Trimorphodon lambda
Sonoran Lyresnake

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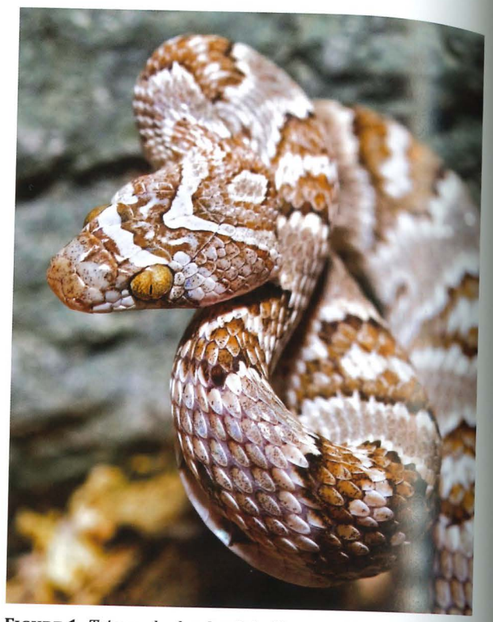

Figure 1. *Trimorphodon lambda* (Sonoran Lyresnake) from the Mohawk Mountains, Yuma Co. Photo by Trent R. Adamson.

Taxonomy. This species has a complicated taxonomic history. Edward D. Cope's (1886) description of the holotype for *Trimorphodon lambda* is based on a specimen (USNM 13487) collected by H.H. Emerich in 1883 from "Guaymas, Sonora Mexico." Klauber (1940b) subsumed *T. lambda* under the name *T. lyrophanes*, following Cope (1861b). Schmidt (1953) and Stebbins (1954, 1966) followed Klauber. Smith (1941d) rejected Klauber's (1940b) proposed change, citing differences in hemipenial morphology and head pattern. Fugler and Dixon (1961) concluded that *T. paucimaculatus*, described by Taylor (1938b), was a subspecies of *T. lambda*. Hardy and McDiarmid (1969) followed Fugler and Dixon (1961) and Dixon *et al.* (1962), who used *T. l. paucimaculatus*. Gehlbach (1971) subsumed *T. lambda* under *T. biscutatus*. Scott and McDiarmid (1984) followed Gehlbach's (1971) taxonomy, as did Stebbins (1985, 2003), despite earlier observations (McDiarmid and Scott 1970) that two members of the *T. biscutatus* complex (*T. biscutatus* and *T. lambda*) were likely sympatric in southwestern Jalisco. Werler and Dixon (2000) applied the combination *Trimorphodon lambda vilkinsonii* to populations from the Chihuahuan Desert without explanation. LaDuc and Johnson (2003) elevated *Trimorphodon vilkinsonii* (Chihuahuan Lyresnake) back to the species level. Devitt *et al.* (2008) recommended *T. lambda* also be treated as a full species, while acknowledging that there may be limited gene exchange between *T. lambda* and *T. vilkinsonii* along a narrow contact zone in extreme southeastern AZ and adjacent southwestern NM based on the presence of morphologically intermediate specimens.

Etymology. The generic name *Trimorphodon* (L. *tri*, three; Gr. *morph*, form; Gr. *odont*, tooth) is from Cope (1861b): "Posterior superior maxillary tooth separate, grooved; median teeth small; anterior elongate, spaced." The specific name *lambda* is for the chevron-shaped head marking that resembles the uppercase Greek letter Λ.

