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South American Snakes Related to *Lygophis boursieri*: A Reappraisal of *Rhadinaea antioquiensis*, *Rhadinaea tristriata*, *Coronella whymperi*, and *Liophis atahuallpae*

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In the course of revisionary studies of *Rhadinaea* and some allied groups of Neotropical, colubrid snakes, I have been particularly puzzled by the descriptions of *Rhadinaea antioquiensis* and *R. tristriata*; both species are from the Andes of Colombia, and are known only from the description of a single specimen of each. I recently had the privilege of examining the type specimens, and it was immediately apparent that they are closely related to the snakes presently known as *Lygophis boursieri* and *L. whymperi* and must be removed from the genus *Rhadinaea*. In addition to commenting on this relationship, I here provide redescriptions and illustrations of the holotypes, to supplement the brief original descriptions and to aid in the identification of future specimens. A lectotype is designated for *Coronella whymperi*, which is again placed in the synonymy of *Lygophis boursieri*; *Liophis atahuallpae* is removed from the synonymy of *Lygophis boursieri* and provisionally placed in the genus *Leimadophis*.

I am obliged to the Reverend Hermano Nicéforo María of the Instituto de La Salle in Bogotá, and to Dr. Greta Vestergren of the Natur-

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historiska Riksmuseet in Stockholm (Swedish Nat. Hist. Mus.), for trusting the holotypes to the mails. Dr. Ernest E. Williams lent me specimens of *Lygophis boursieri* from the collection of the Museum of Comparative Zoology at Harvard (M.C.Z.), and Miss Alice G. C. Grandison and Mr. A. F. Stimson sent the syntypes of *Coronella whymperi* from the British Museum of Natural History (B.M.N.H.). An additional specimen of *boursieri* had been examined prior to this study through the courtesy of Dr. James E. Böhlke and Mr. Edmond V. Malnate, Academy of Natural Sciences of Philadelphia (A.N.S.P.). I discussed aspects of the study with Dr. James A. Peters, who shared with me his knowledge of Ecuadorian geography. Dr. Janis A. Roze corrected my translation of a passage by Franz Steindachner, and Dr. Richard G. Zweifel reviewed the manuscript. I particularly thank Mrs. Ellen E. Bowler for her skillful drawings of hemipenes and a maxilla.

***Lygophis antioquiensis* (Dunn), new combination**

Figures 1-3

Rhadinaea antioquiensis DUNN, 1943, p. 307. Type locality: Colombia, Departamento Antioquia, San Pedro, elevation 2560 meters. Holotype: Mus. Inst. La Salle, Bogotá, No. 386.

REDESCRIPTION OF HOLOTYPE: The specimen is an adult female of moderately slender proportions, except that the posterior part of the body is swollen by large eggs in the oviducts; the head is little wider than the neck. The total length is difficult to measure; it is approximately 665 mm.; the tail is 159 mm., or 23.9 per cent of the total length. The dorsal scales are smooth, lacking apical pits or anal ridges, and are in 19-17-15 rows; scale row reduction is irregular (see page 6) but occurs mainly by loss of row 4 at the level of ventrals 72 (left) and 68 (right), and by fusion of rows 7 and 8 on the posterior part of the body. On the tail, reduction from 10 to eight rows occurs at the level of subcaudal 5, to six rows at subcaudal 14, and to four rows between subcaudals 35 and 37. There are 168 ventrals (Dowling system), one preventral, 62 pairs of subcaudals, and a divided anal plate. The rostral is more than half as high as wide and is tipped forward so that it is but narrowly visible from above. The internasals are slightly wider than long, about two-thirds the length of the prefrontals. The prefrontals are wider than long; each is in contact with the frontal, a supraocular, preocular, loreal, nasal, internasal, and the other prefrontal. The frontal plate is about one and a third times longer than wide, and is equal in length to the distance from its anterior edge to tip of snout; the hind part of the frontal is peculiarly tridentate, with a rounded cusp to each

side of, and anterior to, the posterior apex, which is slightly rounded. The supraocular is nearly as wide posteriorly as the greatest width of the frontal, and is slightly narrowed on its anterior part. The parietals are less than one and a half times longer than broad; the interparietal suture is shorter than the length of the frontal. The nasal plates are damaged, but are seemingly divided or deeply grooved, at least below the naris. The loreal on the left is partly fused with the preocular; the right loreal is a little higher than wide, irregularly rhomboidal, and tipped forward. There are 1/1 preoculars; the postoculars are 2/1, the lower one on the left no more than a third the size of the upper one; the temporals are 1 + 2. There are 7/8 supralabials, with 3-4/3-5 bordering the eye; there are 10 infralabials, with the first pair in contact, the first five touching the anterior genials, and the fifth to sixth (left) or the fifth (right) touching the posterior genials. The anterior genials are a little longer than the posterior ones. The diameter of the eye is equal to the distance from its anterior edge to the center of the naris, extending one and a half times into length of the snout. Tiny, inconspicuous tubercles are present on all head plates, but are most concentrated on the anterior part of the head.

The head and body are dark brown. There is a median, narrow black stripe on the vertebral scale row, overlapping slightly onto the paravertebrals. A lateral, pale tan stripe occupies adjacent halves of two scale rows (5-6 anteriorly, 4-5 posteriorly); this line (fig. 2) is fairly straight and continuous on the anterior half of the body, but encroachment of dark pigment posteriorly gives it the appearance of two adjacent rows of staggered light spots. Immediately below the pale lateral line is a narrower black line; anteriorly this is on the lower half of row 5, but by reduction from 19 to 17 rows of scales (by loss of row 4) the lateral dark and light stripes are shifted one scale row down. All of the stripes start on the neck and run unbroken to the tip of the tail. Another dark line is on the side of the neck, where it runs caudad for a distance of about 20 ventrals on the upper third of row 2; below this the lower sides of the neck are conspicuously whitish for a distance of about 15 ventrals. There is a vague black-edged, white ocellus on each side of the nape; each ocellus occupies the space of four scales and lies a few scales anterior to the start of the lateral light body stripe and two scales behind the parietal. The supralabials are white, with several bold black markings, and are margined above by an irregular black line, which anteriorly is continuous around the rostral plate and posteriorly continuous with the short, black line on the lower side of the neck. There is indication of a black-bordered, white postocular stripe that slants

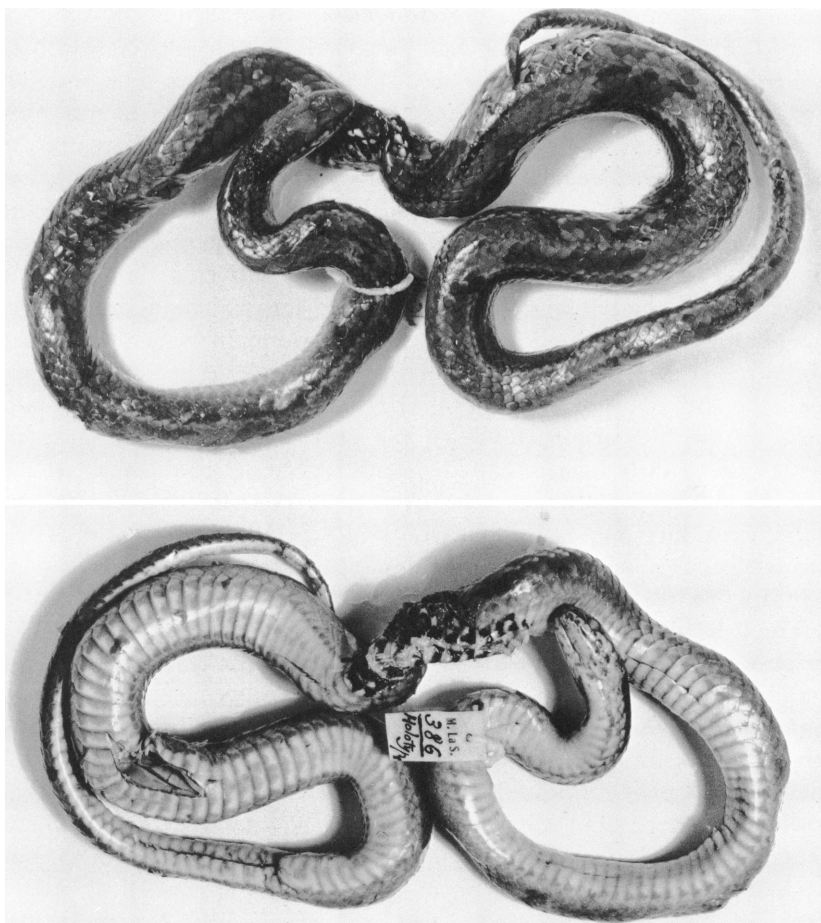


FIG. 1. Dorsal and ventral views of the holotype of *Lygophis antioquiensis*.

