

RESEARCH ARTICLE

An Overview on the Evolution of the Family Iguanidae

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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 infra-order 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

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

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

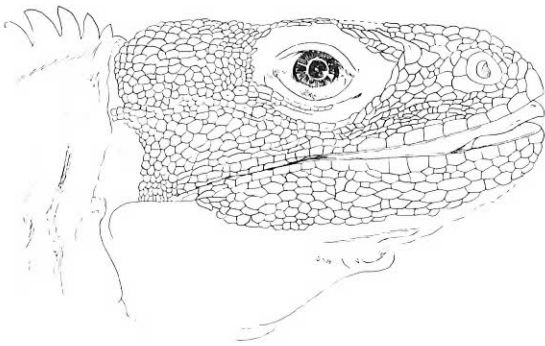
Green iguanas vary considerably in color, size, and physical characters throughout their range. Individuals in the northern part of the range tend to have a longer, more pointed head and have taller dorsal crest scales than some southern forms. They also exhibit more orange coloration in northern parts 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).

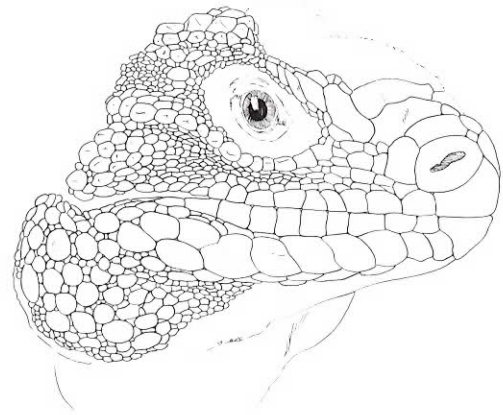
Hypotheses on the Origin of Iguanidae

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 Tropicuridae. 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.

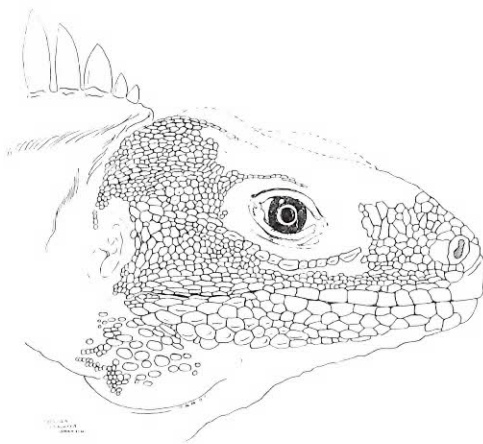
According to the fossil record, members of the



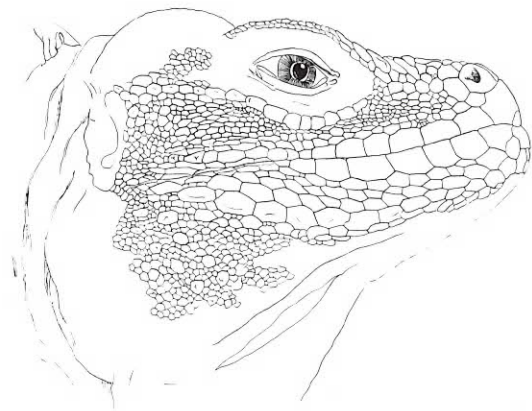
Ctenosaura similis



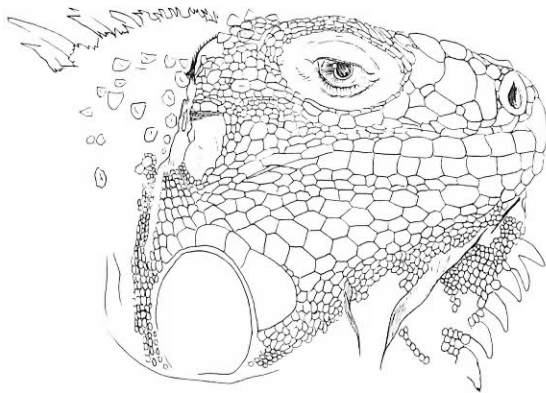
Cyclura cyclura cyclura



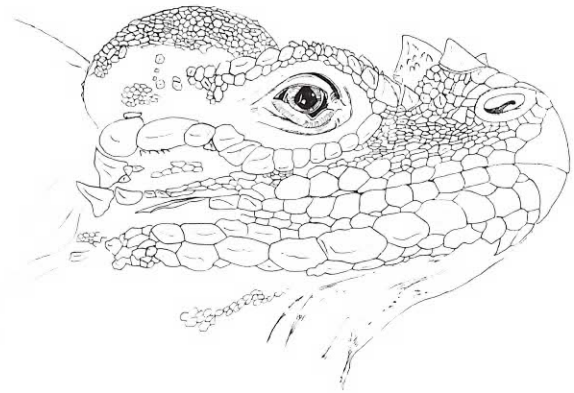
Cyclura carinata bartschi



Cyclura ricordi



Iguana iguana



Cyclura cyclura cornuta

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, *Prisiguana 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 com-

