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A New Genus and New Tribe for *Enicognathus melanauchen* Jan, 1863, a Neglected South American Snake (Colubridae: Xenodontinae), with Taxonomic Notes on Some Dipsadinae

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ABSTRACT

The name *Enicognathus melanauchen* Jan belongs to a currently unrecognized but apparently valid species of small snake described some 140 years ago from an unknown locality in Bahia, Brazil; the unique specimen is in the Nationaal Natuurhistorisch Museum, Leiden. Attempts were unsuccessful to associate it with named genera of the colubrid subfamilies Xenodontinae, Dipsadinae, Colubrinae, and Natricinae; consequently, no basis was found for challenging the provenance. The genus *Amnesteophis* and tribe Amnesteophiini therefore are erected for the species. (The snake generic name *Enicognathus* and the emendation *Henicognathus* are both junior homonyms of bird names.) Assignment to Xenodontinae is partly on geographic grounds as well as on hemipenial and osteological comparisons with the other colubrid subfamilies mentioned.

Tribe Amnesteophiini differs from other tribes in Xenodontinae by combination of three unusual character states: (1) straight-line configuration of posterior maxillary teeth; (2) lack of hemipenial calyces; and (3) an unforked sulcus spermaticus. Hemipenial calyces also are absent in the Xenodontini, and an unforked sulcus spermaticus occurs in one species of Echinantherini (*Taeniophallus nicagus*). *Amnesteophis melanauchen* somewhat resembles *Taeniophallus occipitalis* in color pattern and 15 dorsal scale rows, but *A. melanauchen* differs externally from all *Taeniophallus* in having feebly keeled dorsal scales. The provenance and taxonomic placement of *Amnesteophis* needs to be corroborated by new specimens, or refuted by new insight on relationships and geographic origin.

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Comparisons made for this study shed light on a few groups of dipsadines. The tribal name "Leptodeirini Jenner" auctorum is nomenclaturally unavailable and invalid since it was proposed in an unpublished thesis (Jenner, 1981) that cannot subsequently be used as an indication or bibliographic reference in order to confer availability (contra Dowling et al., 1983). The diagnostic character of a simple sulcus spermaticus does not strictly characterize the type genus *Leptodeira* as originally assumed. Several molecular studies have failed to corroborate monophyly for the group of genera originally and subsequently assigned to the "Leptodeirini," although two genera (*Imantodes* + *Leptodeira*) consistently received strong support. The biogeographically and ecologically successful *Imantodes* and *Leptodeira*, which share large geographic ranges between the tropics of Cancer and Capricorn, are placed in the new tribe Imantodini. In addition to molecular support, the loss of bifurcation of the sulcus spermaticus (*Imantodes* and some *Leptodeira*) or reduction to a small terminal fork or expanded flat area (other *Leptodeira*) sets off the mainly scansorial Imantodini from all other Dipsadinae except the terrestrial Mesoamerican–North American night-snakes, which appear to form an unnamed clade.

The dipsadine genus *Rhadinaea* Cope (sensu Myers, 1974) is further partitioned by the resurrection of *Rhadinella* Smith, 1941, which equates to the *godmani* species group of 15 Middle American species. The maxillary dentition in *Rhadinella* is superficially similar to that of *Amnesteophis* in the straight-line arrangement of several posteriorly enlarged teeth (ultimate fang not offset). Similar apomorphic dentition is shared with Lower Central American *Trimetopon*, which differs from *Rhadinella* in tendency toward diminutiveness and lack of a basal nude pocket on the hemipenis. Offset fangs (whether grooved or smooth) appear symplesiomorphic within most genera of Xenodontinae and Dipsadinae, although possibly synapomorphic for these groups combined.

INTRODUCTION

The snake name *melanauchen* has accrued little literature apart from catalog listings. Its pertinent synonymy is:

Enicognathus melanauchen Jan, 1863a: 266–268; 1863b: 56–58. Holotype in Museo di Leyda, from Bahia. Jan and Sordelli, 1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 2 (illustrations of holotype).
Rhadinaea melanauchen: Boulenger, 1894: 175.
Liophis melanauchen: Amaral, 1929a [1930]: 88; 1929b [1930]: 173; 1936: 115. Peters and Orejas-Miranda, 1970: 178.
Liophis melanauchen, incertae sedis: Dixon, 1980: 11.

Amaral (1929b [1930]: 173; 1936: 115) suggested that *melanauchen* was based on an anomalous example of *Liophis occipitalis* (a species formerly in *Rhadinaea*, now in *Taeniophallus*). Myers (1974: 18) said that *melanauchen* did not belong in *Rhadinaea* and left it out of the synonymy of "*R.*" *occipitalis*. Finally, Dixon (1980: 11) excluded it from *Liophis* sensu stricto.

There appear to have been no reports of additional specimens and the type locality (Bahia [Brazil]) has not been verified. There has been no substantive discussion of this snake since its

original description. The name *melanauchen* has no current usage other than uninformative, tertiary listings in the ephemeral compilations of species names on Internet websites. It is a *species inquirenda* that has not been confirmed as a valid species and that, for practical purposes, has been nearly forgotten.

Examination of the type specimen (fig. 1) of *Enicognathus melanauchen* confirms its distinctiveness, but the dentition and hemipenis reveal that it does not readily fit in any currently recognized genus of Neotropical serpents. A new tribal name and new generic name are here proposed for this neglected snake.

Amnesteophiini, new tribe

Type Genus: *Amnesteophis*, new genus.

Content: One monotypic genus.

Definition and Diagnosis: Distinguished from all other snakes by the generic definition below. Tentatively assigned to subfamily Xenodontinae. Tribal status is conferred in order to conform to the increasingly accepted custom of partitioning South American xenodontines among diagnosable tribes.

The tribe Amnesteophiini is distinguished from other tribes in Xenodontinae by combination of three unusual character states: (1) a straight-line configuration of the several posterior maxillary teeth; (2) absence of calyces on the hemipenis; (3) an unforked sulcus spermaticus. The hemipenes of species in tribe Xenodontini also are acalyculate, but there usually is a flattened apical disc, the sulcus is divided, and the fangs are offset. A species in tribe Echinantherini has an unforked sulcus, but calyces and offset fangs are present (see *Taeniophallus* in generic diagnosis below).

Amnesteophis, new genus

Type Species: *Enicognathus melanauchen* Jan, 1863.

Etymology: *Amnesteophis* (forgotten snake), from Greek *amnēstos* (ἄμνηστος, "forgotten, no longer remembered") + connective *-e-* + *ophis* (ὄφις, "snake"). Gender masculine. (For purposes of euphony, the derivation imposes elision of the final vowel in *amnēstos*, and the connective vowel *-e-* is employed rather than the *-o-* normally used in latinized compounding of Greek elements.)

Jan's specific name *melanauchen* (a Schlegel manuscript name) appears compounded from the Greek combining element *melan-* (μέλαν, neuter of μέλας, *melas*, "black or very dark") + *auchēn* (αὐχήν, "neck")—a masculine noun in apposition, referring to a dark blotch on the neck.

Content: Only *Amnesteophis melanauchen* (Jan), new combination.

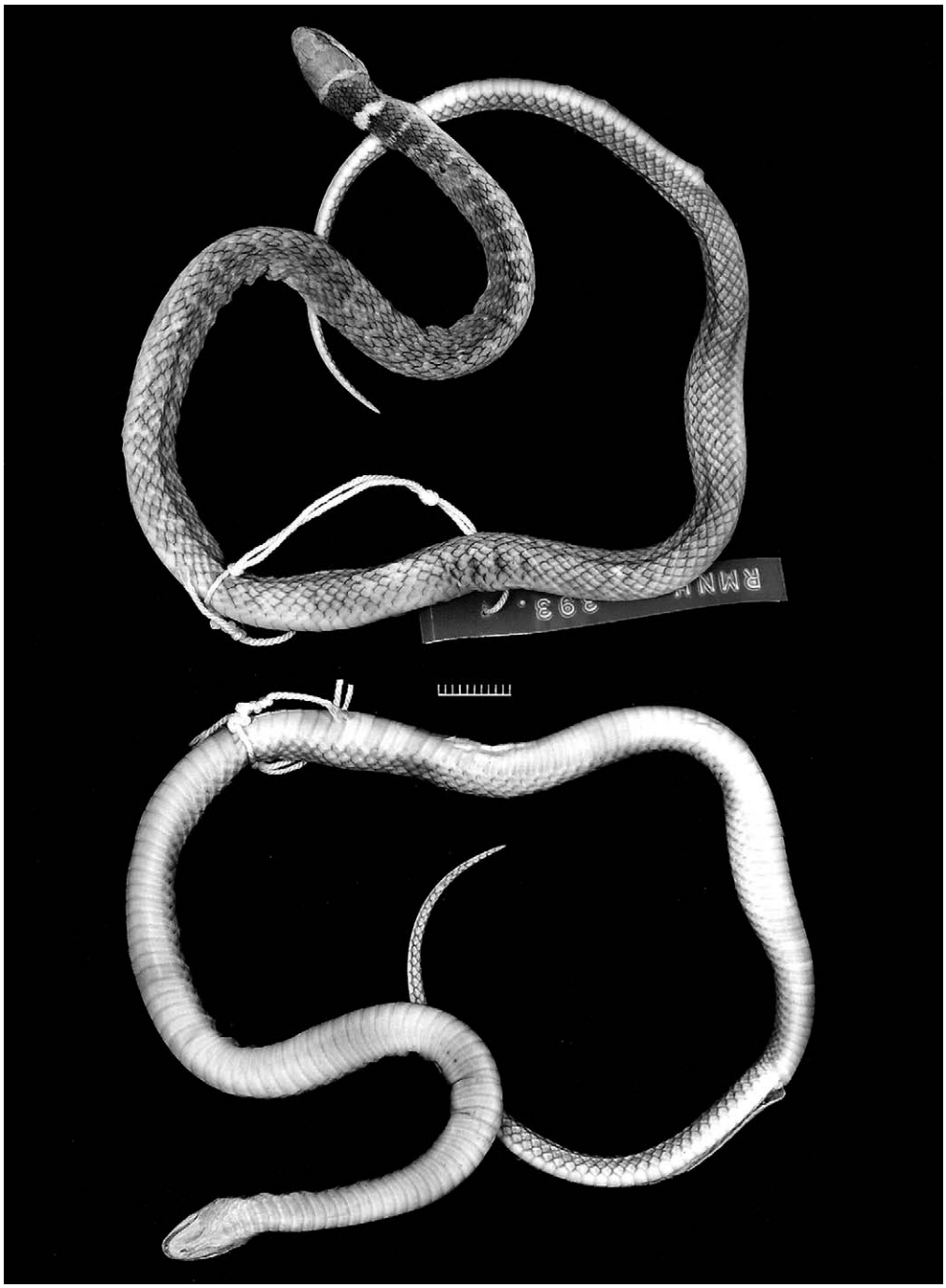

Fig. 1. *Enicognathus melanauchen* Jan 1863. The adult male holotype (RMNH 393) in dorsal and ventral view. Shown life size (scale line = 10 mm).

