

LACK OF CONVERGENCE IN AQUATIC *ANOLIS* LIZARDS

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Abstract.—Why convergent evolution occurs among some species occupying similar habitats but not among others is a question that has received surprisingly little attention. Caribbean *Anolis* lizards, known for their extensive convergent evolution among islands in the Greater Antilles, are an appropriate group with which to address this question. Despite the well-documented pattern of between-island convergence, some Greater Antillean anoles are not obviously part of the convergence syndrome. One example involves aquatic anoles—species that are found near to and readily enter streams—which have evolved independently twice in the Caribbean and also twice on mainland Central America. Despite being found in similar habitats, no previous study has investigated whether aquatic anoles represent yet another case of morphological convergence. We tested this hypothesis by collecting morphological data for seven aquatic anole species and 29 species from the six convergent types of Greater Antillean habitat specialists. We failed to find evidence for morphological convergence: the two Caribbean aquatic species are greatly dissimilar to each other and to the Central American species, which, however, may be convergent upon each other. We suggest two possible reasons for this lack of convergence in an otherwise highly convergent system: either there is more than one habitat type occupied by anoles in the proximity of water, or there is more than one way to adapt to a single aquatic habitat. We estimate that almost all of the 113 species of Greater Antillean anoles occupy habitats that are also used by distantly related species, but only 15% of these species are not morphologically similar to their distantly related ecological counterparts. Comparative data from other taxa would help enlighten the question of why the extent of convergence is so great in some lineages and not in others.

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Independent evolution of similar features in the same environmental context has long been taken as strong evidence of adaptation (Harvey and Pagel 1991 and references therein). Nonetheless, convergence is not an inevitable outcome of occupation of the same environment because more than one solution may exist for a problem posed by the environment. Consequently, the evolutionary path taken by a particular lineage will depend on a variety of factors including the relative fitnesses of the different possible solutions (i.e., the height of their “adaptive peaks”), the ancestral starting point of the lineage, the particular constraints operating within that lineage, and the presence of other species in the community (Bock 1980; Harvey and Pagel 1991; Losos and Miles 1994).

Although particular case studies have been examined (e.g., Wake and Larson 1987; Wake 1991; Grant et al. 2000; Benkman et al. 2001), the general question of why convergence occurs in some instances and not others has received little attention (but see Kappeler and Heymann 1996). In addition, a number of cases have been identified in which entire communities are dominated by convergence (e.g., placentals-marsupials [Wilson 1992], Mediterranean plant communities [Mooney and Dunn 1970]), but even these situations include examples of nonconvergence (e.g., no placental morphological equivalent exists to the kangaroo, a marsupial grazing herbivore). In these situations, why some species are convergent and others are not is a question that has rarely been investigated.

Lizards of the genus *Anolis* provide an ideal opportunity to address such questions. On islands in the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), convergence is widespread. Each island has experienced its own evolu-

tionary radiation, yet the same suite of habitat specialists—termed “ecomorphs” and named for the part of the habitat they occupy—has evolved convergently on each island (with several exceptions mentioned below [Williams 1983; Losos et al. 1998; Jackman et al. 1999]). For example, each island has a short-legged species that uses twigs and a long-legged species found on tree trunks near the ground, but these habitat specialists are not closely related to morphologically and ecologically similar species on other islands. Nonetheless, exceptions to convergence exist, because each island except Puerto Rico has at least one species morphologically unlike any found on other islands (Williams 1983; see also Beuttell and Losos 1999). Particularly interesting are the so-called aquatic anoles, species that are found near and readily enter streams. Aquatic anoles have evolved independently in Hispaniola, Cuba (Schwartz 1978) and probably at least twice in Central America (Savage and Guyer 1989). Despite their similarity in habitat and the general propensity for convergent evolution among Caribbean anoles, no study has investigated whether an “aquatic” ecomorph exists among these lizards. Consequently, we here examine the hypothesis that, like other types of anole habitat specialists, aquatic anoles are convergent in morphology.