from the eye to the corner of the mouth; this stripe is bordered above by the black line on the tops of the labials, but its lower edge is indicated (on each side of the head) only by two discrete black marks. Ventral surfaces are whitish, with black markings. There is conspicuous black spotting under the head, especially on the infralabials. Black streaking and spotting across the base of each ventral plate may or may not be connected with black triangular markings near the sides of each ventral. The ventral markings become progressively larger toward the tail and the triangular markings nearly connect to form a ventrolateral

stripe. The sides of the subcaudals are black, and a black median, zigzag line follows their common sutures.

The right maxilla was removed: this bone bears 21 + 2 teeth, and anteriorly curves strongly toward the median plane of the mouth (fig. 3). Several anterior teeth are slightly shorter than posterior ones, but otherwise the prediastemal teeth may be described as subequal; the ultimate prediastemal socket and one-half of the penultimate lie posterior to the anterior edge of the ectopterygoid process; the diastema is approximately

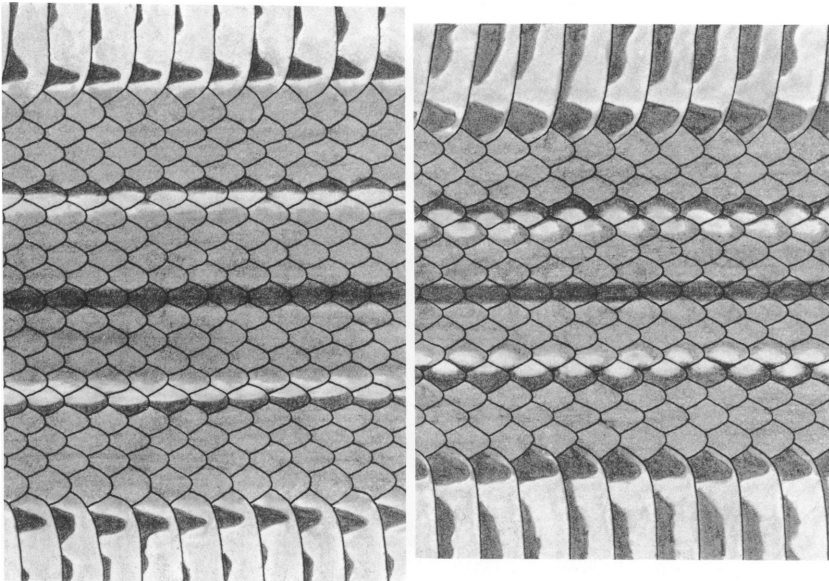


FIG. 2. Color pattern of *Lygophis antioquiensis*, drawn from holotype on generalized scale patterns. *Left*: Anterior body (19 scale rows). *Right*: Posterior body (15 scale rows).

twice the length of the ultimate prediastemal socket. The two fangs are not grooved and are about one and a half times larger than the prediastemal teeth; the last fang is offset laterad from a curved line that could be imagined to connect the prediastemal teeth and the first fang. There are 14 stout, strongly recurved teeth on the right palatine, followed by about 26 teeth on the pterygoid (this bone had been broken before removal); the palatine and pterygoid teeth are recurved, and reduce in size from front to rear. I dissected out the foregoing dentigerous bones and attached them to the specimen in a vial. The left maxilla

had earlier been removed and was not associated with the specimen. The right mandible is broken, but the *in situ* left mandible bears 24 subequal teeth. The anal sacs extend to the level of subcaudals 10/11.

REMARKS: Dunn does not give a collection number for the holotype, which was probably not catalogued until after his examination of it. The specimen (No. 386) that I examined matches well enough the information given by Dunn so that I am convinced it is the holotype as labeled. The main points of resemblance are: 1) the asymmetrical arrangement and number of supralabials and postoculars (although Dunn incorrectly states that only the fourth and fifth labials enter the eye on the right); 2) the size, allowing for the condition of the specimen and normal shrinkage; 3) the number of ventrals (a difference of one in our counts) and subcaudals (a difference of two); 4) the color pattern.

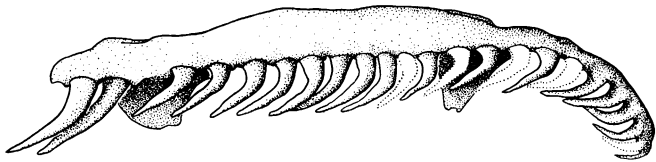


FIG. 3. Right maxilla from holotype of *Lygophis antioquiensis*. $\times 10$.

Scale row reduction is somewhat irregular; because of the poor condition of the specimen, I did not try to determine all the points at which there is a change. Using the method explained by Myers (1967, p. 50), I counted 19 rows of scales immediately behind the head, followed by a reduction to 18 and 17. The method of the foregoing reduction is not clear to me, but at the levels of ventrals 13/15 new paravertebral rows are formed, and again there are 19 rows, until the level of ventrals 72/68, where the fourth rows drop out. The reduction from 17 to 15 rows, posterior to midbody, is by fusion of rows 7 and 8, but this happens several times, because reverse splitting also occurs. On the right side, for example, rows 7 and 8 fuse at the level of ventral 99, there is a reverse split at ventral 101, and fusion again at ventral 135. There is even a fusion and reverse splitting of rows 5 and 6, on the right side at about ventrals 115 and 130 respectively. Dunn errs slightly in stating that the posterior reduction occurs by loss of the paravertebral (eighth) rows, because an enlarged scale at each point of reduction is best interpreted as fusion between the two rows (7 and 8) immediately anterior.

***Lygophis tristriatus* (Rendahl and Vestergren), new combination**

Figures 4, 7

Rhadinaea tristriata RENDAHL AND VESTERGREN, 1940, p. 5. Type locality: Colombia, Departamento Cauca, no other data. Holotype: Naturhistoriska Riksmuseet, Stockholm, No. 3119, collected by G. Gerring in 1938.

REDESCRIPTION OF HOLOTYPE: The specimen is a male, apparently adult, and is of slender proportions, with the head little wider than the neck. Total length is 665 mm.; the tail is 168 mm., or 25.3 per cent of the total length. The dorsal scales are smooth, lacking apical pits or anal ridges, and in 17-17-15 rows; scale row reduction occurs by fusion of rows 3 and 4 at level of ventrals 96 (left) and 93 (right). Reduction on the tail occurs from 10 to eight rows between subcaudals 5 and 7, to six rows at subcaudal 15, and to four rows between subcaudals 40 and 42. There are 174 ventrals, 75 pairs of subcaudals, and a divided anal plate; there are no large, undivided gulars (preventrals). The rostral is more than half as high as wide and is tipped forward so that it is but narrowly visible from above. The internasals are wider than long, about three-fourths the length of the prefrontals. The prefrontals are wider than long, and each is in contact with the frontal, a supraocular, preocular, loreal, nasal, internasal, and the other prefrontal. The frontal plate is about one and two-thirds longer than wide, and is about a third longer than the distance from its anterior edge to tip of snout; the frontal is pentagonal, somewhat rounded at its posterior apex. The supraocular is posteriorly about three-fourths as wide as the greatest width of the frontal and is narrowed in front. The parietals are about one and a half times longer than broad; the interparietal suture is two-thirds the length of the frontal and equal to the length of the snout. The nasal plate is deeply grooved above and below the naris. The loreal on each side is tiny, higher than wide, and narrowed at the base. The preoculars are 2/1, but the one on the right has an incomplete suture that nearly divides it into equal parts; the postoculars are 2/2, the lower plate being at least one-half the area of the upper. The temporals are $1 + \frac{1}{2}$, which is to say that there are three plates in the second vertical row but two of them lie side by side on the bottom. There are 7/8 supralabials, with 3-4/3-5 bordering the eye; there are 9/8 infralabials, with the first pair in contact, the first four touching the anterior genials, and the fourth to fifth touching the posterior genials. The anterior genials are conspicuously shorter than the posterior ones. The diameter of the eye is equal to the distance from its anterior edge to the center of the naris, extending about one and two-thirds times the length of the snout. Tiny, inconspicuous tubercles are present on all head

