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A New Genus and Species of Colubrid Snake from the Sierra Madre del Sur of Guerrero, Mexico

CHARLES W. MYERS¹ AND JONATHAN A. CAMPBELL²

ABSTRACT

Rhadinophanes, new genus, is erected for a small colubrid snake from high montane forest (~2750 m.) on Cerro Teótepec, in the Sierra Madre del Sur of central Guerrero, Mexico. The characteristics of *Rhadinophanes monticola*, new species, include a mottled linear pattern, enlarged, ungrooved rear maxillary teeth, and smooth dorsal scales with paired apical pits, in 19-19-17 rows. The hemipenis has a centripetal sulcus spermaticus and is distinctly bilobed, with each lobe being spinose basally and individually calyculate and capitate distally. *Rhadinophanes monticola* resembles snakes of the genera *Rhadinaea* and *Coniophanes*, but it is comparatively primitive in hemipenial structure and in several other relevant characters. Although *Rhadinophanes* might represent the plesiomorphic sister group of *Rhadinaea* and *Coniophanes*, the monophyly of these phenotypically similar snakes

could not be demonstrated. In contrast, a sister-group relationship is corroborated for *Rhadinophanes* and the very dissimilar *Tantalophis*, on the basis of unusual hemipenial features judged to be synapomorphies. The phyletic position of *Rhadinophanes* and *Tantalophis* to other genera is uncertain, although similarity can be found to such diverse groups as *Rhadinaea-Coniophanes* and *Leptodeira-Cryophis* of Middle America, and with various alsophiine colubrids, which occur widely in the American mainland, West Indies, and Galapagos. The hemipenes of *Rhadinophanes* and *Tantalophis* are reminiscent of the alsophiine type, although there seems to be fundamental disparity in several characters, including the synapomorphic features that affirm the monopoly of these two otherwise divergent genera.

RESUMEN

Rhadinophanes, género nuevo, se necesita crear para una nueva especie de serpiente colúbrida descubierta en los bosques de altas montañas

(~2750 m.) en el Cerro Teótepec, Sierra Madre del Sur de Guerrero central, México. Las características de *Rhadinophanes monticola*, especie

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nueva, incluyen un dibujo moteado en líneas, dientes maxilares de atrás agrandados, sin surcos, y escamas dorsales lisas con fosetas apicales en parejas, en 19-19-17 hileras. El hemipene tiene el surco espermático centripeto y es definitivamente bilobado, con cada lóbulo siendo espinoso en la base e individualmente calculado y capitado hacia la punta. *Rhadinophanes monticola* tiene alguna similitud con las culebras de los géneros *Rhadinaea* y *Coniophanes*, pero en comparación es más primitiva en la estructura del hemipenis y

en otros caracteres de importancia. De ese modo *Rhadinophanes* puede que represente la agrupación hermana plesiomórfica de los géneros *Rhadinaea* y *Coniophanes*, aunque todavía no ha sido establecida la monofilia de este complejo de serpientes neotropicales. Por el contraste, la monofilia de *Rhadinophanes* y la muy incongruente *Tantalophis* está corroborada, basándose en las características poco usuales de sus hemipenes que están considerados como sinapomorfios.

INTRODUCTION

The Sierra Madre del Sur stretches narrow and rugged through the southern Mexican state of Guerrero. This mountain range parallels the coast and interrupts prevailing southeasterly winds, thus receiving abundant moisture, especially on the Pacific slopes. The drier leeward side drops into the arid rain-shadow basin of the Río Balsas, which effectively separates this part of the Sierra Madre from the Cordillera Volcánica and Mexican Plateau to the north (fig. 1).

In eastern Guerrero, otherwise continuous montane (pine-oak) forest is broken by low, arid passes near Chilpancingo (fig. 1), isolating some highland-adapted species in the mountains to the west. From Chilpancingo westward to the lower valley of the Río Balsas, the Sierra Madre uplift is unbroken up to about 1500 m. elevation, but higher segments—especially above 2500 m. in the fir zone—are discontinuous and ecologically isolated. The subject of this paper is a small snake recently discovered in one such area of pine-oak-fir forest on the Pacific side of the Sierra Madre of central Guerrero. With due consideration of phyletic and phenetic relationships, we have concluded that still another genus should be added to Mexico's rich snake fauna.

ACKNOWLEDGMENTS

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nior author expresses his gratitude to Mr. Barry L. Armstrong for help in the field, and to the University of Texas at Arlington for financial assistance for travel in Mexico. Collecting was done under permit issued by the Dirección General de la Fauna Silvestre, Departamento de Conservación, Mexico.

RHADINOPHANES, NEW GENUS

TYPE SPECIES: *Rhadinophanes monticola*, new species.

ETYMOLOGY: From the Greek *ραδινός* (= *rhadinós*, slender, graceful) + the suffix *φάνες* (= *phanes*, appearing), alluding both to the slenderness of the type species and to its superficial similarity to *Rhadinaea* and *Coniophanes*. Gender masculine.

CONTENT: Monotypic.

DEFINITION AND DIAGNOSIS: Small terrestrial colubrids lacking hypapophyses (haemal keel present) on posterior trunk vertebrae. Intramandibular articulation of lower jaw with broad gap between dentary and compound bones. Pupil of eye round. Hemipenis one-third bilobed—each lobe separately capitate, distally calyculate, and proximally spinose, lacking a nude area in asulcate side of the spinose zone; principal spines confined to lobes, with only small, slender spinules on midsection below lobes; basal one-half of hemipenis nude; sulcus spermaticus forked about halfway along organ, with centripetal branches extending to tips of lobes. High number (about 19–20 + 2) of maxillary teeth, the two enlarged fangs ungrooved,

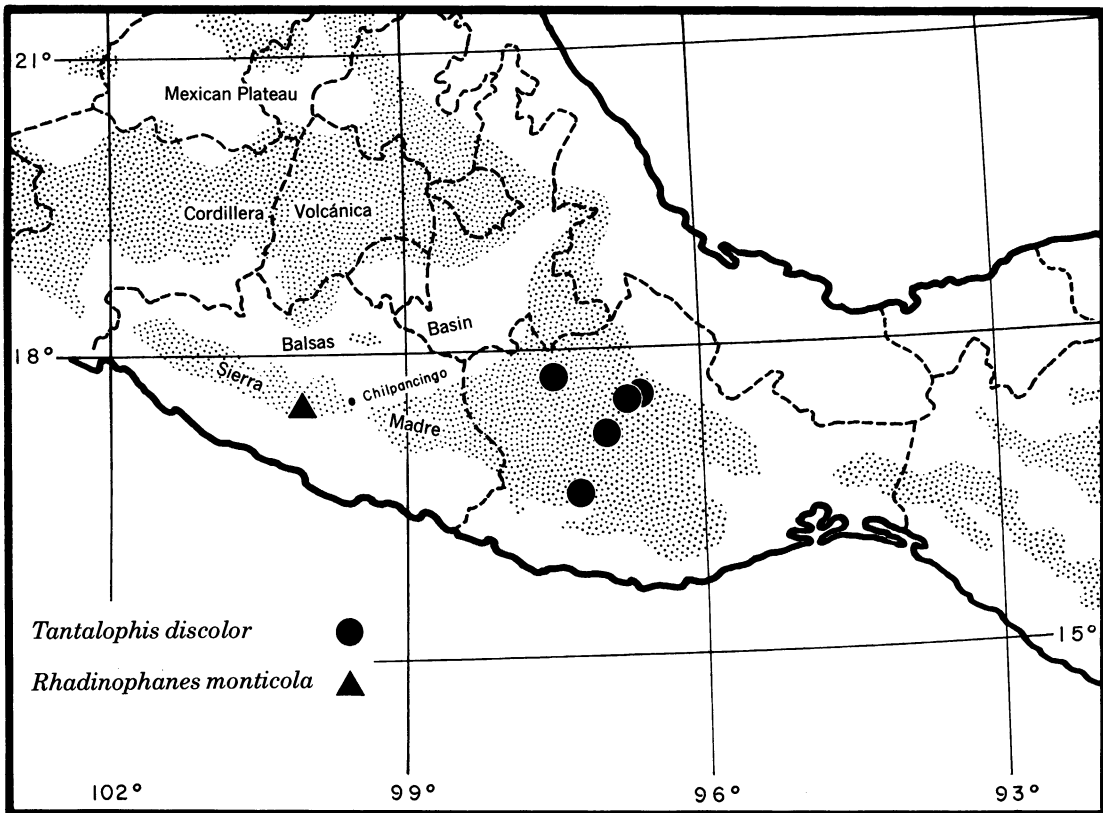


FIG. 1. Locality records for *Rhadinophanes monticola*, new genus and species, and *Tantalophis discolor* (Günther) in southern Mexico, with principal mountain ranges indicated by the approximate distribution of pine-oak forest (stipple pattern). The single record for *Rhadinophanes* covers the type locality in high elevation (~2750 m.) and ecologically disjunct pine-oak-fir forest on Cerro Teótepec in central Guerrero.

with knifelike posterior edges, and with the ultimate fang offset slightly laterad. Ventrolateral edge of belly nonangular. Dorsal scales smooth (except for anal ridges on at least some males), with paired apical pits, in 19-19-17 rows, the posterior reduction involving lateral rows; normal complement of colubrid head plates; anal plate divided, subcaudals paired. Color pattern basically striped albeit appearing somewhat mottled (but not crossbanded or blotched), with pale nuchal spot(s).

