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Shedding Light on the Luminous Lizard (*Proctoporus shrevei*) of Trinidad: A Brief Natural History

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ABSTRACT.—A herpetological debate lasting nearly 70 years regarding the so-called luminous lizard, *Proctoporus shrevei*, of Trinidad is addressed. Published natural history accounts from the 1930s suggested that males of the species possess the ca-

pability of producing light. Despite the potential significance of such a trait in a terrestrial vertebrate, no direct studies of *P. shrevei* were conducted and findings from indirect studies were equivocal. To resolve the debate, a field investigation was conducted in May 2001 and 2002 with adult *P. shrevei* in Trinidad. Evidence supported the hypothesis that the lizards' scales are highly reflective and, when combined with fluctuations in dermal pigmentation, this produces an optical illusion consistent with early natural history observations. No evidence for bioluminescence was found. However, despite being a tropical organism, *P. shrevei* displays intolerance to heat and life history adaptations to relatively cold, cave-entrance microhabitats.

KEYWORDS.—Teiidae, Trinidad, bioluminescence, thermal ecology, ectothermy.

In March 1937, naturalist Ivan Sanderson collected specimens of the teiid lizard *Proctoporus shrevei* from cave entrances near the summit of Mt. Aripo in Trinidad, West Indies (Sanderson 1939). Males of this small, cryptozoic species (Fig. 1) are dark brown with a series of white lateral spots, each surrounded by a ring of black pigment (Parker 1935; Murphy 1997). These markings became the source of controversy when Sanderson described them as being luminous. As Sanderson (1939) recounts, "...in a crevice beneath a ledge I saw a dim light which promptly went out. I flashed the torch in and there was a small lizard. Putting a net over one end of the cleft, I tickled [the lizard], but instead of running out, it turned its head away from me and both sides lit up for a few seconds like the portholes on a ship. Eventually I got [the lizard] out with forceps, and as I held it up, it again lit up brilliantly." Specimens were subsequently shipped to the British Museum in London where they were examined *post mortem* by H. W. Parker. Parker

FIG. 1. The luminous lizard, *Proctoporus shrevei*, from the summit of Mt. Aripo, Trinidad. Photograph by: Mike Knight.

(1939) concluded that the translucent ocellar scales may have some connection with light and suggested three alternative hypotheses related to light production by the lizard:

1. Light is produced by an intracellular chemical reaction of some substance such as luciferin,
2. Light production occurs through phosphorescence,
3. The unique scales of *P. shrevei* are not luminous at all, but rather highly reflective.

Because Parker's evaluation was based on preserved specimens and not living lizards, no empirical evidence could be obtained to support or refute Sanderson's claim that the *P. shrevei* is capable of producing light.

Roth and Gans (1960) re-evaluated reports of the luminous lizard, providing a detailed examination of the histological structure of the ocellar scales from related species and citing unpublished observations by various biologists and naturalists. No evidence was found to suggest that *P. shrevei* or any related species is luminescent, however, Roth and Gans never made direct observations of *P. shrevei* specimens. Their conclusions, based on hearsay anecdotes and studies of related species, left the controversy surrounding *P. shrevei* unresolved. Most recently, the luminous lizard received further attention when it was featured in a popularized television documentary (produced by Discovery Communications Inc., 1999). This program sensationalized the search for *P. shrevei* in the mountainous rainforest of Trinidad. Following the capture of a single specimen, the documentary showed the lizard, in a darkened room, with what was claimed to be glowing ocellar scales. No scientific investigation was conducted, but the documentary rekindled the debate as to whether *P. shrevei* is actually bioluminescent.

To resolve nearly 70 years of herpetological debate, an investigation was conducted in May 2001 and May 2002. Two male *P. shrevei* were collected from rock crevices containing abundant damp leaf litter, near a cave entrance at the summit of Mt. Aripo, Trinidad (elevation approx. 940 m), Sanderson's original site of discovery. After initial examination in the field, specimens were transported to a station in Arima, Trinidad for further observation. Lizards were studied under light and dark conditions at different times during the day to test Parker's (1939) hypotheses of light production. These observations were compared with notes (Quesnel, personal observations) on a third lizard previously held in captivity. Neither field nor lab observations revealed any light emission from the ocellar scales of *P. shrevei*, thus eliminating the possibility of chemical light production. To test the hypotheses that the ocellar scales are phosphorescent or reflective, high-intensity light from a xenon lamp was directed at the lizards from varying angles. No light was emitted by the lizards, indicating that *P. shrevei* is not phosphorescent. However, light was clearly reflected by the lizards' scales, providing support for Parker's reflectivity hypothesis. We found that if *P. shrevei* is observed along the same plane from which light is directed, the normally obvious white ocelli cannot be seen against the reflection from all other scales. But, when viewed from an angle oblique to the light source, the ocelli appear brighter, while surrounding scales show no reflection. By varying the angle of reflected light, an illusion is created that the ocellar scales are intermittently emitting light, thus providing an explanation of Sanderson's original account of the lizard "switch[ing] on its portholes." The illusion produced by the reflective scales also explains recent accounts, as well as Sanderson's description of the white ocelli "remain[ing] plainly discernable in a darkened box when the rest of the animal was invisible." The ocellar scales reflect and intensify ambient light while the darker ground coloration renders the rest of the lizard invisible in a dimly lit environment. Further enhancing the illusory effect of the reflective scales, dark pigment surrounding each white ocellar scale varies in intensity, apparently depending on the stress level of the animal. We observed that pigmentation becomes darker when lizards are initially handled, but fades to a lower intensity after several minutes. The darker surrounding pigment heightens the reflective effect of the ocelli and makes them appear a brighter white. When viewed immediately after handling the lizards, the ocelli appear to pulse or fluctuate in brightness as the surrounding pigment changes intensity. After a quiescent period, the ocelli are still reflective but do not appear as bright as when the surrounding skin pigmentation is darker. Again, this could explain Sanderson's description that light from the lizard "was much brighter the first time it was switched on after the animal had been quiescent for a period of time," and "after one brilliant display...it refused to shine with full brightness." The darker dermal pigmentation, presumably associated with higher stress levels during handling, heightens the reflective appearance of the white ocellar scales. Decreased pigmentation during inactive periods gives the illusion that the lizard is not producing light at full intensity.