MATERIALS AND METHODS

We included seven species of aquatic anoles, five from Central America and two from the Caribbean, and 29 Greater Antillean species representing each ecomorph type from each island on which it is present, with one exception (no specimens of Hispaniolan crown-giant ecomorph species were available; also, note that Jamaica lacks grass-bush and trunk anoles and

Puerto Rico lacks trunk anoles [Appendix 1 lists the species included]). One to two individuals were measured per ecomorph species and two to six individuals per aquatic species.

We measured the same morphological traits that have been used to define the ecomorphs and for which the adaptive basis of variation among ecomorphs has been established (Losos 1994; Larson and Losos 1996; Beuttell and Losos 1999 and references therein). In addition, we also measured tail height because aquatic animals often have vertically flattened tails that aid in aquatic locomotion (Howell 1930; Fish 1982; Greene 1997).

Using a ruler, we measured the following traits: snout-vent length (SVL) from the tip of the snout to the anterior end of the cloaca; tail length from the anterior end of the cloaca to the tip of the tail, excluding individuals with broken, missing, or regenerated tails; tail height at the base of the tail; and toe and finger length on digit IV on the hindfoot and digit III of the forefoot. In addition, lizards were radiographed and the length of the following traits measured on the radiographs using a video imaging system: femur, tibia, and the longest tarsal bone. The number of subdigital lamellae under the third and fourth phalanges of pedal digit IV was counted using an ocular micrometer. Except when breaks or fractures occurred on the right side or when the radiograph image was poor, all measurements were taken on the right side of the specimen. Each variable was measured twice; an additional measurement (occasionally two additional measurements) was taken when the two original measurements were not within 5% of each other. Measurements were then averaged (when more than two measurements were taken, the two closest were averaged as the other measurements were almost always clearly in error). The mass of each individual was taken from field notes when available (Thomas and Hedges 1991; L. J. Vitt, pers. comm.; Losos, unpubl. data).

We took several approaches to examine how the species varied morphologically. First, we examined each variable individually. Because all of the variables increase allometrically with body size (Losos 1990), we regressed species mean values for each variable against SVL, which was used as a proxy for body size, and calculated residuals. Then, to consider the variables jointly, we conducted a discriminant function analysis (DFA) on non-size-adjusted data in which aquatic anoles were classified a posteriori to one of the six ecomorph categories to examine whether all aquatic anoles were most similar to the same ecomorph type. Finally, to examine the position of species in morphological space, we first conducted a principal components analysis (PCA) on non-size-adjusted data to reduce the dimensionality of the data and then calculated the Euclidean distance between each pair of species using the PCA axes. Mass was not included in the DFA and PCA analyses because data were absent for many species. In addition, three species—*A. alutaceus*, *A. brevirostris*, and *A. semilineatus*—were excluded from DFA and PCA because none of the specimens of these species had complete, original tails.

RESULTS

As a generality, aquatic anoles are long-limbed, particularly with regard to the elements of the hindlimb, and have

deep tails (Fig. 1). The Central American aquatic anoles are generally fairly similar to each other in all morphological variables. By contrast, the two Caribbean aquatic species are substantially different from each other in many respects, most notably in the longer limb elements of *A. eugenegrahami* and the greater body mass of *A. vermiculatus*. One or both Caribbean species overlap the values for the Central American species for many variables, but not for all. In particular, the Caribbean species have substantially more subdigital lamellae. In addition, for many variables (e.g., SVL, metacarpal length), one of the Caribbean species is substantially different from all Central American species.

