

RESEARCH ARTICLE

Morphologic Characters of Herbivorous Lizards

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Introduction

Many lizards are omnivorous (Sokol 1967), however, only iguanines, two species among the gerrhosaurids and cordylids, and relatively few agamids and scincids have significant morphological specializations for a true herbivorous diet (Pough 1973; Iverson 1982). These herbivorous groups comprise approximately 2% of all lizard species (Zimmerman and Tracy 1989), which inhabit three distinct regions: 1) the neotropics and subtropics into the Mohave Desert of the Southwest United States (all *Iguaninae* except two species), 2) the Near and Middle East from North Africa to Southwest Asia (*Uromastyx*), and 3) the Philippines and Indonesia (*Hydrosaurus*), and the Solomon Islands (*Corucia*). They are found on continents, but more abundantly on islands (Iverson 1982). While they are most commonly found in xeric conditions, they also inhabit mesic and hydric habitats.

Two factors make digestion of plant material more difficult than digestion of animal material: 1) digesting the fibrous portions of the plant material such as cellulose, lignin and pectins, and 2) the need to separate the non-fibrous material from the plant fiber, so digestive enzymes are more effective (Throckmorton 1973). These factors may explain why digestive efficiencies of carnivorous lizards are known to vary from 70–90%, while herbivorous lizards normally range from 30–70% (Table 1). Throckmorton (1973) and Hansen and Sylber (in Iverson, 1982) have reported higher efficiencies for the herbivorous lizards *Ctenosaura pectinata* and *Sauromalus varius*. However, in the studies, *Ctenosaura* were fed sweet potato tubers, while *Sauromalus* were fed dandelion flowers, shredded carrots and “chick starter.” Iverson (1982) felt that

these two species are not able to obtain such easily digestible foods in nature throughout most of the year. For example, during the non-fruit and flower portions of the year, the herbivorous iguanines *Dipsosaurus dorsalis* (Minnich 1970), *Cyclura carinata* (Iverson 1979), and *Iguana iguana* (Rand 1978) each primarily rely on leaves which are fibrous and difficult to digest. Whole ingested leaves have been observed to pass through the entire gastrointestinal tract of *C. carinata* (Iverson 1979), *C. cornuta stejnegeri* (Wiewandt 1977) and *C. cyclura figginsi* (Knapp, per. obs.). The energy derived from ingested food items is also lower for fibrous plant material. Fibrous plant material contains an energy content of 3,600–4,200 cal/g of dry weight. In contrast, vertebrate animal tissue contains 5,200 cal/g and insects 5,400 cal/g (Golley 1961).

In order to deal with the difficulties of a plant material diet, herbivorous lizards share multiple, analogous characters. The majority of species possess a large body size, modified dentition, nasal glands, and a large population of colic nematodes. Each of these character complexes is considered adaptive in permitting the increased use of plant material for food by lizards. However, all true herbivorous lizards, regardless of family, share one significant morphological adaptation not found in other extant lizards; they all have a distinctly enlarged, partitioned colon (Iverson 1980). Although numerous ecological adaptations, such as search patterns and repetitive browsing, are also associated with lizard herbivory (Auffenberg 1982), this paper will explore the morphological characters that allow these lizards to exploit an abundant, yet difficult to utilize resource.

Table 1. Apparent Digestibility Coefficients (ADC) of lizards, where ADC = (calories consumed – calories of fecal waste) x (100) / calories consumed.