monly 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

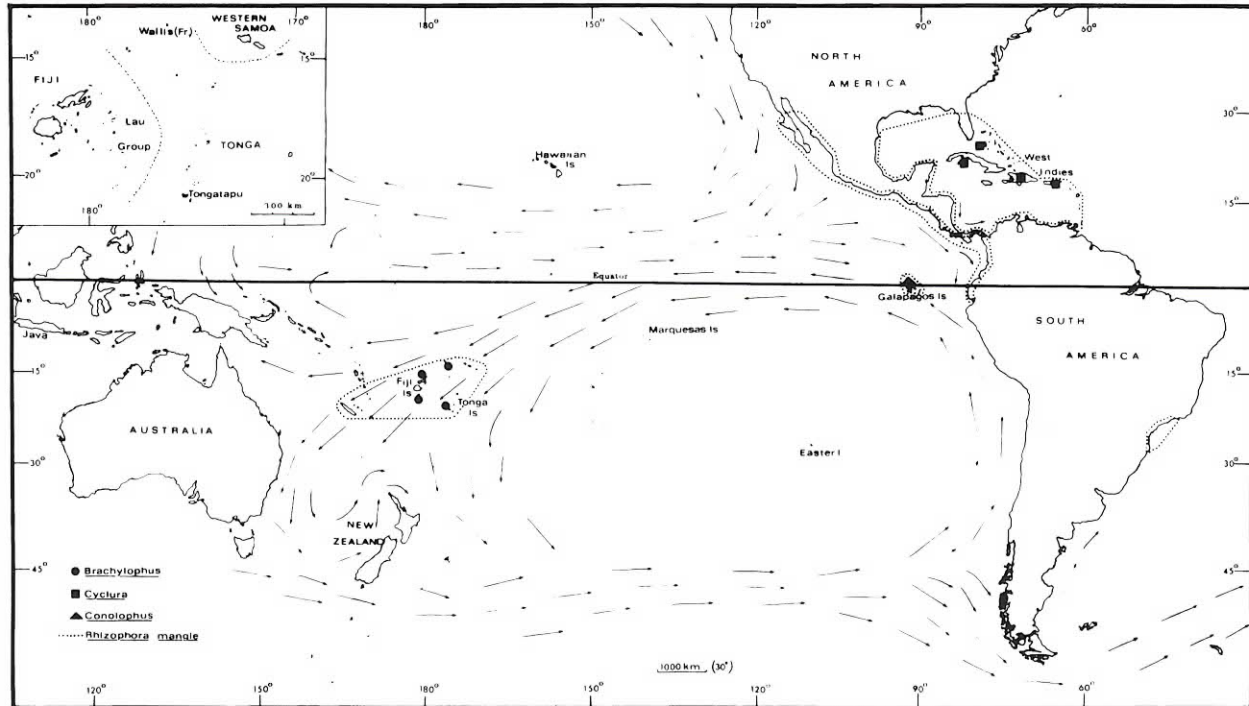


Figure 1. Map of the Pacific and Caribbean showing the distribution of *Brachylophus*, *Cyclura*, *Conolophus*, and *Rhizophora mangle*. Iguanid genera not indicated on the map include *Iguana* (Mexico to the northern half of South America and the West Indies), *Ctenosaura* (Mexico and Central America), *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 polycusate

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 (*Uromastix* 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.

