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Iguana delicatissima at Sint Martin Zoo, Lesser Antilles. *Photograph: Janet Fuhri*

Statement of Purpose

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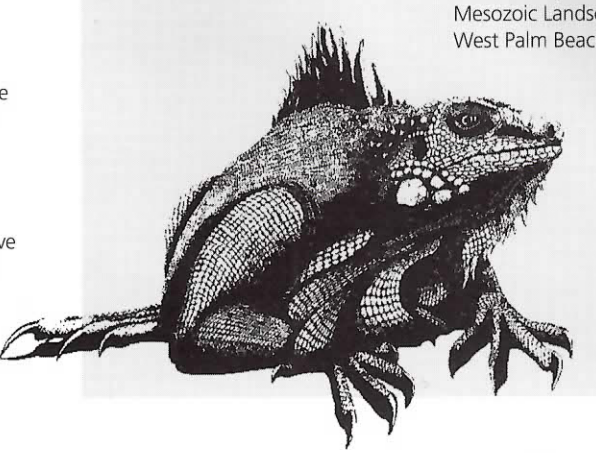


Searching for *Iguana delicatissima*

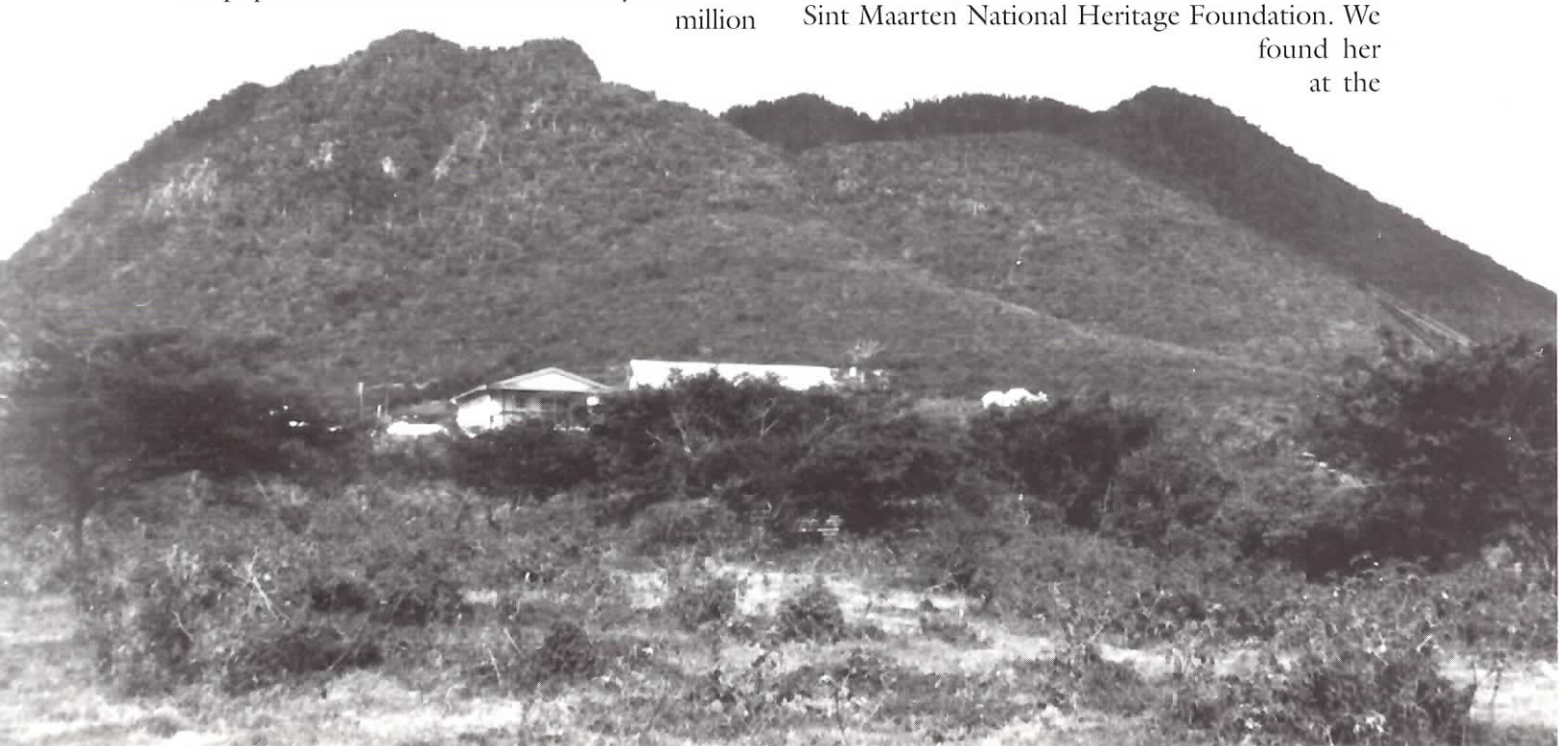
Janet Fuhri

The Lesser Antilles are home to *Iguana delicatissima,* or more accurately the few that have survived the imposition of man and the havoc of natural events. My husband, Carl, and I traveled to Sint Maarten/Saint Martin in July 1997, a trip originally planned as a restful vacation. Prior to leaving home we learned of the Antillean iguana, and with sketchy reports of the proximity of possible habitats to our destination, our restful intent vaporized as excitement and purpose materialized.

Sint Maarten, the Dutch side of the island, was our base during the week long trip. Multiple volcanic peaks form the island, with deep valleys and a surrounding coastline of beaches and rocky precipices. What must have been magnificent and bountiful iguana habitat is now recovering from almost total devastation by Hurricane Luis in 1995. Islanders spoke of a perfectly brown landscape with all mature trees lost. The fate of *Iguana delicatissima* here had been sealed long before the hurricane by overwhelming man-made stressors. The island is a thirty-seven square mile magnet for international tourism, with seventy percent of the population involved in the industry. Over one million travelers visit each year. Traipsing over the hills, valleys, and beaches are free roaming, ubiquitous goats and an impressive army of canines. Mongoose were introduced in the past, effecting a merciless predation on the iguanas.

The French Saint Martin presents as a gentler rolling landscape to the north. Peaks and valleys are stripped of forests to a large extent, providing abundant pastures for a few sleek cattle. Civilization here has left no allowance for cohabitation with iguanas. We spoke with many people of the island, seeking information about the iguanas, to be told repeatedly how good they were to eat and how tourists had come seeking the delicacy in the past, a story we came to dread. Several people, including our first taxi driver, told us of iguanas living around the airport and crossing the outlying road at times. It seems a large crate of iguanas, species undetermined, had been damaged or dropped with many escaping. Our repeated attempts to locate even a hospitable refuge in the area of the airport left us convinced that this tale had been long and often told to embellish island lore.

Sint Maarten was kind to us, however, in the person of Elsje Wilson-Bosch, the president of the Sint Maarten National Heritage Foundation. We found her at the



Sint Maarten Museum in Phillipsburg, where she valiantly crusades to involve local and visiting people in appreciation for the history and historical remnants on the island. Elsje is part archeologist, part curator, and total educator, with a great zeal for preservation of treasure of all sorts. Although flora and fauna are not her first interests, she was drawn in by our enthusiasm for *Iguana delicatissima*. She offered us a bound survey of the local plants and animals written after Hurricane Luis. We were told to peruse this while she finished a discussion with a group of local children. This was a challenge since neither of us speak or read Dutch, the language of the text. We obediently strained to the unfamiliar and were pleased to identify nearby island names and references to iguana populations, albeit rather vague. Elsje then translated for us, confirming our conjecture, and we had the birth of a plan for our search. She was generous with flight and ferry information as well. As an educator, Elsje travels to the surrounding islands for the local governments. We left her museum feeling encouraged and richer for having spent time with her, her enthusiasm matching our own.

The second treasure bestowed on us by the island was our first contact with *Iguana delicatissima* at the Sint Maarten Zoo. She appeared to be a robust, serene female who shared a free form enclosure with a pair of *Iguana iguana*. Her colors were vivid green and yellow. The differences between her and her pen mates were obvious given their close proximity. The most striking was her lack of the subtympanic shield. Other differences included a prominent row of submandibular scales, a full body conformation more reminiscent of *Cyclura*, and the lack of banding on her tail. While Carl shot a roll of film of her, I discovered to my astonishment that my camera was nonfunctional, even with new batteries installed for the trip. This commanded a second trip to the zoo days later with a new camera. On the first trip we had hoped to speak with the zookeepers, but found they were at a conference in New York. Unfortunately, they had not returned by our second visit. This was an opportunity missed, and many questions went unanswered. Without a same species mate, would she breed with *Iguana iguana*? We would hope that an *Iguana delicatissima* mate is planned for the near future.