In the DFA, which was highly significant (Wilks' $\lambda = 0.00$, $F_{55,49} = 5.31$, $P < 0.0001$), standard ecomorph species (i.e., not including aquatic anoles) all were assigned to the correct ecomorph class with a probability of 1.0. The five Central American species were classified post hoc as trunk-ground anoles, whereas *A. eugenegrahami* was classified as a trunk-crown anole and *A. vermiculatus* as a crown-giant, all with probabilities equal to 1.0. These findings were in agreement with the position of species in morphological space. In the PCA, the first five PCA axes accounted for 99.7% of the variation. Based on the position of each species in a morphological space defined by these five axes, four of the five Central American aquatic anoles were positioned closer to another Central American aquatic species than they were to any other species; the only exception was *A. poecilopus*, which was slightly closer to the trunk-ground *A. mestrei* than it was to *A. lionotus*. The nearest ecomorph species to four of the Central American species was *A. mestrei*, whereas for the fifth Central American species, *A. barkeri*, *A. mestrei* was only slightly more distant than the crown-giant *A. garmani*. By contrast, the closest species to *A. eugenegrahami* was the trunk-crown *A. evermanni* and the closest species to *A. vermiculatus* was *A. garmani*. *Anolis eugenegrahami* was closer to nine ecomorph species than it was to the nearest aquatic anole, *A. poecilopus*; similarly, *A. vermiculatus* was closer to 12 ecomorph species than it was to *A. barkeri*, the nearest aquatic species. Thus, the aquatic anoles do not cluster together in morphological space and the three groups of aquatic anoles (Central American, *A. eugenegrahami*, and *A. vermiculatus*) are most similar morphologically to members of different ecomorph categories.

DISCUSSION

Convergence is the hallmark of the Caribbean anole radiation. Nonetheless, Caribbean aquatic anoles are clearly not convergent: *A. vermiculatus* is very large with average length limbs, whereas *A. eugenegrahami* is average-sized with extremely long limbs. In addition, although the five Central American aquatic anoles, which represent at least two unrelated lineages (Savage and Guyer 1989), may be convergent among themselves (assuming that their similarity is derived, an assumption that cannot yet be tested due to the lack of a robust phylogeny for Central American anoles), these species are not convergent with either of the Caribbean aquatic species.

Hypotheses for Lack of Convergence

Why aquatic anoles buck the trend and fail to converge is an open question. Given the extensive convergence exhibited

in the Caribbean anole radiation by each of the six ecomorph classes, historical contingencies—such as constraints and different ancestral morphologies—would not seem likely to be important factors. Thus, we may ask: Why is it that anoles that use similar habitats in the Greater Antilles almost always converge morphologically, except when the habitat they use is near streams?

The expectation of convergence is based on the assumption that species occupying the same habitat will be similar in ecology and behavior and thus will need to evolve the same morphological traits. Previous studies on anoles have revealed that species occupying a particular habitat, such as twigs, have many similarities in behavior and ecology that impose the same functional demands (Losos 1990; Losos and Irschick 1996; Irschick and Losos 1998, 1999; Leal and Losos 2000). Thus, for example, twig anoles must be able to move efficiently on narrow and unstable surfaces, trunk-ground anoles need to be able to run rapidly on broad surfaces to capture prey and escape predators, and highly arboreal species need to be able to cling to smooth surfaces such as waxy leaves. By contrast, it is possible that living near streams does not restrict the way in which an anole may interact with its environment, and thus species occupying such areas may not face consistent functional demands promoting convergence.

The many similarities in habitat use and behavior of aquatic anoles suggest that this explanation is inadequate (our statements below on the natural history of aquatic anoles are based on the following studies: Robinson 1962; Meyer 1968; Goodman 1971; Campbell 1971, 1973; Fitch 1973; Schwartz 1978; González-Bermúdez and Rodríguez-Schettino 1982; Rodríguez-Schettino and Novo-Rodríguez 1985; Rodríguez-Schettino et al. 1987; Vitt et al. 1995; Birt et al. 2001; R. Thomas, unpubl. data). For example, all the species are closely tied to water sources; none of the species has been found further than 5 m from water and in most cases individuals rarely venture farther than 1 m from the water's edge. In addition, all aquatic anole species are restricted to the shade and maintain low body temperatures (interspecific mean = 26.2°C, range 24.4–27.8°C), sometimes several degrees lower than species found in nearby forest. Finally, all species will escape from predators by diving into the water and swimming away, propelled by undulation of their bodies and laterally compressed tails, with limbs adpressed to the body. In summary, aquatic anole species share aspects of behavior and ecology distinct from other types of Caribbean habitat specialists. Consequently, recognition of a class of anoles that are specifically found near aquatic habitats—and thus might be expected to experience the same functional demands and to adapt to these demands in similar ways—is reasonable.