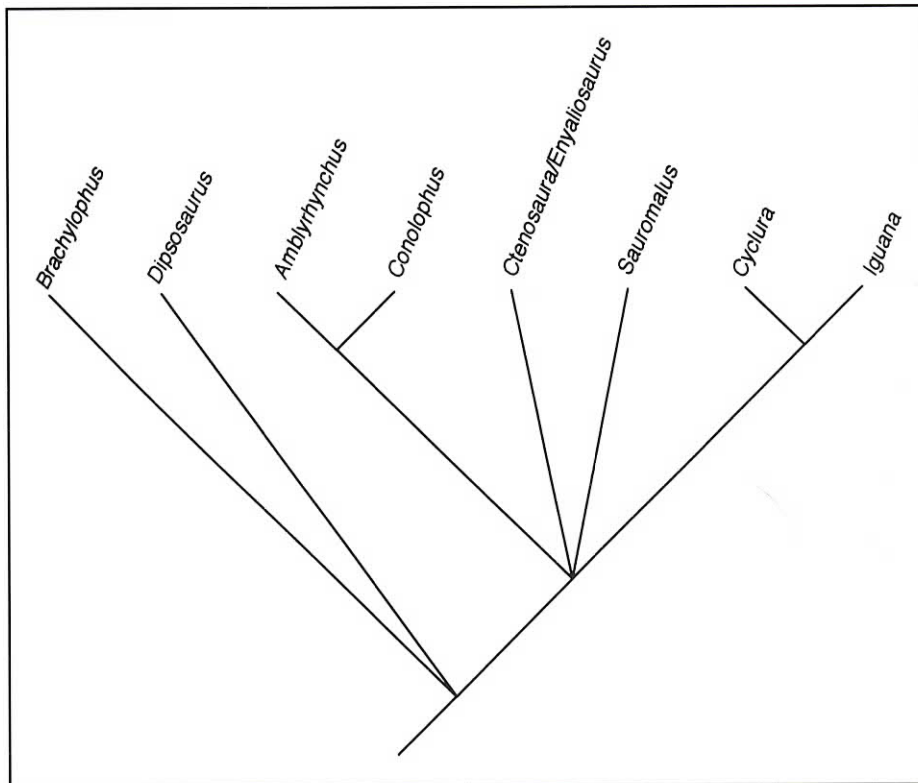


Figure 2. A phylogeny of the iguanid genera based upon morphological characters. (From de Queiroz 1987, and Etheridge and de Queiroz 1988.)

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 cusped 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

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Morphological variation within one species.

The Rhinoceros iguana, *Cyclura cornuta*, ranges over the island of Hispanola and its 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 cusped 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

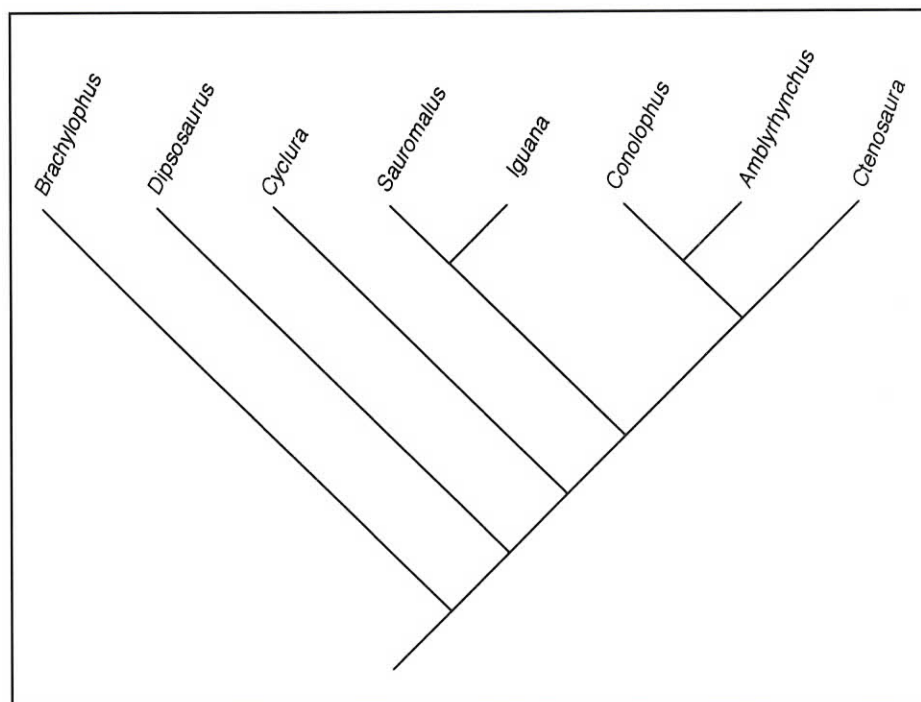


Figure 3. A phylogeny of the iguanid genera based upon morphological and molecular characters. (From Sites et al. 1996.)

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

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