SHORTER COMMUNICATIONS

Taxonomic Status of the Snake Genera Conopsis and Toluca (Colubridae)

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The taxonomic history of the colubrid genera Conopsis and Toluca is complex and has been reviewed by Goyenechea and Flores-Villela (2000). The single character purportedly differentiating them has been called into question by several authors (e.g., Bogert and Oliver, 1945). Some workers recognize just one genus for this group (Bogert and Oliver, 1945; Goyenechea, 1995), whereas others have regarded the two genera as valid (Boulenger, 1894; Dugès, 1896; Duellman, 1961). Taylor and Smith (1942) reviewed these genera and concluded that each was valid. According to these authors, species of Toluca have a groove on each posterior maxillary tooth, that is lacking in species of Conopsis. In spite of the review by Taylor and Smith (1942), the generic status of Conopsis and Toluca was questioned by Bogert and Oliver (1945) because the latter did not consider the putative diagnostic character sufficient for recognizing the genus Toluca.

In addition to the presence or absence of grooves in the posterior maxillary teeth, another morphological character purportedly differentiating these genera is the condition of the loreal scale (Taylor and Smith, 1942). In Conopsis, the loreal scale may be present or fused with the nasal, whereas it is completely absent in Toluca. As part of revisionary work on these snakes, we reevaluated these putative, diagnostic features in all recognized taxa of both genera to assess their taxonomic utility, since the only way to allocate specimens to particular species has been on the basis of geographic provenance.

We examined 659 museum specimens, including 199 Conopsis and 460 Toluca that represented all known taxa (10 species and subspecies) from throughout the geographical range of both genera (both are endemic to Mexico, distributed from Chihuahua to Oaxaca), in order to reevaluate their taxonomic status. The following characters were recorded: snout-vent length (SVL), total length (TL), diameter of the body (DIAM), number of ventral and subcaudal scales, supralabials, infralabials, presence-absence of the nasal, loreal, preocular, postocular, frontal, and genial scales, temporal formula, shape of the hemipenis, and dorsal and ventral color pattern. To determine the presence or absence of tooth grooves, maxillae were dissected on 43 specimens (Appendix 1) representing all recognized species and subspecies of each genus. One maxilla

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was dissected in each of six specimens of Conopsis biserialis from Guerrero and Morelos; one specimen of Conopsis nasus labialis from Chihuahua; seven specimens of Conopsis nasus nasus from Distrito Federal, Durango, Hidalgo, Michoacán, Oaxaca and Queretaro; five specimens of Toluca amphisticha from Oaxaca; five specimens of Toluca conica from Guerrero; six specimens of Toluca lineata acuta from Puebla and Hidalgo; four specimens of Toluca lineata lineata from Puebla; two sepcimens of Toluca lineata varians from Mexico and Puebla; five specimens of Toluca lineata wetmorei from Oaxaca; and two specimens of Toluca megalodon from Oaxaca.

All species of Conopsis and Toluca tipically have 12 maxillary teeth, of which the posterior five are enlarged and flanged (10 taxa; Fig. 1). There is no diastema between the smaller anterior teeth and the enlarged posterior teeth. The structure of the flange is the same for all taxa, the posterior ridge of the tooth is extended caudally into a flange or blade, and this leaves a shallow fossa on both the labial and the medial surfaces of the tooth. The maxillary teeth are uniformly conical, becoming larger posteriorly along the maxilla. We found variation in the maxillary teeth among species of both genera regarding the relative size of the teeth, curvature of the fangs, and depth of the flange.

Flanges can be observed on maxillary teeth seven to 12 on all taxa. This condition is common in many aglyphous colubrids. A low, but distinct, flange can be found on Conopsis biserialis and C. n. nasus. Conopsis nasus labialis, T. l. lineata, and T. l. wetmorei have a more prominent flange, and T. amphistica, T. conica, T. l. acuta, T. l. varians, and T. megalodon have the most highly developed flanges.

Loreal scales were present in 31% of the specimens of Toluca and 81% of specimens of Conopsis. After checking several hundred specimens (the complete list of specimens examined is available upon request to the first author), we attribute this variation to interpopulational differences rather to a feature worthy of generic recognition. In some cases, the loreal scale was present on one side but absent on the other side in the same specimen; similar variation was noted in all the species of both genera (13% in Conopsis and 18% in Toluca).

