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Blunt-Headed Vine Snakes (*Imantodes*) in Panama, Including a New Species and Other Revisionary Notes

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ABSTRACT

The widespread Neotropical genus *Imantodes* (Colubridae) is partially revised in order to determine the relationships of a distinctive new snake discovered on an isolated ridge in eastern Panama. The six species of blunt-headed vine snakes now recognized are equally divided between two monophyletic assemblages—the *cenchoa* and *lentiferus* groups—based on hemipenial characters, maxillary dentition, relative tongue (fork) length, and coloration (reduction of pigmentation in the primitive blotched markings).

The *lentiferus* group includes *Imantodes phantasma*, new species, described from two adult males collected in wet montane forest (> 1000 m. elev.) on the Serranía de Pirre, a mountain ridge that juts north into Panama from the Colombian border. The blotched color pattern is indistinct, consisting of black-flecked, light yellowish brown saddles (gray in alcohol) on a light orange-brown body; the saddle markings appear paler than the ground color in life. During tongue-flicking, both specimens of *phantasma* displayed perceptible pauses, while the conspicuously long tips of the fork (=64% of head length) were held widely separated and quivering. Such quivering-pause behavior was not observed in four other species of *Imantodes*, although all have relatively long forks (42–75% of head length), with fork length being sexually dimorphic in at least a few species.

Imantodes phantasma is the sister species of *Imantodes lentiferus* (Cope), a widespread Amazonian snake. This interpretation of kinship is based on a hemipenial synapomorphy. The South American *I. lentiferus* has a plesiomorphic pattern of conspicuously dark blotches. Geographic differentiation is undetected in *lentiferus*, except in the non-Amazonian part of its range (eastern Guayanan region), where loss of black borders make the blotches less distinct. An unblotched, striped variant of *lentiferus* is reported from Ecuador, but any geographic or genetic significance cannot presently be assessed.

The sister species of *lentiferus* + *phantasma* is *Imantodes inornatus* (Boulenger), which has the least derived hemipenis in the genus but the most derived color pattern. Its markings of vague dorsal and alternating lateral lines seem to be the remnants of dark blotch-edging in the primitive pattern. *Imantodes inornatus* ranges from Nicaragua to the Pacific versant of Ecuador and it is sympatric with *I. cenchoa* throughout this range; it is widely distributed but uncommon in Panama.

The *cenchoa* group consists of *Imantodes cenchoa* (Linnaeus), *I. gemmistratus* (Cope), and *I.*

tenuissimus (Cope), all with well-developed, plesiomorphic, blotched patterns. The last species, from Yucatan, is placed in the *cenchoa* group on the basis of maxillary dentition; because its hemipenis was not examined, its intragroup relationships are unresolved. At least *I. cenchoa* and *I. gemmistratus* share the derived features of reduced size of the hemipenis and reduction or loss of capitation on its asulcate side.

Imantodes gemmistratus ranges from Mexico to the Magdalena Valley of northern Colombia (the first record for South America). In Panama, *gemmistratus* is nearly confined to the Pacific lowlands, occurring even in the *Curatella* savannas; apparently it is more terrestrial than the other Panamanian species, which are found only in humid forest. However, *gemmistratus* does reach the wetter Atlantic lowlands across the structural depression in the central part of the isthmus; its ecological relationships are unclear when it occurs sympatrically with *I. cenchoa* in such areas of humid forest.

Imantodes cenchoa occupies an exceptionally large range, from Mexico to Argentina, with relatively little geographic variability in general appearance. Its distribution broadly overlaps that of *gemmistratus* and completely contains the more limited ranges of the members of the *lentiferus* species group, which occur in well-known regions of endemism. Sympatry of sister groups indicates that considerable dispersal occurred subsequent to initial divergence. It seems more likely that *I. cenchoa* dispersed into the range of the *lentiferus* group than vice versa, although it is not clear whether this occurred before or after speciation events within the *lentiferus* group.

Imantodes cenchoa is ubiquitous in humid tropical forests at low and moderate elevations, hunting lizards and frogs at night and concealing itself by day in a variety of places in the arboreal vegetation or on the ground. In Panamanian *I. cenchoa*, head length and head width increase at a greater rate in females than in males, with the effect that females can take relatively larger prey; the largest females are even able to feed on the "giant" species of *Anolis*. This and other indirect evidence suggest differential foraging by males and females.

From examination of type specimens of old names currently in the synonymy of *Imantodes cenchoa*, it is concluded that (1) the placement of *Himantodes anisolepis* and *H. platycephalus* is correct, (2) *Himantodes hemigenius* is a junior synonym of *I. gemmistratus*, and (3) the name

Himantodes semifasciatus is a composite of *I. cenchoa* and *I. gemmistratus*. A lectotype is designated to keep *semifasciatus* with *cenchoa*, but the

nominal subspecies *Imantodes cenchoa semifasciatus* is nonetheless considered invalid. A lectotype also is designated for *Imantodes lentiferus*.

INTRODUCTION

The genus *Imantodes* is a compact, well-defined assemblage of New World snakes with a continental distribution that slightly overlaps the tropics of Cancer and Capricorn. The species occur at low and moderate elevations in environments as diverse as rain forest and savanna, and their modes of life range from highly arboreal to nearly terrestrial. There are few other snakes with which they can be confused, owing to their attenuated bodies and conspicuous heads that are stuck on ludicrously thin necks. The neck is so disproportionately slender in relation to the head that one might expect the food to be some kind of small invertebrate, rather than the relatively bulky lizards and frogs that *Imantodes* hunts at night and for which it is armed with grooved rear fangs.

Five species of *Imantodes* are currently recognized, all named prior to the twentieth century, as follows. The first three species listed have long been known to occur in Panama.

- (1) *I. cenchoa* (Linnaeus, 1758), Mexico to Argentina
- (2) *I. gemmistratus* (Cope, 1861), Mexico to Colombia
- (3) *I. inornatus* (Boulenger, 1896), Nicaragua to Ecuador
- (4) *I. lentiferus* (Cope, 1894), Amazonian basin and Guayanan region
- (5) *I. tenuissimus* (Cope, "1866" [1867]), Yucatan

A sixth species, the fourth for Panama, was discovered in 1966, when I encountered two specimens of a new *Imantodes* on an isolated mountain ridge in Darién. The finding of previously unknown species can be predicted in some genera of tropical vertebrates and in some regions—including the Isthmus of Panama, which holds an exceedingly complex herpetofauna that is taking a long time to

census and catalogue (Myers, 1972; Duellman and Myers, 1980). However, *Imantodes* seemed to be a well-known genus comprised mainly of widely distributed, frequently collected snakes, with the last valid species having been named in 1896. Thus, a new species of seemingly limited distribution was cause for astonishment early in 1966, atop the northern end of the Serranía de Pirre. I have not found this snake again, although I always half expected to see one when working at night from forest camps in other, neighboring mountain ranges in Darién and in Chocóan Colombia.

In the sense of making an unusual and unexpected appearance, the first specimen materialized truly as an apparition in the drifting, nocturnal fog of a remote cloud forest—*un fantasma de la montaña llorona*. With that remembrance, I propose the following name:

***Imantodes phantasma*, new species**

Figures 1–3, 4D, 4E, 19E; Map 2

HOLOTYPE: KU 110217 (field no. CWM 6094), caught by Charles W. Myers in company with Tomás Quintero on January 24, 1966, in montane forest at 1030 m. elevation on the southeastern slope of Cerro Cituro, a peak on the northern end of the Serranía de Pirre, Province of Darién, Republic of Panama (map 2, fig. 5).

PARATYPE: AMNH 109493 (field no. CWM 6002), an adult male taken on January 20, 1966, in cloud forest at 1100 m. elevation on the south ridge of Cerro Cituro. Other data same as for holotype.

ETYMOLOGY: The specific epithet, a noun in apposition, is Latin, meaning apparition.

DEFINITION AND DIAGNOSIS: An *Imantodes* of ~1 m. total length, with pattern of grayish dorsal saddles (these markings yellowish

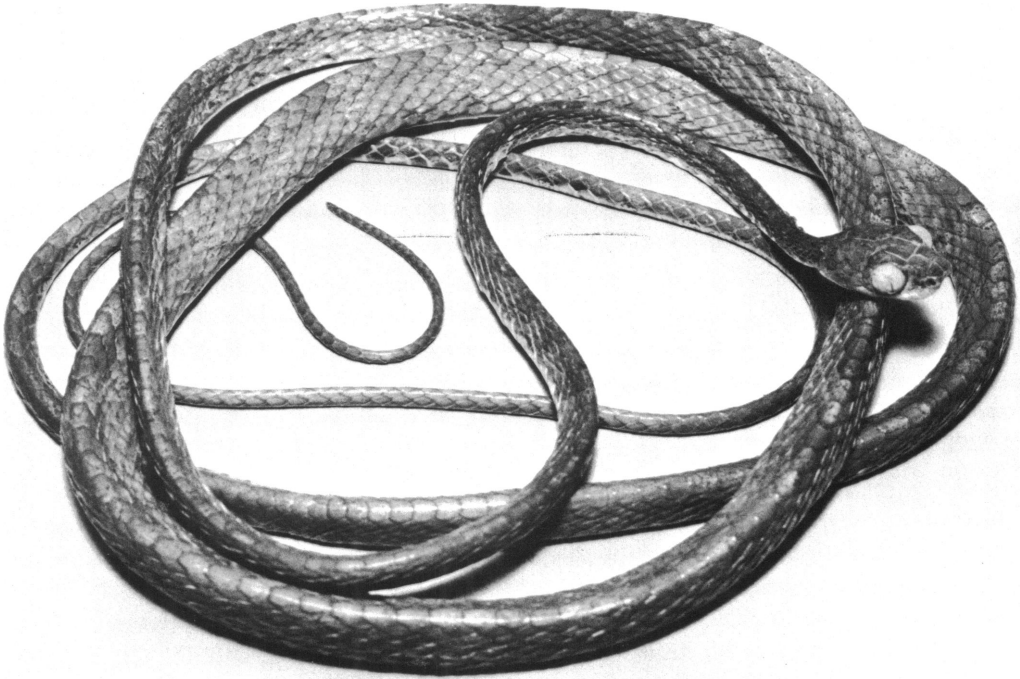


FIG. 1. *Imantodes phantasma*, new species. The holotype in life.

brown with black flecks in life) on a light orangish brown body; saddle markings have little contrast, actually appearing paler than the ground color in life. Dorsal scales in 17-17-17 or 17-17-15 rows; vertebral scales conspicuously modified, about two times wider than midlateral scales and with concave or truncate rear margins. High number of maxillary teeth ($\sim 19+2$), with the rear fangs being only feebly grooved. Hemipenis relatively large; asulcate edge of capitulum joined to midsection by short cluster of small spines, adjacent to a naked pocket notched in edge of capitulum.

This species differs from all other *Imantodes* in its unusual pattern of very light dorsal blotches, which are not sharply defined and which in life may even appear paler than the ground color. *Imantodes phantasma* differs from all other species except *I. inornatus*

and *I. lentiferus* in having a relatively large hemipenis² with a distal naked pocket in the asulcate edge of the capitulum, and in having a high number (> 16) of prediastemal maxillary teeth, and rear fangs that are only feebly grooved. *Imantodes inornatus* is immediately differentiated from *phantasma* by its autapomorphic pattern of vague dark cross-lines (rather than saddles or blotches). *Imantodes lentiferus* differs in having 15 (vs. 17) scale rows at midbody and in dorsal blotches that, although variable, are always conspicuously darker than the ground color.

² I have not examined the hemipenis of *Imantodes tenuissimus* (Cope) of Yucatan, whose affinities seem to be with *gemmistratus* and *cencha*. In any case, it is a vividly banded snake with normally shaped, scarcely enlarged scales in the vertebral row, and cannot be confused with *I. phantasma*.

TABLE 1
Scale Counts, Measurements, and Proportions of the Type Specimens of *Imantodes phantasma*^a

	Holotype ♂ KU 110217	Paratype ♂ AMNH 109493
Dorsal scale rows	17-17-17	17-17-15
Ventrals at posterior scale-row reduction ^b	—	187/188
Ventrals	236 ^c	235 ^c
Anal plate	÷	÷
Subcaudals (pairs)	161	156
Supralabials	9	9
Supralabials touching loreal	2-3	2-3/2
Supralabials touching eye	4-6	4-6
Preoculars	1	1
Postoculars	2	2
Temporals	1+2+3/1+2+2	2+2+2/2+2+3
Infralabials	12/11	11
Infralabials touching anterior genials	1-6	1-6
Infralabials touching posterior genials	6-7	6-7
Eye diameter	4.0 mm.	4.0 mm.
Greatest head width	9.3 mm.	9.5 mm.
Head length (tip of snout to end of mandible)	15.0 mm.	15.6 mm.
Eye/head length	0.267	0.256
Head width/head length	0.620	0.609
Total length	1053 mm.	1082 mm.
Tail length	344 mm.	356 mm.
Tail/total length	0.327	0.329

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

^b Scale-row reduction occurring in paratype by loss of paravertebral rows.

^c Preceded by three preventrals (gulars longer than wide) in holotype, one preventral in paratype.

DESCRIPTION OF TYPE SPECIMENS

The male holotype (fig. 1) and male paratype are adults, as suggested by their size and confirmed by the presence of visually enlarged kidney tubules, enlarged, convoluted vasa deferentia, and calcified hemipenial spines. Following is a combined description of the two specimens. Differences in scale counts and certain measurements and proportions are shown in table 1, and some comparisons with other species in table 2.

PROPORTIONS AND SCUTELLATION: Long slender snakes of 1053–1082 mm. total length, of which the tail comprises 33 percent. Body higher than wide, rounded ventrolaterally. Short, blunt head 1.6 times longer³ than broad and 2.4–2.6 times longer

than deep; head abruptly distinct from neck, about 3.3–3.4 times wider than thinnest part of neck and also somewhat wider than greatest width of body. Eye large, occupying 26–27 percent of length of head, and protuberant, with the elliptical pupil visible from anterior, dorsal, and ventral aspects.

Dorsal scales smooth, with some anterior scales bearing an inconspicuous median apical pit; anal ridges absent. Dorsal body scales in 17 rows throughout in holotype, but posteriorly reducing to 15 rows in paratype by loss of the paravertebral rows (table 1). Scales of vertebral row conspicuously enlarged (figs. 1, 2), with the posterior margins being either concave or truncate; vertebral scales twice as wide as midlateral scales at midbody. Ven-

³ Head length was measured with calipers from the tip of the snout to the level of the end of the mandibles

(which can be felt through the skin), in a plane parallel to the long axis of the head and body.

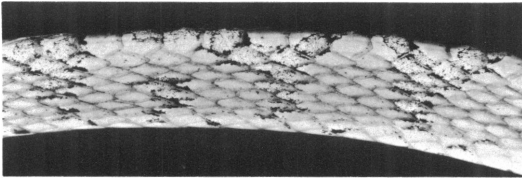


FIG. 2. *Imantodes phantasma*, new species. Section of body of holotype in dorsolateral view.

trials 235–236, anal plate divided, subcaudals in 156–161 pairs.

Rostral plate twice as wide as high, inclined slightly forward and narrowly visible from above. Paired internasals, wider than long, about two-thirds as long as prefrontals. Paired prefrontals slightly longer than wide, each in contact with its mate and with frontal, supraocular, preocular, loreal, nasal, and internasal. Frontal pentagonal, 1.6–1.9 times longer than its greatest (anterior) width, and about a fourth longer than distance from its anterior edge to tip of snout. Supraocular anteriorly narrow, but posteriorly nearly as wide as greatest frontal width. Broad parietals only about 1.4 times longer than wide; interparietal suture shorter than or equal to length of frontal, longer than distance from frontal to tip of snout. Single nasal plate centrally pierced by large naris (0.9 mm. diameter). Small loreal higher than wide, smaller than nasal or adjacent labials. One large, high preocular; no subpreocular; two postoculars, the lower somewhat more than half the size of upper. Temporals somewhat variable in size, with five to seven scales per side forming vague rows (table 1). Supralabials 9, second to third or second only touching loreal, fourth to sixth bordering the orbit. Infralabials 11 or 12, with first six touching anterior genial, and sixth to seventh touching posterior genial; first pair of infralabials in contact behind mental. Anterior and posterior genials of nearly equal length. Some tiny tubercles (presumed sensory organs) present on head, most concentrated on snout and most widely dispersed on underside of head.

COLOR AND PATTERN: The pattern in preservative is one of numerous, poorly defined gray saddles on an orangish brown body; the

two males have 61–65 body markings and two or three dozen vague tail blotches. The body saddles dorsally tend to occupy two or parts of three enlarged vertebral scales; the middorsal interspaces vary from somewhat shorter than to somewhat longer than the saddles themselves. The saddles narrow to about one lateral scale on the lower side, where they extend nearly to, or actually touch, the tips of the ventral plates. Both specimens have parts of the trunk where the saddle-markings are bilaterally shifted and interconnected, forming short chains. Both individuals have some discrete saddles that have a median pale area devoid of melanophores, and which, when viewed from the side, are indistinguishable from the interconnected chainlike sections of saddles (fig. 2). (Because of this variability, the saddles were counted from the left side rather than from the dorsal aspect.)

There is very little contrast between the body and tail markings, especially in life (fig. 1). The living snakes had dull, light orangish brown bodies, with *lighter* yellowish brown saddle markings having extensive black flecking; the saddles on the neck were more of a dark gray owing to a finer dispersion of melanophores; dorsal interspaces devoid of dark speckling. The top of the head (fig. 3) was mottled with grayish brown on orangish brown, with some irregular black edging to the variegated mottling. The supralabials were pale yellow and the underside of the head white, these surfaces being nearly immaculate except for a few black dots on the mental and first few infralabials, and an occasional black speck elsewhere. The ventral plates on the anterior third of the body were greenish white, thence turning either very pale (in paratype) or light (in holotype) orangish brown. The first dozen or so ventrals are nearly immaculate, but the rest of the venter is heavily speckled and flecked with black; the underside of the tail is darker than the belly because of extensive fusion of melanophores. There are well-spaced, small irregular black markings at the tips of some ventrals and subcaudals, forming a line of dashlike ventrolateral spots that tend to alternate with the dorsal saddles (fig. 2).

The eye was pale grayish green, with a vertical slitlike pupil. The long tongue was gray, with an extremely long white fork (see Behavior).

MAXILLARY DENTITION: The formula is 19+2 for both specimens (right maxillae examined *in situ*). The prediastemal teeth are subequal and strongly recurved; the 19th socket is entirely posterior to the front edge of the ectopterygoid process, and therefore the following diastema is rather small (slightly longer than length of prediastemal socket). The fangs are roughly one and a half times larger than the prediastemal teeth; the ultimate fang is slightly offset laterad. Each fang has a very shallow groove on the basal half of its anterior face; the distal half of the fang is laterally compressed, with knifelike anterior and posterior edges.

HEMIPENIS: The everted hemipenis is relatively large (fig. 4D, E), extending to the base or to the end of subcaudal 6 when appressed against the tail. The organ is about half as wide as long, and moderately to strongly recurved on the sulcate side; the calyculate capitulum comprises about 40–50 percent of the straight-line length of the sulcate side of the everted organ (fig. 4D). The undivided sulcus spermaticus terminates more than halfway up the capitulum (presumably at or close to the apex when the organ is retracted). The calyces are papillate over most of the capitulum but the peripheral calyces are spinulate.

The asulcate, overhanging edge of the capitulum is joined to the midsection by a slightly oblique row of little spines. On both left and right organs (when appressed posteriorly with sulci against tail), this longitudinal cluster of small spines extends slightly dextrad to the capitulum (figs. 4E, 19E). A deep naked pocket notches the edge of the capitulum immediately to the left of the connecting row of spines (figs. 4E, 19E), and a smaller, open naked pocket occurs to the right of the spines (fig. 19E [not visible in fig. 4E]). In the holotype, the larger naked pocket is closed off at the base (fig. 4E), but it is basally open in the paratype (fig. 19E).

The hemipenis is conspicuously spinose below the capitulum, with several dozen



FIG. 3. *Imantodes phantasma*, new species. Head of holotype.

small to large spines occurring nearly to the base. There are spinules on the basal section of the organ, some spinules being intermingled among the more basal spines. There is a small naked pocket on the side of the organ close to the base; this pocket lies on the lateral side when the organ is appressed posteriorly with the sulcus dorsad. (The basal naked pocket may be obscured when the base of the hemipenis is tied following inflation; it is best retained on the hemipenes of the holotype.)

DISTRIBUTION, HABITAT, AND BEHAVIOR

DISTRIBUTION: I found *Imantodes phantasma* on the nights of January 20 and 24, 1966, in extreme eastern Panama, in forest at 1030–1100 m. elevation, on the northern end of the Serranía de Pirre—a relatively undissected mountain ridge that extends northward for about 35 km. from the Colombian border (map 2, fig. 5). The two specimens were the only *Imantodes* seen during two weeks spent exploring the northern end of this *serranía*, nor had I seen any the year before during a three-day sojourn farther south, at 1400–1550 m. elevation on Cerro Pirre, the high peak on the middle of the ridge. I have subsequently searched unsuccessfully for the species in areas of cloud forest to the west (Serranía del Sapo) and southwest (Cordillera de Juradó) in 1967, to the northeast in the Serranía del Darién (Cerro Tacarcuna and Cerro Malí) in 1975, and to the south in the Serranía de Baudó (Alto del Buey) of Colombia, in 1978.

