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An Enigmatic New Snake from the Peruvian Andes, with Notes on the Xenodontini (Colubridae: Xenodontinae)

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ABSTRACT

Liophis problematicus, new species, is based on a specimen from 1520 m elevation on the Amazonian side of the Andes in the Department of Puno, extreme southeastern Peru. It is a very small snake (adult male 275 mm total length), with a bilobed hemipenis having nude apical discs, a condition that defines a probably monophyletic group (tribe Xenodontini) of at least six genera of Neotropical xenodontine colubrids. Beyond this, the relationships of the new species are uncertain, but a pragmatic assignment to *Liophis* (s.l.) scarcely violates the definition of this highly variable, possibly nonmonophyletic genus. Incidental notes are provided on the hemipenis, coloration, and behavior of *Liophis williamsi*, a small snake of Venezuelan cloud forest.

It is pointed out in discussion that hemipenial variation among the Xenodontini is much greater than has been indicated in the literature, and that the tribe is based essentially on a single character—the paired apical discs, which may have been lost

in some populations but which are accepted as a defining synapomorphy pending further study.

Defensive neck flattening or hood display is widespread in the Xenodontini, having been recorded for at least five of the six genera currently assigned, and seems to provide a behavioral synapomorphy that corroborates the validity of the group. North American snakes of the genus *Heterodon* also flatten their necks and have been compared morphologically with some Xenodontini; a relationship between *Xenodon* and South American *Hydrodynastes*, another genus of neck spreaders, also has been suggested. *Heterodon* and *Hydrodynastes* have relatively primitive hemipenes and cannot be included in the Xenodontini. The hypothesis that one genus or the other is a sister group of the Xenodontini deserves to be tested by morphological criteria—although this seems to be strongly contraindicated by immunological distance data. Neck spreading therefore may have evolved several times within the subfamily Xenodontinae.

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INTRODUCTION

The main purpose of this paper is to describe a new xenodontine colubrid snake from the Andes of southern Peru, and secondarily to call attention to a behavioral trait that seems to offer additional support for the tribe Xenodontini. The new species is quite small (fig. 1 is life size), and I know it only from a single specimen in the Field Museum of Natural History.

At first examination, the color pattern and small adult size of the new snake reminded me of a few species of *Rhadinaea*. Hemipenial morphology, however, indicates that it is allied with some member of a group or tribe of Neotropical genera that includes *Erythrolamprus*, *Liophis*, *Lystrophis*, *Umbrivaga*, *Waglerophis*, and *Xenodon*. But the new species does not readily fit in any of these genera, which for the most part appear to represent well-defined monophyletic units of ecologically diverse snakes.

Liophis, however, is not defined by synapomorphy and accommodates snakes that are quite divergent in color pattern and morphology. Therefore, inasmuch as this genus is of questionable monophyly and in order to avoid creating or resurrecting a new generic name at this time, a provisional assignment to *Liophis* is warranted. The specific name derives from the Greek *problematicos* (problematical), an adjective here used in reference to uncertain kinship.

***Liophis problematicus*, new species**

Figures 1–6

HOLOTYPE: FMNH 64733, an adult male obtained by Hilda H. Heller in the period November 22–December 20, 1950, at 1520 m above sea level at San Juan, Tambopata [Río], Sandia [Province of], Department of Puno, Peru. I assume that “San Juan” is the same as San Juan del Oro, a settlement situated about 30 km ENE of the town of Sandia, on the west bank of the Río Tambopata—at 14°13'S, 69°10'W.²

DIAGNOSIS: Among those snakes characterized by a bilobed spiny hemipenis with

nude apical discs (Xenodontini), *Liophis problematicus* can be distinguished by the combination of small size (<300 mm total length), low number of ventrals and subcaudals (133 + 36 in one male), and color pattern—including pale labial markings, pale nuchal spots, and a striped body (figs. 1–3).

DISTRIBUTION: *Liophis problematicus* is known only from its type locality at 1520 m elevation on the Amazonian side of the Andes (drainage of Río Madre de Dios)—about 150 km north of Lake Titicaca in the border region between Peru and Bolivia.

DESCRIPTION

The holotype (fig. 1) is an adult male as determined by enlarged and convoluted vasa deferentia, enlarged segments of the kidney tubules, and hardening of the hemipenial spines. The specimen is in fair condition except for a slightly misshapen mouth border in the rostral region and front of the lower jaw, owing to desiccation.

PROPORTIONS AND SCUTELLATION: A small, slender, short-tailed snake 275 mm total length, 51 mm tail length (tail 18.5% of total). Body higher than wide (roughly 6.5 mm × 5.5 mm), rounded ventrolaterally. Head slightly wider than body; greatest head width (parietal region) 6.5 mm, head length 11.3 mm from tip of snout to level of end of mandibles. Diameter of eye greater than distance



Fig. 1. *Liophis problematicus*, new species. The holotype (FMNH 64733), shown at natural size.

² From *Mapa Físico Político del Perú* (1:1,000,000). Ministerio de Guerra del Perú, Instituto Geográfico Nacional, 1982 (2nd ed.).

