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A New Genus for Andean Snakes Related to *Lygophis boursieri* and a New Species (Colubridae)

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ABSTRACT

Saphenophis, new genus, accommodates five species of South American colubrid snakes: *Dromicus boursieri* Jan and Sordelli (type species), *Liophis atahuallpae* Steindachner, *Rhadinaea antioquiensis* Dunn, *Rhadinaea tristriatus* Rendahl and Vestergrén, and *Saphenophis sneiderni*, new species (from southwestern Colombia). These are defined and diagnosed, and placed in two species groups. No support is given a recent suggestion that the type species (*boursieri*) may be closely allied with some West Indian snakes (*Antillophis* Maglio, 1970).

Saphenophis belongs with an undefined group of New World colubrid genera characterized by a usually bilobed, spinose hemipenis that is distally calyculate and noncapitate or semicapitate (but lobes not contained within single capitulum), with a deeply forked sulcus spermaticus. It is suggested that this type of hemipenis is more primitive than the single or slightly bilobated type in which the entire calyculate area is contained within a single capitulum and bifurcation of the sulcus spermaticus is reduced.

Saphenophis boursieri occurs on both Pacific and Atlantic drainages; it possibly adapted to a wide range of environments in the course of vertical habitat displacement during Pleistocene glaciation. Other species of *Saphenophis* are thought to be isolates differentiated from stock(s) fragmented by upward displacement of montane habitats, in a drier postglacial period. Thus, evolution of some or all the species is suggested to have occurred fairly recently in the Quaternary.

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INTRODUCTION

In a previous publication (Myers, 1969), I redescribed two species of nominal *Rhadinaea* and demonstrated their relationship with "*Lygophis*" *boursieri*. A *boursieri* species group was defined. It was acknowledged that the group did not seem to fit into any known genus of Neotropical snakes, but no generic name was proposed and *Lygophis* was used as a provisional depository. I am now aware that two additional species—one new—seem to be congeneric with *boursieri*, and believe that the taxonomic situation can be improved only by giving formal generic recognition to this assemblage of five species.

One annoyance in describing *boursieri* and its relatives as a new genus is that they are generalized snakes quite lacking in peculiar or unique features. The group must be defined by a combination of characteristics that are variously shared by many other genera in the same family. In allusion to one incontrovertible fact about these snakes, I propose the following name:

SAPHENOPHIS, NEW GENUS

TYPE SPECIES: *Dromicus boursieri* Jan and Sordelli, 1867.

ETYMOLOGY: From the Greek *saphenes* (evident truth, clear) + *ophis* (a serpent), meaning "clearly a snake." Gender masculine.

CONTENT: The following five names are considered to represent distinct species that are referable to *Saphenophis*: *Dromicus boursieri* Jan and Sordelli, 1867; *Liophis atahuallpae* Steindachner, 1901; *Rhadinaea antioquiensis* Dunn, 1943; *Rhadinaea tristriatus* Rendahl and Vestergren, 1940; *Saphenophis sneiderni*, new species.

DEFINITION AND DIAGNOSIS: Small to medium-sized terrestrial colubrids lacking hypapophyses on posterior vertebrae; hemipenis bilobed, distally calyculate and semicapitate on each lobe (lobes not contained in single capitulum), basally spinose, with deeply forked sulcus spermaticus; maxillary dentition approximately 19–22+2, the fangs being ungrooved; ventrolateral edge of belly nonangular; dorsal scales smooth, lacking apical pits or anal ridges, in 19 or 17 rows anteriorly, reducing to at least 15 rows posteriorly (method of reduction interspecifically variable); normal complement of colubrid head plates (but fusions in ocular-loreal region not uncommon); pupil of eye round; basically a striped color pattern on a brown ground, turning gray or pale grayish brown on loss of stratum corneum in preservative.

The above combination of traits is believed sufficient to distinguish *Saphenophis* from all other genera of snakes. Specimens of *Saphenophis* are most likely to key to *Lygophis*, *Rhadinaea*, or *Liophis* in the recent work by

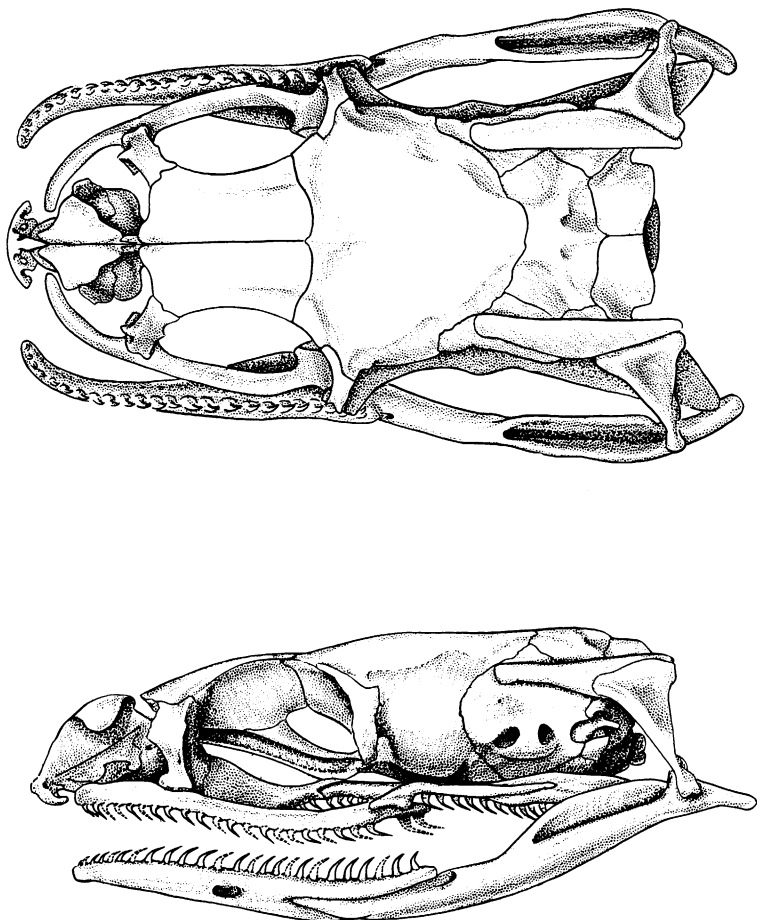


FIG. 1. Skull of the type species of *Saphenophis* (*S. boursieri*, Mus. Comp. Zool. 36948), $\times 5.6$.

Peters and Orejas-Miranda (1970). Externally, the species of *Saphenophis* are rather generalized terrestrial snakes, and only the hemipenis convincingly separates them on a generic level from the slender, striped snakes in *Lygophis* and *Rhadinaea*. *Lygophis* has a bilobed, noncapitate and acalyculate hemipenis with an apical disk (Maglio, 1970, fig. 28A); *Rhadinaea* has a single or only slightly bilobated organ in which a distal calyculate region is contained within a single capitulum (Myers, In press). Species of *Liophis* are generally cross-banded and have a dark-checked ventral pattern, and also a disked hemipenis as in *Lygophis*. More closely related

genera (i.e., those having the same general type of hemipenis as *Saphenophis*) are easily separated from *Saphenophis* by a variety of traits; some examples: grooved fangs and tendency for angulate ventral edges (*Philodryas*, *Tachymenis*); cross-banded color pattern and large size (*Cyclagris*); scale pits and large, racer-like habitus (West Indian *Alsophis*); scale pits, racer-like habitus, and low numbers of maxillary teeth (Peruvian and Galapagos *Alsophis*, *sensu* Maglio, 1970); scale pits, higher numbers of subcaudals, different color patterns, different habitus (*Antillophis*).

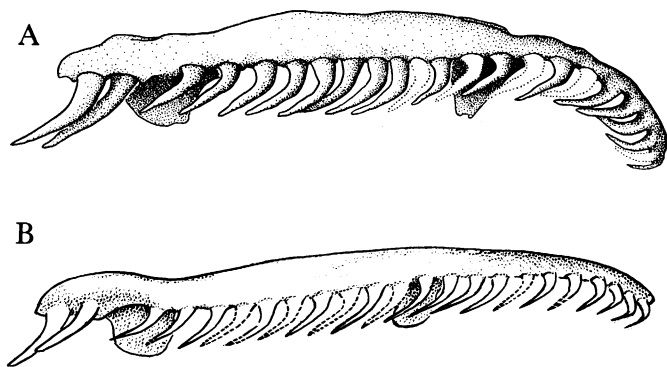


FIG. 2. Right maxillae of *Saphenophis*. A. *S. antioquiensis* (holotype; from Myers, 1969). B. *S. sneiderni* (paratype). Both $\times 10$.

DISTRIBUTION (FIG. 11): Andes of Ecuador and Colombia, to 3200 meters elevation, and adjacent Amazonian lowlands of Ecuador and Peru (see comment under *Saphenophis boursieri*).

DESCRIPTION: Small to medium-sized snakes (adult total lengths from under 500 mm. in *sneiderni* to about 800 mm. in *tristriatus*) of relatively slender proportions, with head slightly wider than neck, and with moderate-sized tails (about 20–30 percent of total length). Body higher than wide; ventrolateral edges of body rounded, not angular.

Ground color brown or grayish brown, turning gray or pale gray-brown on loss of stratum corneum in preservative; ground color uniform or somewhat reticulate due to dark scale edges; basically a striped color pattern, often with a dark vertebral line and usually with at least an indication of dark lateral and ventrolateral lines; pale tan line or row of almost coalesced tan spots bordering upper edge of dark lateral line in some species. Upper lip white or pale brown with darker markings sometimes delimiting a white postocular stripe or horizontal labial line; supralabials margined above by black line or stripe extending from snout onto neck, where

connecting or not with lateral dark line of trunk. Pair of pale ocelli sometimes present on nape. Venter basically whitish or yellowish (at least in preservative), with median row of gray to black markings and/or transverse streaks, or an overall dark-speckled or clouded appearance; ventral tips usually dark, at least posteriorly, tending to form dark ventrolateral line.

A more or less "normal" colubrid pattern of head plates, including paired internasals and prefrontals, but some individual specimens having fusion of loreal and preocular, or postocular and supraocular. Commonly eight supralabials, with 3–5 in eye, or seven supralabials, with 3–4 in eye. Temporal pattern basically 1+2. Tiny scale organs (tubercles) present on all or most head plates, most concentrated anteriorly. Canthus rostralis rounded, not angular. Pupil of eye round.

Dorsal scales smooth, lacking apical pits or anal ridges, in 19 or 17 rows anteriorly, 17 rows toward midbody, and reducing to 15 or fewer rows posteriorly; method of reduction interspecifically variable. Moderate numbers of ventrals (146–174 observed) and paired subcaudals (51–75 observed, 87 reported for *atahuallpae*). Anal plate divided.