The above combination of traits is unique. *Rhadinophanes* is most likely to be confused with *Rhadinaea* or *Coniophanes*, from

which it differs significantly in having a centripetal sulcus spermaticus on a distinctly bilobed hemipenis that is separately calyculate and capitate on each lobe. The hemipenes of *Rhadinaea* and *Coniophanes* have a centrolineal or rarely centrifugal sulcus and are usually single, or, if slightly bifurcated (e.g., fig. 12B), the small lobes have confluent calyces contained within a single head region. The absence of grooves on the posterior maxillary teeth and the presence of scale pits also distinguish *Rhadinophanes* from *Coniophanes*. It is further distinguished from all *Rhadinaea* by the combination of scale pits, 19-19-17 scale rows, and

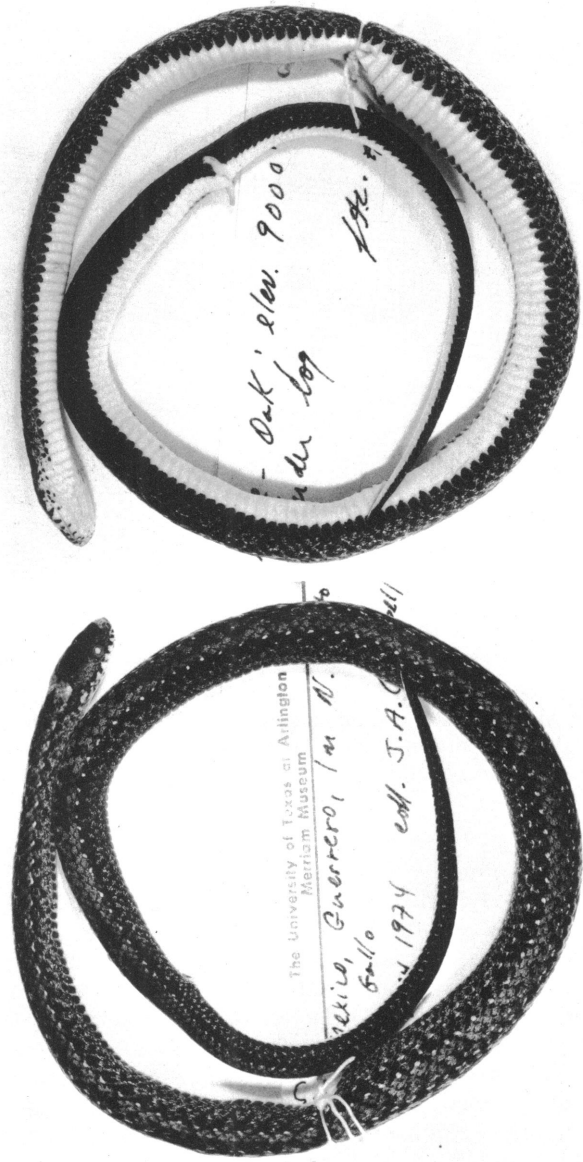


FIG. 2. *Rhadinophanes monticola*, new genus and species. Dorsal and ventral views of the holotype (AMNH 116332), about natural size.

rather mottled color pattern (with most *Rhadinaea* being excluded by any one of these traits). Despite similar hemipenes, *Rhadinophanes* is unlikely to be confused with its sister group, *Tantalophis*, since the latter has a crossbanded color pattern, a feebly elliptical pupil, and a stockier body. *Rhadinophanes* is further differentiated by a spacious articulation between the dentary and compound bones, apparently allowing unusual freedom of movement to the front part of the lower jaw.

DISTRIBUTION: Humid pine-oak-fir forest of the Cerro Teótepec area, in the Sierra Madre del Sur of central Guerrero, Mexico (fig. 1).

***Rhadinophanes monticola*, new species**

Figures 2–5, 8A

HOLOTYPE: American Museum of Natural History (AMNH) no. 116332 (field no. JAC 207), a subadult male from 1 mile (1.6 km.) north of Puerto del Gallo, at an elevation of approximately 9000 feet (~2750 m.) on Cerro Teótepec, State of Guerrero, Mexico. Specimen caught by Jonathan A. Campbell on May 21, 1974. (Puerto del Gallo, at nearly 2500 m. elevation, is the site of an abandoned lumber camp on the southwestern slope of Cerro Teótepec, roughly 40 km. by air northeast of Atoyac and 70 km. north-northwest of Acapulco; 17° 27' N, 100° 09' W.)

PARATYPE: UTA R-4176 in the University of Texas at Arlington Collection of Vertebrates (field no. JAC 208), a subadult female from 0.5 mile (0.8 km.) north of Puerto del Gallo—other collecting data same as for holotype.

ETYMOLOGY: The specific epithet, a Latin noun in apposition, means “mountain-dweller,” in reference to the montane habitat of the species.

DEFINITION AND DIAGNOSIS: Same as given for the genus. Identification is especially facilitated by the distinctive color pattern (fig. 2) and smooth dorsal scales in 19-19-17 rows. Attempts to identify new specimens can be expected to reach an impasse in couplet 97 of Smith and Taylor's (1945) key to the genera of Mexican snakes.

DESCRIPTION OF TYPE SPECIMENS

Individuals of this species probably mature before reaching 500 mm. in total length. The 412 mm. (tail tip missing) female paratype was likely entering its first breeding season, as indicated by enlarging oviducts and maturing ovarian ova 2.7–3.2 mm. in length. The 357 mm. male holotype appears to have the physiognomy of an adult, and there are suggestions of anal ridges, but its unossified hemipenial spines, threadlike vasa deferentia, and unenlarged kidney tubules show that it had not yet attained sexual maturity. The following is a combined description of the two specimens. Differences in scale counts and measurements are pointed out in table 1.

PROPORTIONS AND SCUTELLATION: Small snakes of slender proportions, with tail comprising less than 25 percent of total length. Body somewhat higher than wide, rounded ventrolaterally. Head relatively long and depressed, 1.8 times longer than wide and 2.7–3.2 times longer than deep (length as measured from snout to posterior end of mandible). Head widest in temporal region, 1.4–1.7 times wider than slender neck and about 0.9 times greatest body width. Diameter of eye less than distance from its anterior edge to posterior edge of naris, extending 1.6–1.8 times into total length of snout. Dorsal scales smooth, with paired apical pits (not discernible on all scales), in 19-19-17 rows, the posterior reduction involving row 4 (3 + 4 or 4 + 5); subadult male with a few weakly developed anal ridges. High number of ventral plates (174♂, 180♀), divided anal plate, and moderate number of paired subcaudals (64♂, 54+♀).

Rostral plate roughly twice as wide as high, inclined slightly forward and narrowly visible from above. Paired internasals, each slightly wider than long, about half as long as prefrontals. Paired prefrontals, about as long as wide, each in contact with frontal, supraocular, preocular, loreal, nasal, and internasal as well as other prefrontal. Frontal slightly hexagonal (pentagonal except for small anterior apex), 1.3–1.5 times longer than greatest (anterior) width and slightly

TABLE 1
Scale Counts and Measurements of the Type Specimens of *Rhadinophanes monticola*^a

	♂ Holotype AMNH 116332	♀ Paratype UTA R-4176
Dorsal scale rows	19-19-17	19-19-17
Ventrals at posterior scale-row reduction ^b	105/99-108	117/114
Ventrals	174 ^c	180 ^c
Anal plate	÷	÷
Subcaudals (pairs)	64	54+ ^d
Supralabials	8	8
Supralabials touching eye	4-5	3-5
Supralabials touching loreal	2-3	2-3
Preoculars	1	1
Postoculars	2	2
Temporals	1 + 2	1 + 2
Infralabials	9/10	11/10
Infralabials touching anterior genials	1-4/1-5	1-6/1-5
Infralabials touching posterior genials	4-5/5-6	6-7/5-6
Total length	357 mm.	412 mm. + ^d
Tail length	83 mm.	79 mm. + ^d
Tail length/total length	0.232	>0.19 ^d
Greatest head width (temporal region)	6.5 mm.	7.5 mm.
Head length (from tip of snout to end of mandible)	12.0 mm.	13.7 mm.
Head width/head length	0.542	0.547

^a Differences between left and right sides indicated by solidus (left/right).

^b Reduction involving row 4 (3 + 4 in paratype, 3 + 4/4 + 5 in holotype), and occurring twice on right side of holotype, as follows: rows 4 + 5 fuse at level of ventral 99, new row 4 divides at ventral 105, rows 4 + 5 again fuse at ventral 108.

