The *Imantodes* (Serpentes: Colubridae) of Costa Rica: two or three species?

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Abstract. *Imantodes inornatus* and *Imantodes cenchoa* are currently recognized as occurring in Costa Rica. It has been suggested recently that *I. cenchoa* is actually a composite of two species, *I. cenchoa* and *I. gemmistratus*. Analysis of data on scalation and coloration for Costa Rican samples confirms that this complex is comprised of two species. One of these is clearly the wide-ranging *I. cenchoa*, which in Costa Rica occurs in the southwest Pacific Lowlands, Meseta Central, Atlantic lowlands and cordillieran slopes and just on to the Pacific slope in the northern mountains. It does not range into the northwestern (Pacific) lowlands. A second species occurs on the northwestern Pacific lowlands and in sympatry with *cenchoa* on the Meseta Central and at scattered localities in the Atlantic and southwest Pacific lowlands. The second form is allopatric to Panamanian *gemmistratus* and consistently differs from the latter in scalation. A review of other Central American and Mexican samples referred to *I. gemmistratus* (type locality: El Salvador: Sonsonate: near Volcan de Izalco) indicates that Costa Rican examples are conspecific with it. The species appears to be comprised of three allopatric subpopulations along the Pacific versant: El Salvador-Honduras; Nicaragua-Costa Rica; and Panamá. A fourth more or less allopatric subpopulation occurs on the Atlantic versant of Costa Rica as well.

The systematic status of allopatric eastern México and Yucatán Peninsula populations referred by recent authors to *gemmistratus* is problematic. Other allopatric Isthmus of Tehuantepec and western México populations seem more likely candidates to be conspecific with *gemmistratus*, but the issue cannot be resolved on the basis of available data. Attention is called to a unique unicolor variant of *gemmistratus* from Pacific versant Costa Rica. *Imantodes inornatus* and *cenchoa* are restricted to evergreen forest habitats, while *gemmistratus* is most abundant in deciduous forests along the west coast of Central America and Mexico. The latter species is sometimes found at evergreen forest sites on the Atlantic versants of Costa Rica and Central Panama. *I. cenchoa* and *gemmistratus* are known to be sympatric at several sites in Costa Rica but not *I. inornatus* and the latter species. *I. cenchoa* and *inornatus* are often taken together.

The blunt-headed vine snakes, genus *Imantodes*, form a conspicuous component of the lowland and premontane forest of Costa Rica. Some twenty years ago we noted unexpected variation in characteristics of scalation and coloration utilized elsewhere for distinguishing among nominal species and a consistent geographic variation in coloration that together raised questions regarding the status of vine snake populations in the Republic. With the accumulation of additional materials, we concluded that the observed variation could best be interpreted by the recognition of two species for Costa Rica. (Scott, 1969; 1983; Savage, 1973; 1980).

One of these, *Imantodes inornatus*, is a yellowish to light brown snake with a pattern of small dark spots and speckles, that often form very narrow obscure crosslines. Segmental counts for this form are low: ventrals 199-218 in males, 196-212 in females; subcaudals 110-132; ventrals plus caudals 316-334. All other examples from Costa Rica were regarded as representing the species *Imantodes cenchoa*, which usually has a series of 31–73 dark brown saddles on the body, more than 223 ventrals and ventrals plus caudals more than 350.

Within the series referred to the latter from, samples from northwest to west-central Costa Rica are markedly paler in dorsal ground and blotch colors than those from the Atlantic versant or southwestern Pacific Costa Rica. This color difference appears to be correlated with relatively narrow vertebral scales and high body

blotch counts, features attributed to *Imantodes gemmistratus* (Taylor, 1951; 1954; Peters and Orejas-Miranda, 1970). However the segmental counts for these snakes are much higher than found in putative upper Central America or Panama *gemmistratus*. Our samples suggested a north-south cline in Pacific Costa Rica grading into the much higher count populations of southwestern Costa Rica and adjacent Panama, that appeared to represent typical *cenchoa*. For these reasons and the fact that the vertebral scale rows showed considerably greater variation in width than had been previously reported, we regarded all Costa Rican material as representing a single form, *I. cenchoa*. This view is reflected in previous publications (Savage, 1973; 1976; 1980) and more fully explained by Scott (1983).

Recently, C.W. Myers (1982) in a masterful review of the genus in Panama, has questioned our conclusions, since *Imantodes cenchoa* and *gemmistratus* seem to be valid and distinctive in Panama and South America where they occur in sympatry. Myers also refers to a number of individuals from widely scattered localities in Costa Rica, that he regarded as representing the latter form, although he did not undertake a detailed revision of non-Panamanian material. Since Myers' work provides a comparative baseline of data for the two nominal species and a conflicting hypothesis on the systematic status of the *Imantodes* placed in *cenchoa* by us, and because extensive additional material from Costa Rica has been collected since our previous study, we have undertaken a review of the problem. Essentially the present paper addresses the following question: do one or two species of *Imantodes* in addition to *I. inornatus* occur in Costa Rica?

ANALYSIS OF CHARACTERS

Previous workers on the genus (Smith, 1942; Zweifel, 1959; Myers, 1982; and Yingling, 1972) have emphasized a small suite of variable characteristics to discriminate among nominal forms. These include: the relative size of the enlarged vertebral scales; segmental counts; and coloration, particularly the number of body blotches or saddles and how many of these are broken off laterally to form discrete dark spots. Myers (1982) also utilized differences in size and proportions, maxillary teeth and hemipenes to separate Panamanian *cenchoa* from *gemmistratus*.

According to Myers' data (1982), the latter two forms may be distinguished as follows: in Panama. In this report variation is either indicated by the range or a notation such as 23-29.4-39, where the first number is the minimum, the second the mean and the third the maximum for a particular sample:

cenchoa

1. Scales in vertebral row conspicuously enlarged, usually 3-4 times wider than lateral scales.
2. Ventrals in males 244-288, in females 228-268.
3. Subcaudals 147-195.
4. Ventrals plus subcaudals 405-446.
5. Body blotches 29-56.
6. Maxillary teeth 11-12.4-14 + 2.
7. Total length to 1211 mm in males, 1480 in females.
8. Tail length 26-34% of total length.
9. Hemipenes slightly clavate and slender; calyculate capitulum 32-45% of sulcate side; asulcate side thickly spinose below apex.

gemmistratus

1. Scales in vertebral row slightly enlarged, usually 1.5-2.0 times wider than lateral scales.
2. Ventrals in males 227-235, in females 221-228.
3. Subcaudals 113-130.
4. Ventrals plus subcaudals 341-361.
5. Body blotches 55-74.
6. Maxillary teeth 10-10.8-12 + 2.
7. Total lenghth to 693 mm in males 786 mm in females.
8. Tail lenght 24-28% of total length.

9. Hemipenes short and stubby; calyculate capitulum 50% of sulcate side; asulcate side sparsely spinose to tip.

The following analysis deals primarily with characters 1–5. While characters 6–9 may be helpful in allocating particular individuals to one or another nominal form, the limited number of mature males restricts the use of feature 9 and the variation in the others precludes their use as major criteria in recognizing populations. Although the present study is aimed primrily at determining the status of snakes referrable to the *cenchoa* - *gemmistratus* complex, appropriate comments on variation in *inornatus* are includes.

Vertebral scales: The vertebral scale row is slightly to greatly widened as compared to the lateral scales in *Imantodes*. Smith (1942) recognized three categories of vertebral enlargement for the genus: a) not or very slightly wider than lateral scales: b) about twice as wide as lateral scales and; c) three to four times as wide as laterals, and partially on that basis recognized six Mexican species in the genus. Peters (1954) showed that the variation in vertebral scale width between Smith's categories *a* and *b* was bridged in this material from western Mexico and concluded that the nominal species *splendida* was conspecific with Central American *gemmistratus*. Zweifel (1959) reduced the number further by placing all named populations (except *cenchoa* and *tenuissimus* of the Yucatan Peninsula) in *gemmistratus* by showing intergradation in segmental counts and coloration among them.

Myers (1982) utilized this feature to distinguish Panama *cenchoa* (3-4 times as wide as laterals) from *gemmistratus* (usually about 1.5–2 times as wide), although he observed that there was much greater variability in the feature than previously realized.

The width of the vertebrals in our samples varies 1.2-5 times the width of the mid-lateral scales near mid-body. In *Imantodes inornatus*, the vertebral scale rows are consistently 1.5-2 times wider than the mid-lateral scales. The size of these scales shows a strong correlation with geography and the characteristics of segmental and body blotch counts. Materials from northwestern Costa Rica have consistently narrow vertebral scales (1.2-2.5 the width of the lateral scales) while most of those from the southwest Pacific area and most Atlantic specimens have the vertebral scale rows greatly expanded (3-5 times the width of the lateral scales). In the upland Meseta Central and at scattered Atlantic versant localities, both narrow and expended vertebral scale rows were found in individuals that approach one another in other characters.

It was partially for this reason that we concluded earlier (Scott, 1969; 1983; Savage, 1973; 1980) that only *cenchoa* occurred in Costa Rica, that this feature was unreliable in attempting to separate populations within the genus, and that *gemmistratus* should be excluded from any listing of the Costa Rican snake fauna.