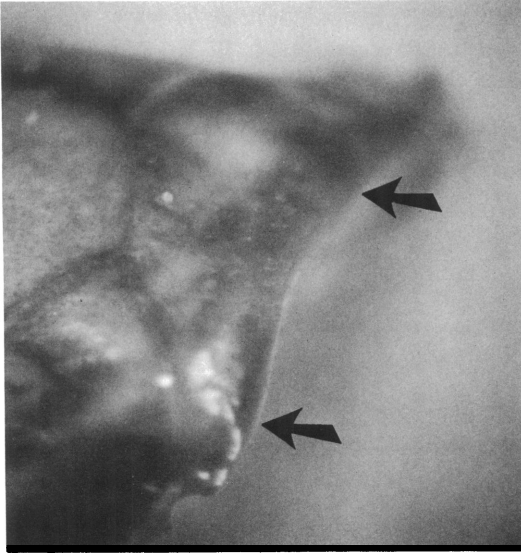


Fig. 2. Dorsolateral view of snout of *Liophis problematicus*, showing transverse keel or crease on rostrum of holotype, $\times 40$. Uppermost arrow is at midpoint of anterior edge of rostral plate. The keel may be an artifact (see fn. 3).

from its anterior edge to anterior edge of naris, extending 1.5 times into length of snout. Dorsal scales smooth, lacking apical pits and anal ridges, in 19-17-17 rows; scale-row reduction from 19 to 17 rows by fusion of lateral rows 3 + 4, on both sides, at level of 62nd ventral. Two preventrals (undivided gulars), 133 ventrals, divided anal plate, 36 pairs of subcaudals.

Rostral plate visible from above, about 2.5 times wider than high, showing a blunt horizontal keel (fig. 2) that may be an artifact.³ Paired internasals, each wider than long, about three-fourths as long as prefrontals. Paired prefrontals, each wider than long, each in contact with its mate and with frontal,

³ It seems likely that the blunt rostral keel is an artificial fold or crease, owing to the front of the snout being somewhat dried and misshapen and the rostral plate being partially separated from the premaxillary bone. Rostral modification in very small snakes most often is an adaptation for semifossorial habits, but usually there are correlated specializations, including modified head shields, reduced eyes, and a pointed head that is small relative to the neck. *Liophis problematicus*, however, has a normally proportioned head and normal head plates expected of an aboveground forager.

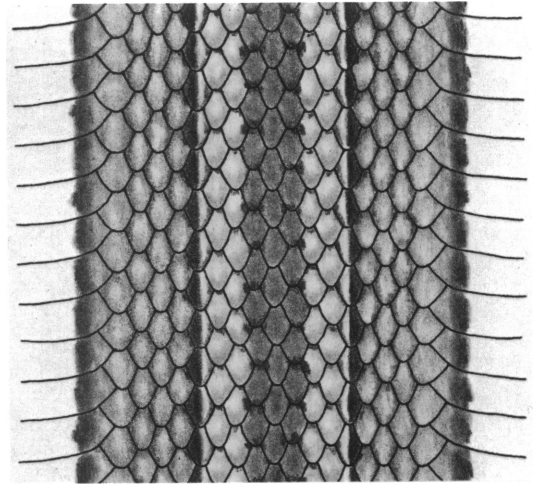


Fig. 3. Midbody color pattern of *Liophis problematicus*, drawn from holotype on generalized scale pattern.

supraocular, preocular, loreal, nasal, and internasal (left prefrontal in contact with both left and right internasals). Frontal hexagonal (with small anterior apex), 2.0 times longer than its greatest width, 1.5 times longer than distance from its anterior edge to tip of snout. Supraoculars posteriorly more than one-half of frontal width, narrowed anteriorly. Parietals about 1.7 times longer than broad; interparietal suture shorter than length of snout, about 60 percent length of frontal plate. Large nasal plate, in contact with first two supralabials, grooved apparently above and below naris; small loreal plate ovoid, separated from eye by the single high preocular (no subpreocular); two postoculars, the upper twice the size of lower. One large anterior temporal and upper and lower posterior temporals, between labials 5-7. Supralabials 7, second touching loreal, third and fourth bordering orbit. Infralabials 8, first pair in contact behind mental, 1-4 touching an anterior genial, 4-5 touching a posterior genial. Genials well developed; anterior pair slightly shorter than posterior pair but with longer intergenial suture. Inconspicuous tubercles (presumed sensory organs) sparsely present on head plates.

COLOR PATTERN: Body light brown, with darker middorsal brown (gray) streak and lateral and ventrolateral blackish brown lines (fig. 3), as follows: (1) The middorsal streak is medium brown (gray after loss of stratum

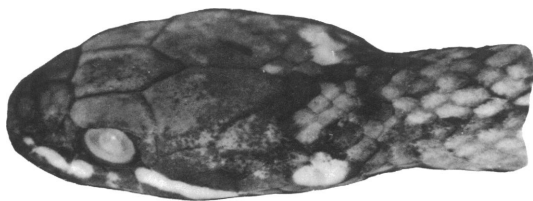


Fig. 4. Head of *Liophis problematicus* (holotype), approximately $\times 3.9$.

corneum) and extends from the nape to the end of the tail; this dark streak is five scales wide on the neck, three scales wide on the greater length of the body, and narrows gradually on the tail. (2) The dark lateral line extends from the rear of the head to the tip of the tail, becoming darker (brown to blackish brown), more nearly continuous (broken at anterior end), and widening perceptibly from anterior to posterior. The lateral line lies on only the lower edge of scale row 6 anteriorly, then drops (because of scale row reduction) onto row 5 before midbody; it covers the lower half of row 5 at midbody, nearly all of row 5 toward the end of the body, and continues conspicuously along the side of the tail, where it narrows only toward the end. (3) Brown pigmentation extends from the lower sides onto the ventral and subcaudal plates before ending abruptly at a blackish brown ventrolateral line that extends from the head to the end of the tail. The median three-fifths of the ventral surface is immaculate white in preservative, and sharply set off by the dark ventrolateral line on either side.