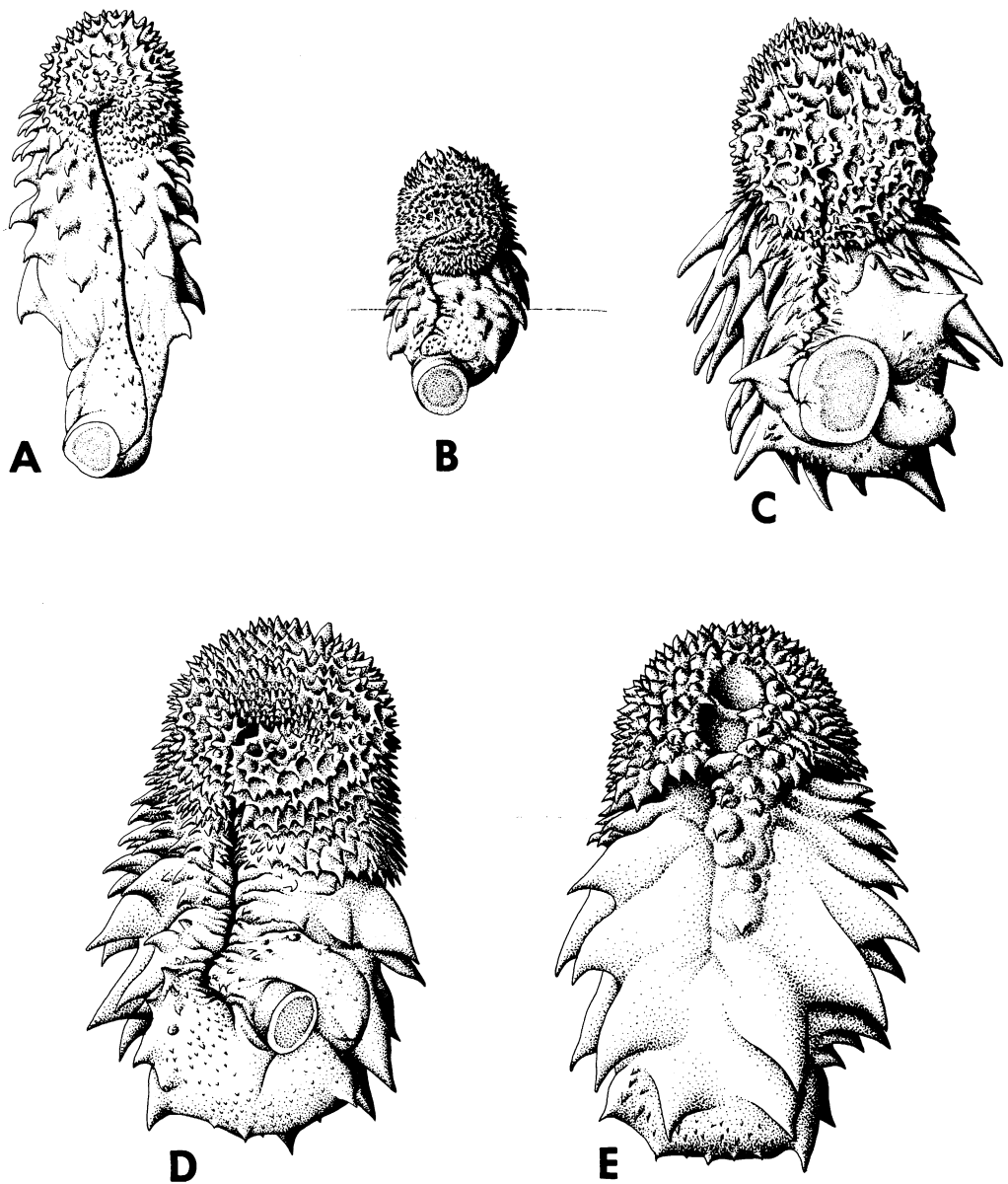


FIG. 4. Hemipenes of Panamanian specimens, all $\times 5$. A. *Imantodes cenchoa*, right organ (KU 110137, 77 cm. SVL, 101 cm. total). B. *Imantodes gemmistratus*, left organ (AMNH 109502, 50 cm. SVL, 63 cm. total). C. *Imantodes inornatus*, left organ (KU 110213, 57 cm. SVL, 81 cm. total). D, E. *Imantodes phantasma*, new species, sulcate and asulcate sides of left organ of holotype (KU 110217, 71 cm. SVL, 105 cm. total).

The Serranía de Pirre shares some species with all the surrounding highland areas mentioned above and, to a lesser extent, with highlands in central and western Panama.

Nonetheless, several distinctive species of reptiles and amphibians are known only from the Serranía de Pirre and may be endemic to the cool, wet forest along the crest of this



FIG. 5. Northern end of the Serranía de Pirre, as seen looking SSE from a distance of 15–20 km. at El Real, 20 m. elev. (December 1965). The twin breastlike peaks were determined by altimeter to be 960 m. and 1000 m. (from left to right) above sea level. The still-higher prominence farther south, at 1110 m. (arrow), is Cerro Cituro—type locality of *Imantodes phantasma*. A base camp (fig. 6) was established at 500 m. in front of the leftside twin peak, and temporary camp was made on its 960-meter summit. From there, after cutting ridgetop trail, it was 2½ hours to the campsite shown in figure 7, on the south ridge of Cerro Cituro.

ridge. In addition to *Imantodes phantasma*, the possibly endemic species include a lizard (*Diploglossus montisilvestris* Myers), a salamander (*Bolitoglossa taylori* Wake, Brame, and Myers), and a frog (*Atelopus glyphus* Dunn). Other species remain to be described.

HABITAT: The slopes of the Serranía de Pirre (fig. 5) are blanketed with a broadleaf evergreen forest growing under tropical monsoon (*Am*) climate. Although well drained, the slope forest is very wet for much of the year, with drenching rains and a usually overcast sky. During the winter dry season, in January–March, there is greatly reduced rain and usually sunny skies, leading to shrinking streams, dry ground, and considerable leaf fall. Figure 6 (top) gives an indication of the appearance of this evergreen seasonal forest

in early dry season. Although the understory is never parklike, relatively little machete work is necessary in order to move about.⁴

⁴ It may bear mentioning that the Pirre mountain forest was essentially virginal in the late 1960s, when the photographs in figures 5–7 were taken. There were a few slash-and-burn farms below 100 m. elevation around the northern base, and some Chococoan settlements near the western base, as well as a few centuries of periodic disturbance at the old gold mines of Santa Cruz de Cana, at about 500 m. on the eastern flank. But there were no established trails or evidence of major disturbance on the higher reaches of the *serranía*, only a rare machete mark showing where some hunter or other wanderer had crossed to the other side. These conditions will doubtless change on account of the increasing settlement of the Darién region, which is now connected to Panama City by road.



FIG. 6. Forest on northern end of Serranía de Pirre. *Top*: Base camp at 500 m., in front of the leftside twin peak (960 m.) in figure 5. Early dry season (January 14, 1966); within two weeks after this photograph, the saturated ground surface dried and there was abundant leaf fall, with the forest seeming to be nearly 50 percent deciduous. *Bottom*: Wetter forest at 1030 m. elevation on southeastern slope of Cerro Cituro (January 24, 1966), habitat of *Imantodes phantasma*.

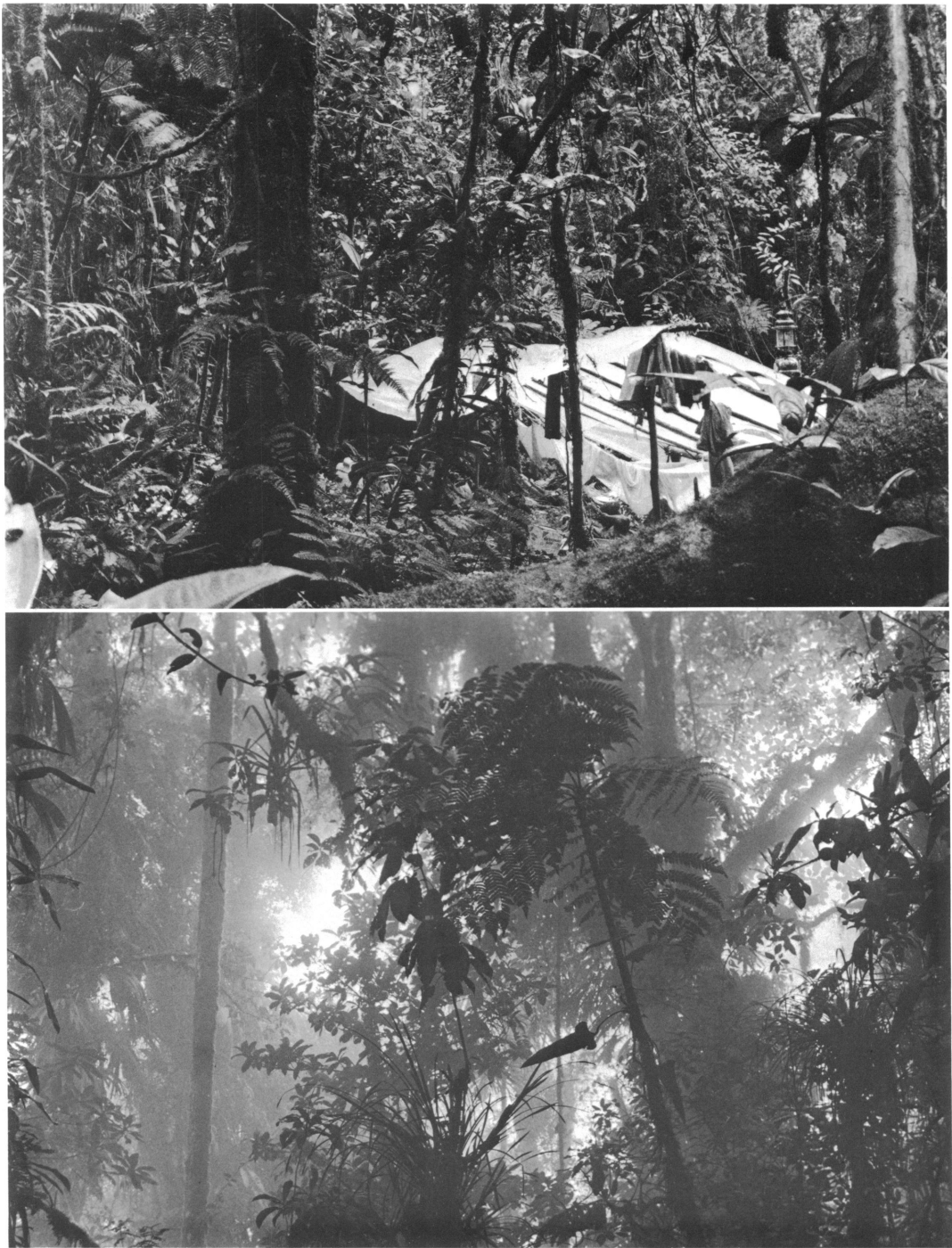


FIG. 7. Ridgetop cloud forest on northern end of Serranía de Pirre. *Top* and *Bottom*: Campsite and forest physiognomy at 1100 m. elevation, on the south ridge of Cerro Cituro (January 24, 1966). The first specimen of *Imantodes phantasma* was found at this locality in dense fog at night; another specimen was taken a short distance downslope, at an elevational difference of only 70 m. but in forest usually free of fog (cf., fig. 6 *bottom*).

There is an abrupt vegetational change at the crest of the northern end of this *serranía*, as detailed elsewhere (Myers, 1969, pp. 22–24). The vegetation becomes conspicuously denser on the ascending ridge above 650 m., and cloud forest prevails along that part of the crest above the 900-m. contour. The cloud forest vegetation is extraordinarily dense on the twin peaks seen in figure 5, evidently owing to a combination of wind exposure and narrowness of the ridge, but farther south on Cerro Cituro, the ridge is wider, the canopy higher, and the cloud forest somewhat more open. On the middle, higher part of the *serranía*, there is extensive vertical zonation of the vegetation, with cloud forest extending from the 1550-m. summit of Cerro Pirre down to about 1400 or 1300 m.—evidently a minor example of the *Massenerhebung* effect (Myers, *op. cit.*, p. 24). But at the northern end of the *serranía*, including Cerro Cituro, the cloud forest is strictly a ridgetop phenomenon, with only a narrow transition below the crest. In the dry season, the ridgetop remains usually foggy and dripping wet while the forest below is losing most of its surface moisture. There was nearly constant fog during eight days at the 1100-m. camp in figure 7, with only one of those days allowing glimpses of blue sky and direct sunlight for an hour or so at a time; in contrast, an assistant at my 500-m. base camp (fig. 6) reported nearly continuous, drying sunlight during the same eight days. That there is a cloud-forest community was as evident to the ear at night as to the eye by day, at least in the dry season when the nighttime forest was noisy with frog calls on the ridge crest but virtually silent by only about 5 m. of elevation below the crest (Myers, *op. cit.*, pp. 23, 44).

The paratype of *Imantodes phantasma* was found in the ridgetop cloud forest adjacent to the 1100-m. camp (fig. 7). The holotype was found several nights later, downslope from this site, at 1030 m. (fig. 6, bottom). The forest at 1030 m. is more open and has a somewhat higher canopy than the cloud forest above; the lower site has more saplings or treelets, less tree ferns, a thinner moss layer

on tree trunks, no bromeliad-laden trees and less epiphytes generally. Although the 1030-m. site was usually fog free and drier than the adjacent cloud forest, it nonetheless was wetter and much less deciduous than the forest at still lower elevations. If this species is endemic to the strip of montane wet forest along the crest of the Serranía de Pirre, potential dispersal may be limited by some set of ecological factors in the seasonally drier forest below. However, such a scenario seems more likely in the case of amphibians than in reptiles (Myers, 1969, pp. 43, 47–48), and I should not be at all surprised if this species has a greater elevational range or even a somewhat greater distribution than presently indicated.

BEHAVIOR: Both specimens were found at night as they were prowling on woody vegetation close to the ground (~0.6 m. up). The holotype was on the trunk of a sapling, the paratype in a low tangle of dead tree branches. They moved slowly and deliberately, and were docile when handled, making no attempt to bite. So far as could be told from brief observation, they seemed to have the same character as other members of the genus, except for one peculiar trait. The tongue quivers while it is kept extended for a second or two at a time, with the long tips of the fork widely separated. This behavior was conspicuous because the tongue is protruded for a longer time than usual among colubrids and also because the tongue is exceptionally long. The tongue of the freshly killed holotype was pulled out and measured before the specimen was preserved:

Head length (from table 1) 15 mm.

Tongue (to sheath aperture) 27 mm.

Thus, the maximally extended tongue is 1.8 times longer than the head. Actually, the tongue is probably a bit longer (closer to 1.9 times head length), since fork length was measured as 8 mm. in the field but as 9.6 mm. under the dissecting microscope (where the filament-like tips were better seen albeit more difficult to straighten after preservation); thus, the fork alone is 64 percent of head length.

COMPARATIVE TONGUE LENGTH IN *IMANTODES*

It is usually difficult to measure the tongues of preserved snakes, although it may be possible (at some risk of damage) to pull the retracted tongue out far enough to measure length of the fork, which I have done on a dozen-odd specimens; in a few specimens (e.g., holotype of *I. phantasma*) that I preserved, the tongue of the freshly killed and relaxed snake was pulled out and folded inside the mouth cavity (to prevent desiccation or breakage of the fine tips) before preservation, which greatly facilitated later measuring. All species were sampled except *I. tenuissimus*. Actual lengths of the fork ranged from a low of 6.0 mm. in two *gemmistratus* (48, 57 cm. SVL) to a high of 10.5 mm. in a specimen each of *cenchoa* (49 cm. SVL) and *inornatus* (69 cm. SVL). Relative to head length (fn. 3), the comparisons are as follows:

Tongue Fork as a Percentage
of Head Length

Species	Females	Males	No.
			Specimens
<i>I. cenchoa</i>	48–56	55–59	4 ♀, 3 ♂
<i>I. gemmistratus</i>	48–57	—	2 ♀ —
<i>I. inornatus</i>	42–44	58–69	2 ♀, 3 ♂
<i>I. lentiferus</i>	—	64–75	— 3 ♂
<i>I. phantasma</i>	—	64	— 1 ♂

The species of *Imantodes* therefore seem generally to have long tongues (fig. 8), at least as reflected in fork length. Surprisingly, there is sexual dimorphism in the two species for which both sexes were sampled. Although females of these two species (*cenchoa*, *inornatus*) also have longer heads than males, the magnitude of dimorphism in head length (figs. 10, 14) does not alone seem adequate

to explain the proportionately shorter tongues (forks) of females. However, the phenomenon needs to be confirmed by morphometric analysis before we spend too much time speculating on possible biological explanations, although it may be kept in mind that there is other indirect evidence of possible differences in foraging behavior of male and female *Imantodes* (see Remarks at end of *I. cenchoa* account).

Only *Imantodes phantasma* seems to be characterized by a conspicuous quivering-pause of the tongue during protrusion. Subsequent to my field experience with *I. phantasma*, I specifically recorded the absence of this behavior in freshly caught specimens of *I. cenchoa* (fig. 8), *I. gemmistratus*, and *I. inornatus*, and, although I failed to make a note, I do not believe that the behavior was displayed by two *I. lentiferus* that I collected in Surinam.

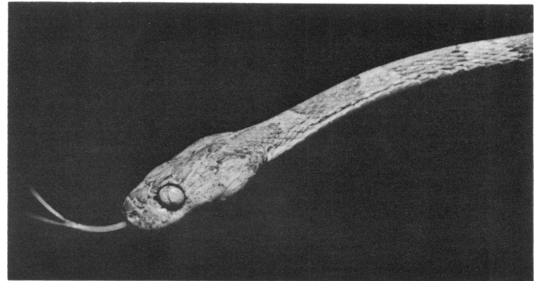


FIG. 8. Tongue movements in *Imantodes* usually involve only a brief flicking of the long tongue, as frozen in this view of *I. cenchoa* (KU 110152 ♀, Los Santos Prov.), but *I. phantasma* is characterized by a "quivering-pause" of the protruded tongue. There are also interspecific differences and perhaps sexual dimorphism in length of the fork of the tongue.

OTHER *IMANTODES* IN PANAMA

In contrast to *Imantodes phantasma*, the species *cenchoa*, *gemmistratus*, and *inornatus* are widespread on the Isthmus of Panama (maps 1, 2). Descriptive accounts of the last three species follow, based primarily on Panamanian material in the University of Kansas Museum of Natural History and in the American Museum. I have added natural history notes where possible. I also have included some tedious and rather sterile nomenclatural discussion, leading to one lectotype designation and the reallocation of an old name from one synonymy to another. The four valid species in Panama are differentiated as follows:

KEY TO SPECIES

1. Pattern of dorsal saddles or blotches of a darker brown than ground color (but these markings not noticeably black speckled); about 10–14+2 maxillary teeth, the fangs being deeply grooved; hemipenis small and with little or no evidence of capitation on asulcate side, which is spinose to tip 2
 Pattern of vague dark lines or of relatively light blotches that are only somewhat darkened by black speckling; about 17–21+2 maxillary teeth, the fangs with only shallow, basal grooves; hemipenis of moderate size, spinose or not at asulcate edge of capitulum, but this region with a deep overhang or naked pocket 3
2. About 29–56 dark brown saddles or blotches on a much paler brown body; scales in vertebral row conspicuously enlarged, usually 3–4 times wider than lateral scales; more than 140 subcaudals; total length may exceed 1 m. *Imantodes cenchoa* (Linnaeus)
 About 55–74 dark brown saddles or blotches on a pale to medium brown body; scales in vertebral row not so conspicuously enlarged, usually about 1.5–2.0 times wider than laterals; usually fewer than 130 subcaudals; maximum total length less than 90 cm. *Imantodes gemmistratus* (Cope)
3. Pattern of short, blackish dorsal crosslines and similar, alternating lateral lines, on golden or light brown body; upper surfaces of body finely speckled or dusted with black overall; fewer than 220 ventrals, fewer than 140 subcaudals . . . *Imantodes inornatus* (Boulenger)
 Pattern of light yellowish brown saddles or blotches (gray in preservative) having little

contrast on light orangish brown body; black dorsal speckling confined to blotches, interspaces virtually devoid of speckling; more than 220 ventrals and 140 subcaudals *Imantodes phantasma*, new species

Imantodes cenchoa (Linnaeus)

Figures 4A, 8–10, 16A, 19A; Map 1

- [*Coluber*] *Cenchoa* Linnaeus, 1758, p. 226 (type locality in "America" [Surinam?]; holotype [with ventrals and subcaudals "220–124" *vide* Linnaeus] presumably one of two specimens in Adolphi Friderici collection in Zool. Mus. Royal Univ. Upsala, *vide* Lönnberg, 1896, pp. 19–20; also Holm, 1957, p. 30).
- Imantodes cenchoa* (Linnaeus): Duméril, 1853, p. 507 (new genus, with *cenchoa* as monotype). See Duméril, Bibron, and Duméril, 1854, pp. 1065–1066 for early literature and synonymy.
- Himantodes cenchoa* (Linnaeus): Cope, 1860, p. 264 (emendation of *Imantodes*); 1861, p. 296; 1894, p. 613; 1899, p. 18. Boulenger, 1896, p. 84.
- Himantodes leucomelas* Cope, 1861, p. 296 (type locality, Mirador, Veracruz, Mexico; syntypes, USNM 25035–25036 [not seen]).
- Himantodes semifasciatus* Cope, 1894, p. 614, part, including lectotype (lectotype locality, Carrillo, Costa Rica; lectotype by present designation, AMNH 17357, collected in 1884 by M. J. Parades [original no. 101; sent to Cope, Feb. 1894, by George K. Cherrie, Museo Nacional de Costa Rica]).
- Himantodes anisolepis* Cope, 1894, p. 614 (type locality, Monte Aguacate, Costa Rica; holotype, AMNH 17274, collected in 1887 by G. Witting [original no. 82; sent to Cope, Feb. 1894, by George K. Cherrie, Museo Nacional de Costa Rica]).
- Himantodes platycephalus* Cope, 1899, p. 15, pl. 4, figs. 4a–d (type locality in Colombia, probably near Bogotá [*vide* Cope, *op. cit.*, p. 3]; holotype, AMNH 38400, collector unknown; originally no. 44a in a collection studied by Cope following its exhibition at the World's Exposition of Chicago).
- Imantodes cenchoa cenchoa* (Linnaeus): Smith, 1942, p. 385. Peters and Orejas-Miranda, 1970, p. 133.
- Imantodes cenchoa leucomelas* Cope: Smith, 1942, p. 384. Peters and Orejas-Miranda, 1970, p. 134.
- Imantodes cenchoa semifasciatus* Cope: Smith, 1942, p. 385. Peters and Orejas-Miranda, 1970, p. 134.