Segmental counts: In common with most snakes, *Imantodes* exhibits sexual dimorphism in the segmental scale counts. Unlike most other sexually dimorphic snakes, the males of *Imantodes* average a higher number of ventrals (V) than are found in females, rather than the converse. As in other sexually dimorphic genera, the males average a higher number of subcaudals (SC) than are found in females. In *Imantodes inornatus*, males average about 7 more ventrals than females and 8 more subcaudals. In definitive *Imantodes cenchoa* from Panama (Myers, 1982) males average 10-13 more ventrals than females in six geographic subsamples and 7-22 more subcaudals. Differences similar to those found in the latter are also characteristic of individuals referred to *Imantodes gemmistratus* by Myers and for our Costa Rican samples.

The range of variation in segmental counts, which appears to provide the most useful distinguishing character for separating the nominal forms in Panama, shows considerable overlap in the two sexes. This is especially the case for the subcaudal counts in two species (158-195 in males and 147-177 in female *cenchoa;* 116-132 in male and 110-122 in female *inornatus*). In the relatively small sample (N = 19) of *gemmistratus* from Panama discussed by Myers, the subcaudal ranges of the two sexes barely overlap (males 124-130, females 113-124). For this reason the range of subcaudal counts, without regard to sex, may be used to distinguish *cenchoa* from *inornatus* and *gemmistratus* (See number 3 above). Similarly the total segmental counts (ventrals plus subcaudals), without regard to sex, provide a complete separation of the three nominal forms in Panama

with ranges of 405-446, 341-361, 316-334, for *cenchoa, gemmistratus* and *inornatus*, respectively.

As an initial attempt to acertain if more than one form of the *cenchoa-gemmistratus* complex might be represented in available Costa Rican material, we analyzed the data for subcaudal and ventral plus subcaudal counts. Subcaudals vary between 129-183, in examples with complete tails and the total segmental counts from 358-459. These counts strongly suggest that only one of the forms (*cenchoa*) recognized by Myers (1982) as occurring in Panama is included within the Costa Rican sample, since the known variation for Panama *cenchoa* is encompassed by these values.

Unfortunately the clear separation of *cenchoa* from *gemmistratus* on the basis of subcaudal and total segmental counts seen in Pana ma does not hold in Costa Rican material. A number of examples have subcaudal counts intermediate in value in a range between 130-147, and many have total segmental counts between 361-405. This variation and our belief that the vertebral scale character failed to consistently separate samples, led to our earlier conclusion that only a single rather variable species of this stock occurred in Costa Rica.

Coloration: Several features of coloration exhibit variation in the *cenchoa-gemmistratus* complex (the coloration for *I. inornatus* has already been described above). The dorsal ground color in Costa Rican samples is pale tan or beige to medium brown. In many individuals the ground color is heavily suffused with dark brown pigment (Fig. 1A) so that the interspaces between the very dark brown blotches or saddles are darkened and the snake has an overall dark appearance (darkened ground color). In other individuals the tan interspaces (and dark blotches) are much lighter (Fig. 1B) and the entire animal often has a distinct yellowish cast (pale and/or yellowisch ground color). Other examples are somewhat intermediate between these two extremes and have the interspaces medium brown or suffused with medium brown pigment (medium brown ground color).

The is some geographic consistency in ground color, with most examples from southwestern Pacific lowland Costa Rica having the most darkened ground color, followed by specimens from the uplands of northern Costa Rica. The snakes from the Atlantic lowlands have medium brown interspaces or the suffusion of the interspaces by dark pigment produces a medium brown tone. Most individuals from the northwest and Central Pacific lowlands and Meseta Central Occidental are very pale and often have a distinct yellow-gold cast.

The typical coloration of the *cenchoa-gemmistratus* complex almost always includes a series of dark blotches, saddles or bands along the length of the body and tail. Usually the blotches narrow toward the venter and frequently many of the posterior saddles or bands have the lower portion broken off to form a discrete lateral spot on one or both sides. Three general patterns may be recognized as follow (Fig. 1):

A. large chestnut brown blotches or saddles
B. relatively narrow light brown blotches or bands
C. relatively narrow medium brown blotches or bands, with a distinct light spot in the center; on the posterior part of the body the blotches are roughly diamong-shaped and form definite light-centered ocelli.

The blotches or bands are in most cases outlined by dark brown to black. Blotches in individuals having the A pattern are uniformly reddish brown (chestnut) and juveniles with this blotch pattern have blotches that are almost red In a few individuals two or more dorsal blotches are fused into an irregularly shaped sinuous figure that forms a zig-zag stripe along short segments of the body.In other examples a single large blotch may be broken up into two small roundish blotches. Sometimes a series of several botches on the posterior third of the body may be broken up in this manner to orm a continuous row of small spots. In the latter cases the equivalent number of large blotches can be determined by counting the lateral spots, which do not show a comparable fragmentation. Usually, there are two small dorsal blotches for each lateral spot in these examples.

The splitting of blotches in the manner described above affects the total body blotch (BB) counts. For this reason, in the text. reference is sometimes made to the number of blotch positions when comparing individuals. The number of blotch positions is determined by summing the number of blotches that ex-

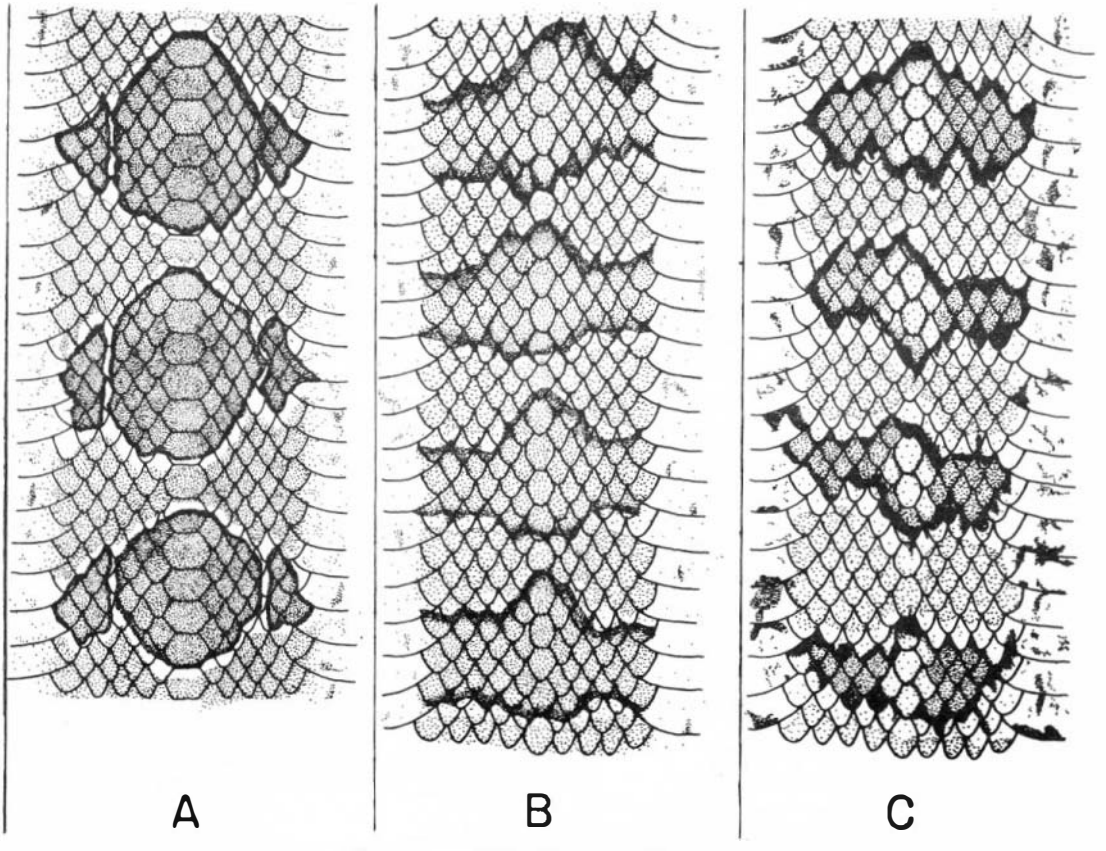


Fig. 1. Patterns of dorsal blotching in *Imantodes*.

tend laterally to or almost to the venter and the number of discrete lateral blotches found on the posterior part of the body. This number compensates for the fragmentation of one to several posterior body blotches into small spots, that raise the body blotch count. For example, one specimen (CRE 3041) has 50 dorsal body blotches, with four posterior ones very small. The number of blotch positions is 48 and the higher number seems to have been produced by the division of two larger blotches to produce four small ones. The use of body blotch positions also compensates for fusions among blotches as well.

The number of dark body blotches appears to show no sexual dimorphism in lower Central America and Myers (1982) recorded only slight overlap between *cenchoa* (29-44. 2-56) and *gemmistratus* (55-74) in Panama. The number of dorsal body blotches for available specimens of the complex from Costa Rica ranges from 31-73, excluding a single unblotched individual (CRE 8261) from La Julieta near Parrita, on the Pacific coast and suggests that both of the forms recognized from Panama also occur in Costa Rica.

A more detailed analysis indicates that the majority of available specimens from Costa Rica have low numbers of body blotches varying from 33-50. Snakes with this range of variation are found along the Atlantic versant, in the southwest Pacific lowlands and in some upland areas. *Imantodes* with higher body blotch counts occur along the northwest Pacific lowlands, on the Meseta Central and at scattered localities on the Atlantic versant and in south-western Costa Rica. This pattern of variation also influenced our earlier decision to regard the high blotch number snakes as representing part of a continium within a single species.