Distribution: Known only from "Bahia" (Jan, 1863a: 266; 1863b: 56)—the purported type locality in northeastern Brazil. The original catalog entry for the holotype (RMNH 393) is "Bahia au Brésil."[2]

Definition and Diagnosis: (Based on one adult male.) Genus of small colubrids less than 500 mm in total length, with tail length roughly a quarter of total length; habitus slender, body about as wide as high, slightly wider than head. *Color Pattern:* Dark nuchal blotch set off by pale crossbands, followed posteriorly by ill-defined narrow brown crossbands. *Scutellation:* Normal complement of colubrid head plates, possibly with diagnostic arrangement of temporals (in oblique rows, with both plates in first row in contact with labials); dorsal scales in 15-15-15 rows, feebly keeled, lacking apical pits or anal ridges; ventrals 145, anal plate divided, paired subcaudals 60. *Osteology:* Maxillary teeth about 25, increasing in size posteriorly, with slight anterior-posterior differentiation in shape; in a continuous series, no diastema; last two teeth slightly enlarged, set in a straight line with the several teeth immediately preceding. About 15 palatine teeth + 30 pterygoid teeth; about 20 teeth on dentary. No hypapophyses on posterior trunk vertebrae. *Hemipenis:* Feebly bilobed, acalyculate, small spines replaced distally by large flattened soft papillae; unforked sulcus spermaticus extending centripetally to apex of left lobe (sinistral sulcus); a nude area in crotch between the small papillate lobes.

Among Neotropical snakes, *Amnesteophis melanauchen* superficially seems most similar to *Taeniophallus* sensu lato. It has been compared by authors (Jan, Amaral) with the snake now known as *Taeniophallus occipitalis*, which shares the character of 15-15-15 dorsal scale rows and a somewhat similar color pattern. It shares with *T. nicagus* the character of a single (unforked) sulcus spermaticus. *Amnesteophis* differs from all *Taeniophallus* in lacking hemipenial calyces, in having the posterior maxillary teeth in a straight line, and in having feebly keeled (vs. smooth) dorsal scales. See Comparisons for further discussion.

Redescription of Holotype of the Type Species

(*Enicognathus melanauchen*)
Figures 1–5, 6 (lower)

The only known specimen (RMNH 393) of *Enicognathus melanauchen* Jan is a male, judged to be sexually mature because the hemipenial spines are mineralized. The right maxilla had been expertly removed by some previous investigator, although the jaws were cut on both sides,

[2] Other collection data are wanting and there seems no way to clarify the type locality; we appear only to know that the unique specimen was collected in or at "Bahia" prior to the 1863 publication date. Up to about the 1870s, the old registry entries at the Leiden Museum were entered systematically rather than by date or collection (Ronald de Ruiter, personal commun.).

The name *Bahia* formerly was commonly used for the old colonial city *São Salvador da Baía de Todos os Santos* (= modern Salvador), but *Bahia* also has been consistently applied since the 16th century to a surrounding administrative district of varying size. In 1817, for example, Prince Maximilian zu Wied collected specimens over 150 km inland when he travelled "durch den inneren *Sertam* der *Capitania da Bahía* [through the inner bush country of the *Captaincy of Bahia*]" (Wied, 1821: 225). The old Captaincy of Bahia became a province in the early 1820s and the province a state in 1889.

rendering infralabial counts problematic; the right mandible also had been removed and is now missing. A hole between the mandibles suggests that the specimen at one time was hanging in its bottle of preservative (a not uncommon practice in the 19th century). Hypapophyses are lacking on the posterior vertebrae, as confirmed by radiography; the body has not been opened. The right retracted hemipenis had been opened previously; I removed the left retracted hemipenis for eversion in order to study the apical ornamentation. The specimen is soft and flexible but in fair condition considering its age (probably > 150 years since collection). See table 1 for detailed measurements.

Proportions and Scutellation: Total length 375 mm, tail length 95 mm (25.3% of total). A slender snake (fig. 1), with body slightly wider than head; body about as wide as high, obtusely rounded (almost angulate) ventrolaterally; greatest head width about 70% of head length from snout to end of parietals. Dorsal scales lacking apical pits, in 15-15-15 rows (17 rows immediately behind head, counting diagonally from first ventral). Dorsal scales very feebly keeled (fig. 2); keels present on scales in all rows, but not discernible on some scales in rows 1–2. Ventrals 145 + 1 preventral; anal plate divided; subcaudals in 60 pairs + slender terminal spine.

Head slightly wider than neck; snout rounded in dorsal and lateral views. Rostral broad, twice as wide as high, barely visible from above. Internasals moderate, slightly longer than wide, slightly shorter (85%) than prefrontal suture. Prefrontals wider than long (length 82% of greatest width); prefrontal suture symmetrical, aligned with internasal suture; prefrontal suture much shorter (33%) than frontal plate. Supraoculars large, longer than wide, slightly narrowed anteriorly. Frontal noticeably longer than wide (width 60% of length), roughly pentagonal. Interparietal suture 2.7 times longer than prefrontal suture, shorter (88%) than frontal plate.

Pupil of eye round. Eye moderate (now sunken and not accurately measurable), contained roughly 1.4 times in snout length (sagittal plane); eye length greater than distance from eye to lip (eyes not visible in ventral view according to fig. 6). Nasal plate large, divided above and below posterior edge of naris. Loreal small, about as high as wide, irregularly pentagonal with dorsal apex. Preoculars 1, the left one partly divided at level of loreal. Supralabials 8, first labial smallest, touching only rostral and nasal; labial 2 in contact with nasal and loreal; labials 3–5 touching eye. Postoculars 3, subequal. Temporal plates large, 2 + 2, in oblique rows with both plates in first row in contact with supralabials (fig. 3); upper temporal in row 2 somewhat elongated but not reaching end of parietal plate.

Infralabials 8 or 9 (jaws cut), first pair in broad contact behind mental, 1–4 in contact with anterior genials, 4–5 touching posterior genials. Genials long and narrow, first pair 75% the length of second pair. One preventral (gular wider than long) and a pair of side-by-side narrow gulars discernible between first ventral plate and suture between posterior genials. Tiny sensory organs inconspicuous, but discernible on labials and on anterior dorsal head plates.

Color Pattern: Faded brown above with conspicuous markings on rear of head and neck, followed by darker brown crossbands on anterior body (figs. 1, 3).[3] A narrow white transverse

[3] Over a century ago, the dorsal ground color was "bruno rossiccio [dark red-brown]," with blackish nape marking set off by white areas and followed by blackish crossbands (Jan, 1863a: 268; 1863b: 58; Boulenger, 1894: 175).

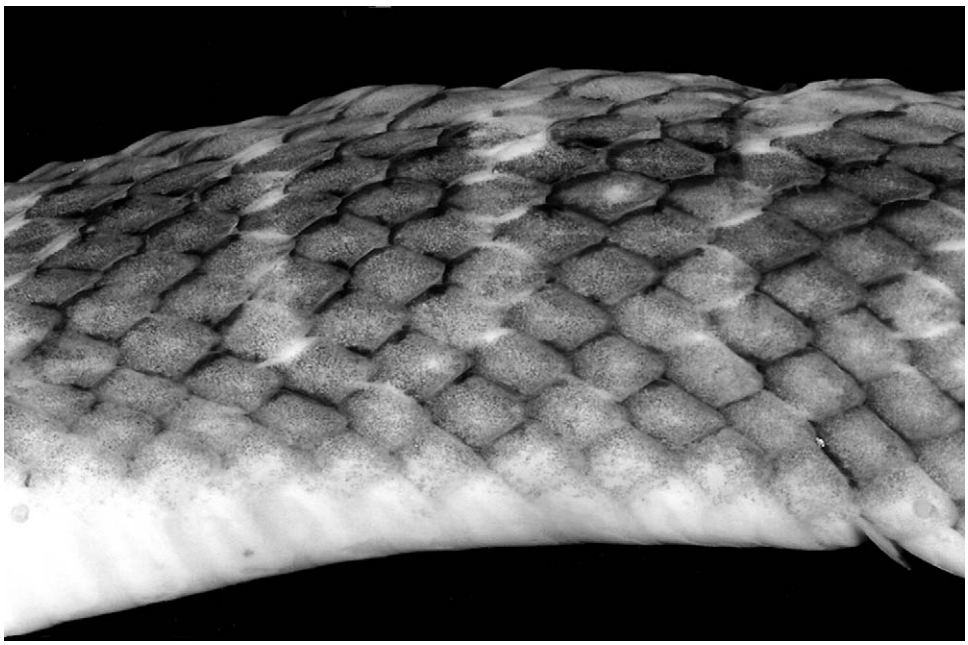

FIG. 2. *Enicognathus melanauchen* Jan 1863. Lateral view of anterior body of holotype between ventral plates 17 and 27, ×7.9. Feeble keels are present on some dorsal scales in all rows, but are not discernible on many scales in rows 1–2.

FIG. 3. *Enicognathus melanauchen* Jan 1863. Head and neck of holotype (scale line = 5 mm).

TABLE 1
Measurements[a] (in mm) of holotype of *Enicognathus melanauchen* Jan

Total length	375
Snout-vent length	280
Tail length	95
Tail/total length x 100	25.3%
Snout to ends of parietals	10.0
Head, greatest width	7.0
Body, greatest width	8[b]
Eye to snout tip (sagittal)	2.9
Eye length	2[b]
Lower edge eye to lip	1.0
Nasal length	1.6
Loreal length	0.7
Loreal, maximum height	0.7
Internasal, greatest length	1.2
Internasal, greatest width	1.1
Internasal suture length	1.1
Prefrontal, greatest length	1.4
Prefrontal, greatest width	1.7
Prefrontal suture length	1.3
Frontal length	4.0
Frontal width (anterior)	2.4
Supraocular length	3.2
Supraocular, greatest width	1.5
Parietal, greatest length	5.1
Interparietal suture length	3.5
Anterior genial length	3.0
Posterior genial length	4.0

[a] Total and tail-length measurements were taken by stretching the specimen gently along a metric ruler. Other measurements were made with ocular micrometer, calibrated against a stage micrometer, in a dissecting microscope (Wild M7S) with the main objective displaced coaxially to the left beam path, to eliminate problems of parallax.

[b] Rounded estimate owing to poor condition.

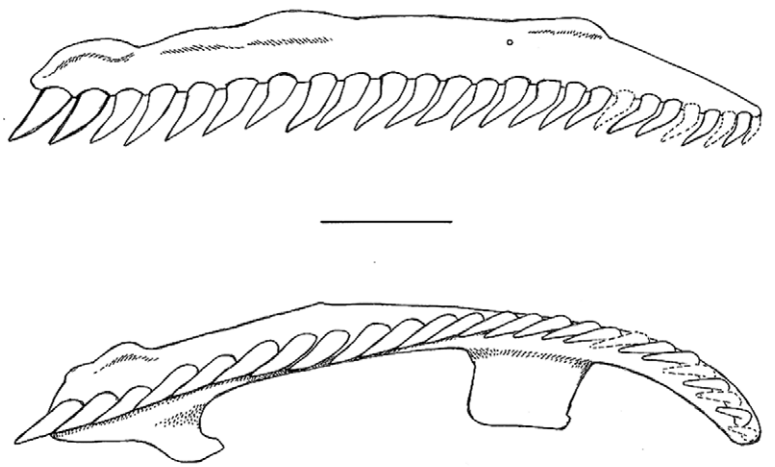

FIG. 4. Maxillary dentition of *Amnesteophis melanauchen* (Jan 1863). Right maxilla of holotype of *Enicognathus melanauchen* in lateral and ventral views (scale line = 1 mm).

collar across posterior tips of parietal plates, merging ventrad into the white throat (fig. 3). Following that is a large, transverse dark nape blotch (5 scales long x 15 scales wide), which is narrowly edged all around in blackish brown. A white crossband (1–2 scales wide) sets off the posterior side of the dark nape blotch. The white crossband is followed by a series of some 30 brown dorsal crossbands on the anterior half of the body. The first brown crossband (4 scales long) is larger than the succeeding ones (about 2 scales long); the crossbands extend ventrad to about the second scale row. The dorsal crossbands are not sharply defined and become increasingly obscure and fade away at midbody. Posteriorly, the body is pale tan with some dark scale edges. A vertebral brown line forms at midbody and continues well onto the tail; it occupies the vertebral row and edges of the paravertebral scales, but is very faded.