Why, then, have aquatic anoles not converged? We suggest two possibilities. First, even though all aquatic species are found near water and share similarities in habitat and behavior, perhaps they nonetheless occupy multiple habitats, each of which happens to be near water. If this were the case, we might not expect species utilizing different habitats to evolve the same adaptations. A comparison of structural habitat use supports this possibility. Most aquatic anoles use a variety of substrates (e.g., standing vegetation, fallen logs, rocks, riverbank) and perch on substrates ranging greatly in

width. Moreover, when perched on vegetation, these species are usually found hanging over water. By contrast, *A. eugeneagrahami* does not use this range of substrates, but is found almost exclusively on large boulders near water. Consequently, it may not be surprising that in many respects *A. eugeneagrahami* is the most divergent of the aquatic anoles. Moreover, some of *A. eugeneagrahami*'s features—long limbs, particularly the forelimb, and a flattened body—are characteristic of lizard species in other families that utilize boulders and rock walls (Losos et al. 2002). Thus, *A. eugeneagrahami* seems to use a different structural habitat than the other aquatic anoles and may have evolved different morphological features as adaptations to this different environment. However, this line of reasoning does not explain the morphological differences between *A. vermiculatus* and the mainland species, which appear to be similar in habitat use.

While on the topic of habitat use, we note that the Caribbean aquatic species are not at all similar in habitat use to the ecomorph class to which they were categorized by the DFA based on morphological data—trunk-crown and crown-giant anoles are usually found high above the ground, whereas *A. eugeneagrahami* and *A. vermiculatus* are generally found much lower. In addition, some morphological differences exist between the Caribbean species and the ecomorph classes that they most closely resemble (Fig. 1). Consequently, although the Caribbean aquatic species are each clearly most similar morphologically to a single ecomorph type, neither of these species belongs to one of the existing ecomorph classes (which are defined on the basis of similarities in ecology and behavior, as well as morphology; Williams 1983). By contrast, the situation for the mainland species, which were classified as trunk-ground anoles in the DFA, is less clear cut. These species do exhibit some similarities to trunk-ground anoles in habitat use, but the mainland species appear to regularly use a wider variety of different types of substrates, from vines to boulders, than do trunk-ground anoles. Moreover, morphological differences do exist between mainland aquatic anoles and trunk-ground species (e.g., relative lamella number; Fig. 1). More detailed data, particularly on behavior and habitat use, are needed to determine the extent to which mainland aquatic species represent trunk-ground anoles restricted to streamside habitats.

A second possible explanation for lack of convergence is that more than one way may exist to adapt to a single habitat, thus leading to the evolution of different morphological features even among species in the same habitat. Several significant differences exist in the natural history of aquatic anoles that may be important in this respect. For example, at least 75% of the diet of Central American species consists of nonaquatic invertebrates and none of the Central American species has been documented to actively hunt for aquatic prey inside the water. By contrast, both Caribbean species actively hunt for aquatic prey (e.g., fish, shrimp) by diving into the water. What morphological (and visual; Katzir et al. 1989, 1999) adaptations are necessary for underwater predation is not clear, but this difference in foraging behavior may be related to the morphological differences between mainland and Caribbean species.

An additional difference in natural history is the mode of locomotion used when aquatic anoles venture into the water