The following day we travelled by ferry from Marigot, the largest town in French Saint Martin, north to Anguilla, a British territory. Anguilla is a narrow, rather flat island about sixteen miles long. The highest rise is just over two hundred feet. Here we began to discover what a truly valuable asset the taxi drivers of the islands are. All are friendly, and helpfulness seems an integral part of the occupation. We again told our story of the search for their Antillean iguana, and although our driver and his cabby friends were highly amused by our request, he shifted into a thoughtful mode and told us where he knew there had been iguanas when he was a boy. We figured boyhood memories were worth checking into. At one point he dropped us off at a trail leading into a valley with a bat cave. At the beginning of this rather easy trail Carl spotted what he believed was a juvenile iguana and, although it ran and was not to appear again, our hopes were up for more sightings as we walked. As it turned out, for the next eight or so hours we were on the island, that was

Female *Iguana delicatissima* at the Sint Maarten Zoo. *Photograph: Carl Fuhri*

Mt. Scenery, Saba, Lesser Antilles. *Photograph: Janet Fuhri*

our only encounter with an iguana, too brief for identification. Goats, bats, cows, ameivas and anoles, but no more iguanas and no evidence by way of tail drags, shed, or feces even on secluded beaches.

The most remarkable day of the trip was spent traveling to Saba and Sint Eustatius, the islands mentioned in the Dutch survey. We flew to Saba first, landing on a runway much resembling an aircraft carrier with cliffs and crashing waves at either end, an experience that alone was worth the price of the fare.

Saba is the top of a volcano rising 2,854 feet at the highest peak. The island is five square miles and the only road has two main directions, up and down, with a few hairpin turns where absolutely necessary. Again we were blessed with a wonderful taxi driver, measuring up to Elsje in helpfulness with his own brand of enthusiasm for our search. He was sure that he could take us to iguanas, "there's lots of them," Eddie kept repeating. He was able to point out the animals perched on distant high cliffs and determinedly drove up to a cliff where we could approach one from above.

This animal appeared to be an ancient male, nearly all black with red flecks around his mouth. He was quite skeletal, however, his tail did not show signs of atrophy. He slept as we approached, and stirred little as I got close enough to stroke his head. We communed and took photos for about ten minutes until he reached his limit for company. He then leapt over the cliff to observe us from a small cave entrance about twenty-five feet below. Touching and viewing him from above, it was difficult to examine him for the presence of a subtympanic shield.

Although it would have been initially easy to catch him for examination, I refrained in awe, leaving him his dignity.

Another animal was spotted in a ravine. It appeared to be female and was robust in body. She was too distant to distinguish detail, but Carl photographed her with the largest zoom in tow. His slides later revealed a lack of visible banding on the tail. In all we saw seven individuals from the taxi without actually entering habitat. We heard multiple first hand accounts of sightings. Several people told of iguanas curiously entering buildings through open doors. Although Sabans seem to know little about their iguanas, they displayed admirable pride and respect for them. Overall they go unmolested. There are no mongoose on the

island, although goats are present in limited numbers. We found many opportunities to educate islanders about the need to protect their iguanas and they were eager to listen.

Worth mentioning is the panther anole, *Anolis sabanus.* Along our climb into the rainforest on Mount Scenery, we found an abundance of these beautiful creatures. The males are flamboyantly spotted and each was invariably accompanied by a dull colored female.

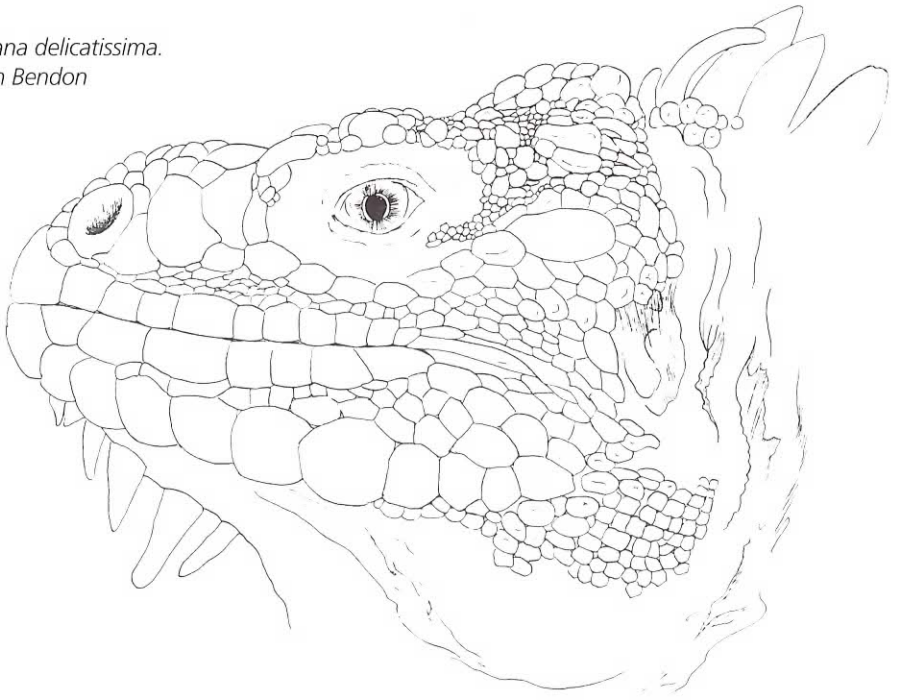
A nearly black iguana on the volcanic island of Saba. *Photograph: Carl Fuhri*

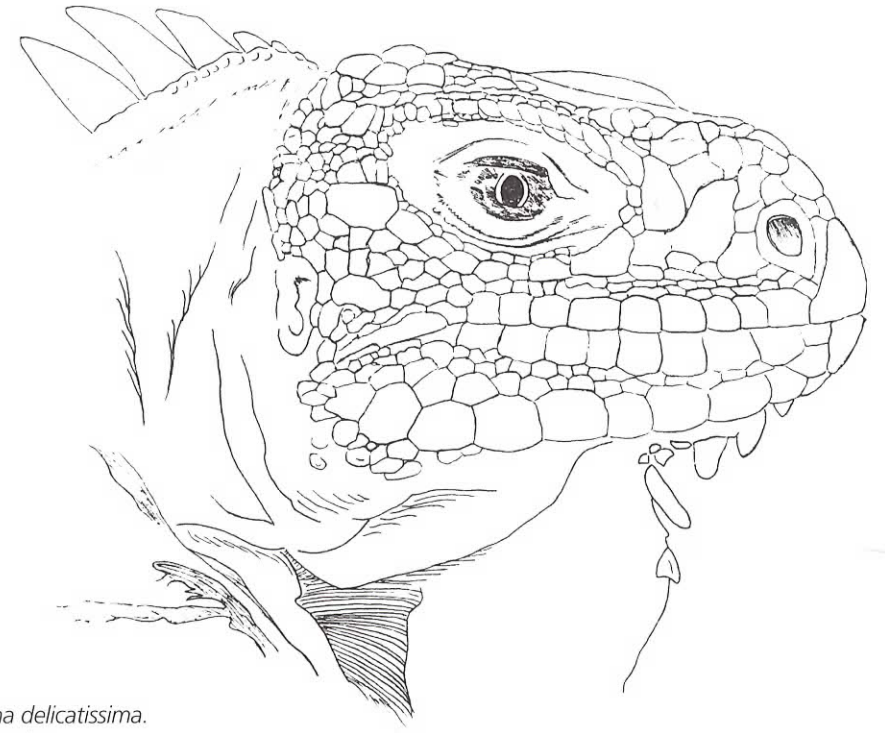
The second half of the day was spent on Saint Eustatius, a ten minute plane ride from Saba. Stacia is roughly twelve square miles. Volcanic peaks dominate the North and South with flat land between, that had once been sugar plantations. We presented our iguana query to our new taxi driver and she told us that although there were iguanas wild on the island, we should visit a woman who had some "preserved" as a guaranteed sighting. After a brief discussion and to our relief we learned that they were captive, not pickled. As promised we found six *Iguana delicatissima* at the Kings Well Resort in Oranjestad. Win and Laura, the resort owners have supplied their wild caught guests of two years with a landscaped enclosure approximately twelve feet by twelve feet, including a small pond in one corner. Within were two obvious adult males, one dominant and robust, the other fearful and thin. Three of the others were females, two adult and one subadult. The sixth animal was also subadult of undetermined gender. The young animals were a glowing yellow green. The adults were much darker and neutrally colored. The most immediate and impressive physical charicteristic was the presence of frontoparietal horn scales, more developed in the males. Although four of the iguanas came readily to us, climbing on our feet, they resisted our touching them.

Panther anolis, *Anolis sabanus,* on Mt. Scenery, Saba. *Photograph: Janet Fuhri*

Their diet consisted of papaya, mango, bananas, and daily fresh hibiscus leaves. They also received a weekly portion of dog food. We found Win and Laura to be very concerned about the wild population, and well aware of the scarcity of the animals. Laura spoke of the yearly hatchling population dwindling rapidly due to local traffic. They also vie for habitat and vegetation with goats and cattle who roam the island, indeed the public streets, at will. Laura and Win are a force for public education on the Antillean iguana. On the way through the town of Oranjestad a small billboard reads "Save Stacias' Treasures" with a painting of the iguana. Unfortunately, Win and Laura have had no success with an iguana breeding program to date. Last year's eggs were disturbed by a hurricane. The World Wildlife Foundation will be sup-

Adult male *Iguana delicatissima*.
Illustration: John Bendon





Adult female *Iguana delicatissima*.
Illustration: John Bendon

porting a marine preserve at Stacia according to Laura and she intends to direct their attention to *Iguana delicatissima*.