The number of posterior body blotches with the lower portion broken off to form lateral spots (BBB) was shown by Smith (1942) to have some consistent geographic variation. Myers (1982) denmonstrated that this feature

had much greater variability than imagined by Smith as amply reaffirmed by Costa Rican material. In the latter sample the counts for this feature vary between 0-39. Very low counts are typical of the southwest Pacific series (0-3) and high counts (23-39) for northwest Pacific specimens. Intermediate values occur at most other sites.

RE-EVALUATION OF THE PROBLEM

The complex geography, physiography and climate of Costa Rica and our impression that there was a corresponding complexity of variation and relationships among samples of *Imantodes,* led us to center the initial stages of the re-analysis on small to moderate sized geographic areas. Our thinking was that once the smaller subsets of the samples were understood they could be linked into a wider geographic context and compared with forms recognized elsewhere in Central America and Panama. For these reasons the following sections treat *Imantodes* of the *cenchoa-gemmistratus* lineage in Costa Rica according to geographic region as follows: 1). Pacific lowlands (northwestern Costa Rica; southewestern Costa Rica; intermediate sites); 2) Upland areas (slopes of the Cordilleras de Guanacaste and Tilarán; slopes of the Cordillera Central and Meseta Central); and 3) Atlantic lowlands and foothills.

The Pacific Lowlands. The region of northwest Costa Rica from the Nicaraguan border to the area around the mouth of the Río Grande de Tárcoles exhibits a definite wet season (June October) and a long dry one (November-April). Specimens of *Imantodes* from the region seem to form a relatively homogenous sample characterized as follows: 1) vertebral scale rows 1.3-2.5 times as wide as lateral scales; (2) ventrals in males 244-249, in females 238-248; (3) subcaudals in males 138-147, in females 135-154; (4) ventrals plus subcaudals 376-404; (5) body blotches 51-73, of types B and C Fig. 1B, c); (6) broken body blotches 23-39; (7) ground color pale light brown, usually with a distinct yellowish cast.

In terms of these features the northwestern examples resemble Panama *gemmistratus* in the relatively unenlarged vertebral scales and body blotch counts (55-74 in Panama specimens). There is no overlap between Panama *gemmistratus* and these snakes in ventral, subcaudal or ventral plus subcaudal counts. The northwest Costa Rican specimens do not seem to represent *cenchoa* because of the size of the vertebral scales and the differences in coloration (*cenchoa* has pattern type A, see Fig. 1A) and number of subcaudal scales (146-195). There is however considerable overlap in ventral and ventral plus subcaudal counts and a slight overlap in body blotch numbers between *cenchoa* and this sample. Apparently, the northwestern Costa Rican *Imantodes* represent a single species not identical with *cenchoa* and not clearly identical with Panama *gemmistratus.* Consequently, this form will be designated "species A" for the remainder of this analysis and for comparison with other samples.

The southwestern lowland area of Costa Rica centered on the Golfo Dulce, is a region of high annual precipitation and a very short dry season (December to February or March). The blunt-headed vine snakes from the region around the Río Grande de Térraba southward, also form a very homogenous sample with two exceptions that will be treated later. This sample is characterized as follows: (1) vertebral scales 3-5 times a wide as lateral scales; (2) ventrals in males 258-278, in females 246-274; (3) subcaudals in males 156-183, in females 149-179; (4) ventrals plus subcaudals 406-459; (5) body blotches 31-43; (6) broken body blotches 0 - 3; (7) ground color heavily suffused with dark pigment to produce a very dark appearance.

There can be no question that this series represents *Imantodes cenchoa* since it closely resembles the population referred to that form from adjacent western Panama by Myers (1982), although averaging slightly higher in segmental counts.

A third small series of *Imantodes* from Pacific lowland Costa Rica is from an intermediate area between Quepos and the mouth of the Río Grande de Tárcoles. Four of these examples (CRE 7139, 8255, 8261, 8263) form the basis for Scott's (1983) assertion that *gemmistratus* and *cenchoa* integrade on the Pacific coast in a narrow contact zone near Parrita. A fifth example (one of the original syntypes of Cope's *Imantodes semifasciatus,* AMNH 17314) is from Pozo Azul in the same area and resembles the other examples from near Parrita (La Julieta) and Jacó to the north-

west in all significant features. These animals have the vertebral scale row less than twice as broad as the lateral scales, and all are females with scale counts as follows:

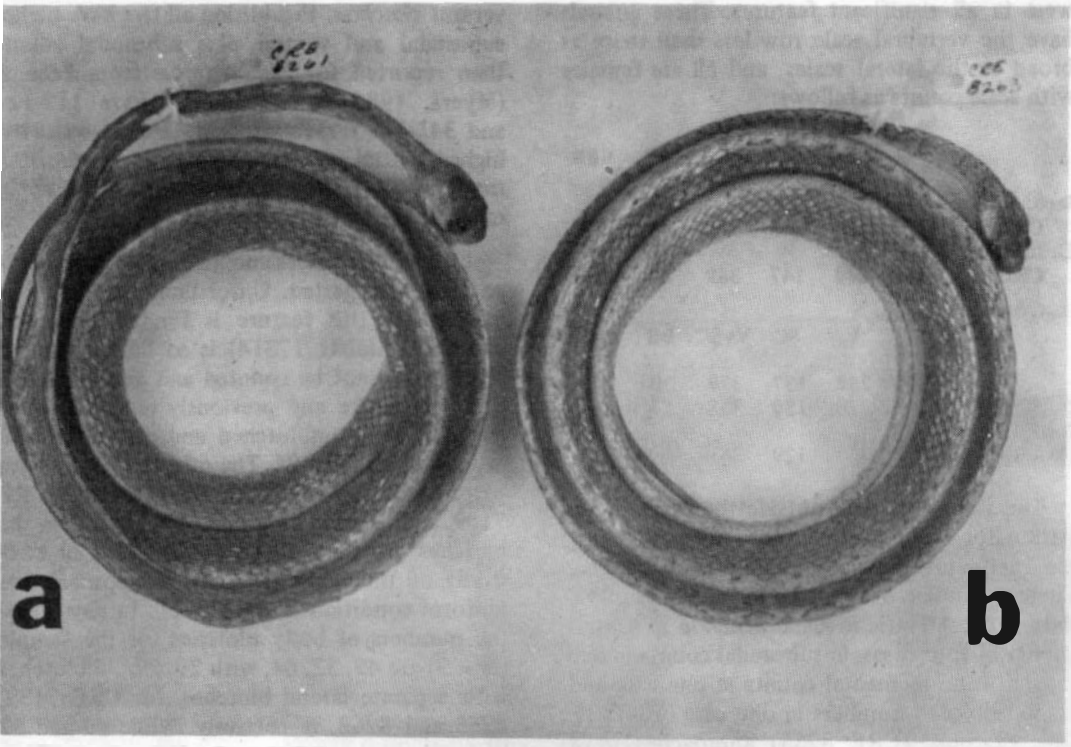
		V	SC	V+SC	BB	BBB
Jacó:						
CRE	7139	226	133	359	49	29
La Julieta:						
CRE	8255	242	147	389	64	36
		V	SC	V+SC	BB	BBB
	8261	252	137	379	0	0
	8263	228	130	358	52	39
Pozo Azul:						
AMNH	17314	232	129	361	–	–

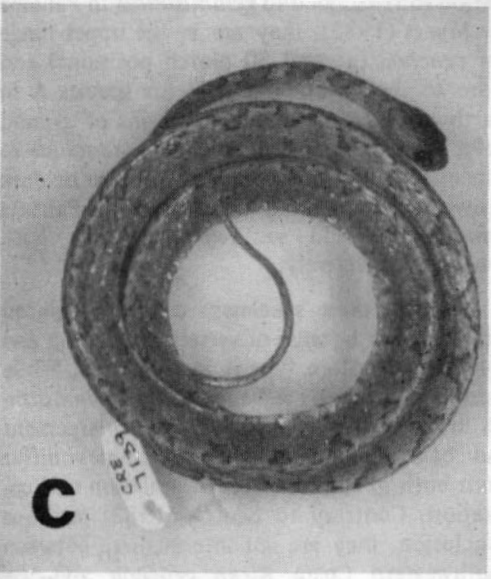
The values are well outside the range of variation for *Imantodes cenchoa* anywhere along the Pacific lowlands of Costa Rica and Panama. These examples overlap the lower limits of variation for Atlantic lowland *cenchoa* in ventral counts in four cases, in subcaudal counts in one case, in total segmental counts in one case and in body blotch numbers in one case (Table 1). One example (CRE 8255) approaches most closely Atlantic lowland *cenchoa* in segmental counts but has 64 dark body blotches, well above the maximum of 52 recorded elsewhere in Costa Rica for definitive *cenchoa* and the maximum of 56 in Panama. Most *cenchoa* have no more than 50 body blotches and higher values involve examples where one to seven posterior blotches are broken up into two smaller spots. All examples in the present series have a light brown to yellowish dorsal ground color and are immediately distinguished from *cenchoa,* which has a dark to medium brown ground color.

In terms of scale characteristics the five specimens discussed above agree more closely with the northwest Pacific sample ("species a") than with *cenchoa.* Females of "species A" have 238-248 ventrals, 135-154 subcaudals and ventrals plus subcaudals 376-401 compared to similar values of 246-274, 149-179 and 406-453, respectively in Pacific lowland *cenchoa.* The latter form has the vertebral scale row strongly enlarged, unlike "species A" or the Parrita region sample. The most striking aspect of the variatoon in scalation in the latter is that the range has substantially lower limits (226 ventrals, 129 subcaudals and 358 ventrals plus caudals) than do either "species A" of Pacific versant *cenchoa.* In addition all five have higher subcaudal and ventral plus subcaudal counts than reported for *gemmistratus* from Panama (Myers, 1982) where females have 113-124 and 341-345 respectively. The Parrita series has higher ventral counts than Panama *gemmistratus* (221-228) although over lapping the upper range of the latter form.

