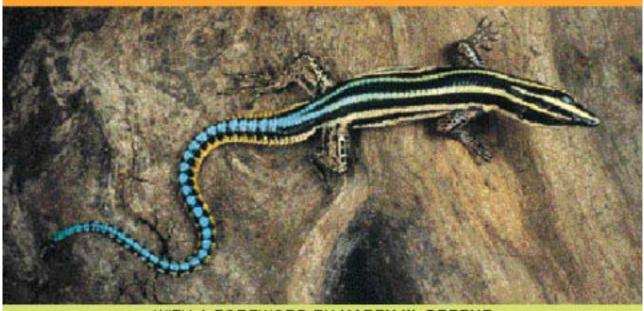
Excerpted from



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LIZARDS

WINDOWS TO THE EVOLUTION OF DIVERSITY



WITH A FOREWORD BY HARRY W. GREENE

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FROM RACERUNNERS TO NIGHT LIZARDS



This tropical African lacertid,

Holaspis guentheri, often sleeps with its tail coiled,
resembling an armored millipede. (Louis Porras)

In this chapter we introduce the highly active teiids and lacertids, the diminutive gymnophthalmids, and the secretive, long-lived xantusiids. Teiids, lacertids,

and gymnophthalmids are in constant motion, maintaining a distance between themselves and other creatures—including humans—and frequently looking back to keep tabs on what could, after all, be a potential predator. Any sudden move by an observer, and the lizard darts off; although it immediately initiates foraging behavior again, its vigilance never ceases.

These are the lizards that dominate terrestrial habitats in the New World and much of the Old World (excluding Australia). Most of these lizards live in open habitats—even Amazonian forest teiids, such as *Dracaena* and *Crocodilurus*, favor large swamps or edges of rivers with sun exposure. Tiny gymnophthalmids appear at first glance to be exceptions because many are found in undisturbed rain forest. However, when scale is considered, most live in the open: a patch of leaf litter in western Amazonia is as much an open habitat to *Prionodactylus eigenmanni* as the bank of a small stream flowing through the same forest is to *Neusticurus ecpleopus*.

Teiids, gymnophthalmids, and lacertids (all of which form the clade Lacertiformes) are tied together evolutionarily because they share a common ancestor. Teiids are most closely related to gymnophthalmids, and both are presently restricted to the New World. Lacertids, the sister taxon to the teiid-gymnophthalmid clade, are an Old World group. Ecological counterparts in their respective habitats, lacertiforms share a number of identifying features: they have elongate, streamlined bodies compared with many iguanians; alert and often fast moving, they forage actively, primarily on the surface of the ground

(with notable exceptions), discriminating between prey and nonprey using chemical cues; and many, but not all, are active at high body temperatures.

Xantusiids, or night lizards, differ considerably from teiids, gymnophthalmids, and lacertids, and their phylogenetic position is less certain. They may be the sister taxon to Lacertiformes, but they could be more closely allied to the Annulata, the group containing, among other



Pantodactylus schreibersii is a common gymnophthalmid in Brazilian cerrado. (Janalee Caldwell)



The gymnophthalmid Micrablepharus atticolus lives in tailings of leafcutter ant nests. (Laurie Vitt)

things, wormlike amphisbaenians (see chapter 9). Another possibility is that they are related to Gekkota. We include xantusiids here recognizing that future studies may place them elsewhere within the evolutionary tree of lizard families. Xantusiids live in enclosed spaces. Some occupy crevices in rocks (*Xantusia henshawi*), others (*X. vigilis*) live under decaying remains of Joshua trees or clumps of large beargrass, *Nolina bigelovi*. Xantusiid eyes are capped over like those of most geckos; they have elliptical pupils and are active in dark places. Their body temperatures while active are considerably lower than those of Lacertiformes.

TEIIDAE

The teiids we know today are a New World family, ecological counterparts of Old World lacertids. Historically, teiids had a wider distribution, at least in the Northern Hemisphere. Their northern distribution is restricted to deserts, the southern half of the Great Plains, and the coastal plain of the southeastern United States. A now extinct group, polyglyphanodontines, was diverse in the late Cretaceous of North America, and they also occurred in the Upper Cretaceous of Mongolia. The fossil record indicates that New and Old World polyglyphanodontines had diverged considerably from each other by mid to late Cretaceous. A faunal exchange during early Cretaceous sent some from east to west; others, however, went from west to east. The fossil record does not clearly indicate whether teiids originated in the Old or New World, though ancient teilds apparently colonized much of the New World. By the end of the Cretaceous, all Northern Hemisphere teiids had gone extinct (Nydam 2000). Modern teiids, therefore, diversified from ancestors remaining in subtropical and tropical areas of the New World, where they achieved the remarkable evolutionary success we see today. A single genus, Cnemidophorus, reinvaded and diversified in the northern half of the New World.

Several characteristics distinguish teiids from other lacertiforms. Teiid head scales are separate from skull bones; those of lacertids are fused to the skull. Teiid teeth have solid bases and are "glued" to jaw bones with cementum; those of lacertids are hollow, and cementum is absent. Indeed, cementum is such a prominent teiid character that it can be used to distinguish fossil teiid jaw-bones from those of all other fossil lizards. Additional characteristics include generally small, granular scales on

the dorsal surface, with large, rectangular scales forming distinct transverse rows ventrally. All teiids have fully formed legs and a fairly distinctive overall morphology consisting of streamlined bodies, long tails, relatively pointed snout, eyelids, and long hind limbs. They are active foragers and lay eggs.

Teiids occur throughout the southern and western continental United States, across Mexico and Central America, on many Caribbean islands, and into much of South America (excluding the high Andes and extreme southern parts of South America). Nine genera are recognized: Ameiva, Callopistes, Cnemidophorus, Crocodilurus, Dicrodon, Dracaena, Kentropyx, Teius, and Tupinambis (Presch 1974). One genus, Cnemidophorus, with 56 named species (Wright 1993), has undergone an extensive adaptive radiation. Ameiva and Kentropyx are well represented also, but Tupinambis, Callopistes, Teius, Dracaena, and Dicrodon contain only a few species. Crocodilurus is monotypic, that is, represented by a single species, C. lacertinus. Teiids are divided into two subfamilies, Teiinae (Ameiva, Cnemidophorus, Dicrodon, Kentropyx, and Teius) and Tupinambinae (the remaining four genera). Teiids vary in body size, ranging from the small whiptail Cnemidophorus inornatus (55 mm SVL) to large tegus, Tupinambis (500 mm SVL), and caiman lizards, Dracaena (approx. 300-450 mm SVL).