^c Preceded by two preventrals (gulars longer than wide) in holotype, one preventral in paratype. Paratype also has a half ventral situated between last (180th) full ventral and the anal plate.

^d Tail incomplete.

longer (1.1-1.2 times) than distance from its front edge to tip of snout. Supraocular posteriorly more than half of frontal width, narrowed anteriorly. Parietals 1.8-2.0 times longer than broad; interparietal suture about equal (1.0-1.1 times) to length of frontal and 1.2-1.3 times longer than distance from anterior edge of frontal to tip of snout. Large nasal plate deeply grooved above and below centrally situated naris. Single loreal plate nearly square, or longer than high and rhomboidal, separated from eye by the single, high preocular; no subpreocular; two postoculars, the lower slightly smaller than upper. One large anterior temporal and upper and lower posterior temporals, between parietal and supralabials 6-8. Supralabials 8, second and third touching loreal, and either

third (posterior corner) to fifth or else fourth to fifth bordering orbit. Infralabials variable, 9, 10, or 11 per side, with, respectively, 1-4, 1-5, or 1-6 touching anterior genial, and 4-5, 5-6, or 6-7 touching posterior genial; first pair of infralabials in contact, separating mental from first pair of genials. Anterior genials slightly shorter than posterior ones, but with much longer intergenial suture. Tiny, inconspicuous tubercles (presumed sensory organs) present on head plates, being most concentrated on snout.

COLOR PATTERN: Overall dorsal coloration brown in preservative—gray after loss of stratum corneum—with a complex mottled linear pattern of black. Dark head set off from body by intervening pair of pale (whitish) dorsal nape spots extending several

scales behind parietals; nape spots partly fused in both specimens because of break in vertebral line of black pigment. Dark head cap produced posteriorly under pale nape spot on each side, forming a broken, vague, irregularly edged black lateral stripe that lies mainly on rows 4 and 5 anteriorly and (after reduction from 19 to 17 rows) on rows 3 and 4 posteriorly. Lower sides below "stripe" black with heavy frosting of pale specks. Upper edge of lateral "stripe" set off by conspicuous line of regularly spaced (every other scale) white dots, most dots straddling adjacent scales in rows 5 and 6 (rows 4 and 5 posteriorly), but some dots confined to a scale in one row or the other. Sides above line of white dots a relatively clear, pale brown on rows 6-7 (5-6 posteriorly), this area being most conspicuous and appearing as a light brown stripe on male holotype (poorly demarcated on female paratype). Middorsal five scale rows darkened by blackish gray suffusion and vague, small black spots; interconnected small black spots form suggestion of median, wavy black stripe on neck of holotype. A tendency for a double row of variably paired or alternating white dashes among the dorsal black spots, each line of dashes lying on common edges of vertebral and paravertebral scale rows. Dorsal spotting and lateral stripe becoming especially obscure on tail.

Top and upper sides of head brown (gray), finely mottled with black; one or more inconspicuous white dots on or near interparietal suture [but not forming the paired parietal dots characteristic of some snakes]. A \cap -shaped black mark on pale rostral plate. White supralabials heavily marked with vertical or (on last several plates) oblique blackish brown bars, each occupying the rear part of a labial plate (fig. 8A). Mental and infralabials weakly spotted or barred with black. Each side of belly with a nearly confluent line of sizable black spots on ends of ventral plates, these markings running together to form a serrated edge on subcaudals. Mid-ventral surfaces white in preservative, with a few scattered black specks in paratype, virtually immaculate in holotype. Venter yellowish orange in life.

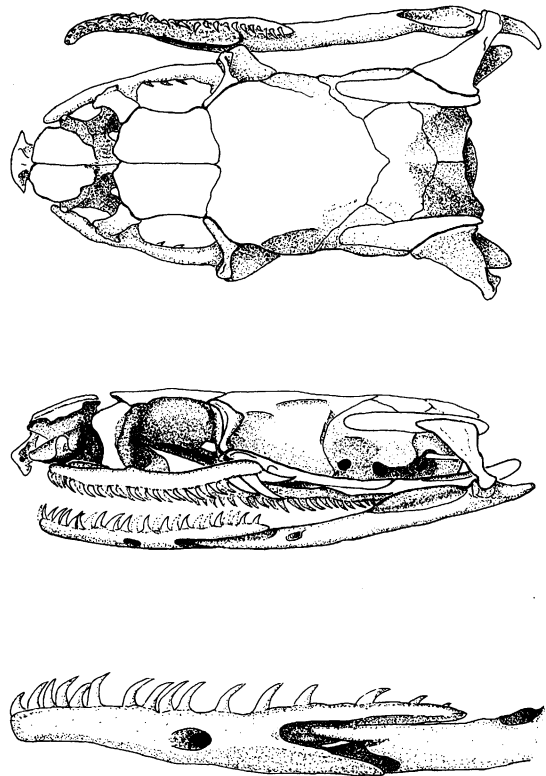


FIG. 3. Skull of *Rhadinophanes monticola*, new genus and species (♀ paratype, UTA R-4176). Dorsal and lateral views, $\times 5$. Front half of lower jaw, in ventrolateral view, shows the spacious articulation between dentary and compound bones, $\times 10$.

SKULL OF PARATYPE: Paired frontal bones forming a unit about as wide as long, slightly emarginated at orbits (greatest frontal length/smallest interorbital width across paired bones = 1.04). Prefrontal relatively high and narrow (height/greatest width = 2.38). Post-orbital dorsally in contact with frontal, in addition to its parietal articulation. Parasphenoid process of sphenoid broad and of nearly uniform depth throughout its length; median part little elevated above broad trabecular groove, bearing neither a crest nor a pronounced step at posteriormost frontal contact.

Each maxilla of paratype with 20 subequal, strongly recurved teeth (counting

empty sockets), followed without a gap³ by two enlarged, ungrooved fangs (a third, replacement fang shown in fig. 3), the last fang being slightly offset laterad. The two maxillary fangs about twice as large as preceding teeth, and further differentiated by having knifelike rear edge. Palatine bones with 11 or 12 teeth, followed by 26 or 27 pterygoid teeth, this series extending virtually to posterior end of skull. Each dentary with 25 teeth. The posterior pterygoid and dentary teeth are smallest; otherwise, teeth are subequal within a series.

Front half of lower jaw apparently capable of considerable movement, owing to an unusually spacious intramandibular articulation between dentary and compound bones (fig. 3, bottom).

VERTEBRAE: Posterior trunk vertebrae (three from paratype, level of ventrals 156–158 in area of kidney overlap) “lacking” hypapophyses, i.e., with hypapophysis reduced to a thick haemal keel that slightly overlaps base of condyle; centrum depressed along either side of haemal keel, especially anteriorly. Paradiapophyses with two articular surfaces, the lower parapophysis well-developed ventrad but having little forward projection. Anterior concavity of centrum nearly round (slightly wider than high). Condyle on short neck, oblique. Prezygapophyses and postzygapophyses with rounded ends; well-developed accessory spine projecting anterolaterally from beneath prezygapophysis. Neural arch lacking epi-zygapophysial spines. Zygosphenes crenate from above, slightly convex from the front. Neural spine a well-developed high crest, blunted on top and with only slight tendency for an anterior overhang (fig. 4).

HEMIPENIS: Major retractor muscle of left hemipenis originating at level of subcaudal 38, anteriorly dividing for insertion onto lobes of hemipenis. Distal one-third of hemi-

³ But the holotype does have a small diastema—less than the length of the ultimate prediastemal socket—and a maxillary formula of 19 + 2 (left side examined). In *Rhadinophanes*, therefore, a diastema is present or absent, probably depending on the total number of “prediastemal” teeth present on the maxilla, as in *Rhadinaea* (Myers, 1974, p. 29).

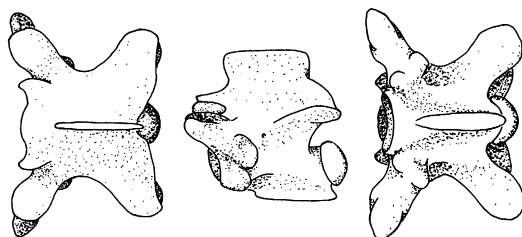


FIG. 4. Posterior trunk vertebra of *Rhadinophanes monticola*, in dorsal, lateral, and ventral aspect (from ♀ paratype at level of 157th ventral, in area of kidney overlap), ×9.

penis bifurcate. Sulcus spermaticus forks at middle of organ, each branch then extending to tip of a lobe; branches of sulcus centripetal, i.e., lying on adjacent walls in the retracted lobes (and, when everted, presumably on sides of lobes facing the crotch). Approximately the distal one-third of asulcate side of each lobe calyculate, with the area of calyces extending more than halfway down sulcate side of lobe (but *not* confluent with calyculate area on other lobe); calyces relatively large and deep, their edges bearing minute papillae. Calyculate area demarcated by a strong overhang, indicating that each lobe would be markedly capitate if everted. Below the calyculate head, each lobe bears several dozen curved, medium-sized spines, which decrease in size toward base of lobe. Numerous slender, extremely small spines in a dense zone extending basad from junction of lobes to about midpoint of organ. Basal one-half of hemipenis nude, lacking spinules or basal pocket.⁴

⁴ When the juvenile male holotype was preserved in the field, only partial eversion was achieved of its small hemipenes (fig. 2). Consequently, the left organ was dissected out for an unsuccessful attempt at manual eversion, after which it was split open (apparently along what had been the dorsal wall) and pinned flat for study. The above description and the illustration (fig. 5) are less than satisfactory because the everted basal section had to be repositioned (which conceivably might account for the apparent lack of a basal “pocket”), and because the fragile organ is not fully developed (which might account for the absence of spinules on the basal half). The major spines are still soft (unossified), so it cannot be determined whether the calyces remain papillate as described or turn spinulate in the mature organ.