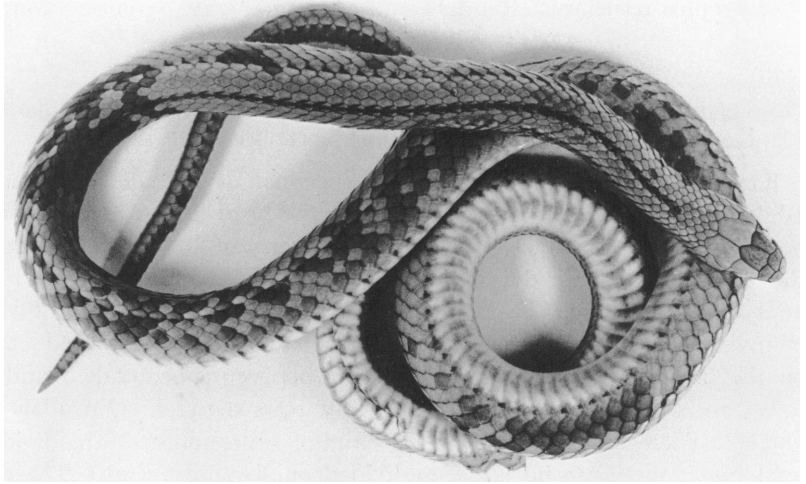


FIG. 4. The holotype of *Lygophis tristriatus*.

plates, being most concentrated on the anterior part of the head.

The head and body are medium brown where the stratum corneum is still present, but gray where it has been lost. There is a narrow black stripe on the vertebral scale row, overlapping slightly onto the paravertebrals. A lateral, pale brown stripe (pale tan under stratum corneum) occupies the upper part of scale row 5 anteriorly, and the upper part of 4 posteriorly; there are also scarcely detectable pale areas on the lower part of row 5 posteriorly, arranged in the same pattern as the staggered rows of pale spots on the posterior body of the holotype of *L. antioquiensis* (fig. 2). Immediately below the pale lateral stripe is a narrower black line; anteriorly this is on the lower edge of row 5, but by the reduction from 17 to 15 rows of scales (by fusion of rows 3 and 4) the lateral dark and light stripes are shifted one scale row down. All the foregoing stripes start on the neck and run unbroken to the tip of the tail. There is a short, black line on the side of the neck, running caudad for a distance of five ventrals on row 3 (anteriorly) and the upper edge of row 2 (posteriorly); below this the lower sides of the neck are pale yellowish for a distance of about four ventrals. There is a faint, pale spot (without dark edging) on each side of the nape; each spot occupies parts of five scales and lies one scale behind the parietal, just above the front end of the lateral dark line and a few scales anterior to the vague origin of the lateral pale line. There is a faint reticulation of pale brown in the darker brown of the head. The supra-

labials are pale yellow, with some faint brownish smudging on the first few and with a light gray spot on adjacent parts of labials 4-5 (left) and 5-6 (right); the supralabials are margined above by an irregular black line, which starts on the first labial and is posteriorly continuous with the short line on the side of the neck. There is no indication of a pale postocular stripe at the corner of the mouth, unless the gray labial spot can be judged a remnant of the lower dark border of such a stripe. The infralabials have faint brownish smudging on pale yellow. The rest of the ventral surfaces are pale yellowish white with gray to black markings; the ends of the ventrals and subcaudals are tipped with gray pigment (brown in life?). Anteriorly there is a midventral series of small, black triangles, one on the base of each ventral plate, starting with the fourth ventral; by about ventral 45 these markings have widened into irregular, mostly dark gray, half-moons, some of which are connected to the dark ventral tips by an extension of pigment along the bases of the ventral scutes. A gray, slightly zigzag line follows the median suture of the subcaudals for most of the length of the tail.

The left maxilla and the right mandible are removed and in a vial, which is attached to the specimen. The maxilla bears 21 + 2 teeth and anteriorly has a moderate curve toward the medial plane of the mouth. The prediastemal teeth increase slightly in size from front to rear, and the last two and a half sockets are posterior to the anterior edge of the ectopterygoid process; the diastema is short, being about the length of the ultimate prediastemal socket; the two fangs are not grooved and are about one and a half times longer than the prediastemal teeth; the last fang is offset laterad from a curved line that could be imagined to connect the prediastemal teeth and the first fang. The maxilla is like that of *L. antioquiensis* (fig. 3) but is less curved, and the suborbital process has a broader tip and the top of the process is not visible in lateral profile. The mandible has 20 subequal teeth.

The retracted left hemipenis extends to the level of the base of subcaudal 10 and is deeply bifurcated, forking at the base of subcaudal 8; its two slips of retractor muscle merge at the end of subcaudal 13, and this muscle inserts posteriorly at the level of subcaudal 34. The sulcus spermaticus lies on the lateral wall and forks at the base of subcaudal 5. This organ was split on its ventral side, removed, and pinned flat so that it could be illustrated (fig. 7) and examined in greater detail. The lobes comprise a third of the total length of the organ. Approximately the distal half of the stalk is rather thickly spinose, with small, recurved spines that become larger near the top of the stalk where it

bilobates; below the spinose area, the basal part of the stalk is ornamented only with inconspicuous spinules on its asulcate surfaces. The sulcus spermaticus forks about two-thirds of the distance up the stalk, each branch extending nearly to the tip of a lobe; the walls of the sulcus are deep and straight, without convolutions; the sulcus is not simply a narrow groove, as its walls can be spread far apart, especially on a lobe. The sulcus is bordered by a dense fringe of small, slightly recurved spines along most of its length on the stalk, and by broader calyculate areas on the lobes. The calyces are medium-size on most of the lobe but much larger basally, where they extend down onto the stalk between the forks of the sulcus; all of the calyces are heavily ornamented with, and partly concealed by, papillae on their edges. The organ is not capitate in that there is no delineated "head" region, but the tip of a lobe is covered by papillate calyces which, on the asulcate side, make an overhang reminiscent of the edge of a capitulum. Below this overhang is a virtually nude strip (having only a few tiny spines) that runs down the lobe on the side opposite the sulcus and which is flanked by calyces and bordered at its base by spines. There is a deep, nude, longitudinal "pocket" on the dorsal wall of the lobe flanked by high walls of tissue that bear calyces on their outer surfaces; one of these walls that separates the pocket from the nude strip probably forms a protuberance on the naked side of a lobe when the hemipenis is everted.

REMARKS: Rendahl and Vestergren (1940) do not mention the sex of the holotype, and the specimen that I examined did not come with a tag attached. Nevertheless, there is no question that it is the holotype. My counts agree with theirs in numbers of supralabials on the left and right sides (including those touching the eye), and in number of ventrals, and we differ by only one in the number of subcaudals, which would be explained if they included the terminal spine. Our respective measurements of total length differ only by 5 millimeters, which is less than might be expected in the case of a somewhat contorted specimen. Rendahl and Vestergren state that there are two preoculars; I give 2/1, but note that the one on the right is nearly divided. No mention of scale row reduction is made in the type description, but this is also true of other species in the same paper. No mention is made of the pale lateral line, which is not very conspicuous.