The top of the head is faded uniform light brown. A blackish brown lateral line extends along the lower side of head; it starts at the nasal plate, extends posteriorly under the eye, crosses the suture between the lower two postoculars, and passes along the lower edges of the temporal plates to terminate on the ultimate supralabial. There is some faint brown smudging on the supralabials and anterior infralabials, but the original overall dark-speckled pattern of the underside of the head and neck (fig. 6: *d* in lower left-hand corner) is no longer discernible.[4] All ventral surfaces immaculate white.

Dentition

There are 25 uniformly spaced, recurved teeth on the right maxilla (fig. 4); teeth seem to be relatively ankylosed, with only four anterior ones missing (empty sockets at positions 1, 3, 5, 8). The maxillary teeth steadily increase in size posteriorly, while decreasing in degree of recurvature. There also is anterior-posterior differentiation in the shape of the teeth. At 50×

[4] The black-dotted or speckled pattern under the head and neck was described by Jan (1863a: 268; 1863b: 58) and illustrated in Jan and Sordelli (1866 (1860–1881): vol. 1, livr. 16, pl. 1, fig. 2d [reproduced in fig. 6 of this paper]).

magnification, most teeth appear to be slightly flattened (chisellike) on the anterior face of the tip (not evident at 17× in fig. 4), whereas at least the last two teeth are slightly compressed laterally. (However, lateral compression of the penultimate and ultimate teeth is not so pronounced as to give a knifelike appearance that characterizes some rear-fanged species.)

The last two maxillary teeth are slightly longer than the tooth immediately preceding and roughly one and a half times longer than the anterior teeth. The last two teeth also are perceptibly stockier than preceding teeth; neither of the last two teeth is offset, both being set in a straight line with other posterior maxillary teeth; there is no diastema.

Right palatine with 15 teeth, followed by about 30 pterygoid teeth. The right mandible is missing. The left dentary bears about 20 slightly recurved, relatively stout teeth. The dentary appears firmly articulated with the compound bone; in lateral view, the posterior 60% of the dentary is resting on the compound bone.

Hemipenis

The retracted right hemipenis had been previously opened, as mentioned above. The morphology of the hemipenial apex could not accurately be determined in this retracted organ and it was desirable to see the everted condition. Consequently, the retracted left hemipenis was removed, soaked in 3% KOH solution and manually everted following the method reviewed in Myers and Cadle (2003: 300). Owing to the delicacy of the organ, the basal starting slit had to be lengthened when a break occurred during the process, but an informative eversion of the distal half was realized (fig. 5).

Before its removal, the left retracted hemipenis extended to the level of the base of subcaudal 12; weak bilobation commenced at the base of subcaudal 11 and the short slips of retractor muscle merged at the end of subcaudal 12.

Retracted Hemipenis: Bilobation is barely evident in the retracted condition, with the lobes occupying about the distal 4% of the organ. Some previous investigator had opened the right hemipenis in situ, incising it along the lateral wall, with the incision then shifting ventrolaterally to the end of the organ. The line of incision interrupted the basal course of the single (unforked) sulcus spermaticus, which runs along the lateral wall to terminate in the end of the small dorsal lobe. There is no basal naked pocket. A concealed narrow nude strip (not visible in fig. 5) on the basal 40% of the organ lies alongside and under the overhanging edge of the thick spinose tissue ridge that parallels the sulcus spermaticus. Nearly the basal fifth of the hemipenis is spinulate (excluding the concealed nude strip alongside the sulcus). Above the spinules, the organ is covered in small spines nearly to the lobes, where the spines give way to a cluster or clusters of larger, flattened, soft papillae.

Everted Hemipenis: On eversion, the very short hemipenial lobes become more evident, and it can be seen that each lobe bears a distinct cluster of nonmineralized soft flat papillae that are larger than the small rigid spines covering most of the hemipenis (fig. 5). There is a well-defined, slightly depressed nude area in the crotch between the papillate lobes (see sulcate and apical views in fig. 5). A thick spinose ridge of tissue extends alongside the unforked sulcus

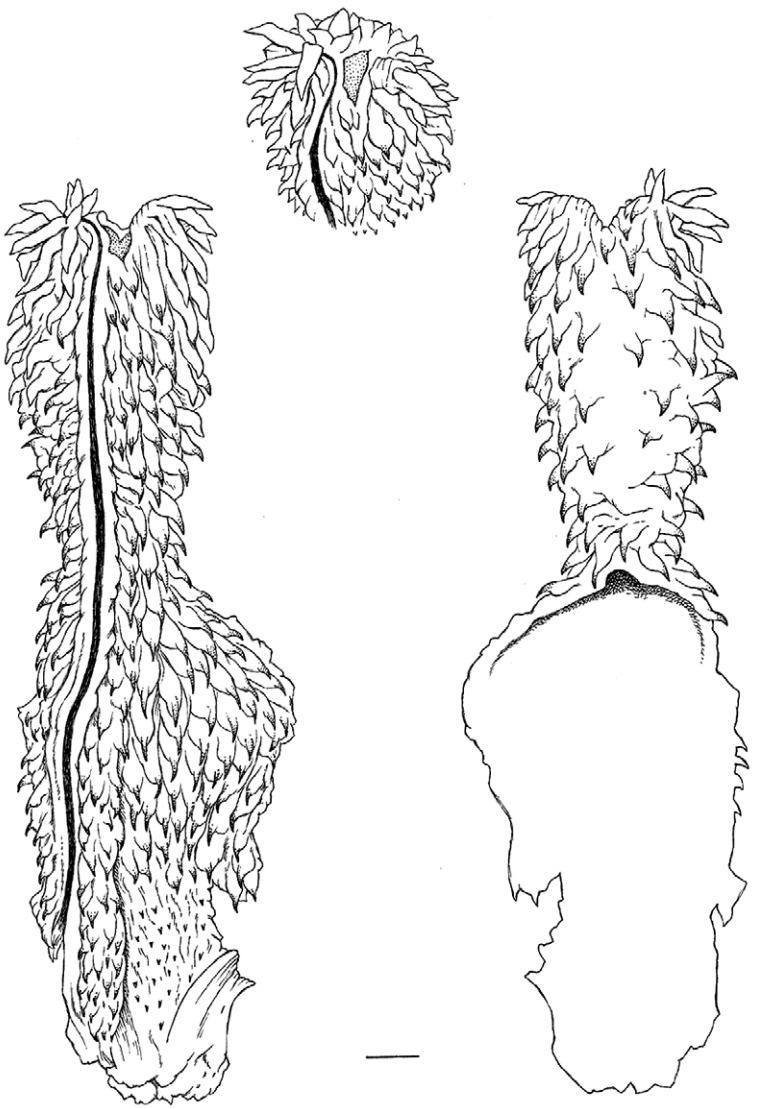

FIG. 5. Hemipenis of *Amnesteophis melanauchen* (Jan 1863). Manually everted left organ of holotype of *Enicognathus melanauchen*, in sulcate (left), apical (top), and asulcate (right) views. (Basal half of organ is split and spread flat; the inflated distal half is fully everted but probably not maximally expanded.) The basally spinulate hemipenis is mostly spinose (spines emphasized by stippling); the spines are replaced on the small lobes by larger, soft flattened papillae; the unforked sulcus spermaticus extends centripetally to apex of the left lobe (sinistral sulcus) without entering a nude area in the lobular crotch; calyces are lacking (scale line = 1 mm).

spermaticus, largely concealing an adjacent narrow nude strip on the basal half of the organ. The distal end of the sulcus extends onto the medial side (centripetal orientation) of the left lobe, where it skirts the nude area and terminates on the apex of the lobe, within the cluster of large papillae. Distal half of asulcate side sparsely spinose to lobes. There is no trace of calyces on the hemipenis.

COMPARISONS AND HIGHER-LEVEL TAXONOMY

Considering that its South American type locality is not corroborated (see fn. 2), and considering especially some features of dentition and hemipenis, *Amnesteophis melanauchen*

needs global comparisons with several major clades of "colubrid" snakes. But, for purposes of discussion, what to call these clades? Systematic biology has slipped into a new era of unprecedented nomenclatural instability—exciting because of new phylogenetic insights but discouraging for normal communication. Small or large amounts of new sequence data added to that stored already in GenBank are permitting relatively rapid successions of new competing molecular classifications. Relationships based on limited taxon sampling and incomplete molecular data, however, are truly in the discovery stage and often ambiguous. Biology in general might best be served if time could be given for new cladograms to be corroborated or falsified before advocating major changes in taxonomy.[5]

Conrad (2008: 4, 142–144) perceptively questioned "the importance of strict rigidity within taxonomy," noting that although "new phylogenetic hypotheses sometimes require revisions in taxonomy ... the taxonomy of the squamate 'families' has been relatively stable for well over 100 years" and that newly hypothesized taxonomies can be "unhelpful and gratuitous." Conrad (2008: fig. 3 caption) demonstrated that "Clearly, taxonomy may be relatively constant and remain informative." It is something to keep in mind.

Zaher et al. (2009) explored the phylogeny of advanced snakes and presented a new important and instructive phylogeny, but their derived classification shifts about a few major names in unfamiliar ways that in my view are not particularly useful at this time. For example, few terms are more familiar to modern herpetologists than "colubrid snakes," with everyone recognizing that there is much to learn about intrafamilial relationships and that there may be paraphyly to resolve. Zaher et al. (2009: 138–139) greatly restricted the family Colubridae from "its long-standing use [for] all caenophidians that were not acrochordids, elapids, or viperids" (Zaher et al., 2009: 139). They usefully confirmed removal of a number of Old World groups whose relationships have been questioned (xenodermatines, pareatines, homalopsines, psammophiines, atractaspidines, pareallactines, and lamprophiines). But the residue of their "superfamily Colubroidea," defined as clade 19 in their phylogeny, includes a huge number of snakes long considered as Colubridae in the common sense. For general discussion, it is more direct and less confusing to call members of clade 19 "colubrids" rather than "colubroids," a term that includes vipers and elapids in most taxonomies (and that might also be confused with the name "Colubroides" of Zaher et al., 2009: 132).

Conrad (2008: 144) seems one of the few recent workers who recognizes that "Taxonomy is most useful as a tool for *discussing* [emphasis added] groups of animals, phylogenetic hypotheses, and ideas about evolutionary history." Discussion is hampered and becomes confused when new taxonomies are generated from new (uncorroborated) phylogenetic hypotheses, especially when familiar groups are renamed and redefined in *major* ways.