The head is brown (gray under stratum corneum) above, irregularly blotched with darker brown, and set off posteriorly by several white markings (fig. 4) as follows: (1) A small white spot immediately behind the interparietal suture occupies less than half the area of the first dorsal scale. (2) A pair of obliquely arranged white nape spots lie one scale behind the parietal plates and are separated by the width of the brown vertebral scale row; each of the large nape spots occupies all or parts of 6–7 scales. (3) A rounded white spot, occupying parts of three scales, lies on each side of the neck immediately posterior to the last supralabial and narrowly separated from the nape spot above.



Fig. 5. Left maxilla of *Liophis problematicus* (holotype), $\times 10$.

There is no dark stripe through the eye. The supralabials bear three conspicuous white markings that are broadly edged in dark brown, as follows: There is a short horizontal white line across labials 1–3; a small subocular white area on labial 4; and a bold postocular white stripe that originates on the lower postocular and extends obliquely across labials 5, 6, and lower corner of 7 to the edge of the mouth, where the line matches up with a white line on the anterior part of the last (8th) infralabial. The underside of the head is basically white, with brown blotches on the mental and on each of the infralabials and genials and on many of the gular scales.

DENTITION: There are 15 (right side) or 16 (left) recurved subequal maxillary teeth, which are followed by a distinct diastema and two ungrooved fangs that are about $1\frac{1}{2}$ times larger than the prediastemal teeth (fig. 5). The ultimate prediastemal socket on each side lies anterior to the front edge of the ectopterygoid process. The fangs have a rounded anterior surface, a flattened knifelike posterior edge, and are somewhat laterally compressed at the tips; the ultimate fang is offset slightly laterad. The numerous palatine-pterygoid teeth are not readily counted in situ. There are at least 26 teeth on the left dentary.

VERTEBRAE: As examined ventrally with the internal organs displaced, the hypapophyses of the cervical vertebrae appear to have a long ventral edge (i.e., broad in profile, not spine-like), and the m. transversohypapophyseus is present. Posteriorly, the hypapophyses are reduced to a lower, thick hemal keel and the m. transversohypapophyseus is absent (examined at level of ventrals 115–116 in area of kidney overlap).

HEMIPENIS: The right retracted organ extends in situ to the end of subcaudal 7, being bifurcated from about the middle of subcaudal 7 and with the two slips of the major retractor muscle merging toward the base of subcaudal 8 (combined division of hemipenis tip and muscle only the length of about one

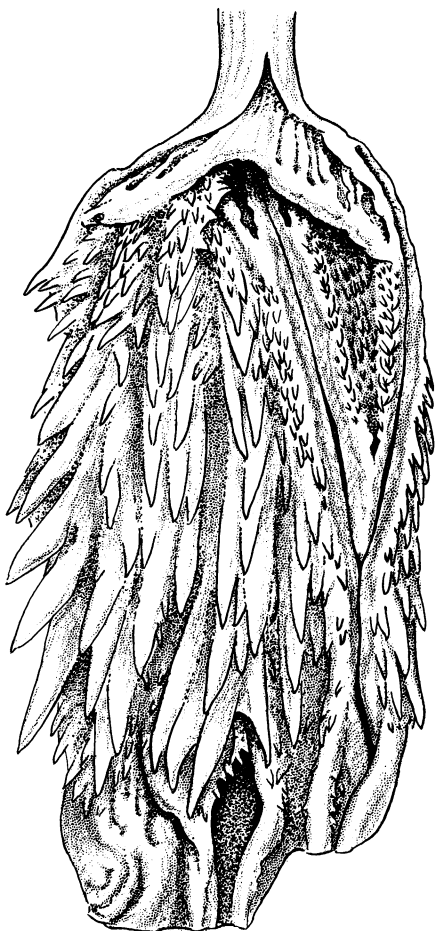


Fig. 6. Hemipenis of *Liophis problematicus* (holotype). Unverted right organ opened mid-ventrally, $\times 10$. The proximal free edge of the apical nude area overhangs and conceals small spines that would surround the edge of a presumably flattened apical disc if the hemipenis were everted; a second disc is concealed in the unopened dorsal lobe (see fig. 7 for an idea of the probable configuration when everted).

subcaudal plate). The major retractor muscle originates at the level of subcaudal 27. The right hemipenis was opened along its mid-ventral surface and then removed and pinned out for detailed study and illustration (fig. 6).