The 56-plus species of *Cnemidophorus* (= carrying leg armor), commonly known as racerunners or whiptails, range from southern Idaho through Central America and the Caribbean all the way to Argentina. They reach their largest body sizes in northern South America and on some Caribbean islands, with size generally diminishing as latitude increases (although exceptions exist: C. tigris, for example, is smaller in southern parts of its geographic range). Several species of Cnemidophorus remain unnamed, including one found in Manaus, Brazil. Many "species" of whiptails are unisexual; in these, males do not exist and females reproduce by parthenogenesis. As soon as a female reaches sexual maturity, she begins producing daughters that are genetically identical to herself (see chapter 6). Parthenogenesis occurs in some other teiids (e.g., Kentropyx) as well, and in some other squamate families.

Herpetologists have had difficulty identifying whiptails and working out their relationships. As Charles Lowe points out in his insightful introduction to *Biology of Whiptail Lizards (Genus* Cnemidophorus) (Wright and

Vitt 1993), the famous herpetologist Edward Drinker Cope considered this genus the most difficult in all of herpetology. Yet Cope had seen only the tip of the iceberg: parthenogenetic *Cnemidophorus* were not discovered until 1958 (not published until 1962), adding a new element of confusion to the genus.

Discovery of parthenogenesis in East Asian Lacerta by Ilya Darevsky (1958) sent the American herpetologists Richard Zweifel and Charles Lowe deep into their collections searching for the answer to a question implicit in an observation first made by Sherman Minton (1958); why were there no males in Cnemidophorus tesselatus? Indeed, not only did C. tesselatus prove to be parthenogenetic, but a swarm of parthenogenetic Cnemidophorus were found to occur all across the southwestern United States and northern Mexico, all very difficult to sort out. Zweifel and Lowe (1966) discovered three characters—number of scales around midbody, number of scales between paravertebral stripes, and number of scales on toes—that were sufficient to distinguish one species of Cnemidophorus from another. Of course, in those days we didn't have the fancy molecular techniques that now dominate systematic herpetology, but at least Cope's most difficult genus could finally be sorted out into species.

Among teiids, whiptails are most widespread geographically and appear tied to open habitats to a much greater extent than *Ameiva*, *Kentropyx*, or most largerbodied genera. These lizards are most frequently encountered on beaches and desert flats, in tropical dry forest, and along edges of relatively closed habitats such as forests. They often use roads and trails to get to open patches within forest in tropical regions. As a group, they are also among the most terrestrial of teiids, rarely entering water or climbing into vegetation.

In addition, whiptails—which appear quite nervous while foraging, often darting off at the slightest provocation—are among the most active of Lacertiformes. Their high activity levels are supported in part by their high body temperatures. *Cnemidophorus deppii*, for example, which live on open beaches in western Central America, average nearly 40°C while active.

In temperate North and South America, whiptails are active during summer, with activity falling off rapidly as fall approaches. In North America, adults disappear underground in August (though juveniles remain active until September or October), and reproduction is highly seasonal, occurring in spring and early summer (as, for

example, in *Cnemidophorus inornatus* and *C. neomexicanus*; Christiansen 1971). In tropical environments where annual temperatures are relatively constant, activity and reproduction can occur nearly year round (as in *C. ocellifer* in northeastern Brazil; Vitt 1983).

A North American species, *Cnemidophorus tigris*, ranges from southern Idaho through Sonora and Baja California. Because of its wide distribution, it exemplifies geographic variation in ecological traits. In the north, *C. tigris* are active at both lower body temperatures and lower ambient environmental temperatures than in the south. Their seasonal period of activity is also shorter in the north. Frequencies of broken regenerated tails are higher in the south (Pianka 1970a). Most whiptails eat a variety of insects (particularly termites) and spiders, but some, such as *C. lemniscatus*, add fruits to their diet, and a few, such as *C. murinus* and *C. arubensis*, are herbivorous.

Ameiva, which occur through southern Mexico, Central America, and much of South America, with numerous island species in the Caribbean, are very much like Cnemidophorus in general morphology and behavior. As in Cnemidophorus, Ameiva are terrestrial. Diets are varied but include a diversity of invertebrates, small vertebrates, and fruits (Vitt and Colli 1994; Censky 1996). A. ameiva in South America has been best studied. This alert, fast-moving, large (190 mm SVL) lizard is common in virtually every open habitat within its range, even entering cities to forage alongside dogs in garbage heaps! It is among the most conspicuous of lizards in Venezuelan llanos, cerrado, caatinga, and lowland rain forest habitats. Ameiva ameiva maintain body temperatures of 37°C and higher, regardless of habitat, and can be seen in strikingly large numbers in lowland forest along roads, trails, and river edges where direct sunlight hits the ground (Sartorius et al. 1999).

Like many other teiids, *Ameiva ameiva* digs a burrow where it remains while inactive. Burrows generally have a single entrance and are left open while the lizard is inside. When on flat ground, burrows are shallow, with the terminal chamber just under the surface. If an intruder digs into one of these burrows, the lizard typically emerges through the roof of the terminal chamber and dashes off. On steep hillsides, burrows often go straight into the bank and may likewise be rather shallow. Although lizards have no escape routes from these shelters, their location—sometimes as much as 4.5 m up the bank—likely discourages many predators.



The large teiid Ameiva ameiva occurs in nearly all tropical habitats of South America. (Laurie Vitt)

In Central America, several species of *Ameiva* occur along beaches and in dry forest of the west coast, including *A. festiva* and *A. quadrilineata. Ameiva festiva* also occurs in rain forest of eastern Central America, along the Caribbean. Just north of Río San Juan in Nicaragua, *A. festiva* is a common forest species near treefalls. In many respects, including coloration and color pattern, it appears nearly identical ecologically to *Kentropyx pelviceps* of lowland Amazonian forest, foraging and basking in treefalls but also entering forest to forage for brief periods before its body temperature falls (Vitt and Zani 1996d). However, it doesn't climb like *Kentropyx*.