NATURAL HISTORY

Both specimens of *Rhadinophanes monticola* were found in late May, coiled beneath rotting logs in small ravines having deep leaf litter, in pine-oak-fir forest, approximately 2750 meters above sea level. The area had been lumbered previously (reportedly in 1971), but good stands of pine-oak forest with scattered firs were still present.

The following species of reptiles and amphibians were found broadly sympatric with *Rhadinophanes monticola*: *Abronia deppii*, *Barisia gadovii*, *Eumeces ochoterenai*, *Sceloporus adleri*, *Sceloporus grammicus*, *Bothrops barbouri*, *Thorius* sp., *Hyla mykter*. The food of *Rhadinophanes* includes salamanders, since the paratype specimen had the remains of two or three *Thorius* in its stomach.

COMPARISON WITH RHADINAEA AND CONIOPHANES

As already stated, *Rhadinophanes monticola* bears a resemblance to snakes of the genera *Rhadinaea* and *Coniophanes*, which are abundantly represented in Middle America. The resemblance is due to *Rhadinophanes* being a small, slender, and rather generalized terrestrial colubrid having a round pupil, a moderate number of rows of smooth scales, and a basically striped pattern. These features, and some details of scutellation and dentition, are shared with species of *Rhadinaea* and *Coniophanes*, although the color pattern of *Rhadinophanes monticola* is sufficiently distinctive that it could not be associated with any group of species within those genera. The dorsal scale rows reduce in number posteriorly in *Rhadinophanes*, as in all *Coniophanes* but few *Rhadinaea*. However, *Rhadinophanes* lacks the grooved fangs that characterize *Coniophanes*. We might have reluctantly placed the new species as a monotypic species group of *Rhadinaea* had we access only to female specimens, but the hemipenial evidence provides argument for separate generic status.

It is of interest to compare *Rhadinophanes* with *Rhadinaea* and *Coniophanes* in several

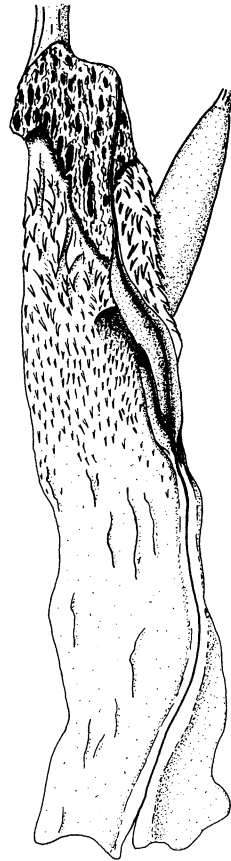


FIG. 5. Hemipenis of *Rhadinophanes monticola*. Semidiagrammatic rendition of repositioned left organ (immature) of holotype, $\times 8.6$.

characters for which evolutionary polarity can be postulated on some specific basis. The comparison leads to a tentative hypothesis that *Rhadinophanes* might be the plesiomorphic sister group of the other two genera (fig. 6). However, we wish to emphasize that we have not found actual evidence of monophyly and that the hypothesis remains neither substantiated nor falsified. (The basic nature of this postulation will not be changed by enlarging the supposedly plesiomorphic sister group to include another taxon, as will be done later in this paper, although alternative hypotheses may then seem equally as attractive.) The characters and our conclusions on polarity are as follows:

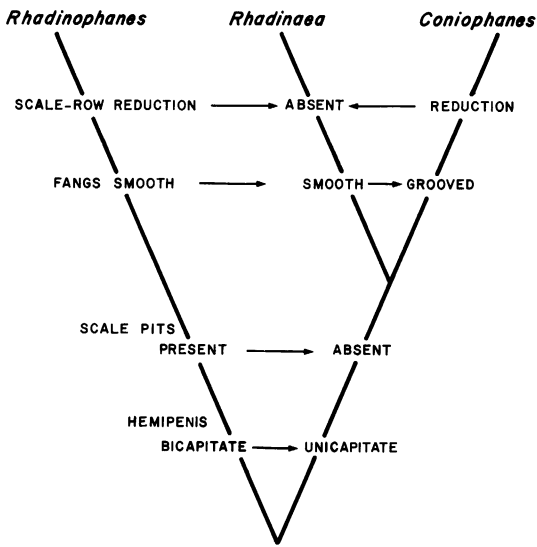


FIG. 6. A theory of relationships placing *Rhadinophanes* as the plesiomorphic sister group of *Rhadinaea* + *Coniophanes*. Arrows indicate polarity of characters, from primitive to derived. Monophyly of the two postulated sister groups is not demonstrated.

HEMIPENIS: Myers (1974) demonstrated the existence of considerable hemipenial diversity within *Rhadinaea* and discovered that a few of the 45 species have single (non-bilobate) organs attached to a divided m. retractor penis magnus. This condition was used to determine the polarity of a perceived morphocline, leading from a primitive, slightly bilobed hemipenis attached to a necessarily divided retractor muscle, to a single organ attached to a predictably undivided retractor (*op. cit.*, pp. 31–32, 226).

Even in the relatively primitive bilobate type of *Rhadinaea* hemipenis (e.g., fig. 12B), the two small lobes are contained within a single, calyculate capitulum.⁵ Myers (1973, p. 31; 1974, p. 236) speculated that this kind of hemipenis (unicapitate) was derived from

⁵ Even in species lacking an overhang or nude gap demarcating the calyculate region from the adjacent part of the hemipenis (e.g., fig. 35 in Myers, 1974), the small calyculate lobes still have the appearance of belonging to a single head region.

a still more primitive, deeply bilobed and bicapitate or semicapitate organ (see footnote 9), such as possessed by the species of *Al-sophis*, *Philodryas*, and *Saphenophis*. The hemipenis of *Rhadinophanes monticola* is clearly primitive by the above criteria, in being deeply bilobed and bicapitate. The contrary unicapitate condition is considered a synapomorphy (fig. 6) that supports the monophyly of *Rhadinaea* and *Coniophanes*, and some allied genera not considered in the present paper.

The hemipenes of *Rhadinaea* and most (?) *Coniophanes* have a centrolineal sulcus spermaticus (as in fig. 12B). The hemipenis of *Rhadinophanes* has a distinctive centripetal sulcus (as in fig. 12A) and is probably derived in this regard; it probably also is derived in having the principal spines confined to the lobes.

APICAL PITS: Myers (1974, pp. 40–41) discussed some practical problems in utilizing scale pits as a taxonomic character, and reported that apical pits occur on *some* specimens in two of the 45 species of *Rhadinaea*. No attempt was made to put this character in a phylogenetic framework, except to “suggest a possibility in need of investigation, namely that the pits may be polyphylogenetically derivable above nerve endings already present in colubrid snakes generally.” However, Marx and Rabb (1972, pp. 92–96) found a strong ecological correlation between snakes lacking pits and having specialized (secretive or aquatic) habits, which suggests that absence of pits is derived. Therefore, we here consider the presence of pits as primitive in *Rhadinophanes* and their absence as derived in *Rhadinaea* and *Coniophanes* (fig. 6). But the appearance of pits in the variational repertory of two distantly related species of *Rhadinaea* is not explained. Do the occasional pits merely represent a genetic atavism, or do we conclude that multiple loss has occurred and is still occurring in different lineages of *Rhadinaea*? Either way, the character seems to have low predictive value, at least in this complex of snakes.

MAXILLARY TEETH: The two posterior-

most maxillary teeth in *Rhadinophanes*⁶ and most *Rhadinaea* are enlarged "fangs" which evidently facilitate entry of weak venom, from Duvernoy's gland, into some kinds⁷ of prey (Myers, 1974, pp. 27-28). Since the teeth are shed alternately, paired fangs help ensure that at least one will be functional and present on each maxilla. The device is improved in *Coniophanes* by the addition of a deep anterior groove on the basal one-half to four-fifths of each fang. Such morphological improvement indicates to us that the grooves are derived, a conclusion also reached by Marx and Rabb (1972, pp. 268-272). Therefore, in *Coniophanes*, the presence of an anterior groove below a laterally compressed, knifelike tip (Myers, 1969, p. 1) is considered a synapomorphy supporting a monophyletic origin for this genus (fig. 6). Presence of weak maxillary grooves in specimens of one species of *Rhadinaea* is considered as evidence supporting a widely held view that grooves are convergently derived in separate colubrid lineages (Myers, 1974, p. 231).