Other relatively invariate characters observed in all specimens of both genera include presence of a pair of internasal scales, one preocular and a pair of postocular scales, one rostral, one nasal, one hexagonal frontal scale, and a temporal formula of 1+2. The shape and ornamentation of the hemipenis corresponds to Types A and B of Dowling and Savage (1960), with a subcylindrical shape and reticulated ornamentation with several large spines at the base, respectively. Characters that have been used to define species of Conopsis and Toluca were found to be variable in all species of both genera. These characters include the number of genial scales, upper and lower labials, the coloration and pattern of spots on both the dorsum and ventrum, and all the morphometric measures we recorded.

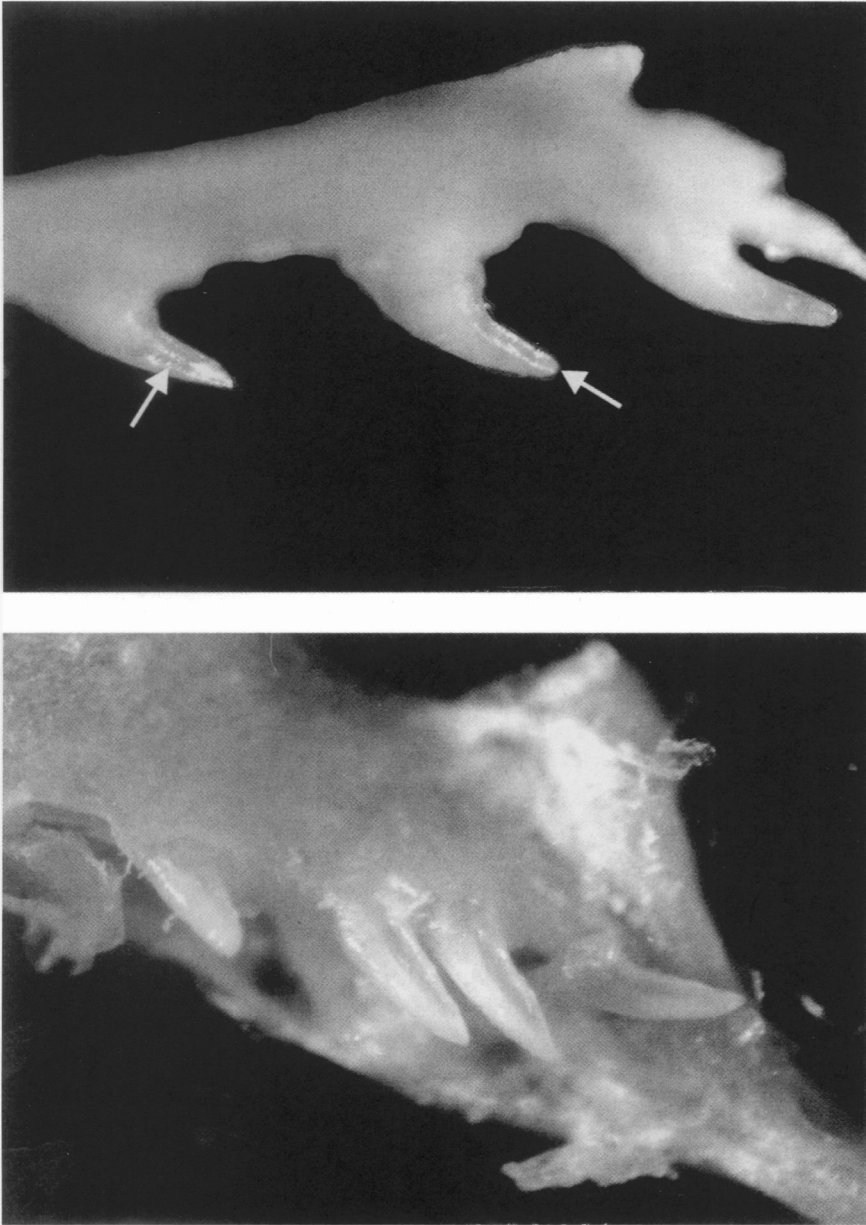Günther (1893) described C. nasus for a second time,

Fig. 1. Maxillae of *Conopsis* and *Toluca* showing the flange in at least one of the rear teeth. Top: *Conopsis nasus nasus* MZFC 617; Bottom: *Toluca lineata wetmorei* MZFC 7568.

as having smooth, equal teeth. However, he also noted, that teeth in "*Conopsis nasus* are not strictly isodont" and observed a "commencement of a groove on large specimens." In their review of the genera *Conopsis* and *Toluca*, Taylor and Smith (1942) argued that Günther (1893) probably confused species of the two genera which at that time were lumped under *Conopsis*, and because of that he saw a faint groove in some individuals. Also, they commented that *Conopsis biserialis* may posses two or three teeth that "may be

very slightly thicker, and a slight depression may be discernible on the outer posterior face."

