

REPTILIA: SQUAMATA: SERPENTES: COLUBRIDAE

TRIMORPHODON
BISCUTATUS

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Trimorphodon biscutatus
(Duméril, Bibron, and Duméril)
Western Lyre Snake

Dipsas bi-scutata Duméril, Bibron, and Duméril, 1854:1153. Type-locality, "Mexique" [restricted to Tehuantepec, Oaxaca, México, by Smith and Taylor (1950)]. Holotype, Mus. Hist. Nat. Paris 5900, sex, collector, and date of collection unknown (examined by Harry W. Greene).

Dipsadomorphus biscutatus: Günther, 1858:176.

Trimorphodon biscutatus: Cope, 1861:297.

Eteirodipsas biscutata: Jan, 1863:105 (part).

Trimorphodon (*Dipsas*) *biscutata*: Dugès, 1882:145.

Sibon biscutatum: Garman, 1884a:16 (part).

Sibon biscutata: Garman, 1884b:22 (part).

Trimorphodon biscutatum: Dugès, 1893:295.

• CONTENT. Six subspecies are recognized: *biscutatus*, *lambda*, *lyrophanes*, *quadruplex*, *vandenburgi*, and *vilkinsoni* (Gehlbach, 1971).

• DEFINITION AND DIAGNOSIS. Head pattern variable (see subspecies accounts) but never with a broad pale nape band with a relatively straight rear margin; dorsal dark blotches usually not connected to dark markings on ventrals; size larger than *T. tau*, often greater than 1.5 m total length (*tau* rarely greater than 1 m); *T. biscutatus* also differs from *T. tau* in having higher average counts (20–28) for midbody scale rows, ventrals (range of means in 10 samples) in males 222–267, in females 221–263, subcaudals (means in 10 samples) in males 72–99, in females 65–85, supralabials 7–10, and infralabials 11–14, but wide overlap between the two species in all of these characters exists; anal plate divided or single; teeth on maxilla 10–12, on mandible 17–18, on pterygoid 12–15, and on palatine 6–7.

• DESCRIPTIONS. Comprehensive descriptions encompassing most forms are found in Taylor (1939), Klauber (1940), and Smith (1941). Most recent description of entire species is in Gehlbach (1971). Descriptions (besides those of types) of subspecies are: *biscutatus*—Cope (1861, 1870), Boulenger (1896), Oliver (1937), Taylor (1938, 1940), Smith (1943), Schmidt and Shannon (1947), Duellman (1954, 1957), Davis and Dixon (1957, 1959), Fugler and Dixon (1961), Dixon et al. (1962), Fouquette and Rossman (1963), and Hardy and McDiarmid (1969); *lambda*—Cope (1900), Woodbury (1931), Tanner (1941), Bogert and Oliver (1945), Stebbins (1954, 1966), Davis and Dixon (1957), Wright and Wright (1957), Gehlbach (1958), Harris (1959), and Fowle (1965); *lyrophanes*—Coues (1875), Cope (1900), Van Denburgh (1922), Klauber (1928), and Linsdale (1932); *quadruplex*—Taylor (1951), Mertens (1952), Campbell and Howell (1965), and Wilson and Meyer (1982); *vandenburgi*—Klauber (1928, 1941), Stebbins (1954, 1966), Murray (1955), Wright and Wright (1957), and Loomis and Stephens (1967); *vilkinsoni*—Jameson and Flury (1949), Degenhardt and Steele (1957), Wright and Wright (1957), Medica (1962), Jones and Findley (1963), Stebbins (1966), Conant (1975), Morafka (1977), and Banicki and Webb (1982). Vertebrae of *Trimorphodon biscutatus* are described by Duellman (1958) and Van Devender and Mead (1978), lung by Cope (1894) and Underwood (1967), eye and vision by Walls (1931, 1942), Underwood (1967, 1970), and Rochon-Duvigneaud (1970), hyoid by Langenbartel (1968), labial glands by Taub (1967a), Duvernoy's gland by Taub (1967b), inner ear by Baird (1970), and cochlear duct by Miller (1968). Courtship and eggs are described by Werler (1951, 1970), and parasites by Telford (1964).