At least 12 species of *Ameiva* occur on the Lesser Antilles. Each island has a single species, with one exception: the Anguilla Bank has two, *A. corax* and *A. pleii* (Censky and Paulson 1992). Unlike *Anolis*, which colonized the island arc from the west (Puerto Rico), *Ameiva* colonized from the mainland to the south. When sea levels were much lower during the Pleistocene, islands were larger and separated by less water. The fact that most islands have but a single species suggests that *Ameiva* are their own strongest competitors. On the Anguilla Bank, the

two species are different in body size, with adult male A. pleii reaching 181 mm SVL and A. corax reaching only 132 mm SVL. Those 50 mm may represent the minimum body size difference allowing coexistence. Of course, juveniles are much more similar in size and probably face intense interspecific competition as a result.

This divergence in body size, both within and among genera, is in fact fairly common among teiids (see below). Unlike iguanian species, which vary considerably in overall morphology and often segregate by microhabitat, teiid species are strikingly similar morphologically (with a few exceptions). Yet because they cover large areas while foraging, and forage at about the same time of day, encounters among individuals and between species occur frequently. Hence, divergence in body size appears to allow coexistence. Examination of body sizes and DNA-based phylogeny for populations of C. tigris and C. hyperythrus from Baja California, Mexico, and associated islands, for example, reveals that body size has evolved in both species and that when the two species occur together, one (C. hyperythrus) is small and the other (C. tigris) is large (Case 1979, 1983; Radtkey et al. 1997). When these two species

occur alone, however, they are intermediate in size, indicating that optimal body size in a single-species guild differs from that in a two-species guild. This phenomenon, in which a character shifts away from the norm in response to interaction with another species, is referred to as "character displacement." One consequence of divergence in body size in teiids is that prey can be partitioned on the basis of size, offsetting competition for food.

Kentropyx (= spur or point rump, referring to spikelike enlarged scales on either side of the male's cloaca) is easily distinguished from all other teiids by a single feature: keeled ventral scales. These scales may help hold lizards against branches and leaves while climbing in vegetation. The eight species of this genus are restricted to mainland South America (Gallagher and Dixon 1991). Some (e.g., K. pelviceps, K. altamazonica, and K. calcarata) occur only in Amazon forest habitats or gallery forests along rivers that extend into savannalike grasslands, or cerrados, of central Brazil. One, K. altamazonica, though generally associated with waterways in lowland rain forest, has also been found far from water in patches of cerrado isolated in tropical rain forest of Rondônia. Others, such as K. vanzoi and K. striata, live in grasslands, the former in portions of cerrados and the latter in patchily distributed Amazon savannas. Most Kentropyx are excellent climbers, often ascending forest-edge trees where they lie atop leafy vegetation or on branches basking in the morning sun to gain heat. Body temperatures of *Kentropyx* are slightly lower than those of whiptail lizards but still higher than those of lizards in most other families. Some forest species, such as *K. calcarata*, can often be found in large numbers by searching exposed surfaces along forest edge. Juvenile K. calcarata climb into shrubs and work them much as birds do, gleaning insects and spiders from tops and bottoms of leaves as well as from twigs, limbs, and trunks. Kentropyx forage continuously, ceasing only when body temperatures drop below their preferred range or when they are copulating.

Two genera of large teiids, Crocodilurus and Dracaena (maximum SVL being about 220 mm and 450 mm, respectively), are semiaquatic. The single species of Crocodilurus, C. lacertinus, is widespread in the Amazon and upper Orinoco regions, Dracaena guianensis is widespread in Amazonia, and D. paraguayensis occurs in the Pantanal region of southwestern Brazil and extreme northwestern Paraguay. Members of both genera climb into trees along watercourses to bask, often lying on branches with their



Dracaena guianensis is an aquatic Amazonian teiid, a snail specialist during wet season. (William W. Lamar)

limbs and tail hanging free, appearing to be precariously balanced on the limb (Vanzolini 1961). Both are also graceful swimmers, folding their legs back against their body and swimming in a serpentine manner with head up. Tails are laterally compressed in both genera and have a double dorsal crest, providing forward thrust as it is moved back and forth. While foraging in shallow water, these lizards frequently walk on the bottom in search of prey. Not only is the water relatively warm, but the lizards' large size probably offsets some heat loss as well. When disturbed in water, they typically swim away from an intruder; they can also move quite rapidly on the water's surface, using a combination of serpentine locomotion powered by tail thrusts and rapid movement of front and hind limbs. Locomotion across water does not appear to be bipedal, and their body never raises off the surface. They can switch from a methodical swimming locomotion to rapid surface escape nearly instantaneously, demonstrating that tail thrust assisted by leg action is powerful.

Crocodilurus is a drab brown to greenish above, though juveniles are mottled with orange, particularly on their limbs, which renders them nearly invisible against water and leaf litter. Most striking are the large, rectangular scales of the ventral body surface, which are brilliant enamel-white in juveniles and enamel yellow in adults. No ecological studies have been conducted on this species, so most natural history observations are anecdotal. The few individuals that have been examined fed on juvenile toads and insects (Martins 1991), suggesting that their diet probably includes most catchable invertebrates and small vertebrates.

Dracaena, often found in the same swamps and water-

ways as *Crocodilurus*, is primarily a snail specialist, crushing mollusk shells with its powerful jaws and large molariform rear teeth and expelling pieces of crushed shell with the tongue. *Dracaena* enters flooded forests (*igapo*) during the wet season to forage. During dry season, when flooded forests dry out, *D. guianensis* forages in trees, apparently searching for insects and possibly bird eggs (Goulding 1989).

Tupinambis are by far the most impressive terrestrial teiid lizards, with two species, T. merianae and T. rufescens, reaching a snout-vent length exceeding 500 mm; their tail is nearly twice SVL, bringing maximum total length up to about 1300 mm (Fitzgerald et al. 1991). Six species are currently recognized, two of which have been described only in the last decade: T. longilineus, from the western Amazon (Avila-Pires 1995), and T. quadrilineatus, from central Brazil (Manzani and Abe 1997; Colli et al. 1998). These impressive animals march around during the heat of midday in search of prey, covering large areas while foraging. One species, T. teguixin, is most common along watercourses, where it feeds at the edge, often walking through shallow water. Tupinambis merianae, occurs in relatively open areas of northeastern and central Brazil and

on into southern South America. The largest *Tupinam-bis, T. rufescens,* the red tegu, occurs in rather arid habitats of the Chacoan biotic province (Fitzgerald et al. 1991). The somewhat diminutive and slightly more streamlined *T. longilineus* occurs along rivers and streams in the western Amazon of Brazil. The first individual was found in central Rondônia in 1986 and described nine years later (Avila-Pires 1995); since then, three others have been collected and several more seen near Rio Ituxi, a tributary of Rio Purus in western Amazonas, Brazil.