In contrast to Taylor and Smith (1942), who noted the presence of grooves on the rear teeth of *Toluca*, but described the teeth of *Conopsis* as being smooth, we found that a distinct flange is present in at least the three most posterior maxillary teeth in all of the specimens in both genera, and that the posterior maxillary teeth tend to be enlarged.

Likewise, the condition of the loreal scale is highly

variable within taxa assigned to both genera, and indeed in individual specimens, and cannot be considered a diagnostic character differentiating *Conopsis* from *Toluca*. The diagnostic characters that purportedly separate these genera (sensu Taylor and Smith, 1942) simply do not exist. Therefore, because of the principle of priority, *Conopsis* Günther (1858) must be given priority over *Toluca* Kennicott (in Baird, 1859). All species and subspecies of the former genus *Toluca* should be synonimized under *Conopsis*, and considering that both names have female endings, no changes in spelling of specific or subspecific names are needed.

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APPENDIX 1

The maxilla was dissected in the following specimens, museum abbreviations follow Leviton et al. (1985), and Flores-Villela and Hernández-Gómez (1992).

Conopsis biserialis: 3603 MZFC GRO, Tetipac, Los Llanos, km 10 carr. Taxco-Tetipac; 3606 MZFC GRO, Ixcateopan de Cuauhtémoc, km 26.5 carr. Taxco-Ixcateopan; 3608 MZFC GRO, Tetipac, Los Llanos, km 10 carr. Taxco-Tetipac; 3612 MZFC GRO, Taxco, Cerro del Huizteco; 3613 MZFC GRO, Pedro Ascencio Alquisiras, 500 m before 3 Cruces de Mamatla; 10167 MZFC MOR, sorroundings of Huitzilac, carr. Tres Marias-Huitzilac.

Conopsis nasus labialis: 8565 MZFC CHIH, Guachochi; km 28 carr. Creel-La Bufa.

Conopsis nasus nasus: 0089 MZFC DF., Iztapalapa, Villa de Guadalupe, Cerro del Guerrero; 0092 MZFC DF., Iztapalapa, Villa de Guadalupe, Cerro del Guerrero; 7026 UTA DGO, Llano Grande; 0617 MZFC HGO, 5 km from Jasso; 2162 MZFC MICH, Patzcuaro Lake; 3344 UTA OAX, Monte Albán; 6235 MZFC QRO, Los Espinos, km 55 carr. Cadereyta-Xilitla.

Toluca amphisticha: 12487 UTA OAX, Sierra Mixe, 0.8 km W Totontepec; 12491 UTA OAX, Sierra Mixe, 0.8 km W Totontepec; 14168 UTA OAX, Sierra Mixe, 0.8

km S Totontepec; 14169 UTA OAX, Sierra Mixe, 0.8 km S Totontepec; 14170 UTA OAX, Sierra Mixe, 0.8 km S Totontepec.

Toluca conica: 2898 MZFC GRO, Chilpancingo, Omiltemi Salida E del pueblo; 2899 MZFC GRO, Chilpancingo, Omiltemi 2km E-SE; 2900 MZFC GRO, Chilpancingo, Omiltemi on trail to Las Joyas 500 m NW; 2901 MZFC GRO, Chilpancingo, Omiltemi Barranca de Potrerillos; 2902 MZFC GRO, Chilpancingo, Omiltemi 2 km E.

Toluca lileata acuta: 3258, 3258-3, 3258-4, 3258-6, 3258-7 MZFC PUE, Chapulco, 4 km E.

Toluca lileata acuta × *Toluca lineata lineata*: 0840 MZFC HGO, Tejocotal approx 500 m NE of town.

Toluca lineata lineata: 3216 MZFC PUE, town of Amozoc; 3217–18 MZFC PUE, Chignahuapan, Puente rojo 0.5–1 km W; 3534 MZFC PUE, Chignahuapan, Chignahuapan 10 km E.

Toluca lineata varians: 7108 MZFC MEX, Atlacomulco km 21 carr. Toluca-Atlacomulco; 5739 MZFC PUE, Tehuacan, 8 km E Chapulco.