In terms of coloration a similar geographic pattern is suggested. Unfortunately, the information for this feature is limited since one example (AMNH 17314) is so faded that the blotches cannot be counted and another (CRE 8261) is unlike any previously reported *Imantodes* in being unblotched and nearly uniform in coloration (Fig. 2). The other examples have patterns of type B (CRE 8255) and C (CRE 7139 and 8263), although the latter has the blotches greatly reduced on the anterior two-thirds of the body (Fig. 2), to approach the uniform condition of CRE 8261. In any event, the numbers of body blotches for the sample (N = 3) are 49, 52, 64, with 29, 39, 36 blotches with separate lateral blotches, for CRE 7139, 8255 and 8263, respectively. While 49 and 52 body blotches are below the lower limit of variation (55) ascribed to *gemmistratus* in Panama by Myers (1982), they are in the upper range for *cenchoa* (around 50 blotch positions) and close to the lower limit (51) for species A in northwestern Costa Rica. In terms of ground color these problematic specimens are similar to "species A" in not having the medium or dark brown dorsal ground color seen in Panama *gemmistratus* and southwestern Costa Rica *cenchoa,* respectively.

In short, these specimens cannot be placed with *cenchoa* because of vertebral scalation and coloration (pattern type A in the latter). While resembling "species A" and Panama *gemmistratus* in the degree of vertebral scale enlargement and basic coloration, these examples differ from both in some aspects of scalation and coloration. Contrary to Scott's (1983) previous conclusion, they are not intermediate between southwestern Costa Rican *cenchoa* and the northwestern Costa Rican species, but tend to have lower segmental counts than either. In coloration they most closely approach the latter population, but have lower body blotch counts and in two cases unique color patterns. Their allocation thus remains in doubt at this stage of our analysis.





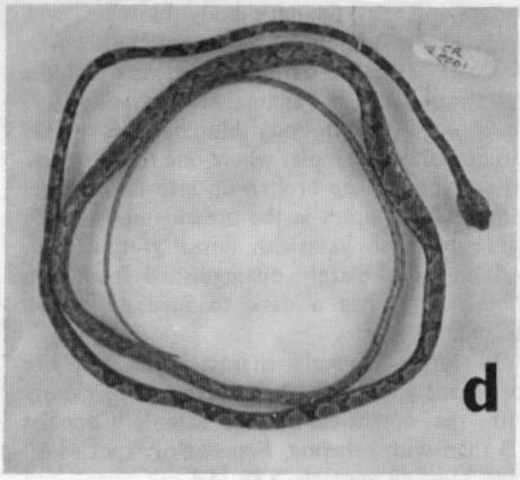


Fig. 2. *Imantodes* from western Costa Rica. A. Unusual uniform pattern (CRE 8261). B. Reduced posterior blotching (CRE 8263). C. Typical pattern C (CRE 7001). D. Pale pattern C (CRE 7139). The bar equals 4 cm.

The extremely unusual coloration of two of hese snakes requires further comment since ney rival the unique striped condition found in vo specimens of the Amazonian *Imantodes ntiferus* (Myers, 1982), as extreme variants in hese normally dark blotched forms (Fig. 2A, B). The most bizarre pattern occurs in CRE 8261, which is without any suggestion of dark blotches on the body or tail. The ground color is uniform beige with a slight yellowish cast and the entire upper surface is punctated with dark

pigment that is concentrated along the scale margins. Under magnification each scale has the punctations concentrated to form a darked outline around the light center. Over most of the body and tail the enlarged vertebral scales also show this tendency to produce an obscure light vertebral stripe. The head has a dull dark complex marking above; the venter is light but punctated with dark brown, particularly laterally.

CRE 8263 is somewhat intermediate between the specimen described above and blotched examples from the area. The dorsal ground color is similar to that for CRE 8261 but anteriorly it has 31 distinct dorsal and 17 lateral blotches. Posterior to this point on the body the dorsal blotches are represented at best by small dark spots and the lateral spots are similarly reduced. In terms of blotch position there appear to be around 50 positions and about 39 lateral spots. Except for the very faint suggestion of spots the posterior coloration of this individual is identical to the uniform individual described above.

Two other examples, both males, of *gemmistratus*-like snakes have recently been discovered from the southwestern Pacific lowland area and have been called to our attention by Douglas C. Robinson. Their salient features in addition to having the vertebral scale row less than two times the width of the lateral scales, a type C color pattern and the dorsal ground color light brown include:

	V	SC	V+SC	BB
Coto Brus:				
UCR 3401	241	141	382	53
Quebrada Leona:				
UCR 6929	244	144	388	49

These examples have higher ventral, subcaudal and ventral plus sub-caudal counts than Panama male *gemmistratus* (227 - 237; 124 - 130; and 357 - 361, respectively). They resemble "species A" from northwest Costa Rica in those regards, but tend to be near the lower limits of each range for that form. Since males have more ventrals and subcaudals than females in *Imantodes*, these two examples also resemble the Jacó - Parrita snakes (all females) discussed above, when allowance is made for sexual dimorphism, and seem to represent the same species.

The situation for the Pacific lowlands may be summarized as follows: there are two distinctive apparently allopatric forms, one in northwest Costa Rica ("species A") and one in southwest Costa Rica, that may be consistently distinguished on the basis of the amount of vertebral scale enlargement, color pattern, number of body blotches and ventrals plus subcaudals. They further differ in ventral and subcaudal counts although there is some overlap, with the southwest Pacific species having higher counts for all segmental characters. The latter form is conspecific with *Imantodes cenchoa* while the former approaches Panama *Imantodes gemmistratus*, but is completely distinct from that population in having much higher segmental counts (V, SC and V+SC, see Tab. 2). A second *gemmistratus*-like series of female snakes from localities intermediate between (Pozo Azul-Parrita) the samples discussed above have somewhat lower segmental counts than found in "species A", as do the two males from within the range of southwest Pacific *cenchoa*. These examples approach Panama *gemmistratus* in segmental counts but are completely separated from them in total segmental counts, when the sexes are compared separately. This sample of seven individuals is therefore somewhat intermediate between Panama *gemmistratus* and "species A".

Upland Areas: A. Northwest upland series: A sample of 14 snakes from the Cordilleras de Guanacaste and Tilarán from sites between (480-1500m), is comprised of 12 individuals with enlarged vertebral scales, high subcaudal counts (149-175) and body blotches of type A, ranging in number from 35-52. The upper limit of the range for the latter feature is represented by a male (CRE 4461 from near Monteverde, Provincia de Puntarenas 1400 m) with 45 blotch positions in which seven blotches including the last three are broken into two small spots. These snakes are *Imantodes cenchoa.*

Two other examples, both females, have relatively small vertebral scales, slightly lower subcaudal counts (145-146), lack the type A color pattern and have 51-55 body blotches. In these features and all other regards these specimens (UCR 4650 and UMMZ 131406) resemble very closely "species A", the *gemmistratus*-like form, from the adjacent northwest Pacific lowlands. Both examples are from near Tilarán, (from 1 km NW Tilarán and Los Angeles, about 6 km NW of Tilarán, respectively) where indisputable *cenchoa* occurs in virtual sympatry. A comparison of these two snakes to others from the area follows:

	V	SC	V+SC	BB
1 km NW Tilarán:				
UCR 4650	231	145	386	55
Los Angeles				
UMMZ 131406	239	146	385	51

cenchoa

	V	SC	V+SC	BB
El Silencio:				
CRE6218	253	169	422	43
CRE6222	244	154	398	41
San Bosco:				
CRE 6277	257	165	422	35
Tilarán:				
UCR 6134	259	166	425	–
UMMZ 126716	257	163	420	40

A juvenile *cenchoa* (CRE 3621 from 2.2 km E of Los Angeles), with 43 body blotches, for which segmental counts could not be made because of its condition, further confirms that two sympatric species occur in this zone.

The two *gemmistratus*-like snakes from the Tilarán area seem to represent the same form as found in the northwest lowland area of Costa Rica. For this reason they are included with that sample as part of species A in subsequent discussions.