A few workers would reverse the polarity and consider ungrooved fangs as derived from primitively grooved fangs. This seems likely to have occurred in isolated cases, but as a broad generality the notion seems to defy logic. Myers (*loc. cit.*) observed that unless there has been a "more or less complete shift to food for which venom is not needed or is useless . . . grooves in which to

more efficiently channel the venom would not seem likely to be lost once present."

SCALE ROW REDUCTION: Most snakes have a changing number of scale rows from neck to tail, probably in some rough relationship to the degree of body taper. Some snakes, however, have a constant number of rows throughout the body, seemingly correlated with a somewhat more cylindrical body shape and often with fossorial or semifossorial habits. Absence of reduction is here considered a derived characteristic of *Rhadinaea* (fig. 6). Presence of posterior reduction in *R. brevirostris* (17-17-15) and some specimens of a few other species of *Rhadinaea* are secondary events in the generic trend toward a reduced number of dorsal scales.

COMPARISON OF *RHADINOPHANES* AND *TANTALOPHIS*, WITH SPECIAL REFERENCE TO THE HEMIPENIS

Phylogenetic relationship has never been satisfactorily elucidated for the snake *Lep-todeira discolor* Günther, which was described from two specimens collected over a century ago in the Mexican state of Oaxaca. Duellman (1958) recognized that *discolor* did not belong with any of several genera to which previous workers had assigned it, and so erected the monotypic *Tantalophis*, based primarily on his detailed examination of a new specimen collected in Oaxaca in 1955. Additional material now available shows that *Tantalophis discolor* is widespread in the Sierra Madre del Sur of Oaxaca, at elevations of about 2400-2800 m. in the pine-oak zone. Its distribution is thus allopatric to that of *Rhadinophanes monticola*, which occurs at similar elevation in the Guerrero extension of the Sierra Madre del Sur (fig. 1).

Although *Tantalophis* appears to be quite a different kind of snake from *Rhadinophanes* (compare figs. 2 and 7), they have similar hemipenes and therefore warrant close comparison. We are grateful to A. S. Savitzky for calling our attention to the resemblance between figure 5 and a comparable *Tantalophis* preparation, and for rushing

⁶ The ultimate fang is offset laterad relative to an imaginary line connecting the penultimate fang with the prediastemal teeth. Myers (1974, pp. 28-29) considered this condition to be derived in *Rhadinaea*, compared with a presumably primitive condition, in the *R. godmani* group, characterized by the last several teeth being enlarged and lying on the same plane. That polarity judgment is now considered questionable on the basis of outgroup comparison, which indicates that the offset-fang condition is widespread and therefore more likely to be primitive relative to the distinctive dentition in the *godmani* group.

⁷ *Rhadinaea flavilata*, at least, may employ the venom apparatus only on its larger, more difficult to manage prey (e.g., lizards); such prey as small frogs are swallowed straightaway.

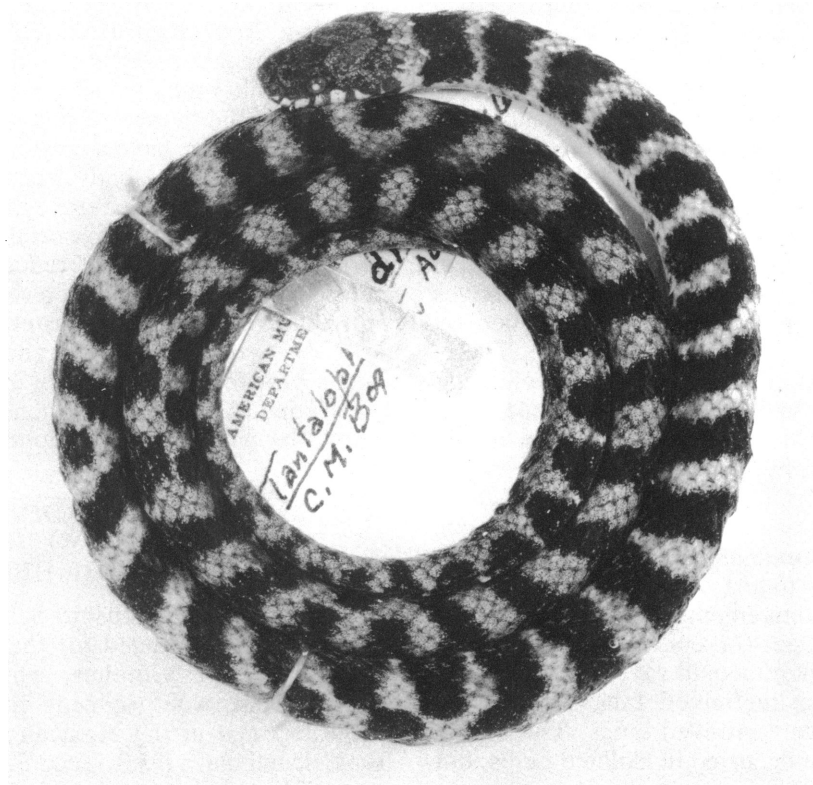


FIG. 7. *Tantalophis discolor* (Günther), an adult female (AMNH 97973), about natural size.

his own examination of available *Tantalophis* in order to return specimens for our use. Data were taken from seven specimens of *Tantalophis discolor* in the collections of the American Museum (AMNH) and the University of Kansas Museum of Natural History (KU). All localities are in Oaxaca, as follows: 0.5 mi. SW El Punto, 8000 ft., northeast slope Cerro San Felipe (AMNH 89593); 1 mi. S El Punto, 8000 ft. (AMNH 103130); Loma Grande, above and S El Punto, 8200 ft. (AMNH 97973); 13 km. N Guelatao, 2620 m. (KU 87471); La Cofradía, 9100 ft. (AMNH 103068); 3 rd. mi. NW Santa Inez del Monte, 9100–9200 ft., Sierra de Cuatro Venados (AMNH 100917); 6 mi. SE Tamazulápam [or Tamazulapan] (KU 40143).

In the following comparisons, we are unable to determine evolutionary polarity for most of the character-state differences between the two taxa.

SIZE AND HABITUS: *Tantalophis* attains a total length of at least 539 mm. in males (555 mm. reported for a male syntype) and 620 mm. in females, with the tail comprising about 23–28 percent of the total length (sexes combined). *Rhadinophanes* might conceivably grow to equivalent size, perhaps with a slightly shorter tail (23.2% of total in ♂ holotype, vs. 25.2–27.6% in 3♂ *Tantalophis*), but *Tantalophis* is much more robust in general habitus. This can be visualized in figure 8, which shows a juvenile *Tantalophis* that has a larger, more massive head than a sub-

adult *Rhadinophanes* that is 25 mm. longer in total length.

COLOR PATTERN: *Tantalophis* is marked with 38–54 dark crossbands on the body, in contrast to the mottled linear appearance of *Rhadinophanes* (figs. 2, 7). *Tantalophis* has a pale collar, which in some individuals is broken completely or partially by a vertebral line of dark pigment, whereas *Rhadinophanes* has a laterally restricted pale nape spot that may be similarly broken on the midline. The dark markings on the labial plates are very similar (fig. 8).

SCUTELLATION: Five specimens of *Tantalophis* have the dorsal scales in 19-19-17 rows, as do the types of *Rhadinophanes*. The formulae 21-21-19⁸ and 19-21-17 also appear in one specimen each of *Tantalophis*. The posteriormost reduction to 17 rows of body scales, or to 19 rows in one, involves the loss or fusion of row 4 (usually by 3 + 4), as in *Rhadinophanes* (table 1, note b). Other similarities involving the dorsal scales include the presence of anal (supracloacal) ridges in some males and the presence of small, paired apical pits in both genera.

Variation in the head plates of *Rhadinophanes* is essentially encompassed in the variation of the larger *Tantalophis* sample. *Tantalophis* has a similarly high number of ventral plates (172–181, 4♂; 187–189, 3♀) as *Rhadinophanes* (174♂, 180♀), but the latter has fewer subcaudals (64 in 1♂ vs. *Tantalophis* with 80–82 in 4♂, 72–73 in 3♀).

SKULL: The skull of *Tantalophis* (fig. 9A) generally resembles that of *Rhadinophanes* (fig. 3), including such features as: frontal bones together forming a unit that is about as wide as long; prefrontal relatively high and narrow; and postorbital dorsally in narrow contact with both frontal and parietal. The nasals of *Tantalophis* are somewhat smaller and are anteriorly narrowed (poste-

⁸ Duellman (1958, p. 4) shows a posterior reduction to 17 rows on this specimen, but that is the reduction from the body to the tail; the reduction to 17 rows in other specimens occurs well anterior to the tail. Duellman (*loc. cit.*) mistakenly annotated the reduction from 21 to 19 rows as due to the combination of rows 2 and 3 (actually 3 + 4 on this specimen).