Maxilla (fig. 2) with moderately high number of prediastemal teeth (about 19–22), followed by two enlarged, ungrooved fangs, the last being slightly offset laterad (from a plane connecting prediastemal teeth and first fang); diastema variable, from virtually nonexistent to moderate-sized. Teeth also present on palatine (11–14 observed), pterygoid (24–26), and dentary (24–26). Skull (of type species, fig. 1) generalized; frontal bones relatively long and narrow, slightly emarginated at orbits (greatest frontal length/smallest interorbital width of paired bones = 1.23 in one specimen); prefrontal relatively high and narrow (height/width = 2.50); premaxilla with pronounced, posteriorly curved lateral projections; parasphenoid relatively narrow posteriorly, deeper anteriorly, with a dorso-medial frontal "step" (not a crest) situated high above the broad trabecular groove and forming posteriormost frontal contact. Posterior trunk vertebrae (three species, fig. 3) lacking hypapophyses, with long ridgelike haemal keel extending almost from contyle to condyle; a longitudinal concavity on centrum situated between base of haemal keel and a moderate to strong subcentral ridge—the concavity being deepest anteriorly and disappearing toward condyle. Paradiapophyses with two articular surfaces; parapophysis well developed, with very slight forward projection. Contyle round; condyle on a short neck, oblique. Prezygapophyses and postzygapophyses tending to be more rounded than pointed at distal ends. Well-developed accessory spine projecting anterolaterally from beneath prezygapophysis. Neural arch lacking epizygapophysial spines. Zygo-

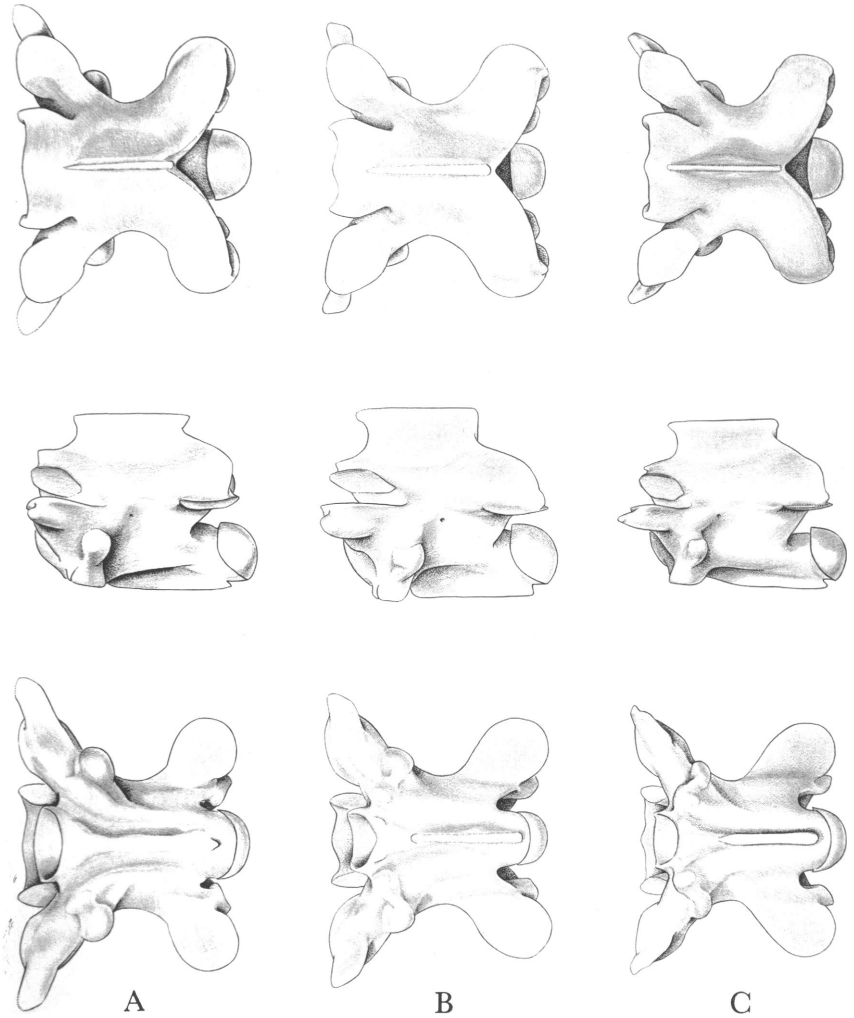


FIG. 3. Posterior trunk vertebrae of *Saphenophis* in dorsal, lateral, and ventral aspect. A. *S. tristriatus* (unnumbered ♀ specimen in Mus. Hist. Nat., Univ. Cauca, Popayán, near 115th ventral), $\times 7.1$. B. *S. boursieri* (Mus. Comp. Zool. 36948 ♂, near 120th ventral), $\times 7.8$. C. *S. sneiderni* (♀ paratype, near 115th ventral), $\times 7.8$.

sphene weakly to moderately crenate from above, slightly convex from the front. Neural spine a well-developed long crest, moderately low to high, blunted on top and with slight anterior overhang.

Hemipenis (known only in *boursieri* and *tristriatus*, fig. 4) spinose,

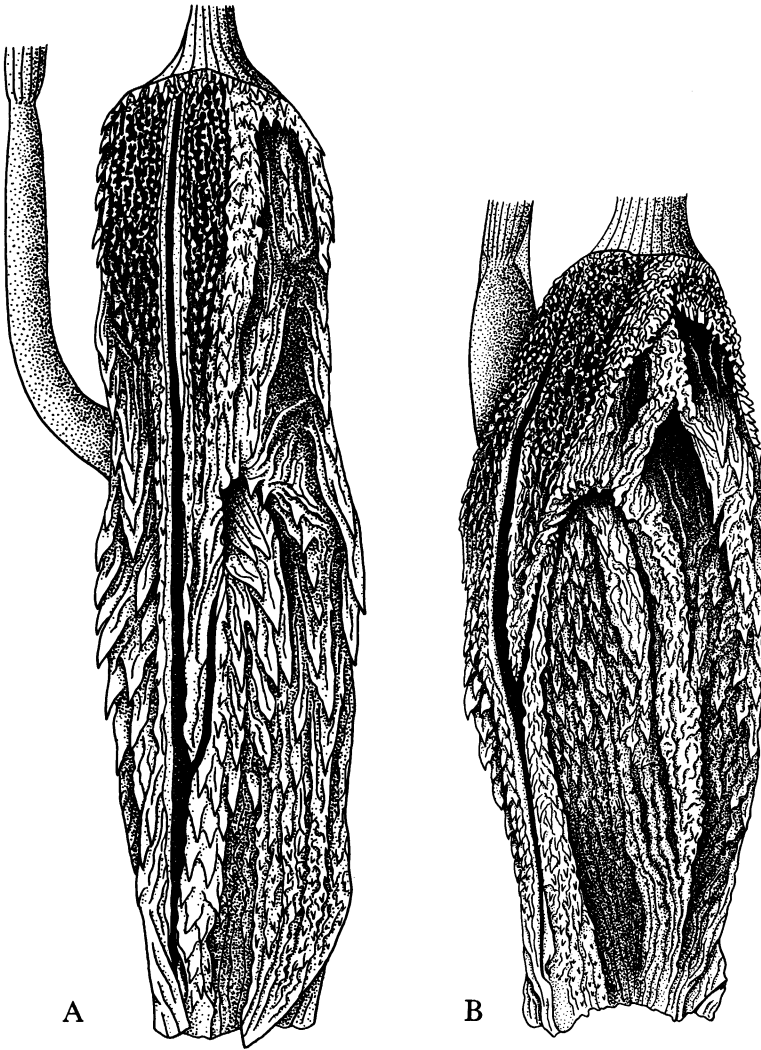


FIG. 4. Hemipenes of *Saphenophis* (left uneverted organs, opened by midventral incision; from Myers, 1969). A. *S. boursieri* (British Mus. Nat. Hist. 1946.1.4.4, lectotype of *Coronella whymperei*). B. *S. tristriatus* (holotype). Both $\times 4$.

bifurcated for 30–50 percent of its length, the lobes being partly calyculate but not contained within a single capitulum; areas of calyces separated, not confluent at bases of lobes; lobes nude on asulcate side, calyculate on sulcate side—probably semicapitate when everted (i.e., with edge of

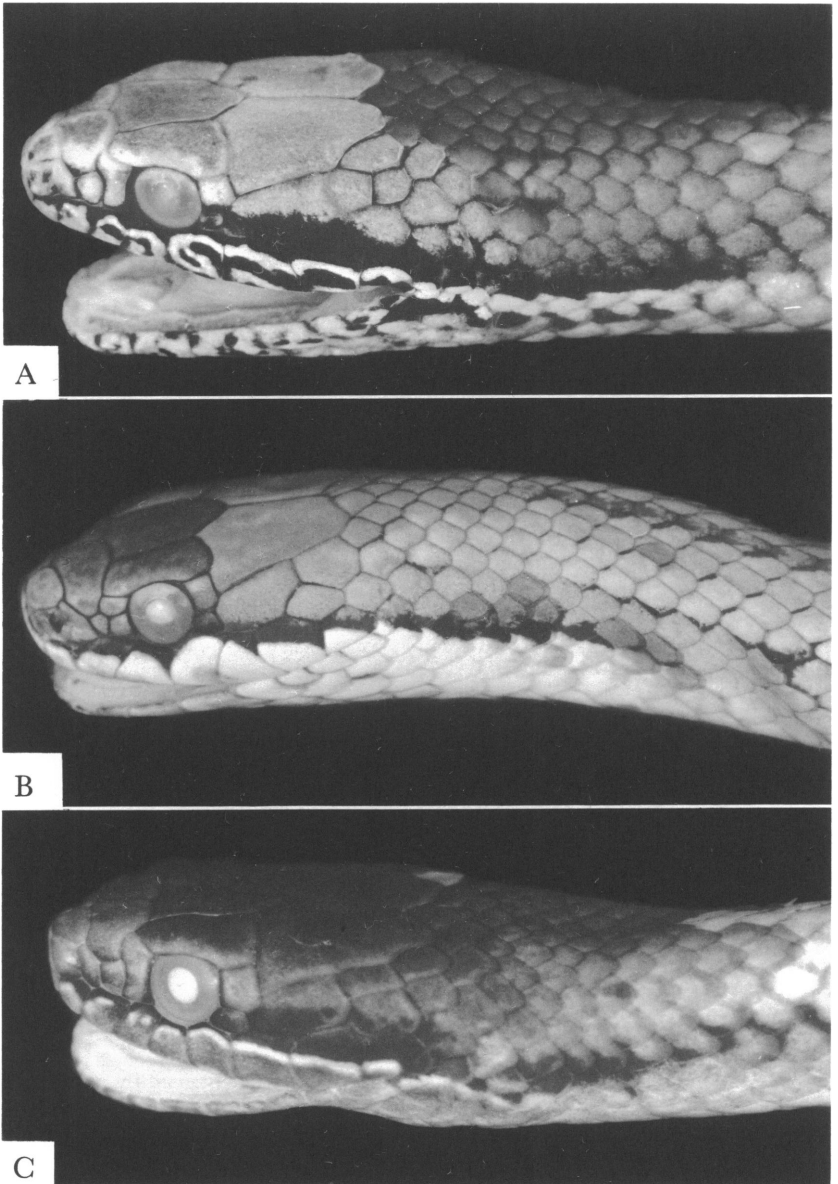


FIG. 5. Heads of *Saphenophis*. A. *S. boursieri* (holotype). B. *S. tristriatus* (holotype). C. *S. sneiderni* (holotype).

calyculate area forming a slight overhang at tip of each lobe). Sulcus spermaticus deeply forked.

