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Caudals and Calyces: The Curious Case of a Consumed Chiapan Colubroid

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Abstract.—A new genus and species of colubroid snake is described from the isolated highlands of western Chiapas. This enigmatic little snake possesses a unique suite of characters that defies placing it in any known genus and clearly distinguishes it from all known genera. Several of the most unusual features include subcaudals undivided throughout the length of the tail and a simple hemipenis completely adorned with calyces and having a sulcus spermaticus that remains unbifurcated until the apical portion of the organ. Neither of these characteristics is known for any other colubroid of the Western Hemisphere. Consideration of morphology places the new snake in the Dipsadidae and suggests that *Adelphicos*, *Atractus*, *Geophis*, and *Chapinophis* are among its closest relatives.

Resumen.—Se describe un nuevo género y especie de serpiente colubrina de las montañas aisladas del oeste de Chiapas. Esta enigmática y pequeña serpiente posee un conjunto único de caracteres que impide su asignación a cualquier otro género y claramente la distingue de cualquier género conocido. Varios de las características inusuales incluyen subcaudales no divididas a lo largo de toda la cola y un hemipene simple, completamente cubierto de cálices, y con un surco espermático que permanece no bifurcado hasta el ápice del órgano. Ninguna de estas características es conocida de cualquier colúbrido en el hemisferio occidental. Examen de morfología sugiere que la nueva serpiente pertenece a la familia Dipsadidae y su afinidad esta con *Adelphicos*, *Atractus*, *Geophis*, y *Chapinophis*.

Prey items, especially small snakes, are frequently encountered in stomachs of Coralsnakes (Schmidt, 1932). Indeed, in several instances, new species of snakes have been recovered from Coralsnakes of the genus *Micrurus*. *Geophis dunni* Schmidt (1932) was removed from an individual of *Micrurus nigrocinctus* from Nicaragua, and this species has remained an enigma. The holotype was collected during or before 1909 (Townsend, 2006) from a region of Nicaragua that is thought to have become relatively well surveyed. Nevertheless, *G. dunni* has remained known from only the single specimen. In another instance of predation leading to discovery of a taxonomic novelty, Hay (1892) described *Storeria victa* (*Storeria dekayi victa*) that he encountered in the stomach of a *Micrurus fulvius* from Florida.

Coralsnakes are undoubtedly far more efficient predators of certain species of small snakes than human collectors, as revealed by a cursory survey of secretive or fossorial species of Middle American snakes found in their stomachs. Numerous species of colubroids are recorded from no more than a handful of individuals, and some are known from only their original descriptions: *Adelphicos daryi* Campbell and Ford (1982), *Adelphicos ibarraorum* Campbell and Brodie (1988), *Chapinophis xanthocheilus* Campbell and Smith (1998), *Geophis isthmicus* Downs (1967), *Geophis juarezi* Nieto-Montes de Oca (2003), *Geophis maculiferus* Downs (1967), and *Rhadinophanes monticola* Myers and Campbell (1981) are but a few examples of rare species becoming known in recent decades.

We were not surprised when a small snake was recovered from the stomach of a *M. nigrocinctus* from southern Mexico. Following the key to Mexican genera of snakes in Smith and Taylor (1945), this snake is identified as *Geophis*, which—on the basis of a suite of characters—it is not. Subsequent examination clearly indicated that this prey item represented a previously unknown snake, unlike anything currently recognized from the New World tropics. This small snake was obtained now over 40 yr ago, and the report of its discovery has been a long time in coming. We were optimistic that additional specimens might be secured, but after at least a dozen more trips into the region spanning several decades, we have been unrewarded.

The colubroids of the Western Hemisphere currently are allocated into three families: Natricidae, Colubridae, and Dipsadidae (Vidal et al., 2007, 2010; Zaher et al., 2009; sensu Grazziotin et al., 2012), although these families are sometimes placed at the subfamily level (Figueroa et al., 2016). Regardless of taxonomic rank, these groups of snakes are recognizable by distinctive molecular differences. Morphological characteristics that clearly define individual groups are more difficult to categorize owing to the large number of species and morphologically diverse assemblages. The largest American clade of snakes, the Dipsadidae, is composed of almost 100 genera in over 700 species that have radiated into practically every terrestrial and freshwater habitat.

Several clades within the Dipsadidae are currently placed at the subfamily level (Vidal et al., 2007, 2010; Zaher et al., 2009). The Xenodontinae contains genera that are mostly South American in distribution, possess enlarged spines on the sides of a bilobed hemipenial body, and the lobes bear two distinctly ornamented regions: a sulcate surface bearing a capitulum and the asulcate surface with enlarged spinulate or papillate calyces, or sometimes nude; further, the sulcus spermaticus bifurcates near the base of the organ (Zaher, 1999). The Dipsadidae is primarily a Middle American lineage containing over 25 genera lacking enlarged lateral spines on the hemipenial body and do not have two different ornamented regions on the lobes. Further, the organ may be single or bilobed and may be noncapitate or semicapitate. Most species have a capitate, calyculate hemipenis with a sulcus spermaticus bifurcating within the capitulum. A synapomorphy supporting this group is a sulcus spermaticus bifurcating at the base of, or within, the capitulum (Cadle, 1984c; Zaher, 1999; Myers and Cadle, 2003). The hemipenis of the new genus described here is unlike that of any known colubroid.

Materials and Methods

Protocols for making most standard scale counts follow Myers (1974). We determined the number of ventral scutes

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using the procedure suggested by Dowling (1951), in which the anteriormost ventral is that bordered on either side by the first row of dorsal scales. In many snakes there is a single scale between the nasal(s) and eye. A single scale, when present in dipsadids, is longer than high and therefore referred to as a loreal (Peters, 1964). We measured the body and tail with a standard meterstick to the nearest 1 mm; smaller structures such as the head and hemipenis were measured to the nearest 0.1 mm using a Vernier caliper. We obtained locations and distances using topographic maps (1:250,000) issued by the Instituto Nacional de Estadística, Geografía e Informática (2000) and Google Earth Pro (2017). Specimens were preserved by injection with formalin diluted to 10% of stock solution and then transferred to 70% ethanol for permanent storage. Fortunately, enough formalin was injected into the body cavity to stop the digestive process of the Coralsnake that preyed on the snake (the primary subject of this paper).

We prepared the hemipenis of the new taxon and comparative material using the technique of Pesantes (1994), with modifications as suggested by Myers and Cadle (2003) and Zaher and Prudente (2003), expanding everted hemipenes by introducing a syringe needle with a blunt tip at the base, tying the organ at this level, and injecting heated petroleum jelly with blue wax-dye through the needle until maximal possible expansion was achieved without risking rupture.

The artwork reconstructing the new taxon as it probably appeared in life was accomplished by Gabriel Ugueto, who used a series of photographs and measurements of the holotype as a reference. The illustration was drawn and painted digitally in Corel Painter and Adobe Photoshop using a Wacom Cintiq Pen Display.

To compare cranial osteology of small, rare, and delicate specimens we collected computed tomography (CT) data from skulls of the new taxon and comparative material. Formalin-fixed specimens were immobilized in a combination of floral foam, plastic straws or cups, and tape. Then, each specimen (sometimes two to four specimens simultaneously) were CT scanned at the University of Texas Arlington Shimadzu Center for Environmental Forensics and Material Science using a Shimadzu inspeXio SMX-100CT (Shimadzu, Inc., Kyoto, Japan). We collected CT data using several parameter combinations deemed suitable to preserved snake specimens. Each scan lasted about 15–30 min.

We used Shimadzu's inspeXio software to reconstruct raw X-ray data and exported them as stacks of 1,024 × 1,024 16-bit TIFF images. Each stack was rotated and cropped in ImageJ and imported into Avizo™ Software v.8.1 and 9.4 (Thermo Fisher Scientific, Inc., Waltham, Massachusetts USA). We isolated and converted skulls into one surface per skull using interactive thresholding. These surface files were the basis for collecting characteristics across the new taxon and comparative taxa. For the new taxon and *Adelphicos quadrivirigatus* (UTA R-22680), we manually segmented the lower jaw bones and the maxilla, ectopterygoid, pterygoid, and quadrate. Because of the digested state of the new taxon, reasonable segmentation of these bones was possible on only one side of the skull.