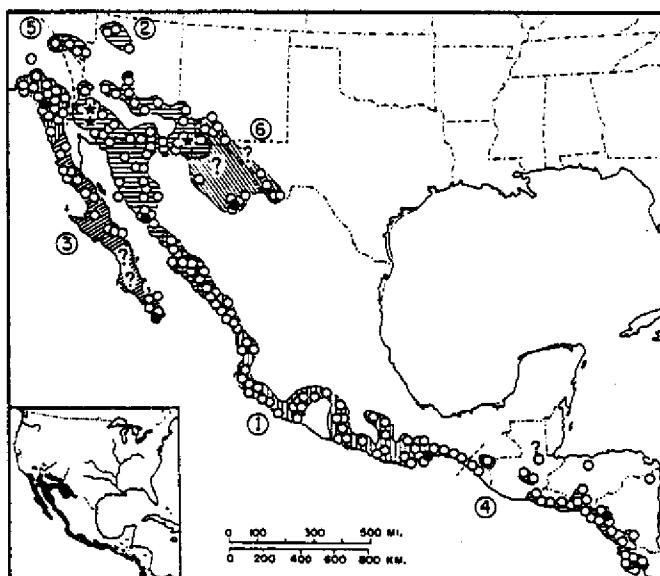
• ILLUSTRATIONS. The subspecies are illustrated by photographs or drawings as follows: *biscutatus*—Taylor (1938, 1939), Duellman (1954), Alvarez del Toro (1960, 1973), and Dixon et al. (1962) (a drawing labelled *Eteirodipsas biscutata* in Jan and Sordelli (1872) is *T. tau*); *lambda*—Wright and Wright (1957), Jones and Findley (1963), Wauer (1964), Fowle (1965), Stebbins (1966), and Leviton (1972); *lyrophanes*—Cope (1900), Klauber (1940), and Schmidt and Davis (1941); *quadruplex*—Wilson and Meyer (1982); *vank-*

denburghi—Klauber (1924, 1928, 1940), Taylor (1939), Schmidt and Davis (1941), Stebbins (1954), Wright and Wright (1957), Dixon (1967), Cochran and Goin (1970), and Shaw and Campbell (1974); and *vilkinsoni*—Taylor (1939), Wright and Wright (1957), Jones and Findley (1963), and Conant (1975). The same hemipenis is illustrated *in situ* twice (Cope, 1895, 1900). Dentition and venom glands are figured by Dugès, (1882), Cowles and Bogert (1935), and Duellman (1958). Duvernoy's gland is illustrated in cross-section (Taub, 1967b). The maxilla is illustrated by Duellman (1958), a karyotype is shown in Bury et al. (1970), and visual cells are diagrammed by Underwood (1970).

• DISTRIBUTION. *Trimorphodon biscutatus* is found throughout the Baja California peninsula; on Cerralvo, San Marcos, and Tiburón islands in the Gulf of California; in southern California north to the vicinity of Los Angeles on the coast and to the Argus and Amargosa mountains inland in Inyo County; in southern Nevada, extreme southwestern Utah, Arizona except the northeastern quarter, southern New Mexico, and southern Trans-Pecos Texas. The species is also found east of the Sierra Madre Occidental of México south to the vicinity of Ciudad Chihuahua, Chihuahua, and west of the Sierra on the Pacific coastal plain and foothills south to Puntarenas Province in Costa Rica. A record from near the city of Durango, Durango, México (Morafka, 1977), is based on a specimen of *T. tau* (Banicki and Webb, 1982). Populations are found in some dry Atlantic slope valleys in Guatemala, Honduras, and Nicaragua (Wilson and Meyer, 1982). The species reaches an elevation of 2400 m in the northern part of its range (Stebbins, 1966), but is restricted to elevations below 1200 m south of Sonora, México. A record for Lanquin, Guatemala (Günther, 1895) is questioned by Stuart (1963), and a record for Panamá (Boulenger, 1896) is surely incorrect.

• FOSSIL RECORD. *Trimorphodon biscutatus* has been taken from late Pleistocene and early Holocene deposits in southwestern Arizona and southwestern New Mexico (Van Devender and Mead, 1978; Van Devender and Worthington, 1978).

• PERTINENT LITERATURE. The pertinent taxonomic literature is summarized in Gehlbach (1971); additional comments appear in Wilson and Meyer (1982). Feeding records from the wild include "lizards" (Klauber, 1928; Dixon, 1967), *Xantusia*, *Uta*, and *Crotosaurus* (Klauber, 1940), *Sceloporus* (Woodbury, 1931; Gehlbach, 1958; Loomis and Stephens, 1967), *Petrosaurus* (pers. obs.), snakes (Wauer, 1964), "mammals" (Klauber, 1940), and bats (Stager, 1942; Krutzsch, 1944). Captives accept amphibians (Dixon,



MAP. Solid circles mark type-localities, hollow circles other localities. Stars indicate Pleistocene and Holocene fossil localities. Question marks indicate a questionable Guatemala record (see DISTRIBUTION), an uncertain range boundary, and an uncertain area of occurrence. Overlapping shading patterns indicate areas of intergradation.