ILLUSTRATIONS: Myers (1969) published photographs of the holotypes of *antioquiensis* and *tristriatus* and of two specimens of *boursieri* (including the lectotype of *Coronella whymperi*). Drawings showing color pattern and details of scutellation were published by Jan and Sordelli (1867) for *boursieri*, and by Steindachner (1902) for *atahuallpae* (reproduced herein as fig. 8). Semidiagrammatic drawings of the color pattern on the anterior and posterior parts of the body of *antioquiensis* are given in Myers (1969). The maxillary dentition of *antioquiensis* is also illustrated in Myers (1969), and the inverted hemipenes of *tristriatus* and *boursieri* (of the latter, two organs are shown, including one from the lectotype of *Coronella whymperi*), as well. Maglio (1970) provided an additional, semidiagrammatic drawing of the inverted hemipenis of *boursieri*.¹ Additional illustrations are provided in the present paper.

NATURAL HISTORY: I know nothing of the life history of these snakes except that they are oviparous (based on large oviductal eggs in the holotype of *antioquiensis* and in the paratype of *sneiderni*). Their cool montane habitats, and the round pupil of the eye, indicate that they are principally diurnal; a specimen of *Saphenophis tristriatus* (q.v.) was found abroad about midday.

REMARKS: The species *atahuallpae* and *sneiderni* are placed in *Saphenophis* provisionally, pending examination of their hemipenes. The hemipenis of *antioquiensis* also is unknown, but that species is unquestionably related to *tristriatus*, which, in penial and other characters, is demonstrably close to *boursieri* (fide Myers, 1969), the type species. The last three species form a closely knit, albeit geographically fragmented, evolutionary unit, whereas *atahuallpae* and *sneiderni* evidently form a similar unit which I hypothesize to be congeneric with the first. These two units, or species groups, are definable by the nature of the color pattern on the side of the trunk. The most important diagnostic characters separating the two groups and the five species are summarized in the following key. Users of the key are warned that it was constructed on the basis of only 15 specimens, one literature description, and a few old engravings; therefore, we cannot pretend to know even the approximate limits of variation in *Saphenophis*, and difficulties in identification would not be unexpected (see p. 32 for one possible source of trouble).

¹ I have examined the specimen on which Maglio's illustration is based; the published drawing is enlarged approximately 2.8 times, not "×5."

KEY TO THE SPECIES OF *Saphenophis*

1. Lateral dark line (when present) anteriorly lying on scale row 5 or rows 5-6, not continuous with dark line or stripe extending from side of head onto lower side of neck; lateral dark line bordered above by pale tan line or spots (*boursieri* species group) 2
 - Lateral dark line anteriorly lower, lying on scale row 4 or rows 3-4, confluent with dark line from head, and not bordered above by pale line or spots (*atahuallpae* species group) 4
2. 17 scale rows on anterior part of body; posterior reduction to 15 rows involving fourth lateral row 3
 - 19 scale rows on anterior part of body; posterior reduction to 15 rows involving paravertebral rows. *Saphenophis antioquiensis*
3. Dark vertebral and lateral lines broken or absent anteriorly (and sometimes posteriorly); scale edges usually dark, especially on lower sides and rear of body and after loss of stratum corneum; lobes of hemipenis comprising about 40-50 percent of its length *Saphenophis boursieri*
 - Dark lines continuous anteriorly; dorsal ground color almost uniform brown (gray) without conspicuously dark scale edges; lobes of hemipenis comprising about 30 percent of its length *Saphenophis tristriatus*
4. Vertebral dark line present; supralabials yellowish white, without conspicuous horizontal white line. *Saphenophis atahuallpae*
 - No vertebral dark line; supralabials suffused with pale brown and with dark markings delimiting a horizontal white line *Saphenophis sneiderni*

THE *BOURSIERI* SPECIES GROUP

Saphenophis antioquiensis (Dunn), new combination

Figure 2A

Rhadinaea antioquiensis DUNN, 1943, p. 307 (type locality, Colombia, Departamento Antioquia, San Pedro, elev. 2560 m.; holotype: Museo del Instituto de La Salle, Bogotá, 386).

Lygophis antioquiensis (Dunn): MYERS, 1969, pp. 2-6, figs. 1-3. PETERS AND OREJAS-MIRANDA, 1970, p. 185.

DEFINITION AND DIAGNOSIS: Ground color uniform brown (gray under stratum corneum), without conspicuously dark scale edges. Vertebral and lateral dark lines extending from neck onto tail; lateral dark line anteriorly on lower part of row 5, posteriorly on lower part of row 4, and edged above by somewhat broader, pale tan stripe (on rows 5-6), which posteriorly may form staggered light spots (on rows 4-5). Supralabials white with black markings, and margined above by black stripe extending from snout onto lower side of neck, which tends to be pale below the stripe; hint of dark-edged white stripe from eye to corner of mouth. Vague, pale ocellus on each side of neck. Black streaking and spotting across bases of ventral plates; black triangular markings on ventral tips, tending to fuse into solid ventrolateral stripe on rear of body. Dorsal scales in 19-17-15 rows, ante-

rior reduction involving row 4 and posterior reduction involving paravertebral rows. Ventrals 168, subcaudals 62, in one known female (an adult, about 665 mm. total length, 159 mm. tail length).

This species resembles *Saphenophis boursieri* and *S. tristriatus* in having a high lateral dark stripe (i.e., anteriorly on rows 5 or 5-6) that is not confluent with a lower stripe, extending from the side of the head onto the lower side of the neck. *Saphenophis antioquiensis* differs in having 19 rows of scales anteriorly (rather than 17) and in that the posterior scale-row reduction (17 to 15 rows) involves the paravertebral rows (rather than lateral rows).

DISTRIBUTION: *Saphenophis antioquiensis* is reported only from the type locality, at the northern end of the Cordillera Central.

REMARKS: This species is known solely from the holotype, a female; therefore some of the characters given in the Definition and Diagnosis will doubtlessly prove to be variable. *Saphenophis antioquiensis* seems most closely related to *S. tristriatus*, which also is geographically closest, and it would be most interesting to have a male specimen of *antioquiensis* for hemipenial comparison. The holotype of *antioquiensis* has been redescribed and illustrated in some detail (Myers, 1969).

Saphenophis boursieri (Jan and Sordelli), new combination

Figures 1, 3B, 4A, 5A, 6

Dromicus Boursieri JAN AND SORDELLI, 1867, livr. 25, pl. 2, fig. 2 (type locality, "Quito," Ecuador; holotype: Muséum National d'Histoire Naturelle, Paris, 858).

Coronella Whymperi BOULENGER, 1882, pp. 460, 461, fig.; 1891, pp. 130, 131, fig. (type locality, Milligalli, 6200 ft. [1890 m.], Ecuador [on western slopes of Cerro Corazon, elev. 1900 m. on trail between Aloág and Mirador, *fide* Andrade Marin, 1931, p. 30]; lectotype, British Museum Natural History 1946.1.4.4, designated by Myers, 1969, p. 21).

Rhadinaea undulata (not of Wied): BOULENGER, 1894, p. 174 (part).

Liophis boursieri (Jan and Sordelli): PARKER, 1935, p. 522 (part).

Lygophis boursieri (Jan and Sordelli): SHREVE, 1934, p. 125 (part). PETERS, 1960, p. 528; 1963, p. 61. MYERS, 1966, p. 887; 1969, pp. 1 *et seq.*, figs. 5, 6. MAGLIO, 1970, pp. 34, 35, fig. 28B. PETERS AND OREJAS-MIRANDA, 1970, p. 186.

Lygophis whymperi (Boulenger): PETERS, 1960, p. 528; 1963, p. 61.

DEFINITION AND DIAGNOSIS: Ground color brown (usually gray under stratum corneum), but not uniform: individual scales tending to have light brown (gray) centers and dark edges,¹ especially those scales on

¹ Actually, the entire circumference of the scale is not dark, but the free, usually translucent edge appears dark because it overlaps the pigmented base of an adjacent scale.

lower sides and on posterior part of body. Vertebral and lateral dark lines generally absent, or faint and broken, on anterior part of body; vertebral marking, even posteriorly, sometimes reduced to series of spots; lateral dark line anteriorly on row 5 (when present), posteriorly on row 4 or adjacent edges of 3 and 4 (rarely absent on rear of body). Lateral dark line edged above by tan or whitish line or series of almost coalesced spots, on rows 5 or 5-6 anteriorly, and rows 4-5 or 5 posteriorly; this marking posteriorly taking appearance of double row of staggered spots in some specimens. Supralabials white with bold black markings, and margined above by black line or stripe extending from snout onto lower side of neck, which tends to be whitish below the line; commonly a black-edged white postocular line or stripe from eye to corner of mouth, or, in some cases, even extending horizontally for short distance on lower side of neck (with aforesaid black line forming the upper edge). Pale ocellus present or not on each side of nape. Underside of head with black markings. Bases of ventral plates with transverse gray or black streaks or half-moon markings, often with midventral line of spots on first several dozen ventrals; tips of ventrals in many cases with dark spots or accumulated pigment, confluent or not with transverse ventral markings, tending to form solid black ventrolateral stripe on rear of body. Dorsal scales in 17-17-15 rows, reduction involving row 4 (i.e., -4, 3+4, or 4+5). Ventrals in five males 148-159 (mean 154.4), in four females 146-155 (151.0); subcaudals in five males 64-70 (66.6), in two females 51, 58.

Saphenophis boursieri is distinguishable from its congeners by the reticulated appearance of the posterior body and lower sides, and by the anterior absence or reduction of the vertebral and lateral dark lines.

DISTRIBUTION: Andean Ecuador and extreme southwestern Colombia, on western (Pacific) slopes above 1000 meters, and on eastern slopes into the Amazonian lowlands. The lowland records¹ need to be verified, but, if correct, the species is doubtlessly also present in Amazonian Peru.

REDESCRIPTION OF HOLOTYPE: The several engravings in Jan and Sordelli's (1867) livraison 25, plate 2, constitute the only previous "description" of the type specimen of *boursieri*. This specimen is number 858 in the Muséum National d'Histoire Naturelle, Paris, and is in fair condition although the posterior half of the body is quite soft. Jan and Sordelli's illustrations are reasonably accurate, especially concerning color pattern. Their figure of the entire specimen shows several more sub-

¹ Ecuador: Rocafuerte on the Río Napo, Field Mus. Nat. Hist. 36622. Ecuador (and/or Peru?): Río Pastaza between Canelos and Río Marañón, Mus. Comparative Zool., Harvard, 36948-36950.

