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SCOTT, NORMAN J., JR., AND ROY W. McDiarmid. 1984. Trimorphodon.

Trimorphodon Cope Lyre Snakes

Trimorphodon Cope, 1861:297. Type species, Lycodon lyrophanes Cope, 1860, by original designation.

Eteirodipsas Jan, 1863:105. Type species, Dipsas biscutata Duméril, Bibron, and Duméril, 1854, by subsequent designation (Smith and Taylor, 1945; Mertens, 1952).

Hetaerodipsas Berg, 1901:90. Emendation of Eteirodipsas Jan.

• CONTENT. Two species are recognized: T. biscutatus and T. tau.

 DEFINITION AND DIAGNOSIS. A colubrid snake genus with lateral head scales fragmented, numerous, and variable in number, loreals generally 2 or 3 (2-5), preoculars generally 3 or 4 (2-5), postoculars generally 3 (2-4), temporals generally 2 or 3 (1-5) + 3 or 4 (2-5); supralabials generally 8 or 9 (7-10), infralabials generally 11 or 12 (9-14); dorsal scales smooth (or bluntly keeled in some males) with paired apical pits, generally in 21-25 rows at midbody with posterior reduction; anal plate divided or single; subcaudals paired; head distinct from body; eye moderate to large with vertically elliptical pupil; body and tail moderately slender to very slender and laterally compressed; length to over 1500 mm; color pattern composed of black or brown blotches, usually with pale centers which tend to divide the primary blotches into secondary blotches which in turn may be divided; small blotches sometimes present dorsally between large blotches or laterally in a row; head pattern usually complex with a broad pale collar (tau) or pale chevron or lyre (most biscutatus) on the nape; pale interocular bar often present; ground color brown, tan, gray, or brick red with juvenile color pattern more intense and sharply defined; venter paler than dorsum and noticeably opalescent, may be spotted or mottled.

Maxillary teeth 10-12, anterior 2 or 3 much larger than others which gradually decrease in size posteriorly to diasterna which is followed by 1 or 2 enlarged teeth, deeply grooved on anterior face; anterior mandibular teeth enlarged; Duvernoy's gland well developed.

Vertebrae short, broad and flat; wider than long, neural spine low and thin; haemal spine barely indicated as a slightly raised keel. Hypapophyses blade-like, present on anterior vertebrae only.

Hemipenis 14-25 subcaudals long, single, and attenuate; sulcus single, reaching to tip; basal quarter naked, with or without tiny spinules; next distal fifth with thickened sulcal lips and covered with large spines and spinules, or naked (specimens from southern and Baja California); this part followed by two or three pockets on asulcate side with naked pouches and thick, spinulate lips; these pockets followed by a short naked neck that ends in another pocket under the distal portion of the organ, which is finger-shaped and covered with rows of spinulate papillae.

Both species are nocturnal, oviparous, and primarily feed on lizards.

In North and Central American colubrid snakes, an undivided sulcus spermaticus, elliptical pupil, generally smooth scales, and enlarged grooved posterior maxillary teeth preceded by a diastema, define three genera: *Leptodeira*, *Imantodes*, and *Trimorphodon* (Dunn, 1928). *Trimorphodon* is further distinguished by having more than one loreal, a pocketed, non-capitate hemipenis, and slightly oblique scale rows (Duellman, 1958).

• DESCRIPTIONS. Generic descriptions are found in Cope (1861, 1900), Boulenger (1896), Brown (1901), Phisalix (1922), Taylor (1939), and Duellman (1958); hemipenes are described by Klauber (1940) and Smith (1941).

• ILLUSTRATIONS. See species accounts.

• DISTRIBUTION. The genus ranges from southern California, southern Nevada, southwestern Utah, Arizona, southern New Mexico, and western Texas south through the entire peninsula of Baja California, on Cerralvo, San Marcos, and Tiburón islands of the Gulf of California, in all of the Pacific states of México plus Chihuahua, Durango, Tamaulipas, Aguascalientes, Guanajuato, Hidalgo, México, Morelos, Puebla, Queretaro, San Luis Potosí, Veracruz, and Zacatecas; through the Pacific lowlands and some dry interior valleys of Guatemala, Honduras, El Salvador, and Nicaragua to Guanacaste and Puntarenas provinces of northwestern Costa Rica. A record for Panamá (Boulenger, 1896) is not confirmed and probably erroneous. Elevational range from sea level to 2600 m.

• FOSSIL RECORD. See species accounts.

• PERTINENT LITERATURE. McDiarmid and Scott (1970) reviewed T. tau, and Gehlbach (1971) revised T. biscutatus; see these and the species accounts for additional references.

