion of gut symbionts by providing

microhabitats for them, selection would have favored their maintenance. Thus evolution of these “protovalves” in conjunction with salt glands and the acquisition of gut symbionts may finally have made it energetically feasible to subsist primarily on vegetation. Both before and (more intensely) after the appearance of these valves, selection would also have been operating on the dentition to permit efficient handling of first an omnivorous, and later an herbivorous diet.

Finally, those species in which the evolution of valves was more rapid, would, because they had more valves and more compartments, also have had more symbionts and hence more efficient food processing. The energy benefit from this apparatus would result in increased body size, the size increase in direct proportion to the efficiency of the gastrointestinal machinery. When measured in terms of number of partitions, this is exactly the relationship that is obtained for the iguanines (Figure 3). Body size increases would, of course, then have imparted additional advantages to these lizards, specifically the ecological, metabolic, and thermoregulatory benefits already mentioned.



This article is condensed and reprinted with permission from a chapter in the book, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, edited by Gordon Burghardt and A. Stanley Rand, and published in 1982 by Noyes Publications. It has recently been reprinted and is now available from IIS (see ad on this page). Although written for a scientific audience, the editors highly recommend it as an exhaustive source of facts about iguana biology.

NOTICE

Iguana Times staff contacted Reptiles magazine publisher, Phillip Samuelson, after running our news account of smuggled, critically endangered San Salvadore iguanas on the cover of their April, 1994 issue. Samuelson assured us they had no knowledge that the animal was contraband previous to running the photo.

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The Green Iguana Manual, by Philippe de Vosjoli. 1992. **\$7.00** (including postage); **\$8.75** (non-members)

Guide to the Identification of the Amphibians and Reptiles of the West Indies (Exclusive of Hispaniola), by Albert Schwartz and Robert Henderson. 1985. **\$19.00** (including postage); **\$27.00** (non-members)

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Adult male, Ricord's Iguana, *Cyclura ricordi*.
Photograph: Jeff Wines