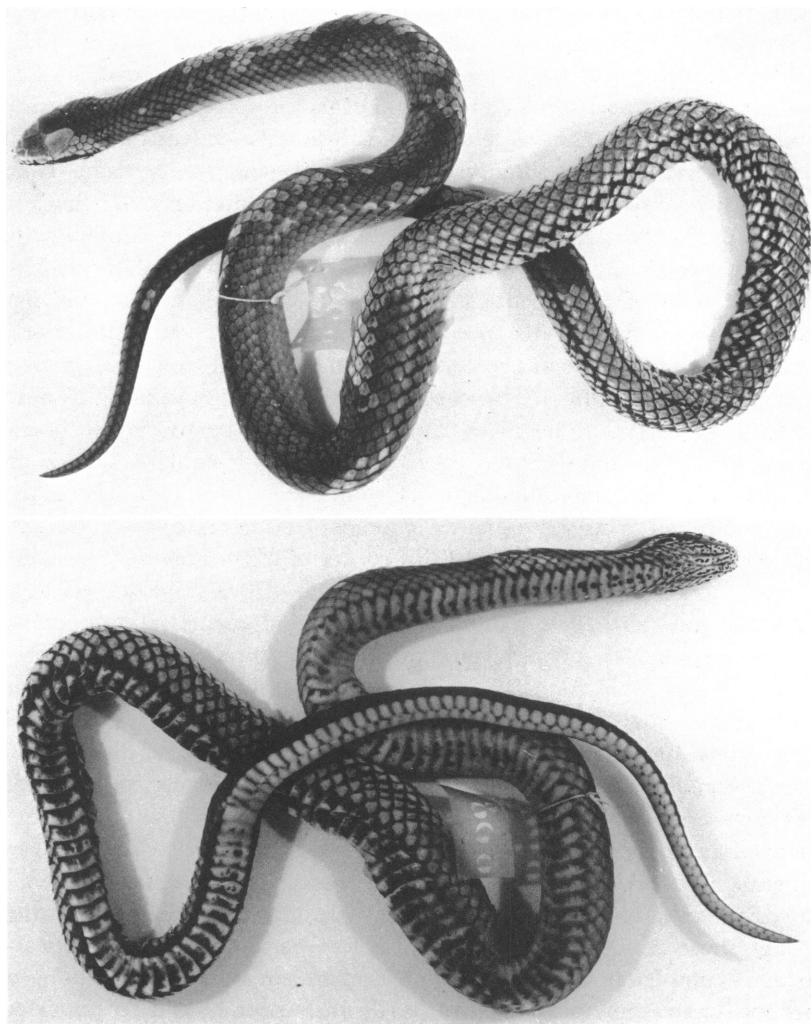


FIG. 6. Dorsal and ventral views of the holotype of *Saphenophis boursieri*; see figure 5A for details of head.

caudals than actually present, but the details (their figs. 2e, 2f) of the head show the actual differences, between the left and right sides, in the temporal formula and in the number of supralabials in contact with the loreals. The following description may be used in conjunction with photographs of the holotype (figs. 5A, 6).

Female, presumably adult, of slender proportions, with head little

wider than neck; total length approximately 590 mm., tail 136 mm. (23.1 percent of total). Dorsal scales smooth, lacking apical pits or anal ridges, in 17-17-15 rows, reducing posteriorly by fusion of lateral rows 3+4 at level of ventrals 93 left side, 88 right. Ventrals 146, preceded by two wide gulars (preventrals), anal plate divided, subcaudals 58. Rostral plate half as high as wide, tipped slightly forward and but narrowly visible from above. Internasals as wide as long, but narrowed anteriorly, 0.7 times as long as prefrontals. Prefrontals wider than long, each in contact with frontal, supraocular, preocular, loreal, nasal, and internasal, as well as other prefrontal. Frontal pentagonal, 1.5 times longer than wide, and also 1.5 times longer than its distance to tip of snout. Supraocular posteriorly about 0.8 times as wide as greatest (anterior) width of frontal, narrowed in front. Parietals about 1.6 times longer than broad; interparietal suture shorter (0.8 times) than length of frontal. Nasal plate partly divided below naris, with only shallow groove above naris. Loreal irregularly shaped on both sides of head, higher than wide. One large preocular; two postoculars, lower about half as large as upper. Temporals 1+2 left side, 1+3 on right. Supralabials eight, second labial (plus corner of third labial on right side of head) touching loreal, labials 3-5 in orbit. Infralabials about nine (angles of jaws slit), first pair in contact behind mental, 1-4 touching anterior genials, 4-5 touching posterior genials. Anterior genials slightly shorter than posterior ones, but with longer intergenial suture. Diameter of eye about equal to distance from its anterior edge to posterior edge of naris, extending 1.5 times into length of snout. Presence and distribution of scale organs (tubercles) on head not determined because of condition (soft surface) of head plates.

Dorsal surfaces medium yellowish brown, or gray where lacking stratum corneum. Ground color not uniform because of black pigment on concealed anterobasal edges of each body scale, these dark edges showing through those of overlying translucent scales—each scale thereby appearing as if completely edged in gray; this dark edging more pronounced after loss of stratum corneum, and particularly pronounced on posterior sides of body because of greater concentration of black pigment. Black pigment on bases of vertebral scales increasing posteriorly, until, at mid-body (*ca.* ventral 78), forming a definite line of small black spots, which later fuse (at ventral 136) to a solid black vertebral line extending from near end of body to tip of tail. A vague, light gray streak covering scale rows 3 and 4 on front half of body. Lateral dark line anteriorly absent, perhaps being represented by a few isolated, small black marks (resulting from heavier than average accumulation of black on lower anterior edge

of some scales in row 5, or, less often, on upper or lower edges in rows 4 and 6, respectively). At midbody, black scale edging becoming evident on row 4 and lower edge of row 5, then more conspicuous and lower—on adjacent edges rows 3 and 4—after reduction from 17 to 15 rows (by fusion of rows 3+4 at ventrals 93/88). Black edging posteriorly intensifying on all lateral scales, but nearly confluent on border between rows 3-4, becoming a narrow, continuous black lateral stripe several ventrals before cloaca. A double row of staggered, pale spots on rows 5-6 (before scale-row reduction) and 4-5 (after reduction), most evident above lateral dark line on posterior half of body and only very faintly indicated anteriorly. A vague, pale ocellus-like marking on each side of nape, two or three scales behind upper secondary temporal; each ocellus occupying parts of four scales and bordered above and below by short (two scale lengths), parallel black lines.

Top of head gray (doubtless brown before loss of stratum corneum), this color reduced to spots on prefrontals and internasals. Top and sides of snout, free edges of supraoculars, and upper postocular mostly whitish; rostral whitish, with four black dots. Anterior supralabials white, boldly marked with black borders and irregular spots. Parallel black postocular stripes enclosing a vivid white line extending obliquely from lower edge of eye, across corner of mouth, and onto lower side of neck, becoming indistinct after level of fourth ventral; upper black postocular stripe contiguous on neck (at level of ventral 4) with the vague gray streak on scale rows 3-4. Underside of head white, densely marked with small black spots. Ventral and subcaudal surfaces pale yellow (whitish after loss of stratum corneum). Anterior part of belly with small, median black spot(s) on base of each ventral plate, these markings becoming progressively larger and diffused posteriorly, causing rear of belly to be clouded with black. Basal edges of subcaudal plates blackish brown, appearing gray through overlapping free edges of adjacent plates; a weak, median line of black dots on underside of tail. Black pigment on tips of ventral plates intensifying caudad from midbody, forming a solid black ventrolateral stripe on posterior third of body. Lateral body and ventrolateral black stripes fused a few scales behind cloaca, forming a single broad stripe on side of tail to its tip.

Right maxilla with 21 teeth, smallest in front but otherwise subequal, followed by small diastema and two moderately enlarged, ungrooved fangs. Ultimate prediastemal socket lying posterior to front edge of ectopterygoid process. Diastema somewhat greater than length of ultimate prediastemal socket. Palatine-pterygoid bones damaged, but with approxi-

mately 11 palatine and 24 pterygoid teeth on left side. Right mandible with about 24 subequal teeth. (All bones examined *in situ*; empty sockets included in counts.)

REMARKS: Despite its large range (fig. 11), *Saphenophis boursieri* remains uncommon in collections. I have seen only the following nine specimens. Colombia: Dept. Nariño, Ricuarte, 1300 m. (Acad. Nat. Sci. Philadelphia 25183). Ecuador: Milligalli, 1890 m. (British Mus. Nat. Hist. 1946.1.4.4 and 1946.1.4.5); "Quito" (the holotype); Rocafuerte on the Río Napo (Field Mus. Nat. Hist. 36622). Ecuador and/or Peru: Río Pastaza between Canelos and Río Marañon (Mus. Comp. Zool. 36948-36950). Locality unknown: Mus. Comp. Zool. 9598 (originally thought to have come from Cuba, and misidentified in the literature [references in Myers, 1966] under the names *Dromicus dumerilii* and *Urotheca dumerilii*). Peters (1963) also recorded *Saphenophis boursieri* (as *Lygophis whympersi*) from Mindo, 1100 m., and Corazon Pass, Pichincha Province, Ecuador, and I have included these localities in figure 11.

Saphenophis tristriatus (Rendahl and Vestergren), new combination

Figures 3A, 4B, 5B, 7

Rhadinaea tristriata RENDAHL AND VESTERGREN, 1940, p. 5 (type locality, Colombia, Departamento Cauca, no other data; holotype, Naturhistoriska Riksmuseet, Stockholm, 3119, collected by G. Gerring in 1938).

Lygophis tristriatus (Rendahl and Vestergren): MYERS, 1969, pp. 7-10, figs. 4, 7. PETERS AND OREJAS-MIRANDA, 1970, p. 187.

DEFINITION AND DIAGNOSIS: Ground color almost uniform brown (gray under stratum corneum), without conspicuously dark scale edges. Vertebral and lateral dark lines extending from neck onto tail; lateral dark line anteriorly on lower part of scale row 5, posteriorly on lower part of row 4, and edged above by narrow pale tan line (upper part of row 5), which posteriorly may widen and form staggered light spots (rows 4-5). Supralabials yellowish white with brown or black markings, and margined above by black stripe extending from snout onto lower side of neck, which tends to be pale below the stripe. Faint indication of small pale spot on each side of nape. Underside of head smudged with brown or boldly spotted with black. Bases of ventral plates with transverse gray streaks and/or mid-ventral series of black triangular or half-moon markings; dark pigment on tips of ventrals, sometimes in form of black triangular markings, forming broken ventrolateral stripe. Dorsal scales in 17-17-15 rows, reducing posteriorly by fusion of rows 3+4. Ventrals and subcaudals 174, 75 (one male) or 170, 65 (one female). To at least 790 mm. total length (table 1).

Saphenophis tristriatus resembles *S. antioquiensis* and *S. boursieri* in having

a high lateral dark stripe (i.e., anteriorly on rows 5 or 5-6) that is not confluent with a lower stripe that extends from the side of the head onto the lower side of the neck. The species most closely resembles *antioquiensis*, from which it differs in having 17 anterior rows of scales (rather than 19) and in that the posterior scale-row reduction (17 to 15) involves lateral rows rather than the paravertebrals. It differs from *boursieri* in having an almost uniform ground color (without conspicuously dark scale edges), and in the vertebral and lateral dark lines extending the length of the body (one or both lines anteriorly broken or absent in *boursieri*); the lobes of the hemipenis comprise about 30 percent of the organ in *tristriatus* (40-50 percent in *boursieri*).

DISTRIBUTION: Known only from the Andes of southern Colombia, in the Departamento del Cauca. The holotype has no specific locality data, other than "Cauca," but a second specimen (see below) is from the vicinity of Gabrielopez, at about 3200 meters elevation in the Malvasá Valley, on the western slopes of the Cordillera Central; this locality is about 30 miles [48 km.] northeast of Popayán (*vide* Kjell von Sneidern, *in litt.*).