In order to give time for the taxonomic dust to settle, "Colubridae" is conservatively used herein, and the four "colubrid" subfamilies considered in the present paper are the widely distributed Colubrinae and Natricinae and the mostly New World Xenodontinae and Dipsa-

[5] That was the philosophy that I remember being expressed by early cladists at the American Museum, but it seems long forgotten. It is ironic that systematists used to argue that Latin names are more stable than invented "common" names, but proponents of the latter lately have reason to claim otherwise!

dinae (for comments on the last two, see below under "Xenodontinae"). As will be seen, although xenodontine affinities are suspected, I cannot *unambiguously* assign *Amnesteophis* to any of these subfamilies, which is a practical reason for retaining Colubridae in the common sense.

Introductory Notes on Dentition and Hemipenes

Dentition: Great variation occurs in the maxillary dentition of colubrid snakes generally, but the vast majority of South and Central American xenodontines and dipsadines have two enlarged posterior "fangs" (grooved or not), of which the posterior one is offset laterad from the anterior one; the enlarged posterior teeth often are preceded by a distinct gap or diastema, the presence or absence of which is correlated in some species with the total number of teeth present (Myers, 1974: 24, 29). The common pattern of offset fangs—possibly synapomorphic for xenodontines + dipsadines—appears to be symplesiomorphic within all but a few genera.

Amnesteophis differs significantly in having approximately the posterior 10 maxillary teeth lying in a straight line, none being offset from the others. I can recall only a few Middle American dipsadine genera having posterior maxillary teeth in a straight line, a condition that now seems to me to be derived within the Dipsadinae (see appendix 2 for taxonomic implications). The condition is unknown to me in the Xenodontinae. The dentition would seem unique and diagnostic if I am correct in placing *Amnesteophis* in the Xenodontinae.

Also of interest is the slightly flattened or chisellike surface of the anterior sides of the tips of most maxillary teeth. This feature, which appears weakly developed at about 50× magnification under the dissecting microscope, is not evident at 17× in figure 4. Chisellike teeth occur in several genera in at least two colubrid subfamilies—for example, *Tantilla melanocephala* (e.g., AMNH R-55966) in Colubrinae and *Regina rigida* (AMNH R-128639) in Natricinae. In those cases, chisellike teeth may correlate with dietary specialization on chitinous arthropods such as centipedes and crayfish.

Hemipenes: Along with earlier authorities, I assume that *Amnesteophis melanauchen* is a South American snake as originally described. However, the single sulcus spermaticus gives immediate pause inasmuch as an unforked sulcus spermaticus is rarely encountered among xenodontines and is uncommon among dipsadines. A single sulcus characterizes the Colubrinae and some Natricinae, which necessitates hemipenial comparisons with Old World representatives of those groups—to be followed by general comparisons within New World Dipsadinae and Xenodontinae.

Colubrinae

Amnesteophis melanauchen (Jan) has a large dark nuchal blotch flanked by pale crossbands. These markings, coupled with a slender habitus, are somewhat similar to the anterior color pattern of the Asiatic colubrine *Sibynophis subpunctatus* (Jan and Sordelli, 1866 (1860–1881): vol. 1, livr. 16, pl. 4, fig. 1 [as *Enicognathus humberti*]; 1876: vol. 3, livr. 48, pl. 1, fig. 4 [as *Oligodon*

subpunctatus]). However, the genus *Sibynophis* differs in many characters, including 17 rows of smooth dorsal scales (vs. 15 rows of weakly keeled dorsals in *Amnesteophis*), the dentary very loosely articulated with the compound bone, numerous small teeth, and a different hemipenis. So far as described, the hemipenis of *Sibynophis* is nonbilobate and calyculate (vs. weakly bilobed and acalyculate in *Amnesteophis*); in addition, *Amnesteophis* lacks a hemipenial synapomorphy thought to be diagnostic of the colubrine tribe Sibynophiini (Zaher, 1999: 28, fig. 15).

The colubrine clade is defined by the loss of the "left" branch of the sulcus spermaticus (McDowell, 1961: 504; Zaher, 1999: 25–26).[6] The resultant single sulcus runs onto the right lobe when the colubrine hemipenis is bilobate; in colubrine organs lacking bilobation (derived loss), the single sulcus terminates either in a centrolineal position (as in *Sibynophis*) or trends toward the right side[7] (for a sample of variation among colubrines, compare figs. 112c.1–112c.13 in Dowling and Duellman, "1974–1978" [1978]). In the Colubrinae, the orientation of the sulcus branch usually is either centrolineal or centrifugal—rarely centripetal (examples in Cadle, 2010: 18).

In contrast to the colubrine condition, the unforked sulcus in *Amnesteophis* extends onto the left lobe (the dorsal lobe when retracted), to terminate in a centripetal position as in the Natricinae (fig. 5).

Natricinae

The great majority of these snakes have strongly to weakly bilobed, spinose hemipenes that were recently thought to be always acalyculate (McDowell, 1961: 504–505; Rossman and Eberle, 1977: 38–41; Dowling and Duellman, "1974–1978" [1978]: 112d.1; Zaher, 1999: 25, 32–33). Cadle (ms.), however, has demonstrated the presence of calyces in *Rhabdophis* and further explored hemipenial diversity among natricines.

It is believed that in most natricine hemipenes the sulcus spermaticus either bifurcates with centripetal branches on the lobes, or else extends unforked straight (centrolineally) to a variable-sized median nude area in the middle of an unilobed or weakly bilobed head.[8] Other configurations, however, also occur and it is difficult to generalize.

[6] The "left" and "right" hemipenial lobes and/or sulcus branches refer to the everted hemipenis as viewed looking toward its sulcate side (hemipenial lobes are dorsal and ventral when retracted). "Sinistral sulcus" and "dextral sulcus" are useful descriptors for unforked sulci extending either to the left or right lobe, respectively (Rossman and Eberle, 1977: 40).

[7] Shwayat et al. (2009: 98, fig. 9A–D), however, describe four species of the colubrine genus *Eirenis* as each having a single sulcus that either "turns left" or "turns right," or "turns left or right" in the same species. These conditions are not evident in their photographs, which are reproduced too small for clarity. When the PDF is greatly enlarged on a computer screen, however, the four unilobed organs all appear to have centrolineal sulci spermatici that seem to terminate in the middle of the hemipenial apices.

[8] Zaher (1999: 26) suggested that the nude area derives from broadly-expanded centripetal branches of a forked sulcus, but this can be questioned. In *Macropisthodon rudis* a sinistral sulcus appears to extend to the tip of the left lobe before meeting a centripetal "nude apical groove" that also seems to be represented by a "narrow nude pocket" on the medial side of the right lobe (Rossman and Eberle, 1977: 39–40, fig. 4C). In some other natricines, the sulcus groove remains distinct within or even crosses the nude area (Cadle, ms.).

The right branch of the sulcus spermaticus has been lost in a several derived natricine genera, including *Afronatrix* and *Hydraethiops*, with the remaining left branch extending centripetally onto a small left lobe as in *Amnesteophis*. For illustrations of the everted hemipenis of *Afronatrix anoscopus* see Zaher (1999: fig. 18, upper); for the retracted and everted organs of *Hydraethiops melanogaster* see Bogert (1940: fig. 4A) and Zaher (1999: fig. 18, lower), respectively.[9] These acalyculate, spinose hemipenes—with a nude area in the crotch—are similar to that of *Amnesteophis* (fig. 5) except that the *Amnesteophis* organ bears distal flaplike papillae, which are absent or at least rare on natricine hemipenes.[10]

Natricines (and few other colubrids) are characterized by presence of hypapophyses on the posterior vertebrae, but posterior hypapophyses are lacking in *Amnesteophis*. Furthermore, even small natricines tend to be relatively robust compared with the slender *Amneseophis*. Therefore, despite aforesaid hemipenial similarities with a few Old World natricines, the slender body, relatively narrow head, and lack of precaudal hypapophyses seem to preclude *Amnesteophis* from the Natricinae.

"Xenodontinae"

More than a quarter century ago investigators began to realize that New World "xenodontine" snakes comprise two geographically overlapping clades—the Central American "xenodontines" and the South American "xenodontines"—as documented primarily by microcomplement fixation studies of serum albumins (Dowling et al., 1983; Cadle, 1984a, 1984b, 1984c, 1985); for summary discussion see Zaher (1999: 5–7).

The predominantly Central American assemblage was recognized as subfamily Dipsadinae by Dowling et al. (1983: 323, 326). Zaher's (1999: 33) concept of Dipsadinae corresponded "essentially to Cadle's Central American group," as supported morphologically by the hemipenial characterization provided by Myers and Cadle (1994: 27). Zaher stated that one of the three synapomorphies suggested by Myers and Cadle—distal division of the sulcus spermaticus within or at the base of the capitulum—"is nearly unique to the dipsadines, being otherwise present only in the Madagascan genus *Geodipsas*."

[9] The "Hiss drawing" of a hemipenis labeled "*Hydraethiops melanogaster*" in Dowling and Duellman ("1974–1978" [1978]: fig. 112d.4) is an accidentally transposed illustration of *Natriciteres olivacea*—apparently the same hemipenis represented by the photograph of AMNH 11915 in Zaher (1999: fig. 19, upper). The adjacent drawing (fig. 112d.5) mislabeled "*Natriciteres*" probably is *Hydraethiops melanogaster*, but not the same organ illustrated under that name in Zaher (1999: fig. 18, lower).

N.B.: The hemipenis of *Natriciteres* is *not* a unilobed organ like that of *Limnophis* as implied by Zaher (1999: 32). The aforesaid illustrations of *N. olivacea* show what appears to be a bifurcated organ with the right lobe very incompletely everted, but, as described and illustrated by Bogert (1940: 33--35 [as *Neusterophis*]), the *Natriciteres* hemipenis is only basally bifid, with one long and one very short lobe controlled by unequal-length slips of retractor muscle. Thus, the shortening leading to loss of a single lobe is one method of becoming unilobed, the alternative being distal shortening of both lobes simultaneously.

[10] The flaplike structure shown on the left lobe in Zaher's (1999: fig. 18) photograph of *Hydraethiops melanogaster* (AMNH 11959) is an artifact (torn tissue) of preparation.

The restricted subfamily Xenodontinae was treated in considerable detail by Zaher (1999), who provided an exhaustive survey of xenodontine (and other) hemipenes and suggested synapomorphies for defining the clade. Owing to the lack of field-everted hemipenes, Zaher prepared and illustrated numerous hemipenes that he everted manually. Such eversions elucidate features often not interpretable from dissections of retracted organs (both kinds of data are essential for complete understanding). Limitations to manual eversion of fully retracted organs of museum specimens include (1) some necessary damage will occur to the base of the hemipenis and (2) complete *expansion* often cannot be attained (resulting in a smaller circumference), even though *eversion* may be complete with all structures revealed. Both situations apply to the manually everted hemipenis of *Amnesteophis melanauchen* (see p. 10 and fig. 5). The techniques and limitations of manually everting hemipenes were discussed by Myers and Cadle (2003) and Zaher and Prudente (2003).