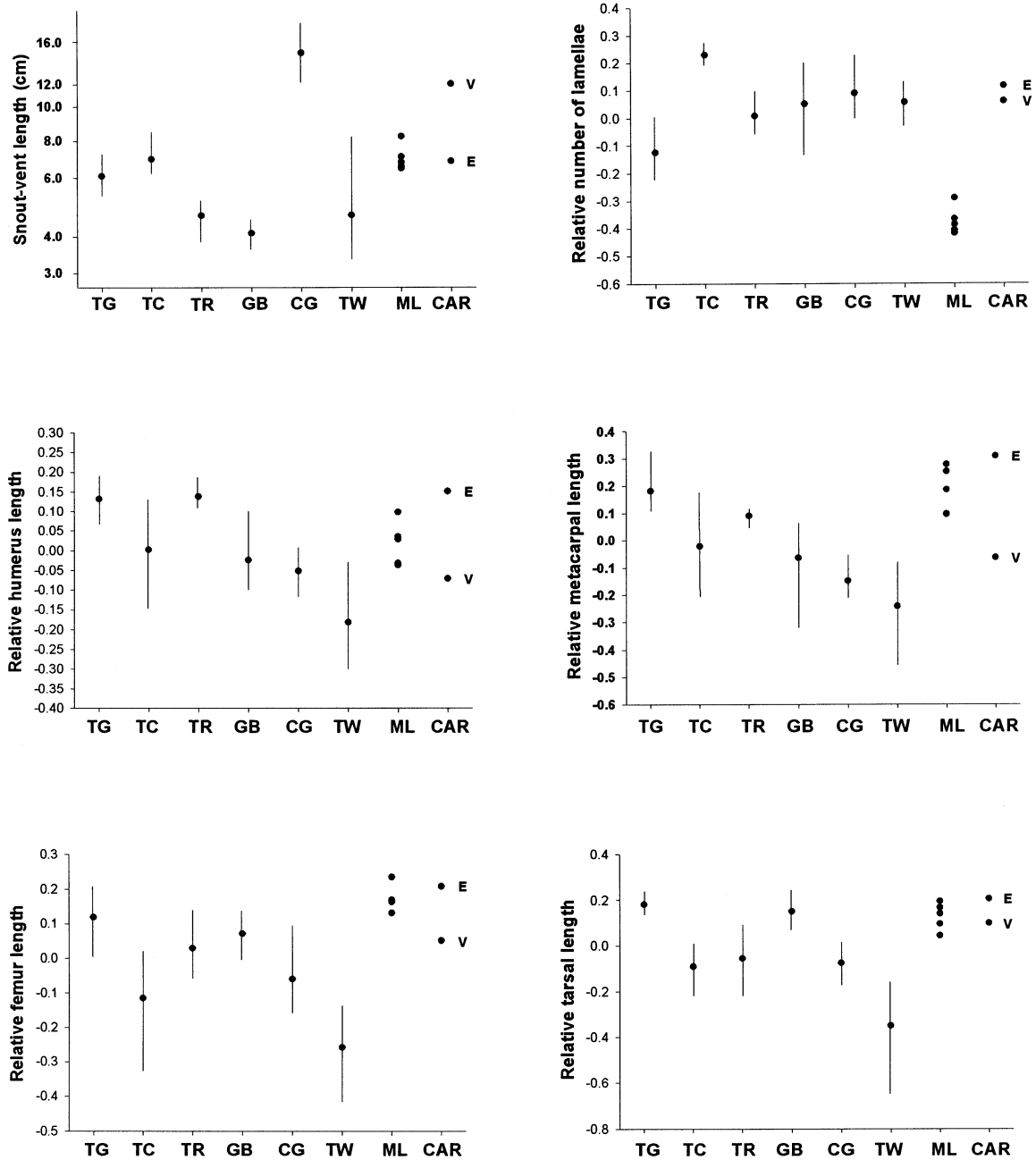


FIG. 1. Morphological variation among ecomorphs and aquatic anoles. Values for each of the six ecomorph categories are means and ranges (ecomorph abbreviations: TC, trunk-crown; TG, trunk-ground; TR, trunk; GB, grass-bush; CG crown-giant; TW, twig). Points for aquatic anoles (ML, mainland or Central American aquatic anoles; CAR, Caribbean anoles) are mean values for each species. E and V, referring to the two Caribbean species *Anolis eugenegrahami* and *A. vermiculatus*, identify which value corresponds to each species when the values are divergent. All variables are residuals from regressions against body size (as represented by snout-vent length) except for snout-vent length. Mass data were not available for all species. Ulna and tibia data are not shown because their patterns of variation are very similar to those for humerus and femur lengths, respectively.