The small lobes constitute only about the distal tenth of the retracted hemipenis. The tip of the opened ventral lobe comprises naked distensible tissue that is set off by a free proximal edge. (This nude area and the one concealed in the unopened dorsal lobe presumably form flattened apical discs when the

hemipenis is everted.) The sulcus spermaticus lies on the lateral wall and bifurcates slightly below the middle of the hemipenis, with the branches extending to the tips of the lobes and maintaining well-defined walls even on the apical discs; the branches of the sulcus have a centrifugal orientation, lying on opposite sides of the distal lobes (i.e., in the uneverted organ in fig. 6, one branch lies on the dorsal wall of the dorsal lobe and the other branch is on the ventral wall of the ventral lobe—a configuration that can be determined by manipulation during dissection as well as by inspection of everted organs [discussion in Myers and Campbell, 1981, pp. 16–17]). A basal naked pocket is situated dorsally on the proximal one-fourth of the hemipenis (in fig. 6, the distal part of this pocket is concealed by the overhanging spines). Approximately the basal 15 percent of the organ is nude, lacking spines or spinules. The rest of the organ is densely spinose, with several dozen medium-size spines on the midsection giving way to numerous small spines along the branches of the sulcus spermaticus and up to the edges of the apical discs (in fig. 6, small spines along the edge of the visible disc are concealed under its overhang).

DISCUSSION

HISTORICAL SUMMARY: Assuming that I have correctly interpreted the morphology of its uneverted hemipenis,⁴ the relationships of

⁴ Morphological misinterpretations of both uneverted and everted hemipenes are commonplace in the literature. The following examples are relevant: Thompson (1913, p. 79) mistook as apical discs the distal nude areas on the sulcate sides of the lobes of an uneverted organ in *Oxyrhopus trigeminus* (lobes distally calyculate on asulcate sides, e.g., in AMNH 104667), and erected the invalid genus *Erythroxyrhopus* largely on that basis. And Wellman (1963, p. 289) incorrectly described the everted organs of *Conopsis* as being moderately calyculate with tiny apical discs on the short lobes. The spinose hemipenis of *Conopsis* has neither calyces nor discs, being conspicuously flounced distally (flounces with spinulate to papillate edges) and having a centrolineal sulcus spermaticus. The tips of most *Conopsis* organs I examined are not quite everted (AMNH 66337, 123917, 126423), but, in the one illustrated by Wellman (UMMZ 82650), the apex of each short bilobation has at the terminus of the sulcus a hard, nearly nude (slightly papillate) bump or projection—the mistaken disc.

Liophis problematicus are most likely to be sought among the xenodontine genera that possess bilobed spiny hemipenes with nude apical discs. Cope (1894, pp. 840, 842; 1895, pp. 200–201, 207), although understandably misinterpreting some of his pioneering dissections, recognized two assemblages (“disciferi”) characterized by the apical discs. But he separated these groups widely, placing them in the 1895 paper as subfamilies of separate families and superfamilies⁵—a separation mainly based on whether the posterior maxillary fangs were grooved or not. Dunn (1928, p. 21) tried to bring the generic nomenclature up to date, and gathered Cope’s disciferi together as a presumably natural subgroup of “Ophiinae” (=Xenodontinae) characterized by a “disked, double” hemipenis.⁶ H. G. Dowling has advocated tribal status for this and other assemblages, and nine modern generic names representing Dunn’s “disked, double” group were listed under the tribe Xenodontini in Dowling and Duellman (“1974–1978” [1978], p. 112a.3). Since then, Dixon (1980) has relegated three of the names to the synonymy of *Liophis* (*Dromicus*, *Leimadophis*, *Lygophis*), thus reducing the group to the following six genera:

Erythrolamprus
Liophis
Lystrophis
Umbrivaga
Waglerophis
Xenodon

⁵ Aglyphodonta, Colubridae, Xenodontinae; and Glyphodonta, Dipsadidae, Erythrolamprinae.

⁶ Dunn (loc. cit.) removed Thompson’s *Erythroxyrhopus* from this assemblage (see fn. 4), but he mistakenly added *Philodryas* and *Siphlophis*. As explained by Dowling (1969, p. 5), addition of *Philodryas* probably resulted from the nomenclatural confusion in Cope’s work. Dunn’s placement of *Siphlophis*, however, is puzzling because he indicated (by the suffix “D”) that it was based on his own examination of the hemipenis. It seems most likely that Dunn would have looked at the relatively common and widespread type species of *Siphlophis* (*Lycodon audax* = *S. cervinus*), which clearly has the hemipenial lobes apically calyculate (e.g., in AMNH 116342, unverted) rather than disced. Conceivably he might have seen a partially everted hemipenis, in which case the distal calyces might not be visible and the lobes would appear short.

I think the above genera may well form a monophyletic group that can usefully be given tribal status. But it should be pointed out that the group is recognized mainly by hemipenial resemblance, and that some of the characters which account for this resemblance are probably plesiomorphic for colubrids generally (e.g., bilobed hemipenis, bifurcated sulcus spermaticus, spines present); a few features not present (calyces, capitulation) might be symplesiomorphic for most Xenodontinae but secondarily absent in the Xenodontini, although synapomorphies of loss are especially difficult to confirm.