We examined comparative material from the Amphibian and Reptile Diversity Research Center at University of Texas Arlington, which contains representatives of almost every genus of Middle American snakes. For osteological comparisons, we prepared CT scans for the following species of dipsadids and colubrids (all numbers refer to UTA, except for UF H-157664 and AMNH 103068): *Adelphicos latifaciatus* (R-12245–12246), *A. quadrivirgatus* (R-22680), *Amastridium veliferum* (14146), *Atractus lancini* (R-59423), *Atractus. univittatus* (R-3600), *Atractus trilineatus* (R-22264), *C. xanthocheilus* (R-37591), *Chersodromus leibmanni* R-14132, 52625), *Coniophanes fissidens* (R-9413), *Coniophanes imperialis* (R-4328), *Conophis vittatus* (R-52631), *Cryophis hallbergi* (R-12272, 52632), *Diadophis punctatus* (R-5952), *Dipsas indica* (R-18175), *Enuliophis sclateri* (R-45181), *Enulius flavitorques* (R-56376), *Ficimia publia* (R-63119), *Geagras redimitus* (R-26690), *Geophis nigrocinctus* (R-5908), *Geophis omiltemanus* (R-5055), *Hydromorphus concolor* (R-44940, R-44941), *Hypsiglena torquata* (R-57106), *Imantodes cenchoa* (R-39231), *Leptodeira annulata* (R-59214), *Leptodeira septentrionalis* (R-14487), *Leptodeira uribei* (R-57688), *Manolepis putnami* (R-53007), *Ninia diademata* (R-12371), *Ninia pavimentata* (R-42407), *Nothopsis rugosus*, (R-40098), *Oxybelis aeneus* (R-53369), *Omoadiphas aurula* (UF H-157664), *Pliocercus elapoides* (R-52569), *Pseudoleptodeira latifasciata* (R-59558), *Rhadinaea fulvivittis* (R-4692), *Rhadinaea taeniata* (R-4424), *Rhadinella hannsteini* (R-21720), *Rhadinophanes monticola* (R-63277), *Rhinocheilus lecontei* (R-50696, 57755), *Sibynomorphus mikanii* (R-37712), *Sibon carri* (R-37270), *Sibon nebulata* (R-4700), *Tantalophis discolor* (ANMH-103068), *Tantilla rubra* (R-12455), *Tantilla shawi* (R-36810), *Tretanorrhinus nigroluteus* (R-52336), *Trimetopon pliolepis* (R-44969), *Tropidodipsas fasciata* (R-52645), and *Tropidodipsas philippii* (R-57499). To view the entire specimen, we collected radiographs from the new taxon using the SMX-100CT and exported them as 1,024 × 1,024 16-bit grayscale TIFF files. Each radiograph ran at 35 kV and 40 μA and averaged over 999 integrations in inspeXio. Original tomograms and surface files for the new taxon and *Adelphicos quadrivirgatus* (R-22680) are available on Morphosource (http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/555) and archived at the University of Texas at Arlington Amphibian and Reptile Diversity Research Center digital image collection.

The following sources have also been helpful in comparing the new genus with other Middle American snakes with regard to scalation, osteology, internal morphology, and biogeography: Hay (1892), Cope (1894), Smith (1941), Tanner (1943, 1944), Burger and Werler (1954), Duellman (1958a,b), Dowling and Savage (1960), Leviton and Tanner (1960), Peters (1960), Bogert and Duellman (1963), Dowling (1967), Downs (1967), Wilson and Meyer (1969), Myers (1974, 1982, 1984, 2003), Cundall (1981), Myers and Campbell (1981), Campbell and Ford (1982), Cadle (1984a,b,c), Jenner and Dowling (1985), Kofron (1985a,b, 1987), Campbell and Brodie (1988), Campbell (1989), Crother (1989), Smith and Campbell (1996), Campbell and Smith (1998), Zaher (1999), Smith and Chiszar (2001), Savage (2002), Mulcahy (2003, 2007), Myers and Cadle (2003), Nieto-Montes de Oca (2003), Schargel and Castoe (2003), Pinou et al. (2004), Townsend (2006), Cundall and Irish (2008), Harvey et al. (2008), McDowell (2008), Passos et al. (2009, 2013), Mulcahy et al. (2011)Angarita-Sierra (2014), Pietro et al. (2014), Zaher et al. (2014), Klaczko et al. (2016), and Canseco-Márquez et al. (2018).

Systematic Account

We are aware of no single morphological character that clearly differentiates the Dipsadidae from the Colubridae. We are confident, however, in placing the new taxon described below in the Dipsadidae on the basis of overall gestalt and similarity of certain characters with Middle American genera (*Adelphicos*, *Atractus*, *Chapinophis*, and *Geophis*) such as elongated braincase, loreal entering the orbit, prefrontal making contact

FIG. 1. *Cenaspis aenigma* (holotype, UTA R-10544, 258 mm total length), drawing reconstructing species in life.

with the eye, and maxilla with relatively few teeth (14–15) and probably lacking enlarged "rear-fangs."

Cenaspis, new genus
(Figs. 1–7)

Type Species.—*Cenaspis aenigma*, new species (described below).

Diagnosis of Genus.—This genus differs from all other New World dipsadids by two unique features: 1) all subcaudals undivided and 2) hemipenis single, noncapitate, hemipenial body and apical region completely covered with calyces, and sulcus spermaticus simple. *Rhinocheilus* is the only other American colubroid north of Panama having undivided subcaudals, distinguished from *Cenaspis* in always having at least a few divided subcaudals, preocular present, dorsals in 23 rows at mid-body and reduced to 19 posteriorly, and a reddish and black pattern with dorsal blotches or bands. Although some other New World genera have single hemipenes, in every case of which we are aware, the hemipenial body bears spines or spinules (vs. calyces), there usually is distinct capitation, and the sulcus spermaticus is bifurcate for much of the length of the capitulum (Tables 1, 2).

Etymology.—The generic name is derived from the Latin *cena*, meaning dinner, and *aspis*, meaning a kind of snake, in reference to predation on the single known individual of this snake. The name taken literally means "dinner snake."

Cenaspis ***aenigma***, new species

Holotype.—UTA R-10544, an adult male, obtained on "La Loma," located some 20–25 km (by road) W-NW of Rizo de Oro (sometimes known as Nueva Tenochtitlán), Chiapas, Mexico. Access is gained into this region by means of a logging road connecting Rizo de Oro with Colonia Rodulfo Figueroa; the latter is a small settlement very near the border with Oaxaca. The type locality lies to the N-NW of Colonia Rodulfo Figueroa on the western slopes of Cerro El Baúl, the highest peak in the region, rising to an elevation of 2,050 m. Collected by the late Julio Ornelas-Martínez on 6 July 1976.

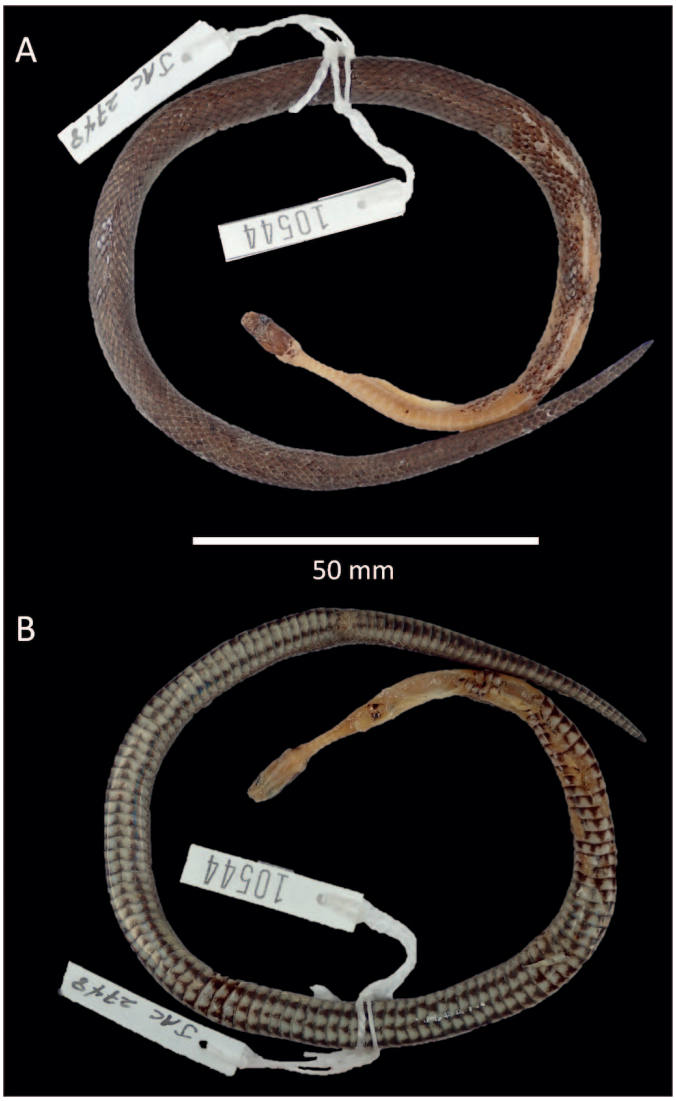

FIG. 2. *Cenaspis aenigma* (holotype, UTA R-10544, 258 mm total length), dorsal (A) and ventral (B) aspects of preserved specimen.