| Species | ADC (in %) | Food | Source |
|---|--------------------|--|---|
| <i>Anolis carolinensis</i> | 54.4 | <i>Tenebrio</i> adults | Licht & Jones 1967 |
| | 88.9 | <i>Tenebrio</i> larvae | |
| | 69.5 | crickets | |
| <i>Dipsosaurus dorsalis</i> | 3070* | natural diets | Minnich 1970 Porter <i>et al.</i> 1973 |
| <i>Sceloporus graciosus</i> and <i>S. occidentalis</i> | 83 | <i>Tenebrio</i> larvae | Mueller 1970 |
| <i>Ctenosaura pectinata</i> | 86.3 (77.894.0) | Sweet potato tubers (<i>Ipomea</i>) | Throckmorton 1971, 1973 |
| <i>Lacerta vivipara</i> | 89 (8491) | <i>Tenebrio</i> larvae | Avery 1971 |
| <i>Anolis carolinensis</i> | 69.972.2 | <i>Tenebrio</i> larvae | Kitchell & Windell 1972 |
| <i>Crotaphytus wislizeni</i> | 77.878 | natural diets | Essghaier & Johnson 1975 |
| <i>Cnemidophorus tigris</i> | 79.8 | | |
| <i>Uta stansburiana</i> | 83.585.8 | | |
| <i>Dipsosaurus dorsalis</i> | 57 | natural vegetation (flowers) | Nagy and Shoemaker 1975 |
| <i>Sauromalus obesus</i> | 56 | natural vegetation | Nagy and Shoemaker 1975 |
| <i>Sceloporus olivaceus</i> | 83.5 | crickets | Dutton <i>et al.</i> 1975 |
| <i>Dipsosaurus dorsalis</i> | 54.3 @ 33°C | commercial | Harlow <i>et al.</i> 1976 |
| | 62.8 @ 37°C | rabbit food | |
| | 69.5 @ 41°C | | |

*Method of calculation of digestive efficiency was not indicated. (Source: Iverson 1979)

Body Size

Of approximately 3,000 extant lizard species, no more than 60 attain an adult body size exceeding one kilogram (Alberts 1994). With the exception of the specialized varanid carnivores, the majority of these large lizards are herbivorous. Several hypotheses have been offered to explain the adaptive significance of this correlation between large body size and herbivory.

One adaptive advantage of a large body size is the increased mechanical strength for reducing vegetation for consumption (Iverson 1982). Also, because mass specific energy requirements decrease with increasing body mass, larger body size may be an adaptation to a diet that is typically

energy deficient. For example, the metabolic rate per gram of a 100 gram lizard is 1/6 that of a 1 gram lizard while a lizard weighing 1 kilogram would have an estimated weight-specific metabolic rate about 1/2 that of a 100 gram lizard (Pough 1973). Similarly, large body size may serve as an energy buffer against a seasonal and fluctuating food supply. Therefore, the mass-specific rate of energy reserve depletion would be lower for larger than for smaller animals (Case 1982).

Larger body size in herbivorous lizards may also be a thermoregulatory adaptation to aid in digestion. Body size of ectotherms influences the rate at which heat is exchanged with the environment. Thus, larger ectotherms are temporally less

responsive to their thermal environment than smaller ectotherms. This causes them to heat and cool more slowly in relation to a fluctuating thermal environment. The high thermal and stable environment in the gut presumably allows gut symbionts to ferment the cell walls of plants more efficiently (Zimmerman and Tracy 1989). For example, greater digestive efficiency at elevated, opposed to reduced, body temperatures have been demonstrated in *I. iguana* (Troyer 1987) and *Sauromalus obesus* (Zimmerman and Tracy 1989). Furthermore, in the lizard *D. dorsalis*, Harlow *et al.* (1976) demonstrated a significant correlation between body temperatures and the proportion of ingested food utilized. At temperatures of 33, 37 and 41°C, apparent digestibility coefficients were 54.3%, 62.8% and 69.5% respectively. Even though *D. dorsalis* is smaller (25-75g) than most herbivorous lizards, it is the most thermophilic of all North American reptiles. Its tolerance of body temperatures exceeds 40°C (Norris 1953). Pough (1973) postulates that few insects are active at these extreme temperatures; therefore, the unique ecological specialization of *D. dorsalis* has forced it into a herbivorous diet, despite its small body size.

Greater digestion efficiencies at elevated temperatures are not, however, restricted to herbivorous lizards. With increasing temperature, Hardwood (1979) reported the increased digestive coefficient in three carnivorous species, and Waldschmidt *et al.* (1986) in one species. Although greater digestive efficiencies at elevated temperatures may not be a unique characteristic among herbivorous lizards, increased body size provides the advantage of greater thermal inertia. This allows the maintenance of elevated body temperatures and facilitates the consistent assimilation of fibrous vegetative material despite fluctuating temperatures. Therefore, excluding the unique ecological situation associated with *D. dorsalis*, large body size may, in part, be a thermoregulatory adaptation co-evolved with an herbivorous feeding strategy (Zimmerman and Tracy 1989).