REMARKS: I previously redescribed and illustrated the holotype, heretofore the only available specimen of this species. I am now indebted to Kjell von Sneidern for the privilege of reporting on a second example, an unnumbered specimen in the collection of the Museo de Historia Natural, Universidad del Cauca, Popayán. The specimen (fig. 7) is a large female that corresponds in most characters to my previous description (Myers, 1969, pp. 7-10); scale counts and measurements are compared in table 1. Major features of the color pattern are virtually identical, including especially the position and appearance of the linear dark lines and also the narrow tan line that posteriorly tends to form a double row of small staggered spots. Following are points of departure in the color pattern (condition of holotype indicated in parentheses): Head and body dark (medium) brown, almost uniformly dark atop the head (faintly reticulated with pale brown). Pale spot on each side of nape very faint and occupying parts of three (five) scales. Dark line from side of head extending caudad for distance of eight (five) ventrals; lower side of neck white (pale yellowish) below dark line for distance of eight (four) ventrals. Supralabials with black markings (faint brownish smudging), in same position as markings on holotype, except for addition of downward extension of black pigment below eye, along sutures of labials 3-4. Underside of head boldly spotted with black (faint brownish smudging). Transverse gray streak across base of each ventral plate (ventral pigment mostly concentrated to form median series of small black triangles, posteriorly turning to gray half-moon markings after ventral 45). Black triangle on each ventral tip, forming broken

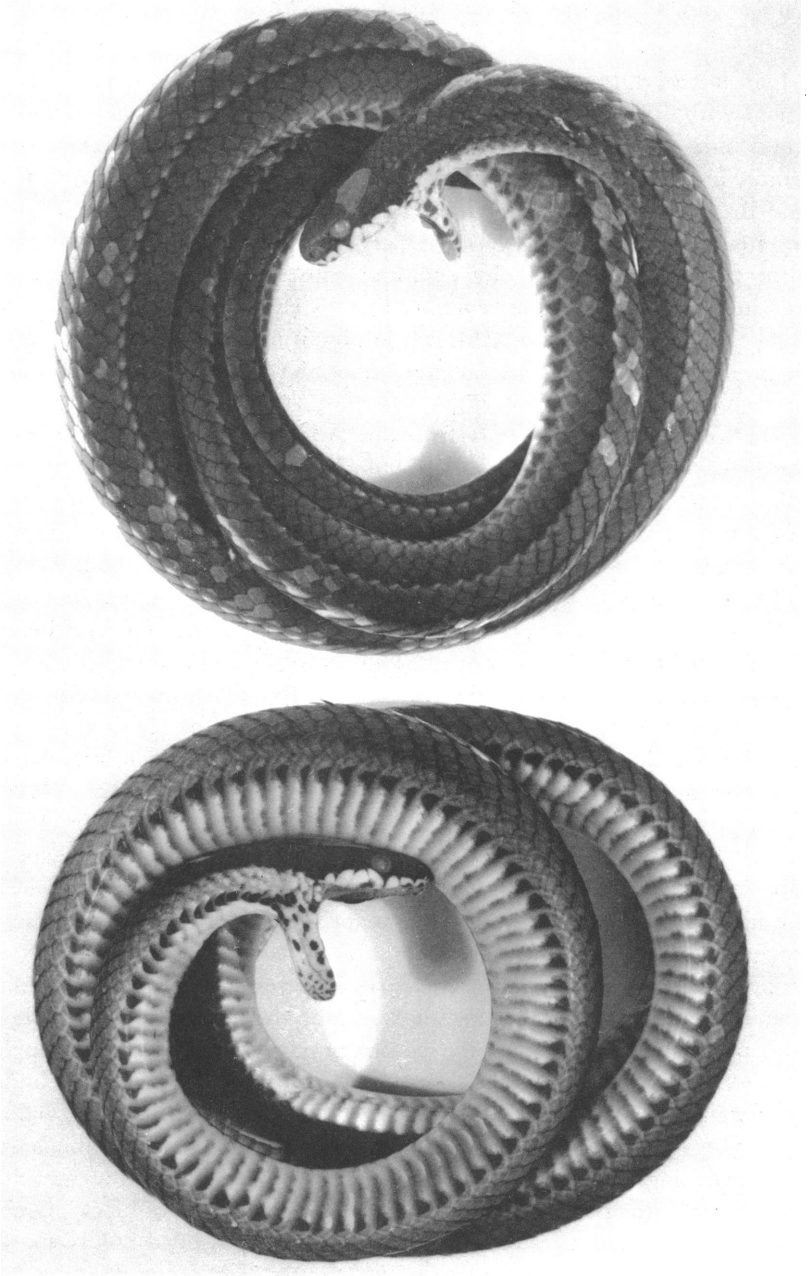


FIG. 7. Dorsal and ventral views of the second-known specimen of *Saphenophis tristriatus* (Mus. Hist. Nat., Univ. Cauca, Popayán). This individual is the largest known specimen (790 mm. total length) of *Saphenophis* and is also the uppermost elevational record (3200 m.) for the genus.

TABLE 1
SCALE COUNTS AND MEASUREMENTS (IN MILLIMETERS) OF KNOWN
SPECIMENS OF *Saphenophis tristriatus*

	Naturhist. Riksmus. 3119 (holotype) ♂	Univ. Cauca, Popayán ♀
Dorsal scale rows	17-17-15	17-17-15
Ventrals at scale-row reduction (3+4)	96/93	85/87
Ventrals	174	170
Subcaudals	75	65
Supralabials	7/8	7
Supralabials touching eye	3-4/3-5	3-4
Supralabial touching loreal	2	2
Preoculars	2/1 ^a	2/1
Postoculars	2	2
Temporals	1+ $\frac{1}{2}$	1+2
Infralabials	9/8	9
Infralabials touching anterior genials	1-4	1-4
Infralabials touching posterior genials	4-5	4-5
Total length	655	790
Tail length	168	191
Tail length as a percentage	25.6	24.2

^a Single preocular on right side has an incomplete suture that divides it into almost equal parts.

ventrolateral stripe, becoming a solid black line across ends of subcaudals (ends of ventrals and subcaudals not so conspicuously marked, mostly with gray pigment and some irregular small dark spots). Right maxilla with 22+2 teeth (21+2 in holotype), last four (two and a half) sockets lying posterior to front edge of ectopterygoid process; diastema tiny, less than (about the same as) length of ultimate prediastemal socket.

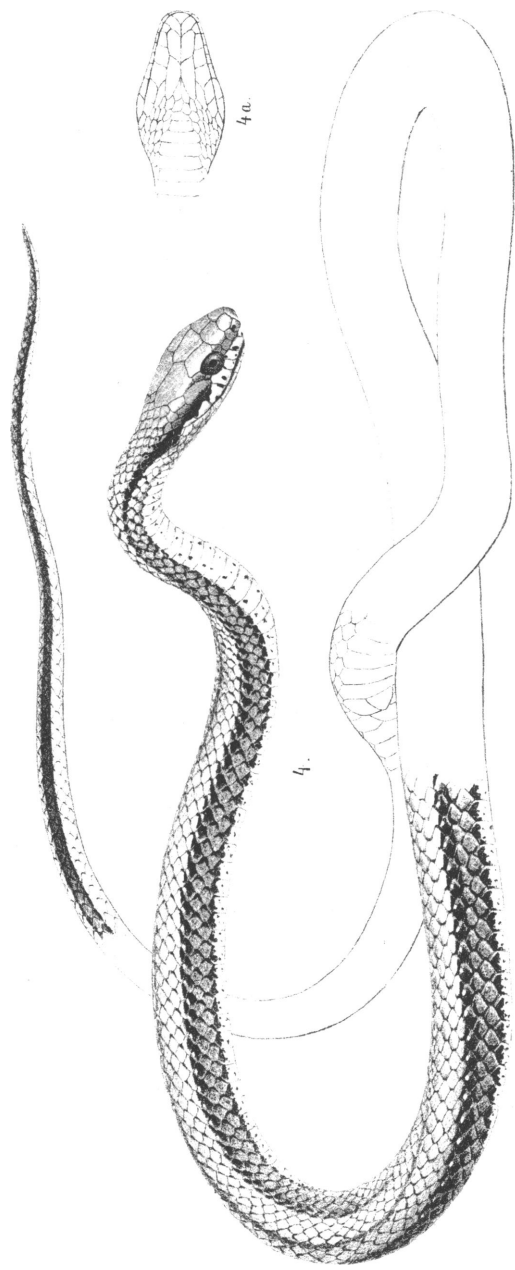
Mr. von Sneidern found this specimen between 11 and 12 A.M., as it was lying in the sun on a wood bridge, 1 mile from the mountain village of Gabrielopez.

THE ATAHUALLPAE SPECIES GROUP

Saphenophis atahuallpae (Steindachner), new combination

Figure 8

Liophis atahuallpae STEINDACHNER, 1901, pp. 195, 196; 1902, p. 105, pl. 1, figs. 4, 4a
[type locality, "unterhalb Las Palmas am Westabhange der Anden, auf dem



Gez. u. lith. v. E. Konopický

Lith. Aust. v. Th. Baunwarth, Wien.

Denkschriften d. kais. Akad. d. Wiss. math. naturw. Classe, Bd. LXXII.

FIG. 8. Holotype of *Sophenophis atahualpae*. Illustration reproduced same size from Steindachner (1902, pl. 1, fig. 4 "In natürlicher Grösse," fig. 4a "zweimal vergrößert").

- Wege von Babahoyo nach Guaranda (West-Ecuador) . . . circa 2500 m Seehöhe" (Steindachner, 1902); holotype, Prince Bayern Collection, 68; present location unknown, possibly in the Vienna Museum (Peters, 1960, p. 529)].
- Rhadinaea undulata* (not of Wied): WERNER, 1929, p. 119 (part).
- Liophis undulatus* (not of Wied): AMARAL, "1929" [1930], p. 174 (part).
- Liophis boursieri* (not of Jan and Sordelli): PARKER, 1935, p. 522 (part).
- Lygophis whymperi* (not of Boulenger): PETERS, 1960, pp. 528, 529 (part).
- Leimadophis atahuallpae* (Steindachner): MYERS, 1969, pp. 21, 22. PETERS AND OREJAS-MIRANDA, 1970, p. 143.

DEFINITION AND DIAGNOSIS: Ground color of middorsum brown (gray under stratum corneum?), of lower sides (below lateral dark stripe) gray-brown, becoming gradually darker toward tail; ground color evidently rather uniform, without conspicuously dark scale edges. Vertebral and lateral dark lines extending from neck onto tail; lateral dark line anteriorly involving adjacent parts of rows 3 and 4, and containing a row of small pale spots. Supralabials yellowish white, with black markings, and margined above by black stripe extending along side of head to fuse with lateral body stripe on side of neck. Probably no ocellus on side of neck. Narrow ventrolateral black stripe across tips of ventrals; venter flecked with dark pigment, tending toward immaculate near end of body. Dorsal scales in "17 Reihen" [probably 17 or 19 anteriorly, 17 midbody, 15 posteriorly]. Ventrals 163, subcaudals 87 in one reported specimen of unknown sex (about 600 mm. total length, 175 mm. tail length).

Saphenophis atahuallpae differs from all its supposed congeners except *S. sneiderni* in having the lateral dark stripe low on the sides (anteriorly involving rows 3-4, rather than 5 or 5-6) and in this stripe being anteriorly continuous with the lateral head stripe. It differs from *sneiderni* in having a vertebral dark line, in having whitish (rather than brownish) supralabials with black markings, in lacking a horizontal white line on supralabials, and, possibly, in a higher number of ventrals and subcaudals.

DISTRIBUTION: *Saphenophis atahuallpae* is known only from the type locality in west-central Ecuador, on the western slopes of the Andes at about 2500 m. elevation.