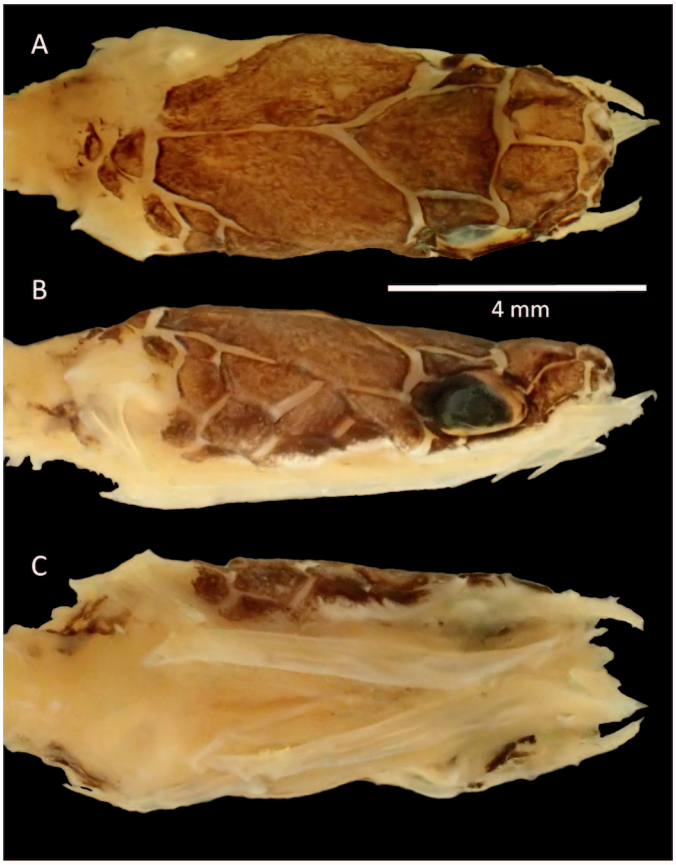

FIG. 3. *Cenaspis aenigma* (holotype, UTA R-10544), dorsal (A), lateral (B), and ventral (C) aspects of head of preserved specimen.

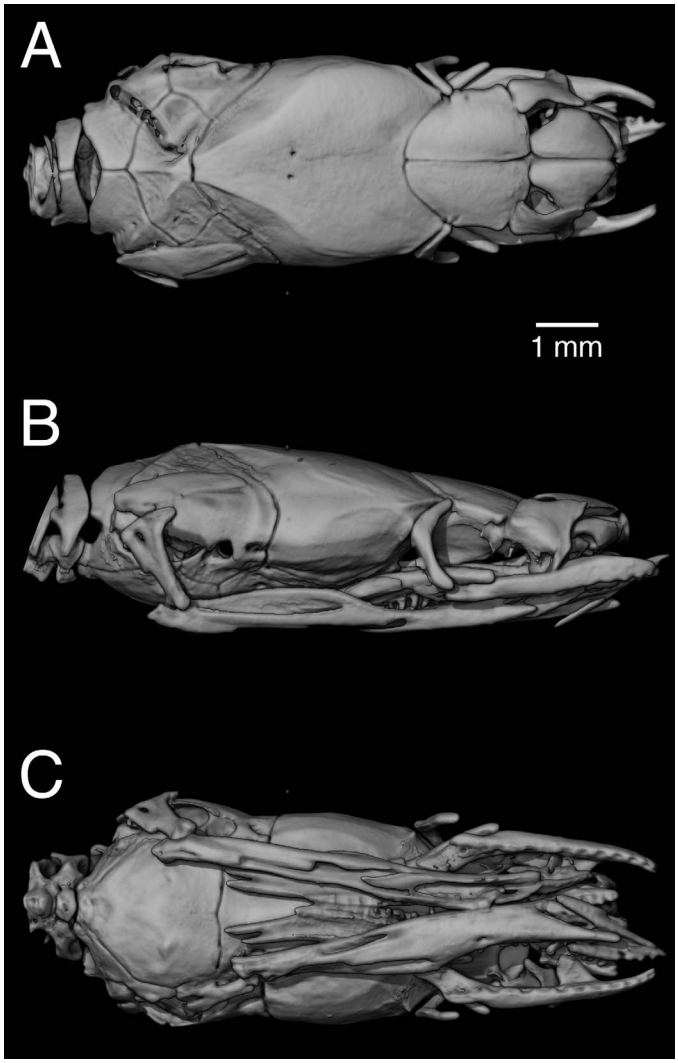

FIG. 4. *Cenaspis aenigma* (holotype, UTA R-10544), volume rendering of dorsal (A), lateral (B), and ventral (C) aspects of skull.

Diagnosis.—Differs from other Middle American genera of dipsadids except *Adelphicos*, *Atractus*, *Chapinophis*, *Chersodromus*, *Geophis*, *Ninia*, some *Sibon* in having prefrontal enter orbit. *Chersodromus* and *Ninia* (characters for *Cenaspis aenigma* in parentheses) have keeled (vs. smooth) dorsal scales; *Adelphicos* and *Sibon* have $\leq$ 15 (vs. 17) dorsal scale rows at mid-body; *Atractus*, *Chersodromus*, *Geophis*, and *Sibon* have 1 + 2 or 0 + 1 (vs. 1 + 1) temporals; *Adelphicos*, *Chapinophis*, and *Geophis* usually have $\leq$ 7 (vs. 8) supralabials; and *Adelphicos*, *Chapinophis*, and *Trimetopon* have a divided cloacal scute (vs. undivided) (Tables 1, 2). For additional characteristics see diagnosis for genus.

Description of the Holotype.—Moderately slender, small snake with snout–vent length 222 mm, tail length 36 mm, and total length 258 mm (Figs. 1, 2); head length 9.0 mm, eye diameter 1.0 mm, snout-to-eye distance 1.2 mm (Fig. 3); portions of head on left side, ventral surface, and neck digested and scales missing; internasals small, less than half size of prefrontals; prefrontals relatively large, anterolateral portion forming upper anterior border of eye; frontal 2.4 long $\times$ 1.8 wide, flanked by large supraoculars; parietals long, tapering, and becoming slender posteriorly; nasal scale single apparently without vertical suture; single horizontally elongate loreal extending posteriorly to border anterior of orbit (alternatively, this scale might be considered a preocular with loreal missing, but see Peters, 1964); supralabials 8/8, supralabials 4–5 contacting lower border of orbit; postoculars 2/2, upper long and narrow, about twice as large as the lower; temporals 1 + 1 + 2; dorsal scale rows at mid-body 17, unreduced posteriorly; ventrals ~140, some missing anteriorly on body but estimated on the basis of segmental (vertebral) number; cloacal scute undivided; subcaudals 36, undivided; tail spine sharply pointed, about as long as preceding 2 subcaudals; mid-length of tail encircled by 8 scales between subcaudals.

Dorsum without conspicuous pattern; dorsal ground color medium brown, grading to paler brown on sides; anterior supralabials to level of eye white, posterior lower portion of supralabials white; apical portion of most dorsal scales with dark brown spot, especially on middle half of body; cranial end of individual dorsal scales also dark brown over much of body (Figs. 1, 2A); venter of body cream with three series of dark brown triangular blotches on ventrals creating irregular striping; tail cream with single series of mid-ventral blotches (Fig. 2B).