Following the visit to the resort, we hiked the Southern vocanic peak known as The Quill with local expert guide, Raphael "Charley" Lopes. Charley is paid by the government as caretaker for the island's many trails. He leads groups to the rim and into the interior rain forest of The Quill with unmatched energy and zeal, sometimes three and four trips a day. We questioned him about finding iguanas along the way and although he assured us there were iguanas in the trees, none were sighted. This left us thankful for the hospitality at King's Well Resort which afforded us our only opportunity on Sint Eustatius to photograph *Iguana delicatissima*. The regular foot traffic on The Quill has no doubt pushed the iguanas back to untrafficked areas of the forest. The woods here are lush, less stripped by man and hurricane than on Sint Maarten. We left the island feeling that here, of all the Antilles, *Iguana delicatissima* may have a decent chance to survive through the diligence of a few, and hopefully the tolerance of many.

We will be travelling back to Saba and Saint Eustatius in the Spring of 1998, planning to intensify our search, giving all of our time to these two islands. Our goals will include determination of species on Saba and finding *Iguana delicatissima* in the wild on Sint Eustatius. In the meantime, I intend to be in communication with the Sint Maarten Zoo and to enlist our Saban friend, Eddie, in photographing the iguanas as they appear along his taxi route. I greatly look forward to our next landing on Saba's cliff runway.

Antillian iguana at the Kings Well Resort, Oranjestad, Sint Eustatius. *Photograph: Carl Fuhri*

RESEARCH ARTICLE

An Overview on the Evolution of the Family Iguanidae

Daniel A. Warner
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Introduction

Lizards are a conspicuous part of the reptile fauna in many parts of the world. Given the wide range of habitats they occupy, one can see how diverse this group has become. Many of these reptiles exhibit interesting morphological characteristics, as well as behavioral and physiological adaptations, which help them survive in their habitats. The family Iguanidae is a group that has sparked my interest because of its many unique traits. This family is confined mainly to the New World and occupies a diverse range of habitats, from deserts to rainforests, and mountains to tropical islands. One species, *Amblyrhynchus cristatus* (marine iguana), is the only lizard that is adapted, both morphologically and physiologically, to swimming in cold water. To help understand the biology of this unusual group of lizards, this paper describes the geographic distribution of the family, various adaptations for survival, and its phylogenetic relationships, as well as hypotheses on the dispersal and evolution of the different taxa.

The former family Iguanidae contained roughly 600 species. Because of its large size and diversity, herpetologists suspected that it was a composite of several different monophyletic groups. Frost and Etheridge (1989) subdivided the former Iguanidae into eight separate families. All lizards that were formerly included in the family Iguanidae plus the families Agamidae and Chamaeleontidae are now included in the infraorder Iguania. This paper deals with the former subfamily Iguaninae, which is now recognized as the family Iguanidae.

Brief Descriptions of the Iguanid Genera

Iguanidae is a group of lizards characterized by large body size and adaptations to herbivory (Iverson 1982). Although the family contains only eight genera with about 35 species, it exhibits diverse characteristics and is distributed throughout the New World and also occurs on some islands in the South Pacific. The individual iguanid genera, which are described below in alphabetical order, have received unequal treatment in the taxonomic literature (summarized in Table 1).

Amblyrhynchus (marine iguana) is native to the Galápagos Islands. This monotypic genus has one of the most unusual diets of all lizards, feeding on marine algae as it dives into cold waters for extended periods of time. Normally the lizard's body temperature would drop and it would become helpless. However, *Amblyrhynchus* has evolved a way to slow its heart rate by about half to limit its peripheral circulation (Mattison 1989). The rate of circulation of the cooled blood near the surface decreases, so heat loss from the body core is considerably reduced. When a marine iguana emerges from the water and begins to bask, the heart rate returns to normal so that blood circulates under the skin rapidly, becoming warmed and then carrying heat to deeper parts of the body.

Brachylophus (banded iguanas) is found on the Fiji and Tonga Island groups. This genus is mainly arboreal and lives in the wet forests of these islands. Because of their restricted distribution in Fiji and Tonga, they are the most isolated members of the Iguanidae (Pregill 1989). An interesting aspect of *Brachylophus* is its extremely long egg incubation time, exceeded only by the tuatara (*Sphenodon*) among terrestrial vertebrates. This is believed to be an ancestral feature (Gibbons and Watkins 1982).

Conolophus (land iguanas) is found only on the Galápagos Islands, like *Amblyrhynchus*. There are two similar species of *Conolophus;* both are terrestrial and are found on different islands. Thus, they probably evolved not too long ago from a common ancestor. These large, heavy-bodied lizards

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Table 1. The iguanid genera, number of species, and their geographic range.

Genus	Number of Species	Geographic Range
Amblyrhynchus	1	Galápagos Islands
Brachylophus	2	Fiji and Tonga Island groups
Conolophus	2	Galápagos Islands
Ctenosaura	11	Mexico to Panama
Cyclura	8	Caribbean Islands and Bahamas
Dipsosaurus	1	Southwestern U.S., Mexico, islands in the Gulf of California
Iguana	2	Mexico to Southern Brazil and Paraguay, Lesser Antilles
Sauromalus	8	Southwestern U.S., Mexico, islands in the Gulf of California

Sources: Burghardt and Rand 1982, and de Queiroz 1995.

feed mainly on the fruits and leaves of prickly pear cactus (*Opuntia* spp.) (Mattison 1989).

Ctenosaura (spiny-tailed iguanas) is found from Mexico to Panama. They are large ground-dwelling lizards that occupy a wide range of habitats from semi-arid scrub to forests. There are taxonomic problems between *Ctenosaura* and another putative genus, *Enyaliosaurus*. *Enyaliosaurus* is considered by some to be a subgroup of *Ctenosaura* instead of a separate genus (Etheridge and de Queiroz 1988). The systematic problems between these two taxa are discussed in more detail later in the paper.

Cyclura (rock iguanas) is found on many islands in the Caribbean. These huge lizards live among rock and scrub habitat, where they feed mainly on vegetation. *Ctenosaura* is replaced by *Cyclura* in the West Indies. Eight species, which are further divided into several subspecies, are recognized throughout these islands (Mattison 1989).

Dipsosaurus (desert iguana) is a relatively small iguanid that has not evolved a large body size (Petren and Case 1997). This monotypic genus is found in the southwestern U.S., Mexico and islands in the Gulf of California. It lives in sandy desert flatlands, a habitat with low humidity and high temperatures. This genus is closely related to *Iguana* and *Ctenosaura* (Norris 1953) and is probably the most primitive living North American iguanid genus (Mittleman 1942 [cited in Etheridge 1982]).

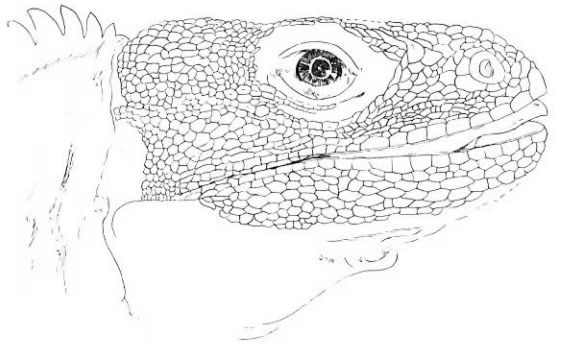
Iguana (green iguanas) is found from Mexico to southern Brazil and Paraguay, and in the Lesser Antilles. There are two recognized species of this widespread, arboreal genus (Etheridge 1982). Green iguanas vary considerably in color, size, and physical characters throughout their range. Individuals in the northern part of the range tend to have a longer, more pointed head and have taller dorsal crest scales than some southern forms. They also exhibit more orange coloration in northern parts of their range (Blair 1995).

Sauromalus (chuckwallas) occupies much of the same range as *Dipsosaurus*. They live in rock outcrops or on rocky hill slopes throughout the Mojave and Sonoran deserts. This genus is also found on roughly 22 islands in the Gulf of California. Some species on these islands differ from those on the mainland in having large body sizes. It is hypothesized that large body size evolved on these islands due to different ecological conditions from those on the mainland, such as sexual selection, competition, resource availability, and predation (Case 1982, Petren and Case 1997).