DISTRIBUTION: East coast of Mexico (Veracruz) and along both coasts of Central America, south to Argentina. *Imantodes cenchoa* is widely distributed in Panama, in humid forest from sea level to at least 1200 m. elevation, but apparently absent from lowland savanna and other dry habitats in Pacific western Panama (map 1).

DESCRIPTION OF PANAMANIAN SPECIMENS ($N > 80$): Body very pale brown with 29–56 dark brown saddles (fig. 9), narrowed on the sides where they usually either extend to the venter or break off into small lateral spots; dorsal saddles occasionally become irregularly shaped and sinuously interconnected, thus forming a zigzag stripe on part of body; 22–53 tail blotches. Saddle markings immaculate, but interspaces dusted or very finely speckled with black. Color pattern atop head variable—rarely a uniformly dark brown color confluent with first saddle, but usually with several pale lines tending to delimit a floral pattern of large brown spots, said spots being occasionally discrete but more often

partially fused with each other and usually connected with dorsolateral bars or dorsal blotch on nape. Ventral surfaces whitish, relatively clear under head but otherwise heavily dotted or spotted with dark brown and sometimes with a median dark line.

Long, slender snakes, attaining total lengths in excess of 1 m. (observed maxima this sample, 1211 mm. ♂, 1480 mm. ♀), with tail comprising 26–34 percent of total. Short, blunt head very distinct from neck, with large eye occupying more or less one-fourth (19–32%) of length of head; HW (greatest head width)/HL (tip of snout to end of mandible) = 0.57–0.77 in all sizes; females with longer and wider heads than males (mean HW/HL = 0.654 in 37 ♂, 0.683 in 36 ♀ of all sizes; see especially fig. 10 and associated text under Geographic and Sexual Variation). Dorsal scales smooth, in 17-17-17 or 19-17-17 rows; scales in vertebral row very large, usually 3–4 times (range 2.5–5×) wider than midlateral scales; all vertebral scales posterior to neck highly modified in shape, with

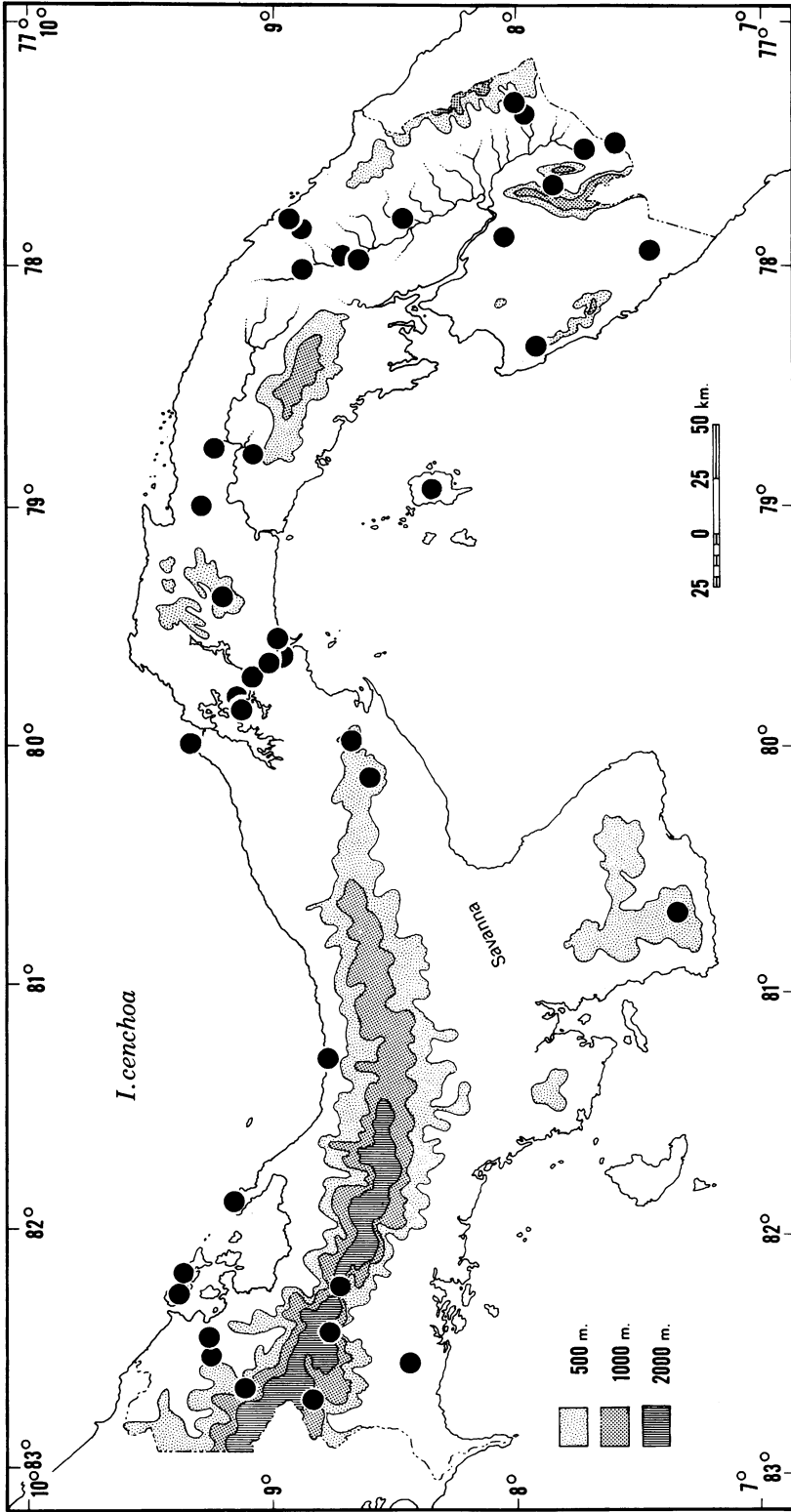
TABLE 2
Numbers of Ventrals and Subcaudals, and Proportional Tail Length in Panamanian *Imantodes*^a

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
<i>cenchoa</i> ^b	78	244–288 (40) 263.8	228–268 (38) 249.0	158–195 (28) 174.2	147–177 (34) 162.4	26.8–33.7 (28) 29.98	28.1–31.3 (34) 29.78
<i>gemmistratus</i> ^c	20	227–237 (9) 232.9	221–228 (11) 225.2	124–130 (9) 126.0	113–124 (10) 118.0	24.5–28.3 (8) 26.59	24.2–27.1 (9) 25.52
<i>inornatus</i>	16	199–218 (8) 207.0	196–212 (8) 201.5	116–132 (6) 123.7	110–122 (8) 116.9	29.7–31.3 (6) 30.20	26.5–29.5 (8) 28.15
<i>phantasma</i>	2	235, 236 235.5	—	156, 161 158.5	—	32.7, 32.9 32.80	—

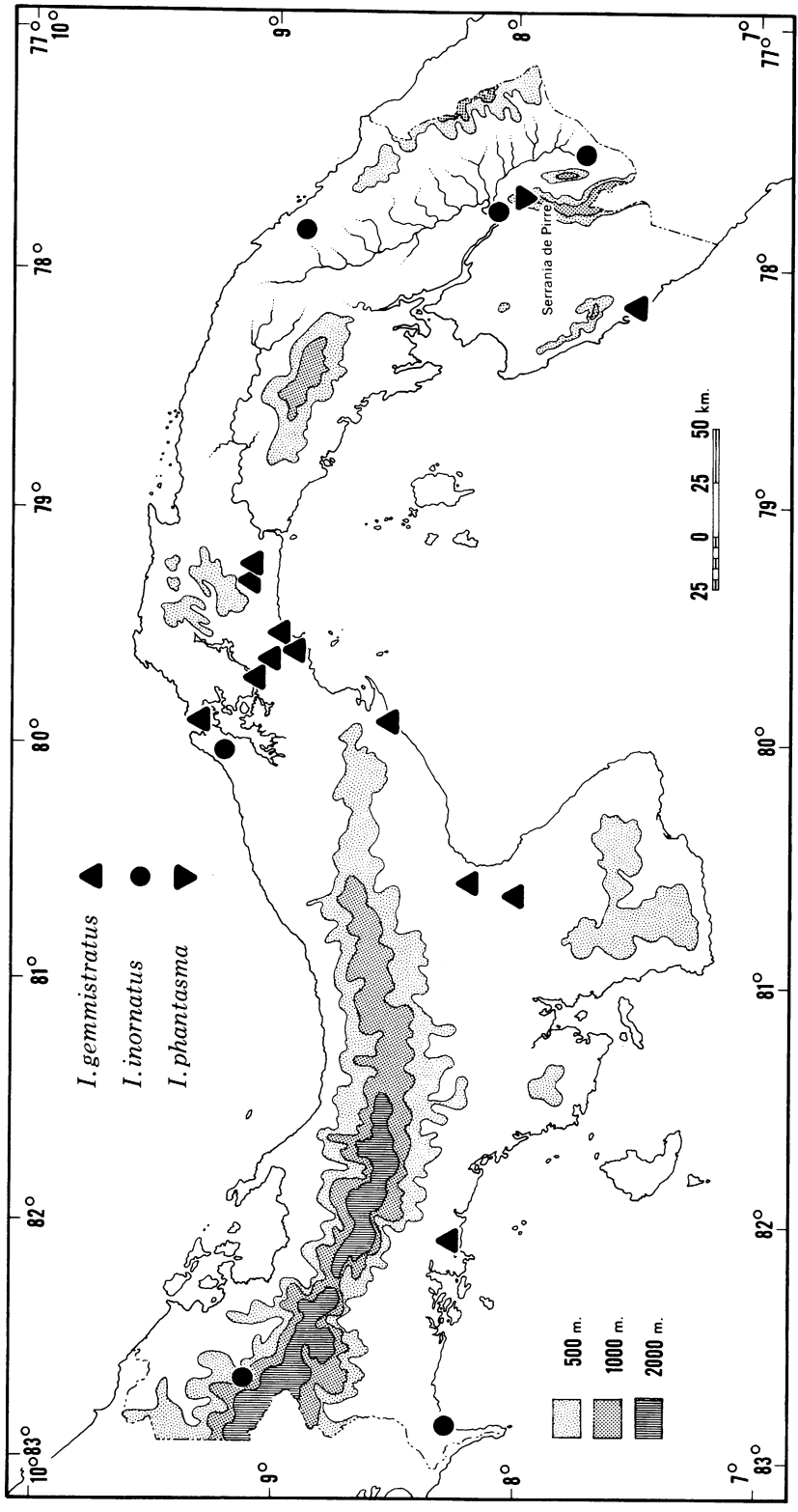
^a Range followed by number of specimens (in parentheses), mean in boldface.

^b See table 3 for geographic breakdown of the data for *Imantodes cenchoa*.

^c A juvenile male with abnormally high counts is excluded from the table (KU 80260, Curundú, C.Z.). It has 255 ventrals, 155 subcaudals, and a relative tail length of 28.1 percent. It also has an unusually high number of tail blotches (50) and unusually wide vertebral scales (2.5× laterals), but a normal *gemmistratus* pattern of 64 body blotches (as counted from left side).



MAP 1. Some locality records for *Imantodes cenchoa* in Panama. This common, widespread snake occurs in virtually all lowland and lower montane humid forest, but it seems absent in the dry *Curatella* savannas of the Pacific lowlands.



MAP 2. Locality records for three species of *Imantodes* in Panama.

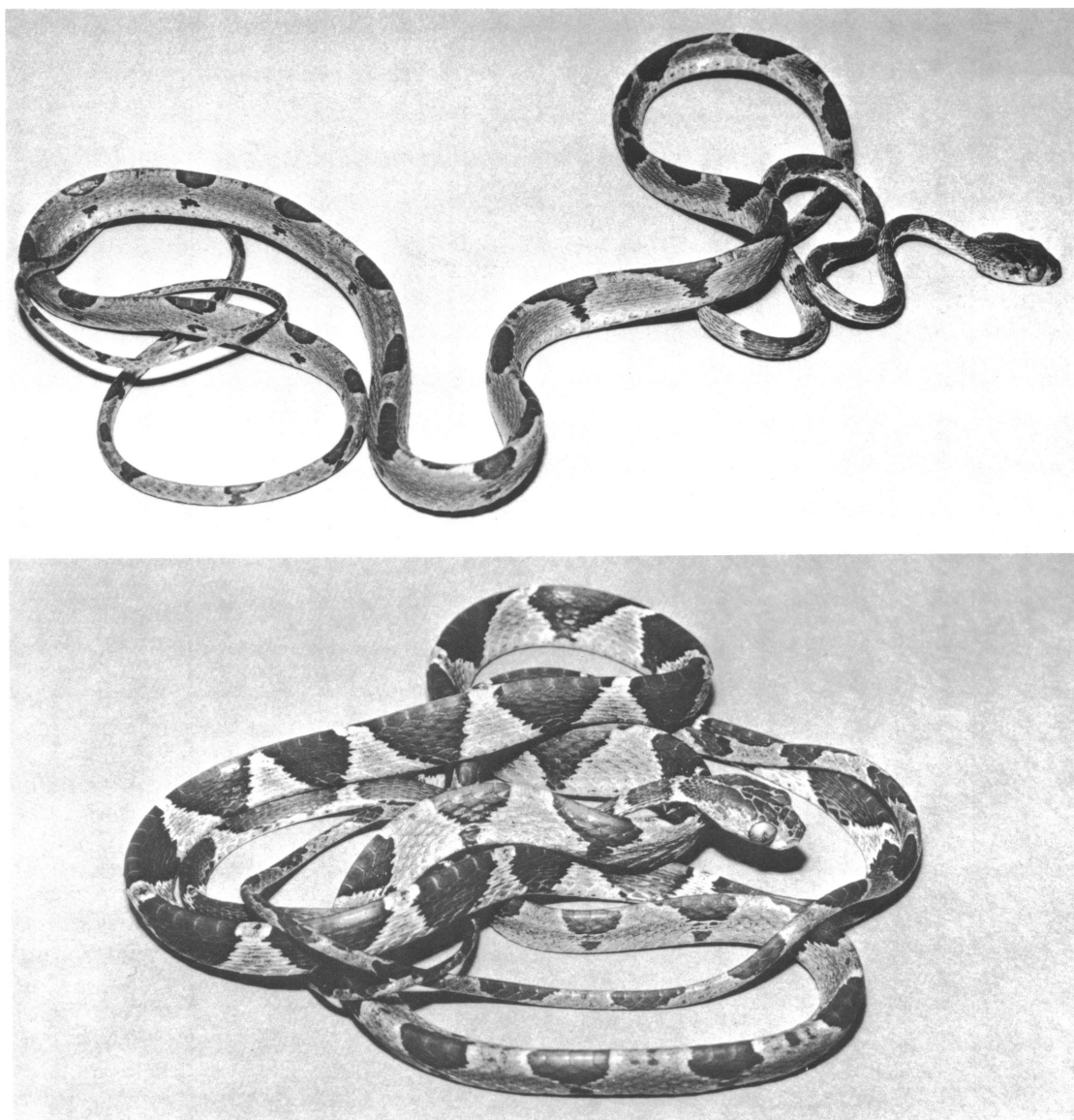


FIG. 9. *Imantodes cenchoa* from Panama. *Top*: KU 110154, Cerro Campana, 280 m., Panamá Province. *Bottom*: KU 110192, Camp Summit, 300–400 m., on divide between San Blas Territory and Darién Province.

truncate or concave rear margins. Ventrals 228–288 and subcaudals 147–195, geographically variable and with males averaging

more of each (tables 2, 3); anal plate normally divided (entire in <3%). Supralabials usually 8, occasionally 9, rarely otherwise (7 in one);

infralabials usually 10, occasionally 11 or 9. One or sometimes two (rarely 3) preoculars; usually two postoculars (range, 1–4); temporal scales (between parietal and supralabials) variable in size and shape, with 4–12 scales per side.

Maxillary teeth 11–14 ($\bar{X} = 12.4$) + 2, on a maxilla from each of 25 specimens; 12+2 is the modal number, accounting for 16 of the 25 maxillae. The two rear fangs are up to twice as large as the prediastemal teeth; each fang has a deep groove along the basal two-thirds of its anterior face.

The everted hemipenes of 24 adult males are relatively small (fig. 4A), extending to subcaudals 4–5 when pressed against the tail. The fully everted organ is slightly clavate and slender, being only about a third as wide as long; the hemipenis usually stays relatively straight upon eversion, with but slight recurvature on its sulcate side. The calyculate capitulum comprises roughly 32–45 percent of the sulcate side of the organ; free overhang of capitulum lost on asulcate side, which is thickly spinose below apex (fig. 19A).

COLOR IN LIFE: The dorsal ground color comes in several shades of pale to light brown, pale yellowish brown, or pale orangish brown. The much darker blotches or saddles (fig. 9) are medium to dark brown (verging on reddish brown) or, occasionally, blackish brown, with rather inconspicuously darkened edges. The underside of the head is white. The remaining ventral surfaces may be the same as the pale dorsal ground color, but usually the venter is a paler tan or white (pale greenish tan in one); there is conspicuous brown to blackish brown spotting and/or speckling on the venter, and sometimes a midventral dark line. The iris most often is either a pale greenish gray or pale to light brown, less commonly some other color (pale gray to grayish brown, yellowish gray, grayish tan with orange flecking, or pale gray or brown with brown or green suffusion along the vertical pupil). The pale iris color is often relatively uniform, but individuals also may have a vertical line of brown or gray through the pupil, or an overall fine reticulum of black. The tongue varies from pale or dark

gray to pale or light brown, becoming white or unpigmented on the tips of the fork.

GEOGRAPHIC AND SEXUAL VARIATION: Throughout most of its vast geographic range, *Imantodes cenchoa* exhibits a relatively uniform appearance of dark brown blotches on a pale body.⁵ Color in life of specimens collected in western Colombia, Amazonian Peru, and Surinam was within the variation observed in Panama.

As noted by Smith (1942, p. 385), however, there is geographic variation in the number of dorsal bands or saddles, and also in the number of posterior saddles whose lower ends are broken off as discrete lateral spots (see fig. 9). Smith used the latter character to differentiate two subspecies in Panama: (1) *I. c. semifasciatus*, Nicaragua to Panama, with saddles broken on posterior part of body; (2) *I. c. cenchoa*, Panama to South America, with saddles not or rarely broken. With the larger samples now available, it can be seen that the situation is a bit more complicated. Specimens from the South American side of Panama (Darién and San Blas) do average less broken bands than those from central and Atlantic western Panama, but those from the Pacific side of extreme western Panama (Chiriquí) have the least bands broken. The Chiriquí specimens also have a low total number of saddles and, in this respect, resemble Mexican and northern Central American snakes placed by Smith (*loc. cit.*) under the name *I. c. leucomelas*. Considering the overlapping variation from one end of the country to the other, recognition of subspecies is impractical and serves no useful purpose in Panama. Variation in color pattern may be summarized for samples drawn from Panamanian populations as follows (mean followed by range in parentheses); the sexes are combined, since dimorphism in this character is slight or absent.

⁵ A population at Rancho Grande, in the Cordillera de la Costa of Venezuela, may be exceptional. The banded (saddle) pattern appears less distinct owing to a darkening of the normally pale interspaces (AMNH 81433, 98257, 98258).

Region	N	Total Saddles on Body	No. Posterior Saddles Broken
Western Atlantic, 0–910 m. (Bocas del Toro Prov.)	11	48.1(44–53)	21.5(13–28)
Western Pacific, 100–1170 m. (Chiriquí Prov.)	7	35.9(29–42)	0.3(0–2)
Southern Azuero Peninsula, 480– 940 m. (Los Santos Prov.)	8	43.4(40–49)	18.4(14–23)
Central Panama, 0–950 m. (from 79°20' to 80°)	8	46.8(37–56)	18.3(13–23)
Eastern Atlantic, 12–400 m. (San Blas at about 77°45')	17	42.8(37–48)	10.0(0–18)
Eastern Pacific, 50–900 m. (Darién Prov.)	27	41.7(36–53)	5.9(0–17)

There is some interpopulational variation in numbers of ventral and subcaudal plates, which are higher in extreme eastern Panama (Darién and San Blas) than in samples from central (including Azuero) and western Atlantic Panama (table 3). The small sample of males from western Pacific Panama resembles the distant eastern populations in high ventral and, especially, caudal counts—a similarity reminiscent of the situation involving broken body blotches, which occur in lowest frequencies in these widely separated populations. Oddly, the Chiriquí females do not seem to differ from the intervening central populations in ventrals and caudals.