Description. *Trimorphodon lambda* is a long, slender snake with vertical pupils; a broad, flat head; and a comparatively slim neck (Fig. 1). The following measurements for AZ *T. lambda* are from Devitt *et al.* (2008): SVL in males is 250–885 mm ($\bar{x}$ = 490, *n* = 74) and TL is 301–1,049 mm ($\bar{x}$ = 604, *n* = 68); SVL in females is 237–883 mm ($\bar{x}$ = 641, *n* = 32) and TL is 279–1,027 mm ($\bar{x}$ = 641, *n* = 28). Maximum TL of males is 1,049 mm (885 mm SVL + 164 mm tail; UMMZ 75809, Santa Cruz Co.) and of females is 1,027 mm (883 mm SVL + 144 mm tail; UNM 55161, Yuma Co.). Tail length relative to TL in males is 0.146–0.195 ($\bar{x}$ = 0.179, *n* = 68) and in females is 0.146–0.195 ($\bar{x}$ = 0.154, *n* = 28). Records of live weights are not available in the literature. Unverted hemipenes of *T. lambda* are described as unbifurcated, with a single *sulcus spermaticus*. The proximal end of the hemipenis is smooth, and the distal end has flounces, with an enlarged region of spines proximal to the flounces (Klauber 1940b; Smith 1941d). More recent descriptions of everted hemipenes of *T. biscutatus* indicate earlier descriptions of the genus may be inaccurate (*e.g.*, absence of calyces, Jenner 1981, Scott and McDiarmid 1984; presence of calyces, Jadin and Smith 2010).

Coloration and Pattern. The dorsum is light gray or brown with 18–31 ($\bar{x}$ = 24, *n* = 104) darker brown, pale-edged saddles divided by a light center (Figs 2–7). These saddles are widest at the midline and taper laterally. Number of tail blotches is 8–17 ($\bar{x}$ = 12, *n* =100). The venter is tan, light gray, or pale yellowish, with darker spots or flecks toward the edges. There is usually a complete, dark-brown, lyre-shaped mark on top of the head and a dark bar between the eyes or across the snout. However, head markings may be reduced, especially in individuals from the extreme southeastern portion of the state. Figures 5 and 6 illustrate individuals collected meters from one another in Cave Creek Canyon, Chiricahua Mountains; one of these (Fig. 6) lacks head markings, suggesting influence of *T. vilkinsonii* (Devitt *et al.* 2008). There are no sexually dimorphic differences in overall coloration. The overall contrast between blotch color and background coloration is more pronounced in juveniles than in adults (Fig. 7).

Scutellation. Devitt *et al.* (2008) reported the following scale counts for a sample of 74 males and 32 females from AZ: 9 large scales on top of the head, usually 3 (2–4) preoculars, usually 3 (2–4) postoculars, 3 (1–4) loreals, 1 prefrontal, 2 nasals, a single medial rostral, 9 (7–11) supralabials, 12 (10–14) infralabials, usually 3+3 (sometimes 1–4) temporals, and usually 22 (19–25) dorsal scale rows at mid-body. Males have 211–240 ($\bar{x}$ = 224.8 ± 5.1) ventrals and 69–87 ($\bar{x}$ = 77.7 ± 3.5) subcaudals; females have 223–241 ($\bar{x}$ = 230.5 ± 4.3) ventrals and 64–78 ($\bar{x}$ = 69.1 ± 3.3) subcaudals. The cloacal scute and subcaudals are divided.

Similar Species. Most other species with dark blotches or saddles have round pupils. Night snakes (*Hypsiglena*) and leaf-nosed snakes (*Phyllorhynchus*) also possess vertical pupils, but are smaller and have spots without light centers. Other snakes possessing saddles with light centers and vertical pupils have rattles or at least a button and are much stouter.

Trimorphodon lambda is distinguished from *T. vilkinsonii* by having a greater number of body blotches (average of 24 in *T. lambda*, 21 in *T. vilkinsonii*) that are more narrowly separated (seventh and eighth blotches separated by four scale rows on average in *T. lambda*, eight in *T. vilkinsonii*). The presence or absence of a complete lyre should not be used as a distinguishing character between *T. lambda* and *T. vilkinsonii*, although *T. vilkinsonii* usually lacks the dark interocular bar across the snout present in *T. lambda* (Devitt *et al.* 2008). Individuals having a pattern intermediate between *T. lambda* and *T. vilkinsonii* have been collected from the San Simon Valley in Cochise Co., suggesting there may be limited gene flow between these species across the desert grassland ecotone between the Chihuahuan and Sonoran deserts in southeastern AZ and southwestern NM (the Cochise Filter Barrier, Morafka 1977). These specimens include SWRS 158, MVZ 229994, and MVZ 229759 from the vicinity of Cave Creek Canyon; MVZ 67228 from near Rodeo, NM; and UAZ 26931 from the Dos Cabezas Mountains.