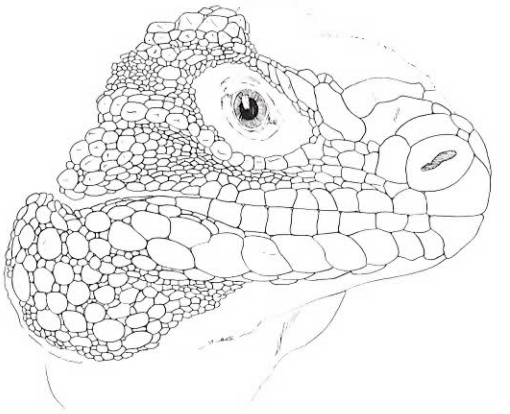
Hypotheses on the Origin of Iguanidae

There seem to be a number of different hypotheses concerning where iguanid lizards first originated. The family that is currently recognized as Iguanidae (*sensu stricto*) has not radiated as extensively as other closely related iguanian families, such as Polychrotidae, Phrynosomatidae, and Tropiduridae. The following hypotheses on iguanid evolution are referred to in the broad sense (*sensu lato*) and include the closely related families that were formerly part of Iguanidae before Frost and Etheridge's (1989) redefinition of the family.

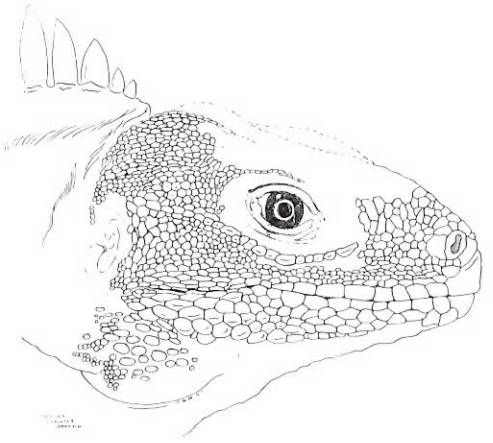
According to the fossil record, members of the



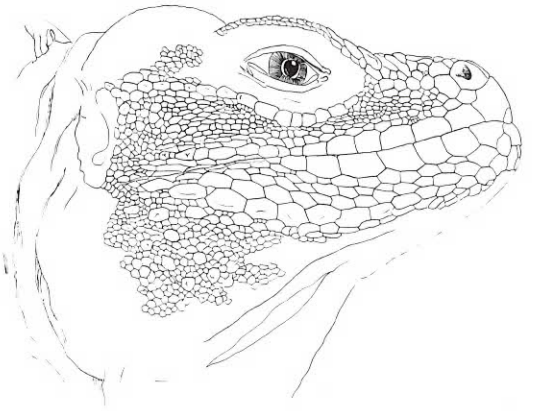
Ctenosaura similis



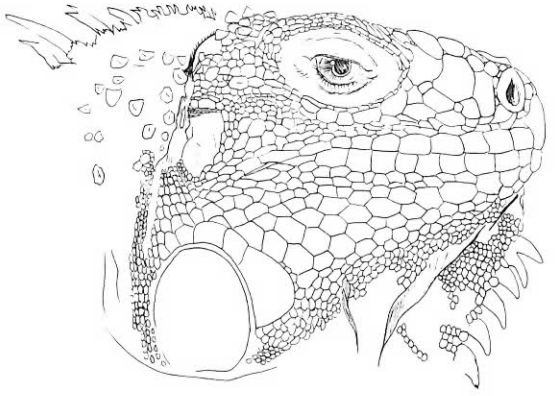
Cyclura cychlura cyclura



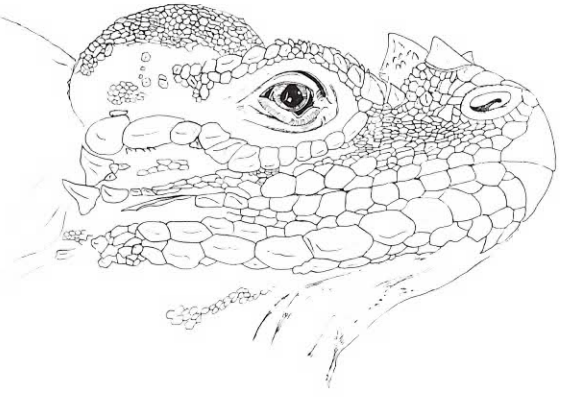
Cyclura carinata bartschi



Cyclura ricordi



Iguana iguana



Cyclura cychlura cornuta

Scalation renderings of a small sampling of the 35 species of iguanas. *Illustrations: John Bendon*

Iguanidae (*sensu lato*) have been in existence in North and South America since the Cretaceous (Burghardt and Rand 1982). The oldest known fossil that is unambiguously referable to this family, *Pristiguana brasiliensis,* is the first Mesozoic record of Iguanidae (*sensu lato*) (Estes and Price 1973). However, *Armandisaurus explorator* from the Miocene of New Mexico is the oldest fossil of Iguanidae (*sensu stricto*) (Norell and de Queiroz 1991).

The family Agamidae is considered the Old World counterpart to the Iguanidae. Agamids tend to fill the same ecological niches that the iguanids fill in the New World. Some agamids, like the iguanids, exhibit large body size and herbivorous diets, such as *Uromastyx* in northern Africa and Asia and *Hydrosaurus* in the Philippines. There are few other Old World lizards that are herbivorous, which shows that agamids do not simply "replace" iguanids in the Old World (Burghardt and Rand 1982).

According to Darlington (1957), iguanians originated on the Old World continents, giving rise to the agamids, which later displaced the more primitive iguanians, except in the islands of Madagascar, Fiji and Tonga, and subsequently spread to the New World. Fossil iguanids (*sensu lato*) have been recorded from Europe as well, but Darlington claims that "they are open to question, although the family's present distribution leaves little doubt that iguanids [*sensu lato*] did occur on the Old World continents long ago." Estes and Price (1973) suggested that iguanids (*sensu lato*) are of South American origin, and see similarities between them and teiids. They also mention that "a southern continental (Gondwanan) origin of iguanids [*sensu lato*] is more plausible than the northern one that is often suggested." As an alternative explanation of present distribution, Blanc (1982) proposed that when the southern continents were closer together, there was dispersal through Antarctica onto Madagascar. The two Malagasy genera are now classified as members of the family Opluridae (Frost and Etheridge 1989).

Hypotheses on the Dispersal and Biogeography of the Insular Iguanids

It is thought that the iguanids inhabiting island ecosystems may have arrived there by rafting on floating debris. The distribution of iguanas exemplifies how rafting may have helped spread related species globally. Iguanidae is most commonly thought to have arisen in Central or South America. *Iguana* or *Ctenosaura* may have been ancestors of the West Indian genus (*Cyclura*) and are also thought to have found their way to the Galápagos Islands where they speciated into three forms, *Amblyrhynchus cristatus, Conolophus subcristatus,* and *Conolophus pallidus* (Mattison 1989). Cogger (1974) suggests that ancestors of *Brachylophus* could have ridden the same ocean current, but passed the Galápagos archipelago, and arrived on the Fiji and Tonga Island groups.

It is also thought that the spiny-tailed iguanas, *Ctenosaura,* are the closest living relatives of *Cyclura.* However, recent phylogenies do not support this relationship, which is discussed later in the article. *Ctenosaura* may have reached the Caribbean islands by being washed out to sea on drifting debris from the mainland. Schwartz and Carey (1977) (cited in Etheridge 1982) suggest that *Cyclura* is most similar to *Ctenosaura,* from which it differs in toe morphology, and that "*Cyclura* probably originated on Hispaniola following the invasion of pre-*Ctenosaura* stock from the mainland." The genus *Cyclura* definitely illustrates that speciation has taken place after becoming isolated on separate island groups. These iguanas have evolved into morphologically distinct forms (Blair 1983). Because there was no actual land connection between North and South America at the time of dispersal, *Cyclura* could be a possible ancestor of the Galápagos and Fijian iguanids. The radiation of *Sauromalus* on the islands in the Gulf of California is perhaps even more poorly understood (Sites *et al.* 1996).

The exact details of these animals' dispersal can only be hypothesized, but certain basic similarities in the anatomy of these species, coupled with the direction of the ocean currents, provide evidence that dispersal events led to the evolution and present distribution of the family. Examining the distribution of plants that have floating seeds provides additional evidence of iguanid dispersal (Mattison 1989). There are several South Pacific plant species that may have a South American origin (bamboo, coconut, sweet potato), however, the distribution of the red mangrove (*Rhizophora mangle*), which is dependent on ocean currents for dispersal, is especially similar to that of the modern iguanid genera (Figure 1).