LYGOPHIS ANTIOQUIENSIS AND *LYGOPHIS TRISTRIATUS*
COMPARED WITH *LYGOPHIS BOURSIERI*

The holotypes of *antioquiensis* and *tristriatus* strongly resemble specimens

of *Lygophis boursieri* (Jan and Sordelli) in most respects. The following comparisons do not include the syntypes of *Coronella whymperei* (= *L. boursieri*), which will be considered separately.

Basic color pattern is identical in these three species: All have a vertebral black line (or series of spots in some *boursieri*), and all have a black lateral line (absent in one *boursieri*) that anteriorly lies on row 5 and posteriorly on row 4 (and also adjacent part of row 3 in some *boursieri*). Above the dark lateral line is a tan or whitish line or series of nearly coalesced spots on row 5 (or 5 and 6) anteriorly, and rows 4 and 5 (or 5 only) posteriorly; the pale lateral marking posteriorly takes the appearance of a double row of staggered spots in some specimens of *boursieri* and in the types of *antioquiensis* and *tristriatus*, although the spots are very vague in *tristriatus*. The drawing of the posterodorsal aspect of *antioquiensis* (fig. 2) might almost have been made from a specimen of *boursieri* (M.C.Z. No. 36948), except for the fact that in *boursieri*, which is unlike the types of the other species, the several linear markings are faint and broken, or absent, on the anterior part of the body. The body ground color is uniform brown in *antioquiensis* and *tristriatus*, but in *boursieri* the body scales tend to have lighter brown centers and dark edges, which may be especially noticeable in the first three rows of scales (fig. 5); actually the entire circumference of the scale is not dark, but the free, translucent edge appears dark because it overlaps the pigmented base of an adjacent scale. A pair of ocelli on the nape is present in some *boursieri* (e.g. M.C.Z. No. 36950) and also in the types of *antioquiensis* and *tristriatus*, although in *tristriatus* the spots are faint and lack dark edges. The brown head coloring is more uniform in *antioquiensis* than in *boursieri*, which has dark spots on a light snout; the head of *tristriatus* is uniform brown except for inconspicuous pale reticulations. The supralabials of *boursieri* are more boldly spotted, and the postocular white stripe better delineated. In all three species the dark line along the top of the labials continues caudad for a short distance on the side of the neck, which is pale below the line. Ventral patterns are likewise similar, but the dark markings are most extensive in *antioquiensis*.

The three species are very similar in scutellation and proportionate tail length, as can be seen from inspection of table 1, and all have the same general habitus. Probably significant is an apparent tendency for fusion of the loreal with the preocular; this occurs on one side of the head in the holotype of *antioquiensis* and on one or both sides in three of five *boursieri*. The holotypes of *antioquiensis* and *tristriatus* have higher numbers of ventrals and subcaudals than the observed specimens of

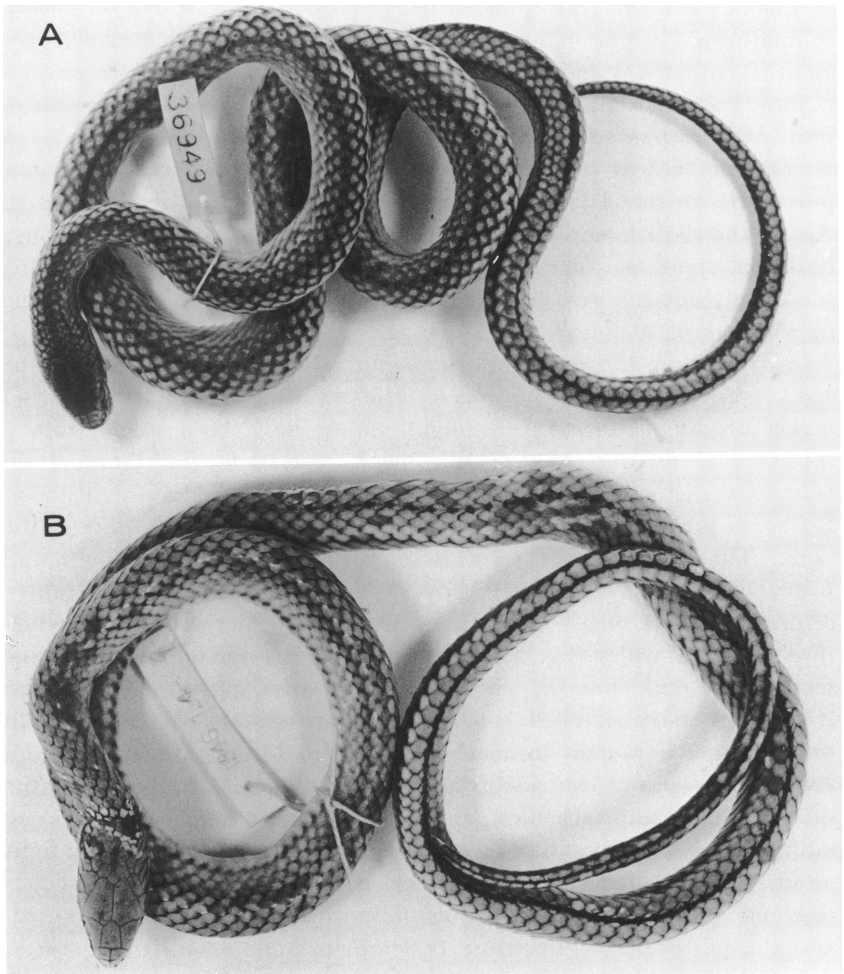


FIG. 5. A. *Lygophis boursieri*, M.C.Z. No. 36949, from Atlantic side of Ecuador. B. *L. boursieri*, B.M.N.H. No. 1946.1.4.4 (lectotype of *Coronella whymperi*), from Pacific side of Ecuador.

boursieri, but the differences are not striking (table 1). The only outstanding differences in scutellation are the presence in *antioquiensis* of 19 rows of body scales anteriorly, rather than 17, and in method of reduction. All three species have a posterior reduction from 17 to 15 or fewer scale rows, but in the type of *antioquiensis* this occurs mainly (but irregularly, see description) by fusion of rows 7 and 8, whereas re-

TABLE 1
SCALE COUNTS AND MEASUREMENTS (IN MILLIMETERS) FOR THREE SPECIES OF *Lygophis*

	<i>boursieri</i> N=5	<i>antioquiensis</i> holotype ♀	<i>tristriatus</i> holotype ♂
Dorsal scale rows	17-17-15 (4)	19-17-15	—
	17-17-13 (1 ♂)	—	17-17-15
Ventrals	148-159 (3 ♂ ♂)	—	174
	150-153 (2 ♀ ♀)	168	—
Subcaudals	64-68 (3 ♂ ♂)	—	75
	51 (1 ♀)	62	—
Supralabials	8	7/8	7/8
Supralabials touching eye	3-5 ^a	3-4/3-5	3-4/3-5
Supralabial touching loreal ^b	2nd	2nd	2nd
Preoculars	1	1	2/1
Postoculars	2	2	2
Temporals	1+2 ^a	1+2	1+½
Infralabials	7 to 10	10	9/8
Total lengths	565-582 (3 ♂ ♂)	—	655
	530 (1 ♀)	664	—
Snout-vent lengths	421-452 (4 ♂ ♂)	—	487
	415 (1 ♀)	505	—
Tail length, as a per cent	24.5-27.1 (3 ♂ ♂)	—	25.3
	21.7 (1 ♀)	23.9	—

^a Except in M.C.Z. No. 36950 which is decidedly abnormal in shape and positioning of some supralabials and in temporal formula.

^b Not counting plates under preocular, in specimens where this is fused with loreal.

duction in *boursieri* and the type specimen of *tristriatus* involves the fusion of rows 3 and 4 or the loss of row 4. Peters (1963) notes that a specimen of *boursieri* (M.C.Z. No. 36948) undergoes further reduction from 15 to 13 rows by fusion of vertebral and paravertebral rows, but this happens very close to the tail.