Toluca lineata wetmorei: 11453–54 MZFC OAX, Cerro de Yucunino; 11455–57 MZFC OAX, Llano de Guadalupe.

Toluca megalodon: 6557 MZFC OAX, Sierra de Juárez, km 148 carr. 185 Oaxaca-Tuxtepec; 8301 MZFC OAX, Sierra de Juárez, La Cumbre carr. Oaxaca-Tuxtepec.

Recovery of Garter Snakes (*Thamnophis sirtalis*) from the Effects of Tetrodotoxin

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The arms race analogy is a popular view of evolutionary interactions between predators and prey but one whose generality is questionable because of the paucity of empirical studies in natural systems. Predators and prey are expected to experience asymmetrical selection from ecological interactions, leading some authors to question whether predators are under direct selection to respond to evolutionary advances by prey. The consequences of interactions are generally less severe for predators than for prey (the "life-dinner principle"; Dawkins and Krebs, 1979) and even severe consequences may not be predictable ("dodging the bullet"; Brodie and Brodie, 1999a). Consequently, evolutionary arms races between predators and prey are most likely to occur when prey are dangerous and, therefore, exert strong selection on predators (Brodie and Brodie, 1999a).

Strong selection by prey on predators is expected when prey are toxic or otherwise dangerous (Brodie and Brodie, 1999a). For toxic prey, selection may result

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from the immediate effects of toxins (i.e., injury or death) or from indirect effects that result from the action of the toxin such as temporary immobility, alterations to physiology or metabolism, or reduced organismal performance. Because evolutionary response of predators to prey might result in any predator adaptation that ameliorates the fitness deficits associated with prey toxins, predator resistance might include behavioral avoidance of toxic prey, reduced susceptibility to a toxin directly, or reduced duration of the effects of a toxin, or some combination thereof.

From a microevolutionary perspective, one of the best documented predator-prey systems includes the newt *Taricha granulosa* and its predator, the garter snake *Thamnophis sirtalis* in the Pacific Northwest of North America (Brodie and Brodie, 1990, 1991, 1999b,a). Newts of the genus *Taricha* possess tetrodotoxin (TTX; Mosher et al., 1964; Wakely et al., 1966; Brodie, 1968; Brodie et al., 1974; Daly et al., 1987), an extremely potent neurotoxin that acts as a Na+ channel blocker. Although all three species of the genus *Taricha* possess this toxin, *Taricha granulosa* is many times more toxic than any other species. The only predator known to forage on newts and resist the effects of this toxin is *Thamnophis sirtalis*.

Within populations, resistance to TTX varies among neonate snakes and has a heritable basis (Brodie and Brodie, 1990). Resistance is not affected by either short-term or long-term exposure to TTX (Brodie and Brodie, 1990; Ridenhour et al., 1999), hence, environmental effects are unlikely to explain familial differences. Among populations, the levels of both newt toxicity and garter snake resistance are variable but roughly matched (Brodie and Brodie, 1990, 1991, 1999a), suggesting a geographic mosaic of coevolutionary outcomes (Thompson, 1994, 1999a,b). Garter snake populations allopatric with newts are not resistant to TTX, whereas sympatric populations are resistant (Brodie and Brodie, 1990). Island populations of newts from British Columbia lack TTX (Hanifin et al., 1999), and garter snakes from these populations are nonresistant (Brodie and Brodie, 1991). Other garter snakes that coexist with *Taricha* are susceptible to TTX (Brodie, 1968; Brodie and Brodie, 1990; Motychak et al., 1999), supporting the view that resistance to TTX is an adaptation by a predator to its toxic prey.

Past studies of TTX resistance have used a bioassay based on locomotor performance to assess variation (Brodie and Brodie, 1990, 1991, 1999b; Ridenhour et al., 1999). The bioassay examines an individual snake's reduction in crawl speed 30 min after an injection of TTX. The bioassay is ecologically relevant because reduced locomotor performance is expected to impair the ability of snakes to escape predators or thermoregulate. The length of time that a snake is impaired from a given dose of TTX is unknown and may further contribute to the selective scenario in the interaction between newts and snakes. In this paper, we explore the time to recovery for individual snakes from a population resistant to TTX. We further examine the correlation between resistance as measured by reduction in locomotor performance after 30 min and the relative recovery at longer intervals.

The subjects for this experiment were neonate *T. sirtalis*, born during the summer of 2000 in captivity to wild-caught females from Benton County, Oregon.