All species of *Tupinambis* are dietary generalists. Arthropods, mollusks, and small vertebrates, particularly frogs, are common in their diets, as is carrion. They also feed seasonally on plant materials, especially fruits. The large *T. teguixin* raid nests of turtle eggs (*Podocnemis unifilis*) on breeding beaches and most likely prey on eggs of other oviparous reptiles as well (Avila-Pires 1995). All species can swim; some, such as *T. teguixin*, enter large rivers when disturbed and swim to the other side.

Tupinambis have larger clutch sizes than most teiids, partly a consequence of their large body size. For example, *T. rufescens* in Argentina average twenty-one eggs per clutch, with larger females producing larger clutches



Crocodilurus lacertinus is one of two large teilds that spend much of their time swimming in search of prey. (Laurie Vitt)



Tupinambis longilineus is known from only four specimens.

(Janalee Caldwell and Laurie Vitt)

(Fitzgerald et al. 1993). Nesting habits of some species have caught the attention of naturalists throughout history. William Beebe, a well-known naturalist working with the New York Zoological Society in the first half of the twentieth century, stated, for example, that "direct or indirect evidence of six separate nestings of tegus in the nests of termites were found at Karatabo and Caripitu. These varied from two feet above the ground to as high as twelve. Five were three to four feet up in low growths" (Beebe 1945). Female Tupinambis, when ready to deposit eggs, climb tree trunks and vegetation seeking out nests of arboreal termites in the genus Nasutitermes. Although these primarily terrestrial lizards have no obvious specializations for climbing (e.g., prehensile tails, recurved claws, toe fringes), nevertheless they do climb trees to dig large holes in the massive, dark-colored, and bulbous-shaped termite nests—ideal substrates for egg development and deposit their clutches of ten or more eggs. Termites in the meantime swarm over the nest, but their chemical defenses and minuscule bites have little apparent effect on these big lizards. Once a lizard finishes depositing its clutch, termites repair the nest, sealing the lizard eggs inside. Nests remain relatively warm and humid due to the termites' own metabolism. When eggs hatch, one or more juveniles dig out and the remainder follow (Dixon and Soini 1986). Several large varanids use termitaria for nesting chambers as well (see chapter 13).

RICHEST KID IN TOWN

One should never underestimate the ingenuity of young children when money can be made. In 1977, while I was a postdoctoral research fellow of the Museu de Zoologia da Universidade de São Paulo working in semiarid caatinga in interior northeastern Brazil, I marshaled the help of about a dozen very enthusiastic local youths (all boysyoung girls were not allowed to go out alone) to help me capture lizards. On any given day, more than a hundred lizards of sixteen species might be brought in. I paid the children 1 cruzeiro (about \$0.05) per lizard, but since Tupinambis merianae were quite large and difficult to capture alive, I increased the price to

20 cruzeiros for adults of this species. One small kid, measuring about 1.5 m, seemed especially good at collecting them. I recall one day when he and his dogs had dug out two large adults. Arriving at my field lab at about 8:30 A.M., he held the lizards by their heads, with each lizard's tail dragging on the ground behind him. Later, at the end of the dry season, he brought me the first juvenile Tupinambis I had seen. He wanted 20 cruzeiros for it, but I told him that it was a small lizard and not worth as much as an adult. We finally settled on a compromise price of 10 cruzeiros. After we exchanged money and lizard, he sort of sheepishly asked me if I wanted any

more "small" ones, to which I replied, "Of course, I'll take all you can catch." He went running off, with a sly grin on his face; it never occurred to me that he might have found a nest. About half an hour later he returned with thirteen juvenile T. merianae for which I was of course compelled to pay 10 cruzeiros each, for a total of 130 cruzeiros! I got him to tell me that he had found the nest in the process of hatching, but he refused to show it to me. The most I coerced out of him was that it was in a tree inside a "casa de cupim" (termite nest). He brought me more adults over the course of the following six months but never found another nest. (VITT)



Tupinambis tequixin is widespread in South America and likely will prove to be several species. (Laurie Vitt)

Some smaller teiids include fruit and flowers in their diets. For example, in the Amazon savanna region of Roraima in northern Brazil, species in three genera, Cnemidophorus, Kentropyx, and Ameiva, eat yellow fruits of a locally common plant, the Muruci (Vitt and Carvalho 1995). Three teiids, Cnemidophorus arubensis, C. murinus, and Dicrodon guttulatum, are herbivores. The first two apparently can detect alkaloids, such as quinine, in plants, and thereafter can presumably selectively avoid alkaloidcontaining plants or at least balance their intake of potentially toxic plants against their recent dietary history (Schall 1990). These lizards' ability to detect potentially toxic chemicals in plants is not surprising, considering that most scleroglossan lizards use chemical signals to discriminate among prey types. Apparent teiid avoidance of insects such as ants, hemipterans, and particularly noxious beetles likely reflects this ability as well, since many defensive chemicals produced by insects are alkaloids.

GYMNOPHTHALMIDAE

Gymnophthalmids (= naked eye), also known as microteiids, are the sister taxon to teiids. All species are small,

most are terrestrial, some are semiaquatic, and a few are partly arboreal. About 36 genera and 160 species are known. Most species are elongate and thin bodied when compared to other lizard taxa, have relatively short limbs, reduced to varying degrees in some species and nearly absent in others. Most have transparent windows in their lower eyelids, allowing them to see when their eyes are closed. These are strictly New World lizards (Presch 1980). As a group, they are pretty much limited to tropical latitudes, but gymnophthalmid diversity is high in both lowland Amazonian forest and foothills, valleys, and hillsides of the Andes. Some species, such as Pholidobolus macbrydei, even reach high elevations in the Andes (Montanucci 1973; Hillis 1985). Proctoperus bolivianus occurs as high as 4000 m in the Peruvian Andes. Aside from a few tiny geckos (Sphaerodactylus, Coleodactylus, Pseudogonatodes, and Lepidoblepharis), these are the smallest species in New World tropical lizard assemblages.

As many as ten species of gymnophthalmids can occur together. For example, in the Juruá River system of western Brazil in the state of Acré, the following species have been found within one square kilometer: *Neusticurus ecpleopus*, *N. juruazensis*, *Alopoglossus atriventris*, *A. angu-*



This Amazonian rain forest gymnophthalmid, *Alopoglossus atriventris*, lives in leaf litter. (Laurie Vitt)



Neusticurus ecpleopus is a semiaquatic gymnophthalmid that lives in small Amazonian streams. (Janalee Caldwell)

latus, Iphisa elegans, Prionodactylus argulus, P. oshaughnessyii, Ptychoglossus brevifrontalis, Cercosaura ocellata, and an as yet undetermined species of Bachia. These species account for about one-third of the lizard species in this particular assemblage.