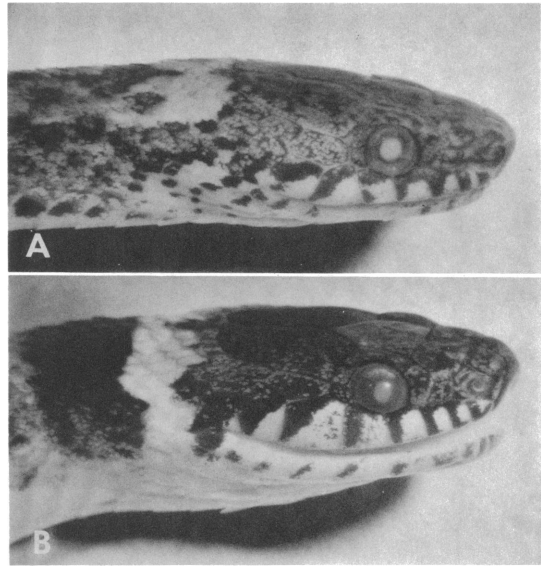


FIG. 8. Heads of (A) *Rhadinophanes* and (B) *Tantalophis*, both $\times 3.6$. Labial color patterns are similar, but *Tantalophis* differs in having an elliptical pupil and a stockier head and body. (A. *R. monticola*, holotype, subadult male 357 mm. total length. B. *T. discolor*, AMNH 100917, juvenile female 332 mm. total length.)

riorly narrowed in *Rhadinophanes*). The parasphenoid process of the sphenoid has a pronounced step at the posteriormost frontal contact in *Tantalophis*, whereas the parasphenoid process in *Rhadinophanes* is not noticeably raised at this point.

Tantalophis has fewer maxillary teeth (13–17 + 2, $\bar{X} = 15 + 2$, $N = 7$) than *Rhadinophanes* (19 + 2, 20 + 2). The two enlarged rear fangs in both snakes are ungrooved and have a knifelike rear edge on at least the distal half of the tooth, this last feature being somewhat better developed in *Rhadinophanes*. The size of the diastema seems to be negatively correlated with the number of prediastemal teeth, and it is sometimes absent at least in *Rhadinophanes*. The last fang, in each genus, is only slightly offset to the side.

Tantalophis also may tend to have fewer teeth on the other dentigerous bones, although the differences are not great (follow-

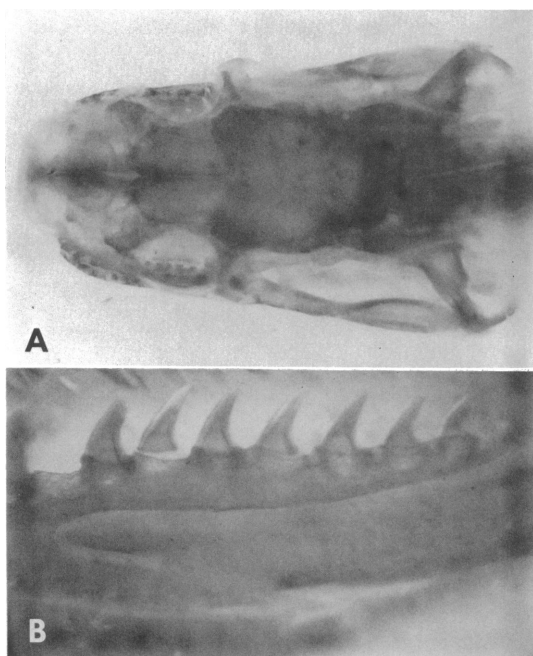


FIG. 9. *Tantalophis discolor* (AMNH 103130 ♂), cleared-and-stained head of an adult. A. Dorsal view of skull, $\times 4.0$. B. Left mandible in lateral view, showing articulation between dentary and compound bones, $\times 19.4$.

ing counts taken from one side each of two specimens of *Tantalophis* and both sides of the paratype of *Rhadinophanes*):

	<i>Tantalophis</i>	<i>Rhadinophanes</i>
Palatine	10, 11	11, 12
Pterygoid	21, 26	26, 27
Dentary	19, 21	25, 25

The most striking osteological difference noted between *Tantalophis* and *Rhadinophanes* is the unusually spacious intramandibular articulation of the latter (fig. 3). The gap between the dentary and compound bones is conspicuously wide in both mandibles of the paratype of *Rhadinophanes*; in medial view, the articulations in the splenial-angular region appear normal (i.e., close).

There is a relatively close articulation between dentary and compound bones in *Tantalophis*, both in cleared-and-stained and in dry preparations (figs. 9B, 10). To check whether an ontogenetic change might be involved, a lower jaw was removed from the smallest juvenile specimen of *Tantalophis* (AMNH 89593 ♂, 238 mm. SVL); even after cleaning this small mandible nearly to the point of disarticulation, the gap between dentary and compound bones remained relatively as narrow as in the adult (fig. 10).

JAW MUSCULATURE: There are a few differences in the jaw muscles, as pointed out to us by S. B. McDowell, who examined aspects of the soft anatomy of heads being prepared for osteological comparisons (specimens in figs. 3, 9). In *Rhadinophanes*, the m. retractor pterygoidei inserts on the pterygoid, but in *Tantalophis* it inserts entirely on the palatine.

The m. pterygoideus superficialis also differs, as best explained in Dr. McDowell's own words (personal commun.): "Both genera have (as do all snakes) a pterygoideus superficialis *pars major*, with a fleshy origin from the lateral surface of the extreme rear of the lower jaw and a tendinous insertion on the anterolateral corner of the ectopterygoid. *Tantalophis*, but not *Rhadinophanes*, also

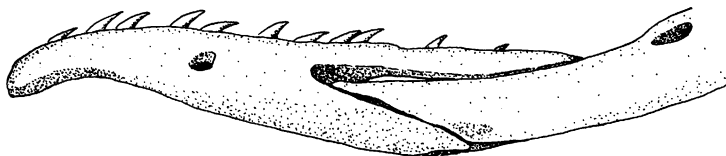


FIG. 10. *Tantalophis discolor* (AMNH 97973 ♀), front half of lower jaw in ventrolateral view, showing a "normal" colubrid intramandibular articulation, $\times 9$. See also figure 9B and compare with condition in *Rhadinophanes* (fig. 3).

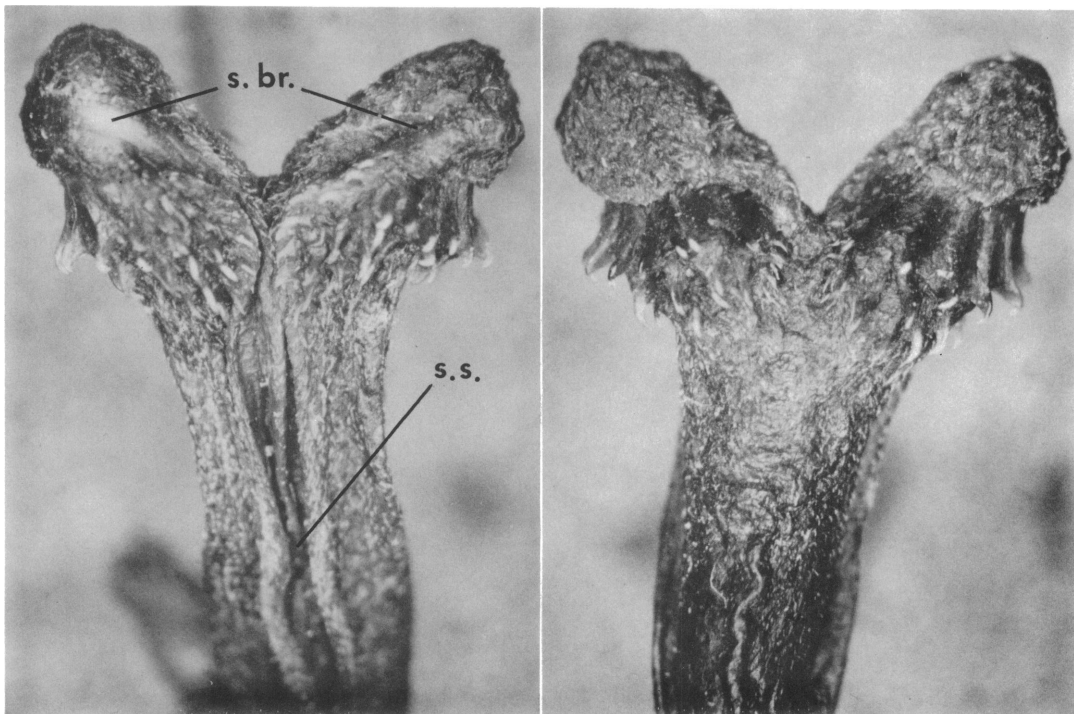


FIG. 11. Everted hemipenis of *Tantalophis discolor* (AMNH 103130). Distal half of left organ from both sulcate side (left) and asulcate side (right). Abbreviations: s.s., the sulcus spermaticus below its point of bifurcation; s.br., the centripetal branches of the sulcus spermaticus. About $\times 10.6$.

has a pterygoideus superficialis *pars minor* (as do many primitive colubroids), a muscle with a fleshy origin from the dorsal surface of the anterior end of the ectopterygoid and a tendinous insertion on the medial face of the mandible, just anterior to the insertion of the pterygoideus accessorius (the 'pterygoideus superficialis *pars minor*' is, perhaps, an isolated anterior slip of the pterygoideus accessorius, rather than a true portion of the pterygoideus superficialis)."