Distribution and Abundance. *Trimorphodon lambda* is found in southern NV (Nye Co.) and extreme southwestern UT (Washington Co.), south through much of AZ (except the northeastern quarter), to southwestern NM (Hidalgo and Grant counties) and southeastern CA (generally east of the Salton Trough region).

In México, it occurs throughout Sonora and west of the Sierra Madre Occidental in Chihuahua, south to near the Sinaloan border (Devitt *et al.* 2008).

In AZ, it occurs throughout much of the western part of the state and in southeastern AZ below the Mogollon Rim (Map 35). It has been vouchered from every county except Apache and Navajo. In southeastern AZ, numerous vouchers document its presence in rocky desertscrub habitats at the base of mountain ranges and along rocky drainages. This species is also distributed below and along the length of the Arizona Transition Zone in rocky desertscrub habitats and appears to follow major drainages that dissect this landscape. For example, specimens have been collected in the Verde Valley from near the Childs-Irving Power Plant at the mouth of Fossil Creek (CM 69310) and from the vicinity of Sedona (*e.g.*, UAZ 37850; Hahn and May 1972). A specimen (CA 9401) collected in 1941 by V.H. Housholder from "50 mi NE of Globe" was probably taken from Salt River Canyon where it is transected by U.S. Highway 60. Multiple specimens document *T. lambda* from the Salt River in the vicinity of its confluence with Tonto Creek (Roosevelt Lake). Two photographs, one from the north end of the Sierra Ancha, Gila Co. (ASU HP00063), and one from hilly country between Ash Flat and Antelope Flat on the San Carlos Indian Reservation (ASU HP00083), represent the only vouchers above and away from these desertscrub corridors. A single specimen (CAS 190691) from the vicinity of Duncan represents the only voucher for Greenlee Co.

In southwestern AZ, *T. lambda* is vouchered from the Agua Dulce, Ajo, Baboquivari, Copper, Crater, Eagletail, Gila, Gila Bend, Harcuvar, Harquahala, Kofa, Little Ajo, Mohawk, Puerto Blanco, Pozo Redondo, Quijotoa, Quinlan, Sacaton, Sawtooth, Sierra Estrella, Sierra Pinta, Silver Bell, Silver Reef, Slate, Tinajas Altas, Tucson, and Vulture mountains as well as from the Buckskin, Gunsight, and Wellton hills—likely due to ease of access along public roadways or in wildlife refuges. However, it probably occurs in all of the mountain ranges in southwestern AZ, but remains undocumented in these areas due to remoteness and/or restricted public access.

Although there are very few vouchers from Mohave Co., a recent specimen from Lake Havasu City (ASU 36011; Leavitt 2015), indicates that additional locations in these counties may also harbor *T. lambda* populations. Although the Hualapai Mountains lack vouchered material, there is a reliable sighting of an individual crossing Chicken Springs Road in 1992 (J. Howland, pers. comm.). A specimen (UTA 50702) from the southern end of the Black Mountains suggests that the distribution of this species probably follows this range (and the canyons of the Colorado) north up to Lake Mead. Multiple vouchers document occurrence throughout most of the Grand Canyon from the Grand Wash Cliffs upstream to the vicinity of Lees Ferry (O'Connor *et al.* 2011). To the north, specimens have been reported from UT in the vicinity of St. George and in Zion National Park in Washington Co. (BYU 501–02, 653, 1798, 23801, 53013–14, 50298, 52895; Woodbury 1931, Tanner 1935, Tanner 1940). In AZ, *T. lambda* has been found as low as *ca.* 75 m ASL in Telegraph Pass, Gila Mountains, and as high as *ca.* 2,250 m ASL at San Pedro Vista, Santa Catalina Mountains (UAZ 26951).

Questionable Localities. None.

Status and Trends. No information on the status of populations is available. Data indicate site fidelity within populations (Repp 1998c, 2002), suggesting that populations might be especially vulnerable to destructive collecting techniques (Goode *et al.* 2005). Urban sprawl has undoubtedly contributed to both direct mortality and habitat loss in the foothills surrounding Tucson and Phoenix, a trend that continues as both metropolises expand into the surrounding desert. Because a large proportion of this species' habitat is in remote areas, direct impacts by humans are limited in geographic scope.