REMARKS: We know *Saphenophis atahuallpae* only from Steindachner's (1901, 1902) descriptions and illustrations of the holotype. I previously (Myers, 1969) clarified the bibliographic confusion involved with the name, removed it from the synonymy of *Lygophis whymperi* (= *boursieri*), and tentatively transferred it to the genus *Leimadophis*. I now transfer it to *Saphenophis* on the basis of color-pattern similarity with the newly described *S. sneiderni*. Steindachner's second description (1902) of the holotype is fairly detailed, but is lacking in several critical respects (sex of specimen, maxillary dentition, dorsal scale-row formula); the scale-row position of

the lateral stripe was not mentioned in the written description but, fortunately, is discernible from the figure.

***Saphenophis sneiderni*, NEW SPECIES**

Figures 2B, 3C, 5C, 9, 10

Rhadinaea brevirostris (not of Peters): RENDAHL AND VESTERGREN, 1940, p. 6 (misidentification).

HOLOTYPE: Naturhistoriska Riksmuseet, Stockholm, 3129,¹ an adult or subadult female from El Tambo, Department of Cauca, Colombia, obtained by Kjell von Sneidern in 1935 or 1936. El Tambo is a village situated about 21 kilometers westward² from Popayán, on the eastern slopes of the Cordillera de Occidental. According to Rendahl and Vestergren (1940), El Tambo is at an elevation of 1745 meters, between the headwaters of the Río Cauca and the Río Patía.

PARATYPE: Naturhistoriska Riksmuseet, Stockholm, 3129,¹ an adult female with same data as holotype.

ETYMOLOGY: Named in honor of Kjell von Sneidern, whose collecting activities have resulted in the only known specimens of *Saphenophis sneiderni*, in one of the two known specimens of *S. tristriatus*, and also in the only specimen of *S. boursieri* known from Colombia. Mr. von Sneidern has therefore contributed greatly to an understanding of this genus.

DEFINITION AND DIAGNOSIS: Ground color of dorsum brown (brownish gray under stratum corneum), of lower sides (below lateral dark stripe) paler brown (gray); ground color almost uniform except for narrow dark gray edging on scales. No vertebral line. Lateral dark line continuous from neck to tail, anteriorly narrow, involving rows 3-4, and containing some pale areas, becoming broader and darker posteriorly—not bordered above by pale line or spots. Supralabials pale brown but with vivid white horizontal line, margined above by black stripe extending along side of head to fuse with lateral body stripe on side of neck. No nape ocelli. Dark pigment on ventral tips posteriorly fusing into solid black ventrolateral stripe. Pale belly clouded with grayish brown and with tendency for dark transverse streaks, becoming almost immaculate near cloaca and under tail. Dorsal scales 19-17-15 or 17-17-15, reducing to 17 rows by loss of paravertebrals and to 15 rows by fusion of 3+4. Ventrals in two females 149,

¹ The holotype and paratype are catalogued under the same number and are not individually tagged, but the specimens are readily separated by characteristics of size and scutellation (see table 2).

² El Tambo is plotted on most maps as being west-southwest of Popayán, although a recent United States Air Force map (Operational Navigation Chart, ONC L-26, 1969) puts it in a west-northwest location.

152; subcaudals 54, 56. Largest specimen (adult) 503 mm. total length.

Saphenophis sneiderni is readily distinguished from its congeners by its color pattern. The species differs from *S. antioquiensis*, *S. boursieri*, and *S. tristriatus* by the following combination of pattern characteristics (any one of which will separate all known specimens, but variational limits of the species are unknown): No dark vertebral line. Dark lateral body stripe confluent with lateral head stripe and anteriorly lying on scale row 4 or rows 3-4 (rather than rows 5 or 5-6). Lateral dark stripe posteriorly broad, occupying at least two full scale rows in front of tail, not bordered above by pale stripe or spots. Other distinctive but more subjective characteristics of the type specimens of *sneiderni* include the less heavily marked venter, and brown-suffused supralabials with a vivid white horizontal line. Indication of the white labial line may be seen in other species but is usually not so well defined (except in some *boursieri*, see fig. 5A, C) because the labials are basically white rather than brown as in *sneiderni*. Of all the above characters, I am most inclined to place greatest reliance on the position (especially anteriorly) and width (especially posteriorly) of the lateral dark stripe.

In color pattern, *Saphenophis sneiderni* seems closest to the enigmatic *S. atahuallpae*, known only from descriptions (Steindachner, 1901, 1902) of a single specimen from west-central Ecuador. *Saphenophis sneiderni* differs in the absence of a dark vertebral line (distinct in *atahuallpae*), brownish supralabials (yellowish white with dark spots in *atahuallpae*), horizontal white line on supralabials (absent in *atahuallpae*) and, possibly, in a lower number of ventrals and subcaudals.

DESCRIPTION OF HOLOTYPE: Female, adult or subadult (compare size with adult female paratype), of slender proportions, with head little wider than neck; total length 422 mm., tail 94 mm. Dorsal scales smooth, lacking apical pits or anal ridges, in 19-17-15 rows; anterior reduction to 17 rows by loss of paravertebral rows at ventrals 15 (left)/17 (right), posterior reduction to 15 rows by fusion of rows 3+4 at ventrals 90/93. Ventrals 149, preceded by two wide gulars (preventrals), anal plate divided, subcaudals 56. Rostral plate less than half as high as wide, tipped slightly forward and but narrowly visible from above. Internasals as wide as long, but greatly narrowed anteriorly, 0.7 times as long as prefrontals. Prefrontals as wide as long, each in contact with frontal, supraocular, preocular, loreal, nasal, and internasal as well as other prefrontal. Frontal 1.7 times longer than wide, and 1.3 times longer than its distance to tip of snout; frontal posteriorly somewhat rounded in outline, lacking posterolateral corners (i.e., not pentagonal). Supraocular posteriorly almost as wide as greatest (anterior) width of frontal, narrowed in front. Parietals

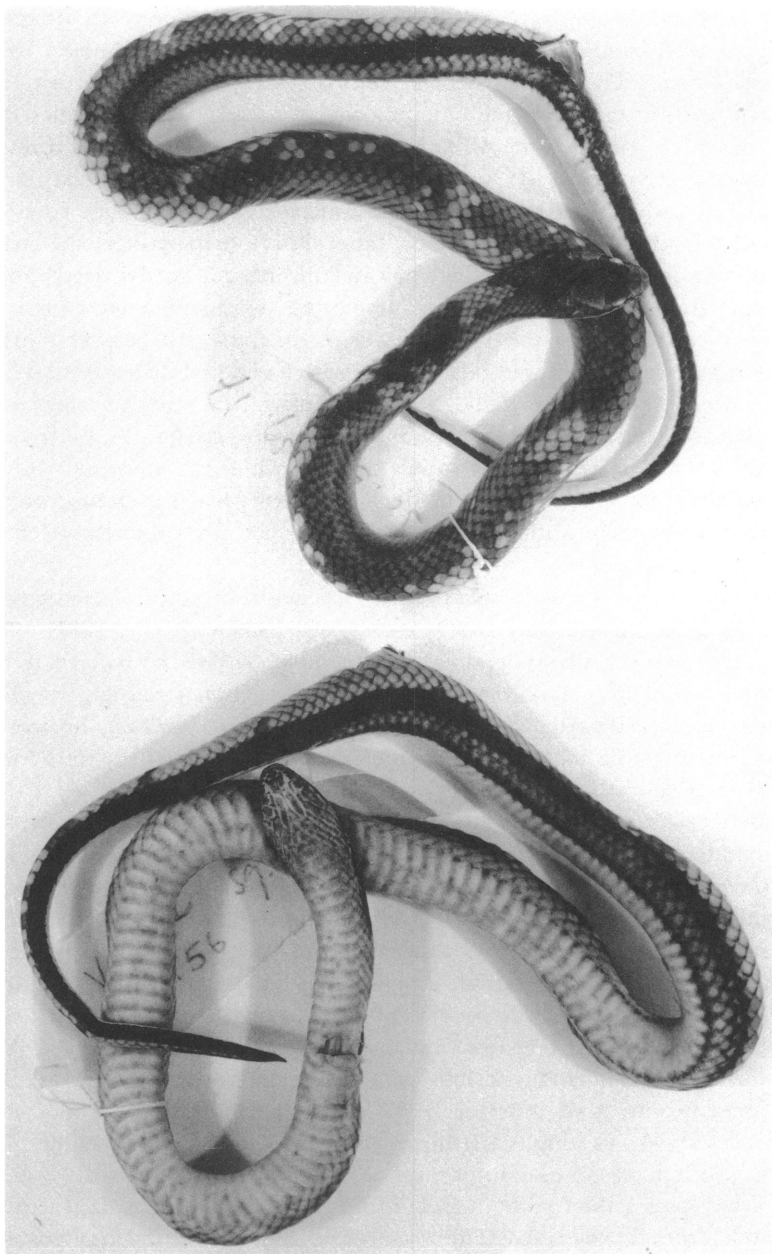


FIG. 9. Dorsal and ventral views of the holotype of *Saphenophis sneiderni*, new species; see figure 5C for details of head.

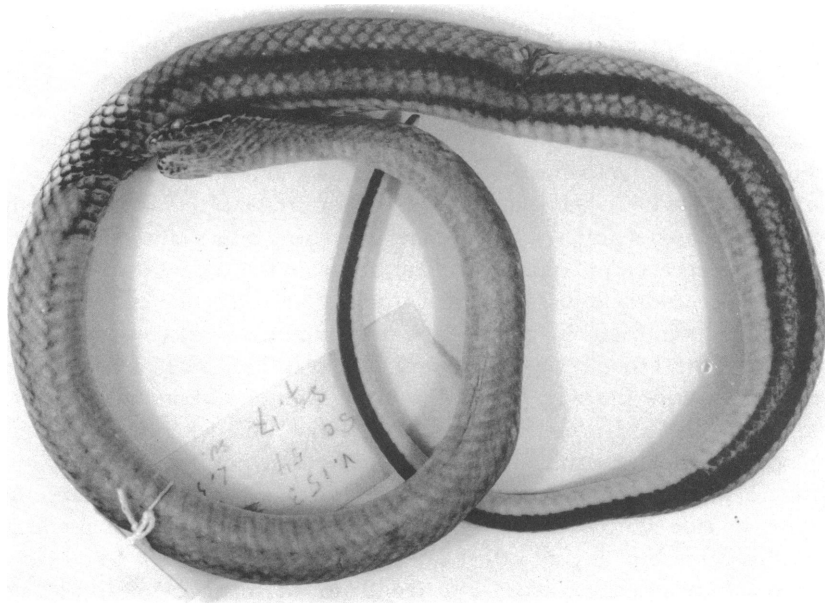


FIG. 10. Paratype of *Saphenophis sneiderni*.

about 1.4 times longer than broad; interparietal suture shorter than frontal, equal to distance from anterior edge of frontal to tip of snout. Nasal plate divided below naris, deeply grooved above. Loreal on each side of head higher than wide, irregularly four-sided. One large preocular; two postoculars, lower about half as large as upper. Temporals 1+2. Supralabials 8, second touching loreal, 3-5 in orbit. Infralabials 10 (left)/11 (right), first pair in contact behind mental, 1-5 touching anterior genials, 5-6 touching posterior genials. Anterior genials conspicuously shorter than posterior ones, but with longer intergenial suture. Diameter of eye equal to distance from its anterior edge to posterior edge of naris, extending 1.7 times into length of snout. Tiny, inconspicuous tubercles present on head plates, being most concentrated on anterior part of head.