There has been no adequate comparative study of hemipenial variation among the genera of this group, or even among the species of a single genus. And yet the variation is considerable: The apical discs range from small to large relative to the size of the hemipenis; the branches of the sulci spermatici vary in orientation from centrolinal to centrifugal; the base of the organ goes from squat to fairly long; and the lobes, although usually very short, may be very slender and much longer than the base. A particular problem in recognizing the Xenodontini is that the defining tribal character—the apical discs—appears to have been lost in some populations of *Xenodon*, the type genus (Myers, unpublished data!).

With the above reservations and pending additional study, the hemipenial apical discs provide a likely synapomorphy on which the hypothesis of monophyly of the Xenodontini is accepted for present purposes. There may also be a behavioral synapomorphy (fig. 8 and accompanying text). Cadle’s immunological data from 13 species representing five of the six genera were consistent with the hemipenial synapomorphy and he regarded the group as a clade, mentioning that his data were insufficient for addressing questions of intragroup relationships (Cadle, 1984a, p. 17).

The above summary skips over various attempts to relate one or more of the genera with North American *Heterodon*, a view that was summarized and further supported by Underwood (1967, pp. 100–103), who pointed out, however, that one such claim had been based on “slender and partly faulty evidence” and that there are discrepancies among the anatomical accounts of several writers. In

common with the times and with other authors whom he cited, Underwood appeared to attach no taxonomic importance to whether characters are primitive or derived, giving more weight, for example, to the symple-siomorphic condition of "divided hemipenis" than to the unusual apical discs (op. cit., pp. 102, 148). Neill (1964) added the South American *Dugandia* and *Cyclagras*—monotypic genera now subsumed within *Hydrodynastes* (see Dowling and Gibson, 1970)—as possible relatives of *Xenodon*, based mainly on the shared presence of a bifurcate sulcus spermaticus and distensible hood (Neill's primary objective was dissociating one species from an erroneous placement in the Colubrinae).

If the hemipenial apical discs truly define the Xenodontini as a monophyletic group, then *Heterodon* and *Hydrodynastes* clearly cannot be included because they have relatively primitive hemipenes. Nonetheless, anatomical similarities, such as claimed for *Heterodon* and some of the Xenodontini, should be reevaluated in the context of a synapomorphy scheme in order to test the possibility that *Heterodon* (or *Hydrodynastes*) + Xenodontini form a larger monophyletic group. If anatomical evidence of a sister-group relationship were found, then certain behavioral resemblances might acquire new meaning, as mentioned at the end of this paper (under A Behavioral Synapomorphy). Cadle's immunological data, however, predict that such a close relationship will *not* be found; *Hydrodynastes* seems much closer to several other South American lineages than to the Xenodontini (Cadle, 1984a, p. 12), whereas the enigmatic *Heterodon* "seems far removed from all South American xenodontines" (Cadle, 1984c, p. 643).

COMPARISONS: Externally, *Liophis problematicus* is quite different from its presumptive intragroup relatives, which are mostly much larger snakes. The species of *Erythrolamprus* are brightly ringed coral snake mimics, whereas the usually crossbanded, heavy-bodied *Xenodon* and *Waglerophis* resemble terrestrial vipers. The species of *Lystrophis* are crossbanded or blotched and have an up-turned transversely keeled rostrum that is supported above by a longitudinal median keel. *Umbrivaga* is characterized by a low

number of subcaudals as is *Liophis problematicus*, and one species is as small as *problematicus*; however, the species of *Umbrivaga* have stripes confined posteriorly on body and tail, with spots or bands anteriorly on the body, and pale supralabials. The preceding genera also differ from *L. problematicus* in various kinds of maxillary specialization.

Some of the characters alluded to above (as well as characters not mentioned) are doubtlessly synapomorphic, and I find no grounds for assigning the new snake to any of the five considered genera. This leaves *Liophis* (sensu Dixon), which Dixon (1980, p. 26) recognized as the "most generalized genus of the group in its osteology, external morphology, habitat, and food preferences." As now constituted, *Liophis* is extraordinarily diverse: The species range in habitus from slender to relatively robust; adult total length varies from small (e.g., <500 mm in *L. williamsi*) to large (e.g., >1 m in *L. miliaris*); the tail is short to long (tail/total length = 0.135–0.310 fide Dixon); color patterns include unicolor, speckled, banded, and several distinctive types of striping, including combined patterns such as anterior blotches and posterior stripes. The rather extreme diversity raises a suspicion that *Liophis* may be polyphyletic.⁷ Most of the dentitional and other osteological traits used by Dixon to distinguish *Liophis* from related genera seem to be plesiomorphic, and it is perhaps the one genus of the group that lacks obvious synapomorphies.