There seem to be no important differences in dentition. Maxillary formulae are 21+2 in the types of *antioquiensis* and *tristriatus*, and 19+2-22+2 in three *boursieri*, and the size and shape of the teeth are similar. The number of prediastemal teeth lying behind the anterior edge of the ectopterygoid process is variable. In the type of *antioquiensis*, and in two *boursieri*, the last one and a half sockets are posterior to the edge of the process and the diastema is distinct; in the type of *tristriatus*, and in one *boursieri*, there are two or two and a half sockets posterior and the diastema is thereby shorter. Maxillary shape is similar, but observed

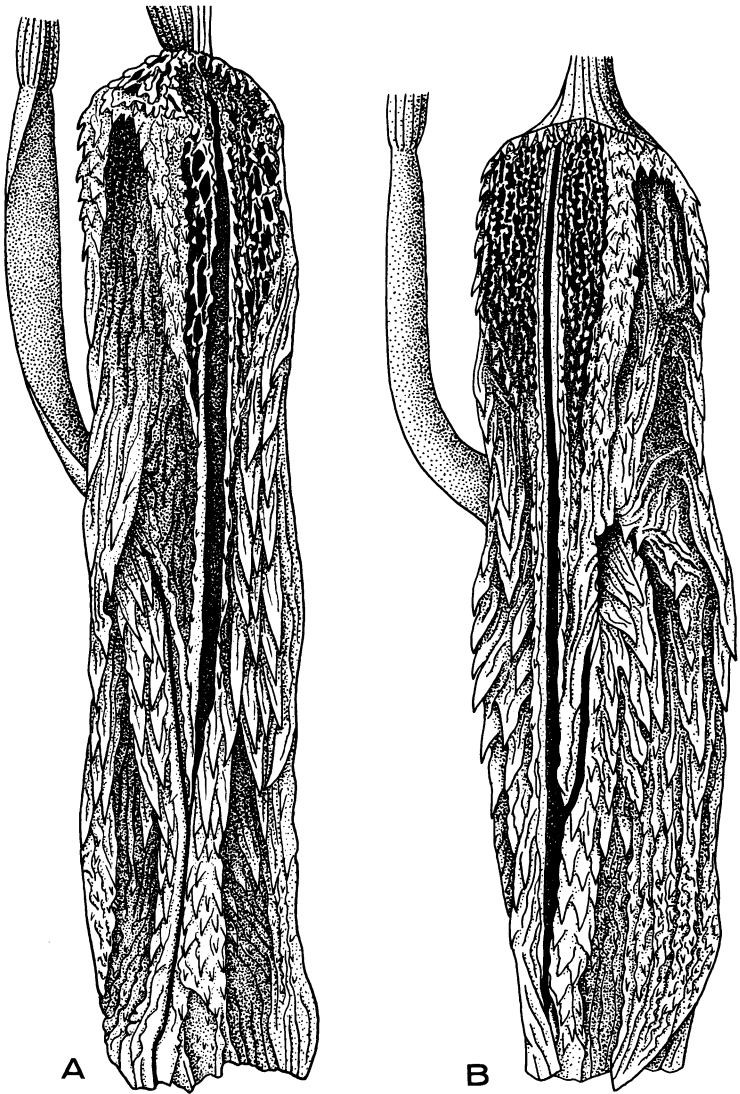


FIG. 6. Hemipenes of *Lygophis boursieri*. A. Left organ from M.C.Z. No. 36949 (total length, 565 mm.; tail 143 mm.), seemingly opened along lateral wall of ventral lobe. B. Left organ from B.M.N.H. No. 1946.1.4.4 (lectotype of *Coronella whymperi*, total length, 520 mm.; tail, 135 mm.), opened by midventral incision. $\times 4$.

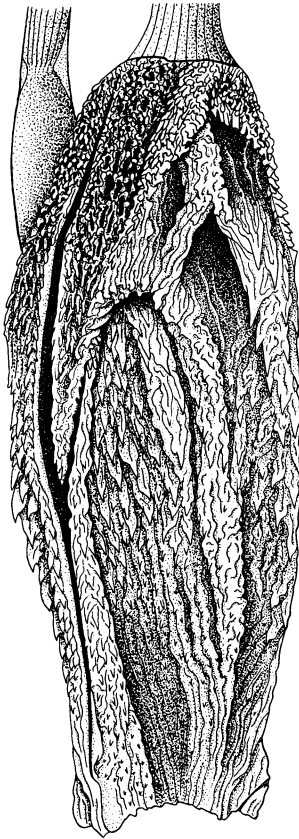


FIG. 7. Hemipenis of *Lygophis tristriatus* (holotype, total length 665 mm., tail 168 mm.), left organ opened by midventral incision. $\times 4$.

maxillae of *boursieri* and *tristriatus* are anteriorly a little less curved than that of the holotype of *antioquiensis* (fig. 3), and the end of the suborbital process is less pointed and the dorsal side of the suborbital process is not visible in lateral profile.

The hemipenes of *Lygophis boursieri* and *L. tristriatus* provide a clear indication of relationship. The only known specimen of *L. antioquiensis* is unfortunately a female, but because of all the other correspondences we may assume that the hemipenis will also prove similar. The retracted organ of *boursieri* is known to me from three specimens (M.C.Z. Nos. 36948-36950): The hemipenis extends to a level opposite subcaudals 13 to 17 and is deeply bifurcated, forking at the levels of subcaudals

8 to 11; the two slips of retractor muscle merge at subcaudals 16 to 20, and this muscle inserts posteriorly at subcaudals 31 to 36. The sulcus spermaticus forks at subcaudals 5 to 7. Some of the organs had been previously opened and twisted, or partially everted, so that the normal position of the sulcus spermaticus is not clear, but it lies on the lateral wall of the left organ of one specimen (No. 36948) and on the lateral wall of the right organ of another (No. 36950); therefore, the left and right hemipenes of this species seemingly are mirror images. The forks of the sulcus extend nearly to the tips of the lobes, with the ventral fork going to the ventral lobe and vice versa. The left organ of one specimen (M.C.Z. No. 36949) was removed for detailed examination and is illustrated as figure 6A: The sulcus forks halfway up the basal, unbifurcated part of the hemipenis; the lobes comprise nearly half of the total length of the organ. The sulcus is not merely a narrow groove but has lips that can be spread widely, especially on a lobe; the walls of the sulcus are straight, not convoluted. The sulcus is bordered by a dense fringe of small to medium, slightly recurved spines along most of its length on the unbifurcated stalk, which lacks basal ornamentation except for minute spinules; there is a nearly bare strip along either side of the spiny sulcus border. The forks of the sulcus are bordered by calyculate areas on most of the length of the lobes, but the calyces do not extend down to the bases of the lobes. The calyces are quite large and are sparsely ornamented with papillae on their edges. The organ is not capitate in that there is no "head" region delineated on the lobes, but the tip of a lobe is covered by papillate calyces that, on the asulcate side, make an overhang reminiscent of the edge of a capitulum. Below this overhang is a virtually nude strip (with only a few tiny spines) that runs along the lobe on the side opposite the sulcus and which is flanked by small to medium spines that lie between it and the calyces; one border of spines starts near the base of the lobe and the other starts near the middle of the basal stalk.

The hemipenis of *L. tristriatus* has already been described in detail; it is basically similar to the organ of *boursieri* but differs in several notable aspects. It is only about one-third bilobated and is shorter and thicker; compare figures 6 and 7, for which the relatively short organ of *tristriatus* was taken from a snake 100–145 mm. longer than the specimens of *boursieri*. There is a bare pocket on the lobe, in addition to the bare strip present in *boursieri*, but the important feature is probably the ridge of tissue that separates these two unadorned areas. The ridge possibly forms a characteristic protuberance on the naked side of the lobe, when the hemipenis of *tristriatus* is everted. The naked side

of the lobe is bordered by calyces, rather than a fringe of spines as in *boursieri*. There are more calyces on the hemipenis of *tristriatus*, and some calyces extend down onto the unbifurcated stalk, between the forks of the sulcus; also, most of the calyces are smaller than in *boursieri*. The lips of the sulcus can be parted widely in both species.