• KEY TO SPECIES.

- Pale band on nape broad with a straight or slightly indented posterior border; most dorsal dark saddles confluent with dark markings on ventrals ______ T. tau
- Pale band on nape narrow and chevron or lyre shaped, posterior border \land or U-shaped; most dorsal dark saddles separated from dark spots on tips of ventrals ______ T. biscutatus

• NOMENCLATURAL HISTORY. Cope (1861) described Trimorphodon based on specimens of Lycodon lyrophanes Cope from Baja California Sur, the description of Dipsas biscutata Duméril, Bibron, and Duméril from México, and a specimen that Cope examined from Nicaragua. Both taxa are now included in T. biscutatus. In 1869, Cope described three additional forms: T. tau, upsilon, and major. McDiarmid and Scott (1970) showed that Trimorphodon tau and upsilon represented one species (T. tau); T. major was made a synonym of T. biscutatus (Cope, 1887). Subsequent work consisted of two stages, a long period during which several new forms were described, and a recent period during which all of these have been assigned to one of the two species now composing the genus (see references in Species Accounts).

Eteirodipsas was described by Jan (1863) to include Dipsas biscutata, Duméril, Bibron, and Duméril, Dipsas colubrina Schlegel, Coluber annulatus Linnaeus, and rhomboidalis Jan, a variety of E. annulatus. Jan's (1863; Jan and Sordelli, 1872) biscutata included both species (biscutatus and tau) currently in Trimorphodon. Boulenger (1896) placed biscutatus in Trimorphodo and annulatus in Leptodeira (rhomboidalis is a nomen nudum), retaining colubrina as the only species of Eteirodipsas. Smith and Taylor (1945) explicitly designated Dipsas biscutata as the type species of Eteirodipsas (Mertens, 1952).

• ETYMOLOGY. *Trimorphodon* refers to the three tooth shapes in the upper jaw: the long, recurved anterior teeth, the shorter middle teeth, and the elongate, grooved fangs at the rear. The gender is masculine.





COMMENT

The placement of Trimorphodon within the family Colubridae is probably as unsettled as that of any genus. Cope (1900) placed it with a group of 13 Old and New World genera characterized by grooved fangs and a calvculate or spinose hemipenis with a single sulcus spermaticus. Although Cope (1900) mentioned "calyces few and irregular" on the hemipenis of Trimorphodon, neither Cope's drawings (Plate 28, Figure 7) nor our observations indiate calvces. Dunn (1928) rejected the emphasis that Cope placed on grooved fangs and included Trimorphodon with Hypsiglena and Leptodeira in a colubrine group having enlarged rear teeth either grooved or not and a capitate hemipenis with a simple sulcus. We do not know how Dunn defined a capitate hemipenis, but we do not consider that of Trimorphodon to be capitate because the capitulum does not have a free overhanging edge on the sulcate side. Dunn (1928) may have been repeating Cope's observations that the head is very distinct. Duellman (1958), using Dunn's arrangement, compared the same three genera and concluded that Trimorphodon was distantly related to the other two. Underwood (1967), using hemipenial and retinal characters, tenatively placed Trimorphodon and Hypsiglena in one heterogeneous family (Natricidae) and Leptodeira in another (Homalopsidae). Dowling (1975) doubtfully placed Trimorphodon in a small tribe with Phyllorhynchus and the oriental Oligodon because it did not fit well elsewhere. However Dowling and Duellman (1978) returned to the classification of Cope (1893, et seq.), and included the genus in a heterogeneous array of neotropical forms. This placement conflicts with the biochemical data which agree in allying Trimorphodon with a group of mostly North American genera, including Elaphe, Pituophis, and Lampropeltis (George and Dessauer, 1970; Minton and Salanitro, 1972; Schwaner and Dessauer, 1982; Cadle, in press). These studies also coincide in placing the relationships of Trimorphodon far from the North American Nerodia-Thamnophis series (George and Dessauer, 1970; Minton and Salanitro, 1972), from Leptodeira and other neotropical xenodontines (Minton and Salanitro, 1972; Cadle and Sarich, 1981; Cadle, in press), and from various elapids and Crotalus (Cadle and Sarich, 1981; Cadle and Gorman, 1981). On the other hand, Bury et al. (1970) showed that the karyotype of Trimorphodon is distinct from a variety of genera from western North America, including Lampropeltis and Pituophis. Most early attempts to clarify the relationships of Trimorphodon have been misled by an inadequate description of the hemipenis and by the unusual combination of characters (e.g., vertical pupil; enlarged, grooved posterior maxillary teeth; noncalyculate hemipenis with large pockets), and even now no close relatives of Trimorphodon have been identified.

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