Gibbons (1981) suggests that the biology and distribution of *Rhizophora mangle* is significant in

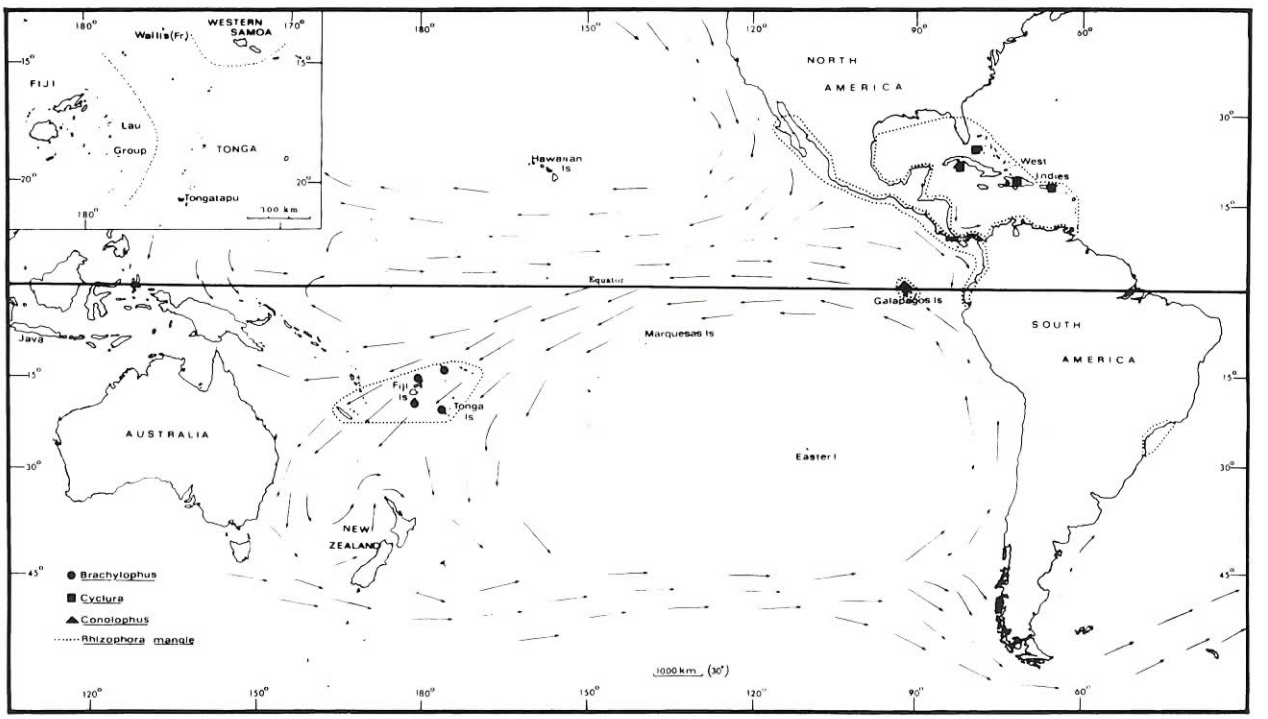


Figure 1. Map of the Pacific and Caribbean showing the distribution of *Brachylophus, Cyclura, Conolophus,* and *Rhizophora mangle*. Iguanid genera not indicated on the map include *Iguana* (Mexico to the northern half of South America and the West Indies), *Ctenosaura* (Mexico and Central America), *Amblyrhynchus* (Galápagos Islands), and *Sauromalus* and *Dipsosaurus* (Mexico and southwestern United States). Arrows represent the course of the South Equatorial Current that these iguanids are thought to have drifted. Notice that *R. mangle* has a similar distribution to the mainland and insular iguanids. (From Gibbons 1981. Reprinted with permission. ©1981, Society for the Study of Amphibians and Reptiles.)

understanding the origin and distribution of insular iguanids. The dispersal pattern of *R. mangle* by ocean currents coincides nicely with that of the iguanids for three reasons: 1) *R. mangle* provides evidence of the access from the West Indies to the Pacific because it occurs along both the Atlantic and Pacific coasts of the Americas, 2) some species of *Cyclura* depend on *R. mangle* as an important food source (Auffenberg 1982) and it also forms part of the habitat of Iguana iguana and *Brachylophus* populations, and 3) the distribution of *R. mangle* in the Pacific corresponds with the presence of the iguanids found in the Galápagos and in Fiji and Tonga. *R. mangle* could have had a human introduction, but there is still good evidence that suggests that it reached these islands by rafting (see Gibbons 1981). Because *R. mangle* is a good long-distance colonizer, it would not be expected to show much change from its ancestral form, while the iguanids have.

It is certainly possible that whole trees could drift within a raft of matted vegetation. Disturbances such as hurricanes can uproot vegetation and cause them to drift out to sea, following the course of the South Equatorial Current. Any iguanids swept away on a raft with such trees would be provided a supply of leaves that might last for many weeks (Gibbons 1981). Nasal salt glands, scaly skin, and the fact that water requirements are satisfied in their food, are all possible reasons that might help prevent dehydration on such long, rafting journeys (Cogger 1974).

A problem with the rafting hypothesis is that it would be a very long journey for the *Brachylophus* ancestor, and the food supply may not last for that long. However, Gibbons and Watkins (1982) have shown that *Brachylophus* has an extremely long egg incubation time. Thus, if part or the whole journey was spent in the egg stage, then a continuous food supply would not have been needed. Eggs of *Brachylophus* have been found in coconut trees and it is possible that eggs could be deposited in the humus among the dying vegetation of a raft. Gibbons (1981) suggests that "*Brachylophus* is uniquely preadapted for rafting, whatever stage of the life cycle is actually employed."

One might well ask why iguanids have not arrived on other island groups. A possible answer is that other islands may have unsuitable conditions. For example, the marine iguana is adapted to an environment with cold water, warm land, and few predators, conditions unique to the Galápagos Islands. It is difficult to imagine another place where marine iguanas could have evolved or extended their range, if given the opportunity (Jackson 1993).

Phylogenetic Relationships of Iguanidae

All the members of Iguanidae are believed to be descendants of a common ancestor, and thus the group is considered monophyletic. Etheridge and de Queiroz (1988) and de Queiroz (1987) show that the iguanid monophyly is supported by numerous synapomorphies, which are shared, derived characteristics common to members of a group. Synapomorphies are important in constructing a phylogenetic tree, whereas symplesiomorphies (shared ancestral characteristics) do not add evolutionary information about relationships among members of the group.

Large body size, flared and often polycuspate marginal teeth, and transverse folds or valves in the colon are three hypothesized synapomorphies that seem to be related to herbivory (Etheridge and de Queiroz 1988). Large body size and herbivory are shared characteristics of iguanids and two agamids (*Uromastyx* and *Hydrosaurus*). However, the lack of colic septa and the position of the parietal process of the supratemporal bone are synapomorphies of Iguanidae (de Queiroz 1987). Camp (1923) (cited in de Queiroz 1987) showed that tooth attachment is another distinguishing characteristic of iguanids. Iguanids have teeth attached at one side to the inner surface of the jawbone (pleurodont dentition), while other iguanians (agamids and chamaeleontids) have their teeth fused to the crest of the jaw bone (acrodont dentition).

Iguanid phylogenetics has been presented by Avery and Tanner (1971), de Queiroz (1987), Etheridge and de Queiroz (1988), Norell and de Queiroz (1991), Sites *et al.* (1996), and Petren and Case (1997). Although all data used in constructing these phylogenies are relevant, only selected parts from Etheridge and de Queiroz (1988) will be discussed in the following section. Figure 2 shows a phylogeny of the iguanid genera based upon the following morphological characteristics.