Parker's description (1935, p. 522) of the hemipenis of *Lygophis boursieri* as "divided, capitate, not calyculate distally" is puzzling; even if one considered the slight distal overhang as a sign of capitulation, the calyces could scarcely be missed. The only specimens of *boursieri* indicated by Parker as being in the British Museum at that time are the syntypes of *Coronella whymperei*, but neither of the unverted hemipenes of the male syntype had been opened before my recent examination. Parker's description is possibly based on misplaced data from some other species. Comment on the hemipenis (fig. 6B) of the *whymperei* syntype is made in the next section.

The similarities between *Lygophis boursieri*, *L. antioquiensis*, and *L. tristriatus* are such that their close relationship can scarcely be disputed. Judged only by the slight differences in pattern, they might conceivably be populations of a single, widely distributed species; but differences in hemipenes and number of scale rows are sufficient grounds to recognize each as a valid species. I suggest that they form a very close-knit unit and that a natural species group can be usefully defined. First, however, it is necessary to consider the status of two other nominal species.

STATUS OF *CORONELLA WHYMPERI*

Boulenger (1882) named *Coronella whymperei* from Milligalli, Ecuador, a locality at about 1900 meters elevation on the western slopes of Cerro Corazon (Adrade Marin, 1931, p. 30); this description was reprinted by Boulenger in 1891. Boulenger later (1894, p. 174) placed *C. whymperei* in the synonymy of *Rhadinaea undulata*, along with *Dromicus boursieri* and some other names. Shreve (1934) revalidated *boursieri* as a distinct species, which he placed in *Lygophis* on the advice of E. R. Dunn; Shreve transferred the names *Coronella whymperei* and *Enicognathus joberti* from Boulenger's synonymy of *R. undulata* to the synonymy of *Lygophis boursieri*. Parker (1935) showed it to be unlikely that *Enicognathus joberti* Sauvage (type locality Marajo Island, mouth of Amazon) has anything to do with *boursieri*, which he transferred from *Lygophis* to *Liophis*; Parker maintained *whymperei* as a synonym of *boursieri*, and also doubtfully added the neglected name *Liophis atahuallpae*, which Steindachner had named from

western Ecuador in 1901. The situation remained unchanged until Peters (1960, 1963) put *boursieri* back into *Lygophis*, and revalidated *whymperi* as another species of *Lygophis*, with *Liophis atahuallpae* as a junior synonym. According to Peters, *Lygophis boursieri* and *L. whymperi* are distinct species occupying the Atlantic and Pacific slopes, respectively, of the Ecuadorian Andes. I (1966) extended the range of *Lygophis boursieri* to the Pacific drainage, on the basis of a specimen from south-western Colombia, and suggested this as added evidence that *boursieri* and *whymperi* are conspecific.

Peters (1963, pp. 61, 62) demonstrated that "there are no good characters of scutellation that can be used to separate the two species *boursieri* and *whymperi*" (compare also tables 1 and 2), but believed that this could be done on the basis of pattern. These differences were first summarized by Peters (1960, p. 528) in a check list and key, as follow:

"Dorsum almost unicolor light brown, with a vague lateral light line which is poorly distinguished from other dorsolateral color; vertebral black line never prominent; often with a light, dark-edged ocellus on each side of the nape
 *whymperi*
 Dorsal ground color brown, with the light lateral line rather strongly contrasted with dorsal color; vertebral black line prominent, at least posteriorly; usually no clearly marked light, dark-edged ocellus on each side of the nape
 *boursieri*"

In his 1963 paper (p. 62), Peters did not emphasize the nape ocelli as being diagnostic, but he added that *boursieri* is darker above and that the vertebral dark line forms more anteriorly on the body, and that the lateral dark marking is a solid stripe and not a zigzag as in *whymperi*.

At different times I examined the two syntypes of *Coronella whymperi*, which were not seen by Peters, and compared them with four specimens of *Lygophis boursieri*, including two Museum of Comparative Zoology, Harvard, specimens that Peters (1960, 1963) used for comparison in his resurrection of the name *whymperi*. The supposed diagnostic features (see above) of *whymperi* are not reliable, as indicated by the following remarks. One of the syntypes (B.M.N.H. No. 1946.1.4.4) of *whymperi* has a prominent black line on the posterior part of the body (fig. 5B), which is a supposed characteristic of *boursieri*; this line is broken on the other syntype (B.M.N.H. No. 1946.1.4.5) and does not form a solid line until close to the tail, which is also true of certain specimens of *boursieri* not seen by Peters (M.C.Z. Nos. 9598 and 36948). The lateral black line is extremely reduced in the syntypes, on which it forms a posterior zigzag along the upper edges of the scales in row 3 and the lower edges in row 4; but the lateral dark line is also much reduced on some

boursieri, especially M.C.Z. No. 36950, on which it would also appear as a zigzag except that the dark edging continues all the way around the scales, thus eliminating all apparency of any discrete, lateral dark line. In syntype No. 1946.1.4.5 the pale lateral stripe is anteriorly on row 5 and posteriorly on rows 4 and 5, and is nearly as vague as in some *boursieri*; the pale stripe also is posteriorly on rows 4 to 5 and vague in the other syntype, but anteriorly the stripe is reduced to a line of white dashes on the adjacent edges of rows 5 and 6 (fig. 5B). One syntype (No. 1946.1.4.4) differs from the specimens of *boursieri* in being pale brown under the stratum corneum, rather than gray, but my notes on the other syntype indicate that it is more like the *boursieri* in this regard; in both *whymperi* and *boursieri* the ground color appears less uniform than in *antioquiensis* and *tristriatus*, especially on parts of the body where the stratum corneum has fallen away in preservative. One of the syntypes (No. 1946.1.4.5) has the nape ocelli more strongly developed than on any of the *boursieri*, but the other syntype has poorly developed ocelli. One syntype (No. 1946.1.4.5) differs from the *boursieri* in having a uniformly brown snout rather than a black spotted one, but the other syntype has a dark spot on each internasal plate.

Number of dorsal scales of the two syntypes is given in table 2; methods of reduction in the dorsal scale rows were determined for No. 1946.1.4.4 and are as follows: There is reduction from 17 to 15 rows at midbody by the fusion of rows 4 and 5 at the level of ventral 80. Posterior reduction to 13 rows occurs at about the levels of ventrals 120 (left) and 123 (right); this is an irregular reduction that involves the paravertebral scales, which, at specific points, may fuse either with scales in the vertebral row or next lateral row, or simply drop out. There is further reduction to 12 rows by fusion of rows 2 and 3, on the right side at ventral 146, 10 ventrals in front of the anal plate. On the tail, reduction from eight to six rows occurs at the level of subcaudal 5, to four rows at subcaudal 20, and two rows at subcaudal 51. Peters (1963) suggests that the place of caudal reduction from six to four rows might eventually provide a means of separating *whymperi* and *boursieri*, but there seems to be overlap even in this character (Myers, 1966).

The maxillary dentition of the syntypes of *Coronella whymperi* is within the variational range of *Lygophis boursieri*. There are 20+2 and 21+2 teeth on the *in situ* right maxillae of Nos. 1946.1.4.4 and 1946.1.4.5, respectively, and in each there are one and a half prediastemal sockets behind the anterior edge of the ectopterygoid process. One of the syntypes (No. 1946.1.4.4) is a male, and its hemipenis (fig. 6B) agrees

almost word for word with the description previously given for *boursieri*; the following data were recorded from the left organ, before it was removed for illustration and detailed study: The retracted hemipenis extends to the end of subcaudal 17 and is deeply bilobated, bifurcating at the end of subcaudal 11; the two slips of retractor muscle merge at the end of subcaudal 21, and this muscle inserts at level of subcaudal 36; the sulcus spermaticus lies on the lateral wall and forks opposite the base of subcaudal 7. The main differences are that the *whymperi*

TABLE 2
SCALE COUNTS AND MEASUREMENTS (IN MILLIMETERS) OF THE SYNTYPES OF
Coronella whymperi (= *Lygophis boursieri*)

	B.M.N.H. 1946.1.4.4 lectotype ♂	B.M.N.H. 1946.1.4.5 ♀
Dorsal scale rows	17-15-12	17-17-14
Ventrals	156	155
Subcaudals	65	54+
Supralabials	8	7
Supralabials touching eye	3-5	3-4/3-5
Supralabial touching loreal	2nd	2nd
Preoculars	1	1
Postoculars	1 ^a	1/2
Temporals	1+2	1+ ² ₁
Infralabials	8/9	9/8
Total length	520	600+
Tail length	135	128
Tail length, as a per cent	26.0	—

^aUpper postocular on each side is fused with supraocular, and the remaining postocular is very tiny.

hemipenis has more and smaller calyces and also a row of spines on the otherwise nude strip on the asulcate side of a lobe (compare figs. 6A and 6B).