Premaxilla mostly absent (Figs. 4, 5A–C), perhaps owing to digestion, but prominent ascending process oriented vertically and attaching dorsally to septomaxilla and nasals; nasals in broad medial contact, longer than wide with broad downwardly curving lateral winglike processes, rounded posteriorly, in contact with frontals; prokinetic joint attaching snout with braincase formed by articulation of nasals and septomaxillae with frontals; prefontals robust, blocklike, anterior edge concave without anteriorly projecting processes, ventrally long articulating surface with maxillae, extended by posteroventral

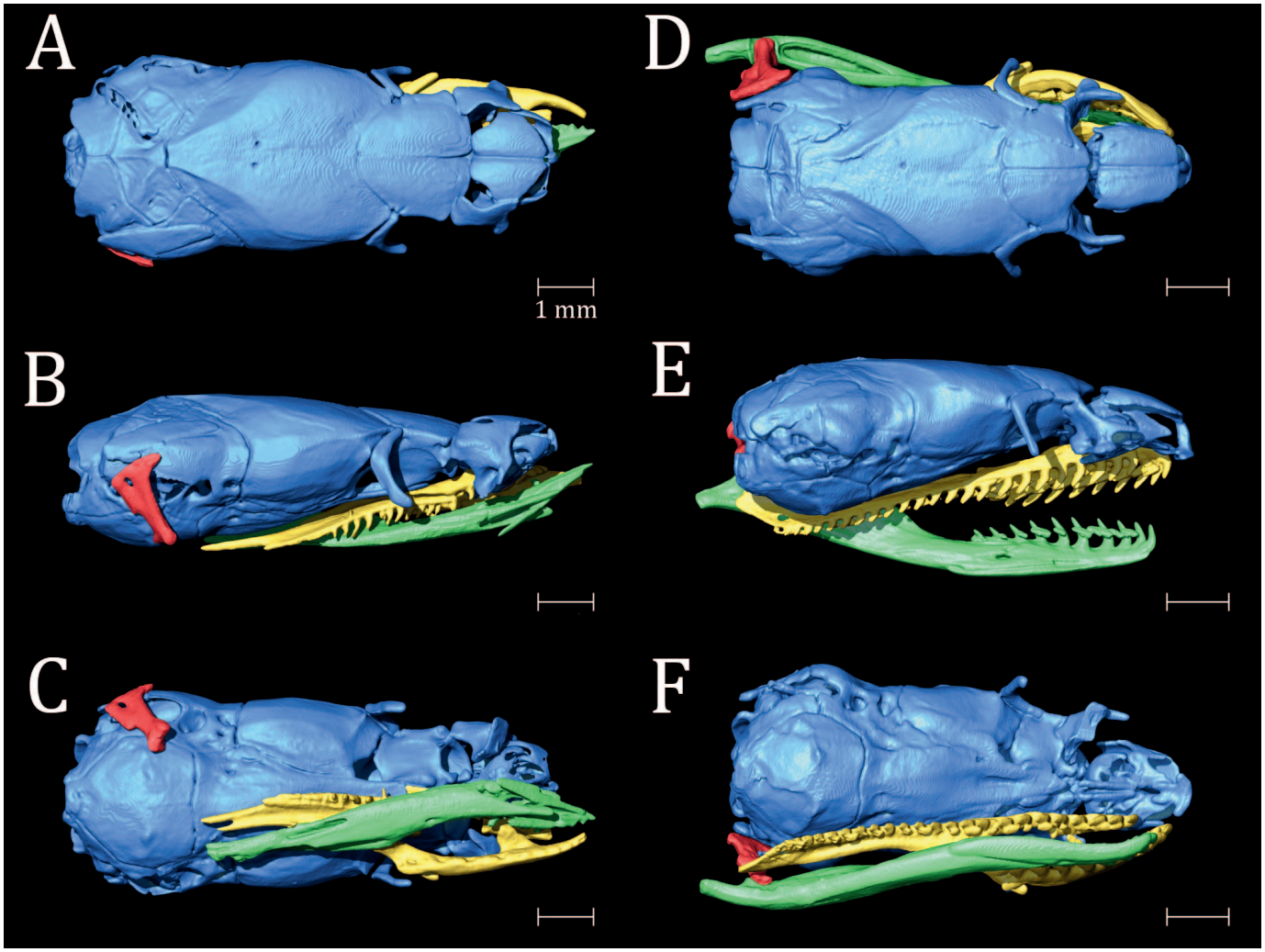

FIG. 5. Comparison between segmented skulls of *Cenaspis aenigma* (UTA R-10544) (A–C) and *Adelphicos quadrivirigatus sargii* (UTA R-22680) (D–F). Dorsal (A and D), lateral (B and E), and ventral (C and F) aspects; quadrate shown in red, palatomaxillary arch in yellow, mandible in green, and cranium in blue. The quadrate of the *C. aenigma* holotype was digested on the left side, so the right one is shown (although somewhat digested).

process; paired frontals with broad median suture, posteriorly broad articulation with parietal forming U shape; parietals united, extending downward to basisphenoid; supraoccipitals relatively large, lacking transverse crest, with median keel; postorbital large, well-developed, articulating broadly with parietal, reaching frontal, bordered dorsally by distinct parietal ridge, extending ventrally to occupy most of posterior margin of orbit, nearly reaching ectopterygoid; dentigerous bones of the palatomaxillary arch include maxillary, palatine, and pterygoid (Fig. 6A); in lower jaw dentary also with teeth (Fig. 6B); teeth short, conical, blunt, only slightly recurved; maxilla long, almost straight, extending to level about equal to posterior edge of eye, broad palatine process projecting slightly posteromedially and medial edge with blunt point; ectopterygoid process slightly more narrow than palatine process, angling posteriorly from terminus of bone, medial edge straight; number of maxillary teeth 14/14 (anterior tip of maxillae broken, possibly accounting for one additional tooth on each side); increase in tooth socket size from anterior to posterior indicating corresponding increase in tooth size, no posterior diastema; anterior end of ectopterygoid relatively short, strongly bifurcating with lateral fork about twice as long as medial fork, extending posteriorly to level about equal to lateral flexure of pterygoid; palatine teeth 5/4, tooth sockets large; pterygoid teeth 16/17, decreasing in size posteriorly; supratemporal (right only, left missing) relatively short, straight, and wide, extending just barely beyond caudal edge of braincase, extending anteriorly only to prootic; quadrate short, stout, roughly triangular, well-developed heterocoelous condyle articulating with mandible, dorsally flattened and flared dorsoanteriorly, large oval foramen in upper posterior of bone (Fig. 6C).

The right hemipenis in situ extends to subcaudal 12; left hemipenis removed, everted, and expanded, total length from base to apex ~10 mm; organ mostly cylindrical, distally becoming very slightly bulbous; sulcus spermaticus single through most of length, becoming bifurcated at apex (level of subcaudal 12); except for extreme lower base, entire organ calyculate, with large calyces proximally (alternately being considered flounced because of relatively few vertical cross-ridges), becoming smaller distally; as few as 3–4 calyces encircling organ near base, 18–19 near apex; micro-ornamentation of ridges papillate; apex not differentiated (Fig. 7).

Etymology.—From the Latin *aenigma* meaning a riddle or mystery.

Comparison with Other Middle American Taxa.—About half of the genera of Dipsadidae have a preocular contacting the supra-