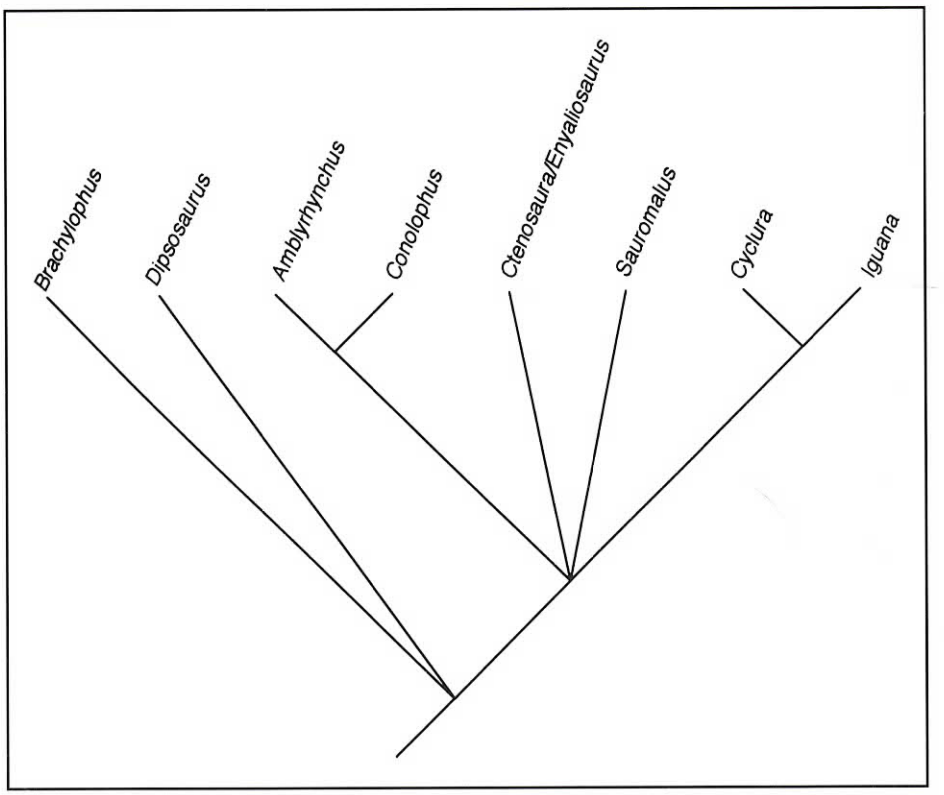
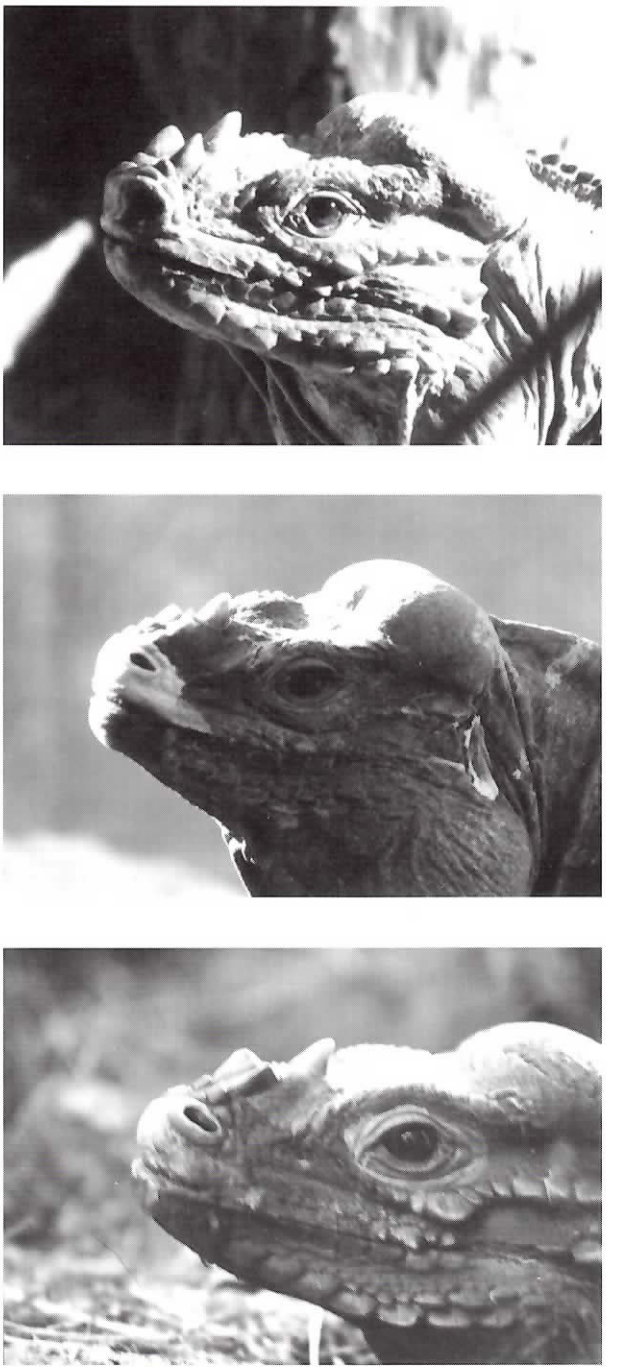


Figure 2. A phylogeny of the iguanid genera based upon morphological characters. (From de Queiroz 1987, and Etheridge and de Queiroz 1988.)

Phylogenetically, *Dipsosaurus* and *Brachylophus* form a sister group to the remaining iguanids. Etheridge and de Queiroz (1988) have shown that the parietal foramen has moved to the frontal bone in *Dipsosaurus*. Both *Brachylophus* and *Dipsosaurus* are outside the clade formed by the remaining iguanid genera because they lack a posterior coracoid fenestra, which is a posterior opening on a bony scapular process. It is suggested that *Dipsosaurus* diverged earlier than *Brachylophus* from the other iguanids because of its elongate, strongly overlapping superciliary scales, but it is not clear that elongated superciliaries are primitive within Iguanidae. For this reason, the relationships among *Brachylophus, Dipsosaurus* and the remaining iguanids were left unresolved.

A posterior coracoid fenestra is a synapomorphy shared by the remaining genera. The Galápagos iguanas, *Amblyrhynchus* and *Conolophus,* have often been considered closely related. There are a number of derived characteristics that support this relationship, including cuspate premaxillary teeth and a premaxillary spine that is covered by the nasal bones. The distinctiveness of *Amblyrhynchus* is characterized by numerous derived traits including the presence of separable skull osteoderms in large specimens. This feature is unique within Iguanidae. Although *Conolophus* has fewer modified morphological characters than *Amblyrhynchus,* it also has its own derived traits (Etheridge and de Queiroz 1988).

Problems have arisen when recognizing two separate genera of spiny-tailed iguanas, *Ctenosaura* and *Enyaliosaurus. Ctenosaura* is a monophyletic taxon supported by at least three synapomorphies. Derived characteristics show that *Enyaliosaurus* is also monophyletic, but is a subgroup of *Ctenosaura* rather than a sister group (Etheridge and de Queiroz 1988). These two taxa jointly possess a reduced posterior process of the basisphenoid bone, which suggests that they are a monophyletic group. Thus, if *Enyaliosaurus* were separated from *Ctenosaura*, then *Ctenosaura* would not be monophyletic because a monophyletic group must include a common ancestor and all descendants of that group. In particular, the parietal roof of *Ctenosaura* is derived relative to that of *Enyaliosaurus*. The change in parietal roof shape during post embryonic ontogeny is most pronounced in large species of *Ctenosaura*. Species with small body size or young have a trapezoidal shaped parietal, while in large adults the parietal is Y-shaped. Because of the derived small size of *Enyaliosaurus,* it has a trapezoidal shaped parietal (de Queiroz 1987). These are reasons why *Enyaliosaurus* is considered a subgroup of



Morphological variation within one species. The Rhinoceros iguana, *Cyclura cornuta,* ranges over the island of Hispanola and it's offshore islands, and is an extremely variable species. Note the scalation variation between these three adults. *Photographs: John Bendon. Finca Cyclura, 1997*

Ctenosaura rather than a sister group.

A short posterior process of the interclavicle, loss of the middorsal scale row, and a reduction in the number of premaxillary teeth are a few derived characters that support the monophyly of *Sauromalus*. Because common patterns of distribution of derived characters are lacking within this group, the relationships among *Sauromalus,* the Galápagos iguanas, *Ctenosaura*, *Iguana* and *Cyclura* are uncertain, and for this reason, have been left unresolved (Etheridge and de Queiroz 1988).

Highly cuspate marginal teeth is just one synapomorphy that supports the sister group relationship of *Iguana* and *Cyclura*. The presence of a gular crest supports the monophyly of *Iguana,* while that of *Cyclura* is supported by peculiar toe combs, a condition approached but not attained by some other iguanids. Members of this latter genus also share an increased number of premaxillary teeth (Etheridge and de Queiroz 1988).

One can examine the similarities and differences in morphological features among the iguanid genera and hypothesize their evolutionary relationships. However, looking at their molecular structure can provide different, possibly more robust hypotheses regarding phylogenetic relationships. When using morphological characters, homologies and convergent evolution cannot always be distinguished and the character number is limited. However, these problems tend to be mitigated when using molecular characters.

Recently, a paper was published showing a phylogeny of Iguanidae based upon molecular data combined with morphological data (Sites et al. 1996) (Figure 3). There were both agreements and conflicts between this tree and that of de Queiroz (1987) (cf. Figures 2 and 3). The molecular study supported the basal positions of *Brachylophus* and *Dipsosaurus,* although de Queiroz's (1987) tree was left unresolved at this relationship. The molecular study suggests that *Brachylophus* diverged earlier than *Dipsosaurus*. De Queiroz (1987) showed that *Cyclura* and *Iguana* are sister taxa because of shared derived morphological features; the molecular study does not agree with this arrangement and instead hypothesizes *Cyclura* to be the sister group of all iguanids except *Brachylophus* and *Dipsosaurus*. Another area of conflict centers on the placement of the genera *Ctenosaura* and *Sauromalus*. Sites et al. (1996) suggest that *Ctenosaura* is the sister group of the Galápagos iguanas (*Amblyrhynchus* and *Conolophus*) and *Sauromalus* is the sister group of *Iguana*. Molecular evidence strongly favors monophyly for the *Ctenosaura*, *Amblyrhynchus* and *Conolophus* topology, and for all the genera from which multiple species were sampled. These trees may suggest possible conflicts with the current hypotheses on