to escape from potential predators or aggressive conspecifics. Some aquatic anoles (*A. lionotus*, *A. poecilopus*, *A. oxylophus* and *A. vermiculatus*) run bipedally across water surfaces (like the more famous basilisk lizard), but other species apparently do not. Bipedal locomotion, particularly on water, is related to a variety of morphological characteristics (Laerm 1973; Glasheen and McMahon 1996; Irschick and Jayne 1998, 1999). In particular, bipedal species often have relatively

short forelimbs, which may explain why *A. eugenegrahami* is not bipedal. Nonetheless, the use of bipedal locomotion explains neither the similarity among Central American species, only some of which are bipedal, nor the morphological differences between *A. vermiculatus* and the bipedal mainland species.

In summary, many similarities exist in the natural history of aquatic anoles. These similarities can explain some fea-

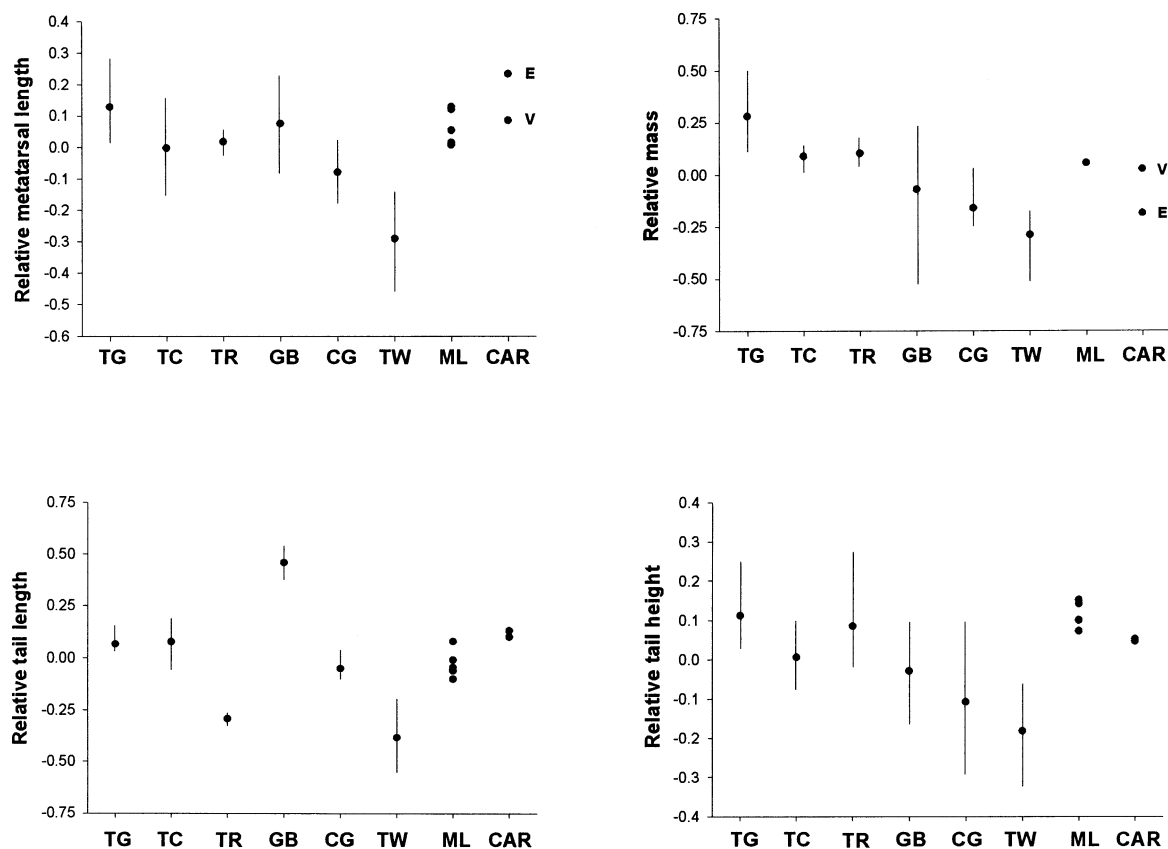


FIG. 1. Continued.