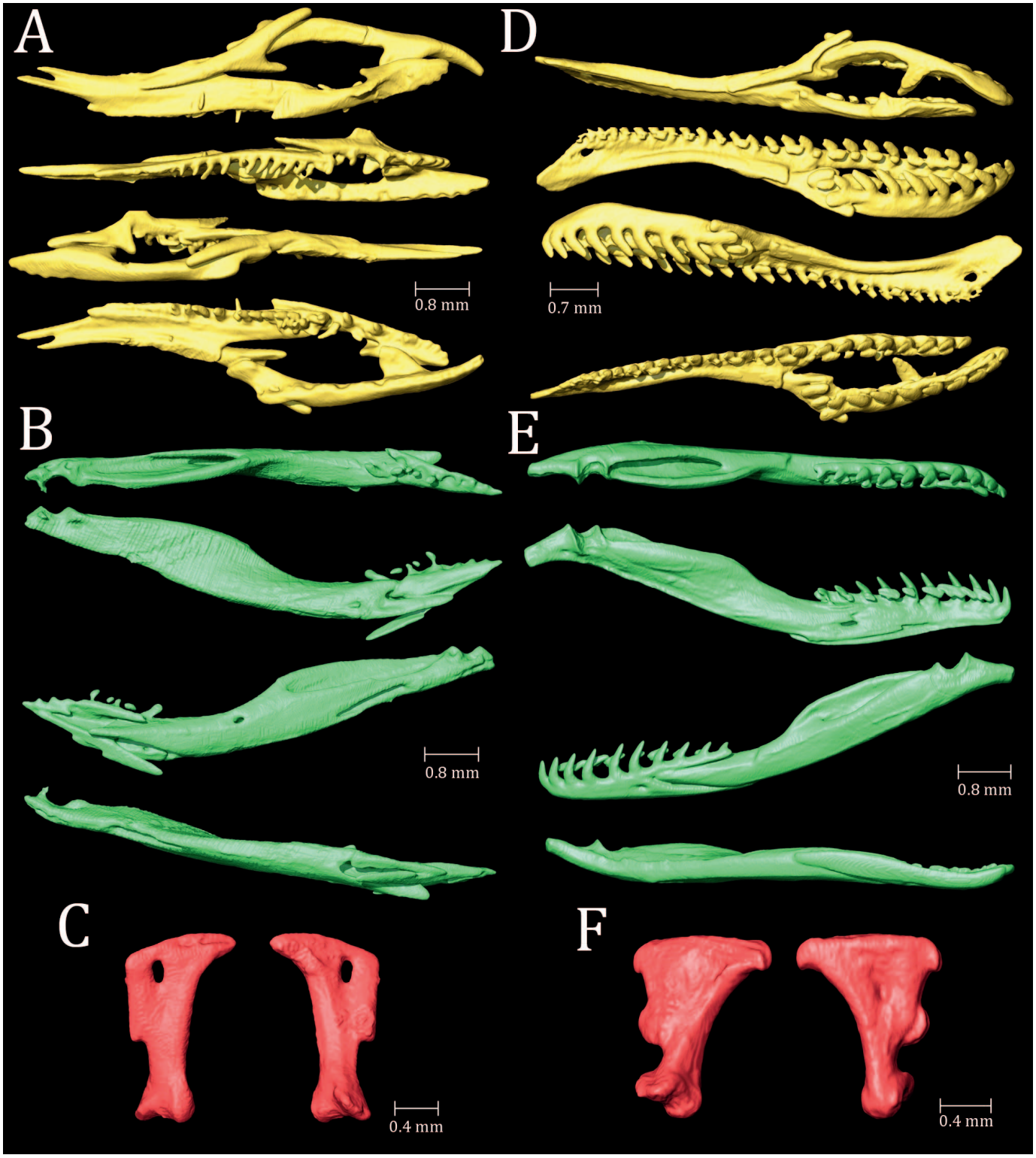

FIG. 6. Comparison between segmented bones of *Cenaspis aenigma* (UTA R-10544) (A–C) and *Adelphicos quadrivirigatus sargii* (UTA R-22680) (D–F). Palatomaxillary arch (A and D; yellow), mandible (B and E; green), and quadrate (C and F; red). Left palatomaxillary arches shown in dorsal, lateral, medial, and, ventral views (top to bottom); left mandibles shown in dorsal, medial, lateral, and ventral views (top to bottom); right quadrate shown for *C. aenigma* (C) in lateral (left) and medial (right) views, and left quadrate for *A. quadrivirigatus sargii* (F) in medial (left) and lateral (right) views.

ocular, precluding contact of the prefrontal with the orbit (Table 1). When the preocular is absent as in *Cenaspis*, *Adelphicos*, *Atractus*, *Chapinophis*, *Chersodromus*, *Enuliophis*, *Enulius*, *Geophis*, *Ninia*, *Omoadipsas*, and some *Sibon*, the prefrontal enters the eye. Associated with this trait is a single, horizontally elongate loreal between the nasal(s) and orbit. Most often small burrowing or terrestrial Dipsadidae have 15 to 17 rows of smooth dorsal scales at mid-body and these are unreduced posteriorly; exceptions are *Chersodromus* and *Ninia*, which have keeled scales. Genera with 19 or more scale rows at mid-body (*Coniophanes*, *Cryophis*,

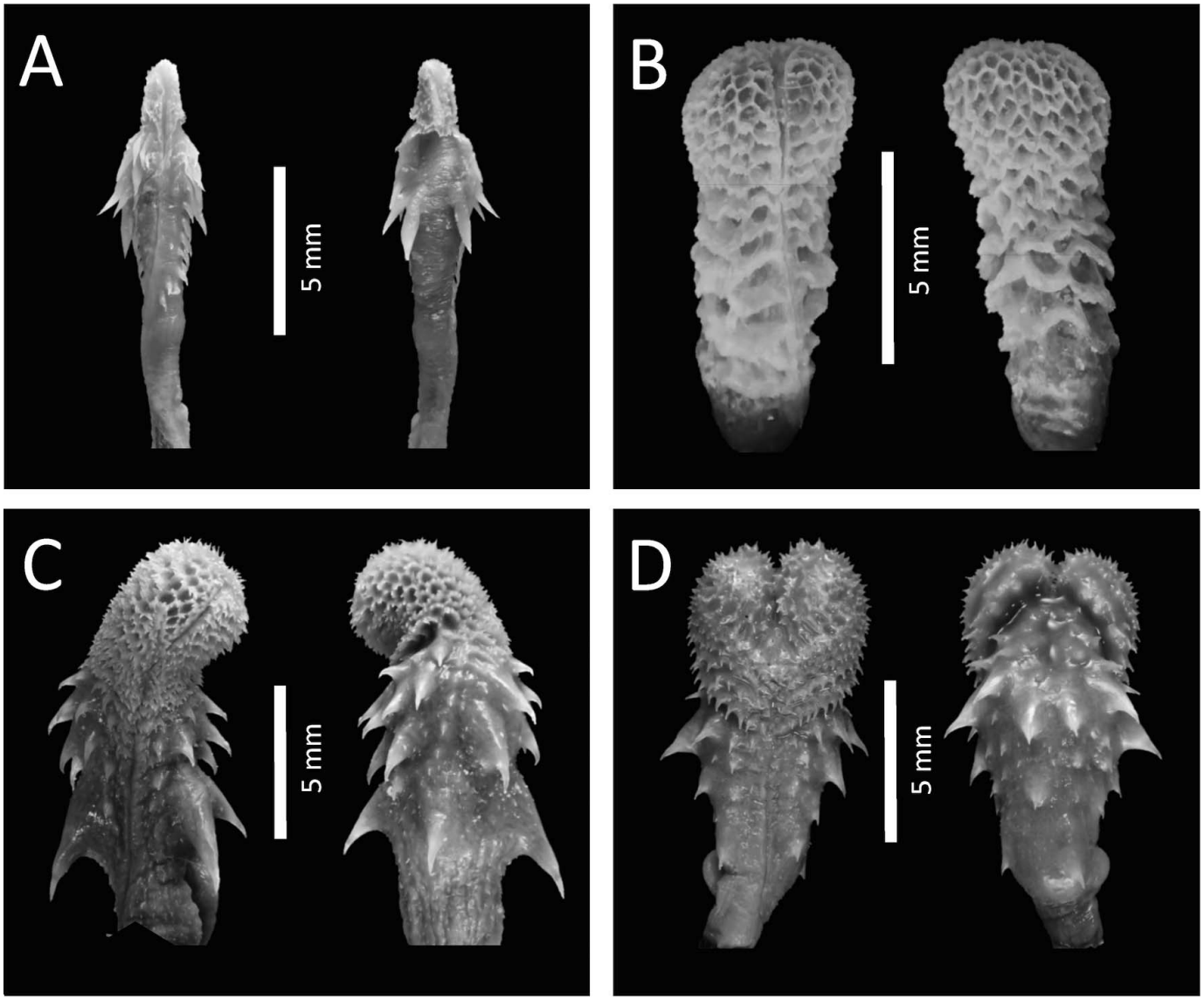

FIG. 7. Selected hemipenes of Nuclear Central American snakes. (A) *Adelphicos latifasciatus* from Oaxaca, UTA R-12246 (left hemipenis, 204 mm snout–vent length [SVL], 54 mm tail length); (B) *Cenaspis aenigma* holotype from Chiapas, UTA R-10544 (left hemipenis, 222 mm SVL, 36 mm tail length); (C) *Cryophis hallbergi* from Oaxaca, UTA R-12272 (left hemipenis, 478 mm SVL, 137 mm tail length); (D) *Geophis rhodogaster* from Guatemala, UTA R-28349 (right hemipenis, 223 mm SVL, 59 mm tail length). Sulcate (left) and asulcate (right) views shown. Note that, except for the hemipenis of *C. aenigma*, all other organs are spinous and show a well differentiated capitulum, slightly bilobed in *Geophis rhodogaster*.

Eridaphas, *Hypsiglena*, *Leptodeira*, *Pseudoleptodeira*, *Rhadinophanes*, and *Tretanorhinus*) generally have scale-row reductions on the posterior of the body.

Few other Middle American snakes possess a ventral pattern resembling that of *Cenaspis aenigma*. The venter is immaculate in most species, although colors may grade into different hues from anterior to posterior of body, and often the dorsal coloration encroaches on the lateral edges of ventrals. *Coniophanes quinquevittatus* and *Coniophanes bipunctatus* have distinct dark round spots near the outer edge of each ventral and the midventer is unmarked. *Ninia diademata* frequently has three regular series of dark markings on the ventrals: a series is present on the lateral portion of each ventral and a large well-formed roundish to triangular spot midventrally. Unlike *Cenaspis aenigma,* in which the markings in all series are approximately the same size and shape, in *N. diademata* the midventral series is conspicuously larger and differently shaped from the lateral series (Burger and Werler, 1954). *Ninia maculata* and *Ninia psephota* usually have dark ventral markings that may variably be in a single midventral series, two series near lateral edges of ventrals, or as an irregular checkerboard, but rarely dark markings are arranged in more-or-less three series (lateral and midventral), although in irregular lines (Smith and Campbell, 1996; Savage, 2002).