Figure 2. *Trimorphodon lambda* (Sonoran Lyresnake) from the Gila Bend Mountains, Maricopa Co. Photo by Thomas C. Brennan.

Habitat. In AZ, *T. lambda* is typically found in rocky areas up to 2,250 m ASL (Lowe 1964; Lowe *et al.* 1986). The species often occurs in both the Lower Colorado River Valley and Arizona Upland subdivisions of Sonoran Desertscrub, Semidesert Grassland, and Chihuahuan Desertscrub, but it also occupies Interior Chaparral and Madrean Evergreen Woodland (Brennan and Holycross 2006; Brennan and Babb 2015). Intensive sampling on AZ public lands from 1970 to 1980 placed *T. lambda* in the following habitat associations: open chaparral, cottonwood-willow riparian, juniper woodland, *Canotia*–mixed scrub, mixed riparian scrub, creosote flats, and both Mojave and Sonoran desertscrub habitats (Jones 1981, 1988a). Additional snakes have been found in ponderosa pine (*Pinus ponderosa*) forest and pinyon-oak-juniper woodland (R.D. Babb and A.T. Holycross, pers. comm.; Lowe *et al.* 1986). Within these habitats, *T. lambda* is typically encountered under and between rocks, cracks, and crevices; site fidelity for particular crevices has been reported (Repp 1998c, 2002). Arboreality has also been reported in *T. lambda* (Lowe 1964; Jones 1981; Lowe *et al.* 1986). Uncommonly, *T. lambda* is collected from atypical localities such as "Bernardino" along SR 80 in Cochise Co., a tobosa (*Hilaria mutica*) grassland (Grant and Woodin 1946).

Diet and Foraging Biology. *Trimorphodon lambda* feeds mainly on lizards (Klauber 1928; Clark 1968b; Lowe *et al.* 1986), although bats, small birds, amphibians, and rodents are also taken (Woodbury 1931; Lowe *et al.* 1986; Rorabaugh and Lemos Espinal 2016). Seventeen *T. lambda* specimens from southern NV were examined for stomach contents by Clark (1968b). Seven of these specimens, all collected

FIGURE 3. *Trimorphodon lambda* (Sonoran Lyresnake) from the Sierra Ancha Mountains, Gila Co. (ASU HP00063). Photo by Randall D. Babb.

FIGURE 4. *Trimorphodon lambda* (Sonoran Lyresnake) from the Vulture Mountains, Maricopa Co. Photo by William Wells.

in the spring and early summer, contained prey, including four that contained *Uta stansburiana* (Common Side-blotched Lizard), one that contained an *Aspidoscelis tigris* (Tiger Whiptail), one that contained a *Sceloporus* sp. (spiny lizard), and another that contained an unidentified lizard. Fahrner (2017) observed an adult *T. lambda* in UT eating a *Sauromalus ater* (Common Chuckwalla) with head and body facing downward on a near-vertical rock face. Additional lizards noted as prey items of *T. lambda* include *Holbrookia elegans* (Elegant Earless Lizard), *Urosaurus ornatus* (Ornate Tree Lizard; UAZ 57494), *Sceloporus "undulatus"* (= *cowlesi* or *tristichus*; Stebbins 1954), and *Xantusia* spp. (night lizards; Clark 1968b). Some authors cited small snakes as being part of the diet of *T. lambda* (Ditmars 1907; Wauer 1964; Lowe *et al.* 1986; Rorabaugh and Lemos Espinal 2016), although no specific taxa were listed.