tures that are convergent, such as compressed tails used for swimming. Thermal physiology is probably also convergent, based on field body temperature data, but more detailed analysis is required (cf. Hertz et al. 1993). Nonetheless, overall, aquatic anoles fail to exhibit the widespread pattern of convergence exhibited by anoles occupying other habitats. We attribute this lack of convergence to two factors. First, even though all species live near water, more than one type of habitat appears to be available—*A. eugenegrahami* has adapted to a different aquatic habitat than have the other species. Second, even species with similar habitats use these habitats in different ways, and these different foraging and escape behaviors may have different functional demands and thus promote the evolution of different features. Whether these explanations can account for all of the nonconvergent features, such as the great disparity in number of lamellae among species and the large body size of *A. vermiculatus*, will require more detailed field and functional studies.

Relative Importance of Convergence and Nonconvergence in the Caribbean Anole Radiation

Much has been written about the extensive convergence of the Caribbean anole radiation. Yet, as the aquatic anole case illustrates, convergence is not the entire story. One might ask, in this canonical case of community-wide convergence: what is the relative importance of convergence versus divergence? Of the 113 species of *Anolis* on the Greater Antilles, 82% (93 species) belong to one of the ecomorph clas-

ses. Even if the ecomorph with the most species, trunk-ground, represents the ancestral condition, 59% of Caribbean species are convergent with distantly related species on other islands (the other 23% being similar due to retention of the ancestral condition), an extent of convergence perhaps unparalleled in other lineages (although quantitative data are lacking). Thus, at most, only the remaining 18% of the species do not have distantly related morphological counterparts. However, some species, such as the leaf-litter dwelling *Chamaelinorops barbouri* (a lineage within *Anolis*; see Hass et al. 1993; Jackman et al. 1999), occupy habitats apparently not used by any other Caribbean species. Hence, in these cases, convergence would not be expected. We estimate that only 15% of all Caribbean anoles (17 species)—such as the trunk-using *A. christophei*—occupy habitats used by other Caribbean anole species, but are not convergent with any of those species. Why anoles exhibit so much convergence and why convergence is not exhibited in certain habitats are questions worthy of further study. In addition, quantitative estimation of the extent of convergence in other clades would be interesting to determine the extent to which the anole Caribbean radiation is truly exceptional.

Sadly, we conclude by noting that *A. eugenegrahami* is known from only one locality and has not been collected since 1985 (B. Hedges, pers. comm.). Given the high rate of deforestation of Haiti (Hedges and Woods 1993), the continued existence of this species must be considered in doubt.

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APPENDIX

Species included. Islands: C, Cuba; H, Hispaniola; J, Jamaica; ML, mainland; PR, Puerto Rico.

Aquatic:

A. aquaticus (ML), *A. barkeri* (ML), *A. eugenegrahami* (H), *A. lionotus* (ML), *A. oxylophus* (ML), *A. poecilopus* (ML), *A. vermiculatus* (C)

Trunk-Ground:

A. gundlachi (PR), *A. lineatopus* (J), *A. longitibialis* (H), *A. mestrei* (C), *A. sagrei* (C)

Trunk-Crown:

A. allisoni (C), *A. chlorocyanus* (H), *A. coelestinus* (H), *A. evermanni* (PR), *A. grahami* (J), *A. porcatus* (C)

Trunk:

A. brevisrostris (H), *A. distichus* (H), *A. loysiana* (C)

Grass-Bush:

A. alutaceus (C), *A. olssoni* (H), *A. poncensis* (PR), *A. pulchellus* (PR), *A. semilineatus* (H), *A. vanidicus* (C)

Crown-Giant:

A. cuvieri (PR), *A. equestris* (C), *A. garmani* (J), *A. luteogularis* (C)

Twig:

A. angusticeps (C), *A. darlingtoni* (H), *A. guazuma* (C), *A. occultus* (PR), *A. valencienni* (J)