Many genera of the Dipsadidae have two enlarged teeth on the posterior of the maxilla that may be grooved and often set off from more anterior teeth by a diastema (e.g., *Amastridium*, *Coniophanes*, *Imantodes*, *Leptodeira*, *Tantalophis*; Table 2). In *Cenaspis* 14–15 maxillary teeth appear to decrease in size posteriorly (on the basis of tooth socket size) and no diastema or enlarged grooved teeth are present (Figs. 5, 6). Fewer maxillary teeth characterize *Adelphicos* (7–11), *Atractus* (5–11), *Chapinophis* (12), and *Chersodromus* (7–9), whereas more teeth are present in *Ninia* (15–18) and *Tretanorhinus* (27–30). Species of *Geophis* differ by having relatively longer, sharper, more slender teeth in contrast to the short, stout, and blunt teeth in *Cenaspis*.

TABLE 1. Comparison of certain scalation characters among Middle American dipsadid snakes. Some meristic characters subject to variation; usual condition given. Dark shade represents characters similar to *Cenaspis*; light shade represents characters at variance.

Taxon	Prefrontals	Preocular(s)	Supralabials	Temporals	Dorsal midbody scales, posterior condition	Dorsal scale ornamentation	Cloacal scute	Subcaudals
Cenaspis aenigma	Entering orbit	Absent	8	1 + 1	17, unreduced	Smooth	Undivided	Undivided
Adelphicos (*veraepacis* group)	Entering orbit	Absent	7	1 + 1	15, unreduced	Smooth	Divided	Divided
Adelphicos (*quadrivirgatus* group)	Entering orbit	Absent	7	1 + 1	15, unreduced	Smooth	Divided	Divided
Amastridium	Not entering orbit	Present	7	1 + 2	17, unreduced	Smooth	Divided	Divided
Atractus	Entering orbit	Absent	5–9	1 + 2	15–17, unreduced	Smooth	Undivided	Divided
Chapinophis	Entering orbit	Absent	7	1 + 1	17, unreduced	Smooth	Divided	Divided
Chersodromus	Entering orbit	Absent	7–8	1 + 2	15–17, unreduced	Keeled	Undivided	Divided
Coniophanes	Not entering orbit	Present	7	1 + 2	17–25, reduced	Smooth	Divided	Divided
Cryophis	Not entering orbit	Present	9	2 + 2	23, reduced	Keeled	Divided	Divided
Dipsas articulata group	Variable	Variable[1]	6–11	Variable	13–19, variable	Smooth	Undivided	Divided
Enuliophis	Entering orbit	Absent	6–7	1 + 1 1 + 2	15, unreduced	Smooth	Divided	Divided
Enulius	Entering orbit	Variable	5–8	1 + 1 1 + 2	15–17, reduced or not	Smooth	Divided	Divided
Geophis (*omiltemanus* group)	Entering orbit	Absent	6[2]	1 + 2	15–17, unreduced	Smooth or keeled	Undivided	Divided
Geophis (*sieboldi* group)	Entering orbit	Absent	6 or fewer	0 + 1	15–17, unreduced	Keeled (at least above vent)	Undivided	Divided
Hydromorphus	Not entering orbit	Variable[3]	Usually 6	1 + 2	15–17, reduced	Smooth	Divided	Divided
Hypsiglena (including *Eridiphas*)	Not entering orbit	Present	7–8	1 + 2	19–23, reduced	Smooth	Divided	Divided
Imantodes	Not entering orbit	Present	8–9	1 + 2 2 + 2	17, reduced or not	Smooth	Usually divided[4]	Divided
Leptodeira	Not entering orbit	Present	7–9, usually 8	1 + 2	17–25, reduced	Smooth	Divided	Divided
Ninia	Entering orbit	Absent	6–7	1 + 2	17–19, unreduced	Keeled	Usually undivided	Divided
Nothopsis	Not entering orbit	Present	9–13	Multiple	26–30, reduced	Keeled	Undivided	Divided
Omoadiphas	Entering orbit	Absent	6–7	0 + 1	17, unreduced	Smooth	Divided	Divided
Pseudoleptodeira	Not entering orbit	Present	8	1 + 2	23, reduced	Smooth	Divided	Divided
Rhadinaea (*decorata* group)	Not entering orbit	Present	8–9	1 + 2	17, unreduced	Smooth to weak keels	Divided	Divided

TABLE 1. Continued.

Taxon	Prefrontals	Preocular(s)	Supralabials	Temporals	Dorsal midbody scales, posterior condition	Dorsal scale ornamentation	Cloacal scute	Subcaudals
Rhadinaea (*taeniata* group)	Not entering orbit	Present	8	1 + 1 1 + 2	17, unreduced	Smooth	Divided	Divided
Rhadinella	Not entering orbit	Present	7–8	1 + 1 1 + 2	17–21, unreduced	Smooth	Divided	Divided
Rhadinophanes	Not entering orbit	Present	8	1 + 2	19, reduced	Smooth	Divided	Divided
Sibon annulatus & *S. argus* groups	Entering orbit[5]	Absent	7–9	1 + 2[6]	13–15, unreduced[7]	Smooth	Undivided	Divided
Tantalophis	Not entering orbit	Present	7–8	1 + 2	19–21, reduced	Smooth	Divided	Divided
Tretanorhinus	Not entering orbit[8]	Present	7–9	1 + 2	19–21, reduced	Keeled	Divided	Divided
Trimetopon	Not entering orbit	Present	7–8	1 + 1	15–17, unreduced	Smooth	Divided	Divided
Tropidodipsas	Not entering orbit	Present	6–7	1 + 2	17, unreduced	Weakly keeled	Undivided	Divided
Urotheca (now included within *Pliocercus*)	Not entering orbit	Present	6–8	1 + 1 1 + 2	17, unreduced	Smooth	Divided	Divided

[1] When present, preocular located above loreal, which enters eye.
[2] Supralabials 7 in the enigmatic *Geophis isthmicus*.
[3] Preoculars 0–2; when absent loreal contacting orbit.
[4] Cloacal plate usually divided in northern species; often entire in lower Central American and South American species.
[5] In all species except *S. sanniolus*.
[6] Temporals in *Sibon carri* 0 + 1.
[7] *Sibon anthracops* has 13 dorsal scale rows at mid-body.
[8] Prefontals often coalescing with loreal(s); number of loreals 0–2.

The ectopterygoid is slenderer in *Geophis* than in *Cenaspis* and usually less forked; only in some species in the *Geophis mutitorques* group does bifurcation of the anterior end with lateral anterior branch of the ectopterygoid approach the condition seen in *Cenaspis*.

Numerous other osteological features distinguish various species of dipsadids from *C. aenigma*. In *Adelphicos latifasciatus*, the prefrontal has two (middle and lower) distinctive forward processes, a more strongly defined dorsolateral parietal ridge, no foramen in the quadrate, and 10–11 short, stout maxillary teeth. *Adelphicos quadrivirgata* (Figs. 6D,E,F) is similar to *A. latifasciatus* except there is only a single middle forward prefrontal process (middle; Fig. 5E). In *Amastridium veliferum* the braincase is shorter; the postocular is narrow dorsally, becoming heavy at midlength, continuing to ventral end; and there are 13–14 + 2 maxillary teeth (enlarged, diastema present). *Atractus lancini* and *A. univittatus* have 11–14 long, sharp maxillary teeth, becoming smaller posteriorly; the prefrontal has an anteriorly projecting flange. There are 11 long, robust maxillary teeth, becoming smaller posteriorly in *Chapinophis xanthocheilus*; the postocular is stout, the prefrontal has a middle anterior projection, the anterior edge of frontal has median projections, and the prefrontal distinctly curves over the dorsum of skull. *Chersodromus liebmanni* has a relatively short braincase, a strong dorsolateral ridge is present on parietals, postoculars are absent, the prefrontal has three forward projections, and almost the anterior third of the maxilla is edentate, followed by about nine long needlelike teeth. *Coniophanes imperialis* has a short braincase, the prefontals have a large forward flange, the dorsolateral ridge on parietal is well developed, the supratemporal extends forward to almost the parietal, and the maxilla has 11–12 + 2 teeth that are posteriorly enlarged and grooved, separated by a diastema from more anterior teeth. *Conophis vittatus* has a short braincase; a postocular is present but not contacting frontal, the quadrate is relatively long and slender, the prefrontal has a forward-projecting flange, the maxilla bears 10 + 3 teeth with posterior teeth greatly enlarged and grooved, and a diastema is present. In *Cryophis hallbergi* the premaxilla does not reach the nasals, the prefrontals have a broad forward projecting flange, the postorbital does not reach the frontal, the supratabular extends forward to the parietal, the maxilla bears 21 + 2 teeth with posterior teeth enlarged and grooved, and a narrow diastema is present. *Diadophis punctatus* has a prefrontal with a middle forward-projecting process, the dorsolateral ridge of the parietal is well developed, the supratabular extends forward on to the parietal, the maxilla bears 8–9 + 2 teeth with posterior teeth enlarged, and a diastema is present. In *Ficimia publia*, the premaxilla is distinctly forward projecting, the prefrontal has single large anterior projection, and the maxilla bears 12–13 short stout teeth. In *Geagras redimitus*, (a small burrowing Mexican colubrid), the premaxillary is produced forward with a knoblike process that

TABLE 2. Comparison of selected morphological features among Middle American dipsadid snakes. Dark shade represents characters similar to *Cenaspis*; light shade represents at variance, unshaded represents comparative condition unknown in *Cenaspis*.