PUPIL SHAPE: *Tantalophis discolor* has a vertically elliptical pupil (fig. 8B; Duellman, 1958), which is preserved in its nearly round state in a few specimens. *Rhadinophanes monticola* has a circular pupil (fig. 8A). Walls (1932, p. 69) called attention to the occasional problem of determining pupil shape but also emphasized that, "The form of a reptilian pupil is a minor morphological feature in itself, but it is an adaptation in support of a

fundamental structural and physiological situation in the retina itself."

HEMIPENIS: The hemipenes of *Rhadinophanes* (fig. 5) and *Tantalophis* (figs. 11, 12A) are similar in all major aspects, although the material available is inadequate for comparison of certain details (e.g., see footnote 4). The organs have the same physiognomy in being long, slender, and bifurcate for between 20 and 35 percent of their length. Each lobe is separately capitate⁹ and calyculate,

⁹ Such a double-headed organ can appropriately be termed *bicapitate* (fig. 12A), the contrary condition, whether of single or slightly bilobed organs, being *unicapitate* (fig. 12B). An intermediate condition has been termed *semicapitate* (discussion in Myers, 1973, pp. 30-31). All these conditions indicate the presence of a free overhanging edge demarcating a greater or lesser part of the distal calyculate area(s), otherwise the organ is *noncapitate* (fig. 12C and further discussion in Myers, 1974, p. 31).

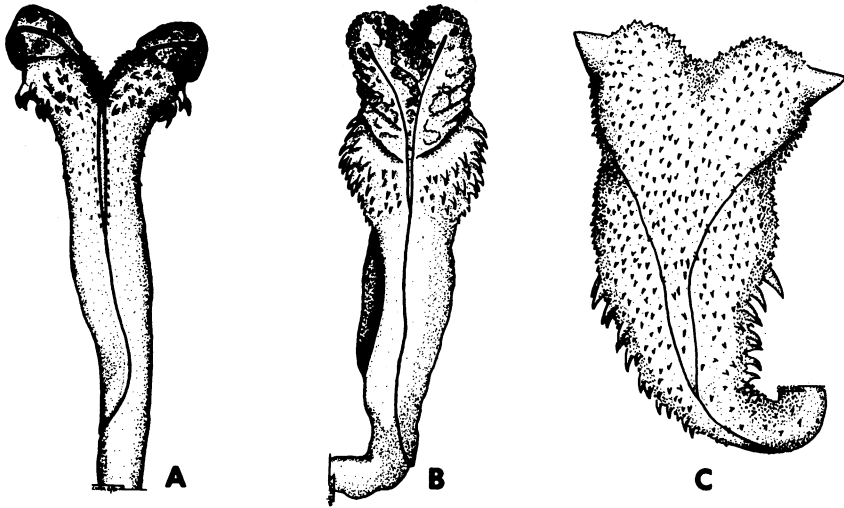


FIG. 12. Snake hemipenes with different orientations of the branches of forked sulci spermatici. A. Centripetal (*Tantalophis discolor*, AMNH 103130, left organ, $\times 4$). B. Centrolineal (*Rhadinaea hempsteadae*, AMNH 110617, right organ, $\times 3$). C. Centrifugal (*Arrhyton callilaemus*, Albert Schwartz collection, field series no. V12553, left organ, $\times 6$).

with no confluence between the two areas of calyces. The proximal part of each lobe is completely encircled by medium-sized spines. The stalk of the hemipenis below the lobes is spinulate on roughly its upper half, whereas the lower half seems completely nude, lacking spinules, basal pocket, or any other ornamentation (but see footnote 4). The sulcus spermaticus forks on the upper half of the organ and the two branches run in parallel to the crotch and then extend along the facing sides of the lobes to their tips.

The aforesaid orientation of the branches of the sulcus spermaticus is a rare condition, at least among xenodontine colubrids. McDowell (1961, p. 504) suggested adoption of the terms *centripetal* and *centrifugal* for describing two extreme conditions of the branches of forked sulci in the Natricinae. Although little subsequent attention has been given to this aspect of the snake hemipenis, it seems to have potential taxonomic importance and we think that the terms suggested by McDowell will prove useful. But an additional term is needed for a common intermediate condition, for which *centrolineal* is

here proposed. The following definitions refer to forked sulci on either bilobed or single hemipenes:

- (A) Centripetal. Branches of the sulcus spermaticus diverge minimally and extend up the center of the hemipenis, to lie on facing sides of the lobes if the organ is bifurcate. This rare condition is exemplified by *Rhadinophanes* and *Tantalophis* (fig. 12A).
- (B) Centrolineal. Branches of the sulcus spermaticus diverge moderately and extend in relatively straight lines, to lie on the same side of the hemipenis as the forking point of the sulcus. This common condition occurs in at least some species of such diverse xenodontine genera as *Alsophis*, *Diadophis*, *Philodryas*, *Manolepis*, *Rhadinaea*, and *Tachymenis* (fig. 12B).
- (C) Centrifugal. Branches of the sulcus spermaticus diverge outward from the center, to lie ultimately on opposite sides of the hemipenis. Examples among xenodontines include species of *Arrhyton*,

Liophis, *Oxyrhopus*, *Pseudoboa*, *Tripanurgos*, and *Coniophanes imperialis* (fig. 12C).

There appear to be degrees of intermediacy between the above conditions,¹⁰ but most organs can readily be assigned to one of the three classes. Although determination is made most easily from everted hemipenes (fig. 12), the orientation of the sulcus branches is normally the same in the retracted organ¹¹ and can be determined by dissection. But this may be difficult or impossible to ascertain from illustrations of retracted organs that have been cut open and spread flat. Although the centripetal nature of the sulcus is obvious in a one-dimensional illustration of the everted organ of *Tantalophis discolor* (fig. 11), it is not at all evident in a published drawing (Duellman, 1958, fig. 4) of a retracted hemipenis of the same species. But direct examination and manipulation of the dissected hemipenis (KU 40143, left organ) used in the aforesaid drawing showed that, when the lobes are closed, each branch of the sulcus lies on the side of the lobe that faces the other lobe. The centripetal nature of the hemipenis of *Rhadinophanes monticola* was similarly determined by dissection

¹⁰ In *Crisantophis nevermanni* (AMNH 104032), for example, the branches of the sulcus diverge moderately upon forking and extend onto the lobes of the hemipenis in a centrolineal direction, but each branch then curves medially and thereafter faces its fellow along most of its length. This spermatid sulcus must thus be classified as centripetal, although differing in detail from figure 12A, which shows the two branches extending in parallel to the crotch of the hemipenis.

The monotypic *Crisantophis*, incidentally, has a considerably larger geographic range than previously reported (from Costa Rica through western Nicaragua to southern Honduras, *vide* Villa, 1971). A specimen of *C. nevermanni* from Guatemala extends the range several hundred kilometers northwestward and indicates that the species probably is also part of the El Salvador fauna (AMNH 112402, La Avellana, Dept. Santa Rosa, southeastern Guatemala).

¹¹ This is readily visualized by painting a forked, sulcus-like line on two fingers of a transparent surgical glove, representing an everted, bilobed hemipenis. Turn the glove inside out to represent the retracted hemipenis.

and manipulation of both lobes of the organ illustrated in figure 5.

DISCUSSION: SYSTEMATICS AND ZOOGEOGRAPHY

We have commented on the general resemblance between *Rhadinophanes monticola* and species of *Rhadinaea* and *Coniophanes*, and we have pointed out that *Rhadinophanes* is comparatively primitive in several characters for which evolutionary polarity can be determined. If the resemblance were the result of close (phyletic) relationship, *Rhadinophanes* could be the plesiomorphic sister group of *Rhadinaea* and *Coniophanes*, as shown in figure 6. The two sister groups thus postulated are separated most convincingly by hemipenial differences. In keeping with the relatively primitive aspect of *Rhadinophanes*, its bilobed, bicapitate hemipenis is consistent with the ancestral morphotype previously hypothesized for single, or weakly bilobed, unicapitate organs such as possessed by *Rhadinaea* and *Coniophanes* (Myers, 1973, p. 31). Other characters separating *Rhadinophanes* from *Rhadinaea* plus *Coniophanes* (scale pits), or from *Rhadinaea* alone (scale-row reduction), are somewhat ambiguous because of intraspecific variation in a few species of *Rhadinaea*. But the separation is further supported by lack of any detailed correspondence between the color patterns of *Rhadinophanes monticola* and any of the 57 recognized species of *Rhadinaea* and *Coniophanes*. Separation, however, is not the real problem. We have not found a single, uniquely derived character which would unite these genera by recency of common ancestry. Without such evidence, any purported relationship is highly speculative. The similarities in phenotype could as well be due to convergence or to symplesiomorphy.