Dowling (2004) seemed unenthused about the usefulness of manual eversions and responded critically to the last two papers and also to Zaher's (1999) earlier study. Based on "prior knowledge" gained from having "prepared more than 400 'fresh' hemipenes in the last half-century," and "due to long experience and careful observation," Dowling was able to provide imaginative explanations for hemipenial features with which he had had no experience. Two examples: he suggested (Dowling, 2004: 321) that "the disappearing calyces" (the "pseudocalyces" of Myers and Cadle) on an everted *Psomophis* hemipenis were "an artifact of incomplete specimen preparation" (i.e., not injecting the "outer lymph sinus"), and he predicted (ibid.: 325) how the everted hemipenes of *Xenopholis* really *should* look after stating that five of Zaher's illustrations were "so inaccurate as to place the taxa in the wrong family."[11] Dowling (2004: 325–327) particularly critiqued Zaher's (1999) photographs of manually everted hemipenes by "doing a page-by-page survey of [Zaher's] entire study" and listed those illustrations he judged to be based on distorted or incompletely everted organs. However, few of the supposed "incomplete" eversions or "distortions" mask the synapomorphic structures that Zaher discussed, nor was Dowling's critique as thorough as he implied. Witness that Zaher's study (1999: 154–156) included photographs of hemipenes of three species of *Xenodon*, and yet Dowling (2004: 326) asserted that "it seems strange that Zaher failed to illustrate the hemipenis of the type genus of xenodontine snakes (*Xenodon*) (*v.* my Fig. 11 [= Dowling's own accompanying illustration])"!

[11]Concerning pseudocalyces: Normal calyces have walls of varying flexibility but do *not* disappear no matter how the organ is everted or to what extent it is inflated. As noted by Myers and Cadle (1994: 13), retracted *Psomophis* hemipenes have obliquely transverse folds of large spinulate papillae that are connected longitudinally by fine tissue folds, which bear striking resemblance to calyces "when the inverted lobe is incised and gently parted." The connecting longitudinal folds, however, "can be flattened by micromanipulation with fine teasing needles." The calyxlike structures were absent on the only available field-everted organ and were judged to have disappeared during inflation owing to stretching of the fine connecting folds (Myers and Cadle, 1994: 10–13). Two manually everted *Psomophis* hemipenes are fully everted but not completely expanded. The transverse papillate folds are evident in photographs (Zaher, 1999: fig. 74), but the connecting longitudinal folds show only at high magnification as hairline folds that "probably would disappear in a maximally expanded fresh eversion" (Myers and Cadle, 2003: 296, fig. 3).

Concerning *Xenopholis*: The appearance of the hemipenis of *X. scalaris* illustrated by Zaher (1999: 168, fig. 95) compares favorably with one that I field-everted in Rondônia, Brazil (AMNH R-130238).

Zaher et al. (2009: 141) have reworked the classification of "Xenodontinae," returning it to earlier concepts of a single group of New World "xenodontines" that (because of nomenclatural priority) would now have to be called "dipsadines." Their new groupings follow:

Family Dipsadidae Bonaparte, 1838

Subfamily Carphophiinae Zaher et al., 2009

Subfamily Dipsadinae Bonaparte, 1838

Subfamily Xenodontinae Bonaparte, 1845 (with 14 tribes)

Subfamily Xenodontinae was now said to have "No known synapomorphies" because synapomorphies presented by Zaher (1999) were moved to family Dipsadidae for complex and unresolved issues explained by Zaher et al. (2009: 140). Nonetheless, subfamily Xenodontinae was retained (appropriately in my view) to avoid changing "the well-established taxonomic hierarchy for this group" (Zaher et al., 2009: 141–142).

I have no reason to challenge the phylogeny that led to this classification except to note that ongoing DNA sampling still is insufficient for a thoroughly robust testing of these groupings (cf. Vidal et al., 2000; Kelly et al., 2003; Lawson et al., 2005: 594; Hedges et al., 2009; Zaher et al., 2009). Therefore the Dipsadinae and Xenodontinae are retained herein for practical reasons as subfamilies of Colubridae sensu lato for reasons discussed above (introductory paragraphs under Comparisons and Higher-Level Taxonomy).

Herndon Dowling has been a long-time proponent of assigning colubrid snake genera to tribes (e.g., see Dowling and Duellman, "1974–1978" [1978]). Zaher et al. (2009) have significantly advanced the process by distributing the colubrid subfamily Xenodontinae among 14 tribes, which facilitates discussion and further research. Tribal designations and molecular sampling are much less complete for the Dipsadinae.

Dipsadinae

Various authors mention that an undivided sulcus spermaticus characterizes several genera of Dipsadinae that have been grouped under the tribal name "Leptodeirini," although monophyly of the group could not be corroborated with molecular data (Mulcahy, 2007). Another problem is that the sulcus is not strictly single in the type genus *Leptodeira*, in which it varies from undivided to apically forked. In any case, these genera (*Eridiphas* [= *Hypsiglena* fide Mulcahy, 2008: 1112], *Hypsiglena*, *Imantodes*, *Leptodeira, Pseudoleptodeira*) are composed of slender, terrestrial to arboreal nocturnal snakes with elliptical pupils and opisthoglyphous dentition; aside from an unforked sulcus, they bear no other resemblance or evident relationship to *Amnesteophis*. See appendix 1 for hemipenial variation in *Leptodeira* and taxonomic comments.

Xenodontinae

An undivided sulcus spermaticus is unknown in the South American "xenodontine" clade except in one species of *Taeniophallus*, as reported by Myers and Cadle (1994). Zaher (1999: 97) assigned *Taeniophallus* to Dipsadinae incertae sedis, but limited molecular data suggest that *Taeniophallus brevirostris* and *T. occipitalis* (Cadle, 1984b, under "*Rhadinaea*"), and *T. nicagus* (Vidal et al., 2000, as "*Taeniophallus brevirostris*"[12]) belong with Xenodontinae sensu stricto. This placement has now been corroborated by Zaher et al. (2009: 125, 144), based on mitochondrial data from *T. affinis* and *T. brevirostris*.[13]

The generic name *Taeniophallus* (Cope, 1895) was resurrected by Myers and Cadle (1994: 4), who included seven species that later were distributed by Schargel et al. (2005: 14–16) among three groups for discussion: (1) *Taeniophallus brevirostris* and *T. nicagus*; (2) *T. occipitalis*; (3) *T. affinis* group. Schargel et al. (2005) also added an eighth species—the enigmatic new *T. nebularis*—which arguably is related to *T. brevirostris* and *T. nicagus*. And the monotypic *T. occipitalis* group was enlarged with addition of the new *T. quadriocellatus* by Santos-Jr. et al. (2008); this species is close to *occipitalis*, with which it shares the diagnostic large median spine in the interspinal gap on the asulcate side of the hemipenis. These nine species constitute *Taeniophallus* sensu lato, for which there is no explicit evidence of monophyly. The first two groups comprise *Taeniophallus* sensu stricto (*nicagus* is the generic type species).

Amnesteophis is appropriately compared with *Taeniophallus* sensu stricto following the lead of Jan himself. In a key to the old snake genus *Enicognathus*,[14] Jan (1863a: 266; 1863b: 56) paired "*E.*" *melanauchen* with "*E.*" *occipitalis*, and Jan and Sordelli illustrated both species together (reproduced herein as fig. 6). Both are characterized by 15 rows of dorsal scales and have somewhat similar color patterns, or at least similar enough for Amaral (1929b [1930]: 173; 1936: 115) to suggest that "*Liophis*" *melanauchen* was based on an anomalous example of "*L.*" [*Taeniophallus*] *occipitalis*. The hemipenis of *T. occipitalis* shares with *Amnesteophis* the characters of weak bilobation (some specimens) and large flaplike papillae (on asulcate side of

[12]Based on voucher specimen MNHN 1996.4240 from French Guiana (not examined).

[13]Zaher et al. (2009: 144) assigned *Taeniophallus* and *Echinanthera* (molecular data not available for the last) to their new tribe Echinantherini, but the tribal diagnosis is unsatisfactory on several points. (1) The "unilobed" hemipenis actually is distinctly bilobed in *T. nebularis* and weakly bilobed in some *T. occipitalis*. (2) The sulcus spermaticus does not divide "relatively distally, within the calyculate region," but divides roughly halfway up the organ at the base of, or slightly below, the calyculate region; also it should be noted that the sulcus is unforked in the type species of *Taeniophallus* (*nicagus*). (3) The "large nude region present on asulcate side of the hemipenial body" refers to the asulcate interspinal gap, which is distinctly nude only in a few species (e.g., *T. nebularis*). Although often distinctly expanded on everted organs, the interspinal gap usually bears a median line of tiny spines or spinelike papillae in the *T. affinis* group and some *Echinanthera*; there is a very large median spine interrupting the gap in *T. occipitalis* and the related *T. quadriocellatus*); there is *no* interspinal gap in *T. nicagus* and *T. brevirostris*, in which the asulcate side is spinose. See Schargel et al. (2005) for some illustrations.

[14]*Enicognathus* Duméril et al. (1854: 328) is a junior homonym of the avian genus *Enicognathus* Gray (1840: 51). The homonymous emendations *Henicognathus* were proposed by Agassiz (1846: 138, 178) and Cope (1868: 132) for the bird and snake names, respectively. The derivations are Gk. *Enico-*/*Henic-* ("single" or "singular") + Gk. *gnathos* ("jaw").

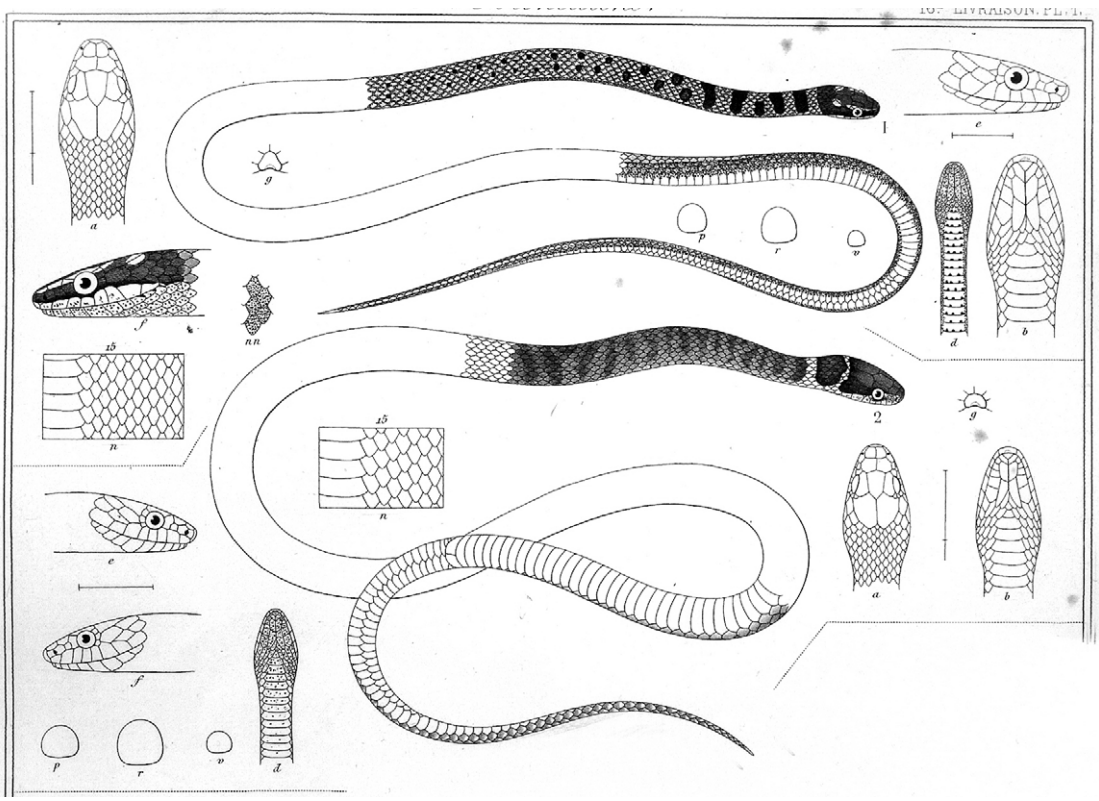

FIG. 6. Portion of plate 1, livraison 16, in the *Iconographie générale des ophidiens* (Jan and Sordelli, 1866 [1860–1881]), shown 0.77× original folio size. **1.** Syntype of *Enicognathus occipitalis* Jan 1863, now = *Taeniophallus occipitalis*. **2.** Holotype of *Enicognathus melanauchen* Jan 1863, type species of *Amnesteophis* as proposed herein (see also figs. 1–3 and text for comments on faded color pattern).

capitulum). The *occipitalis* hemipenis otherwise is very different from that of *Amnesteophis*, since it has a calyculate capitulum, a deeply bifurcate sulcus, and a distinctive arrangement of spines (compare fig. 5 with Myers, 1974, fig. 47B, and Schargel et al., 2005, fig. 9D).