Szarski (1962) suggested that poor assimilation of plant material reduced the energy herbivorous lizards had available for reproduction, leading to reproductive rates lower than those of carnivorous lizards. Therefore, in order to exploit an herbivorous niche successfully, he hypothesized that lizards require some mechanism, such as a large body size, to reduce predation. He also noted that members

of the genus *Uromastix* have spiny tails for defense while members of the genus *Enyaliosaurus* possess a similar tail used for blocking holes in trees used for refuge. The iguana, *I. iguana*, has a powerful tail for defense and also swims to escape predators. Due to the high temperature niche of *D. dorsalis*, it avoids many predators and competing lizard species, while insular species, such as *Amblyrhynchus cristatus* and *Conolophus subcristatus*, lack natural predators all together as adults.

Lastly, Iverson (1982) hypothesized that the most important determinants for herbivorous capabilities, as well as for body size, are the anatomical, physiological, and ecological characteristics of the gastrointestinal tract. This is due to the positive relationship of colic complexity (i.e. number of valves or folds) to body size observed in herbivorous lizards. Increased colon complexity is thought to allow for increased body size due to the ability to support an increased population of microbes. Refer to Partitioned Colon and Associated Symbionts section for further discussion of this relationship.

Dentition

Ostrom (1963) felt that the loss of the lower temporal arch in modern lizards and the resulting mobility of the quadrate bone prevented the evolution of an efficient plant-grinding mechanism. In the absence of a grinding mechanism, modification of the feeding apparatus of herbivorous lizards is related to the necessity to crop plant material (Throckmorton 1976). In conjunction with large body size for mechanical strength, the most distinctive modification to facilitate this task is the morphology of the marginal dentition.

Hotton (1955) showed that tooth morphology was related to diet in iguanid lizards. Herbivorous iguanines are characterized by an elevated degree of lateral compression and a blade-like multicuspid crown. Species that tend to be more obligatory plant feeders have cusped teeth originating more anteriorly in the tooth row (Hotton 1955). Montanucci (1968) worked with the four iguanid genera and showed that dentition becomes highly modified as the amount of plant material in the diet increases. The iguana, *I. iguana*, the most herbivorous in the group, had all of its teeth cusped and possessed the highest degree of lateral compression.

Throckmorton (1976) demonstrated that different dentitional modifications exist among herbivorous genera, but that the overall apparatus is modified to crop plant material. Herbivorous lizards have a shearing edge of the tooth expanded in the anterior and posterior directions, so that the space between adjacent teeth is reduced. This creates a nearly continuous cutting edge, not found in carnivorous lizards. Carnivorous lizards can only puncture their food. Because of the slanting orientation of the shearing crests relative to the long axis of the jaw, the anterior end of the perforation made by one tooth lies medial to the posterior end of the tooth preceding it. With a thin food item, the upper and lower dentitions will overlap, shearing the material in a scissors-like fashion. If the food item is thick, the perforations allow the food item to be torn with a quick movement of the head.

The applied upper and lower dentitions also produce an anterior force that tends to push the food out of the mouth. To cope with this, all herbivorous lizards possess some type of large, fleshy tongue to aid in food manipulation and stabilization. Additionally, Throckmorton (1976) has demonstrated that different restraining mechanisms are used in the genera *Iguana* and *Uromastix*. In *Iguana*, serrated and pterygoid teeth help stabilize the food, while in *Uromastix*, the retraction of the lower jaw acts to hold the food in position as the teeth shear through it.

Nasal Salt Glands

Several researchers have studied the nasal salt glands of several iguanine species (Schmidt-Nielsen *et al.* 1963; Norris and Dawson 1964; Templeton 1967). Schmidt-Nielsen *et al.* (1963) postulated that the salt glands are a water conserving mechanism. Norris and Dawson (1964) reached similar conclusions while investigating the insular *Sauromalus hispidus*. Both studies reported the presence of potassium in the nasal secretions. Since *S. hispidus* is a desert island inhabitant that eats halophytes, Norris and Dawson believed that this was related to the excess of potassium in the diet. Additionally, nasal secretions of *I. iguana* were apparent so long as the animals received a primarily vegetable diet, even with free access to water (Schmidt-Nielsen 1963). Consequently, Sokol (1967) suggested that a major function of these glands in the iguanines is to regulate the balance between sodium and potassium.