Taxon	Pupil shape	Maxilla teeth number[1]	Size maxillary teeth (very thin, thin, moderate, stout, very stout, extremely stout)	Maxillary diastema	Maxillary teeth grooved	Hemipenial shape	Truncus region ornamentation	Apical region ornamentation	Capitation	Sulcus spermaticus
Cenaspis aenigma	Subcircular	14–15	Unknown	No	Unknown	Single	Calyculate	Calyculate	Noncapitate	Simple, with tiny terminal fork
Adelphicos	Round	7–11	Stout	No	No	Single	Spinous	Spinous and papillate	Capitate	Simple
Amastridium	Round	13–17 + 2	Thin	Yes	Variable	Single, slightly clavate	Spinous	Calyculate	Capitate[2]	Bifurcate, centrolineal
Atractus	Round	5–14	Thin to stout	No	No	Single or bilobed	Spinous	Spinous or calyculate	Noncapitate or unicapitate	Simple to bifurcate, centrifugal
Chapinophis	Subcircular	12–13	Thin	No	No	Bilobed	Spinous	Calyculate	Bicapitate	Bifurcate, centripedal
Chersodromus	Round	7–9	Very thin to moderate	No	No	Bilobed	Spinous	Spinous	Noncapitate or semicapitate	Bifurcate, centrifugal
Coniophanes	Round	8–15 + 2	Thin to moderate	Yes	Yes	Single or bilobed	Spinous	Calyculate or flounced	Unicapitate or noncapitate	Bifurcate, centrolineal or centrifugal
Cryophis	Subcircular[3]	19–22 + 2	Very thin	Yes	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Dipsas articulata group	Vertical	17–24[4]	Very thin	No	No	Slightly bilobed	Spinous	Calyculate	Unicapitate	Bifurcate, centrolineal
Enuliophis	Round	4+2	Very stout	No	No	Slightly bilobed	Spinous	Smooth	Noncapitate	Bifurcate, centrifugal
Enulius	Round	3+2	Very stout	No	Variable	Slightly bilobed	Spinous	Spinous and papillate	Noncapitate	Bifurcate, centrolineal
Geophis omiltemanus group	Round	10–17	Very thin	No	No	Slightly bilobed	Spinous	Calyculate	Unicapitate	Bifurcate
Geophis sieboldi group	Round	8–15	Very thin	No	No	Slightly bilobed	Spinous	Calyculate	Unicapitate	Bifurcate
Hydromorphus	Round	11–12 + 2	Extremely stout	Yes	No	Bilobed	Spinous	Calyculate and spinous	Unicapitate	Bifurcate, centrolineal
Hypsiglena (including *Eridiphas*)	Vertical	7–12 + 2	Very thin to thin	Yes	No	Slightly bilobed	Spinous	Calyculate and spinous	Capitate	Simple
Imantodes	Vertical	10–22 + 2	Very thin	Yes	Yes	Single	Spinous	Calyculate	Capitate	Simple
Leptodeira	Vertical	8–18 + 2	Very thin to moderate	Variable	Yes	Single	Spinous	Calyculate	Capitate	Simple with tiny terminal fork or bifurcate
Ninia	Round	8–18	Very thin	No	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Nothopsis	Round	18–19 + 2	Stout	Yes	No	Single	Spinous and calyculate	Spinous	Capitate	Bifurcate, centrolineal
Omoadiphas	Subcircular	13–14	Very thin	No	No	Bilobed	Spinous	Calyculate	Bicapitate	Bifurcate, centrolineal
Pseudoleptodeira latifasciata	Vertical	14 + 2	Thin	Yes	No to faintly	Single	Spinous	Spinous	Capitate	Simple
Rhadinaea decorata group	Round	12–22 + 2	Very thin	Yes	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Rhadinaea taeniata group	Round	15–22 + 2	Thin to moderate	Variable	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Rhadinella	Round	9–21 + 2[5]	Moderate	Variable	No	Bilobed	Spinous	Calyculate	Unicapitate	Bifurcate, centrolineal
Rhadinophanes	Round	19–20 + 2	Thin	No	No	Bilobed	Spinous	Calyculate	Bicapitate	Bifurcate, centripetal
Sibon annulatus & *S. argus* groups[6]	Vertical	12–17	Thin	No	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Tantalophis	Subcircular	13–17 + 2	Thin	Yes	No	Bilobed	Spinous	Calyculate	Bicapitate	Bifurcate, centripetal
Tretanorhinus	Round	27–30	Very thin	No	No	Single	Spinous	Calyculate	Capitate	Bifurcate, centrolineal
Trimetopon	Round	11–12 + 2	Stout	Variable	No	Single or bilobed	Usually spinous	Calyculate	Semicapitate	Bifurcate, centrolineal
Tropidodipsas	Subcircular	12–24	Very thin to thin	No	No	Single	Spinous	Calyculate or spinous	Capitate	Bifurcate, centrolineal
Urotheca (now included within *Pliocercus*)	Round	11–19 + 2	Moderate	Yes	Variable	Single to Slightly bilobed	Spinous	Calyculate	Unicapitate	Bifurcated, centrolineal

[1] When "+" inserted between numbers, last number indicating teeth conspicuously enlarged over anterior series; diastema and grooves present or not.
[2] Report by Wilson and Meyer (1969) of organ being noncapitulate appears in error and at odds with their figure 3.
[3] Sensu Myers (1984); distinction between round and subcircular can be slight and further examination of material, especially living, may reveal that some snakes here categorized as having round pupils actually should be judged subcircular. Conversely, some species appearing to have subcircular pupils may contract pupils to the vertical condition under certain circumstances.
[4] Variation in number of teeth for Middle American species except *Dipsas gaigae*, which is reported to have as few as 10.
[5] Sometimes more than two posterior teeth enlarged.
[6] Uncertain if *Sibon carri* falls within these groups; this species not examined.

projects upward and forward; the nasal, frontal, and parietal bones have no or little space between them with mostly tight sutures; the quadrate is exceptionally broad, and the maxillary bears 10–11 short, stout teeth. In *Geophis anocularis*, the premaxilla slopes forward; the nasals, frontals, and parietals are in tight juxtaposition, with no dorsolateral parietal ridge; the frontal forms only a small portion of the orbital socket; no postorbital is present; the quadrate relatively small but expanded dorsally, and the nasals are roughly triangular. In *G. laticinctus*, the premaxillary is rounded in lateral view; the nasals and frontals are widely separated; the parietal ridge is laterally located; and the maxillary teeth moderately long and stout, decreasing in size posteriorly. In *Rhadinaea*, the nasals are small, widely separated from the frontals; the postorbital does not contact prefrontals, and the prefrontal is distinctly higher than long. In *Sibon* and *Tropidodipsas*, the nasals are widely separated from the frontals, the prefrontal is distinctly higher than long, the postorbital is long and delicate, the dorsolateral ridge of the parietal is well developed, and the quadrate is well developed and robust, with a broadly expanded superior end.

Hemipenes in species of dipsadids often are single or bilobed with a bifurcate sulcus spermaticus, capitate calyculate ornamention on distal portion of lobes, and spines or spinules on hemipenial body and sometimes basal portion of lobes (Fig. 7A,C,D). Genera having a single subcyindrical organ include *Adelphicos*, *Amastridium*, *Cryophis*, *Imantodes*, *Leptodeira*, *Ninia*, *Rhadinaea*, *Tropidodipsas*, and others (see Table 2), but most of these genera are characterized by a distinctive calyculate apical portion of the hemipenis, which is usually differentiated into a distinct capitulum with a bifurcate sulcus spermaticus. Besides having a single organ, *Adelphicos* (Fig. 7), *Eridiphas*, *Hypsiglena*, *Imantodes*, *Leptodeira*, and *Pseudoleptodeira* have a simple (not bifurcate) sulcus spermaticus, but these genera differ from *Cenaspis* by having a spinous hemipenial body and some capitation evident.