Several specimens have died trying to ingest lizards. A *T. lambda* (GCNP 1208) was found dead on Bright Angel Trail in Grand Canyon with a partially ingested *Sceloporus magister* (Desert Spiny Lizard; GCNP 1209) that had broken through the skin of the snake's throat. Another *T. lambda* (UAZ 55756-PSV) was found dead on South Bass Trail in Grand Canyon with a *S. magister* lodged in its throat. The *Sceloporus jarrovii* (Yarrow's Spiny Lizard) dietary record for *T. lambda* in Grand Canyon (Fowlie 1965) is clearly in error and might refer to *S. magister* (perhaps GCNP 1208). Although cause of death could not be determined, a female *T. lambda* (ASU 36182; 296 mm SVL, 3.7 g) was found dead on a road at 1840 h on 8 June 2006 in the Atascosa Mountains with the tail tip of an *H. elegans* (ASU 36183; 59.7 mm SVL, 4.9 g) sticking out of its mouth (T.R. Jones, pers. comm.).

Members of the genus *Trimorphodon* have grooved rear maxillary teeth (opisthoglyphous dentition) positioned below Duvernoy's gland. This gland is capable of delivering a remarkably high yield of venom (130 ml) and an average of 6.34 mg of dry venom per strike (Hill and Mackessy 1997, 2000). Because of the inefficient venom delivery system (grooves vs. hollowed fangs), the venom of rear-fanged snake species is injected into their prey through rhythmic chewing. The venomous nature of lyresnakes was first reported by Dugès (1884), who described a *T. biscutatus* chewing on an *Aspidoscelis* sp. (whiptail lizard), which subsequently died. Species of *Trimorphodon* may require 5–7 minutes of rhythmic chewing to kill lizard prey items (Cowles and Bogert 1935; Klauber 1940b), but the complete recovery of a mouse following an envenomation was also described (Cowles and Bogert 1935). In captive *T. lambda* from AZ, two to four coils of the snake's body

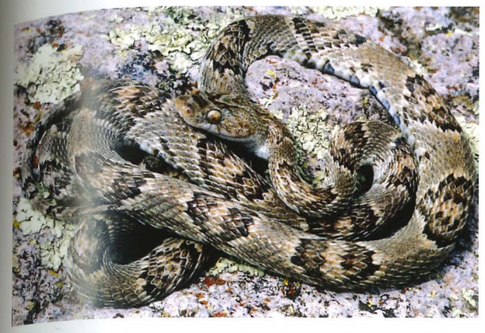

FIGURE 5. *Trimorphodon lambda* (Sonoran Lyresnake) from the Chiricahua Mountains, Cochise Co. (LSUMZ 83684). Photo by Thomas Devitt.

FIGURE 6. *Trimorphodon lambda* (Sonoran Lyresnake) from the Chiricahua Mountains, Cochise Co. (LSUMZ 83685; see text). Photo by Thomas Devitt.

were used to constrict mammalian prey, but constriction was never observed when captives preyed on lizards (Jones 1988b). A *T. lambda* (from Mohave Co.) was allowed to chew on the pinky finger of a human for 30–45 seconds, resulting in localized pain and swelling that lasted some 12 hours, with pain comparable to a wasp or scorpion sting (Foley 2002). Duvernoy's gland secretions and specific components of *Trimorphodon* venom continue to be studied for insights into colubrid venom evolution (Taub 1967; McKinstry 1978; Hill and Mackessy 1997, 2000; Huang and Mackessy 2004; Lumsden *et al.* 2004; Peichoto *et al.* 2012).

■ **PREDATORS AND PARASITES.** Few predation records specifically list *T. lambda* as prey of other animals. The transmitter of a radiotagged *T. lambda* was found in a *Bubo virginianus* (Great Horned Owl) pellet in the Tortolita Mountains (Amarello and Goode 2004b). Vertebrae of *T. biscutatus* were recovered from Late Holocene deposits of *Bassariscus astutus* (Ringtail) feces from Grand Canyon National Park (Mead and Van Devender 1981). Wiseman *et al.* 2019) documented *Trimorphodon lyrophanes* in the diet of *Lampropeltis californiae* from CA and Holycross *et al.* (2019) recently documented an *L. californiae* (*ca.* 600–650 mm TL) swallowing an adult *T. lambda* on the Bright Angel Trail in Grand Canyon. *Oochoristica* spp. (cestodes) were recorded from the stomach of *T. lambda* in Zion National Park, UT (Woodbury 1934).