Imantodes cenchoa from these uplands have significantly lower segmental couns than the population from the southwest Pacific lowlands (Table 1). In this regard there is an approach to the northwest Pacific lowland "species A" in the upland samples of *cenchoa* from this region, which led Scott (1983) to conclude that intergradation between the two forms occurs on the Pacific slope of the Cordillera de Guanacaste. The data presented above show that the two species occur sympatrically along the slopes of the Cordillera de Tilarán and the only two available specimens from the Guanacaste range confirm this conclusion. Both examples (KU 31946, a male and KU 34034, a female) are typical *cenchoa* in the vertebral scale enlargement, color pattern type A with 41 (40) blotches and 45 body blotches (there are 41 blotch positions but two blotches are fused together) and 14 and 16 broken body blotches, respectively. In addition the segmental counts are: ventrals 246, 236; subcaudals 175, 149; ventrals plus subcaudals 421, 385, respectively. Examples from the southern portion of the Cordillera de Tilarán near Monteverde are all unquestionable *cenchoa.*

B. Meseta Central series: Myers (1982) in straightening out the identifications for the type specimens of several of Cope's names for *Imantodes* based upon Costa Rican examples, reached the conclusion that a number were conspecific with *Imantodes gemmistratus* as diagnosed in Panama. He challenged the idea (Scott 1969; 1983; Savage 1973, 1980) that only one species of the *cenchoa - gemmistratus* complex occurred in Costa Rica on this basis but did not undertake a full analysis of the problem. In particular he recognized Cope's (1894) types of *Himantodes semifasciatus* as representing *gemmistratus.* The specimens are labeled Pozo Azul (AMNH 17314), with locality data erroneously transliterated to Paso Azul and from "Alajuela" (AMNH 17356), Monte Aguacate (AMNH 17330 - 31) and San José (AMNH 17296-97, 17355) (see Savage, 1974 and below). Another type of *semifasciatus* from Santa Clara, Provincia de Limon (AMNH 17273) was later made the holotype of a new species, *Himantodes hemigenius* by Cope (1899) and will be discussed later in this paper. The remaining types of *semifasciatus,* including the example designated as the lectotype (AMNH 17357) of the name by Myers (1982) and the holotype of *Himantodes anisolepsis* Cope, 1894 (AMNH 17274) from Monte Aguacate were regarded as *cenchoa,* conclusions with which we concur. The other syntypes are from Carrillo, Provincia de San José (AMNH 17357), and Sipurio, Provincia de Limón (AMNH 17358), with its locality data erroneously transliterated to Sapurio, (see Savage, 1974 and below).

The example from Pozo Azul, Cantón de Acosta, Provincia de San José, (incorrectly listed as Provincia de Puntarenas, Cantón Aguirre by Savage, 1974) has been discussed above with other lowland Pacific versant examples. The remainder of the Cope material reviewed by Myers (1982) suggests that two species occur in the upland Meseta Central area, and are sympatric at least in the Monte del Aguacate, Provincia de Alajuela (1000 m). One of these forms is *cenchoa* and the other is *gemmistratus,* according to Myers.

Data for 28 examples of *Imantodes* from the Meseta Central (Pacific drainage) and two from the Meseta Central (Atlantic drainage) seem to clarify the general problem and elucidate the relationship between species A from the Pacific northwest and other *gemmistratus*-like popu-

lations. Only five of the snakes from the Meseta appear to represent *cenchoa*. They are from Montes de Aguacate (AMNH 17274), the city of San José (NHMW 25472.1, ZMH RO 1980); and Navarro (UMMZ 74304) and Azahar, Provincia de Cartago (NHMW 25528.1). All other material has reduced vertebral scale rows, pattern types B or C and relatively low ventral plus subcaudal counts (360 - 389).

The latter series of 24 individuals has the following features: 1) vertebral scale rows 1.3 - 2.1 times as wide as lateral scales; 2) ventrals in males 233-246, in females 229 - 240; 3) subcaudals in males 137 - 146, in females 130 - 138 4) ventrals plus caudals in males 373 - 389; in females 360 - 378; 5) body blotches 41-61 of types B and C (Fib. 1B, C); 6) broken body blotches 8-34; 7) dorsal ground color light brown, often with a yellowsih cast.

This sample obviously resembles, the Panama *gemmistratus*, "species A" from northwest Costa Rica and the ambiguous *gemmistratus*-like specimens from southwestern Pacific lowland areas. The former may be separated from these *gemmistratus*-like samples as follows:

	Panama	SW Pacific	Meseta	NW Pacific
Ventrals				
♂	227-237	241-244	233-246	244-249
♀	221-228	226-242	229-252	238-248
Subcaudals				
♂	124-130	141-144	137-146	138-147
♀	113-124	129-147	130-150	135-154
Ventrals plus Subcaudals				
♂	357-361	382-388	373-389	382-404
♀	341-345	358-389	360-382	376-401

These data show that the three Costa Rican samples resemble one another more closely than any one of them resembles the snakes from Panama. All Costa Rica samples have higher counts in each category than do the Panama examples. While there is some overlap in ventral counts among the four series, Costa Rican specimens consistently have much higher subcaudal and ventral plus subcaudal counts for the same sex than occur in Panama, as is shown below:

	Pacific Costa Rica	Panama
Subdaudals		
♂	137-147	124-130
♀	129-154	113-124
Ventrals plus Subcaudals		
♂	373-404	357-361
♀	358-401	341-345

Within the Costa Rican series the Meseta Central specimens are essentially intermediate between southwest and northwest samples in segmental counts, although having substantially lower maximum values for each count when compared to the latter and resembling the for mer rather closely in variational range.

It seems, therefore, that all upland and lowland Pacific versant *gemmistratus*-like samples are conspecific with one another and "species A" of northwest Costa Rica. Whether they are conspecific with the species called *gemmistratus* in Panama by Myers (1982) is unknown.

The relatively high ventral and ventral plus subcaudal counts for the Meseta examples available previous to the present study led Scott (1983) to regard them as showing intergradation between *cenchoa* and *gemmistratus*-like populations on the Meseta Central. Although the considerable variation in *cenchoa* in this area also contributed to this conclusion, nothing in the present study substantiates that view.

The remaining Meseta Central specimens previously referred to *Imantodes cenchoa* are discussed in the context of the following section.

C. La Palma-La Hondura sample: three snakes (CRE 7144, UCR 4316-17) from the pass between La Palma on the slope north of the Meseta Central Occidental to La Hondura on the Atlantic slope, are typical *cenchoa* and agree closely with one another in all features. They may best be compared with Meseta Central individuals of that form as a basis for subsequently determining the populational affinities of all 10 examples (no counts were taken for ZMH RO 1980 because of its condition):

TABLE 1

Geographic variation in Costa Rica: Imantodes cenchoa

	N	Ventrals	Subcaudals	Ventrals + Subcaudals	Body Blotches	Broken Body Blotches
Pacific						
♂	12	258-270.7-278	156-175-183	432-447.1-459	35-39-41	0-0.2-3
♀	10	246-256.6-274	149-165-179	406-423.1-453	31-38.2-43	0
NW Uplands						
♂	7	233-249.6-259	165-167.6-175	420-422-425	35-42.1-52	12-14.4-17
♀	3	236-238.7-244	149-152.3-154	385-391-398	41-42.7-45	14-17-21
undet.	1	–	–	–	43	12
Atlantic and Central uplands						
♂	34	235-249.5-269	147-166.2-180	383-416.6-442	33-43.7-51	2-13.6-19
♀	26	228-240.6-245	146-158.4-168	390-399.6-411	32-43.5-49	0-15.3-27
undet.	13	228-242.4-259	145-157.6-176	385-398.8-431	37-42.3-47	16-16.7-19

TABLE 2

Geographic variation in Imantodes gemmistratus*-like samples from Costa Rica and Panama*

	N	Ventrals	Subcaudals	Ventrals Plus Subcaudals	Body Blotches	Broken Body Blotches
NW Pacific						
♂	6	244-246.8-249	138-145.8-147	382-393.3-404	56-65.8-73	24-30.4-39
♀	11	238-242.3-248	135-144.8-154	376-388.1-401	51-57.8-66	23-28.1-34
undet.	2	238-244.5-251	144-144.5-145	382-389-396	62-63-64	–
SW Pacific						
♂	2	241-242.5-244	141-142.5-145	382-385-388	49-51-53	8
♀	5	226-234-242	129-135.2-147	358-369.2-389	(0)52-55-64	(0)29-34.7-39
Meseta						
♂	14	233-240-246	137-142.8-146	373-382.4-389	41-53.2-61	8-23.6-34
♀	8	229-233.2-252	130-135.1-150	360-366.9-382	46-52-56	14
undet.	1	241	139	380	51	–
Atlantic						
♂	4	231-236-241	139-142.3-145	373-378.6-386	54-55-56	21-24-27
♀	8	225-236-242	134-140.1-144	358-373.6-382	47-52-59	14-24.3-33
undet.	1	143	159	383	49	–
			PANAMA			
♂	9	227-232.9-237	124-126.130	357-361		
♀	11	221-225.2-228	113-118.124	341-345	55-74	–

		V	C	V+C	BB	BBB
Monte del Aguacate						
AMNH 17274	♂	270	173	443	39	0
San José						
NHMW 25472.1	♂	250	171	421	48	14
La Palma:						
CRE 7144	♂	236	147	383	40	14
La Hondura:						
UCR 4316		232	153	385	41	–

		V	SC	V + SC	BB	BBB
UCR 4317	–	240	147	387	42	–
UCR 2052	♂	248	153	401	44	–
UCR 2053	♂	243	159	402	42	–
Azahar:						
NHMW 25528.1	♂	241	158	399	32	9
Navarro:						
UMMZ 74304	♂	236				

These data suggest considerable differences between *cenchoa* populations at the western edge of the Meseta Central (Montes del Aguacate), at San José and on the slopes to the north and east toward the Atlantic versant. The Montes del Aguacate specimen agrees in all particulars (Table 2) with the southwest Pacific lowland sample of this form and differs from other samples in having higher segmental counts. For this reason it has been included with the lowland Pacific population in subsequent discussions and the tabulation (Table 2) of geographic variation. This specimen confirms the virtual sympatry of *cenchoa* and "species A" at a second location along the Pacific slope of Costa Rica.