The evolution of extrarenal nasal salt glands in herbivorous lizards would presumably reduce osmotic problems and simultaneously allow the lizards to utilize potassium rich plant parts without being susceptible to ionic problems (Iverson 1982). Templeton (1967) demonstrated that *Ctenosaura pectinata* have the ability to fluctuate the potassium/sodium ratio in the nasal fluid. The capacity of the nasal gland to alter this ratio through its secretion would be valuable in countering the dietary seasonal fluctuations in xeric environments. These factors suggest that the nasal glands may be regarded as an adaptation to herbivory (Sokol 1967).

Partitioned Colon and Associated Symbionts

While general external topography of the gastrointestinal tract of herbivorous iguanids is similar to most carnivorous lizards (Henke in Iverson, 1980), the large intestine is more extensive in herbivorous iguanids than in carnivorous iguanids and agamids (Iverson 1980). Different modifications of a specialized colon have been found in all herbivorous reptiles and are completely lacking in all carnivorous reptiles (Guard 1980). Specifically, all herbivorous lizards in the families *Agamidae*, *Iguanidae* and *Scincidae* possess an enlarged, specialized colon (Iverson 1982).

The marine iguana, *Amblyrhynchus cristatus*, possesses colic folds, the remaining iguanine lizards have from one (*D. dorsalis*) to eleven (*C. cornuta*) transverse valves in the proximal colon. Valves are either circular or semilunar and exhibit little intraspecific variation in the number and types of valves (Iverson 1980). Moreover, in the species that Iverson (1980) examined, he found colic valves to be present at hatching and showed no significant ontogenetic change in the number of valves. He felt that the number, type, and size of valves are so consistent within a given iguanine species, that it is an important taxonomic indicator. Colons of unknown origin can almost always be identified, at least to genus, based purely on morphological features of the organ (Iverson 1980).

Although not completely modified, Iverson (1982) discovered that the colon of *Uromastix*, *Hydrosaurus* and *Corucia* are also partitioned. The partitions are less developed and consist of folds rather than valves. Nevertheless, this indicates that a partitioned colon has evolved independently at

least three times (*Agamidae*, *Iguanidae*, *Scincidae*) in the Lacertilia (Iverson 1982).

The functional significance of a partitioned colon is still not clearly known. The partitioned colon most likely slows down the passage of plant material through the gut, thereby increasing time for digestion and absorption of nutrients to occur (Iverson 1980). The absorptive surface area for water and nutrients is also increased (Zimmerman and Tracy 1989). The most significant advantage that the partitions provide is that they offer important microhabitats for colic symbionts. Populations of worms are typical in herbivorous lizards, but are not found in omnivorous or carnivorous lizards (Bowie 1974). Large quantities of colic nematodes, from the families *Atractidae* and *Oxyuridae*, have been found in *C. carinata* (Iverson 1979), *C. nubila caymanensis* (Knapp, pers. obs.), and other iguanines (Iverson 1980). Nematodes have also been found in the large intestine and partitioned colon of *S. obesus* (Nagy 1977). Bacteria belonging to the genera *Clostridium* and *Leuconostoc*, exceeding 10^{10} bacterial clumps per gram of colic material, have been isolated from the hindgut in *I. iguana* (Troyer 1982). These cellulolytic bacteria are found in the hindguts of a variety of herbivorous reptiles, as well as in the rumen of cattle and sheep (Zimmerman and Tracy 1989).

Herbivorous mammals and reptiles typically obtain part of their energy from the fermentation of plant cell walls, or fibers, by symbiotic populations of microbes (McBee and McBee 1982). During hindgut fermentation in *Iguana*, protein and other digestible nutrients from plant cell contents are broken down and assimilated in the stomach and small intestine. Fiber components are then broken down and the products absorbed in the fermentative portions of the digestive tract (Troyer 1984).