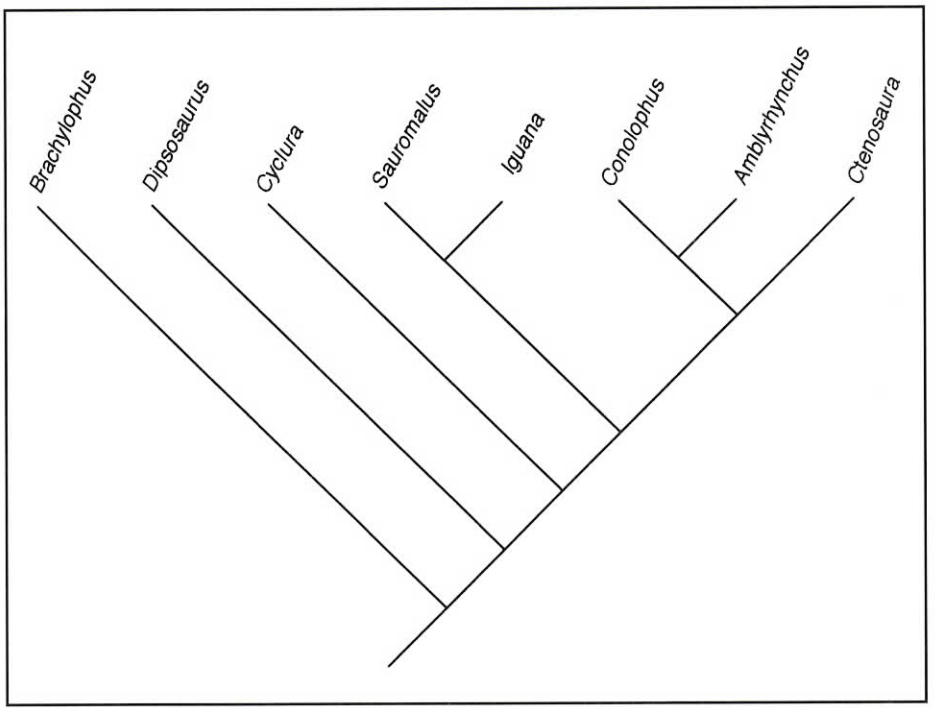


Figure 3. A phylogeny of the iguanid genera based upon morphological and molecular characters. (From Sites *et al.* 1996.)

the dispersal of the insular iguanids (see earlier discussion). Sites *et al.* (1996) explain a current hypothesis of the distribution patterns of the iguanid genera based on their phylogeny.

Conclusion

The Iguanidae is distributed throughout the New World and South Pacific islands. The family exemplifies how organisms have adapted to the extremes of climate and habitat. The unique adaptations and diversity of this family have thus made it an interesting and important group for evolutionary studies. This overview has presented only a few aspects of iguanid evolution, including many hypotheses about the origin and dispersal of this family. Although iguanas exhibit many shared, derived characteristics, the phylogenetic relationships among the iguanid genera remain unclear. Consequently, many of the hypotheses on iguanid dispersal and evolution are equally acceptable at present. Thus, as is true with most organisms, there remains much exciting research to do on the evolutionary and biogeographic history of this group.

Acknowledgments

I wish to express my thanks to Dr. Fredric Janzen and Dr. Robert Wallace for encouraging me to write this review, for their help in editing the rough draft of this article, and for their helpful advice.

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Cuban and Rhino Iguana Egg Laying

I.I.S. Member, Bo Staten, in Casper, Wyoming reports three captive born *Cyclura* laying eggs at the very young age of one year, 10 months. All eggs were infertile, but fully formed. On 8 August, 1997 one Cuban iguana, *Cyclura nubila*, was observed laying an egg at 5:00 p.m. Shortly thereafter an egg was found in the nest box of another *C. nubila* that was layed several days earlier. On 21 August, 1997 a rhiniceros iguana, *Cyclura cornuta*, layed an egg at 6:45 a.m.

The *Cyclura nubila* were both about 55 cm (22.75 in.) total length. The *Cyclura cornuta* is 58 cm (23.5 in.) total length. All animals were fed a 100% vegetable diet throughout their lives, heavy on leafy greens and fed daily. Crushed Tums® were added twice weekly for calcium supplement. The iguanas are kept under timed UV lights to simulate sunlight. Enclosures are 8' x 8' x 4' high.

Above: Captive born rhinoceros iguanas, *Cyclura cornuta,* in enclosure.

Left: Egg from one-year, 10 month old, Cuban iguana, *Cyclura nubila.*

Below: Robust juvinile in it's captive habitat in Wyoming.

Photographs: Bo and Anita Staten

LIZARD LETTERS

Dear Editor,

I am writing in response to the article by John Bendon in your most recent issue of the *Iguana Times* regarding the Jersey Wildlife Preservation Trust's Lesser Antilles iguanas *Iguana delicatissima*. Primarily I wish to update your readers as to the progress of the juvenile but would first like to correct one or two slight inaccuracies.

I do not remember discussing the evolutionary history of *Cyclura* and *Iguana* with John Bendon. I am not an authority on the ancestry of West Indian iguanines but did mention to John that some changes were possible in the future regarding the taxonomy of these animals, partly as a result of recent work carried out on *I. delicatissima* in the field. I hope the hackles of iguana taxonomists have not been raised by this slightly elaborated statement on iguana evolution.

At no time since the hatching of the worlds first did I put it through the stressful and traumatic experience of daily measuring and weighing. It was weighed and measured on the day it was moved from it's incubation container to it's vivarium (wt = 20g, svl = 7.5 mm, tail = 208 mm) and has only been measured subsequently on a weekly basis for the first month during which it did not feed and was given a weekly tube feeding of fruit puree and vitamins and monthly thereafter. Vitamin D_3 is administered by mouth on a monthly basis using D_3 suspended in oil as produced by Woodstocks Nutritional Supplements.

Finally, though I work long and hard, and spend much of my own time here in the Department, I do not spend ALL day EVERY day here!!

Now to the baby. After the first traumatic (for us that was) month it finally began feeding voluntarily when a flowering hibiscus plant was placed inside it's vivarium. Initially only the stamen from each flower was eaten, possibly targeting the protein rich pollen at the end. Following this breakthrough other food items have been gradually added to the diet, the next item accepted being freshly sprouted sweet potatoe leaves.

He or she (we haven't yet attempted to sex it) is now dining daily on a variety of greens and some fruits including: hibiscus flowers, nasturtium leaves and flowers, dandelion leaves, watercress, endive, chicory, romaine lettuce, sweet potatoe leaves, apple, pear, and papaya. All fruits are offered finely chopped and sprinkled with a multi-vitamin and mineral supplement. Oral D_3 dosing takes place once per month and is followed by the provision of large quantities of ground cuttle fish at the next feed. Water is permanently available in a bowl but the baby only drinks during daily spraying with warm water.

The vivarium is furnished with various plants for cover and humidity, climbing branches and a bark chipping substrate. A 60W incandescent bulb provides a basking spot in excess of 32°C while the ambient temperature varies from 25-30°C during the day and about 22-25°C at night. The vivarium is lit with a Trulite fluorescent tube and a Philips Blacklite for additional UV, mostly UVA. Under this regime the baby iguana, now nearly six months old, has grown by more than 25% in both weight and body and tail length.

I look forward to being able to bring you more news from this exciting breeding experiment in the future.

Sincerely
Richard C. Gibson, Herpetology Department Head

NEWS OF THE SOCIETY

Thank You for Your Donations

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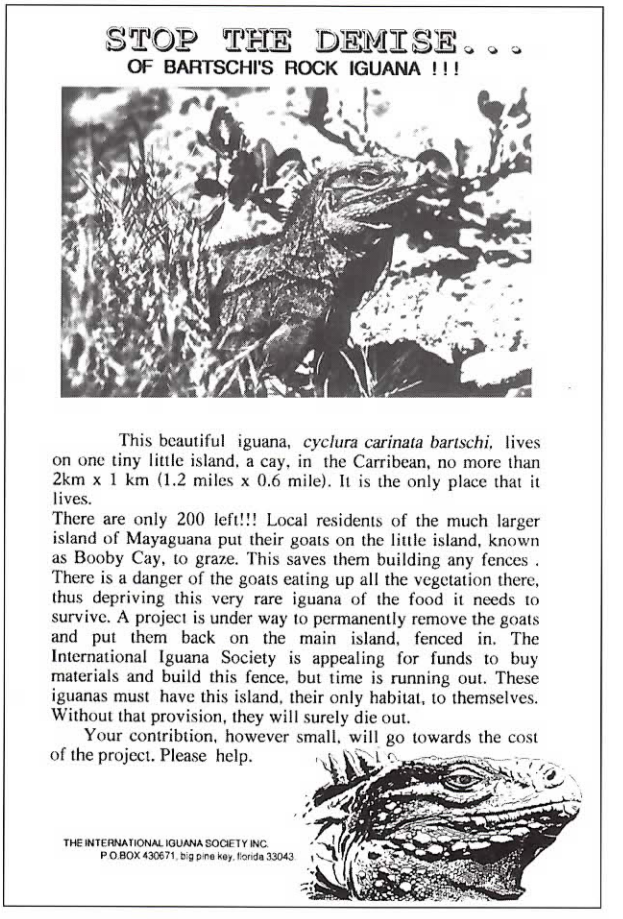

This poster was circulated at herp shows in England this Summer and was responsible for generating a sizable donation to I.I.S. for the project.