Unlike teiids, which often vary by size when occurring together, all gymnophthalmids are small, with many about the same size. Also unlike teiids, in which the maximum number of species occurring together seems to be about four, gymnophthalmids can coexist in larger numbers of species. Reasons for this are complex, but their body size relative to the structural diversity of habitats occupied may provide a partial explanation. Large animals must range over larger areas than small ones and so tend to use a greater range of habitats. Small species, in contrast, perceive smaller environmental elements than do

larger species. During a typical foraging bout, for example, a large-bodied lizard such as the teiid *Ameiva ameiva* might traverse leaf litter, bare ground, stream banks, and clusters of debris associated with treefalls—all relatively small areas compared to the extent of land an individual *Ameiva* covers during a normal day. In an absolute sense, then, the structurally diverse forest habitat is a mosaic of accessible patches to an *Ameiva*. Yet what appears as a mere patch within an *Ameiva*'s foraging area would be an entire landscape to a small lizard whose foraging bouts cover just a few square meters on any given day.

Gymnophthalmids divide their space equitably. Neusticurus ecpleopus, to cite one representative gymnophthalmid, lives at the forest-stream interface and is nearly always associated with stream banks. The closely related N. juruazensis, in contrast, lives one step removed: in low, damp areas associated with forest streams but not directly on banks with N. ecpleopus. Where low vines and shrubs occur, the long, streamlined lizard Prionodactylus argulus lives above the ground on shrubs and vines. P. oshaughnessyii forages at the bases of trees and on and around fallen logs, often seeking patches of sunlight breaking through the forest. In leaf litter, where layers of leaves produce a microhabitat with an enormous surface area available for exploitation, tiny Iphisa elegans moves in and among leaves, often seeking those same migrating patches of sunlight. In piles of debris associated with treefalls, Cercosaura ocellata negotiates twigs, branches, and vines, occasionally climbing off the ground to forage. In the structurally diverse microhabitat created by packs of leaf litter along streams and in low areas, Alopoglossus angulatus moves in and out of crevices, while under leaf litter and rotted logs the nearly limbless Bachia moves about like a miniature animated sausage in search of termites. Each of these small gymnophthalmids, along with their many cousins, is associated with specific habitat patches.

Species of *Bachia* are undoubtedly among the strangest gymnophthalmids. Their bodies are sausagelike: front limbs, back limbs, or sometimes all limbs are reduced to paddlelike structures that appear to be used for locomotion associated with foraging. With SVL just under 30 mm, *Bachia* pull and push themselves by their tiny limbs as they move about under leaf litter and along edges of decaying logs. Although the Guiana earless microteiid *Bachia cophias* uses its tiny three-toed appendages when moving slowly, when in a hurry it resorts to serpentine locomotion, undulating body and tail laterally from side to side





Clockwise from left: Male *Prionodactylus oshaughnessyi* are brick red on the sides during the breeding season. (Laurie Vitt) *Cercosaura ocellata* is often found in leaf litter within rain forest treefalls. (Laurie Vitt)

Iphisa elegans, with its two dorsal and two ventral scale rows, is among the easiest of Amazonian gymnophthalmids to identify. (Laurie Vitt)



while holding its diminutive legs against its sides, dangling uselessly. In extreme emergencies, this 100–120-mm-long lizard flicks its tail like a spring, lifting itself completely off the ground about 25 cm and a full 30 cm forward (some Australian pygopodids in the genus *Delma* also leap like this) (Schmidt and Inger 1957). *Echinosaura* of northwestern South America and southern Central America is equally bizarre. In litter on forest floors in Panamanian and Colombian rain forests, little rough dark brown *Echinosaura* move slowly, resembling twigs. If touched, these lizards become rigid, looking even more strongly like a fallen twig.

Although most gymnophthalmids are associated with wet tropics, an impressively wide array of species occurs throughout relatively open areas of South America, particularly northeastern and central Brazil. Because so many areas remain to be explored in central Brazil, their diversity could be considerable. A species-rich gymnophthalmid fauna—comparable to or even more diverse than the lizard fauna found at most localities within Amazon rain forest—occurs in open habitats along sand dunes associated with the Rio São Francisco in northeastern Brazil. Miguel Rodrigues, currently director of the Museu de Zoologia da Universidade de São Paulo, discovered an entire reptile fauna in this area composed primarily of fossorial species, nine of which are gymnophthalmids (Rodrigues 1996). Of these nine, seven (representing four genera: Calyptommatus, Procellosaurinus, Psilophthalmus, and Notobachia) are endemic to the area; all are fossorial. The remaining two species are terrestrial gymnophthalmids, Vanzosaura rubricauda and Colobosaura mentalis, widespread in open habitats of South America. Of course, not all these lizards live at the same exact spot. One hypothesis is that the dunes date back to the Quaternary and were separated into two isolated sets as the Rio São Francisco made its way to the Atlantic Ocean sometime after the last glaciation. As a result, "sister species" occur on each side of this river. The river probably changed course, cutting off populations from one another (perhaps multiple times), generating high diversity through a process known as allopatric speciation. The wormlike *Calyptom*matus sinebrachiatus, for example, occurs in dunes on the river's north side, whereas C. leiolepis and C. nicteris are found on dunes on the south side. Interestingly, the latter two are isolated from each other as well, each occurring in its own set of isolated sand dunes.

Among dune gymnophthalmids, Vanzosaura rubricauda

is the most widespread, occurring from caatinga of northeast Brazil to deserts of Argentina, where it can be locally abundant. Two distinct color morphs are known for this species: one is a black and white lined version with an orange or red tail; the other is a nearly unmarked gray lizard with a red or orange tail.

The Andes appear to be a center of diversity for some gymnophthalmid genera. In Ecuador, Pholidobolus has diversified into a nearly linearly arranged set of five species occurring both in valleys and on Andean slopes to elevations exceeding 3000 m (Montanucci 1973). Distributional ranges of two species, P. montium (north) and P. affinis (south), appear to be dynamic. After 1973, when Richard Montanucci first described these species' distributions, a considerable amount of human activity caused drastic habitat change at the zone of contact between these two species. As a result, the contact zone shifted at least 30 km south in only twelve years (Hillis and Simmons 1986). At slightly lower elevations in Ecuador and extending northeast through Colombia as far as Panama and Costa Rica, the genus Ptychoglossus has also diversified, into 15 known species (Harris 1994). The distribution of this genus includes tropical lowlands of the Brazilian Amazon, a difficult habitat in which to collect, as the paucity of records from tropical forest suggests.