Volatile fatty acids, the end products of anaerobic digestion of carbohydrates, have been demonstrated to appear in the hindgut of *Chelonia mydas* (Bjorndal 1979) and *I. iguana* (Troyer 1984) in quantities comparable to the rumens of mammals. The highest concentrations of the volatile fatty acids in the GI tract of *I. iguana* occur in the partitioned colon (Troyer 1984). Other studies conducted on *I. iguana* revealed that the animal receives energy, in the form of volatile fatty acids, from the hindgut at the rate of 30–40% of their requirements. These percentages are higher than any obtained from hindgut fer-

mentation in birds or rodents (McBee and McBee 1982). Troyer (1984) states that the structure and function of the digestive organs of iguanas, and probably other reptilian herbivores, are similar to those of mammals. This suggests a certain amount of convergence in the possible adaptations for herbivory in vertebrate tetrapods.

Hypothesizing that colic compartmentalization permits the proliferation of nematodes and bacteria, Iverson (1982) compared the number of colic nematode species described from each lizard species (tabulated in Iverson, 1979) with the number of colic valves for the eleven best studied iguanine lizard species. He found a significant linear relationship between the two variables, indicating that increased colic partitioning permits and increases diversity of nematodes (Fig. 1).

Of the colic variations possessed by iguanids, there is a significant linear relationship between number of valves and mean body size for interspecific comparisons (Fig. 2). The larger the species, the more colic compartments are present (Iverson

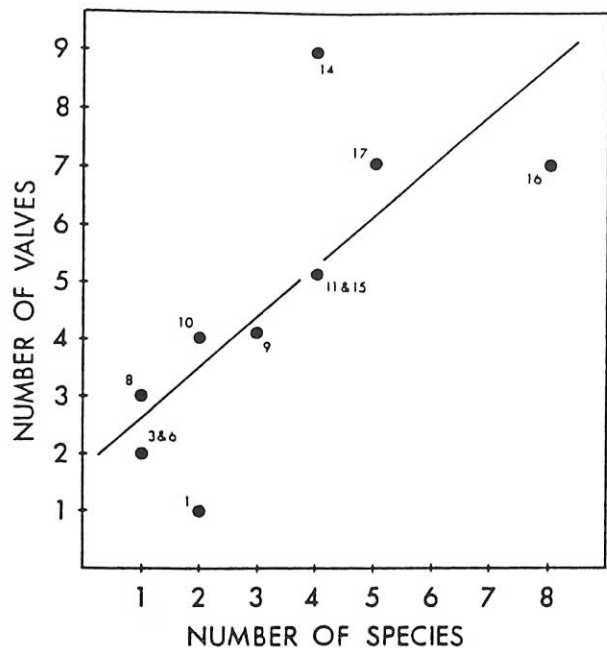


Figure 1. Intestinal nematode species richness versus colic modification for the 11 best-studied iguanine species. Species codes: *Dipsosaurus dorsalis* (1), *Ctenosaura defensor* (3), *Sauromalus obesus* (6), *Ctenosaura hemilopha* (8), *C. similis* (9), *C. pectinata* (10), *Cyclura carinata* (11), *C. cornuta* (14), *Conolophus subcristatus* (15), *Iguana iguana* (16) and *Cyclura nubila* (17). Least square regression is: $y = 0.01895X - 0.6196$; $r = 0.908$; $p < 0.01$. (Source: modified from Iverson 1982)