The material from the La Palma pass area and the upper Río Reventazón valley south of Cartago on the Atlantic portion of the Meseta Central, closely resemble one another. They differ markedly from southwest Pacific lowland *cenchoa* in having lower segmental counts and more numerous lateral body blotches. Of the samples discussed to this point they resemble those from the uplands of northwestern Costa Rica (see previous section). They also approach examples of *cenchoa* from the Atlantic lowlands and for this reason their final allocation will be mentioned below.

The specimen from San José city does not fit readily with either the southwest Pacific series or with other upland examples. The segmental counts are high when compared to the latter, but the presence of 14 body blotches that have broken off lateral spots separates it from the former, which usually has no lateral spots at all (maximum of 3 in one specimen). The status of this example will also be discused below in relation to the analysis of Atlantic lowland samples. It further confirms the virtual sympatry of *Imantodes cenchoa* and "species A" since both have now been examined from the city of San José.

The Atlantic Lowlands and Foothills: The Atlantic lowland and foothill zone of Costa Rica originally supported a continuous broadleafed evergreen forest because of the extended rainy season, interrupted by a brief two month dry period in Januar, February and March. Two distinctive forms of *Imantodes* of the *cenchoa-gemmistratus* complex occur in sympatry at some localities on the Atlantic versant of Costa Rica. By far the most abundant is a species with greatly enlarged vertebral scale rows, color pattern type A (Fig. 1A) and a relative low number of dark body blotches (33-50). Although this population has fewer ventrals than *cenchoa*

rom southwest Pacific Costa Rica (Table 1) nd usually has some posterior, dorsal dark lotches broken laterally to form lateral spots, t closely resembles western Atlantic lowland anama examples referred to *cenchoa* by Myers 1982) and we have little doubt that only a ingle wide-ranging species is involved. Because he ventral and the ventral plus subcaudal ounts are low in this population, these values verlap the upper limits of variation for the Pacific versant populations of "species A". The several examples of this species from the upper portions of the Meseta Central and surrounding slopes (discusses above) closely resemble the Atlantic samples and probably the same population. One of us (Scott, 1969, 1983) thought that this tendency suggested intergradation between *cenchoa* and "species A" (called *gemmistratus* by him). As shown, this is not the case since the two may be unequivocally separated and are sympatric at several locations on the Meseta Central Occidental. A similar situation occurs in the Cordillera de Tilarán where sympatry between *cenchoa* and "species A" is documented in an earlier section of this paper.

Imantodes cenchoa of the northwestern uplands resemble Atlantic lowland samples in having low segmental counts (Table 1) and there is some overlap with the relatively high segmental counts found in the northwest Pacific versant population of "species A". We have already described the trenchant differences between "species A" and *cenchoa* in the area of verlap (see section on northwestern upland samples) and have refuted Scott's (1969, 1983) claim of intergradation.

Costa Rican Atlantic lowland *cenchoa* may be consistently distinguished by the following features: 1) vertebral scale rows 3.2-5 times as wide as lateral scales; 2) ventrals in males 235-269, in females 228-245; 3) subcaudals 152-180 in males, 146-168 in females; 4) ventrals plus subcaudals 393-442 in males, 390-411 in females; 5) body blotches 33-50 of pattern type A; 6) broken body blotches 0-27; 7) ground color tan to medium brown.

Taylor (1951, 1954) and Myers (1982) both reported *Imantodes gemmistratus* from Atlantic lowland Costa Rica. Our study has discovered 13 examples of *gemmistratus*-like snakes from this region. They may be characterized as follows: 1) vertebral scale rows 1.5-1.9 as wide as lateral scales; 2) ventrals in males 231-241, in females 225-252; 3) subcaudals 139-145 in males, 134-150 in females; 4) ventrals plus subcaudals 373-386 in males, 358-382 in females 5) body blotches 46-59, of pattern type B or C; 6) broken body blotches 14-34; 7) dorsal ground color medium to light brown, some examples with a yellow cast. These snakes may be distinguished most readily from sympatric *cenchoa* by differences in vertebral scale row enlargement (1), color pattern type (5) and less consistently in total segmental counts (4).

Atlantic Costa Rica *gemmistratus*-like *Imantodes* are consistently separated from Panamanian *gemmistratus* (Myers, 1982) by having much higher subcaudal and ventral plus subcaudal counts, as follows:

	Panama	Atlantic Costa Rica
Subcaudals		
♂	124-130	139-145
♀	113-124	134-144
Ventrals plus Subcaudals		
♂	357-361	373-386
♀	341-345	358-382

This is not suprising since *gemmistratus* in Panama is virtually limited to the Pacific slope, with only a few central Panama records from the Caribbean drainage, some 350 km ESE from the nearest locality for *gemmistratus*-like snakes in Costa Rica (CRE 3147; Pandora, Provincia de Limón). For this reason it is even less suprising that the Atlantic lowland series from Costa Rica is virtually identical to the samples of series A from the Meseta Central and southwest Pacific lowlands (Tab. 2). We have no hesitancy in referring these three series to a single form, although and since the Atlantic suite differs from the northwestern lowland specimens of "species A" in exactly the same ways and degree as Meseta and southwest samples do. That the four series represent a single species is evidenced by the similarity in vertebral scale row enlargement, color pattern, numbers of dark body blotches and overlap in segmental counts (Tab. 2).

THE COSTA RICA SITUATION

The analysis of available material of *Imantodes* from Costa Rica confirms the conclusions

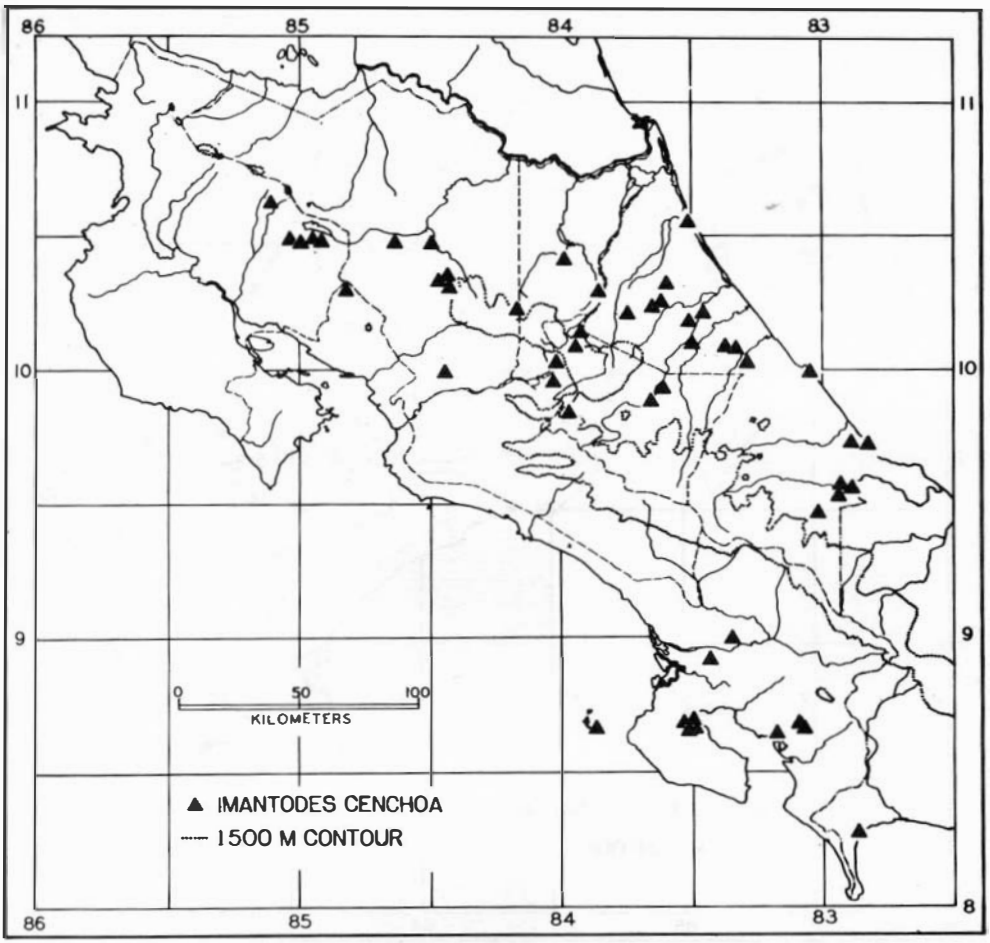


Fig. 3. Distribution of *Imantodes cenchoa* in Costa Rica.

of Taylor (1951, 1954) and Myers (1982) that three species occur in the republic. One of these, *Imantodes inornatus*, is found in sympatry with *Imantodes cenchoa* at a number of localities and has never been confused with other members of the genus. The second species is *cenchoa*, which has a wide geographic distribution is evergreen forest situations from southern Veracruz on the east coast and Chiapas on the west coast in Mexico; to Argentina. A third form (referred to above as "species A") called *gemmistratus* by Taylor (loc. cit), was thought to be conspecific with Panamanian material referred to that form by Myers (loc. cit.). This species occurs in sympatry with *cenchoa* at a number of localities in Costa Rica and probably is sympatric with *inornatus* at some sites on the Atlantic lowlands.

Imantodes inornatus occurs in lowland and premontane evergreen forests from Atlantic drainage southern Nicaragua to western Ecuador. In Costa Rica (Fig. 3) it is found along the entire Atlantic slope from near sea-level to 900 m, in the uplands of the Cordillera de Tilarán to 1450 m, and on the southwest Pacific lowlands and slopes to 1200 m. It extends southward on both coasts of Panama and through western Colombia no western Ecuador.