At elevations of 2000–3000 m in the Peruvian Andes, the gymnophthalmid genus *Macropholidus* can be found in a variety of habitats, including montane cloud forest, disturbed forest, brushy hillside, and even some open areas (Cadle and Chuna M. 1995). Like other gymnophthalmids, *Macropholidus* is diurnal and active in leaf litter, seeking refuge under rocks. Like low-elevation gymnophthalmids, *Macropholidus* reproduces over an extended time period (January–June) corresponding to the wet season and early to mid dry season. Nesting is communal, with many eggs being laid in a single location. At one site, Cadle and Chuna M. found remains of 220 eggs in addition to 8 unhatched ones! In this case, nesting sites for small reptiles would appear to be limited because snake eggs were found in lizard nests as well.

Parthenogenesis occurs within a number of gymnophthalmid genera and may ultimately prove to be widespread. The best-known parthenogenetic gymnophthalmid is *Gymnophthalmus underwoodi*, a small, slender, smooth-scaled lizard with a bluish tail that occupies disturbed areas in lowland forest of northeastern South America. In the Brazilian state of Roraima, three species



The fast-moving gymnophthalmid *Arthrosaura reticulata* lives near streams at the interface of downed logs and the forest floor. (Laurie Vitt)

of Gymnophthalmus are known. One is G. underwoodi. The second is G. leucomystax, a similar lizard but with a brown tail. Endemic to Roraima, it is associated with termite nests in the Lavrado area, a savanna grassland that is part of a system of Amazon savannas extending from the north Amazon across the central Amazon, with patches elsewhere. It is a sexually reproducing species with typical males and females. A third Gymnophthalmus, a small, redtailed lizard, is found along gallery forests associated with major waterways such as the Rio Branco in Roraima. This undescribed species often occurs at high density in leaf litter underlying gallery forest. When approached, it dives into the leaf litter, leaving its tail exposed and moving about, presumably to distract a predator's attention from its body. Like G. underwoodi, it is parthenogenetic. Chromosomal data reveal that karyotypes of the three species are distinct, even though the parthenogenetic ones were once both classified as G. underwoodi (Yonenaga-Yassuda et al. 1995). Moreover, G. underwoodi from Roraima has a different karyotype than G. underwoodi from other localities, indicating that all three parthenogenetic species (the two G. underwoodi and the undescribed red-tailed species) arose independently from other G. underwoodi.

Sexual dimorphism in size, relative head size, and coloration exists in some gymnophthalmids but is absent or reduced in subterranean species. Because this large family contains so many completely different genera, no single description suffices. In *Neusticurus, Cercosaura*, and some species of *Prionodactylus*, males have slightly larger heads than females and sport conspicuous, circular, target-shaped markings on the sides of their bodies. Male *Alopoglossus* have black lateral stripes and black markings on the face. In the widespread open-habitat species *Vanzosaura rubricauda*, males are smaller than females but have relatively larger heads. In addition, while reproductively active, males have red or orange on their jaws, throat, and front legs.

Unlike members of their sister taxon the teiids, which generally have high body temperatures while active, many gymnophthalmids are active at lower body temperatures. For example, *Arthrosaura reticulata*, common along streams, averages 26.6°C; *Neusticurus ecpleopus*, which lives on stream banks and frequently enters water, averages 23.8°C; semiarboreal *Prionodactylus oshaughnessyii*, which is often found on tree trunks or logs, averages 26.2°C; and the tiny *Leposoma percarinatum*, also as-

sociated with damp areas, averages 28°C. All these very active lizards live in Amazon rain forest and can often be found in patches of filtered sunlight. Body temperatures of gymnophthalmids in open habitats remain unknown, but considering the secretive habits of most, they are probably low. Some terrestrially active species in open areas, like *Vanzosaura rubricauda*, may have high body temperatures.

LACERTIDAE

Lacertids are found across Eurasia and Africa and into Southeast Asia but do not reach Australia. About 27 genera and 220 species are recognized. Appropriately named (*lacerta* is Latin for "lizard"), lacertids are small to medium-sized diurnal lizards with movable eyelids, long cylindrical bodies, and well-developed legs. Most species have small smooth body scales, but a few have enlarged or spiny scales. Head scales are large. Lacertid teeth are hollow at the base (teiid teeth are solid). Virtually all lacertids are terrestrial or rock-dwelling lizards, although a few species, including *Holaspis* and *Takydromus*, climb in

vegetation, and at least one appears to live high in trees. Most are insectivorous, and all but one species lay eggs. Some populations of European *Lacerta vivipara* bear living young, whereas others lay eggs. Sometimes quite colorful (as, for example, the large—250 mm SVL—*Lacerta lepida* from Spain), lacertids cannot change color rapidly, though some do change color over the course of their lives. Most lacertids are sexual, but five unisexual (all-female) species exist, all of which occur in the genus *Lacerta* and are found in southwestern Asia (Darevsky 1958).

Some species are highly adapted to loose sands. In northern Africa, sandy desert regions support lacertids (Acanthodactylus) with fringed toes, shovel noses, and countersunk lower jaws. Far away in the Southern Hemisphere, on windblown sand dunes of the Namib Desert of southwestern Africa, an independent clade of lacertids has evolved similar life forms, containing the species Meroles ctenodactylus, M. cuneirostris, and M. anchietae. The impact that wind-blown sand habitats can have on evolution of lizard morphology is striking. The North American iguanid genus Uma, the Saharan skink genus Scincus, and the Namibian desert gerrhosaurid Angolosaurus



Lacerta schreiberi is often referred to as the Iberian emerald lizard. (Chris Mattison)

skoogi have all converged on body plans very similar to those of sand-dwelling lacertids, including countersunk lower jaws, shovel noses, and fringed toes.

A beautiful Kalahari lacertid, *Nucras tessellata*, consumes considerably more scorpions than most other lizard species. *Nucras* are active during the heat of midday at body temperatures of 39.3°C (probably a predator avoidance tactic), foraging widely to find and dig up large scorpions in their diurnal retreats (by day, scorpions are exceedingly patchily distributed, nonmobile prey items) (Pianka et al. 1979). Scorpions are extremely large and nutritious, a benefit that presumably facilitated evolution of dietary specialization in *Nucras*.