Discussion

The type locality appears to be very near the Continental Divide, but slightly north on the Atlantic versant. The western flank of Cerro El Baúl is drained by the Río El Baúl and the eastern side by the Río Portamoneda, both upper tributaries of the Río Grijalva flowing into the Gulf of Mexico. A small portion of the southern end of the range is drained by several small streams that are upper tributaries of the Río San Miguel that flows into the Mar Muerto of the Pacific. Cerro El Baúl attains ~2,050 m and is the highest point in the mountains of southeastern Oaxaca (although immediately to the east a peak in the Cerro El Ermitaño reaches at least 1,950 m), and is included in the region known at least locally as the Chimalapas, of which Cerro El Baúl and Cerro El Ermitaño can be considered the easternmost outliers. The small settlement and historical collecting locality of Colonia Rodulfo Figueroa, located in the eastern portion of the Chimalapas, has usually been reported to be in Oaxaca (Bogert, 1968; Campbell, 1984). Digital maps provided by Google Earth, however, place Colonia Rodulfo Figueroa in Chiapas ~1 km west of the Oaxaca–Chiapas border.

Although one of the least explored regions in Mexico, the biotic diversity of the Chimalapas is already well recognized (MacDougall, 1971; Smith and Campbell, 1996; Peterson et al., 2003; Aguilar-López et al., 2016), and these highlands contain a high number of herpetofaunal endemics. Moderately high elevations of the Chimalapas, influenced by weather conditions from both the Gulf of Mexico and Pacific Ocean, have provided the backdrop for a spectacular landscape and biotic inventory. The fortuitous geographical location of the Chimalapas provided the means by which the origin of biota was derived from multiple sources besides the Sierra Madre de Chiapas. These highlands are sometimes considered an extension of the northwestern highlands of the Sierra Madre de Chiapas (Johnson, 1990). Although these highlands lie to the east of the Isthmus of Tehuantepec, a strong biotic component derives from the Mexican Plateau, as well as temperate regions farther north. To the east, the Chimalapas are isolated from the highlands of the Meseta Central of Chiapas and the Sierra Madre del Sur of Chiapas by low ridges and foothills covered with xerophytic vegetation (Leopold, 1950; Miranda, 1952; Breedlove, 1981), but share many highland genera of tropical origin. Perhaps most remarkable are the biotic similarities with the isolated Sierra de Los Tuxtlas (Campbell, 1984), arising out of the Gulf Coast and isolated to the NE by some 150 km of lowland tropical deciduous forest and tropical evergreen forest.

As previously noted, the holotype of *Cenaspis aenigma* was taken from the stomach of a large *Micrurus nigrocinctus* (UTA R-6085). During our exploration of the region, *M. browni* was more common, with about half a dozen individuals encountered; however, only the single *M. nigrocinctus* was found. This Coralsnake was secured by Julio Ornelas-Martínez, a resident of Rizo de Oro who at the time was engaged in harvesting palm (*Chamaedorea*) on the slopes of Cerro Baúl and surrounding uplands.

Although the type of *Cenaspis aenigma* was collected within 20–25 km NE (by road) of Rizo de Oro on the slopes of Cerro Baúl, determining the precise habitat of origin is not possible because of interdigitation of many complex habitats in the area owing to elevation, slope exposure, prevailing winds, and precipitation. The diversity of forest types in this region is described in captivating fashion by MacDougall (1971). Among the various habitats MacDougall (1971) describes is an incredible elfin forest near Cerro Baúl in which trees, shaped by strong and almost constant N-to-S winds, have been beaten down to such an extent that, in places, walking on top of the forest is easier than walking through it. Another unique forest in the region is the cypress woods (*Cupressus benthami*) covering some of the upper elevations of Cerro Baúl and perhaps elsewhere. Our experience in the region has been that many restricted microhabitats occur in certain ravines and on particular mountain ridges and crests.

Hypothesizing about living *Cenaspis aenigma*, on the basis of morphological traits of the single preserved specimen, is somewhat daunting but worthwhile. The dorsal color is rather unremarkable, being uniformly pale brown. This color and lack of dorsal pattern is not unusual for burrowing species; however, the ventrals are marked with three series of dark rectangular to triangular markings forming essentially three stripes for the length of the body, and the subcaudals are marked with a single midventral band extending the length of the tail. Why a secretive burrowing snake would have such a distinctive ventral pattern is unknown. The ventral pattern is not replicated in any other Middle American snake, although as mentioned previously, several terrestrial (vs. fossorial) species have a vivid pattern of series of spots on the venter.

Snakes are the only terrestrial vertebrates that are usually adapted to swallow large, entire prey often larger than the head of the predator. Because *Cenaspis aenigma* lives in mesic forest, one is tempted to speculate that it preys upon soft-bodied

invertebrates such as earthworms and slugs, similar to other sympatric snakes of the genera *Adelphicos*, *Geophis*, and *Ninia*. Yet all snakes in these genera have long needlelike teeth, in sharp contrast to the short, stout, and blunt teeth of *C. aenigma*. Some of the feeding habits of *C. aenigma* may be implied on the basis of certain features of the skull. The teeth are short, stout, and appear relatively blunt. This type of dentition is characteristic of species that prey on arthropods with hard chitinous exoskeletons and is perhaps most common among the Sonorini (*Sonora*, *Toluca*, *Stenorrhina*) that prey on spiders, centipedes, and snakes such as *Symphimus* that feed mainly on arthropods. Relatively few dipsadids possess this dentition, although the teeth in *Rhadinophanes*, some species of *Atractus*, and *Adelphicos* are moderately short but sharp.

Pupil shape may provide some insights into the ecology of snakes (Brischoux et al., 2010). The eyes of the holotype of *Cenaspis aenigma* are in pathetic condition owing to the digestive enzymes of its predator. Nevertheless, they appear subcircular in shape. Brischoux et al. (2010) suggest that round-pupil species adapted to low light conditions are unable to close the pupil sufficiently to prevent dazzle under daylight conditions, in contrast with vertical-pupil species that may have better vision both at night and by day. It follows that visual acuity for small-eyed species with either round or subcircular pupils is greatly diminished during daylight hours and these species are highly secretive, remaining underground almost without interruption or perhaps occasionally venturing out by night, especially after rains.

The overall morphology of *C. aenigma* is that of a burrowing snake. *Cenaspis aenigma* is similar to the burrowing genera *Geophis, Adelphicos*, and *Atractus* in having an elongate braincase. Categorizing relative length of the snake skull into long vs. short braincase is a somewhat subjective assessment, but cursorial examination does reveal conspicuous differences in relative head length/width that probably associates with evolutionary histories and ecologies. We used only adult snakes in our examinations because of the large amount of variation attributable to allometry (Murta-Fonseca and Fernandes, 2016). If the distance from the level of the parietal–frontal suture above the eye to the posterior edge of the exoccipital midline suture is divided by the distance across the parietal at its widest point in dorsal aspect (usually about midlevel), then fossorial species with elongate braincases produce values of 0.48–0.60 (*Cenaspis* is 0.59, *Adelphicos* 0.54–0.56, *Atractus* 0.48–0.59); those for terrestrial species vary from 0.65 to 0.80 (*Imantodes* 0.80, *Leptodeira* 0.65, *Ninia* 0.67, *Tropidodipas* 0.66, *Rhadinaea* 0.67–0.71). The genus *Geophis* contains some groups that are highly fossorial and others that are more terrestrial. Species of this genus may fall into either long or short braincase categories, using 0.63 as the arbitrary dividing line.

Characteristics of "long-headed burrowers" often include long postorbital braincases, shortened orbits, low prefrontals, short or missing postorbitals, reduced postorbital processes on parietal, anterior extensions of the dorsolateral edge of parietal along lateral edge of frontal, elongated parietal, shortening of caudal end of the supratemporal, and reductions of transversely oriented crests associated with muscle origins (Cundall and Irish, 2008). Most of these features are possessed by *Cenaspis aenigma*, but the postorbitals are relatively well developed and the dorsolateral ridge is only moderately well developed, merging with a prominent ridge forming part of the dorsal articulation with the postorbital.

Given its unique features, the affinities of *Cenaspis aenigma* are difficult to assess. The only other genus of New World colubrid with undivided subcaudals is *Rhinocheilus*, but invariably at least a few subcaudals (usually distally) are divided. That genus is a member of the Colubridae and the differences between it and *Cenaspis* are numerous and striking. Very superficially, *Cenaspis* seems to be allied with *Adelphicos* or *Geophis*, widespread groups showing great morphological and ecological diversity. Yet, osteological features, the enigmatic entire subcaudals, and unique hemipenis of *Cenaspis* preclude its placement in these genera and suggest that the relationships of *Cenaspis* are distant and will have to be found elsewhere.

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