There is no apparent sexual dimorphism in relative tail length in the Panamanian samples of *Imantodes cenchoa* (table 3). This confirms the results of Zug, Hedges, and Sunkel (1979, p. 12), who found slight dimor-

phism in populations from Mexico to Costa Rica, but not in more southern populations, including 18 specimens (not included herein) from the Panama Canal Zone. At least in Panamanian *cenchoa*, males average more ventrals and subcaudals than females (table 3), a trait also shared by *gemmistratus* and *inornatus* (table 2), although females attain larger sizes.

Head length and head width seem to increase exponentially in *Imantodes cenchoa*, at notably greater rates in females than in males (fig. 10). Females of all sizes average larger heads than males, with differences becoming proportionately greater with increasing body size. Sexual dimorphism in head dimensions was first suggested by differences in crude HW/HL ratios (in Description preceding); divergent growth rates in both HW and HL were then revealed by regression analysis, using only specimens from extreme eastern Panama (Darién and San Blas) in order to obtain a geographically limited sample of adequate size (fig. 10).⁶

⁶ Curvature was evident upon plotting the head and body measurements on either arithmetic or full logarithmic graph paper. Linearity was improved by a semi-logarithmic plot (fig. 10), and so I have taken the equation $\log Y = \log a + (\log b)X$ as descriptive of the sample data. Inspection of the scatter either in figure 10 or in a log-log plot of the same data, especially for females, suggests that the allometric growth equation ($\log Y = \log a + b \log X$) might also be applicable—but only if juveniles and adults are regressed separately. The data are insufficient for determining if there is really an ontogenetic shift in ratio of change, but, in any case, single-line regressions are adequate for pointing out the divergent rates of growth in head dimensions of male and female *Imantodes cenchoa*, a matter of apparent ecological significance (see note on food and concluding remarks under Natural History).

Sexual divergence in rates of head growth presumably is uncommon among snakes generally and is not even universal within *Imantodes*, being absent in *I. gemmistratus* (fig. 12) although present to some degree in *I. inornatus* (fig. 14). In the last two species, logarithmic transformation of HL and HW improves linearity only slightly, but it does allow direct comparison of figures 10, 12, and 14.

TABLE 3
Numbers of Ventrals and Subcaudals, and Proportional Tail Length in Panamanian Samples of *Imantodes cenchoe*^a

Region	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
Western Atlantic, 0-910 m. (Bocas del Toro Prov.)	11	244-257 (7) 249.9	228-245 (4) 237.0	166-181 (5) 173.4	147-166 (4) 157.8	31.3-33.1 (5) 32.14	29.2-30.9 (4) 30.32
Western Pacific, 100-1170 m. (Chiriquí Prov.)	7	259-269 (3) 265.7	236-252 (4) 245.5	169-195 (3) 179.7	156-161 (4) 157.3	27.5-33.7 (3) 30.53	28.1-31.0 (4) 29.80
Southern Azuero Peninsula, 480-940 m. (Los Santos Prov.)	8	259-261 (3) 260.0	235-246 (5) 241.8	158-169 (3) 164.7	148-162 (4) 156.0	27.2-29.9 (3) 28.64	28.6-31.3 (4) 29.70
Central Panama, 0-950 m. (from 79°20' to 80°)	8	271 (1)	245-260 (7) 248.8	-	158-168 (5) 164.0	-	29.9-31.0 (5) 30.54
Eastern Atlantic, 12-400 m. (San Blas at about 77°45')	17	265-278 (12) 271.0	249-262 (5) 258.4	164-185 (8) 178.1	168-175 (5) 170.4	26.8-30.8 (8) 29.21	28.1-29.9 (5) 29.01
Eastern Pacific, 50-900 m. (Darién Prov.)	27	264-288 (14) 272.5	254-268 (13) 262.3	171-181 (9) 175.0	160-177 (12) 168.9	27.5-30.6 (9) 29.38	28.4-30.3 (12) 29.32

^a Range followed by number of specimens (in parentheses), mean in boldface. See table 2 for combined data.

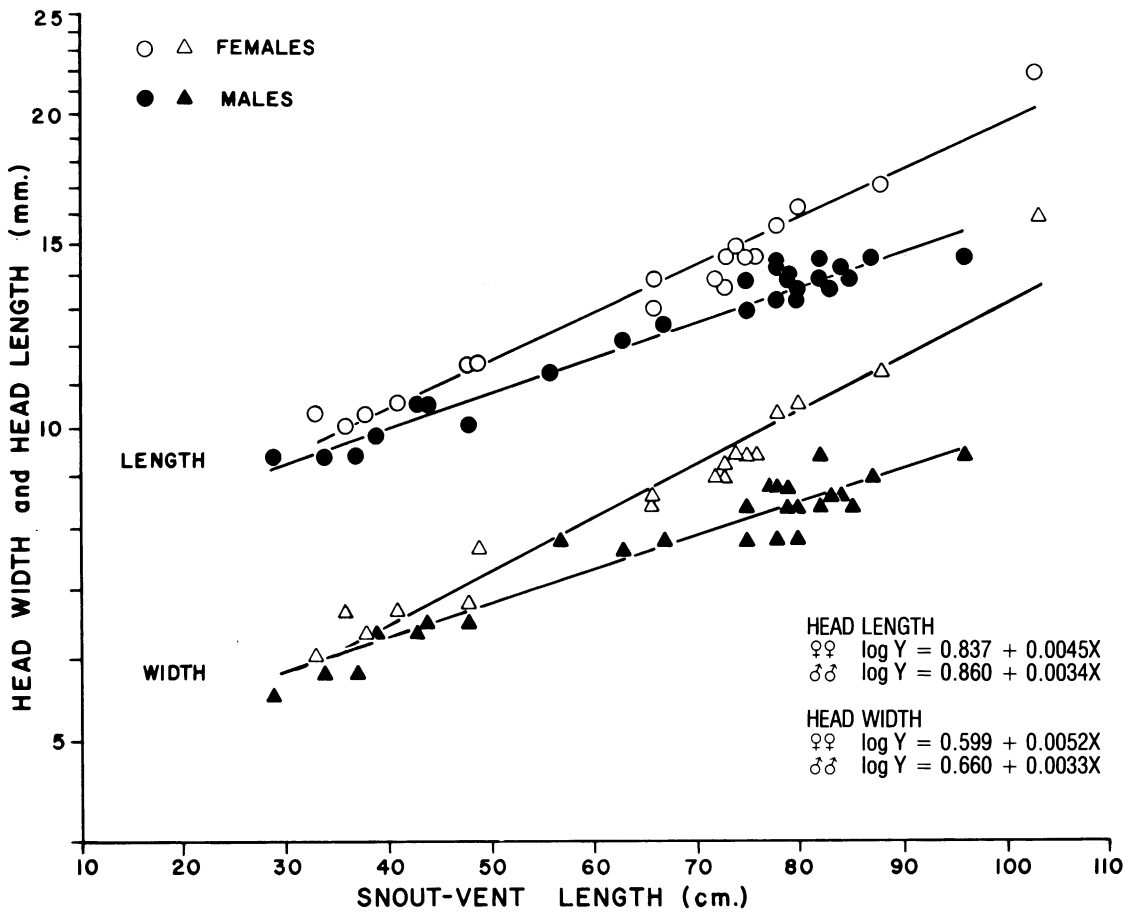


FIG. 10. Sexual dimorphism in relationship of head width and head length to body size, in *Imantodes cenchoa* from extreme eastern Panama (KU series from Darién and San Blas). See footnote 6.

In the *cenchoa* samples in the tables, 10.5 percent of the females and 30.0 percent of the males have incomplete tails. Zug, Hedges, and Sunkel (1979, p. 13) found similar tendencies in their samples of *cenchoa*, although they noted a lack of statistical significance. My added observations (based on different specimens) seem to confirm that males do suffer a higher incidence of tail breakage than females. Biological significance (differential predation) may be inferred, although difficult to prove.

Ontogenetic change was considered in the analysis of sexually dimorphic head growth,

but, otherwise, juveniles and adults were combined in the foregoing account, which purports only to shed some light on more noticeable aspects of geographic and sexual variation of *Imantodes cenchoa* on the Isthmus of Panama. The treatment is based principally on University of Kansas and American Museum material collected by myself. Except to enlarge the sample from Chiriquí, no attempt was made to incorporate material from other museums, where additional material is available especially from the Panama Canal Zone region.

NOTES ON TYPE SPECIMENS OF
JUNIOR SYNONYMS

Imantodes cenchoa is a widespread and fairly common snake, whose specific epithet dates from the official starting point of zoological nomenclature (Linnaeus, 1758). Naturally, a considerable literature has accumulated, including several early spelling variants and generic combinations, which can be traced in such standard references as Duméril, Bibron, and Duméril (1854, pp. 1065–1066) and Boulenger (1896, p. 84). However, relatively few actual synonyms have been credited to this species, all originating from the activities of Edward Drinker Cope in the late 1800s. There are five such names that found their way into the synonymy of *cenchoa* long before the most recent synopsis (Peters and Orejas-Miranda, 1970). The description of a new *Imantodes* from Panama necessitated a re-consideration of four nominal species from Costa Rica and Colombia, to make certain that they are correctly allocated to the synonymy of *cenchoa*. This consideration failed to uncover an available name for the new snake, but it did reveal that one purported synonym of *cenchoa* is based on another species and that another name is based on a composite of two species. In order of publication, Cope's five names are as follows (see synonymy for references and collection data):

1. *Himantodes leucomelas*: Syntypes in Smithsonian Institution (Cochran, 1961), from Veracruz, Mexico. I have not examined the types because they are not relevant to the present paper. The epithet is currently used for a northern subspecies of *Imantodes cenchoa*, but, in the absence of a variational study of the species, I fail to see the point in recognition of subspecies. In any case, the current arrangement of subspecies fails to hold up in lower Central America.

2. *Himantodes semifasciatus*: This name was early placed in the synonymy of *Himantodes elegans* (= *I. gemmistratus*) by Boulenger (1896, p. 86), but it currently is used for a "subspecies" of *I. cenchoa*. Cope had about a dozen specimens (syntypes), which he mentioned in the description. Two, in the Acad-

emy of Natural Sciences of Philadelphia, were said to be from "Nicaragua," but Malnate (1971, p. 372) identified the syntypes as being two specimens from "Honduras; George K. Cherrie (?)." The discrepancy is unimportant and there has been no need for me to examine the ANSP specimens, since the remaining syntypes, from Costa Rica, are well documented. The Costa Rican syntypes of *semifasciatus*, as well as the holotypes of all the remaining Cope names, are in the collection of the American Museum.⁷

Cope (1894, p. 614) mentioned "nine" Costa Rican specimens in one sentence and "ten" in another. The latter seems correct. Cope (*loc. cit.*) mentioned six localities, one in error, and omitted another. These localities, and the present AMNH specimen numbers, are as follows:

Paso Azul (17314)
Santa Clara (17273)
Carrillo (17357)
"Alajuela" (17356)⁸
Monte Aguacate (17330, 17331)⁹

⁷ There is not yet a published type catalogue for this collection, and many workers remain unaware that some of Cope's types are housed at the American Museum. At the time of his death in 1897, Cope possessed certain Costa Rican specimens that were sent to him in 1894 by George K. Cherrie, an American living in San José and associated with the Museo Nacional de Costa Rica; this material was reported on in several papers. Cope also had a Colombian collection that was reported on in a paper written about 1895 and published posthumously (Cope, 1899). Ownership of these materials became vested in the Philadelphia Commercial Museum. They were obtained by the American Museum in 1918 (in exchange for preparation of cotton plants, by wax technique, for a commercial exhibit), in order to insure the perpetuity of the types especially.

⁸ The locality is shown as unknown (specimen no. 113) on Cope's original invoice, although collector and date are recorded (Lisa de Bruno Carranza, March 29, 1886). The source of the error is evident, as "Alajuela" is on the line above.

⁹ I can only account for one specimen of *semifasciatus* from this locality on the original invoice; *H. anisolepis* (17274) and *H. gemmistratus* (17316) also are catalogued from Monte Aguacate, in agreement with the invoice. The original paper museum tags, with handwritten numbers corresponding to those on the invoice, have dissolved and fallen off most specimens, thus preventing corroboration of data.

San José (17296, 17297, 17355)
[Sapurio, Talamanca] (17358)¹⁰

One of the above specimens, AMNH 17273 from Santa Clara, was later made the type of Cope's *Himantodes hemigenius* (= *I. gemmistratus*) and is discussed under name (5) following. Based on my experience with Panamanian *Imantodes*, I believe that the remaining nine AMNH syntypes of *Himantodes semifasciatus* represent two species. The specimens from Paso Azul, "Alajuela," Monte Aguacate, and San José have scales in the vertebral row that are less than 2.5 (1.4–2.2) times wider than the midlateral scales (i.e., those in rows 2–7); these moderately enlarged vertebrae vary (on the same specimen) from posteriorly rounded to truncate or concave. Ventrals are 233–235 in males (2), 229–240 in females (5); subcaudals 140–146 in males (2), 124–138 in females (3). Most are faded, so that the original color pattern is weak or absent. However, the pattern is well retained in two San José specimens (17296, 17297), which quite resemble a published photograph of a Costa Rican specimen of *I. gemmistratus* (fig. 21 in Taylor, 1954, p. 755). The foregoing specimens represent *Imantodes gemmistratus* in my opinion. Curiously, Cope actually identified (on invoice) as *gemmistratus* another specimen (now AMNH 17316) from Monte Aguacate, presumably because some (although not all) of its vertebral scales are acuminate rather than "always truncate" as expected in *semifasciatus*. Cope simply emphasized characters that are more variable than he realized (see also discussion under the name *hemigenius* and under Remarks in the *Imantodes gemmistratus* account). Boulenger (*op. cit.*) therefore was at least partly right when he assigned *semifasciatus* to the synonymy of *H. elegans* (= *gemmistratus*).

¹⁰ This locality was omitted by Cope, but the specimen was part of the same collection and is identified on the invoice, as *semifasciatus*, in Cope's hand. Corroboration was possible in this instance because, when I examined the specimen, a scrap of tag with the original no. 80 was still attached to it.

Only two of the AMNH syntypes represent *Imantodes cenchoa*, namely the specimens from Carrillo and Sapurio. These have the vertebral scales about 3.5–3.6 times wider than the midlateral scales; thus, the vertebrae are greatly enlarged, and virtually all those behind the nape have the rear margins broadly truncate or broadly concave. There are 235(♂) and 239(♀) ventrals, 159(♂) and 151(♀) subcaudals. The color patterns, although somewhat faded, resemble a photograph of a Costa Rican adult *I. cenchoa* (pl. XV in Taylor, 1951, p. 133), which specimen is said to be from the same locality (Los Diamantes) as the *gemmistratus* specimen in Taylor's later photograph (cited above). The Carrillo specimen, an exceptionally big male, is the largest of all the syntypes and is the only one specifically mentioned by Cope, who stated that, "One of these (No. 101) measures; total length 1125 mm.; tail 380 mm." My measurements are 1165 mm. total length, 385 mm. tail length; no other specimen exceeds 1100 mm. nor has a tail coming close to 380 mm. It has 44 body bands, of which the last 16 but one are broken laterally. Because it is the one signified in the original description, and in order to maintain Cope's later concept (1899, p. 18) that his *semifasciatus* should be regarded as being no more than a subspecies of *cenchoa*, I designate the largest specimen as lectotype of *Himantodes semifasciatus* (AMNH 17357, an adult male from Carrillo, Costa Rica). This action keeps the name *semifasciatus* associated with *Imantodes cenchoa*, in accordance with Cope's last decision and in agreement with twentieth-century usage. However, I think that use of *semifasciatus* for the name of a subspecies is unjustified, at least as defined by Smith (1942 [see analysis under Geographic Variation]) or by Peters and Orejas-Miranda (1970, p. 133 [contrary to their key, the lectotype of *semifasciatus* has a dark speckled venter]).

3. *Himantodes anisolepis*: Holotype (AMNH 17274) from Monte Aguacate, Costa Rica. It is a juvenile male about 422 mm. total length, 126 mm. tail length (29.9% of total); vertebral scales about 3.9 times wider than midlateral scales; venter damaged

in places, but approximately 270 ventrals; 173 subcaudals; 39 bands on body, extending to ventrals (none broken); about 27 tail blotches; ventral surfaces virtually immaculate. The specimen agrees well with the original description, which appears on the same page as that of *H. semifasciatus*. The diagnostic key on the page preceding the description shows that Cope was impressed by the wide vertebral scales and by the dorsal bands ("spots") that reach the ventrals throughout the body. The essentially immaculate venter seems unusual, but the other characters fit my understanding of the variational range of *Imantodes cenchoa*, where the name *anisolepis* was correctly assigned by Boulenger (1896) a few years after its description.

4. *Himantodes platycephalus*: Holotype (AMNH 38400) from an unknown locality in Colombia, thought by Cope to be in the "neighborhood of Bogota." It is a juvenile male about 357 mm. total length, 92 mm. tail length (25.8%); vertebral scales about 3.1 times wider than midlateral scales; dorsals in 17-17-17 rows; underside of head damaged, but at least one pre-ventral, followed by 227 ventrals; 123 subcaudals; 46 bands on body, the last 17 broken on sides; 26 tail blotches. The measurements and counts correspond closely to the original description; its identity as the type is further confirmed by comparing the unique pattern of temporal scales (highly variable in *cenchoa*) with Cope's plate 4 (fig. 4b) in the original description. This name has received little attention. It was listed without comment (*vide infra*) in the *Zoological Record* for 1899 (vol. 36, p. 22), and it was carried as a valid species in Werner's (1925, p. 123) catalogue. Amaral "1929" [1930b] put it in the synonymy of *Imantodes cenchoa*, evidently because of his mistaken belief ("1929" [1930a], p. 34) that Boulenger had so listed it in the *Zoological Record* (*vide supra*). Dunn (1944, p. 79), who regarded *platycephalus* as a "straight synonym of *Imantodes cenchoa*," probably had examined the holotype, either at the Commercial Museum of Philadelphia or at the American Museum (Dunn, *op. cit.*, p. 3). Dunn's view appears correct and has been followed by later authors, including Peters

and Orejas-Miranda (1970, p. 133), who also had examined the specimen as evidenced by their comment about the AMNH jar "label with type."

5. *Himantodes hemigenius*: Holotype (AMNH 17273) from Santa Clara, Costa Rica. It is a somewhat desiccated juvenile male, 316 mm. total length, 88 mm. tail length (27.8%); vertebral scales about 2.0 times wider than midlateral scales; one pre-ventral followed by 241 ventrals; 145 subcaudals; 55 bands on body, approximately the last 27 broken laterally; tail blotches? (>30). The number (92) mentioned by Cope is still associated with the holotype, on one of the old Museo Nacional field tags loose in the jar, and the specimen generally agrees with Cope's description. On an original invoice of the collection, specimen no. 92 is identified in Cope's handwriting as "*Himantodes semifasciatus*," the only snake of that name listed from Santa Clara, Costa Rica. Thus, AMNH 17273 is one of the original syntypes and now a paralectotype of *H. semifasciatus* Cope, 1894, as well as holotype of *H. hemigenius* Cope, 1899. In the listing in the *Zoological Record* for 1899 (vol. 36, p. 22), Boulenger straightaway indicated that *hemigenius* is a synonym of *cenchoa*, where it has been maintained by subsequent cataloguers (Werner, 1925; Amaral, "1929" [1930b]; Peters and Orejas-Miranda, 1970). However, the name must now be transferred to the synonymy of *Imantodes gemmistratus* as that species is presently understood. The holotype of *hemigenius* has smaller vertebral scales than *cenchoa*, and its oval-shaped head is less abruptly enlarged than is usual in *cenchoa*. The overall color pattern is very similar to that of two other *semifasciatus* paralectotypes (AMNH 17296-17297) that I also identified as *Imantodes gemmistratus*, as already discussed.

NATURAL HISTORY

Imantodes cenchoa is one of the commoner¹¹ species of Neotropical snakes, being

¹¹ Such statements need to be qualified, although it is difficult to do so. My largest sample of *I. cenchoa* comprises 17 specimens obtained in 20 days of general col-

usually one of the first snakes encountered in suitable forest at night. It is nocturnal, as suggested by the elliptical pupil which closes to a vertical slit, and arboreal, as suggested by morphology, including protuberant eyes that allow downward vision. Most specimens were found less than 2 m. aboveground, in vine tangles, bushes, small trees, or on palm fronds, or other broad leaves. They are not uncommonly found prowling on the forest floor or through low herbaceous vegetation, climbing into and investigating isolated bushes and small trees along the way. None was found active by day. Henderson and Nickerson (1976) observed that captives mostly spent the daylight hours coiled in bromeliads, from which they emerged their heads when light levels had dropped to between 4–1 foot-candles, later emerging completely at 1–0 foot-candles.