Holaspis guentheri lives in forests in central Africa. Scales on each side of its unusual tail project out, down, and backward. These lizards press their tails against trees while climbing, using projecting scales to catch the bark. They also have rows of enlarged scales under their feet and other projecting scales along the base of their toes that help them cling to trees with smooth bark. Holaspis guentheri are boldly striped with yellow and black on their backs and display orange ventral surfaces (Schmidt and Inger 1957). Their tails are also brightly banded, and these lizards coil their tails, particularly while inactive, perhaps mimicking centipedes or millipedes.

Gastropholis echinata is bright green and lives in trees in African rain forests. These moderately large lizards (about 100 mm SVL) have a broad ring of spiny scales around the base of the tail that facilitates climbing (Schmidt and Inger 1957). In some respects, Holaspis guentheri and G. echinata appear convergent with Kentropyx (Teiidae) in that they are climbing members of a generally terrestrial group of lizards.

Still another genus of climbing "grass-swimming" lacertids is *Takydromus* (= speed runner), a group of slender, long-tailed, green lacertids from Southeast Asia (some are found in Taiwan and Japan as well). These lizards look like grass blades and are at home climbing in the top of tall grasses. A lizard with a snout-vent length of 60 mm may have a tail 300–350 mm long, which allows it to distribute its weight over many grass stems. *Takydromus* jump from stem to stem, often turning sharply, making it difficult to follow their movements through the grass.

The unusual *Ophisops* (= snake eyed) is found in northern Africa and southwestern Asia. While some lacertids have a large transparent disk in the center of the lower eyelid through which they can see even when their eyes



This Kalahari lacertid, *Nucras tessellata,* is a scorpion specialist. (Eric Pianka)

SURPRISES IN THE SAND

Lizarding in the Kalahari with Ray Huey and Larry Coons was usually a lot of fun, but at times it got pretty scary. Our biggest concern was lions and leopards, but cobras and puff adders were also hazards. Horned sand vipers, for example, bury themselves in the sand waiting for an unsuspecting lizard to move past; many widely foraging lacertids are ambushed by these snakes. We disturbed many a buried viper while probing around grass tussocks looking for legless burrowing skinks. When one of these little red snakes comes leaping out of the sand, it lifts its entire body completely off the ground as it hisses and lunges. We aren't afraid of snakes, but we were exceedingly surprised every time one of these vipers came thrashing at us with such menace. Puff adders, large vipers the size of big rattlesnakes, though much more dangerous, were less common than horned sand vipers. A large one can have fangs 3 cm long, and they are highly venomous. These big snakes are camouflaged with blotches that break up their outline. Usually you don't see a puff adder until it hisses loudly when you're right on top of it: needless to say, this can be quite startling! (PIANKA)

are closed, in *Ophisops* these disks are so large that the eyelid is no longer movable.

The Kalahari lacertids *Meroles suborbitalis* and *Pedio-planis lineo-ocellata* sit and wait for prey, whereas two other species found in the same microhabitats, *Heliobolus lugubris* and *Pedioplanis namaquensis*, forage widely for their food. Judging from their relative stomach volumes, those species that engage in this active mode of food gathering capture more prey per unit time than do sit-and-wait species—as would be expected, given that active foraging is energetically expensive, requiring a greater overall energy budget (Huey and Pianka 1981; Anderson and Karasov 1981). Compared with sit-and-wait species, widely foraging lacertid species eat more termites, which are sedentary, spatially and temporally unpredictable, but clumped prey.

Another ramification of foraging mode in these Kalahari lizards concerns exposure to predators. Because of their more or less continual movements, widely foraging species tend to be more visible and, as a result, suffer higher predation rates by some kinds of predators. Active foragers fall prey to predators that hunt by ambush such as the horned sand viper, *Bitis caudalis*, whereas sitand-wait species tend to be eaten by predators that forage widely, such as secretary birds. "Crossovers" in foraging mode thus occur between trophic levels.

Among the most spectacular lacertids is the giant (by lacertid standards) *Gallotia simonyi* (260 mm SVL), an endangered species living on the island of El Hierro in the Canary Islands. A smaller species, *Gallotia caesaris*, also occurs on El Hierro, and several other *Gallotia* occur on surrounding islands. These lizards are apparently omnivores, eating both animal and plant material (primarily fruits).

Some *Lacerta* and *Podarcis*, especially those on islands in the Mediterranean, eat large numbers of ants. Whether the ants eaten by these scleroglossans contain defensive chemicals remains unknown.

The most striking evolutionary divergence within lacertids is dietary specialization on ants in various species of *Acanthodactylus* (Arnold 1984). A detailed analysis of the diet of one species, *A. erythrurus*, combined with sampling of insects in the lizard's habitat over a six-month period, for example, indicates that although beetles and Heteroptera (true bugs) dominate the diet during four of six months, and beetles are more frequently eaten in five, dur-

ing the sixth month ants are more frequently eaten; indeed, no heteropterans were captured in the lizard's habitat during that month, whereas 68 percent of insects trapped were ants.

XANTUSIIDAE

Xantusiids are commonly referred to as night lizards, though that name may be something of a misnomer (see below). Affinities of these distinctive lizards with other lizard groups remain uncertain. They could be the sister group to Lacertiformes, or they might even belong with Gekkota, as suggested by the fact that they, too, lick the spectacles over their eyes (Greer 1985a). Scales on their backs are small, granular, and, with the exception of Lepidophyma, nearly uniform in size, while those on their bellies are large and rectangular shaped. Eyelids are absent; instead these lizards possess a fixed spectacle like those seen in many geckos, pygopodids, some skinks, and snakes. The lower eyelid has become permanently fused in the "up" position, fitted with a clear scale through which the lizard can see. Pupils are elliptical, suggesting activity when light levels are low. Their catlike pupils no doubt led to the notion that they are strictly nocturnal, but in fact some night lizards are as much diurnal as nocturnal; their daytime activity is simply restricted to dark, protected places where they are difficult to observe. All xantusiids are viviparous and have evolved a mammal-like



The tropical xantusiid *Lepidophyma mayae* is found in Central America and southern Mexico. (J.A. Campbell)



Long-lived yucca night lizards, *Xantusia vigilis*, live in rubble under Joshua trees. (Jim Rorabaugh)

arrangement whereby the mother nourishes her litter "in utero." Placentation in xantusiids is not as extensive as in certain skinks, but at least a portion of nutrients required for development pass from mother to offspring via a placenta.