Consequently there is nothing in Dixon's (1980, p. 22) generic description that logically prevents *problematicus* from being assigned to *Liophis* (excluding from consideration a few unexamined skull characters). Although *problematicus* becomes one of the smallest species of *Liophis* and has slightly fewer sub-

⁷ I suspect that the situation with *Liophis* may prove similar to that of another large assemblage of Neotropical snakes—*Rhadinaea*—for which the last reviser (Myers, 1974) was reasonably able to demonstrate the existence of eight natural (monophyletic) species groups but could express only a degree of dubious faith that they were all congeneric. Indeed, faith was not enough. New as well as reinterpreted morphological evidence (Myers, unpublished), and supportive albumin immunology (Cadle, 1984b), will necessitate a partitioning of *Rhadinaea*.

caudals (36 vs. 38–106) than recorded by Dixon (1980, p. 22), only the questionable rostral keel might add a structural character not already present in the genus (but see fn. 3). All things considered, the allocation of *problematicus* to *Liophis* (s.l.) seems to me the best taxonomic solution at this time. It would be reassuring to identify some apparently closely related congener but I am unable to do so. Aspects of the color pattern of *problematicus* are distinctive among *Liophis*, few of which show any tendency toward pale nape spots or pale labial markings. The head pattern of *Liophis problematicus* is more similar to some species of *Rhadinaea* (e.g., compare fig. 3 with Myers, 1974, fig. 26) than to any *Liophis*. Most species of *Liophis* have the upper lip basically pale, although some have dusky labials owing to a suffusion of melanophores; only a few species have dark supralabials with definite pale markings, which usually take the form of a horizontal stripe or line, in contrast to the oblique markings in *problematicus*. One such species characterized by a white labial line is *Liophis williamsi*, which, like *Liophis problematicus*, is a small snake that might also be (and has been) confused with *Rhadinaea*. Even though it is not closely related to *L. problematicus*, so little is known about *L. williamsi* that I take this opportunity to make available the following data.

NOTES ON *LIOPHIS WILLIAMSI*

This species was described by Roze (1958) as *Urotheca williamsi* on the basis of four specimens collected in 1929 and 1949, in montane cloud forest of the Cordillera de la Costa, northern Venezuela. Roze misinterpreted the structure of the hemipenis, which he thought was apically calyculate. I pointed out the fact of the misinterpretation, without giving details, in order to remove *williamsi* from consideration in the *Rhadinaea-Urotheca* complex (Myers, 1974, p. 21). Dixon (1980, pp. 17, 25; 1983) later associated the name *williamsi* with *Liophis*. Cadle (1984a) was able to obtain a sample of serum albumin and included the species in his study of immunological distances among South American xenodontines.

I have seen the holotype, and four addi-

tional specimens not available to Roze, including two in the collection of the University of Michigan Museum of Zoology and two at the American Museum. Especially significant is AMNH 117671 from Rancho Grande, which has an everted hemipenis. In addition, notes on another (living) specimen from Rancho Grande were provided by the late Scott J. Maness (in litt., Dec. 2, 1974).⁸

HEMIPENIS: The left uneverted organ of UMMZ 124221 extends in situ to the end of subcaudal 8, being bifurcated from the base of subcaudal 7 and with the two slips of the major retractor muscle merging at the end of subcaudal 9; the major retractor muscle originates at the level of subcaudal 24. The sulcus spermaticus proximally lies on the lateral wall and divides below the middle of the hemipenis, with the branches ending apically in nude areas of longitudinally folded tissue. (Dixon [1983, p. 128] unintentionally implied that the hemipenis is nonlobed when he described it as having "a" smooth apical disc.)

That the distal nude areas of the retracted hemipenis do form a slightly depressed apical disc on each lobe is proved by an everted organ of AMNH 117671 (fig. 7). The sulcus spermaticus has an essentially centrifugal orientation, which is to say that the branches of the sulcus diverge widely and enter onto the apical discs almost from opposite sides of the hemipenis. As is typical of bilobed hemipenes with nude apical discs, that of *Liophis williamsi* is noncapitate and is acalyculate (contra Roze), being ornamented solely with spines.

COLOR IN LIFE: According to Maness, a living adult, about 495 mm in total length, had a clear whitish cream line (on a dark upper lip) extending under the eye and posteriorly for a distance of about 1.2 cm onto the neck; eye with a light orange iris and a round pupil; tongue tips black. Dorsum light brownish olive, with yellowish skin between the scales; four black lines starting posteriorly on body, each about 1½ scales wide and the two dorsal lines merging to one on tail. Venter anteriorly

⁸ Mr. Maness was at that time a Peace Corps Volunteer in Venezuela. He and a companion died tragically in 1981, while fighting a fire in Florida scrubland.

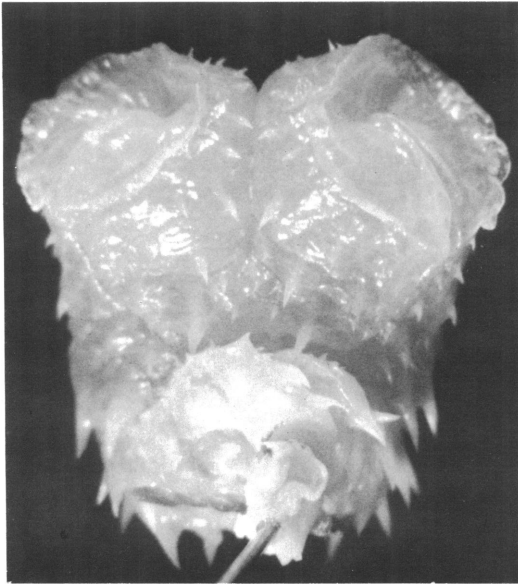


Fig. 7. Hemipenis of *Liophis williamsi* (AMNH 117671). Everted right organ, sulcate side, $\times 6.8$.

light creamy yellow with indistinct small black or grayish spots or dots (venter apparently becoming gray posteriorly [Maness's notes not explicit]), and uniform bright yellow under tail as in sympatric *Rhadinaea multilineata*.