By day, I have found a few *cenchoa* sleeping well concealed in low-growing bromeliads (to 3 m. aboveground), as have many other collectors, since bromeliad molestation is a veritable compulsion among field men in the New World tropics. A presumed "proclivity" to hide in bromeliads led Henderson and Nickerson (1976, p. 207) to suggest that "bromeliads are important in the ecology of the genus." However, at least in Panama, the abundance of *Imantodes cenchoa* (not to mention savanna-inhabiting *gemmistratus*) seems to be negatively correlated with that of bromeliads, which would be unexpected if the plants were very "important" to the snakes. For example, my journal entries state that bromeliads were "decidedly uncommon" at the two San Blas sites that accounted for 17 *cenchoa* (see fn. 11). In another sample, eight specimens from the Azuero highlands (480–940 m.) were all found below the zone of bromeliad abundance (habitat description in Myers, 1969, pp. 30–31). *Imantodes cenchoa* evidently makes do with a variety of daytime retreats—including bromeliads—so

long as they can conceal themselves completely while sleeping. I found several specimens at different localities by breaking open hollow sections of inclining rotten sticks or small trunks (~10 cm. diameter), about 0.5–1.0 m. aboveground. Three were found sleeping on the ground—one in leaf litter, one under a log, and one inside a fallen, hollow cacao pod. The scattered literature reveals a similar multiplicity of diurnal occurrences, as partly summarized by Henderson and Nickerson (1976, p. 206), who indicated a diversity of sleeping sites even among their captive specimens that had access to the bromeliads, which were used most of the time (although, judged from the photographs published by these authors, their snakes may have had little choice of hiding places, with even the bromeliads being of less than optimal size).

Lizards of the genus *Anolis* are widely recognized as the principal food of this snake, but it evidently can exist in their absence. Lizards were seemingly absent in the area of my camp at 940 m. elevation on Cerro Hoya, in the depauperate Azuero highlands (Myers, 1969, p. 47), although six *Imantodes cenchoa* were obtained in 10 nights at that camp. One regurgitated a frog, *Eleutherodactylus crassidigitus*, and specimens from eastern Panama also contained remains of *Eleutherodactylus*, including *E. raniformis*. Nonetheless, anoles are an important food, and my specimens have regurgitated *Anolis capito*, juvenile *A. latifrons*, *A. limifrons*, and *A. tropidogaster*, as well as remains unidentified to species.

Large female *Imantodes* are even capable of feeding on the giant anoles, as permitted by divergent growth rates that result in females acquiring longer and especially wider heads than males. Even so, it requires a degree of elasticity of the snakes' exceptionally thin necks (fig. 9) that is nearly beyond comprehension. The largest Panamanian *cenchoa* (AMNH 119558, 1015 mm. SVL + 465 mm. tail = 1480 mm. total) has a head length of 23.0 mm. and a head width of 17.3 mm. but a neck diameter of only 4.5 mm. This snake contained an adult male *Anolis frenatus* (163 mm. SVL), whose individual legs are greater

lecting at two camps in San Blas (12–400 m.), Panama. In temperate regions, larger samples of some species can be obtained in only a few hours, but snake populations are at either real or apparent low densities in tropical wet lowland forest (Myers and Rand, 1969, p. 9).

than the snake's unexpanded neck and whose uncompressible skull (20 mm.) is four times wider; the weight of the preserved, partially digested lizard (47 g.) is 78 percent that of the preserved snake (60 g.). It was a heroic meal even by snake standards!

A report of reptile eggs (*Anolis*?) from the stomach of a Mexican *cenchoa* is usually cited. Perhaps it is *cenchoa* that has been seen feeding on terrestrial (arboreal) amphibian eggs; Scott and Starrett (1974, p. 87) said that observers in Costa Rica have seen "*Imantodes* preying on *A[galychnis]. callidryas* eggs."

Like other species of the genus, *Imantodes cenchoa* is a docile snake that is not known to bite. One was seen to slide halfway down a giant elephant-ear leaf after being startled by a close-flying bat, but they show no tendency to drop to the ground when approached by a collector.

One moderate-sized female (AMNH 106676, 680 mm. SVL, 965 mm. total) collected in early March, on Cerro Campana (800 m.), laid the maximum number of three eggs on March 30. One egg spoiled after laying; the others measured 33 × 13 mm. and 35 × 12 mm. and contained embryos near hatching when opened in July, 69 days after laying. There are normally two eggs, in a range of one to three, according to Zug, Hedges, and Sunkel (1979), who summarize pertinent literature and provide additional data on reproduction and growth.

Imantodes cenchoa occupies a variety of humid forests, including some cloud forests, but I was unable to find it in the luxuriant cloud forest habitat of *I. phantasma*. It does occur sympatrically with *I. gemmistratus* and *I. inornatus*, as discussed under those species. The tongue is flicked briefly (fig. 8), not extended in a prolonged quiver as in *I. phantasma*.

REMARKS: Taylor (1954, p. 752) commented on how odd it seemed for male *Imantodes cenchoa* in his sample to have more ventrals than the females (as well as more subcaudals), since this is contrary to the usual situation in snakes. However, it may be the usual condition in *Imantodes* for males to have more ventrals, hence more

vertebrae, then females (table 2). Johnson (1955, p. 383) described the vertebral structure that together with body compression and enlarged vertebral and ventral scales (Schmidt and Inger, 1957, p. 212), allows *Imantodes cenchoa* to bridge wide gaps as though the body were an "I" beam (see Carr [1963, pp. 100–101] for photographic sequence). Possibly, the higher ventral-vertebral numbers of the usually shorter (hence lighter, and never egg-laden) males gives them a greater degree of maneuverability than females. The males suffer a higher incidence of tail breakage than females. The females have larger heads than males and apparently can take larger prey. All these features seem to suggest differential foraging behavior and somewhat different ecological roles for the sexes.

Imantodes gemmistratus (Cope)¹²

Figures 4B, 11, 12, 19B; Map 2

Himantodes cenchoa (not of Linnaeus): Cope, 1860, pp. 264–265 (ANSP specimen cited from "Near Isalco, San Salvador").

Himantodes gemmistratus Cope, 1861, pp. 296–297 (type locality, "San Salvador" [near Isalco, *vide supra*], El Salvador; holotype originally in ANSP [not found by Malnate, 1971], Capt. J. M. Dow, collector); 1894, p. 613; 1899, p. 17. Boulenger, 1896, pp. 86–87. Werner, 1925, p. 123.

Himantodes cenchoa var. *elegans* Jan and Sordelli, 1871 (1860–1881), vol. 3, livr. 38, pl. 2, fig. 1 (illustrations of a specimen [the holotype] from "Amérique centrale—Musée de Munich" *fide* index on back cover of livr. 38).

Leptognathus stratissima Cope, "1885" [1886], pp. 280–281 (type locality, "Panama" [p. 279]; holotype, USNM 14121, a juvenile male obtained by Dr. George W. Nelson [on May 9, 1885 *fide* Cochran, 1961, p. 192]).

Himantodes semifasciatus Cope, 1894, p. 614 (part, including most of the syntypes but not the lectotype [= *I. cenchoa*]; see Notes on Type Specimens under *Imantodes cenchoa*).

Himantodes elegans Jan and Sordelli: Boulenger, 1896, pp. 85–86.

¹² For additional synonyms or names applicable to populations of *gemmistratus* in northern Middle America, see especially Zweifel (1959) and Stuart (1963, pp. 100n, 101); also Yingling (ms).

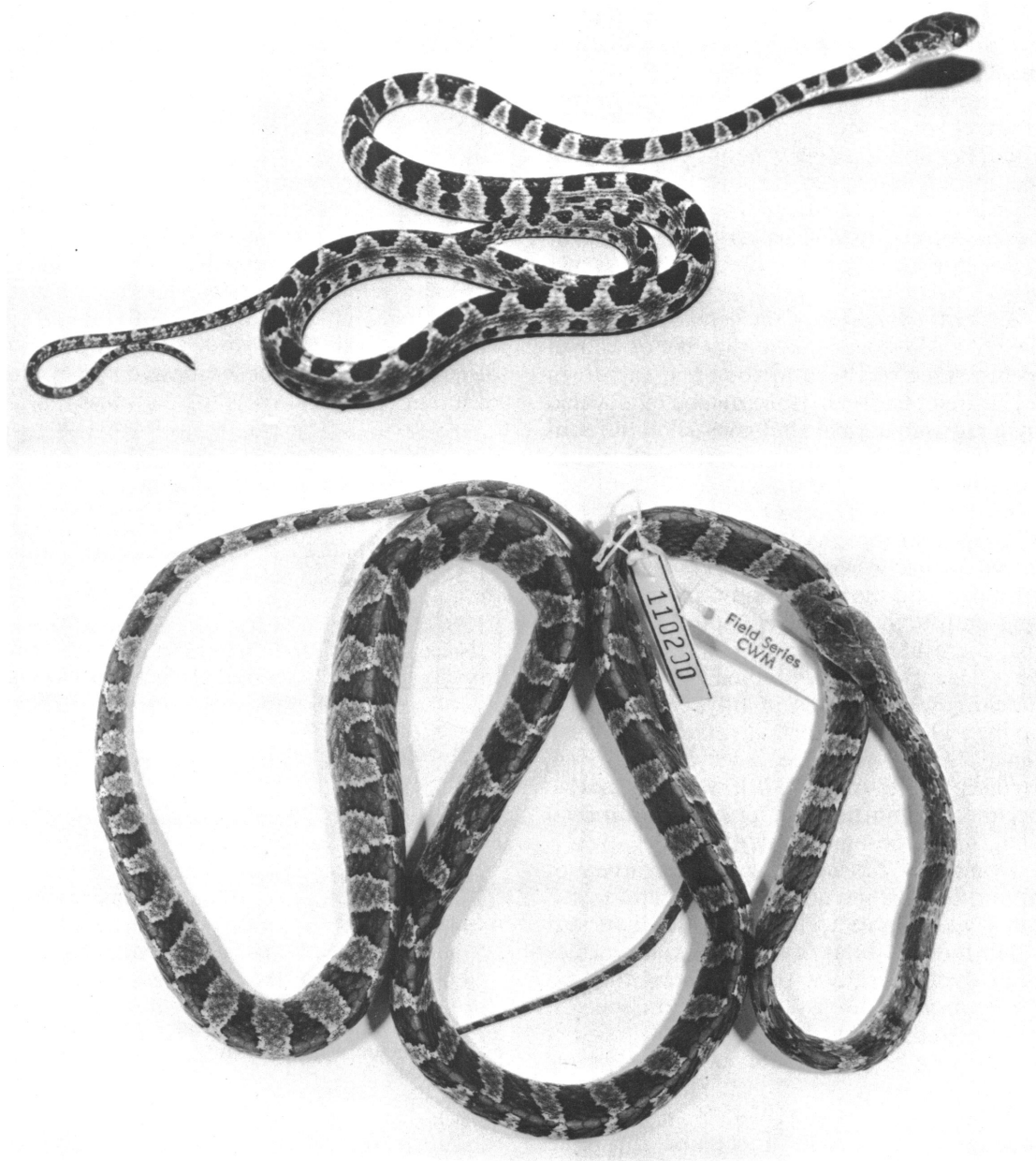


FIG. 11. *Imantodes gemmistratus* from lowland central Panama. *Top*: KU 110195, juvenile male, 9 km. NE Pacora, 30 m., Panamá Province. *Bottom*: KU 110200, adult female, Curundú, Canal Zone of Panama.

Himantodes hemigenius Cope, 1899, p. 16 (type locality, Santa Clara, Costa Rica; holotype, AMNH 17273, collected in May, 1887, by A. Alfaro [original no. 92; sent to Cope, Feb. 1894, by George K. Cherrie, Museo Nacional de Costa Rica; specimen is also a paralectotype of *Himantodes semifasciatus* Cope, 1894]). For discussion, see Notes on Type Specimens under *Imantodes cenchoa*. NEW SYNONYMY.

Imantodes gemmistratus (Cope): Schmidt, 1928, p. 193 (in list). Smith, 1942, p. 385. Taylor, 1951, p. 135; 1954, pp. 754-757, fig. 21. Mertens, 1952, p. 65 (includes brief description of specimen from near type locality). Peters and Orejas-Miranda, 1970, p. 134.

Imantodes cenchoa (not of Linnaeus): Amaral, "1929" (1930b), p. 203 (part, name in synonymy). Savage, 1980, p. 96 (?part).

DISTRIBUTION: From Sonora and Veracruz, Mexico, south through Central America to the Magdalena Valley of northern Colombia.¹³ In Panama, *Imantodes gemmistratus* seems to be confined to the Pacific side of the isthmus except in the central lowlands, where it crosses to the Atlantic side (map 2).

DESCRIPTION OF PANAMANIAN SPECIMENS ($N = 22$): Body pale to medium brown with 55-74 dark brown saddles, variably narrowed on the sides where they either extend to the venter (at least on anterior part of body) or break off into small to medium lateral spots; the dorsal markings are sometimes irregularly shaped and sinuously interconnected, thus forming elongated blotches or a zigzag stripe on part of body; 28-42 tail blotches (50 tail blotches on one juvenile,

¹³ *Imantodes gemmistratus* seems not to have been previously reported from South America. I examined a single specimen (MLS 966) sent for identification by the late Hermano Nicéforo María, Museo del Instituto de La Salle, Bogotá. Hermano Nicéforo wrote (*in litt.*, July 12, 1974) that it had been collected "in the region of Ortega [75°13'W, 3°56'N], Departamento de Tolima, in July 1956," and that it had swallowed an *Anolis auratus*. The snake is a female 348 mm. total length, with the tail (89 mm.) comprising 25.6 percent of the total; 19-17-17 scale rows, with the vertebrals being enlarged twice the width of the laterals; 230 ventrals, 119 subcaudals, anal divided; 54 body blotches (last 9 broken laterally), 31 tail blotches.

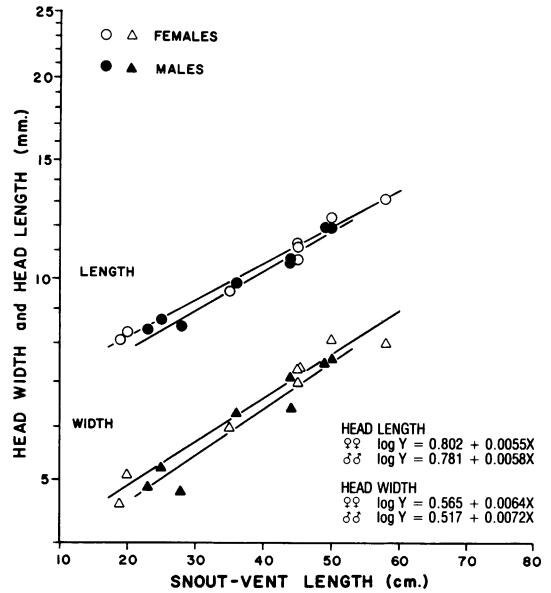


FIG. 12. Relationship of head width and head length to body size in *Imantodes gemmistratus* from Panama. Compare figure 10.

table 2 note *c*). Color pattern atop head variable, with pale lines and dark brown spots forming a usually bilaterally symmetrical floral pattern. Ventral surfaces whitish, relatively clear under head but otherwise heavily dotted or spotted with dark brown; occasionally with a suggestion of a midventral line.

Rather small, slender snakes of less than 900 mm. total length (observed maxima this sample, 693 mm. ♂, 786 mm. ♀), with tail comprising 24-28 percent of total. Short, blunt head wider than thin neck but not abruptly so (usually more oval from above than in *I. cenchoa*); large eye occupying more or less one-fourth (21-27%) of length of head; HW (greatest head width)/HL (tip of snout to end of mandible) = 0.56-0.73 in all sizes; heads of females not conspicuously wider or longer than in males (fig. 12; mean HW/HL = 0.668 in 6 ♂ and 0.649 in 5 ♀ of all sizes). Dorsal scales in 17-17-17 or 19-17-17 rows. Scales in vertebral row moderately en-

larged, 1.3–2.0 times wider than midlaterals (2.5× wider in one juvenile, table 2 note c); vertebral scales varying usually on the same specimen, from posteriorly rounded to truncate or concave. Ventrals 221–237 and subcaudals 113–130, with males averaging more of each (table 2); anal plate divided. Supralabials usually 8, occasionally 9; infralabials 10 or 9. One preocular, usually two (1–3) postoculars; temporal scales (between parietal and supralabials) variable, with 3–9 scales per side.

Maxillary teeth 10–12 (\bar{X} = 10.8) + 2 on a maxilla from each of 16 specimens; the modal number is 11+2, accounting for nine of the 16 maxillae, although 10+2 is also common (5 of 16). The two rear fangs are about 1.5 times larger than the prediastemal teeth; each fang is deeply grooved along the basal two-thirds or one-half of its anterior face.

The everted hemipenis is relatively short and stubby (fig. 4B), being about half as wide as long; the one everted organ examined extended to subcaudal 5. Upon eversion, the hemipenis recurved strongly on the sulcate side, so that the calyculate capitulum occupies half the length of this side of the everted organ; free overhang of capitulum disappearing on median part of asulcate side, which is sparsely spinose to tip (fig. 19B).

COLOR IN LIFE: A juvenile from the savannas east of Panama City had dark brown blotches on a basically white ground; however, the interspaces between the blotches were darkened by central suffusions of grayish brown, as can be seen in the photograph (fig. 11, top). The ventral surfaces were white, heavily speckled with blackish brown. The iris was gray, heavily suffused with brown, and the tongue was light brown with white tips.

NATURAL HISTORY: This species is the only Panamanian *Imantodes* that occurs normally in broken-canopy forest or in such nonforest habitats as *Curatella* savanna and scrubby pasture lands. By virtue of habitat and its relatively small vertebral scales, I assume that it is much more terrestrial than the other species; the juvenile shown in figure 11 was

crawling on the ground at night, in a small grassy savanna with scattered *Curatella* trees. I noted five Panamanian specimens that contained *Anolis tropidogaster* in their stomachs, and a Colombian specimen had eaten an *Anolis aeneus* (fn. 13). These two lizards are common in brushy and grassy habitats on the Pacific side of Panama and seem likely to be the main food of *I. gemmistratus*.

In the drier, more open habitats of the Pacific lowlands, *Imantodes gemmistratus* occurs alone. However, it is broadly sympatric with *I. cenchoa* in the region of wet lowland forest in the structural depression across central Panama. *Imantodes gemmistratus* penetrates north to the Atlantic coast in this region (map 2). Possibly it does so by occupying primarily the brushy and grassy disturbed areas of the Panama Canal Zone, although a specimen (UF 28261) from the Madden Forest Preserve raises the possibility that *gemmistratus* might also occur sparingly in mature, monsoonal rain forest. Nonetheless, the Madden Forest is bordered by open, brushy clearings, and the ecology of *I. gemmistratus* remains enigmatic in this region. The lack of recent records from Barro Colorado Island led Myers and Rand (1969, p. 6) to suggest that *gemmistratus* might be among the species extirpated on the island, following the vegetational succession from old clearings to mature forest.

Three Panamanian females each contain two elongated eggs, which average roughly 15 mm. and 30 mm. long in two snakes caught in May of different years, and about 34 mm. long in a specimen caught in September. Clutch size in these specimens is thus similar to that of *I. cenchoa*, which also normally produces two eggs (known range = 1–3 in *cenchoa*). However, a Costa Rican specimen assigned to *gemmistratus* (AMNH 17356, fn. 8) contained six ova measuring about 17–25 mm. in length.

Based on my note for KU 110195, the tongue is flicked in and out for its full length as in *I. cenchoa* and *I. inornatus* and is not held extended as in *I. phantasma*.

REMARKS: *Imantodes gemmistratus* exhibits considerable geographic variation, es-

pecially in the northern part of its range (Zweifel, 1959). Central American populations from Guatemala south have been allocated to a single taxonomic population, the nominate subspecies (Peters and Orejas-Miranda, 1970), although there exists no published assessment of variation throughout the range of *gemmistratus*.¹⁴ In any case, specimens from the Isthmus of Panama are fairly similar in color pattern, and all appear to belong to the same regional population as the two snakes shown in figure 11.

Imantodes gemmistratus in Panama conceivably might be confused with *I. cenchoa*, since both have brown saddles or dorsal blotches on a lighter ground. Nonetheless, it takes little experience to identify them by appearance alone. *Imantodes cenchoa* has fewer markings, which are of an odd reddish brown hue on a very pale brown or tan, and its enlarged vertebral scales are quite noticeable. Panamanian specimens of *I. gemmistratus* have more numerous and relatively crowded blotches, which are medium or dark brown on a light brown ground, and the smaller vertebral scales are not so conspicuous. The dark edging of the blotches is somewhat less evident in *gemmistratus*, which usually has less contrast between the blotches and the ground color, except when the blotches are set on a partly white ground color (as in fig. 11, top). In addition to appearance and smaller vertebral scales, *gemmistratus* differs from *cenchoa* in hemipenis (fig. 4), in having significantly fewer ventrals and subcaudals (table 2), somewhat fewer maxillary teeth, and in size and proportions. *I. gemmistratus* is a smaller snake that attains less than two-thirds the length of *cenchoa*, and it has a relatively shorter tail; somewhat more subjectively, the head of *gemmistratus*

tends to be more oval and less abruptly distinct from the neck when viewed from above; also there are relative differences in rate of growth and degree of sexual dimorphism in cranial length and width (compare figs. 10, 12).