Taeniophallus occipitalis seems to be related to *T. brevirostris* based on a few pertinent similarities (Myers, 1974: 211, and Schargel et al., 2005: 15). A close relationship between *T. brevirostris* and the partly sympatric *T. nicagus* is inferred from remarkable resemblances in color pattern, external morphology, and condition of the sulcus spermaticus (Myers and Cadle, 1994: 4–6; Myers and Cadle, unpubl.). The everted hemipenes of *brevirostris* and *nicagus* are compared in Schargel et al. (2005: fig. 8). The former is highly unusual among "xenodontines" in having one branch of the sulcus spermaticus noticeably shorter than the other branch, a condition also occurring in the two species of the North American *Rhadinaea flavilata* group (Myers, 1974: 49). I earlier suggested that shortening of a single branch was one way of evolving a simple sulcus spermaticus, which appears to have happened in *Taeniophallus nicagus*, in which there is no sign of a fork.

Nonetheless, except for the simple sulcus, the calyculate hemipenis of *Taeniophallus nicagus* is very different from the acalyculate *Amnesteophis* organ, which is ornamented with small spines proximally and flat papillae distally, with the sulcus extending past a nude area and onto one lobe in centripetal orientation.

SUMMARY DISCUSSION

Amnesteophis melanauchen differs significantly in dentition and hemipenis from other South American snakes. The unforked sulcus spermaticus originally caused me to doubt the purported type locality (Bahia, Brazil) and, some years ago, I sent photographs of the holotype to several colleagues better acquainted with Old World snakes. No one recognized it nor can I find convincing morphological evidence that it might be related to some group of Old World colubrines or natricines. I had originally doubted the provenance of *Taeniophallus nicagus* (type locality Brazil?) because it also has an unforked sulcus (Myers, 1974: 208), but *T. nicagus* subsequently was rediscovered and shown to be a South American snake (Myers and Cadle, 1994). Thus, there seems no good reason to question the geographic provenance of *Amnesteophis*, but confirmation or falsification depends on its rediscovery or demonstrated synonymy with some Old World species.

Tribe Amnesteophiini and genus *Amnesteophis* could well be classified as Colubridae incertae sedis. I assign them primarily on geographic grounds to the Xenodontinae sensu stricto, an extraordinarily diverse, primarily South American[15] group comprised of over a dozen tribes of mostly uncertain relationship (Zaher et al., 2009: 141). The difficulty and uncertainty in making this assignment says something about current understanding of colubrid phylogeny.

Amnesteophis melanauchen and *Taeniophallus nicagus* are the only species of Xenodontinae known to have an undivided sulcus spermaticus. (The character is apomorphic in several genera of Middle American and South American opisthoglyphous cat-eyed snakes [see appendix 1], but these clearly belong in the Dipsadinae and seemingly can be excluded from further comparison.) Although *Amnesteophis* is superficially similar to *Taeniophallus occipitalis* and shares a single sulcus with *T. nicagus,* other aspects of the hemipenis and the straight-line rear maxillary teeth are so profoundly different that they cannot credibly be placed in the same tribe at this time. The monotypic tribe Amnesteophiini is easily diagnosed, but its relationships remain to be discovered.

[15]The Xenodontinae historically have been thought to be confined to the New World, with a primarily South American distribution. He et al. (2009) and Huang et al. (2009) recently used molecular evidence to place in the Xenodontinae the Asiatic snake genus *Thermophis*— from high on the Tibetan (Qinghai-Xizang) Plateau. But Zaher et al. (2009: 140) state that these authors "have shown convincingly that [*Thermophis*] is more closely related to the Dipsadidae than it is to any other colubroid clade." In these studies *Thermophis* is placed in Xenodontinae sensu lato (comprising both dipsadines and xenodontines); *Thermophis* is shown closest to the dipsadine *Contia*, but the generic sampling clearly needs enlarging.

Malnate (1953: 95) did not formally place *Thermophis* in the Xenodontinae as claimed by He et al. (2009: 479), but only noted that "*Thermophis*, using Dunn's [1928] key, would fall in the section Ophiinae" (= "Xenodontinae"). Guo et al. (2009: 54) illustrate *Thermophis* hemipenes, which are dipsadine-like as noted by Zaher (1999: 26, 28).

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APPENDIX 1

Status of the "Leptodeirini"

Although the tribal name "Leptodeirini" (Jenner, 1981 [Ph.D. dissertation]) has been used by several authors, the name is nomenclaturally unavailable and therefore invalid. In an apparent attempt to make available Jenner's tribal names, Dowling et al. (1983: 323, table X) stated that "Taxa recognized by Jenner are named and defined in Jenner, 1981." That statement (in heading to table X) refers to four simply tabulated names,[16] which were (and are) unpublished for purposes of zoological nomenclature (e.g., ICZN, 1961: art. 8.1, 9.6; 1999: art. 8.1.3, 8.4, 9.4, 9.7). Since the names were unpublished in the meaning of the *Code*, Jenner's dissertation cannot subsequently be used as an indication or bibliographic reference in order to confer availability (ICZN, 1961: art. 11(a), 16(a)(i); 1999: art. 11.1, 12.1.1). A new concept and new name "Leptodeirini" could be made available under new authorship if the published nomenclatural act conformed to the provisions of Articles 10–20 (ICZN, 1999), but little would be gained considering the historical baggage.

Jenner (1981: 262) visualized her "Leptodeirini" as "defined by possession of a fully capitate, single or bilobed hemipenis with a simple sulcus"; four genera were included—*Leptodeira*, *Eridiphas*, *Hypsiglena*, and *Imantodes*. Based on immunological comparisons, Cadle (1984b: 24) tenuously associated *Cryophis* with these four genera in a "*Leptodeira-Eridiphas* clade," noting that the divided sulcus spermaticus of *Cryophis* suggested the possibility of a sister-group relationship to the other four genera. Cadle (1984b: 22, 25) placed *Leptodeira latifasciata* with *Eridiphas* and *Hypsiglena*, in a clade outside *Leptodeira*; he commented on the distinctiveness of *L. latifasciata*, saying that its relationships needed reassessment. This was done by Dowling

[16]The tabulated names are "Diaphorolepini Jenner, 1983," "Philodryini Jenner, 1983," "Pseudoboini Jenner, 1983," and "Leptodeirini Jenner, 1983." A reference "Jenner, 1983" is not listed in Dowling et al. (1983) nor is Jenner indicated as author of their table X. However, Jenner and Dowling (1985: 171) credit Jenner as author of table X *in* Dowling et al., 1983. In any case, the "1983" Jenner names listed in that table fail to meet basic requirements for availability (ICZN, 1999: art. 10.1, 11.1, 13.1).

and Jenner (1987), who resurrected the genus *Pseudoleptodeira* for *L. latifasciata* and assigned it to "Tribe Leptodeirini Jenner, 1983."

Mulcahy (2007) obtained mitochondrial DNA sequence data from members of all six genera of the expanded "Leptodeirini," but found no evidence of monophyly, although there was "strong support for a clade containing *Imantodes* and *Leptodeira*, and another clade containing the nightsnakes." Daza et al. (2009) also recovered these two clades, with especially strong support for *Imantodes* + *Leptodeira*. Without considering the other genera, Pinou et al. (2004: fig. 1) and Zaher et al. (2009: 127) also corroborated a monophyletic *Leptodeira* + *Imantodes*.[17]

I have not personally verified the unforked-character state of the sulcus spermaticus in *Eridiphas*, *Hypsiglena*, or *Pseudoleptodeira*, but have seen it in dissections of retracted *Imantodes* hemipenes and have illustrated it on everted organs of four species (Myers, 1982: fig. 4). The related *Leptodeira* is nearly always characterized as having an unforked sulcus, but this is not entirely correct.

Nature of the Sulcus Spermaticus in *Leptodeira*

Species of this genus have long been believed to be united by the character of a simple, unforked sulcus spermaticus (e.g., Dunn, 1928: 23; Duellman, 1958: 17; Cadle, 1984b: 24; Dowling and Jenner, 1987: 198). Savage's (2002: 610) attribution of a forked sulcus in *Leptodeira* seems to have been based on a misreading of Dowling (1975: 198), who, however, had implied that the sulcus is *not* bifurcate.

In using *Leptodeira* as the type genus of her "Leptodeirini," Jenner (1981: 65) apparently relied solely on a drawing of the hemipenis of a single specimen of *L. annulata* ("HGD 864" [= AMNH R-107291, *L. a. cussiliris*; see below and fig. 8A]). Jenner, however, overlooked Underwood's (1967: fig. 10) illustration showing "a small fork" in an everted organ of *L. annulata*. Myers and Cadle (1994: 27) corroborated Underwood's observation by noting that "some, if not all, *Leptodeira* have a vestigial terminal division with very short branches." Without attempting to survey all species, I have since noticed that the condition of the sulcus spermaticus is variable among species of *Leptodeira*, as indicated by the following observations. (Where possible, identifications are based on specimens listed in Duellman, 1958.)

Sulcus spermaticus simple: This may be an uncommon condition in *Leptodeira*. In a specimen of *L. splendida bressoni*, the sulcus terminates abruptly and narrowly on the calyculate capitulum (AMNH R-82029, left organ everted). There is no fork and no widening at the terminus.[18] The terminus of the sulcus also appears single (but perhaps slightly widened) in the right retracted hemipenis of *L. frenata yucatanensis* (AMNH R-7870).

[17]Mulcahy's (2007: 494) evidence "placed *I. inornatus* as sister to the clade containing all other *Imantodes* and *Leptodeira*." Daza et al. (2009: 658–659) also found *Imantodes* paraphyletic with this same topology, although they (p. 662) concluded that "The present results suggest *Imantodes* as monophyletic, based on both combined nuclear and mitochondrial data or nuclear alone … [with] evidence of previously unexpected genetic diversity."

[18]Sulci spermatici were examined by parting any overhanging calyces with teasing needles or fine forceps.