1967), lizards, small mammals, and birds. Northern populations (*lyrophanes*, *vandenburghi*, *wilkinsoni*, *lambda*) are associated with rocks and rock crevices (Klauber, 1940); the larger southern forms (*biscutatus*, *quadruplex*) often forage arboreally and take diurnal refuge in tree hollows (pers. obs.). Duellman (1966), Savage (1966), and Morafka (1977) gave general ecological and biogeographical accounts. Fitch (1970) summarized the scanty reproductive information. Dugès (1882) and Cowles and Bogert (1935) studied the effects of *Trimorphodon* venom on prey. A recent longevity record is listed by Bowler (1977). Greene and Burghardt (1978) studied constriction.

• NOMENCLATURAL HISTORY. Six species have been described from specimens representing this taxon. *Trimorphodon major* Cope was synonymized with *T. biscutatus* (Duméril, Bibron, and Duméril) by Cope himself (1875a, 1887). Subsequent authors suggested that various combinations of *biscutatus*, *lambda* Cope, *lyrophanes* Cope, *paucimaculatus* Taylor, *vandenburghi* Klauber, and *wilkinsoni* Cope might be synonymous or subspecifically related (Klauber, 1940; Bogert and Oliver, 1945; Duellman, 1957; Jones and Findley, 1963; Loomis and Stephens, 1967; Hardy and McDiarmid, 1969), but formal changes were made less often. Klauber (1940) synonymized *lambda* and *lyrophanes* and was followed by Lowe (1964) and Tanner and Banta (1966), but Smith (1941) kept them separate, largely on the basis of hemipenis and head pattern. Fugler and Dixon (1961) made *paucimaculatus* a formal subspecies of *T. lambda*. Gehlbach (1971) first united all of these forms under one specific name with six subspecies, giving the species its current form. Wilson and Meyer (1982) preferred to unite *biscutatus*, *lambda*, and *quadruplex* under a single name, *biscutatus*, but their data are scanty and not persuasive in their present form.

• ETYMOLOGY. The name *biscutatus* (Latin) probably refers to the doubled loreal plate; *lambda* (Greek) refers to the chevron-shaped mark on the head; *lyrophanes* (Greek) refers to the lyre-shaped markings on the nape; *quadruplex* (four-fold weave) presumably describes the color pattern wherein each primary blotch is completely divided into four secondary blotches by the presence of pale centers; *vandenburghi* was named in honor of John Van Denburgh, the eminent herpetologist of the California Academy of Sciences; and *wilkinsoni* is a patronym for Edward Wilkinson, an amateur collector of historical relics and natural history specimens (Smith and Mittleman, 1943).

1. *Trimorphodon biscutatus biscutatus* (Duméril, Bibron, and Duméril)

Dipsas bi-scutata Duméril, Bibron, and Duméril, 1854:1153 (see species synonymy).

Trimorphodon major Cope, 1870:153. Type-locality, "near Tehuantepec," México [W. Tehuantepec (Cope, 1887)]. Syntypes, U.S. Nat. Mus. 30427-9, male, male, female, collected by Francis Sumichrast, date of collection unknown (examined by authors).

Dipsas bisculata: Dugès, 1884:337. Unjustified emendation.

Dipsas bicutata: Dugès, 1890:54. Unjustified emendation.

Trimorphodon paucimaculatus Taylor, 1938:527. Type-locality, "Mazatlán, Sin., México." Holotype, Univ. Illinois Mus. Natur. Hist. 25072, sex undetermined, collected by Edward H. Taylor, 24 July 1934 (not examined by authors).

Trimorphodon biscutatus biscutatus: Smith, 1941:159.

Trimorphodon biscutatus semirutilus Smith, 1943:492. Type-locality, "Acapulco, Guerrero," México. Holotype, U.S. Nat. Mus. 110410, male, collected by Hobart M. Smith, 3 September 1939 (examined by authors).

Trimorphodon lambda paucimaculata: Fugler and Dixon, 1961: 17.

Trimorphodon lambda paucimaculatus: Fouquette and Rossman 1963:198.

• DEFINITION. Primary dark body blotches fewer than 26, 5-11 scales wide along middorsal line at midbody, central pale spots may entirely divide primary body blotches, resulting secondary blotches undivided; pale chevron on back of head with apex on posterior tip of frontal, not connected to interorbital bar; light spot on nape of neck; snout pale, often with a light transverse bar; ventrals more than 243; anal divided.