Imantodes cenchoa probably has a continuous range along the Atlantic versant from Veracruz, Mexico, through Central America, although only a few examples are known from Honduras (Wilson and Myers, 1982) and adjacent northern Nicaragua. On the Pacific slope of northern Central America the species is restricted to eastern Chiapas, Mexico, and adjacent

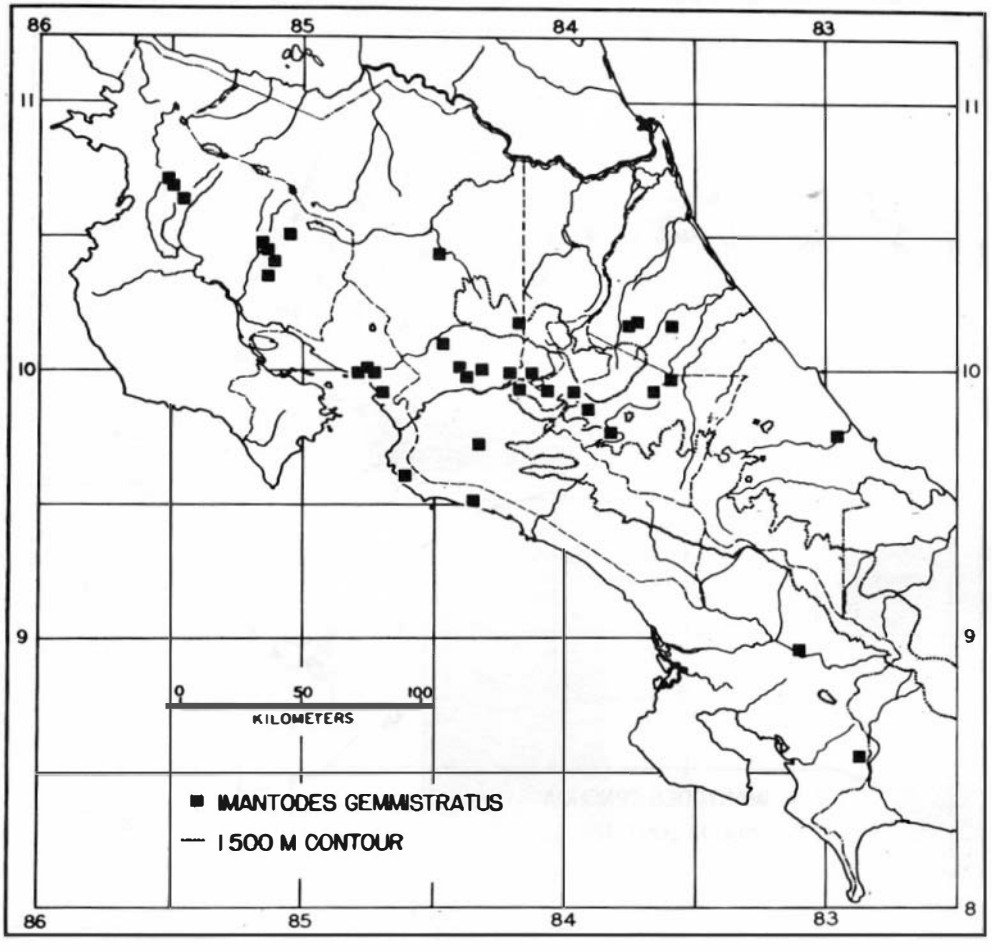


Fig. 4. Distribution of *Imantodes gemmistratus* in Costa Rica.

Guatemala, in the premontane zone (600-1500 m). The species is found in upland areas of Costa Rica and western Panama on both versants and in the southwestern humid forests of Pacific lowland Costa Rica and adjacent Panama, and thence southward in evergreen lowland forests of South America.

In Costa Rica (Fig. 4) two populations are recognizible on the basis of segmental counts and coloration (Tab. 2). The population from the Pacific versant has high subcaudal and ventral plus subcaudal counts, rarely has any lateral blotches broken off from the dorsal body blotches and has the interspaces between blotches very heavily darkened. In all these features it agrees with *cenchoa* from western Panama and together they seem to be disjunct from Atlantic slope populations.

A second population seems to be represented by the Atlantic slope specimens. They differ from the Pacific samples in having low segmental counts, usually a series of definite lateral spots broken off from the dorsal dark blotches on the posterior portion of the body and usually a lighter interspace color. Material from the central and northwest uplands (Tab. 2) agrees closely with Atlantic slope specimens, although the northwest upland snakes have the dorsal interspace areas rather dark. For this reason these upland examples are considered to represent the Atlantic population. These specimens also agree very closely with Myers (1982) series of *cenchoa* from the Atlantic slope of western Panama and seem to represent the same population as well.

A single example of *I. cenchoa* from the city of San José (NHMW 25472.1) is intermediate in

locale and characteristics between Atlantic and Pacific populations. It is a female with 250 ventrals (similar to Pacific examples), 421 total segments (most like the Pacific population), 48 body blotches (most like Atlantic specimens and 14 posterior body blotches with lateral spots (most like Atlantic examples). Very likely there was, prior to the very rapid and recent uplift of the cordillera separating the Atlantic section of the Meseta Central from the Pacific part, or still is, a connection between the two *cenchoa* populations in this region.

The point is moot in any event since the distinctive features of these two populations are encompassed within the variation of *cenchoa* throughout its range as described by Myers (1982). For this reason, and those expressed by Savage and Heyer (1969), we agree with the latter authors that the recognition of these or other populations nomenclaturally as subspecies serves no useful purpose.

The rather low segmental counts for the Atlantic and upland population as compared to those for *cenchoa* in the Pacific lowlands of Costa Rica and over much of its range contributed to our mistaken belief that *cenchoa* and "species A" a position that we now vehemently eschew. (The northwestern and Meseta populations had higher counts than putative *gemmistratus* and overlap with the Atlantic series of the former) integraded (Savage 1973; 1976; 1980; Scot 1969; 1983.

The third Costa Rican form, "species A", is clearly allied to those snakes referred to *Imantodes gemmistratus* by Myers (1982) in Panama and from elsewhere in Middle America by others (Smith 1942; Zweifel 1959; Peters and Orejas-Miranda, 1970). As already pointed out above, "species A" may be consistently distinguished from the Panama sample in having higher subcaudal and ventral plus subcaudal counts. In addition, as shown below, "species A" is similarly distinct from several other nominal populations of *gemmistratus* from elsewhere in Central America.

In Costa Rica this form predominates in the drier formations of the Pacific lowlands and on the Meseta Central, but is also found at scattered localities within the lowland evergreen forests on the Atlantic slope and in the Pacific southwest zone (Fig. 4). There is a general smooth clinal increase south to north along the Pacific versant in segmental counts with the Meseta Central examples usually intermediate. The Atlantic lowland series closely resembles Meseta Central samples. The relatively high segmental counts for these samples, which overlap the lower range of variation for Atlantic and upland *cenchoa* contributed substantially to our earlier and erroneous appraisal that the latter and "species A" were conspecific (Savage, 1973, 1976, 1980; Scott, 1969, 1983). Now that we have shown that this is not the case, it remains to establish the name for "species A".

THE STATUS OF *IMANTODES GEMMISTRATUS*

The name *Himantodes gemmistratus* was proposed by Cope (1861) for a snake from El Salvador: Provincia de Sonsonate: near Volcán de Izalco, formerly at the Academy of Natural Sciences in Philadelphia, but now apparently lost (Malnate, 1971; Myers, 1982). Cope's description is limited but there is no question that the El Salvador example of *Imantodes* is some form other than *cenchoa*, with relatively narrow vertebral scales and 42 body blotches (Smith, 1942). *I. cenchoa* is not known to occur in El Salvador. The few specimens of the genus known from El Salvador (Mertens, 1952; Yingling, 1972) have a range of 219-233 ventrals, 124-136 subcaudals, 346-357 total segmental counts and 41-47 body blotches and we presume that the holotype of *gemmistratus* was conspecific with them.

Smith (1942) proposed that the name *gemmistratus* be applied to the species of *Imantodes* having the enlarged vertebrals only about twice as wide as the laterals, that occurred from Chiapas, Mexico south through Pacific slope Central America to Panama, and that has usually been called *elegans (Himantodes cenchoa* var. *elegans* Jan and Sordelli, 1871*)* by previous authors. Smith had seen no examples from El Salvador or Honduras, and accepted E.R. Dunn's apparent conclusion that specimens from Chiapas, Mexico, Guatemala and the type of *gemmistratus* were conspecific with Nicaragua, Costa Rica and Panama examples. The holotype of *elegans* was known from a nonspecified locality in "Central America".

Smith (1942) recognized a number of other species of *Imantodes* in which the vertebral scale row was slightly or not at all enlarged, as occurring in Mexico and northeastern Central America. Subsequent workers (Peters, 1954;

Zweifel, 1959; Yingling, 1972) have placed all of these forms, with the exception of the very distinctive Yucatan snake, *Imantodes tenuissimus* (Cope, 1867) as synonyms or subspecies of *gemmistratus*. We have serious reservations regarding this arrangement, particularly as it includes the relatively non-attenuate outer Yucatán form *Imantodes splendidus* (Gunther, 1895) having correspondingly low segmental counts (totals 310-321), with populations having total segmental counts of 335-402. Fortunately, the status and relationships among these forms does not concern us here and their resolution is not required to clarify the situation *vis a vis I. gemmistratus* and Costa Rican "species A".