The differences between the syntypes of *Coronella whymperi* and specimens of *Lygophis boursieri* seem to be so few and so slight that I doubt that *whymperi* should be regarded as a distinct species. Indeed, the remarkable thing is that specimens from opposite sides of the high Andes should be so similar. Therefore, the name *Coronella whymperi* Boulenger, 1882, should be added to the latest published synonymy (Myers, 1966) of *Lygophis boursieri* (Jan and Sordelli, 1867). B.M.N.H. No.

1946.1.4.5 is probably the syntype of *whymperi* illustrated in Boulenger's original description, although I did not directly compare the specimen and figures. The other syntype (No. 1946.1.4.4) differs from the figures in the arrangement of black spots under the head, and in having less conspicuous nape ocelli and a weaker lateral black line on the side of the neck; furthermore the skin of the nape is badly torn, which would have made this specimen difficult to illustrate. Even though it is not the specimen originally illustrated, I here designate B.M.N.H. No. 1946.1.4.4 (figs. 5B and 6B) as lectotype of *Coronella whymperi*, because it is a male and because the hemipenis seems to be very important to the taxonomy of this group of snakes.

STATUS OF *LIOPHIS ATAHUALLPAE*

The brief history of this name is outlined in the beginning of the foregoing section on *Coronella whymperi*. I cannot agree that *Liophis atahuallpae* Steindachner should be continued as a synonym in the *Lygophis boursieri* group, although I am uncertain as to its affinities. There has been confusion in the literature of this species. It was named in 1901, in the "Anzeiger der Kaiserlichen Akademie der Wissenschaften," in a partial abstract of a longer article published the following year in the memoirs of the same society. Illustrations and a more detailed description are given of "*Liophis atahuallpae* nob" in the second account, which Steindachner had intended as the official description. The titles of the two papers are identical, except for variant spellings of the last word in the subtitle. Parker (1935, p. 522) probably was unaware of the second paper containing the more detailed description and the illustrations, for I do not believe that he otherwise would have associated *atahuallpae* with *boursieri*. Peters (1960, p. 529) incorrectly cited the original description when he moved *atahuallpae* to the synonymy of *whymperi*; the date and journal are correct, but the pagination and figures belong to the second paper.

According to Steindachner's text and illustration (1902, p. 105, pl. 1, fig. 4), *Liophis atahuallpae* has the following characteristics that cause me to remove it from synonymy in the *Lygophis boursieri* group. The dark lateral line lies low on the side, has pale areas within its borders, and is continuous with the dark, upper margin of the supralabials. In members of the *boursieri* group, the labial stripe extends but a short distance on the neck and the long lateral line is higher on the body. The belly of *atahuallpae* is punctated with dark flecks that, "bis in die Nähe des Analschildes mehr minder dicht gesprenkelt." Species in the *boursieri* group have large, dark markings that increase in size pos-

teriorly. Steindachner (1902) related *atahuallpae* with *Liophis albiventris quadrilineata* Jan [= *Leimadophis reginae* (Linnaeus)] and with *Liophis melanostigma* [= *Leimadophis melanostigma* (Wagler)]. Steindachner's illustration of *atahuallpae* is indeed a bit reminiscent of the Brazilian *Leimadophis melanostigma*, although it is not usual for a *Leimadophis* to have the posterior lateral stripe extending unbroken to the head as it does in *atahuallpae*; nevertheless, this stripe is narrowed on the neck and, according to the description, the vertebral stripe is broken anteriorly. Lacking information on hemipenis and dentition, and for want of a better place, I suggest that *Liophis atahuallpae* Steindachner, 1901, be transferred to the genus *Leimadophis*. The type locality (Steindachner, 1902) is translated as: Below Las Palmas on the western slopes of the Andes, on the way from Babahoyo to Guaranda, at about 2500 meters elevation, western Ecuador. The location of the holotype is uncertain; Peters (1960, p. 529) suggested that it might be in the Vienna Museum.

THE *BOURSIERI* SPECIES GROUP

CONTENT: *Dromicus boursieri* JAN AND SORDELLI, 1867, livr. 25, pl. 2, fig. 2. Type locality "Quito," Ecuador. Holotype presumably in Mus. Natl. d'Hist. Natur. Paris.

Rhadinaea antioquiensis DUNN, 1943, p. 307. Type Locality: San Pedro, 2560 meters, Departamento Antioquia, Colombia. Holotype No. 386 in Mus. Inst. La Salle, Bogotá.

Rhadinaea tristriata RENDAHL AND VESTERGREN, 1940, p. 5. Type Locality: Cauca, Colombia. Holotype No. 3119 in Naturhist. Riksmus., Stockholm.

GENERIC PLACEMENT: This is an unresolved problem because the *boursieri* group of species does not fit readily into any Neotropical colubrid genus as presently defined. The nominal *Rhadinaea antioquiensis* and *R. tristriata* are here removed from *Rhadinaea*, primarily on the basis of the hemipenial structure of *tristriata* and *boursieri*. The hemipenes in specimens of *Rhadinaea* may be single or slightly bilobated, but none that I have examined has the organ so conspicuously divided as in *boursieri* and *tristriata*;¹ the hemipenis in *Rhadinaea* has a distinct head region that is normally set off by an overhang, the calyces are relatively small, and the sulcus spermaticus is a simple groove that usually cannot be spread so widely. The existence of scale row reduction is also uncommon in *Rhadinaea*, and any fusion of loreal and preocular is decidedly aberrant in that genus. The species in the *boursieri* group form an evolutionary unit that seems to have no close affinities within the genus

¹ Except *Rhadinaea steinbachi* Boulenger, which I also intend to remove from *Rhadinaea*.

Rhadinaea. Consequently, *antioquiensis* and *tristriata* are transferred to *Lygophis* simply because *boursieri* already resides there. *Lygophis* is thus being used as a provisional depository, as has already been recognized in the case of the inclusion of *boursieri* (Peters, 1963; Myers, 1966). The *boursieri* group surely will have to be reassigned, but I prefer not to comment further until I know more about other species and genera; my immediate purpose is to clarify the situation in *Rhadinaea*, as a monograph of that genus is in preparation.

DEFINITION: Snakes of moderate proportions and size (to nearly 700 mm. in total length), and having "normal" colubrid head scutellation except for fusion of loreal and preocular, or postocular and supraocular, in some individuals. Canthus rostralis rounded. Ventrolateral edges of belly non-angular. Moderate numbers of ventrals (150-174 observed) and subcaudals (51-75). Dorsal scales smooth, lacking pits and anal ridges, in 19 or 17 rows anteriorly, reducing to 15 or fewer rows posteriorly; method of reduction variable; tiny scale organs (tubercles) present on all or most head plates. Body brown (often gray after loss of stratum corneum in preserved specimens), with a black vertebral line and usually a black lateral line posteriorly involving row 4, or 3 and 4; lateral dark line bordered above by pale stripe or series of spots (sometimes vague), posteriorly on row 5, or 4 and 5; foregoing linear markings vary from distinct to absent on anterior body and in no case extend forward on head. A short black line on side of neck, which is pale whitish or yellowish below the line. Dark-edged ocelli present or not present on nape (dark edge absent in type of *tristriatus*). Labials whitish or yellowish, with dark upper margin continuous with short line on neck; sometimes with bold black spotting and black-edged pale postocular stripe. Venter whitish to yellowish except for dark ventral tips and median row of gray to black markings or transverse streaks. Maxilla with moderately high number of prediastemal teeth (19-22) followed by a variably sized gap and two enlarged, non-grooved fangs, the last being offset laterad (from a plane connecting prediastemal teeth and first fang). Hemipenis bifurcated for one-third to one-half its length; sulcus spermaticus forked, with straight, non-convoluted walls that can be widely parted; spines mostly small to medium, no large basal spines; lobes non-capitate, calyculate on sulcate sides and nude on asulcate surfaces.