A serious comparison also was warranted between *Rhadinophanes* and the monotypic *Tantalophis*, although phenotypic dissimilarity seemed at first to preclude any likelihood of close phyletic relationship. *Tantalophis discolor* differs strikingly in having an elliptical pupil, a crossbanded color pattern, and

a stockier head and body; these disparities are reinforced by a few differences in jaw muscles and by the unique intramandibular articulation of *Rhadinophanes*. Points of similarity between *Rhadinophanes* and *Tantalophis* include labial color patterns, scutellation, overall appearance of the skulls, and, especially, their nearly identical hemipenes.

The hemipenes of *Rhadinophanes* and *Tantalophis* are alike in all essentials. A portion of their resemblance (bilobation, bicapitation) is judged to be the result of sympleiomorphy. No polarity judgments can presently be made for such shared features as slenderness of the hemipenis, degree of bilobation, and size of calyces. Two shared features seem so unusual, however, that we must decide in favor of synapomorphy, at least pending a broader survey of xenodontine hemipenes: (1) Spines are confined to the lobes of the organ (figs. 5, 11); there is only a zone of slender spinules below the lobes. (2) The forked sulcus spermaticus is centripetal (fig. 12A). We therefore have reason to suppose that *Rhadinophanes* and *Tantalophis* share a monophyletic origin and that they are probably more closely related to one another than either is to any other known snake. *The two monotypic groups are regarded as separate genera because of the considerable morphological disparity mentioned above.* The approach is existentialistic (and rather conventional in colubrid systematics). It would be at least methodologically acceptable to treat *R. monticola* as a second species of *Tantalophis*, but most learned discussion about such matters seems rather fruitless, particularly when given for reasons of justification. Suffice it to say that both possibilities were considered and a decision made.

Considering *Rhadinophanes* and *Tantalophis* as sister groups is not inconsistent with the possibility that the two genera together represent the plesiomorphic sister group of *Rhadinaea* plus *Coniophanes*. *Tantalophis* shares the same plesiomorphic character states shown for *Rhadinophanes* in figure 6, but the monophyly of this larger complex of genera remains unestablished. Also, the addition of *Tantalophis* to the picture brings to

mind other possibilities worthy of attention. For example, *Tantalophis* and *Rhadinophanes* together might be viewed as the sister group of *Leptodeira*, which is closest to *Tantalophis* in color pattern and the elliptical pupil but which has grooved rear fangs and a unicapitate hemipenis somewhat similar to that of some *Rhadinaea* and *Coniophanes*. Bogert and Duellman (1963, p. 13), although unaware of the peculiar centripetal sulcus of the hemipenis of *Tantalophis*, called attention to the primitive bilobation of the organ and suggested common ancestry with *Leptodeira* and *Cryophis*, whose hemipenes are single. Much remains to be done to elucidate the relationships of these and other genera of Middle American colubrids.

The relationships of *Rhadinophanes* and *Tantalophis* might also be sought among various alsophiine colubrids, which are widely distributed on the American mainland and in the West Indies and Galapagos. Relationships within this series of snakes are poorly known, but the hemipenes of *Rhadinophanes* and *Tantalophis* are of the alsophiine type in being symmetrically bilobed, with a forked sulcus spermaticus, and with calyculate lobes that appear bicapitate at least from the asulcate side. However, in *Rhadinophanes* and *Tantalophis*, the sulcus spermaticus is centripetal and bifurcates higher than on most alsophiine organs, capitation is more pronounced (fully bicapitate), and the confinement of the principal spines to the lobes is unusual if not unique. The hemipenes are also more slender than the alsophiine organs that we have examined. These several features seem to differentiate *Rhadinophanes* and *Tantalophis* from the alsophiine genera, although few have been treated in any detail (brief discussions and references in Myers, 1973, 1974, and Thomas, 1976).

It is at least consistent with the proposed sister-group relationship of *Rhadinophanes* and *Tantalophis* that they are allopatric and occupy roughly the same elevational zone (fig. 1), although this is not necessarily meaningful with regard to origins. The distributional pattern of a widespread form in Oaxaca and a more confined relative in

Guerrero is perhaps commonplace, although phyletic relationships of most such cases have not been specified. One documented parallel is that of *Rhadinaea fulvivittis* and *Rhadinaea omiltemana* which are allopatric sister species whose ranges approximate those of *Tantalophis* and *Rhadinophanes*, respectively (Myers, 1974, map 8, pp. 97, 228).

It is always tempting to speculate that similar distributions, especially involving sister groups, can be similarly explained. But there is a notable difference between the examples given. The two sister species of *Rhadinaea* are but slightly differentiated, being distinguished mainly by details of color pattern and a few other characters. In contrast, *Tantalophis* and *Rhadinophanes* might be adapted to divergent life-styles, as suggested by marked differences in color patterns, habitus, pupil shape, and jaw apparatus. It would be reasonable (or at least in vogue) to suppose that the two species of *Rhadinaea* speciated in the Pleistocene following climatic-vegetational disruption of an ancestral range. But is it likely that the two monotypic genera shared common ancestry so recently? This is possible, of course, but it is "likely" only if one accepts the probability of very different evolutionary rates, thus adding an additional layer of unsupported speculation.

Without more information, there seems no good way around the above impasse. Platnick and Nelson (1978, p. 9) pointed out an apparently simple but generally unperceived principle, namely that very little can be concluded from comparative analysis of two-taxon, two-area patterns.¹² Although *Rhadinophanes monticola* and *Tantalophis discolor* are cladistically and distributionally congruent with the pattern shown by *Rhad-*

inaea omiltemana and *R. fulvivittis*, there must be more than one historical explanation that is compatible with a pattern of two taxa and areas. Both pairs might have speciated where they presently occur, as already mentioned. Present congruence might likewise have been produced by allopatric speciation in one case (e.g., *Rhadinaea*) and extinction (e.g., of *Tantalophis* in Guerrero) in the other. There are other possibilities, but nothing is presently gained by promoting a particular scenario.

LITERATURE CITED

- Bogert, Charles M., and William E. Duellman
1963. A new genus and species of colubrid snake from the Mexican State of Oaxaca. *Amer. Mus. Novitates*, no. 2162, pp. 1-15.
- Duellman, William E.
1958. Systematic status of the colubrid snake, *Leptodeira discolor* Günther. *Univ. Kansas Publ. Mus. Nat. Hist.*, vol. 11, no. 1, pp. 1-9.
- McDowell, Samuel B.
1961. [Review of] Systematic division and evolution of the colubrid snake genus *Natrix*, with comments on the subfamily Natricinae, by Edmond V. Malnate. *Copeia*, 1961, no. 4, pp. 502-506.
- Marx, Hymen, and George B. Rabb
1972. Phyletic analysis of fifty characters of advanced snakes. *Fieldiana, Zool.*, vol. 63, pp. i-viii, 1-321.
- Myers, Charles W.
1969. Snakes of the genus *Coniophanes* in Panama. *Amer. Mus. Novitates*, no. 2372, pp. 1-28.
1973. A new genus for Andean snakes related to *Lygophis boursieri* and a new species (Colubridae). *Ibid.*, no. 2522, pp. 1-37.
1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. *Bull. Amer. Mus. Nat. Hist.*, vol. 153, art. 1, pp. 1-262.
- Platnick, Norman I., and Gareth Nelson
1978. A method of analysis for historical biogeography. *Syst. Zool.*, vol. 27, no. 1, pp. 1-16.
- Smith, Hobart M., and Edward H. Taylor
1945. An annotated checklist and key to the snakes of Mexico. *Bull. U.S. Natl. Mus.*, no. 187, pp. i-iv, 1-239.

¹² We cannot meet Platnick and Nelson's criterion (*loc. cit.*) that "comparative analysis requires that we deal with at least three taxa and areas." The sister group of *Rhadinophanes monticola* + *Tantalophis discolor* has not been objectively determined. The sister group of *Rhadinaea fulvivittis* + *R. omiltemana* is *Rhadinaea taeniata*, which is comprised of two distinctive subspecies. But one of the latter (*R. t. aemula*) is broadly sympatric with both *fulvivittis* and *omiltemana*.

Thomas, Robert Allen

1976. A revision of the South American colubrid snake genus *Philodryas* Wagler, 1830. Ph.D. thesis, Texas A & M Univ., xiv + 324 pp. [Diss. Abstr. Internatl., vol. 37, no. 8, p. 3815B, 1977.]

Villa, Jaime

1971. *Crisantophis*, a new genus for *Conophis nevermanni* Dunn. *Jour. Herpetology*, vol. 5, no. 3-4, pp. 173-177.

Walls, Gordon L.

1932. Pupil shapes in reptilian eyes. *Bull. Antivenin Inst. Amer.*, vol. 5, no. 3, pp. 68-70.