Sulcus spermaticus with a small terminal fork at least in retracted hemipenes, but fork sometimes lost during eversion: RETRACTED: A terminal fork is present on retracted hemipenes of *Leptodeira annulata annulata* (AMNH R-8680 and [less pronounced] on 8136, left), *L. annulata cussiliris* (AMNH R-66452), *L. punctata* (AMNH R-19853, left; fig. 7A), and *L. rubricata* (USNM 166170). EVERTED: A weaker fork is detectable also on both everted hemipenes of a specimen of *L. annulata cussiliris*, in which each sulcus expands gradually to two termini partly concealed by calyces (AMNH R-107291 ["HGD 864"], fig. 8A); however, the intervening tissue ridge is stretched and flattened in both organs and the forking might easily be overlooked. A field-everted hemipenis of a specimen of *L. a. annulata* (AMNH R-133340) had a *distinct* terminal fork when first examined; after softening in KOH and further inflated, however, this fork broadened and acquired a superficially heart-shaped appearance (see fig. 8B). Clearly, the vestigial fork can be less obvious and may nearly disappear during eversion, as visualized in figure 8B.

Sulcus spermaticus superficially simple but with terminus expanded at least on everted hemipenes: Complete loss of the tissue wall between branches of a tiny fork would result in a simple sulcus with an expanded terminus, even in retracted organs. This seems to have happened in *L. septentrionalis ornata*. A retracted *ornata* hemipenis (AMNH R-13541, left) has a *wide* sulcus extending onto the capitulum without bifurcation; on everted organs (e.g., AMNH R-108482) the sulcus has expanded to form a triangular nude space low on the capitulum.

The situation is even more striking in *L. maculata*. In the left retracted organ of AMNH R-91592, the sulcus superficially seems to bifurcate on the capitulum with a very thin fold of tissue dividing the "branches," whereas in the right retracted organ the terminus seems to expand slightly without appearance of bifurcation. In the everted organ of another specimen (AMNH R-82150) the sulcus terminates on the capitulum as a *very broad* nude area (fig. 8C). Although not clearly forked or divided, terms such as "simple," "single," or "unforked" are not adequate descriptors of sulci spermatici on everted hemipenes such as shown in figure 8B–C.

On the evolutionary loss of bifurcation in the colubrid sulcus spermaticus: The sulcus spermaticus is a smooth, deeply incised groove flanked on each side by smooth supporting "lip" tissue. This morphology usually is continued up the branches of a forked sulcus, in which each branch has a lateral and a medial lip. In some cases described herein, loss of bifurcation of the sulcus appears to be preceded by weakening and eventual loss of the medial lips.

There appear to be at least four ways in which primitively forked sulci spermatici can become single: (1) by simultaneous shortening of both branches, probably associated in some cases with reduction or loss of hemipenial bilobation; (2) by shortening of a single branch, as seen for example in *Rhadinaea flavilata* and *Taeniophallus brevirostris* (loss is complete in *Taeniophallus nicagus*, the probable sister species of *T. brevirostris*); (3) by the probably rare shortening and/or loss of a *single* hemipenial lobe (see fn. 9); and (4) by weakening and loss of the medial sulcus lips, leaving only a tissue divide separating the lateral branches in situ; ornamentation such as calyces between the branches may also be lost during this process.

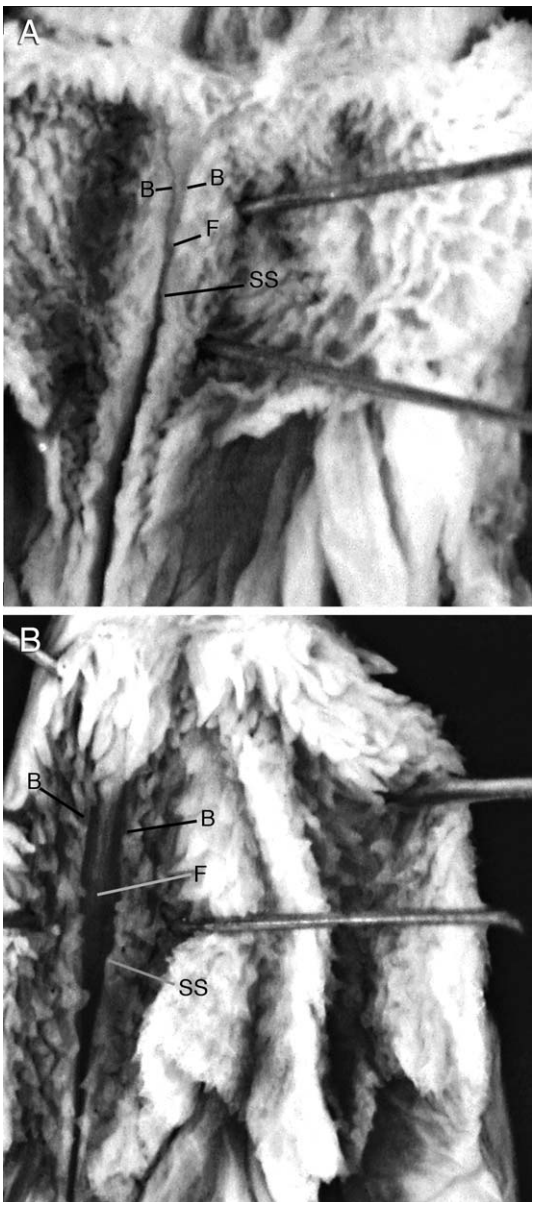

FIG. 7. Examples of terminally forked sulci spermatici in retracted hemipenes (dark areas are transiently stained with Lugol's iodine solution). **A.** *Leptodeira punctata* (AMNH R-19853), distal part of left hemipenis showing small fork, ×15.9. **B.** *Leptodeira annulata cussiliris* (AMNH R-66452), distal part of left hemipenis showing larger fork (termini of branches concealed under calyces), ×13.7. Abbreviations: B, distal branches of sulcus spermaticus; F, fork of sulcus spermaticus; SS sulcus spermaticus proximal to fork.

Loss of bifurcation (as in *L. splendida bressoni*) or its reduction to a tiny terminal fork (e.g., fig. 7A) might arguably have occurred through the first mechanism in some *Leptodeira*. The fourth mechanism, however, seems clearly to be an important one in this genus. Loss of the medial sulcus lips and extreme elasticity of the intervening tissue divide results in a telltale sulcus with a greatly expanded terminus on the everted hemipenis (fig. 8B–C).

Tribal Status of *Imantodes* and *Leptodeira*: In summary, although the tribe "Leptodeirini" was defined on the basis of an unforked sulcus spermaticus, that character state defines neither the type species (*annulata*) nor certain others in the type genus. Nonetheless, there does seem to be an evolutionary tendency toward loss of bifurcation. Mulcahy (2007) used mtDNA data for all genera originally and subsequently assigned to the "Leptodeirini," but found no support for monophyly of the group as originally and subsequently constituted, although *Imantodes* + *Leptodeira* show as monophyletic in his and several other studies cited above. The nomenclaturally invalid and unavailable name "Leptodeirini Jenner" is not available for these two genera. A new "Leptodeirini" could be created as a new taxon, but, considering the history of Jenner's unavailable name and the changed content, the addition of new authorship would engender needless confusion.

The Neotropical genera of blunt-headed vine snakes and cat-eyed snakes comprise the clade *Imantodes* + *Leptodeira*, which is well supported by molecular data (Mulcahy, 2007; Daza et al., 2009; Zaher et al., 2009). Morphologically, the clade can be defined by the synapomorphic tendency toward loss

of bifurcation of the sulcus spermaticus. Use of tribal names has proven useful for the Xenodontinae and the category is likely to prove equally useful in the Dipsadinae, to which belong *Imantodes* and *Leptodeira*. Species of these two genera are among the most commonly encountered snakes on the Neotropical mainland. They comprise biogeographically and ecologically successful genera, with large geographic ranges that slightly overlap the tropics of Cancer and Capricorn. During the process of further verifying monophyletic groups within these genera and within the Dipsadinae generally (see Zaher et al., 2009: 141), a tribal name likely will continue to be useful for *Imantodes* + *Leptodeira*, which may be known as:

Imantodini, new tribe

Type Genus: *Imantodes* Duméril (1853: 507).
Content: *Imantodes* Duméril (1853: 507) and *Leptodeira* Fitzinger (1843: 27).

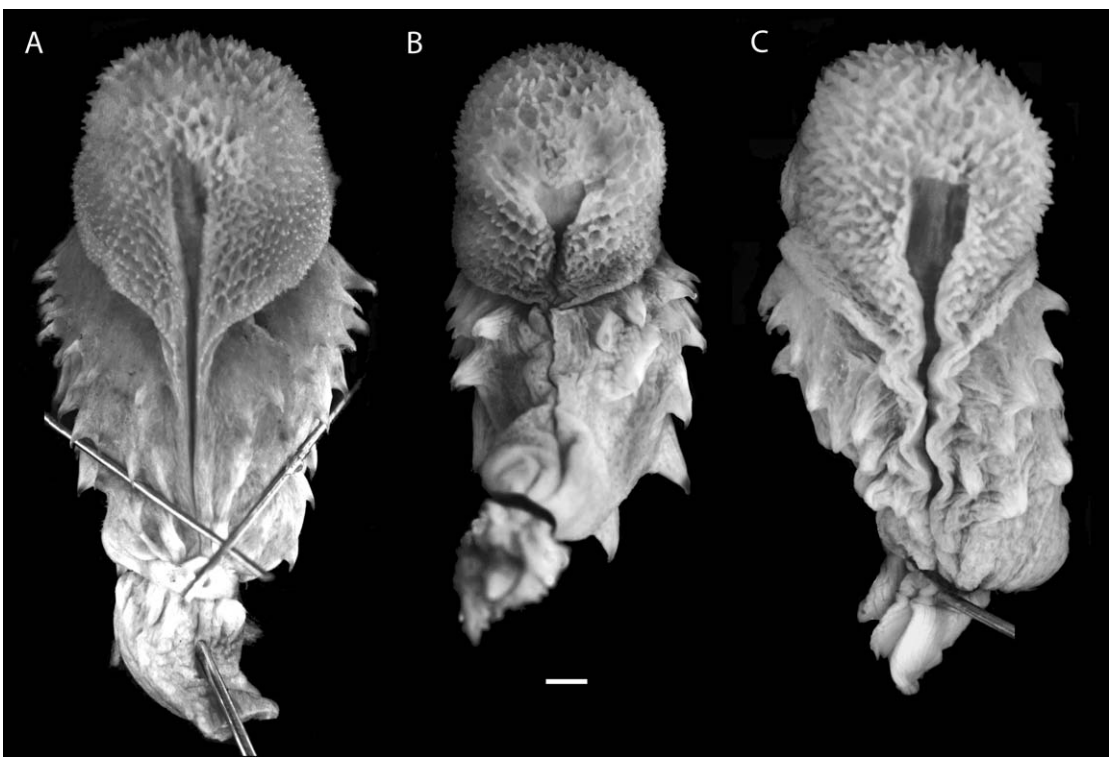

FIG. 8. Examples of field-everted hemipenes showing diminution (A) or loss (B–C) of distal forks after expansion of capitulum. Pliable tissue separating the sulcus branches before eversion is stretched flat in B and C. (Scale line = 1 mm.) **A.** *Leptodeira annulata cussiliris* (AMNH R-107291, right organ); fork slightly widened (cf., fig. 7B), with very short branch terminations concealed in calyces. **B.** *Leptodeira annulata annulata* (AMNH R-133340, right organ); a pronounced fork on field-everted organ expanded into this shape after softening in KOH and injection with petroleum jelly (shape is triangular, the heart-shaped appearance imparted by overhanging calyces at top). **C.** *Leptodeira maculata* (AMNH R-82150, right organ), showing extreme flattening and loss of terminal fork.