As presently defined, the species of the *boursieri* group are separable by the following key, but difficulties might well be encountered in identification, especially in Colombia, where only three specimens are known and each is assigned to a different species.

KEY TO THE *boursieri* GROUP

1. 17 rows of scales on anterior part of body 2
 19 rows *Lygophis antioquiensis*
2. Dark vertebral and lateral lines broken or absent anteriorly (and sometimes posteriorly); scale edges usually dark (fig. 5), especially after loss of stratum corneum; hemipenis one-half bilobated (fig. 6)... *Lygophis boursieri*
 Dark lines continuous anteriorly; dorsal ground color uniform brown (gray) without conspicuously dark scale edges (fig. 4); hemipenis one-third bilobated (fig. 7) *Lygophis tristriatus*

DISTRIBUTION: Species of the *boursieri* group occur from low to high elevations in and near the northern Andes of Ecuador and Colombia (fig. 8). Published elevations are: *Lygophis antioquiensis*, 2560 meters (Dunn, 1943); *Lygophis boursieri*, 1100 meters (Peters, 1963, under *L. whymperi*), and 1300 meters (Myers, 1966). Boulenger (1882, pp. 460, 461) does not actually give an elevation with his description of *Coronella whymperi* (= *boursieri*), but he elsewhere (1891, p. 130) appends the figure of 6200 feet (1890 meters). *Lygophis boursieri* seemingly occurs at low elevations (below 500 meters) on the western fringe of the Amazon Basin, judged from specimens reportedly from the Río Napo and Río Pastaza (see fig. 8 and Specimens Examined).

Lygophis boursieri is found on both the Atlantic and Pacific drainages in Ecuador, and is also known from a single Pacific locality in southwestern Colombia; the reported type locality (Quito) of this species needs verification. The type locality of *L. tristriatus* is somewhere in the department of Cauca, southwestern Colombia. *Lygophis antioquiensis* is known only from its Colombian type locality near the northern end of the Andes, about 24 kilometers north of Medellín in the Cordillera Central.

REMARKS: I know nothing about the natural history of these snakes except that they are oviparous (based on large oviductal eggs in the type specimen of *Lygophis antioquiensis*). They are uncommon in collections.

My concept of *Lygophis boursieri* as a species that lives at low elevations on one side of the Andes, and at relatively high elevations on the other side, invites further examination. It might be that two sibling species really are involved, in which case slight differences in hemipenes (especially number of calyces, compare figs. 6A and 6B) might prove the most reliable diagnostic feature; larger samples are obviously needed. Probably the various populations of the *boursieri* group are distributional relicts from a more favorable time, as perhaps a period of Pleistocene glaciation during which some species of the tropical highlands had wider horizontal and vertical distributions than today (Haffer, 1967).

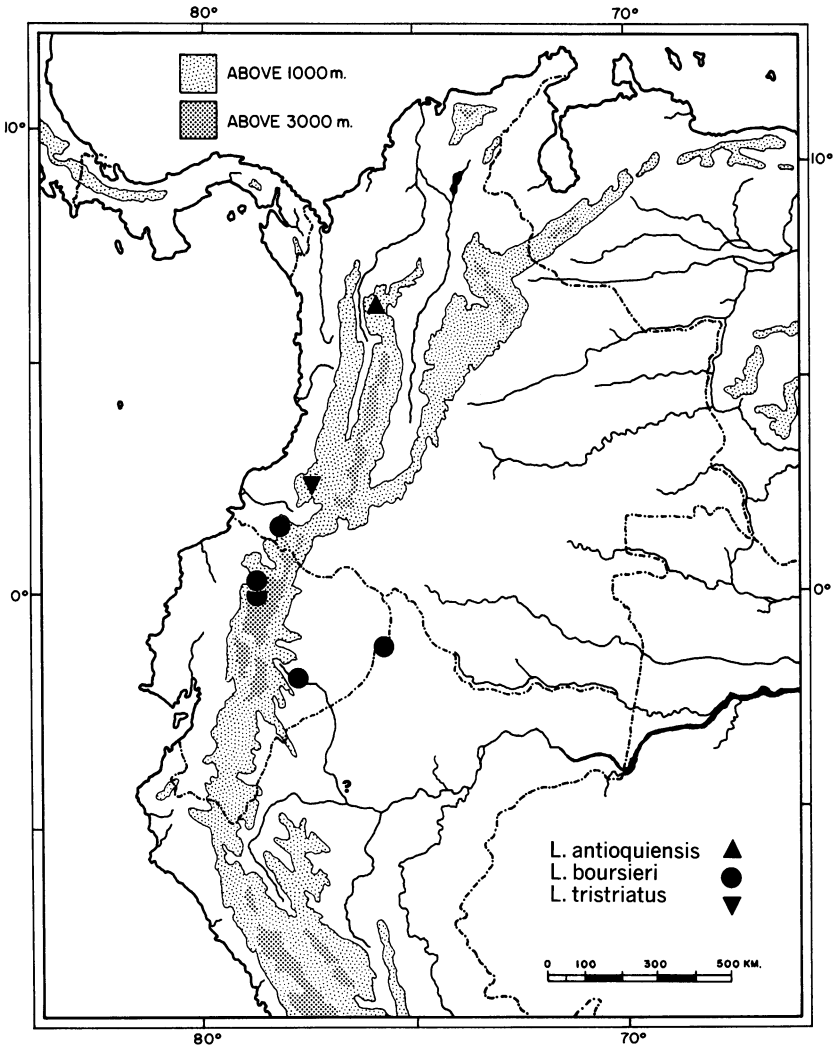


FIG. 8. Northwestern South America, showing known localities for species of the *Lygophis boursieri* group. The positioning of the symbols for "Cauca" (*L. tristriatus*) and "Río Pastaza between Canelos and Río Marañón" (*L. boursieri*) is speculative, owing to the inexact locality data. The Río Pastaza locality might be well into Peru, rather than Ecuador, as indicated by the question mark.

The list below includes localities from which I have examined specimens and records from the literature.

SPECIMENS EXAMINED: *Lygophis antioquiensis* (Dunn). Colombia, Dept. Antioquia, San Pedro, 2560 meters, Instituto de La Salle No. 386 (holotype). *Lygophis boursieri* (Jan and Sordelli). Colombia, Dept. Nariño, Ricuarte, 1300 meters, A.N.S.P. No. 25183. Ecuador, Milligalli, 1890 meters, B.M.N.H. Nos. 1946.1.4.4 and 1946.1.4.5 (syntypes of *Coronella whymperi*; No. 1946.1.4.4 is designated lectotype). Ecuador and/or Peru, Río Pastaza between Canelos and Río Marañon, M.C.Z. Nos. 36948-36950. No data (originally given as "Cuba," see Myers, 1966), M.C.Z. No. 9598. *Lygophis tristriatus* (Rendahl and Vestergren). Colombia, Departamento Cauca, Naturhist. Riksmus. No. 3119 (holotype).

LITERATURE RECORDS: *Lygophis boursieri* (Jan and Sordelli). Ecuador, "Quito" (Jan and Sordelli, 1867, as *Dromicus boursieri*); Ecuador, Pichincha Province, Mindo, 1100 meters, and Corazon Pass (Peters, 1963, as *L. whymperi*); Ecuador, Rocafuerte on the Río Napo (Peters, 1963).

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