Found only in North America, Central America, and Cuba, these generally small lizards (less than 50 mm SVL) are sedentary, patchily distributed, and long lived. Species occurring on islands off the coast of southern California are an exception in terms of size, being by xantusiid standards quite large: 100 mm SVL. The three genera—Xantusia, Lepidophyma, and Cricosaura, comprising some 21 known species and subspecies (Bezy 1989; Papenfuss et al. 2001)—are similar in appearance, differing primarily in minor details of scalation and color pattern. Most species in the genus Xantusia live under exfoliating granite, other rocks, or in Joshua tree rubble in deserts of

SECRETS IN THE ROCKS

As a graduate student, I was in awe of several herpetologists. One was Donald W. Tinkle of the University of Michigan, who came to my school, Arizona State University, as a Maytag visiting professor. (For me, interested as I was in lizard life histories, this was something like having John Lennon drop in on a rehearsal of my rock band.)

At the time of his arrival, a fellow graduate student, Justin Congdon, and I had been collecting around the state; one favorite site was the boulder piles near the one store (and only building) in the "town" of Sunflower, about 50 km north of Phoenix. We collected good numbers of Xantusia there, always under exfoliating granite or in deep crevices. We were struck by the fact that these Xantusia were larger than the X. vigilis we could collect a mere 18 km away under plant debris on the desert floor. In addition, they were flattened and had large spots on their bodies, similar to X. henshawi.

When we showed these lizards to

Tinkle, he was convinced they represented a new taxon and proceeded to contact one of his colleagues, Robert Webb, with the intention of describing it as a new species. After examining the lizards closely and assembling data on scale counts used in xantusiid taxonomy, however, they could find no characters that separated it from *Xantusia vigilis* except that it was larger, flattened, and colored differently.

As it turned out, Robert Bezy had explored the problem a few years earlier while a graduate student at the University of Arizona in Tucson (Bezy 1967). A flattened *Xantusia* from rock crevices in Arizona had been described decades earlier by Lawrence Klauber and named *X. arizonae* (Klauber 1931). When Bezy examined all collections and added new material, he concluded that *X. arizonae* was simply an ecomorph of *X. vigilis:* at a number of places, when *X. vigilis:* colonized rock crevices, its morphology had changed. Bezy concluded that these flatter *Xantusia* were a separate sub-

species, recognizing that origins of crevice dwelling must have occurred more than once within *X. vigilis.*

Bezy had not examined lizards from the Sunflower locality, and Don Tinkle thought our lizards differed enough to warrant attention. Observing his thought process as he progressed from absolute conviction that our Xantusia was an undescribed species to finally determining that it was exactly what it should be, and already described, impacted my approach to saurology in an important way. We are often convinced that we understand something based on minimal observations. When hard data are brought to bear and answers differ from what we first thought, the data must prevail or we aren't doing science. Ironically, in this case, Tinkle had been right from the start. The Sunflower lizards have just recently been described as a new species based on molecular data (Papenfuss et al. 2001). (VITT)

the southwestern United States and Mexico (Bezy 1988). Species of *Xantusia* that live in crevices are dorsoventrally flattened. Species in the genus Lepidophyma live primarily under and inside rotted logs in tropical habitats of Central America. Most are rounded in cross section, although the species that inhabit crevices, such as L. gaigeae, are dorsoventrally flattened like crevice-dwelling Xantusia. Some populations of the Central American species Lepidophyma flavimaculatum are unisexual. Both the use of crevices and the flattened morphology have arisen several times independently within xantusiids (Bezy 1989). This has occurred even within the single species of X. vigilis: populations living under Joshua tree logs and debris are cylindrical in morphology, whereas those living in crevices under exfoliating granite are flat. Cricosaura has smaller limbs than other xantusiids and typically moves in a serpentine manner. Xantusiids have relatively low body temperatures (about 29°C) and rapidly die when exposed to temperatures above 35°C for any length of time.

Xantusia vigilis, a small lizard (only about 40 mm SVL as an adult), lives in the Mojave Desert in rubble under Joshua trees and introduced saltcedars, where it can avoid the temperature extremes of the surrounding desert (Zweifel and Lowe 1966). Growth rates are surprisingly slow for such a small lizard, and sexual maturity is reached only after three years. During September, females produce from one to three live young. Survivorship is unusually high, with 80 percent of a cohort born in any given year living to reach sexual maturity. Some individuals live as long as nine years. Xantusia henshawi, which frequents granitic rock outcrops in southern California deserts, is larger, with adult males averaging 56 mm SVL and females averaging 62 mm SVL (Lee 1975). By living within crevices in exfoliating granite it, too, avoids high daytime temperatures. As in X. vigilis, live young are born in fall, and neonate number varies from one to two. Survivorship is also quite high. Diets of *Xantusia* species include beetles, ants, and spiders (Brattstrom 1952; Pianka 1986). Substantial numbers of seeds and other plant parts are eaten by the large-bodied *X. riversiana*, and all *Xantusia* eat their own shed skins, similar to geckos.

In a combination field and laboratory study, Julian Lee (1974) demonstrated that xantusiids move about actively during the day, a time period when these lizards are difficult to observe in nature (see also Mautz and Case 1974). These lizards are also active on exposed rocks shortly after sunset and may remain out until midnight, demonstrating nocturnal activity. Because lizards out at night tend to be adults, reproductive-related social behavior is likely, but it generally involves little movement; metabolic rates are slow as well, consistent with low activity levels (Mautz 1979). These lizards can therefore be considered both diurnal, in that substantial activity occurs within crevices during the day, and nocturnal, in that lizards position themselves outside crevices at night, likely in a social context.

Other xantusiids, it seems, are similar ecologically to *Xantusia vigilis* and *X. henshawi*. The giant *X. riversiana* and Central American *Lepidophyma* are secretive, living in holes, crevices, or under decaying logs. *Cricosaura typica* lives under rocks, logs, and other surface features in dry forest. *Cricosaura* differs from other xantusiids in that its limbs are reduced, body elongate, and its locomotion snakelike (Schwartz and Henderson 1991). Nevertheless, it could not be mistaken for anything other than a xantusiid: it looks like a stretched-out *Xantusia vigilis!* Even though the distribution is limited to a few areas in southern Cuba, these lizards are apparently fairly common. They feed on a variety of insects, including house crickets, insect larvae, and moths.