Thus, the differences seem substantial between *I. gemmistratus* and *I. cenchoa* in Panama. Cope (1894) confused Costa Rican specimens of these species, as discussed herein under *I. cenchoa* (Notes on Type Specimens), but that was a long time ago and we need not belabor the matter. Taylor (1951, 1954) seems to have properly separated the three species of *Imantodes* in Costa Rica, and he provided a good photograph of each. Savage (1980), however, excludes *I. gemmistratus* from the Costa Rican fauna, presumably in deference to his student Norman Scott, who stated (MS, p. 134) that "*I. cenchoa* is probably conspecific with *I. gemmistratus*." In absence of documentation to the contrary, I suggest that *gemmistratus* be reinstated to the Costa Rican list.¹⁵

Imantodes inornatus (Boulenger)

Figures 4C, 13, 14, 19C; Map 2

Himantodes inornatus Boulenger, 1896, p. 88, pl. 5, fig. 1 (type locality, Hacienda Rosa de Jericho, 3250 ft., Nicaragua; two syntypes [not seen] in BMNH, obtained by Dr. E. Rothschild). Cope, 1899, p. 16. Werner, 1925, p. 123.

Imantodes cenchoa (not of Linnaeus): Amaral, "1929" [1930b], p. 203 (part, name in synonymy).

Imantodes inornatus (Boulenger): Dunn and Bailey, 1939, p. 17. Taylor, 1951, p. 130, pl. 14; 1954, p. 751. Peters and Orejas-Miranda, 1970, p. 135.

¹⁴ There is an unpublished revision of *gemmistratus* on file at San Diego State College (Yingling, MS), which recommends reducing the six presently recognized subspecies to only two. I examined this document primarily to see if the author might have found reason for recognizing the Panamanian snakes as a separate species, for which the name *stratissima* would be available (he did not).

¹⁵ Scott gave no supporting data for his taxonomic opinions, which are incidental to a zoogeographic analysis. He is cited in order to explain a later published event, not to violate the customary ambivalence of dissertation citation (i.e., it is fair to credit original thought but not to criticize ideas that a student might never decide to print). Dr. Scott (verbal commun.) may have perceived variational patterns in northern and western Costa Rican *Imantodes* that do not parallel the situation in Panama, and I urge attention to the problem whenever sufficient specimens have accumulated.

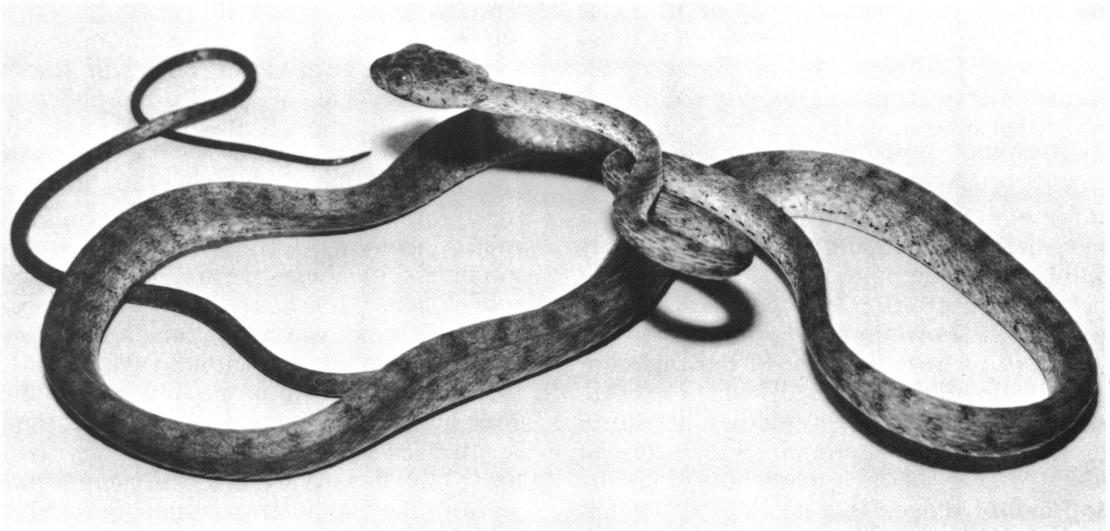


FIG. 13. *Imantodes inornatus* (KU 110213) from Camp Summit, 300–400 m., on divide between San Blas Territory and Darién Province.

DISTRIBUTION: Nicaragua to northwestern Ecuador. *Imantodes inornatus* is widely distributed on both sides of the Panamanian isthmus, in humid forest from near sea level to at least 910 m. elevation, but apparently absent from lowland savanna and other dry habitats in Pacific western Panama (map 2).

DESCRIPTION OF PANAMANIAN SPECIMENS ($N = 16$): Golden or light brown above, with black speckling overall; there are numerous, rather poorly defined blackish crosslines dorsally, and similar but alternating lines laterally (fig. 13). The head is dotted with black; often there is a median black line or suggestion of one on the rear of the head and/or nape. Labials and underside of head are nearly immaculate or weakly speckled with black; rest of ventral surfaces densely speckled with black and usually with a thin mid-ventral line.

Slender snakes usually less than 1 m. in total length (observed maxima this sample, 1035 mm. ♂, 858 mm. ♀), with tail comprising 21–31 percent of the total. Head distinct from neck, with large eyes occupying 20–30 percent of head length; HW (greatest head width)/HL (tip of snout to end of man-

dible) = 0.59–0.74; heads of females tending to be longer (and wider?) than in males (fig. 14; mean HW/HL = 0.663 in 8 adult ♂, 0.637 in 3 adult ♀, 0.633 in 8 ♀ of all sizes). Dorsal scales smooth, in 17–17–17 rows in seven females (17–19–17 in another), but reducing posteriorly to 15 in one female and to 15 or 13 in all males ($N = 8$). Scales in vertebral row slightly to moderately enlarged, less than twice the width of the midlateral scales (range ≈ 1.2 – $1.5\times$), with pointed to rounded posterior margins (occasional specimens having a few scales with the ends truncate or concave). Ventrals 196–218 and subcaudals 110–132, with males averaging more of each (table 2); anal plate entire or (in one-third of sample) divided. Supralabials usually 8, rarely 7 or 9; infralabials usually 10, occasionally 11 or 9, rarely 8. One (rarely two) preocular, two (rarely three) postoculars; temporal scales (between parietal and supralabials) variable, with 3–6 scales per side.

Maxillary teeth 17–21 ($\bar{X} = 19.4$) + 2 on a maxilla from each of 16 specimens; the two rear fangs are about twice the size of the pre-stastemal teeth, and each one has a shallow, basal groove on its anterior face, but the

grooves are so weakly developed as to be nearly absent in some specimens.

Everted hemipenes on six adult males relatively large (fig. 4C), extending to subcaudals 6–8 when pressed against the tail. When fully everted, the hemipenis is about half as wide as long and strongly recurved on sulcate side, so that calyculate capitulum comprises about half of length of this side of everted organ; capitulation strongly pronounced, with deep, uninterrupted overhang on asulcate side (fig. 19C).

COLOR IN LIFE: The ground color of five specimens from scattered localities (20–830 m. elev.) was a yellowish or dull golden brown; specimens from one highland locality (910 m.) in Bocas del Toro varied from bright orangish brown to greenish brown. The dorsal crosslines are usually black, but these markings were noted as “greenish” on a specimen from Camp Summit, San Blas, and “light olive gray to black” on one from Achioté, Colón. The underside of the head and the throat vary from white to yellow; the rest of the ventral surface varies from yellow to light orange or orangish tan, with conspicuous dark speckling. The iris is pale yellowish brown, yellow, tan, or pale brown at most localities; those from the aforesaid highland population (910 m.) had eyes that were pale orange, orangish brown, or greenish gray. The tongue is black, with white tips.

NATURAL HISTORY: Throughout its range, *Imantodes inornatus* seems to occur sympatrically and even microsymbatrically with *I. cenchoa*, both being found mainly in low vegetation in forest at night. However, whereas *cenchoa* is found commonly, *inornatus* is collected infrequently and rarely in series. I have seen only one locality where *inornatus* was indisputably more abundant than *cenchoa*. During May 1966, William E. Duellman, Linda Trueb, and I made a transect through montane and lower montane rain forest in upland Bocas del Toro, from 2290 m. elevation on the continental divide (summit of Cerro Pando) down to 830 m. *Imantodes* was not found in the exceedingly wet and cold forests at the higher elevations (descriptions in Myers, 1969, p. 33), but *inornatus* and *cenchoa* both were at our lower

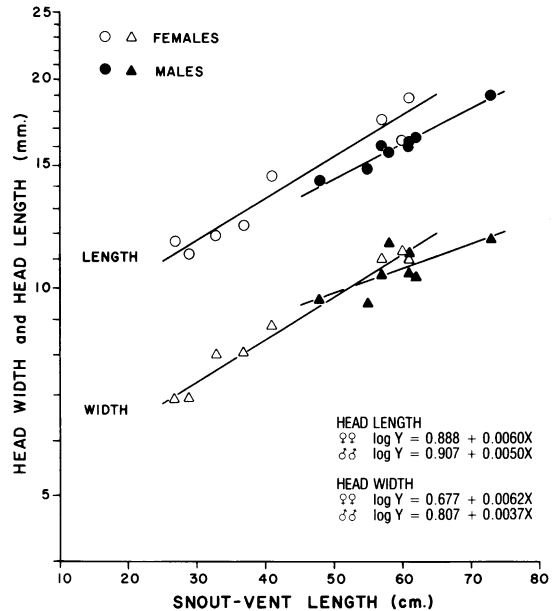


FIG. 14. Relationship of head width and head length to body size in *Imantodes inornatus* from Panama. The size range of available males is too small to allow reliable estimation of possible sexual divergence in growth rates. (Compare fig. 10 where such divergence is present and fig. 12 where it is absent.)

camp at 910 and 830 m. in the Río Changuinola; the 15 specimens collected were distributed as follows:

	<i>I. inornatus</i>	<i>I. cenchoa</i>
CAMP 910 m.	9	1
CAMP 830 m.	1	4

These collections are not randomly distributed ($\chi^2_{\nu} = 4.54$, $P < 0.05 > 0.025$). Inasmuch as the 910 m. camp provided more than half the *inornatus* sample for the present account, photographs of the locality are provided as representations of possibly optimum habitat for this little known species (fig. 15).

One newly captured individual was noted to broaden its head by lateral expansion of its jaws, but, in common with other species of the genus, *Imantodes inornatus* is docile and makes no attempt to bite. The tongue is

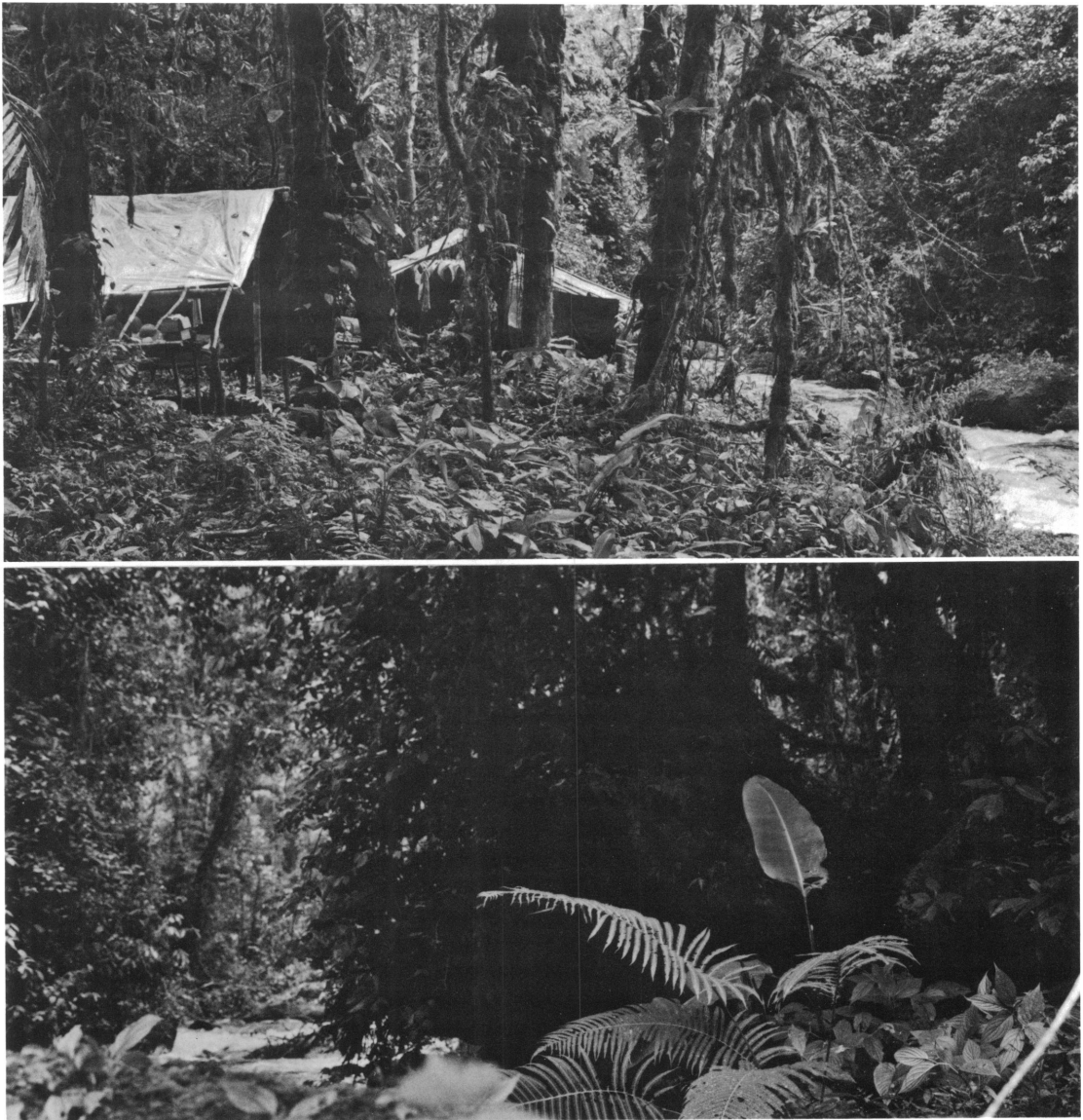


FIG. 15. Views of the lower montane rain forest at Río Claro, 910 m. elev., northern slopes Cerro Pando, Bocas del Toro Province (May 1966). This is the only locality where *Imantodes inornatus* was more common than *I. cenchoa*.

flicked normally as in *I. cenchoa* and *I. gemmistratus* and not held extended as in *I. phantasma*. A female *inornatus* 846 mm. total length (604 mm. SVL) collected in late June at Achote, in central lowland Panama,

contains four eggs measuring about 20 mm. in length. The maximum clutch size of the larger and more common *I. cenchoa* is only three so far as known.

NOTES ON A SOUTH AMERICAN SPECIES

Four species of *Imantodes* are now known to occur in South America, namely: *cenchoa*, *gemmistratus* (see fn. 13), *inornatus*, and *lentiferus*. The last species is the only one that does not also occur in lower Central America. Although *I. lentiferus* is a broadly distributed Amazonian species, little has been published about it, and so the following brief account may prove useful.

Imantodes lentiferus (Cope)

Figures 16B–18, 19D

Himantodes lentiferus Cope, 1894, pp. 613–614 (lectotype locality [see Remarks] in upper Amazonian drainage, either Pebas, Peru, or eastern Ecuador; lectotype by present designation, ANSP 11459, obtained either by J. Hauxwell or J. Orton); 1899, p. 16. Boulenger, 1896, p. 86. Werner, 1925, p. 122.

Imantodes lentiferus (Cope): Amaral, "1929" [1930a], p. 34; "1929" [1930b], p. 203. Peters and Orejas-Miranda, 1970, p. 135.

Himantodes fulviventer Obst, 1977a, p. 169 (a manuscript name ["Poepfig, 1866"] first published by Obst [*loc. cit.*], without diagnosis and as a synonym of *I. lentiferus*, hence an unavailable name under arts. 10d and 13a of the 1964 Internatl. Code Zool. Nomenclature); also Obst, 1977b, p. 184 (purported holotype listed, but inasmuch as *fulviventer* is an unavailable name, the specimen lacks any significant relevance to nomenclature). *Nomen nudum*.

DISTRIBUTION: Northern South America east of the Andes, from Bolivia (AMNH 6781) northwest through eastern Peru and Ecuador to southern Colombia (Medem, "1968" [1969], p. 188), and northeast to the mouth of the Amazon (Cunha and Nascimento, 1978) and northern Surinam (AMNH 108796–108797).

DESCRIPTION ($N = 33$): Light brown with 31–52 dark brown saddles or blotches, which may either extend low on the sides (figs. 16B, 17A) or be dorsally confined (fig. 17B). These body markings with or without distinct black edging; interspaces between blotches lightly to heavily speckled with black. Dorsal blotches occasionally become irregularly shaped and sinuously interconnected to form zigzag stripe on part(s) of body (fig. 17B); two

specimens have a straight-edged vertebral stripe (fig. 17C). Tail blotches 18–32. Color pattern atop head variable—a usually symmetrical pattern of several dark brown spots, often partly or completely fused into a V- or Y-shaped marking; head markings not or barely extending onto nape, well separated from transverse edge of first body blotch. Ventral surfaces whitish, relatively clear under head but otherwise heavily dotted with dark brown; lacking midventral dark line (at least in AMNH specimens).

Long, slender snakes, attaining total lengths in excess of 1 m. (observed maxima this sample, 1015 mm. ♂, 1100 mm. ♀), with tail comprising 31–33 percent of total. Short, blunt head distinct from neck, tending to be oval-shaped from above, with large protuberant eye. Dorsal scales smooth, in 15–15 rows; scales in vertebral row large, with truncate or concave rear edges, about 2.0–2.8 times wider than midlaterals in 12 specimens measured for this character.

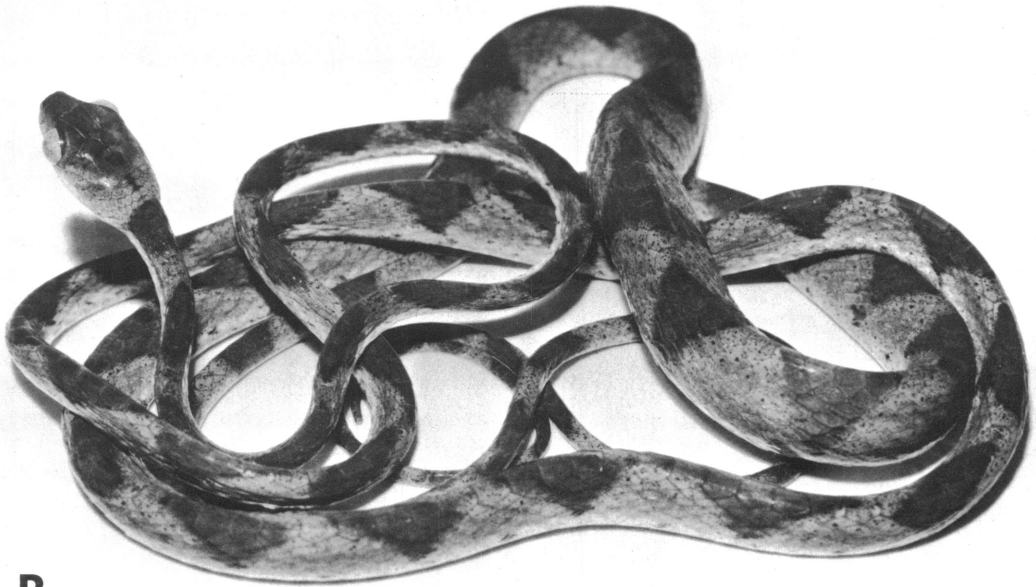
Ventrals 212–236 and subcaudals 127–153, with extensive overlap between sexes (but with males possibly tending to have a few more ventrals and subcaudals than females¹⁶); anal plate normally entire (divided in one of 33 specimens). Supralabials usually 8, occasionally 7 or 9 on one side; infralabials most often 11, frequently 10, rarely 12. One preocular, normally two postoculars (one specimen each with 2/3, 1/2); temporals (excluding scales lying posterior to line between rear edges parietal and ultimate supralabial) somewhat variable in size and shape, with 2–7 scales per side, but often arranged in a generalized pattern of 1+2 scales on at least one side of head.

Maxillary teeth 17–22 ($\bar{X} = 19.0$)+2, on a maxilla from each of 26 specimens; the for-

¹⁶ Ventrals, $\bar{X} = 226.4$ in 13 ♂, 224.9 in 17 ♀; subcaudals, $\bar{X} = 142.2$ in 9 ♂, 140.0 in 14 ♀. However, although the higher means for males are consistent with data from other species (see table 2 and closing Remarks under *I. cenchoa*), it should be remembered that the *lentiferus* sample is too heterogeneous for comparisons to be free of geographic bias and also too small for statistical reliance.



A



B

FIG. 16. A. *Imantodes cenchoa* (AMNH 108798 ♀). B. *Imantodes lentiferus* (AMNH 108797 ♀). Both from Raleigh Cataracts, Coppename River, 50 m. elev., Surinam.

mulae 18+2 ($N = 6$), 19+2 (9), and 20+2 (5) account for 77 percent of the sample. Each of the two enlarged fangs has a shallow groove on the basal half of the anterior face; the distal part of the fang is laterally compressed, with

knifelike anterior and posterior edges, with the latter side retaining its sharp edge well basad.