Diagnosis: A simple, unforked, sulcus spermaticus (*Imantodes* and some *Leptodeira*) or the sulcus terminus either reduced to a tiny terminal fork or greatly expanded distally without forking (other *Leptodeira*) sets off the mainly scansorial Imantodini from all other Dipsadinae except the terrestrial Mesoamerican–North American nightsnakes (*Hypsiglena* [including *Eridiphas*], *Pseudoleptodeira*), which also are recorded as having unforked sulci spermatici. Based on molecular data, the genera of nightsnakes form an unnamed clade that is consistent with morphological data (Cadle, 1984: fig. 1; Dowling and Jenner, 1987; Mulcahy, 2007: figs. 5, 7; Daza et al., 2009: fig. 3).

APPENDIX 2

Further Partitioning of *Rhadinaea* Cope, 1863: Resurrection of *Rhadinella* Smith, 1941

I monographed the old Copeian genus *Rhadinaea* some years ago (Myers, 1974). I had originally become interested in it as an undergraduate assistant, while identifying Costa Rican specimens brought by Prof. Archie Carr to the Florida State Museum collection. Local fieldwork in Florida on the endemic North American pine woods snake, *Rhadinaea flavilata*, solidified my interest (Myers, 1967). Many species proved to be very poorly known and some species were identifiable only by recourse to original descriptions. I assigned 47 species to "*Rhadinaea*" based on color patterns, external morphology, dentition, and hemipenes (Myers, 1974). These fell out into eight species groups, with an overall distribution between latitudes 35° N (Cape Hatteras) and 35° S (east-central Argentina). Unfortunately, monophyly of *Rhadinaea* could not be demonstrated and I have long since been aware that the genus must be partitioned, although this has been slow in coming. Aside from Cadle's (1984a, 1984b, 1984c, 1985) pioneering immunological comparisons, methods of molecular analysis have yet to be applied, although sequence data from a few species are finding their way into higher-level phylogenetic analyses of colubrids.

The species groups set up for *Rhadinaea* mostly seem to represent natural assemblages, which, as noted by Myers and Cadle (1994), "makes it easy to whittle away at the genus." Two species groups (*brevirostris* and *lateristriga*) were problematically included from the start and were the first to be removed. Cadle (1984b) showed that *brevirostris*-group species were immunologically more similar to "South American xenodontines" (i.e., Xenodontinae) than to "Central American xenodontines" (i.e., Dipsadinae). Myers and Cadle (1994) eventually resurrected Cope's genus *Taeniophallus* for the *brevirostris* group, which was further revised by Schargel et al. (2005) and placed in the new xenodontine tribe Echinantherini by Zaher et al. (2009: 144). Even so, the monophyly of *Taeniophallus* has not been corroborated.

The other group to go was the *lateristriga* group, characterized in part by a distinctive striped color pattern. However, in hemipenes and in the very long, disproportionately thick tail (Myers, 1974: fig. 5), the group was noted to share significant character states with the vividly ringed *Pliocercus*, leading to the statement that "it might be easier to show an ancestral-descendent

relationship [with *Pliocercus*] than to convincingly demonstrate [relationship] with the other species groups of *Rhadinaea*" (Myers, 1974: 230). Cadle (1984b: 28) also mentioned this as a case of interest after pointing out that immunological data suggested that "Central American *Rhadinaea* may be paraphyletic." Thus, I fully concurred when Savage and Crother (1989) resurrected *Urotheca* for the *lateristriga* group, but disagreed strongly (as a reviewer) that they also merged *Pliocercus* in the same genus. Myers and Cadle (1994: 3) later observed that "the evolutionary history of *Pliocercus* is linked via mimicry complexes with venomous coral snakes, and regarded *Pliocercus* and *Urotheca* sensu stricto as "monophyletic sister groups—each of which is characterized by synapomorphies of color pattern." More recently, Solórzano (2004: 541) independently called placement of *Pliocercus* in *Urotheca* questionable and requiring further review. Distinctive shared color patterns in assemblages of snakes provide synapomorphies that can be as useful in phylogenetic classification as in field identification.

A third assemblage now to consider is the *Rhadinaea godmani* group, which was thought "to contain the most primitive hemipenes and dentitional pattern to be found among living species of *Rhadinaea*" (Myers, 1974: 226). Special attention was given to configuration of the maxillary dentition, described as follows:

> The rear teeth are modified in two fundamentally different ways in *Rhadinaea.* The *godmani* group has what I consider the primitive arrangement. Approximately the last three to five teeth are noticeably enlarged and heavier than the others (fig. 2A); less commonly there are only two visibly enlarged teeth. The enlarged teeth lie on the same plane, none being set off to one side of the others (fig. lA). There is never a broad gap, or diastema, between any of the teeth and frequently there is no diastema at all. A very short diastema may be present, but it is just as likely to occur anterior to the antepenultimate tooth as in front of the penultimate, or there is often a gap in both places (fig. 2A).
>
> All the other species groups are characterized by a dental arrangement in which there are only two enlarged teeth (fig. 2B– C), the posteriormost of which is offset to the side (laterad) as shown in figure lB. A broad (fig. 2B) to short (fig. 2C) diastema is usually present, but not always. Addition or loss of prediastemal teeth in a species seems most often to be the cause of variability in the size of the diastema. The presence of a diastema presumably allows the posterior fangs to be more efficiently embedded in the prey, and there are probably counterbalancing selective forces for the diastema and the number of prediastemal teeth, as the latter serve the important function of holding the prey until the fangs can be used. I use the word "fang" in its common connotation of a large piercing tooth. The usually ungrooved fangs of [the mildly venomous] *Rhadinaea* seem to serve the same function as the grooved or tubular teeth for which some herpetologists reserve the word. (Myers, 1974: 28–29)

The main points drawn from dentitional variation in the *godmani* group was enlargement of the last several teeth and their arrangement in a straight line. Pondering and discussing the dentition of *Amnesteophis* in the present paper have caused me to change my judgment of polarity in these characters.

In natricine colubrids, maxillary teeth that increase in size posteriorly (without offset so far as I know) has been suggested as the generalized condition among semiaquatic species, with changes to an opisthoglyphous condition being correlated with terrestrialism (Malnate, 1960: 47, 65). I originally assumed that this not uncommon colubrid condition was primitive in Central American and South American "xenodontines." However, the posterior arrangement of offset fangs (usually separated by a diastema) is widespread and predominates among dipsadines and xenodontines, conceivably providing a synapomorphic condition for the combined groups. In having posterior teeth somewhat enlarged but set in straight lines, *Amnesteophis* seems to stand out among South American Xenodontinae, as do the "*Rhadinaea*" *godmani* group and genus *Trimetopon* among Middle American Dipsadinae. The straight-line dentitional patterns are not identical and are judged to be independent apomorphies.

The generic name *Rhadinella* is available and resurrected below for the *Rhadinaea godmani* group, which was shown to differ from the other groups in a complex of character states (e.g., table 3 in Myers, 1974), among which the configuration of posterior maxillary teeth provides an invariant synapomorphy.

Rhadinella Smith, 1941

Type Species: *Rhadinella schistosa* Smith (1941), by original designation and monotypy.

Definition and Diagnosis: See group definition in Myers (1974: 119). Separated from *Rhadinaea* and most other dipsadines by the straight-line arrangement of several enlarged posterior maxillary teeth (ultimate fang not offset). The maxillary dentition is similar in *Trimetopon*, a variable genus of diminutive snakes in lower Central America that differs from *Rhadinella* in lacking a basal nude pocket on the hemipenis (Myers, unpublished).

Content: Fifteen species: *Rhadinella anachoreta* (Smith and Campbell), new combination; *Rhadinella godmani* (Günther), new comb.; *Rhadinella hannsteini* (Stuart), new comb.; *Rhadinella hempsteadae* (Stuart and Bailey), new comb.; *Rhadinella kanalchutchan* (Mendelson III and Kirzirian), new comb.; *Rhadinella kinkelini* (Boettger), new comb.;[19] *Rhadinella lachrymans* (Cope), new comb.; *Rhadinella montecristi* (Mertens), new comb.; *Rhadinella pegosalyta* (McCranie), new comb.; *Rhadinella pilonaorum* (Stuart), new comb.; *Rhadinella posadasi* (Slevin), new comb.; *Rhadinella rogerromani* (Köhler and McCranie), new comb.; *Rhadinella schistosa* Smith; *Rhadinella serperaster* (Cope), new comb.; *Rhadinella tolpanorum* (Holm and Cruz D.), new comb.

Remarks

Nearly 150 years ago, "Master Naturalist" Edward Drinker Cope penned a line that is still relevant: *The genus here called* Rhadinaea, *has afforded me considerable perplexity*. Today we recognize that the perplexity applies to:

an artificial (nonmonophyletic) assemblage of small serpents widely distributed on the New

[19] Including *Rhadinaea pinicola* Mertens; see Köhler and McCranie (1999).

> World mainland … The *Rhadinaea*-like snakes are mainly tropical species of similar habits and habitus—terrestrial in forest, usually diurnal (always with round pupils), small and slender, often striped, and with a generalized colubrid morphology. (Schargel et al., 2005: 12)

There doubtless are morphological synapomorphies still to be discovered, but attention to comparative anatomy has been largely eclipsed by the explosive rise of molecular biology. Considering the rapid and impressive advances in molecular systematics, one hopes that relationships eventually will be resolved within Dipsadinae generally and among the species groups of "*Rhadinaea*" specifically. Broad taxon sampling will be important, although accumulating sufficient tissue samples is likely to be the major problem; many *Rhadinaea* are rarely collected and some species may well be on the verge of extinction if major prey (e.g., small frogs) is disappearing. So far as I have noticed in recent literature, sequence data have been provided only for two species currently in *Rhadinaea—R. flavilata (flavilata* group) and *R. fulvivittis* (*taeniata* group).

The relationships of the *Rhadinaea vermiculaticeps* group is, of course, key to the nomenclatural problem, since *R. vermiculaticeps* is the generic type species. I originally included in this group the similar species *sargenti*, *vermiculaticeps*, and *pulveriventris*, but the hemipenis of the last species was then unknown (Myers, 1974: 158–159). Placement of *pulveriventris* now can be questioned, since its hemipenis lacks the unusual group character of "virtually straight spines" (unpublished data based on AMNH R-114327). However, as earlier emphasized (Myers, 1974: 230, figs. 30G, 39), "the hemipenes of *vermiculaticeps* and *sargenti* bear remarkable resemblance to the tiny organ of *Rhadinaea schistosa* … even to the presence of virtually straight spines that were once thought to characterize the monotypic genus *Rhadinella*." I suggested that the northern *schistosa* and the southern *vermiculaticeps* group might have descended "from a section of the old *godmani* group once widely distributed in Middle America, but now extinct or modified beyond recognition," but, considering dentitional differences, hemipenial similarities could as well be due to convergent evolution. Cope's "perplexity" lives on.

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