Brief color notes accompanying AMNH 117671 indicate a similarly colored specimen with white labial line, yellowish skin between scales, and venter "grey-yellowish." A third specimen (UMMZ 124224) was said by Test et al. (1966, p. 44) to have had the belly "gray with pinkish flush and the interstripe areas posteriorly a pale brown"; I would add that the specimen mentioned by Test et al. is a juvenile of 210 mm total length and that (in preservative) the black head color extends for a distance of five scales onto the nape and there are poorly defined black crossbars on the anterior one-third of the body—both the head-cap and crossbars being pattern features that are absent or inconspicuous on adults. See Dixon (1983) for more detailed description of pattern in preserved specimens.

BEHAVIOR: Test et al. indicated that *williamsi* is a rare snake at Rancho Grande; they found two dead on a road and a third one under dead leaves on a trail. But it is diurnal, or at least partly so, and not a nocturnal species as they suspected. AMNH 117671

was found alive on a road at about 10 a.m., and the live specimen described by Maness was found resting in a small patch of sunlight at midday (12 p.m.).

Maness noted that one was very passive, never attempting to bite and that the cloacal secretion had a "not so unpleasant odor." He also observed that it was "a very strong constrictor, when wrapped around a finger or thumb, cutting off circulation within minutes." Maness wrote that although this snake was passive, "on occasion it would flatten the neck some 8 cm in length from behind the head, as seen in *Leimadophis*⁹ [and] *Umbri-vaga*." Such neck spreading would prominently display the yellow skin between the scales of *L. williamsi*.

The defensive neck spreading just described for *Liophis williamsi* is of apparent significance in the suprageneric scheme of relationships, as discussed below.

A BEHAVIORAL SYNAPOMORPHY

Horizontal (dorsoventral) neck flattening behavior (fig. 8) is widespread in the Xenodontini. The display is elicited in newly captured snakes that have been restrained from escaping but which are allowed some freedom of movement while being prodded or otherwise annoyed (beware that there may be no correlation between this behavior and presence or absence of defensive biting). *Liophis williamsi*, *L. zweifeli*, and *Umbri-vaga* [*mertensi*] are referred to above; Vanzolini et al. (1980, p. 60) described defensive neck spreading for the monotypic genus *Waglerophis*; and my own fieldnotes record the behavior for species as diverse as *Erythrolamprus bizona*, *Liophis epinephelus*, and *Xenodon rabdocephalus*. Other species, especially of *Liophis* (s.l.), can be added from scattered literature references; J. R. Dixon (in litt., Feb. 12, 1986) has witnessed the behavior in the eight species of *Liophis* that he has examined alive. *Lystrophis* is the only genus of Xenodontini for which I am unaware of an observation of neck flattening explicitly,

⁹ Maness probably was referring to *Leimadophis* (= *Liophis*) *zweifeli*, which occurs at Rancho Grande. Test et al. (1966, p. 42) described the neck flattening behavior of this species.

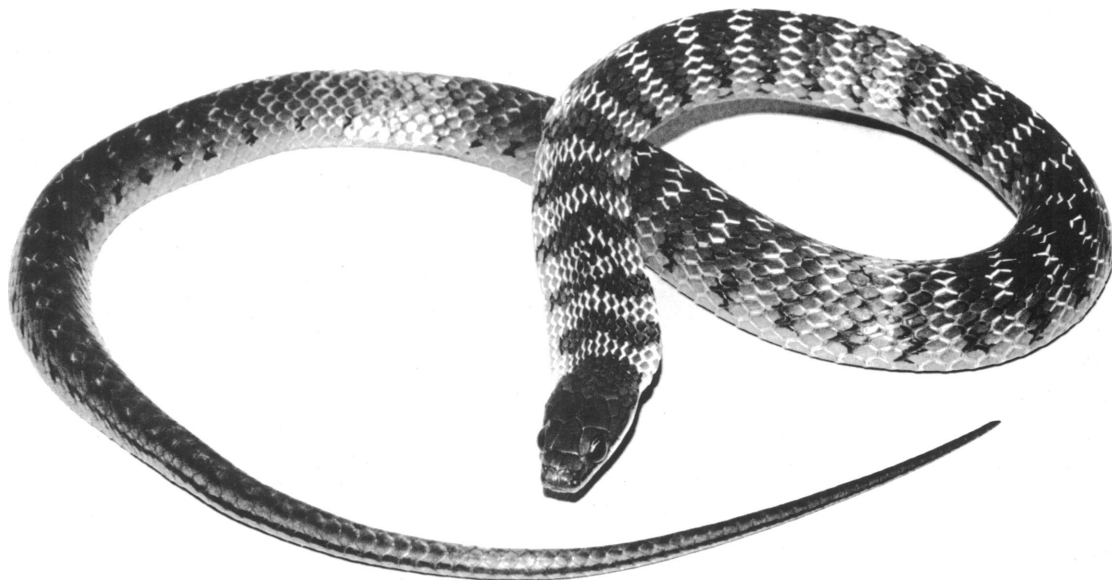


Fig. 8. Neck flattening by *Liophis epinephelus* (El Valle de Antón, Panama), a defensive threat display that is widespread in the Xenodontini. This individual also has inflated the fore part of its body just behind the horizontally spread neck; it made no attempt to bite, eventually abandoning the display and hiding its head under its body.

although the whole body can be flattened in an evidently complex behavioral repertoire (Greene, 1973, p. 151).