The everted hemipenes of three males (AMNH 108796, Surinam; KU 121898,

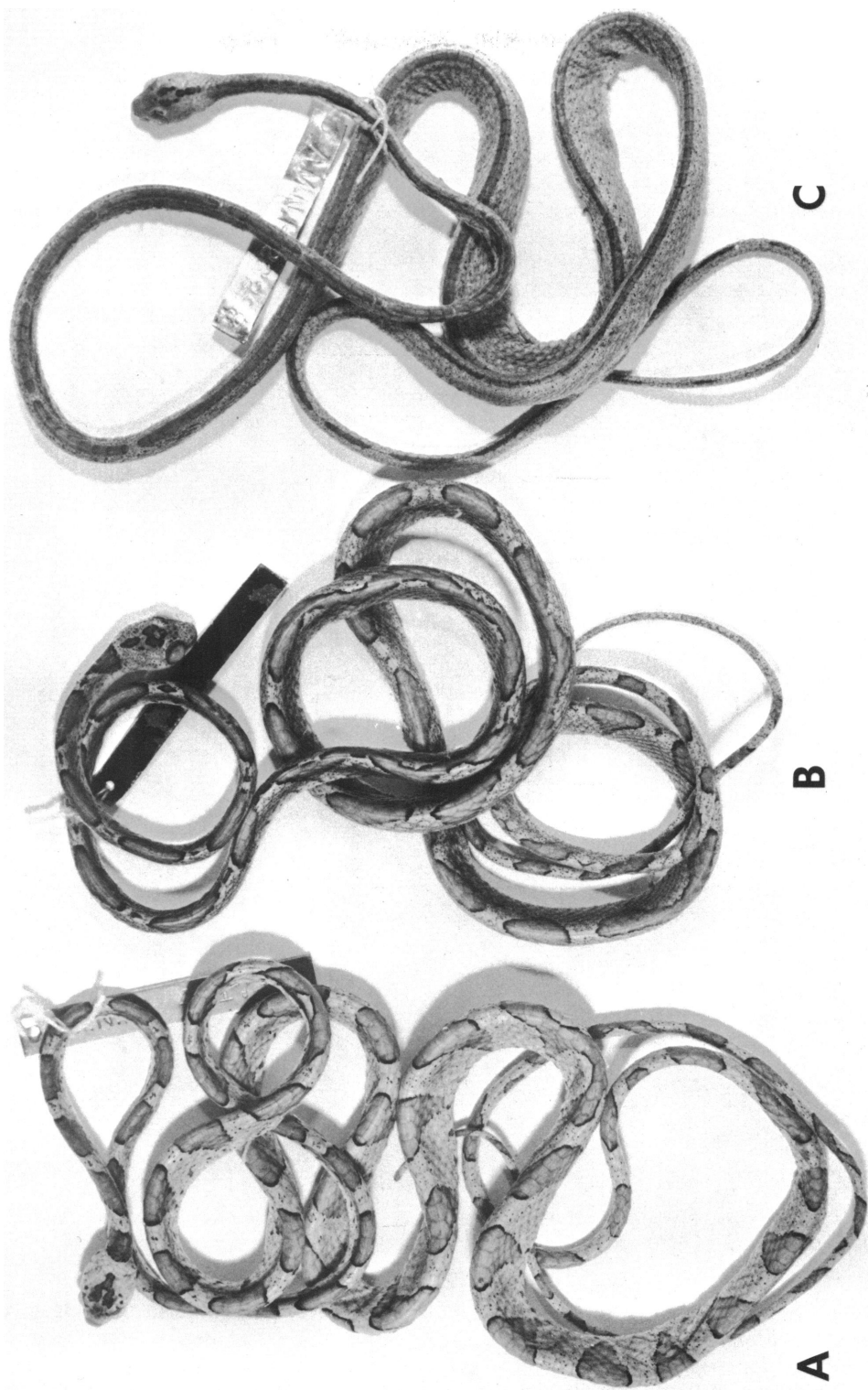


FIG. 17. *Mantodes lentiferus* from eastern Ecuador. A. Specimen with "normal" blotch pattern (AMNH 49173). B. Example of blotch fusion and elongation (AMNH 35906). C. Unusual striped pattern (AMNH 23298).

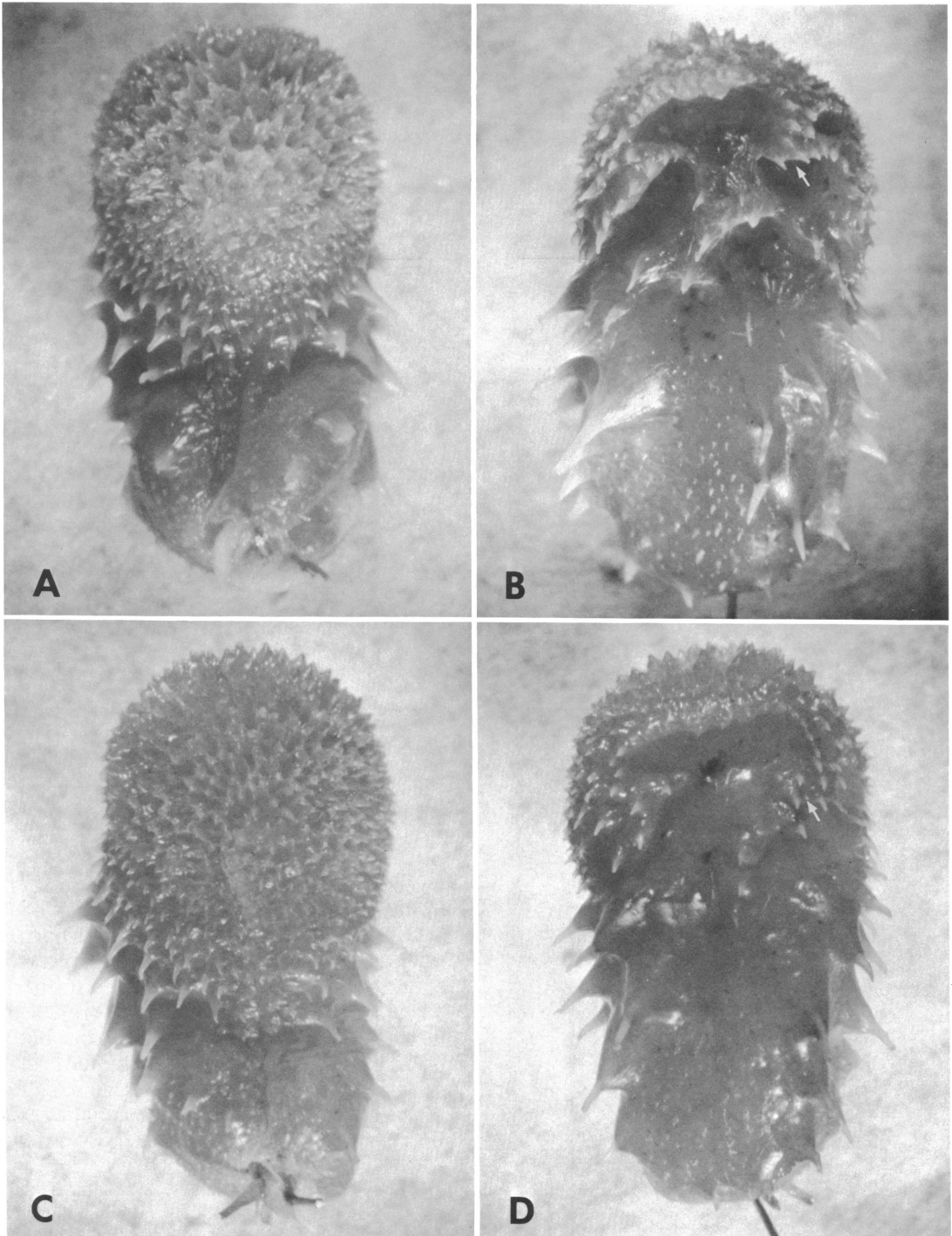


FIG. 18. Hemipenes of *Imantodes lentiferus*, in sulcate (left) and asulcate views. A, B. Left organ of AMNH 108796 (Surinam) $\times 5.7$. C, D. Left organ of KU 121898 (Ecuador) $\times 5.3$. Arrow (in B and D)

148331, Ecuador) are relatively large, extending to subcaudals 6–7 when pressed against the tail. When fully everted (fig. 18), the hemipenis is about half as wide as long and moderately to strongly recurved on sulcate side; calyculate capitulum comprising half or more of length of sulcate side of everted organ. Asulcate, overhanging edge of capitulum joined to midsection by a slightly oblique row of little spines; on both left and right organs (when appressed posteriad with sulci against tail), this longitudinal cluster of spines extends dextrad to the capitulum, tending to leave a large, basally open naked pocket to the left and a small, isolated naked pocket to the right (figs. 18B, 19D).

COLOR IN LIFE: A pair of adult *Imantodes lentiferus* from Surinam (AMNH 108796 ♂, 108797 ♀) were yellowish brown with darker (medium) brown saddles and head spots. The supralabials were suffused with tan, the underside of the head white; the rest of the ventral surfaces were very pale tan with an orangish cast posteriorly on belly and tail and dark speckling overall. The iris was pale, almost yellowish, brown. The tongue was entirely pale grayish (almost lacking color) in the female, and light gray with unpigmented tips in the male from the same locality.

Ecuadorian *lentiferus* are similarly colored (but see Geographic Variation following) according to Duellman (1978, p. 245), who described specimens as “pale tan with brown to reddish brown blotches . . . chin white or cream . . . belly is pinkish tan with small black flecks . . . iris is yellowish tan.”

Duellman (*loc. cit.*) indicated that Ecuadorian *lentiferus* differ from sympatric *cenchoa* in having “smaller reddish tan body blotches” rather than “larger dark brown blotches.” Similarly, a specimen of *cenchoa* from Surinam had darker, more solid brown blotches than two *lentiferus* (*vide supra*) from the same locality, although its blotches were not noticeably larger (*cf.*, fig. 16A, 16B). But

other aspects of hue were very similar (i.e., the specimen of *cenchoa* had pale tan supralabials; white under head; yellowish tan, dark-speckled venter [but also with some white speckling and lacking an orange cast]; iris a very slightly paler shade but the same hue; tongue pale gray with unpigmented fork).

GEOGRAPHIC VARIATION: *Imantodes lentiferus* occupies a vast range in the Amazonian lowlands and seems to be of fairly uniform appearance throughout this region. I have not examined specimens from the lower Amazon, but Cunha and Nascimento (1978, pl. 19, fig. 1) picture one that has distinctly dark-edged blotches the same as in most *lentiferus* from the upper Amazon (fig. 17A).

In contrast, there seems to be an extra-Amazonian center of minor differentiation in the eastern part of the Guayana region. The three specimens that I have examined from northwestern Surinam, and one from extreme southeastern French Guiana, have saddle-markings with rather fuzzy edges that are not so well demarcated as in Amazonian specimens. The peripheries of some blotches may be darker brown than the centers, but none can actually be described as being edged in black or blackish brown. This minor pattern difference gives the Guayana snakes an appearance quite unlike those from Amazonia, as may be seen by comparing the Surinam specimen in figure 16B with those from Ecuador in figure 17.

Two *striped* specimens of *Imantodes lentiferus* are so unusual as to warrant comment. AMNH 23249 ♂ has a continuous, narrow brown stripe confined to the vertebral scale row; AMNH 23298 ♂ (fig. 17C) is similarly marked except that the stripe is broken on the tail and in several places on the body, where the stripe seems formed by the fusion of very elongate albeit straight-edged blotches. The middorsal stripes of these snakes presumably represent an extreme derivation of

←

indicates oblique little cluster of small spines extending slightly dextrad to capitulum, separating small naked pocket on right from large, basally open, naked area to the left of the spinose cluster (see fig. 19D for close-up view from slightly different perspective).

the short wavy stripe that appears more commonly owing to the apparent fusion of several dorsal saddles (as in fig. 17B), but it is unknown whether we are dealing with a rare aberration or a variation that might be common or even predominant in a population. The two striped snakes (also the specimen in fig. 17B) are catalogued as "Riobamba," Ecuador, said to have been collected in October 1922, by Enrique [Heinrich] Feyer. However, the locality is impossibly high (2700 m.) for a lowland snake and certainly represents only the shipping point for these and many other specimens from the lowlands of eastern Ecuador.¹⁷

NATURAL HISTORY: *Imantodes lentiferus* is a nocturnal, arboreal snake of lowland rain forest. Dixon and Soini (1977, p. 53) indicated that it is a species of primary forest in the Iquitos region, but Duellman (1978, p. 245) noticed a habitat preference at Santa Cecilia, Ecuador, where specimens ($N = 24$) were found only in secondary forest, whereas *I. cenchoa* ($N = 32$) seemed equally abundant in both secondary and primary forest. Duellman also suspected a difference in food preference, noting that two *cenchoa* contained lizards (*Anolis*), whereas four *lentiferus* had only frogs in their stomachs (*Hyla*, *Eleutherodactylus*). I also noticed a small hyliid frog in the stomach of a juvenile *lentiferus*, but Cunha and Nascimento (1978, p. 95) indicate that lizards are also eaten by *lentiferus*, and it should be remembered that *cenchoa* in Panama feeds upon both lizards and frogs. Environmental partitioning of food resources by sympatric *Imantodes* may occur but is not demonstrable by these casual records.

I found an adult male and an adult female *lentiferus* in stream-side forest at Raleigh

Cataracts, Surinam, on a night in late February. Both were on a branch 2 m. above-ground, lying together (but not in copulation) in long loose coils, with their heads at opposite ends of the common coil. The female (fig. 16B) contained two large eggs (32×9 mm.), and I have seen a few other museum specimens that also contained two eggs each. Duellman (*loc. cit.*) reported an Ecuadorian individual laying three eggs in mid-August, with two of them hatching in late November. The hatchlings slit their eggs during daylight hours but did not completely emerge until dusk. The known clutch size of 2–3 eggs is thus similar to that of *I. cenchoa* (1–3).

REMARKS: Throughout its range, *Imantodes lentiferus* occurs sympatrically with *I. cenchoa*. It may be reliably differentiated by its reduced number (15-15-15) of dorsal scale rows (17 in *cenchoa*). Without having looked into the variation of Amazonian *cenchoa*, I cannot make detailed comparisons between these similar-appearing species. However, based on hemipenial and dentitional data from Panamanian *Imantodes*, the South American *lentiferus* is more closely related to the dissimilarly patterned *inornatus* and *phantasma*, as discussed in the following section.

Cope (1894, p. 614) mentioned specimens from two localities in his original description of *Himantodes lentiferus*, namely (1) "Pebas, Ecuador" [=Pebas, Dept. Loreto, Peru], from J. Hauxwell, and (2) "E. Equador" [*sic*], from J. Orton. Malnate (1971, p. 368) could find only one of the original syntypes and noted that "which locality is represented by ANSP 11459 is not certain." Malnate inadvertently listed this specimen as "holotype" rather than syntype. It seems best that ANSP 11459 hereby be formally designated as lectotype of the species *Imantodes lentiferus* (Cope); it is a male with 15-15-15 scale rows and an undivided anal plate.

The name *Himantodes fulviventer* Poepig *ex* Obst (= *lentiferus*) is to be credited to Poepig only in concept. It is a *nomen nudum* as recognized by Obst (1977a, 1977b), but Obst himself must bear the responsibility for its publication. Since *Himantodes fulviventer* Obst was not validly published (see synon-

¹⁷ Heinrich Feyer was a commercial collector who started collecting in Ecuador in 1906. He evidently resided for a time in Riobamba, which he falsely claimed as the locality for many biological specimens. This sort of thing has happened before, and the damage caused by Feyer was probably without malice aforethought, although he is said to have disliked collecting for Americans. He returned to Germany in 1939 (*vide* Brown, 1941, p. 811).

ymy), it stands outside of formal nomenclature. Such names nonetheless must be ex-

plained, and little or nothing is gained by introducing them into the literature.

RELATIONSHIPS AMONG THE SPECIES OF *IMANTODES*

Data accumulated for this paper warrant a preliminary phylogenetic analysis of the six species of *Imantodes*. I intend mainly to present an initial hypothesis of relationships that can be tested by additional anatomical and osteological evidence, and secondarily to speculate on a few historical events that seem suggested by the data or by the hypothesis. The species are evenly divisible into two seemingly natural groups.

THE *CENCHOA* GROUP

The species *I. cenchoa*, *I. gemmistratus*, and *I. tenuissimus* are placed together, although the group at this time must be defined primarily on Panamanian populations of the first two species. At least in Panama, *cenchoa* and *gemmistratus* have small hemipenes relative to body size; their hemipenes when everted extend only to subcaudals 4–5 and those of *cenchoa* are also rather slender. Although *I. cenchoa* is perhaps the largest species in the genus, even large males of over 1 m. total length have hemipenes that seem relatively small compared with most colubrids, and for this reason I consider small hemipenial size a synapomorphy uniting at least *cenchoa* and *gemmistratus*. Another probably synapomorphic condition of the hemipenis of these two species involves the degradation of capitation on the asulcate side of the organ. The usual free overhang of the uncapitate type of xenodontine hemipenis is evident to either side of the sulcus spermaticus, but the overhang becomes weak and then absent on the opposite side of the everted organ. The asulcate tip of the organ is spinose without a pronounced overhang or emargination (fig. 19A, 19B). In both slenderness and in relative degradation of capitation (including degree of asulcate spinosity), the everted hemipenes of some 20

cenchoa appear more apomorphic than the single organ examined from *gemmistratus*.¹⁸

The *cenchoa* group also seems definable by a relatively low number of maxillary teeth and by the degree of grooving on the rear fangs. The ranges and means of prediastemal maxillary teeth are as follows for Panamanian samples drawn from diverse populations (one maxilla from each specimen):

I. cenchoa ($N = 25$): 11–14, $\bar{X} = 12.4$

I. gemmistratus ($N = 16$): 10–12, $\bar{X} = 10.8$

The enlarged fangs on the rear of the maxilla are deeply grooved. The Yucatan species *I. tenuissimus* seems to have comparable dentition, based on examination of one specimen (AMNH 100675); although the head is badly damaged, there seem to have been about 12+2 teeth on the right maxilla, and a fang remaining on the left side is deeply grooved. I am inclined to consider the relatively low number of prediastemal teeth (and possibly the deep grooving of the fangs) to be a synapomorphic feature of the *cenchoa* group, but, unless the number of teeth can be shown to be correlated with reduced head size or some common specialization of jaw structure, it is difficult to place much confidence in this polarity judgment. Possibly there is

¹⁸ Intraspecific geographic variation in such characters is conceivable, which should be kept in mind by anyone who might become engaged in detailed variational studies of *cenchoa*, *gemmistratus*, or any other wide-ranging snake. Because the type specimens of the new *I. phantasma* have their hemipenes everted, and for convenience, I have utilized only everted organs in the present paper. However, except for determination of shape and occasional topographic changes associated with eversion, many hemipenial characters, including geographic variation in length, can be most thoroughly studied by dissection of retracted organs, as demonstrated elsewhere (Myers, 1974, pp. 30–33, 74–75).

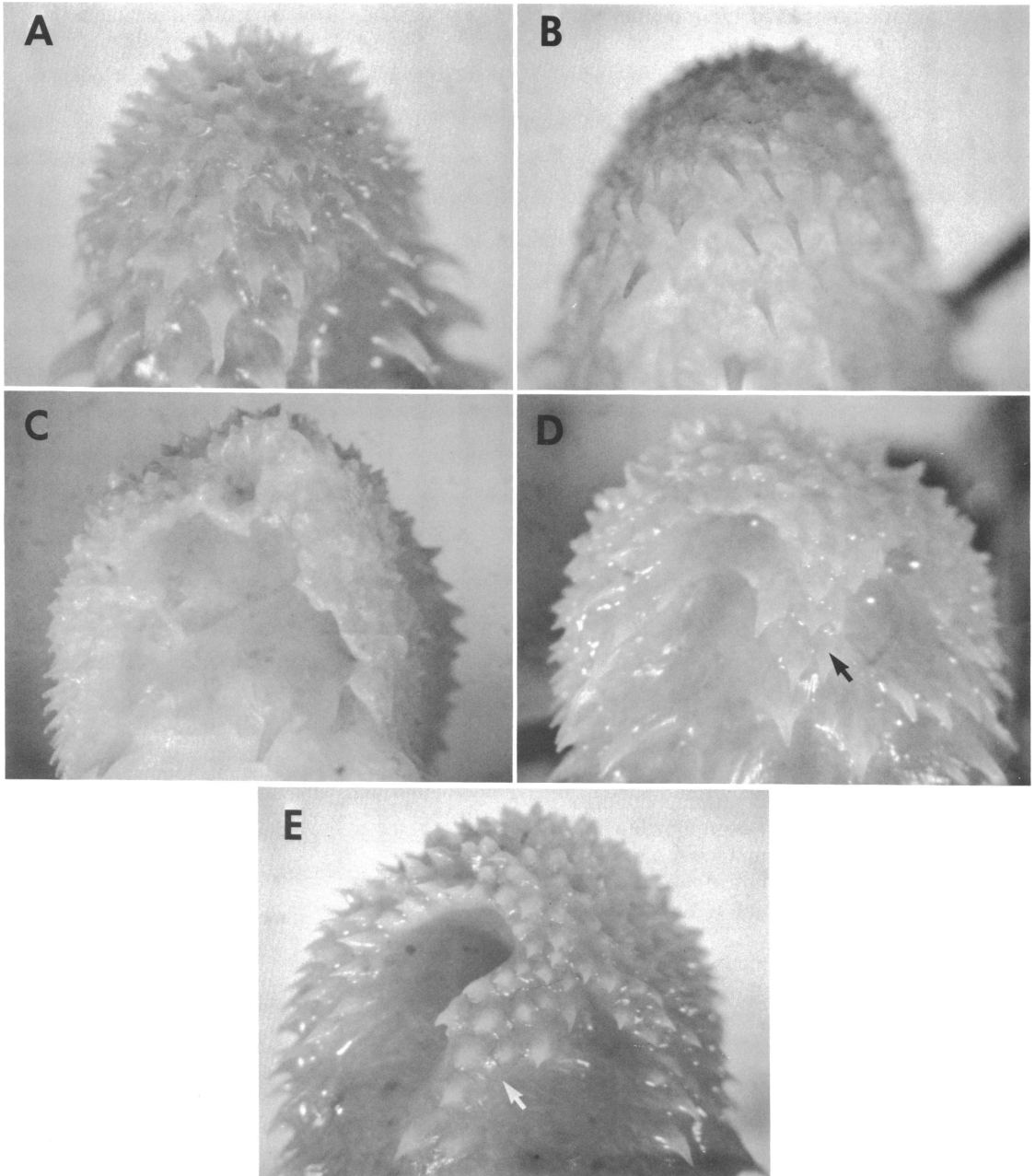


FIG. 19. *Imantodes* hemipenes. Asulcate side of apices (not to scale), as follows: A. *I. cenchoa* (KU 110137, right organ). B. *I. gemmistratus* (AMNH 109502, left). C. *I. inornatus* (KU 110213, left). D. *I. lentiferus* (KU 148331, right). E. *I. phantasma* (AMNH 109493, left). Notice the uniform spinosity and lack of capitulation (on the asulcate side only) of organs in A and B, the well-developed overhang of the capitulum in C, and the spinose cluster (arrows) that interrupts the overhang in D and E.

geographic variation in the number of teeth in the widely distributed *cenchoa* and *gemmistratus*, which would add a further caution against concluding too much on the basis of partial data.