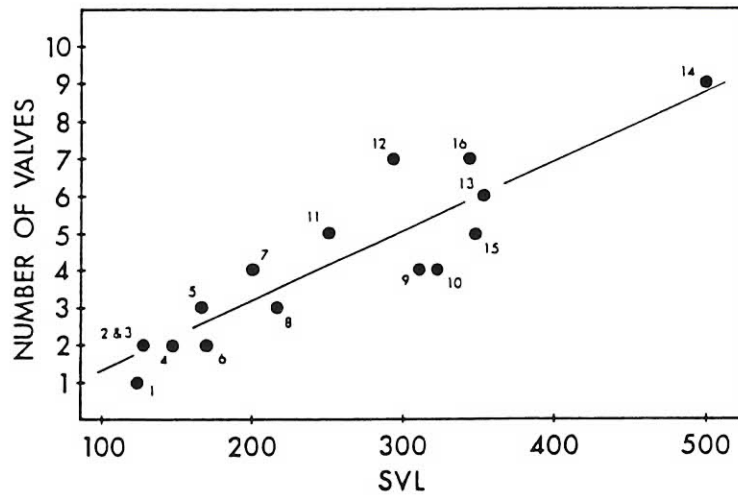


Figure 2. Relationship between modal number of colic valves and body size (mm snout-vent length) for the following iguanine species. Species codes: *Dipsosaurus dorsalis* (1), *Ctenosaura defensor* (2), *C. quinquecarinatus* (3), *C. clarki* (4), *C. palearis* (5), *Sauromalus obesus* (6), *Brachylophus fasciatus* (7), *Ctenosaura hemilopha* (8), *C. similis* (9), *C. pectinata* (10), *Cyclura carinata* (11), *C. cyclura* (12), *C. ricordi* (13), *C. cornuta* (14), *Conolophus subcristatus* (15), *Iguana iguana* (16). Least square regression is: $y = 0.01895X - 0.6196$; $r = 0.908$; $p < 0.01$. (Source: modified from Iverson 1982)

1982). This relationship may have allowed larger body sizes in herbivorous lizards. Previous studies on both lizards (Case 1976) and turtles (Parmenter 1978) have shown that body size may be significantly related to resource availability. Analogously, Iverson (1982) felt that the evolutionary advancement in colon complexity increased resource utilization, not necessarily availability, and thereby energetically permitted increased body size. By modifying their colons, and thus diversifying and augmenting intestinal symbionts, he hypothesized that these herbivores were able to grow to larger sizes, and therefore more fully gain other selected advantages, such as reduced predation, as well as metabolic (Pough 1973), and thermoregulatory (Ellis and Ross 1978) benefits.

Summary and Conclusions

Relatively few lizard species have been able to efficiently exploit a vegetative food source. This is most likely due to the difficulty of digesting plant material and its lower energy derivatives compared to animal tissue. Lizards utilizing plant material share multiple characters such as large body size, modified dentition, nasal glands and a partitioned colon with associated symbionts.

Advantages for a large body include protection from predators and increased mechanical strength for reducing vegetation. A large body size provides a stable internal thermal environment, thereby increasing digestion efficiency. Also, colic complexity and number of gut symbionts increases with larger size. A modified scissors-like dentition allows cropping of vegetation. Nasal salt glands help alleviate an increased potassium load. A parti-

tioned colon slows movement of digesta, allowing more time for digestion or absorption. Colon valves also provide microhabitats for gut symbionts, which assist in food assimilation.

With exception of Iverson's (1980) colon comparison study (51 species, 7 families) and Montanucci's (1968) dentition comparison (4 species, 1 family), the remaining herbivorous lizard studies that I could identify concentrated on one or two species encompassing no more than two families. Detailed comparative studies similar to Iverson (1980), encompassing multiple genera and species, would be useful in discovering exceptions to the general herbivore characteristics. Comparing diets to number of colic valves and species of symbionts would be of interest in order to determine if a correlation exists between specific diet, valve type and number and diversity of microbes. For example, why does *A. cristatus* possess only colic folds, while its closest relative, *C. subcristatus* possesses valves? Are marine algae easier to assimilate, thereby negating the need for colic valves? Additionally, due to its marine existence and algae diet, does *A. cristatus* possess gut symbiont species that differ from those in terrestrial iguanas?

An interesting theory is the speculation (Iverson 1982) that the causal evolutionary factor for large size is the correlation between increased body size and number of colic valves. This leads to the question, what came first, large body size or a partitioned colon? Perhaps the question could be answered by modifying the dentition of a herbivorous lizard. Would it be able to crop vegetation as efficiently? If the lizards failed to effectively feed,

thereby decreasing energy input, perhaps a modified dentition is an evolutionary response for increased body size.

Nevertheless, adaptation to herbivory is an interesting and complex subject, which was overlooked until the late 1970's. In the 1960's, reptilian herbivores were considered primitive. However, recent insights have demonstrated that this is not the case. Hopefully, future investigations will answer additional questions concerning herbivory in lizards.



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