Top of head and dorsum of trunk and tail medium brown, except for patches of pale brownish gray where lacking stratum corneum; ground color uniform except for accumulation of dark pigment on concealed anterobasal edges of each body scale, these dark edges showing through overlying translucent scales—each scale thereby appearing as if completely edged in dark gray. Lateral black stripe continuous from side of head to tail, being narrow and ill-defined anteriorly and becoming broad and vivid

posteriorly, as follows: anteriorly formed mainly by black bordering on scales of row 4, tending to include row 3 toward midbody, then primarily row 3 after place of reduction to 15 scale rows (by fusion of rows 3+4); black pigment gradually intensifies, fills in light centers of scales, and expands to again include row 4, until, shortly before tail, forming a wide, solid black stripe including all of rows 3 and 4 and adjacent edges of rows 2 and 5. Side of body below lateral stripe paler brown (gray under stratum corneum) than dorsum, with scale edges appearing only slightly darkened. Dark pigment accumulating on ventral tips from midbody (about ventral 80) and posteriorly intensifying and forming narrow, solid black stripe. Lateral and ventrolateral black stripes fused immediately behind cloaca, forming single broad stripe on side of tail to its tip. Side of head with irregular, narrow black line extending along tops of anterior supralabials and under eye and posteriorly widening into a broader stripe covering tops of posterior supralabials and part of bottom postocular and lower temporal region; this stripe confluent with lateral body stripe after dipping slightly on side of neck. Lateral head stripe edged below by a vivid white line, this being broken and rather faint anterior to eye but solid and conspicuous from eye across corner of mouth to side of neck, disappearing about four scales behind corner of mouth. Supralabials otherwise heavily suffused with light brown, almost uniformly colored except for faint vertical dark lines on common labial sutures and whitish lower edges of supralabials 5 and 6. Underside of head similarly colored by light brown pigment, turning dark brown on chin, but with mottled effect owing to presence of irregular whitish areas on infralabials and genials. Gular region gray. Rest of venter yellowish white—immaculate in cloacal region and under tail, but belly clouded with pale grayish brown, tending to be concentrated as a vague transverse streak on base of each ventral plate.

Right maxilla, examined *in situ*, with 20 subequal teeth (counting sockets) followed by two moderately enlarged, ungrooved fangs. Last one and one-half prediastemal sockets posterior to front edge of ectopterygoid process. Diastema smaller than on maxilla of paratype (fig. 2B).

PARATYPE: Adult female 503 mm. total length, 109 mm. tail length; at least four large oviductal eggs, one (revealed by dissection) measuring 9 by 23 mm. Scutellation and relative proportions similar to holotype, differing mainly in lower number of anterior dorsal scale rows and in numbers of oculars; principal scale counts summarized in table 2.

Color pattern differing in few details from that of holotype: Top of head not uniform brown but turning whitish or pale tan on posterior parts of internasals and outer edges of supraoculars and parietals. Lips and underside of head more conspicuously mottled, owing especially to intensification

TABLE 2
SCALE COUNTS AND MEASUREMENTS (IN MILLIMETERS) OF THE
TYPES OF *Saphenophis sneiderni*

	Holotype ♀	Paratype ♀
Dorsal scale rows	19-17-15	17-17-15
Ventrals at posterior scale-row reduction (3+4)	90/93	93/91
Ventrals	149	152
Subcaudals	56	54 ^a
Supralabials	8	8
Supralabials touching eye	3-5	3-5
Supralabial touching loreal	2	2
Preoculars	1	2 ^b
Postoculars	2	1/2
Temporals	1+2	1+2
Infralabials	10/11	10
Infralabials touching anterior genials	1-5	1-5
Infralabials touching posterior genials	5-6	5-6
Total length	422	503 ^a
Tail length	94	109 ^a
Tail length as a percentage	22.3	21.7

^a Terminal spine missing, including probably no more than one or two pairs of subcaudals (if any).

^b The two preoculars on the left side of the head are about equal in height, whereas the bottom preocular on the right is a tiny plate that is situated above the suture between supralabials 2 and 3 and is not in contact with the orbit.

and clumping of dark brown pigment on supralabials. Belly more heavily clouded by grayish brown pigment, with pigment more suffused and not so limited to transverse streaks on bases of ventrals.

Right maxilla (fig. 2B) with 21+2 teeth; last two prediastemal sockets posterior to front edge of ectopterygoid process; diastema distinct; prediastemal teeth subequal, ungrooved fangs enlarged about one and one-fourth times, with socket of last fang being offset laterad (but very slightly) from a plane connecting prediastemal teeth and first fang. Palatine and pterygoid teeth subequal except for first several on palatine being slightly longer than others; 11 palatine, 25 pterygoid teeth on right side. Right mandible with 26 subequal teeth, more slender and not so strongly recurved as palatine-ptyergoid teeth.

REMARKS: There will be some uncertainty over the generic position of this species until the hemipenis has been examined. Nonetheless, charac-

teristics of dentition, scutellation, habitus, and coloration indicate that *sneiderni* is related to *Saphenophis boursieri*, *S. tristriatus*, and *S. antioquiensis*. Inclusion of *sneiderni* with this group of species would require relatively few changes in my earlier definition of the "*boursieri* species group" (Myers, 1969, p. 23). The changes would mainly be in color pattern (e.g., absence of a vertebral dark line in *sneiderni*, and position of the lateral dark stripe) and are the kind that more often reflect interspecific rather than intergeneric differences. The differences are sufficient, however, for the informal recognition of two species groups.

Saphenophis sneiderni probably is more closely related to *S. atahuallpae* than to the three congeners mentioned above, although this cannot be ascertained with confidence until *atahuallpae* has been rediscovered. But the resemblances between the type specimens of *sneiderni* and the type description of *atahuallpae* suggest to me a relationship at the species group level.

SAPHENOPHIS COMPARED WITH ANTILLOPHIS

In an essay on West Indian snakes, Maglio (1970, p. 35) made the provocative suggestion that the continental *Saphenophis* "*boursieri* might be placed in a separate genus with [*Antillophis*] *andreae* and *parvifrons* as a specialized radiation, perhaps derived from mainland *Alsophis*." The West Indian *Antillophis* Maglio, of Cuba (*andreae*) and Hispaniola (*parvifrons*), does seem to belong to the same suprageneric group as *Saphenophis*, but Maglio's concepts of xenodontine genera were based primarily on skull and hemipenial characters—to the exclusion of color pattern and habitus, which also must be considered when defining natural assemblages of Neotropical colubrids.

I fail to see significant indications of close (i.e., congeneric) relationship after direct comparison of specimens of *Saphenophis* with specimens of *Antillophis andreae* and *A. parvifrons* in the collection of the American Museum of Natural History. I am impressed, however, by the nature of the differences between the two species of *Antillophis*. Both are relatively small snakes with relatively long tails, but *parvifrons* has a normally compact body that is as high or higher than wide, whereas *andreae* is wider than high. Most of the preserved specimens of *andreae* are very flattened and have somewhat loose-fitting skin. Some have indications of anterior cross-banding, caused by the nonrandom distribution of white scale edges; these pale markings probably are concealed except when the skin is stretched. An ability to flatten at least the anterior part of the body and thereby display contrasting colors in the "hood" region is not uncommon among West Indian colubrids, and the trait is possessed by *andreae* and *parvifrons* both (Albert Schwartz, *in litt.*; see Thomas and Schwartz, 1965, p. 74, for

reference to *A. parvifrons stygius*). But, judged from the aforesaid differences in habitus, I suspect that *andreae* possesses this ability to a greater extent than does *parvifrons*. In addition to habitus, *Antillophis andreae* and *A. parvifrons* differ also in basic color pattern, and neither is close to the situation in *Saphenophis*. Some populations of *parvifrons* are melanistic, but generally this species has a distinctive striped pattern, whereas *andreae* is basically dark, with pale spots on the lower two scale rows and with a variable amount of white flecking or even a tendency for cross-banding. *Antillophis andreae* has dark transverse streaks on the venter, but these streaks are on the free edge of the ventral scute rather than on the base as in *Saphenophis*.

Both species of *Antillophis* have scale pits, which are absent in *Saphenophis*.

Maglio's (1970, fig. 27) illustration of the uneverted hemipenis of *Antillophis parvifrons* shows that it is of the same general type known in *Saphenophis*, although hemipenial structure in *parvifrons* is closer to that of *Alsophis* and some other snakes in having the two calyculate areas confluent at the bases of the lobes on the sulcate side. *Antillophis parvifrons* resembles *Saphenophis* and *Alsophis* in having semicapitate hemipenial lobes which are almost completely nude on the asulcate side—a fact not evident from Maglio's figure (*loc. cit.*).¹ In striking contrast, the hemipenis of *Antillophis andreae* has well-defined transverse ridges (flounces) of papillae on the asulcate side of the lobes, and relatively broad, nude interspaces between these ridges (personal observ.; see Grant, 1943, for a rough sketch of the everted hemipenis). Therefore, despite Maglio's indication (1970, pp. 34–36) of "very close" similarity, the copulatory organ of *Antillophis andreae* differs noticeably from that of its congener *parvifrons*, as well as from *Lygophis* [= *Saphenophis*] *boursieri*.

Maglio found potential taxonomic usefulness in the shapes of the frontal and prefrontal bones. Nonetheless, possibilities of convergence in these characters will have to receive further attention. The extraordinary hemipenial diversity among West Indian snakes that were formerly in *Dromicus*, but reassigned by Maglio to *Antillophis* and *Arrhyton*, suggests that there is still much to learn about affinities and evolution of these snakes. But, in

¹ This is probably because of how the figure is drawn. However, there may be intra-specific variation in a few features of the hemipenis of *Antillophis parvifrons*. I examined the uneverted hemipenis of a specimen of *A. p. niger* (AMNH 40386). This organ has more numerous and smaller calyces near the sulcus spermaticus than illustrated by Maglio, and, furthermore, the large calyces bordering the asulcate nude area are ornamented with large, blunt, conspicuous spinules. Somewhat similar spinules are either present or not on the hemipenis of adult *Rhadinaea brevirostris* (*vide* Myers, *In press*), but it is not known whether the variation is geographic, seasonal, or uncorrelated.

any case, I conclude that any group(s) containing the Antillian *andreae* and *parvifrons* will have to be kept generically separate from *Saphenophis*. Thorough study of such groups as *Philodryas* and mainland "*Alsophis*," as well as additional study of West Indian xenodontines, should give insight into some perplexing zoogeographic problems. I concur with Maglio (1970, p. 50) in the need for continued study using as many kinds of evidence as possible—but I would not go so far as to insist that *all* the new kinds of data Maglio mentioned will be necessary, before we are able "to draw firmer conclusions" than his.

EVOLUTION AND ZOOGEOGRAPHY

The classification of colubrid snakes in general, and of South American colubrids in particular, is in a notoriously unsatisfactory state. A pervasive pessimism seems to have existed among snake systematists ever since Bogert (1940) demonstrated that Dunn's (1928) arrangement of colubrid subfamilies in the Americas did not correlate with natural groupings of African colubrids. Dunn's arrangement was an updating of the earlier Copeian system, which utilized several anatomical characters but gave particular weight to the hemipenis. Bogert (1940, p. 10) remarked that, "The conclusion is inevitable that penaeal characters, although extremely useful in gaining an understanding of generic relationships, are unsatisfactory as subfamily characters." This criticism was based principally on Dunn's use of the simple versus bifurcate sulcus spermaticus as a key character, and, in this context, Bogert's remarks are well taken. Nonetheless, the potential usefulness of hemipenial characters in separating large groups of genera (including subfamilies?) has scarcely begun to be exploited. The extreme importance of the hemipenis to taxonomic study of Neotropical and West Indian "xenodontine" snakes is being amply reaffirmed (e.g., Clark, 1945; Dowling, 1969; Maglio, 1970; Myers, *In press*; Vellard, 1946).