Iguana Times

MEMBERS ONLY: For a limited time, the International Iguana Society is making sets of back issues of *Iguana Times* available to all current IIS members at a reduced price. ***Quantities may be limited, so act now!***

Volume 3

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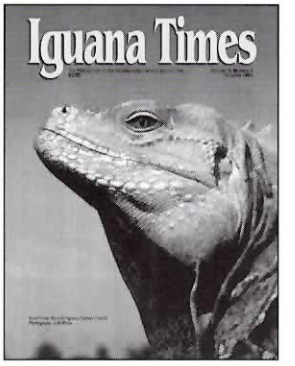

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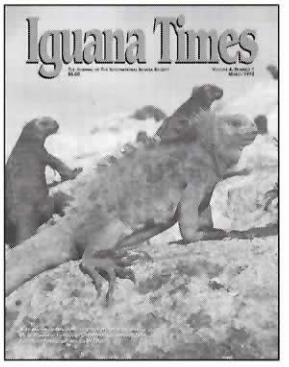

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Volume 4, Number 2
June 1995

Articles Featured:

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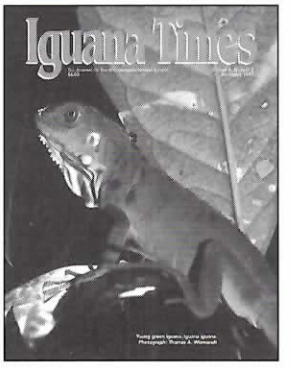

Volume 4, Number 3
September 1995

Articles Featured:

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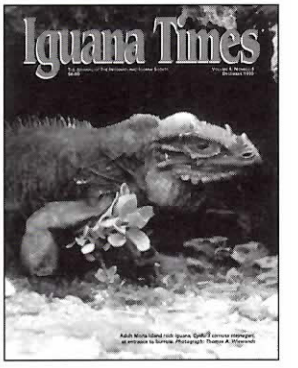

Volume 4, Number 4
December 1995

Articles Featured:

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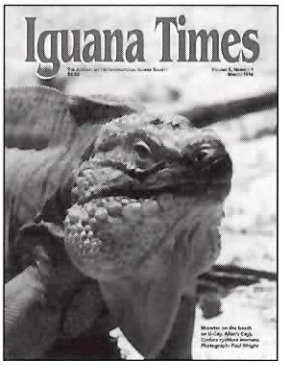

Volume 5, Number 1
March 1996

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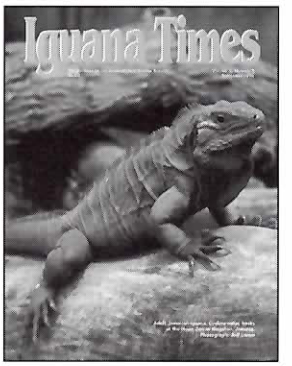
Volume 5, Number 2
June 1996

Articles Featured:

Lost in Time: Galapagos Land Iguanas; Northern Exposure: *C. c. cornuta*; Greasy Lizard Stuff; Iguanas, Salmonella and Herpetoculture: A Conflict of Interest... and Conscience?; Swampa Goes to Kindergarten to Help its Survival; Utila Iguana Gets Helping Hand from Foreign Friends; Lizard Letters; Treasurer's Report; Iguana Newsbriefs



Volume 5, Number 3
October 1996

Articles Featured:

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Volume 5, Number 4
December 1996

Articles Featured:

Any Hope for Grand Cayman's Blue Iguana?; Scalation Renderings of *Cyclura nubila lewisi* and *nubila*; Surviving Atlantis: The Molecular Evolution of the Galapagos Iguanas; Iguana Report from Japan; IIS Conservation Award: Edwin Duffus; Lizard Letters; News of the Society

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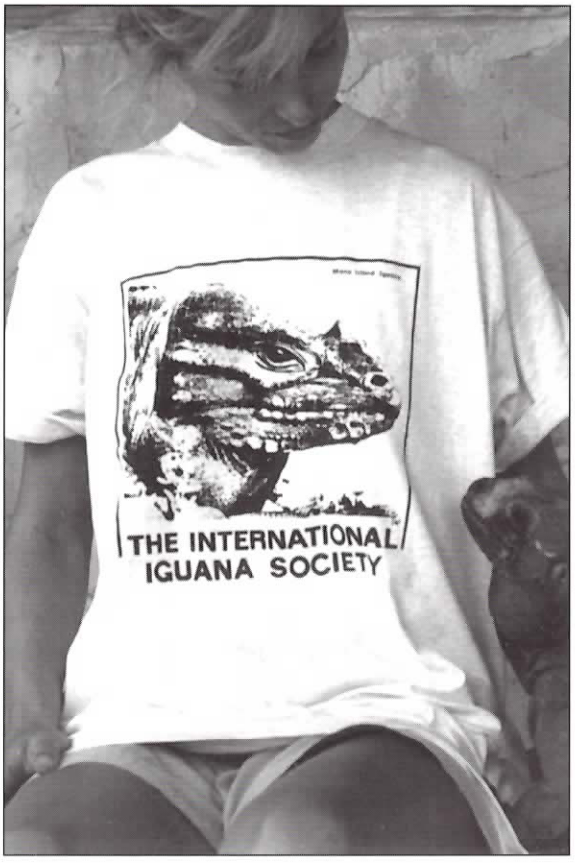

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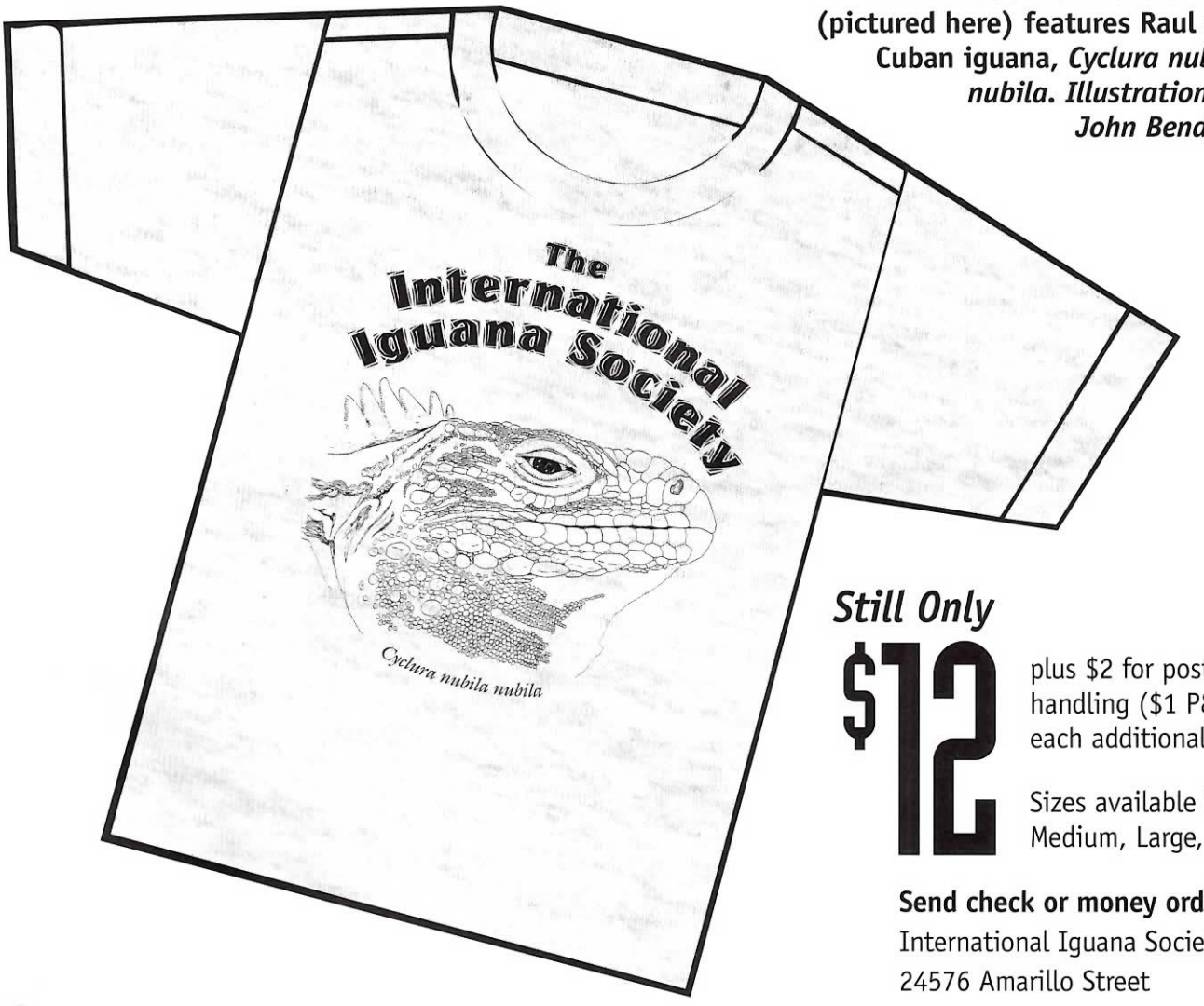

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