Horizontal neck spreading, or "hood" display, has evolved more than once and is taxonomically and geographically widespread among snakes, as has long been recognized (Noble, 1921). Strictly defined, however, this behavior is relatively less common among snakes generally than was suggested by Carpenter (*in* Carpenter and Ferguson, 1977). Basing his conclusions on an extensive search of the literature, which is difficult to analyze, Carpenter coded neck-flattening (hood) behavior in species representing 35 of 94 listed genera of Colubridae (containing roughly 300 genera). But this was an inappropriate designation for some snakes, such as those that properly were also coded for flattening the entire trunk (e.g., the xenodontine genus *Ninia* and New World natricines of the genera *Clonophis*, *Nerodia* (as *Natrix*), *Storeria*, *Thamnophis*, and *Tropidoclonion*).

In any event, neck flattening is an uncommon behavior among the nearly 100 genera

constituting the colubrid subfamily Xenodontinae, with notable exceptions including *Heterodon*, *Hydrodynastes*, and the tribe Xenodontini. Therefore, in addition to hemipenial morphology and albumin correspondence, neck flattening appears to provide a behavioral trait that is consistent with recognition of the Xenodontini as a monophyletic group—even if the behavior should prove to be lacking in some species, as might be expected in such a diverse assemblage of snakes. For example, Brazilian *Erythrolamprus aesculapii* possibly does not display according to P. E. Vanzolini (verbal commun.), who pointedly emphasized, however, that prudent collectors do not give much opportunity for freedom of expression to newly captured *corals* and their mimics unless they are specifically looking for defensive behavior.¹⁰ I noted that a Panamanian *E. bizona*

¹⁰ Added in press: Vanzolini subsequently wrote (*in litt.*, March 17, 1986) that, "I have spent the last half hour teasing an *Erythrolamprus* [*a.*] *venustissimus*. A healthy and cooperative snake, very willing to strike. No flattening."

would "conspicuously flatten about a third of its neck when disturbed" (fieldnotes for Univ. Kansas 110693); R. G. Zweifel similarly observed another Panamanian *bizona* that "flattened out the neck somewhat in the fashion of *Heterodon*" (fieldnotes for AMNH 90019); H. G. Greene (in litt., Jan. 22, 1986) saw neck flattening in one *E. bizona* and three *E. mimus* in Costa Rica and described a photograph (by R. W. McDiarmid) of a Costa Rican *E. mimus* that was simultaneously displaying a coiled tail while *elevating* a flattened neck. Thus, observations on Central American *bizona* and *mimus* suggest that possible absence of such behavior in other *Erythrolamprus* could be due to evolutionary loss. Attrition of synapomorphies during adaptive radiation is a major hindrance in phylogenetic analysis, and the problem becomes more serious when homoplasy is involved.

Although I suggest above that neck flattening is a behavioral synapomorphy of the Xenodontini, there is an alternative hypothesis that might be kept in mind: Notwithstanding that North American *Heterodon* and South American *Hydrodynastes* are excluded because of fundamental hemipenial differences, the possibility that one or the other is a sister group of the Xenodontini has not been properly tested by morphological criteria, although such relationships are contraindicated by genetic distance data (see Historical Summary under Discussion). If such a relationship could be corroborated, then neck spreading would have the appearance of being synapomorphic for the larger group, hence symplesiomorphic for the Xenodontini. Behavioral synapomorphy would at least require the fewest assumptions if a sister-group relationship were established on the basis of derived anatomical characters. Unless there prove to be morphological differences involved in the neck spreading itself (a likelihood worthy of investigation), homoplasy in behavior would be difficult if not impossible to demonstrate if either *Heterodon* or *Hydrodynastes* were postulated as the sister group of the Xenodontini. But homoplasy is a necessary assumption if the groups are judged as not related: Based solely on relationships suggested by available immunological distance data (Cadle, 1984a, 1984c), neck

spreading, or hood display, would seem to have been separately derived in these three lineages of New World snakes.

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¹¹ *Bibliographic note:* This was cited several times in 1975 with varying pagination and a 1974 publication date, which has caused some confusion (to H. M. Smith, for example, 1977, *Jour. Herpetology*, vol. 11, p. 115), but the present version seems to be the first one actually distributed or made available for purchase. W. E. Duellman (in litt., Sept. 5, 1985) determined the publication date to be December 1978.

Dowling et al. (1983, *Jour. Zool., London*, vol. 201, p. 327) recently departed from the usual format by citing Dowling and Duellman as *editors* of the work, but Dowling and Duellman agree in their preface that “the work should be considered a joint effort.” The “major contributor” was supposed to have been indicated by the “initials and date at the end of each section,” although this was done in only one instance (WED on p. 7.2); but there is no suggestion of other authors.

This is a useful compendium. Users should realize, however, that all or most of the approximately six dozen “AMNH drawings” have been previously published, although the original authors (e.g., Bogert, Noble) are not cited; a few names accompanying these drawings have not been in use for years, having been simply copied from the old original artwork.

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