Saphenophis (and *Antillophis*, see above) belongs to the group of xenodontine genera that Dunn (1928, p. 21) characterized as having a "Normal, double" hemipenis. Vellard (1946) and Dowling (1969) added *Philodryas* to this assemblage, and the latter author noted that most South American colubrids appear to fall into one of four undefined groups. In his group number 3, to which *Saphenophis* belongs, Dowling further characterizes the hemipenis as being "bilobed [double], non-capitate [normal] or semi-capitate, spinose, and calyculate . . . with a bifurcate sulcus" (Dunn's terminology added in brackets). I agree with the usefulness of Dowling's groupings, but his definitions must be modified in order to account for variability within the groups—for example, to avoid including in group 3

a type of hemipenis that actually belongs with group 2 (defined as "a single, capitate, spinose, and calyculate hemipenis with a simple or apically bifurcate sulcus"). Most species of *Rhadinaea* have a single, capitate hemipenis and clearly fit into group 2, but the primitive organ in *Rhadinaea* is a slightly bilobate type (Myers, In press) that at first might be thought to invalidate Dowling's definitions. But the groups can be usefully maintained if the following distinctions are kept in mind. In bilobed hemipenes belonging to group 2, the distal calyculate area is contained within a single capitulum or head; even in species in which capitation of the organ has been lost (e.g., *Rhadinaea calligaster*), the small calyculate lobes still give the appearance of being part of a single head region. In the more deeply divided hemipenes of group 3, there are two distinct head regions, and, if capitation is present, it is manifest in a separate overhang below the asulcate tip of each lobe ("semicapitate"). Conversely, it appears that individual species in some group 3 genera can lose bilobation of the hemipenes (see Vellard, 1946, p. 278). In such cases so far known (Myers, In press; Vellard, 1946, fig. 46A), the place of bifurcation of the sulcus spermaticus provides a critical clue to relationships: In the normally divided or occasionally undivided hemipenis of group 3, the sulcus divides at a point less than halfway up the organ, in many cases close to the base. In contrast, in the normally single or occasionally bilobed hemipenis of group 2, the sulcus divides at a point more than halfway up the organ.

There is persuasive evidence (Myers, In press) that the divided, or bilobed, hemipenis is primitive, and that the single type is derived. Given this assumption, it seems quite possible that the single hemipenis in Dowling's group 2 (Dunn's "capitate, single") was derived from the divided type in group 3 (Dunn's "normal, double"). The group 2 type of hemipenis might have been derived from one similar to that of *Saphenophis tristriatus* (fig. 4B), which is semicapitate and is bilobated for only about 30 percent of its length, and in which the sulcus spermaticus divides relatively high on the organ. A gradual shortening of the lobes, with a basal retreat and gradual union of the two calyculate areas, could result in a single or almost single organ in which the calyces were contained in a single head region; capitation might be either elaborated or lost, even in the same genus (e.g., *Rhadinaea*). Such a derived organ would be shorter than the original but could be secondarily lengthened by simple elongation of the base, which in fact has occurred intraspecifically in some populations of extant *Rhadinaea* (e.g., *R. decorata*, Myers, In press, fig. 16). Within *Saphenophis* itself, both elongation of the base and distal shortening of the lobes could have combined to produce the hemipenis of *Saphenophis tristriatus* from that of *S. boursieri*. The hemipenis of the latter seems more

primitive in the greater extent of bilobation and in having the sulcus spermaticus deeply forked.

Unfortunately, in *Saphenophis* only the hemipenes of *S. boursieri* and *S. tristriatus* are known. Although *S. boursieri* may be more primitive in hemipenial structure, aspects of color pattern in this species are probably derived from an ancestral type that is most nearly approached in the relict *S. antioquiensis* and *S. tristriatus*. The last two species are so similar in all their characteristics (Myers, 1969), save for a few aspects of scutellation, that they must have had a common ancestor with similar characteristics, including a uniform ground color, dark lateral and vertebral lines extending the length of the body, and pale markings above the lateral dark line. This ancestor might also have had the high number (19) of anterior scale rows still found in *antioquiensis*, but reduced in the other two species. *Saphenophis boursieri* presumably was derived from such a stock by reduction of the anterior scale rows, by acquisition of dark pigment on the scale edges, and by the tendency for reduction and loss of the vertebral and lateral dark lines. A three-part fragmentation of the ancestral stock is sufficient to account for the origin of the three species of the *boursieri* group. The two species of the *atahuallpae* group perhaps were similarly derived from fragmentation of a single ancestral stock, but the relationship of that stock to the progenitor of the *boursieri* group is a moot question. However, a species ancestral to both of the present species groups probably had a broader, more vivid dark stripe on the side of the neck. In the *atahuallpae* group, the low lateral line, which is continuous from the eye back, represents the lower edge of the primitive stripe. In the *boursieri* group, the higher lateral line (when present) represents the upper edge of the primitive stripe and overlaps slightly with the anterior remnant of the lower edge (which terminates on the neck); this condition is shown in figure 5B. Possibly, the primitive condition of the stripe may prove to be still present in the variational repertory of one or more living species (which would cause difficulty in using the key on p. 10); one specimen (the holotype) of *S. boursieri* has a faint gray streak in the same position on the neck as the low black line that characterizes the *atahuallpae* group. In fact, several aspects of the color pattern of *S. boursieri* help to bridge the gap between the two species groups. Thus, absence of the vertebral line in one species (*S. sneiderni*) of the *atahuallpae* group is a culmination of the trend in *S. boursieri* toward loss of the median line. *Saphenophis boursieri* and *S. sneiderni* both tend to have dark-edged body scales, although the trait is more strongly developed in the former species. A correspondence shared by *S. boursieri* and both members of the *atahuallpae* group is that the lateral and ventrolateral dark lines or stripes fuse close behind the cloaca, forming a

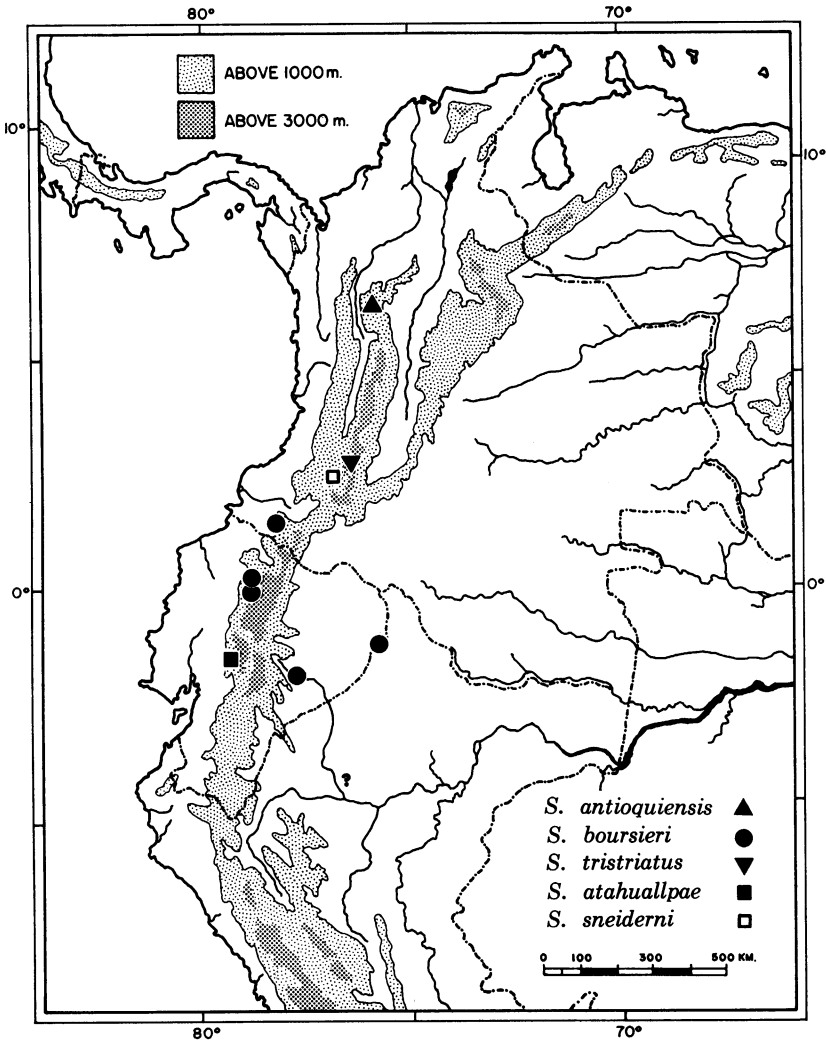


FIG. 11. Northwestern South America, showing known localities for the species of *Saphenophis*. Positioning of the circle for the southernmost record is speculative, owing to the imprecise locality data ("Río Pastaza between Canelos and Río Marañón" [*S. boursieri*]); this locality might be well into Peru rather than Ecuador, as indicated by the question mark near the junction of the Pastaza and Marañón rivers.

single, broad stripe on the side of the tail. These markings tend to remain separated on the tail in the other species (*S. antioquiensis*, *S. tristriatus*) of the *boursieri* group.¹

The relatively young age of the Andean landscape and pronounced climatic fluctuation in the northern Andes during the Quaternary (van der Hammen, 1961; B. Vuilleumier, 1971) suggest that the extant species of *Saphenophis* have evolved fairly recently, that is, well within the last million years. One or two ancestors of the present species may be presumed to have been widely distributed during the Riss or Würm glaciations, when disjunct montane habitats were displaced downward and laterally connected to a much greater degree than at present. Fragmentation of the ancestral range occurred during a drier and warmer postglacial period when the montane environments were displaced upward. Such vertical migrations evidently allowed *Saphenophis boursieri* to adjust to a variety of habitats, as that species is now found in the upper Amazonian lowlands and on both Atlantic and Pacific slopes of the Andes. The other species have not been so adaptable and may have evolved from isolated stocks in the seemingly restricted ranges in which they now occur. Sympatry is unknown, although the ranges of three species approach one another in southern Colombia (fig. 11). But two of these, *Saphenophis sneiderni* and *S. tristriatus*, probably are now effectively separated by the valley of the Río Cauca, and they may also be adapted to life at different elevations. *Saphenophis boursieri* probably is isolated at least from *S. sneiderni* by the dry corridor of the Patía-Cauca valleys, although *boursieri* conceivably might occur with *S. atahuallpae* in western Ecuador. My views of the zoogeography and recent evolution of the species of *Saphenophis* are consistent with recent interpretations of the Andean bird fauna (e.g., Haffer, 1970; F. Vuilleumier, 1969).

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¹ My earlier notes on the holotypes of *Saphenophis antioquiensis* and *S. tristriatus* are not explicit on this point, although I wrote that the stripes “run unbroken to the tip of the tail.” But the lateral and ventrolateral markings are definitely unconnected on the new specimen of *tristriatus* reported herein. I have not checked all specimens of *S. boursieri* for this characteristic, but the two stripes become one on at least the following individuals: Field Mus. Nat. Hist. 36622; Mus. Comp. Zool., Harvard, 36948; Mus. Natl. d’Hist. Nat. 858 (holotype).

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