■ **BEHAVIOR.** Lyresnakes are considered strictly nocturnal (Fowlie 1965) or usually nocturnal (Lazaroff *et al.* 2006). Most *T. lambda* in AZ are encountered at night, from spring to fall, most commonly from April to June, although individuals are occasionally found moving at odd times (*e.g.*, on a rainy February morning; Lazaroff *et al.* 2006). Crepuscular activity has been observed in northern Sonora (J.C. Mitchell, pers. comm.).

Most authorities suggest that members of the *T. biscutatus* complex north of southern Sonora are strictly rock dwellers; however, one author (Lowe 1964; repeated again in Lowe *et al.* 1986) stated that *T. lambda* is an agile climber, climbing 15 or more feet (2.4 m) in trees and in rock crevices, with both sites used for diurnal and winter shelter as well as foraging. Low vegetation has been noted as a basking site for *T. lambda* (Fowlie 1965). An additional instance of arboreality was recorded for *T. lambda*; however, no specifics were provided (Jones 1981). The only other instances of *Trimorphodon* in trees north of México are two observations of *T. vilkinsonii* found in an oak tree and a catclaw acacia (*Senegalia greggii*) in Presidio Co., TX (Davis *et al.* 2008). Most individuals are

FIGURE 7. A young *Trimorphodon lambda* (Sonoran Lyresnake) from the Santa Rita Mountains, Santa Rita Co. Photo by Sonny N. Aaron.

found in rocky areas or on roads intersecting rocky habitats (Klauber 1928, 1939c). Other *T. lambda* have been found when turning granite flakes (Tanner 1941; Lowe *et al.* 1986) and have even been found sharing a shelter site with *S. ater* (Repp 1997). Occasionally, individuals are found in and around human-built structures (Stebbins 1954; Fowlie 1965).

Lyresnakes may defend themselves vigorously if threatened by an aggressor, though some species and individuals are docile when handled (*T. biscutatus*, Schmidt and Shannon 1947; *T. vilkinsonii*, TJL, pers. obs.). Lyresnakes vibrate their tail when disturbed or captured. This defensive behavior can escalate with the snake hissing, coiling its body into a strike position, and striking (Klauber 1928; Campbell 1934; Fowlie 1965; Lazaroff *et al.* 2006).

REPRODUCTION. Reproductive characters were examined in 37 male and 27 female AZ specimens (Goldberg 1995b). The smallest spermiogenic male was 448 mm SVL; the smallest reproductively mature female measured 718 mm SVL. The testicular cycle of specimens examined by Goldberg (1995b) fit a mixed-type spermiogenesis (spermiogenesis interrupted by hibernation with completion in the spring). Goldberg (1995b) reported clutch sizes of 8–10 eggs, but suggested that *T. lambda* females from AZ may not reproduce every year. Lowe (1986) reported clutch sizes of 7–20 eggs, with the 25 mm long eggs laid in late spring/early summer and 200 mm long juveniles hatching in September/October. The only observation of mating in the wild is of a central AZ pair found copulating on 2 June 2008 (J. Kruse Hall, pers. comm.).

REMARKS. In AZ, *Trimorphodon* is known from Late Pleistocene/Early Holocene localities in Yuma Co. (Van Devender and Mead 1978) and Late Quaternary localities in Organ Pipe National Monument, Pima Co. (Van Devender *et al.* 1991b). Additional fossil localities in the Southwest place *Trimorphodon* in the Mid Wisconsinan/Holocene (Doña Ana Co., NM; Harris 1993), Late Wisconsinan/Holocene (Grant Co., NM; Van Devender and Worthington 1974 [1977]), Late Pleistocene/Early Holocene (San Bernardino Co., CA; Reynolds *et al.* 1991), Middle to Late Holocene (San Bernardino Co., CA; Whistler 1991), and a single Quaternary site in Guadalupe Mountains National Park (Culberson Co., TX; Logan and Black 1979). Except for the Guadalupe Mountains National Park locality, extant populations of *Trimorphodon* occur at all of the above fossil localities.

ACKNOWLEDGMENTS. We thank the many curators and collection managers who facilitated our examinations of museum voucher material.