• REMARKS. See Duellman (1954) for the referral of *T. b. semirutilus* to synonymy.

2. *Trimorphodon biscutatus lambda* Cope

Trimorphodon lambda Cope, 1886:286. Type-locality, "Guaymas, Sonora," México. Holotype, U.S. Nat. Mus. 13487, juvenile, collected by H. F. Emerich, 1883 (examined by authors).

Trimorphodon lyrophanes Cope, 1875b:38 (part). Arizona specimens.

Trimorphodon vandenburghi: Cowles and Bogert, 1936:41. Nevada specimens.

Trimorphodon lambda lambda: Dixon et al., 1962:98.

Trimorphodon biscutatus lambda: Gehlbach, 1971:208.

• DEFINITION. Primary dark body blotches 20-35, 4-8 scales wide, central pale spots may entirely divide body blotches, the resulting secondary blotches undivided; pale chevron on back of head with apex on posterior tip of frontal, not connected to interorbital bar; light spot on nape present or absent; snout may be mottled or pale without transverse light bar; ventrals less than 244; anal divided.

3. *Trimorphodon biscutatus lyrophanes* (Cope)

Lycodon lyrophanes Cope, 1860:343. Type-locality, "Cape St. Lucas, Lower California," México. Two syntypes, U.S. Nat. Mus. 4680, male, female, collected by John Xantus, May 1859 (examined by authors).

Lycognathus lyrophanes: Cochran, 1961:164.

Trimorphodon biscutatus lyrophanes: Gehlbach, 1971:208.

• DEFINITION. Primary dark body blotches more than 22; 4-7 scales wide, central light spots divide body blotches, the secondary blotches undivided; light chevron marking on back of head with arms curved, connected to interocular bar, but not to each other, and forming a dark lyre-shaped pattern in temporal region; no light spot on nape; light snout or bar across snout; ventrals fewer than 244; anal divided.

• REMARKS. The catalogue entry for the type of *T. lyrophanes* (USNM 4680) originally contained four specimens. Two are in the USNM under no. 4680. A third was sent to the Academy of Natural Sciences, Philadelphia (notation in the USNM catalogue) and mentioned by Cope in his description of *Trimorphodon*. A specimen with the same data as the types was catalogued at the Academy (ANSP 10146); however, the specimen could not be located in 1983 (Malnate, pers. comm.).

4. *Trimorphodon biscutatus quadruplex* Smith

Trimorphodon biscutatus quadruplex Smith, 1941:157. Type-locality, "Esteli, Nicaragua." Holotype, U.S. Nat. Mus. 89476, female, collected by James H. Ivy, 1932 (examined by authors).

Trimorphodon quadruplex: Smith, 1942:206.

• DEFINITION. Primary dark body blotches fewer than 25, 3-9 scales wide, central light spots divide body blotches into secondary blotches, most of which are also divided by central light markings; light chevron marking on back of head not connected to interocular bar; light spot on nape; no light bar across snout; ventrals more than 255; anal divided.

5. *Trimorphodon biscutatus vandenburghi* Klauber

Trimorphodon vandenburghi Klauber, 1924:17. Type-locality, "Wildwood Ranch (elevation 1520 feet) near Ramona, San Diego County, California." Holotype, California Acad. Sci. 58172, male, collected by E. B. Woodworth and Laurence M. Klauber, 4 May 1924 (not examined by authors).

Trimorphodon biscutatus vandenburghi: Gehlbach, 1971:209.

• DEFINITION. Primary dark body blotches more than 25, 3-6 scales wide, central light spots divide body blotches into secondary blotches; light chevron marking on head usually connected to interocular light bar; no light spot present on nape; snout pale or crossed with light bar; ventrals are fewer than 240; anal usually entire.

6. *Trimorphodon biscutatus wilkinsoni* Cope

Trimorphodon wilkinsonii Cope, 1886:285. Type-locality "City of Chihuahua, Mexico" [restricted to "vicinity of Ciudad Chihuahua" (Gehlbach, 1971)]. Holotype, U.S. Nat. Mus. 14268, juvenile, collected by Edward Wilkinson, date of collection unknown (examined by authors).

Trimorphodon wilkinsoni: Cope, 1887:68. Invalid emendation.
Trimorphodon biscutatus wilkinsoni: Gehlbach, 1971:209.

* DEFINITION. Primary dark blotches fewer than 25, 2-5 scales wide, usually lacking central light spots that divide blotches into secondary blotches; head markings variable, never consisting of a light chevron, most commonly composed of dark spots on frontal and parietal head shields; light spot on nape present or absent; no light bar across snout; ventrals fewer than 237; anal divided.

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