Our observations of *P. shrevei* provide empirical evidence refuting Sanderson's (1939) claim of bioluminescence in this species. Instead, the lizard's unique scales act like small parabolic mirrors, reflecting light at oblique angles. The intensity of this reflectivity is, in turn, influenced by the intensity of surrounding dermal pigmentation and by the angle at which a lizard is oriented relative to a light source. Thus, ocellar reflection produces an illusion that light is emitted by *P. shrevei* at varying intensities, a phenomenon which obviously has confused a number of persons. The results of our investigation substantiate the predictions of Roth and Gans (1960) and provide scientific credence to the anecdotal accounts of numerous naturalists. The functional significance of the reflective ocellar scales, found only in adult males of *P. shrevei* remains unknown.

Perhaps more remarkable than the unique reflective scales, our observations revealed that *P. shrevei* differs from known tropical lizards in at least two aspects. First, adult *P. shrevei* are intolerant of heat, despite their tropical distribution. Second, the species incubates its eggs at very low temperatures relative to other squamate reptiles. Thus, *P. shrevei* possesses the curious trait of being a cold-adapted tropical lizard.

Boos (1979) first hinted at the species' unique physiology when he noted that specimens of *P. shrevei* are so sensitive to heat that they rarely survive transport out of their restricted range. Our observations show that *P. shrevei* typically occupies a microclimatic range of 20-23 °C in its cave entrance microhabitat. Handled specimens went into stress after 2-3 min at temperatures greater than 24 °C, but revived once returned to cooler, moister conditions. However, an adult male died in captivity after its cage temperature reached a maximum of 28 °C despite provisions of moist refugia. This would indicate that 24-28 °C is lethal to *P. shrevei*. By comparison, other tropical members of the family Teiidae show a minimum body temperature of 27 °C, a mean of 40.5 °C, and a lethal maximum of 45-46 °C (see review by Brattstrom 1965). Clearly, *P. shrevei* represents an exception to the physiological characteristics that define other teiid lizards. Perhaps *P. shrevei* behaviorally avoids lethal ambient temperatures by retreating into caves and deep crevices for significant periods each day.

Read (1986) and Sanderson (1939) both reported finding egg masses of *P. shrevei* in either vegetation or rock crevices. Eggs are often adhered in pairs, indicating a clutch size of two, and the number of eggs at each nest site may range from a single pair (Read 1986) to 80 eggs (Quesnel, unpublished data). We found two oviposition sites in rock crevices at the cave entrance atop Mt. Aripo. One nest site measured 17 × 51 mm at the opening and was 90 mm deep, while the other was 19 × 30 mm at the opening and 115 mm deep. Both nest sites contained a communal egg mass inside and the remains of several already-hatched eggs near the entrance. Temperatures inside each nest were measured and were found to maintain a constant temperature of 20.5 °C throughout the day. Such a low incubation temperature is unique among known lizards, and resembles conditions experienced by eggs of temperate zone salamanders (Gutzke unpublished data).

Trinidad typically has high variability in local climates, despite its relatively small size. Mean temperature for the island is 26.7 °C, with an annual range of 2.9 °C (Granger 1982). In higher elevations such as Mt. Aripo, recorded temperatures range from 14.4 °C to 28 °C (Beard 1946). *Proctoporus shrevei* faces potentially lethal temperatures outside its limited cave-entrance microhabitat. Since the species is only known from Mt. Aripo and Mt. Tucuche (approx. 15 km apart), this presents the question of whether there is any gene flow between the populations. Lethal temperatures encountered at lower elevations would seemingly prevent movement of individuals between mountain peaks, thus restricting genetic exchange and promoting allopatric speciation. To date, no investigation has been conducted to determine what evolutionary forces are maintaining the two disjunct populations of *P. shrevei* as a single species. It is also unknown what physiological adaptations to a cold environment exist in the embryos of this species. On a final note, another lizard in Trinidad, *Gonatodes ceciliae*, is also intolerant of warm environmental conditions. This gecko shows thermal stress and dies within 5 min at 27-28 °C (Murphy, 1997) and coincidentally, inhabits the same type of cave microhabitat as *P. shrevei* in the mountainous rainforest of Trinidad's northern range (Knight and Gutzke, personal observation).

Although it is the legend of bioluminescence that propelled *Proctoporus shrevei* into fame, the unique reflective scales and "cold-adapted" physiology of this rare lizard are equally remarkable. The reclusive nature, dark habitat, and unknown behaviors of *P. shrevei* prompt many proximate and ultimate questions regarding the functional significance of its unusual scales. Likewise, its adaptation to relatively cold microhabitats raises new questions pertaining to natural selection, ectothermy, and environmental influences on life history strategies in tropical lizards.

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