By the above caution, I mean only that geographic or other variation *might* obscure interpretation of a hastily chosen character, or negate its use as a synapomorphy. For example, one character which I exclude from analysis because of such variation is shape of the vertebral scales. *Imantodes cenchoa* and two members of the *lentiferus* group are conspicuously alike in having these scales enlarged and the posterior margins broadly truncate or even concave. *Imantodes tenuissimus* and some populations of *I. gemmistratus* have unenlarged or slightly enlarged scales of essentially normal shape. But there is geographic variation in the latter species, with specimens in lower Central America having somewhat larger scales, some with truncate or concave ends (Yingling, MS; personal observation). *Imantodes inornatus* (*lentiferus* group) has slightly enlarged vertebral scales with pointed to rounded ends, but some specimens have a few scales that are truncate or concave. Conspicuously enlarged, posteriorly blunt vertebral scales have functional significance (see Remarks at end of *I. cenchoa* account), and their potential may be a generic characteristic, but the phenotypic expression of this potential seems presently unreliable for assessing relationships among the individual species.

The three species assigned to the *cenchoa* group are vividly blotched or banded, probably a reflection of symplesiomorphy. *I. tenuissimus* is placed in the group solely on the basis of its dentition, since I have not examined the hemipenis. Pending closer comparison of this species with *cenchoa* and *gemmistratus*, the intragroup relationships must be shown as an unresolved trichotomy (fig. 20).

THE LENTIFERUS GROUP

The species *I. inornatus*, *I. lentiferus*, and *I. phantasma*, although highly diverse, seem

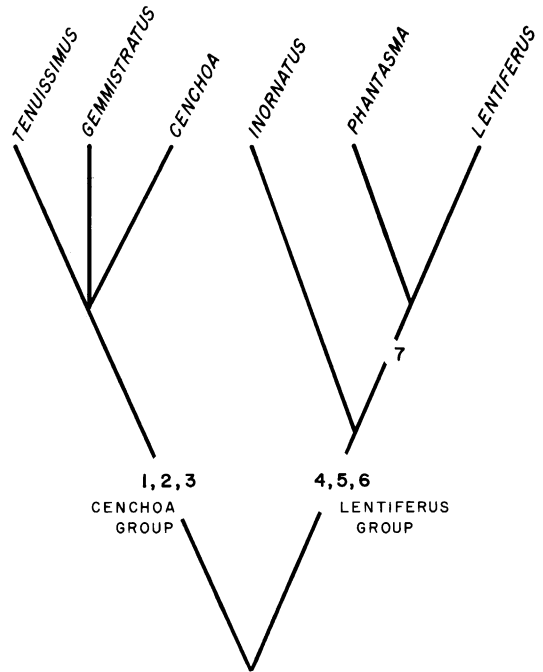


FIG. 20. Theory of relationships among the species of *Imantodes*. Numbers refer to synapomorphies discussed in text, as follows: 1. Hemipenes reduced in size. 2. Loss or reduction of capitation on asulcate side of hemipenis. 3. Reduced number of maxillary teeth. 4. Shallower grooves on maxillary fangs (polarity uncertain). 5. Fork of tongue relatively longer. 6. Reduction of blotch pigmentation, leading to autapomorphic loss or de-emphasis of primitive blotched pattern. 7. Slightly oblique, elongated cluster of small spines interrupting overhang of hemipenial capitulum on asulcate side.

to represent the plesiomorphic sister group of the *cenchoa* group, at least on the basis of hemipenial morphology and perhaps dentition. Their hemipenes when everted extend to subcaudals 6–8 (vs. 4–5 in *cenchoa* group) and subjectively seem to be of “normal” size compared with colubrids generally. Capitulation remains well developed on the asulcate side of the organ compared with the apomorphic condition in the *cenchoa* group (fig. 19). The free overhanging edge of the capitulum in *I. inornatus* (fig. 19C) represents

probably the most common condition among xenodontine colubrids having unicapitate hemipenes (e.g., compare fig. in Myers, 1974, p. 31), and for that reason it is regarded as most plesiomorphic in *Imantodes*. Panamanian specimens of *inornatus* show no significant variation in the region of the asulcate edge of the capitulum.

In contrast to the condition in *I. inornatus*, the asulcate edge of the capitulum is variously scalloped or emarginated in *I. lentiferus* (figs. 18B, 18D, 19D) and *I. phantasma* (figs. 4E, 19E). Despite minor variation in this part of the hemipenis, *lentiferus* and *phantasma* share an unusual tendency for the overhanging edge of the capitulum to be proximally connected by a slightly oblique, elongated cluster of small spines. The hemipenes are asymmetrical in that this little cluster of spines extends to the capitulum in a slightly dextral direction (when the hemipenes are appressed posteriad with the sulci spermatici against the tail), on both the right and left organs. The structure is best seen by comparing figures 19D (*lentiferus*) and 19E (*phantasma*); it is equally present but not so obvious in the photographs of two additional *lentiferus* organs in figure 18. I regard this structure as a synapomorphy indicating the monophyly of *lentiferus* and *phantasma* (fig. 20).

Species of the *lentiferus* group have more prediastemal maxillary teeth than those in the *cenchoa* group (compare above):

I. inornatus ($N = 16$): 17–21, $\bar{X} = 19.4$

I. lentiferus ($N = 26$): 17–22, $\bar{X} = 19.0$

I. phantasma ($N = 2$): 19, 19, $\bar{X} = 19.0$

In addition to similar numbers of prediastemal teeth, the rear maxillary fangs of these species bear only shallow, basal grooves, which are so weak in some specimens as to be easily overlooked, in marked contrast to the deeper and longer channels characterizing the fangs of species in the *cenchoa* group. The higher number of teeth in the *lentiferus* group is perhaps a reflection of symplesiomorphy. A conclusion of symplesiomorphy might apply also to the weak grooves, which would seem less “improved” and less efficient than the deeper grooves in the *cenchoa* group.

However, the weak grooves might also suggest adaptation to different prey (e.g., frogs vs. lizards) for which the venom apparatus is less useful,¹⁹ in which case there might be no reasonable way to determine the polarity of a weak-groove vs. strong-groove morphocline.

The species of the *lentiferus* group seem to have the fork of the tongue relatively longer than in the *cenchoa* group, although this perception is based on incomplete data that are complicated by the presence of sexual dimorphism (see section on Comparative Tongue Length in *Imantodes*).

Conspicuous autapomorphies are more common within the *lentiferus* group than in the *cenchoa* group, which is suggestive (but scarcely proof) of greater age of species in the former assemblage. The restricted, possibly relictual distribution of *Imantodes phantasma* would fit in with that idea; this distinctive species seems to be unique in its quivering tongue behavior and certainly unique in its pattern of dark-speckled dorsal blotches that are relatively pale compared with the ground color. *Imantodes lentiferus*, the allopatric sister species of *phantasma*, has an autapomorphic number of dorsal scale rows, but *lentiferus* has retained a plesiomorphic color pattern that causes it to resemble *I. cenchoa*. Even so, *lentiferus* tends to have dark blotches that are relatively lighter than in *cenchoa* (compare figs. 16A with 16B, and 9 with 17), and I suggest that reduction in blotch pigmentation is a synapomorphy that has been expressed to different degrees in the species of the *lentiferus* group, resulting in the development of autapomorphic pat-

¹⁹ This notion is suggested to me by observations on *Rhadinaea flavilata*, which possesses enlarged albeit ungrooved rear fangs; captives employed venom-injecting behavior (leading to prey immobility) on lizards but not on small frogs. Comparative observations on feeding behavior of *Imantodes* and other frog and lizard-eating snakes might be of interest. A species of *Imantodes* could conceivably come to specialize on either lizards or frogs, with appropriate tuning of the venom apparatus, but without entirely relinquishing the other food item; see brief comments under Natural History in *I. lentiferus* account.

terns in *phantasma* (*vide supra*) and *inornatus* (*vide infra*). The Guayanan population of *lentiferus*, with markings less sharply demarcated owing to loss of the black borders, represents still another expression of this intragroup trend toward de-emphasis or loss of the primitive blotched pattern. *Imantodes inornatus* has the most apomorphic pattern of any *Imantodes*, since it is the only species completely lacking dorsal blotches or saddles. However, I believe that the vague, alternating dorsal and lateral markings of *inornatus* (fig. 13) represent the remnants of dark blotching in the primitive pattern.

NOTES ON BIOGEOGRAPHY

The distinctive and geographically restricted *I. phantasma* of eastern Panama might be a relictual species of now reduced range, but the possibility of speciation *in situ* cannot be discounted. In either case, its habitation—the Serranía de Pirre—probably has existed at least since the Miocene; orographic rain or cloud formation may have maintained a wet-forest refuge atop this *serranía* throughout the arid periods of the Pleistocene. *Imantodes inornatus* presumably speciated in either the northern or southern part of its present range in lower Central America and northwestern South America, a complex region of high endemism. The cis-Andean *I. lentiferus* is geographically well separated from its phylogenetically closest relatives. There is indication that *lentiferus* is somewhat of an “edge” (secondary forest) species in at least part of its range, which might have enabled it to maintain a widespread Amazonian distribution in gallery forest during Pleistocene climatic oscillations, with minor differentiation occurring in a proper forest refuge in eastern Guayana.

Based on present distributions, the species of the *cenchoa* group may have originated from an ancestor that was isolated to the north of the *lentiferus* group. Granted that sympatry of sister groups is evidence of dispersal (assuming allopatric speciation), the evident dispersal of *Imantodes cenchoa* stands out as a remarkable event. This species, which has one of the largest distri-

butions of New World snakes, ranges from Mexico to Argentina and it is broadly sympatric with all its congeners; the distribution of *I. cenchoa* encompasses the *entire range* of the *lentiferus* group, and it occurs microsympatrically with at least two of the three species of that group (*inornatus* and *lentiferus*). Superficially, at least, geographic variation is not pronounced in *cenchoa* (but see fn. 5); there is no present evidence that it has differentiated in the regions that serve as areas of endemism for species of the *lentiferus* group (and many other taxa). For that reason, I am inclined to suppose that the overall dispersal of *I. cenchoa* has been relatively recent—i.e., subsequent to species formation in the *lentiferus* group but perhaps congruent with the Quaternary spread of lowland rain forest (Flenley, 1979). Alternatively, *I. cenchoa* might represent a relatively old species that dispersed following the establishment of two lineages within *Imantodes*—in which case it either (1) has remarkable genetic cohesion and failed to differentiate in the areas of ongoing speciation of the *lentiferus* group, or (2) differentiation occurred but has yet to be detected. At least the last possibility could be answered by a detailed variational study of *I. cenchoa*, and it would be a worthy challenge to see if other aspects of its biology and history could be deduced from such a study.

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APPENDIX: MUSEUM ABBREVIATIONS AND SPECIMENS EXAMINED

ABBREVIATIONS: The following abbreviations of institutions are used in the text or in the lists of specimens examined:

- AMNH, American Museum of Natural History, New York
 ANSP, Academy of Natural Sciences of Philadelphia
 BMNH, British Museum (Natural History), London
 GML, Gorgas Memorial Laboratory, Panama
 KU, Museum of Natural History, University of Kansas, Lawrence
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
 MLS, Museo del Instituto de La Salle, Bogotá
 MNHN, Muséum National d'Histoire Naturelle, Paris
 UF, Florida State Museum, University of Florida, Gainesville
 UMMZ, University of Michigan Museum of Zoology, Ann Arbor
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SPECIMENS EXAMINED: Only Panamanian specimens are listed under the first four species below (although other specimens may be cited in the text)—for confirmation of the localities plotted in maps 1 and 2, and for documentation of the species descriptions, which are based on Panamanian samples. The majority of this material is from the Panamanian collections assembled by William E. Duellman and myself, and the lists do *not* represent a survey of available museum material from Panama.

The description of the South American *Imantodes lentiferus* is based on material from throughout its range, and all specimens which I had occasion to examine are listed.

Imantodes cenchoa

Bocas del Toro: 1 mi. W Almirante, 10 m., KU 110131; about 4.8 km. W Almirante, 40 m., KU 110132; Isla Bastimentos, 10 m., AMNH 108475; Isla de Colón, La Gruta, 30–80 m., KU 110133, 110134; Península Valiente, Bluefields, 10 m., KU 110135; mouth of Río Cahuita, 1 m., KU 110136; Río Claro near junction with Río Changena, 910 m., KU 110137; Río Changena, 830 m., KU 110138–110141; Río Changuinola near Quebrada El Guabo, 150–200 m. [16 km. airline W Almirante], AMNH 119078. *Canal Zone of Panama:* Ancon, MCZ 16394; Barro Colorado Island, AMNH 57780, 68849, 90021, KU 75701–75703, MCZ 34880; Curundú, KU 80261; Frijoles, MCZ 23939; Ft. Sherman, MCZ 26762, 26763; near Gamboa, AMNH 75543. *Chiriquí:* Boquete, ANSP 22421, UMMZ 57927–57929; 13 km. WNW David, Río Platanal, 110 m., KU 110143; region of Fortuna Dam site, about 1000 m., upper Río Chiriquí, GML uncat.; Puerto Armuelles, ANSP 21619; 10 km. NW El Volcán, 1170 m., KU 110142. *Coclé:* El Valle, AMNH 76010; El Valle, Río Antón, 650 m., AMNH 108694. *Darién:* Cana, MCZ 42757; Cerro Quia, 740 m., KU 110162, 110163; northeast slope Cerro Sapo, La Jarcia, 540–560 m., KU 110174; northeast slope Cerro Sapo, 820 m. and 900 m., KU 110175, 110176; Laguna, 540 m. [pond on ridge betw. Río Pucuro and Río Tapalisa], KU 75696–75699; Río

Chucunaque, about 7 km. above Río Mortí, 150 m., KU 110165; Río Chucunaque, about 10 km. below Río Subcutí, 120 m., KU 110164; Río Subcutí, AMNH 36199; Río Jaqué, 1.5 km. above Río Imamadó, 50 m., KU 110171, 110172; ridge between Río Jaqué and Río Imamadó, 730 m., KU 110173; fork Pihuila-Tucutí branch of Río Tuirá, MCZ 37074–37076; Río Tuirá at Río Mono, 130 m., KU 110155–110161; Río Ucurganti, about 7 km. above mouth (trib. Río Chucunaque), 30 m., KU 110166–110170; Tacarcuna [deserted village site on Río Tacarcuna, upper Pucuro drainage], 550 m., KU 75700; South base Cerro Tacarcuna, Río Pucuro, 640 m., AMNH 119379–119381. *Los Santos*: north slopes Cerro Cambutal, 480 m., KU 110144, 110145; east slopes Cerro Hoya, 940 m., KU 110146–110149, 110151, 110152. *Panamá*: Altos de Maje [now an island in Bayano Lake], AMNH 109646; Cerro Azul region, AMNH 119558; Cerro Campana, 800 m., AMNH 106675–106677; south slope Cerro Campana, 850–950 m., KU 75704, 110153, 110154; east slope Cerro Jefe, 650 m., KU 80593; El Llano-Cartí road, km. 12.8, 290 m., AMNH 110564, 110565; Piedras ridge near Pacora, MCZ 42765; Río Chagres, MCZ 34375; Río Silugandí, UMMZ 124141. *Pearl Islands*: San Miguel Island (Isla del Rey), MCZ 9948. *San Blas*: Camp Sardí, 12 m., KU 110177–110188; Camp Summit, 300–400 m., KU 110189–110193.

Imantodes gemmistratus

Canal Zone of Panama: near Ancon, MCZ 16398, 16399; Corozal, MCZ 23936–23938; Cundurú, KU 80258–80260, 110199, 110200; France Field, MCZ 37888; Gamboa, KU 110202, MCZ 23940, 23941; Madden Forest Preserve, UF 28261; Miraflores, MCZ 23942, 23943; Paraiso, KU 110201, MCZ 23944; Pedro Miguel, MCZ 23945; Rodman, KU 110198; Summit, MCZ 23946. *Chiriquí*: 3 km. SE San Lorenzo, 30 m., KU 110194. *Coclé*: Aguadulce, AMNH 67065. *Darién*: Jaqué, ANSP 25085. *Herrera*: Río Santa María, Potuga, MCZ 34371–34374; Río Santa María, Quebrada Las Minas and Quebrada Grande, MCZ 37133. *Panamá*: Estrella Azul Lechería, KU 110197; La Joya, ANSP 25085; Nueva Gorgona, AMNH 90020; 9 km. NE Pacora, 30 m., KU 110195; Panama City, KU 110196, MCZ 31547, 32455, 32456, 37125, 37875, 37876; Río Chagres, MCZ 31534; Río Chagres, Alajuela, MCZ 32454; Sabanas-Pacora area, MCZ 39762, 42819, 42820, 45338. *No specific locality* (“Panama”): AMNH 109501, 109502, USNM 14121 (holotype of *Lep-tonathus straitissima*).

Imantodes inornatus

Bocas del Toro: Río Changena, 830 m., KU 110203; Río Claro near junction with Río Changena, 910 m., KU 110204–110212. *Chiriquí*: Puerto Armuelles, AMNH 75546, ANSP 24254 (6 heads). *Colón*: Achioté, 40 m., KU 75705, 75706. *Darién*: El Real, 20 m., KU 110215; Río Tuirá at Río Mono, 130 m., KU 110214. *San Blas*: Camp Summit, 300–400 m., KU 110213.

Imantodes phantasma

Darién: Southeastern slope Cerro Cituro, 1030 m., on northern end Serranía de Pirre, KU 110217 (holotype); south ridge Cerro Cituro, 1100 m., AMNH 109493 (paratype).

Imantodes lentiferus

BOLIVIA: *Cochabamba*: No specific locality, AMNH 6781. **BRAZIL**: *Amazonas*: Igarapé Belém, near Rio Solimoes, about 70 km. E Leticia, AMNH 115018. **ECUADOR**: No specific locality (“Riobamba” in error, see fn. 17), AMNH 23249, 23279, 23298, 28849, 35906, MCZ 29292. *Napo*: Bermejo No. 4, 15 km. ENE Umbaqui, 740 m. (00°11'N, 77°22'W), KU 121898; Santa Cecilia, 340 m., KU 148331. *Morona-Santiago*: “Macas region” (Feyer), AMNH 28833, 35809. *Pastaza*: Río Capaquaria [=Capahuari?], tributary of Río Pastaza, AMNH 49112; Santa Rosa, Río Tigre, AMNH 49173. **FRENCH GUIANA**: Trois Sauts (upper Oyapock River), MNHN 1978.2522. **PERU**: *Amazonas*: Alto Marañón [probably between ríos Cenepa and Santiago; catalogued date “Sept. 1927” probably in error for Sept. 1924], AMNH 55834; mouth Río Santiago, [177 m.], AMNH 52128. *Loreto*: Cashiboya [on Río Ucayali between Contamana and Río Pisqui], AMNH 52270; Iquitos, AMNH 52263, 53060, 53217; near Iquitos, Isla Lupuna, AMNH 56091; near Iquitos, Río Itaya, AMNH 54039, 54986; Pampa Hermosa on lower Río Cushabatay, near Río Ucayali, AMNH 55836; Pebas (or eastern Ecuador?), ANSP 11459 (lectotype of *Himantodes lentiferus*); Peru-Brazil frontier, [headwaters of] Río Tapiche [or] Río Utoquinia [at about 7°30'S, 74°W, in Río Ucayali drainage], AMNH 52067; Santa Teresa, lower Río Tigre, AMNH 53183. *San Martín*: [Río] Cainarchi, 1200 ft., tributary of Río Huallaga, AMNH 52717; [Río] Chipurana, tributary of Río Huallaga, AMNH 52219. **SURINAM**: *Saramacca*: Bakhuis Mountains, transect V, RMNH 13586; Raleigh Cataracts, Coppename River, 50 m., AMNH 108796, 108797.

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