The El Salvador samples of definitive *I. gemmistratus* differs markedly from the geographically closest populations of species A in Northwest Costa Rica as follows:

	El Salvador	NW Costa Rica
Ventrals	219 – 233	238 – 251
Subcaudals	124 – 136	135 – 154
Ventrals plus Subdaudals	346 – 357	376 – 404
Body Blotches	41 – 47	51 – 73

These differences disappear, however, when the El Salvador *gemmistratus* are compared to the total sample of "species A" and Panama *gemmistratus*. In the following sumary only the features for the two El Salvador snakes of undetermined sex are included in that category (undet.); R equals the total range of variation for each sample; the single, unblotched specimen (CRE 8261) of species A was not included in calculating the mean number of body blotches.

	El Salvador	Costa Rica	Panama
Ventrals			
♂	–	231 – 249	227 – 237
♀	219 – 231	225 – 252	221 – 228
Undet.	220 – 233	–	–
R	219 – 233	225 – 252	221 – 237

	El Salvador	Costa Rica	Panamá
Subcaudals			
♂	–	137 – 147	124 – 130
♀	136	129 – 154	113 – 124
undet.	124 – 126	–	–
R	124 – 136	129 – 154	113 – 130
Ventrals plus Subcaudals			
♂	–	373 – 404	357 – 361
♀	355	358 – 401	341 – 345
undet.	346 – 357	–	–
R	346 – 357	358 – 404	341 – 361
Body Blotches	41-43.5-47	41-55.3-73	55-74

Only a few additional examples of *gemmistratus*-like *Imantodes* have been taken in western Central America. They have the following features.

	W Honduras	Upland Honduras	Nicaragua
Ventrals	232	212	241 – 261
Subcaudals	136+	136	146 – 155
Ventrals plus Subcaudals	368+	348	396 – 408
Body Blotches	47	41	48 – 61

The Nicaragua examples from Departamento Rivas: Javilla, near the Costa Rica border (UMMZ 123041) and Departamento Granada: Santa Cecilia (KU 101930), are very similar to Northwest Costa Rica "species A".

The single western Honduras snake (LSUMZ 33739), from Departamento del Valle: 3.2 km NE Jícaro Galán, is more similar to El Salvador examples than to Nicaragua - northwest Costa Rica series, but is well within the limits of variation for "species A" in Costa Rica. The upland Honduras snake (AMNH 70260) from Departamento Cortés: Agua Azul, agrees most closely with the El Salvador sample, although having a very low ventral count. The latter two specimens and the El Salvador series are most distinctive from Nicaragua - Costa Rica and Panama samples in the consistently low number of body blotches (41 – 47 in the north; 41 – 53.3 – 73 in Nicaragua – Costa Rica and 55 – 75 in Panama). In this regard it should be pointed out that only one example of Costa Rican "species

TABLE 3

Geographic variation in Imantodes gemmistratus*-like samples from Mexico and Guatemala*

	N	Ventrals	Subcaudals	Ventrals plus Subcaudals	Body Blotches	Distribution
Oliveri						
♂	3	230-235	134-144	369-374		Isth. Tehuantepec,
♀	13	221-237	117-135	354-356		Chiapas, Mexico;
R	38	216-237	113-144	354-374	45-68	W. Guatemala
latistriatus						
♂	8	217-231	109-136	340-353		Sonora, to
♀	11	223-236	115-131	353-354		Guerrero,
R	82	206-246	106-138	334-356	35-67	Mexico
gracilimus						
♂	1	242	143	385		Lowland Colima to
♀	4	230-253	133-145	375-386		Guerrero,
R	15	223-253	123-145	367-386	34-39	Mexico
splendidus						
♂	2	201-208	109-113	314-317		N. Yucatán
♀	1	198	104	302		Península
R	6	195-215	99-120	302-321	34-44	
lucidorus						
♂	1	215	126	341		C. Veracruz,
♀	1	218	120	238		Mexico to
R	20	205-225	113-134	335-344	39-55	Guatemala
Islas Très Marías						
♂	1	254	138	392	53	Isla María Cleofas
♀	1	257	145	402	43	Isla María Madre

A" (UMMZ 131408) from "San José" (probably meaning the environs of the capital city) has the low count of 41 body blotches. Two additional examples have 47 and one has 49. All other specimens of this stock from Costa Rica have at least 50 body blotches.

The available data indicate that three apparently allopatric populations or population systems of *gemmistratus*-like *Imantodes* occur on the western lowlands and slopes of Central America: 1) El Salvador - Honduras 2) Nicaragua - Costa Rica and 3) Panama. The series are separated by range gaps of 200 km and 100 km, respectively. A fourth more or less allopatric component of this system occurs on the Atlantic lowland versant of Costa Rica, but may be or was rather recently contiguous with the Meseta Central Occidental population.

As pointed out by Myers (1982) Panama examples of this complex tend to occur in drier climatic zones and more open areas than do *I. cenchoa* and *inornatus* which are typically dense forest species. Habitats suitable for *gemmistratus*-like snakes are continuous along the western slope of Mexico and Central America to central Costa Rica (Savage, 1966). For this reason, we suspect that the range of the species with is represented by the type of *gemmistratus* may be found to be continuous from at least western Guatemala to Central and Meseta Central Costa Rica and can find no reason for regarding "species A" as distinct from it. We reach this conclusion despite the 200 km range gap between the latter and definitive *gemmistratus* and the significant differences between them where they most closely approach one another geographically. Variation in these features in central and southern Costa Rica completely overlaps with the El Salvador - Honduras species, which further supports this view. We thus conclude that *Imantodes gemmistratus* and "species A" are conspecific.

The relationship of *gemmistratus* to the allopatric population called *Imantodes splendida oliveri* by Smith (1942) found from the

Isthmus of Tehuantepec of Oaxaca and Chiapas, Mexico, eastwards into western Guatemala is problematical. Peters (1954) believed that all Mexico populations allied to *gemmistratus* were linked through *oliveri*, a view accepted by and expanded on by Zweifel (1959) and Yingling (1972). The *oliveri* population is separated by a 480 km gap from between the Tehuantepec region and the southern records of the west Mexico subspecies *latistriatus* (Cope, 1887) and *gracillimus* (Günther, 1895) in Guerrero.

The range of *oliveri* is completely allopatric to that of the Atlantic versant population called *Imantodes splendidus luciodorus* Oliver by Smith (1942). This form ranges along the lowlands from Veracruz into northern Guatemala and is allopatric to the northern Yucatán Península form for which the name *Dipsas splendida* was coined by Günther (1895).

While variation in segmental counts and body blotch numbers among these allopatric series overlap, marked differences in color pattern between the Atlantic versant and Pacific slope samples may reflect significant differentiation. Our review of the literature and material from scattered localities in Mexico, does not allow us to reach a definite conclusion as to whether all represent a single species or if one or more are conspecific with *Imantodes gemmistratus*. As an aid to those who may wish to attack this problem we have provided a summary of segmental and body blotch counts for each allopatric sample (Tab.3). These data are from Smith (1942), Zweifel (1959) and Yingling (1972). Since the latter did not indicate the sex for his counts, R in the table refers to the range of variation for the feature regardless of sex.

A final problem relates to the allocation of the distinctive Panama population regarded as *I. gemmistratus* by Myers (1982). As shown earlier almost all Costa Rica - Nicaragua examples of the species may be separated from all Panama specimens on the basis of subcaudals counts and the associated ventral plus subcaudal counts (Tab. 2). Nevertheless, since definitive *gemmistratus* from El Salvador have similar segmental counts to those found in Panama, we believe that no useful purpose will be served by recognizing the Panama population as a distinct species. *Imantodes gemmistratus* seems to be comprised of a series of 5 or more allopatric populations ranging along the Pacific versant of Central America from eastern Guatemala through Panama, to the Magdalena Valley of northern Colombia. Future collecting in areas north of Costa Rica is needed to establish whether the apparant gaps in distribution are real or collecting artifacts. An essentially allopatric population of the species occurs in the Atlantic lowlands of Costa Rica. In Panama the species is confined to the Pacific slope except in the central lowlands where a contiguous series of records link Atlantic and Pacific locations (Myers, 1982, map 1).

KEY TO THE SPECIES OF *IMANTODES* IN COSTA RICA

The following diagnostic key will serve to distinguish among the three species of blunt-headed vine snakes known to occur in Costa Rica.

1a. Dorsal pattern usually of large dark blotches, rarely uniform; ventrals more than 223; maxillary teeth 10-14+2 deeply grooved fangs. 2

1b. Dorsal pattern of small dark spots and speckles, sometimes lined up to form very narrow (no more than 1 scale row long) crossbars; 196-218 ventrals; 110-132 subcaudals; maxillary teeth 17-21+2 fangs with shallow grooves. . *Imantodes inornatus*

2a. Scales in vertebral row greatly enlarged, 3-5 times width of laterals; 31-52 (usually 48 or less) broad dark dorsal body blotches (Fig. 1A); 228-278 ventrals; 145-183 subcaudals. *Imantodes cenchoa*

2b. Scales in vertebral row 1.2-2.5 times as wide as laterals; 41-73 (usually 49 or more) dark dorsal bands or blotches (Figs. 1B, 1C); 225-252 ventrals; 129-154 subcaudals. *Imantodes gemmistratus*

In practice, especially in the field, the differences in color pattern will immediately separate representatives of the three forms. *I. Imantodes inornatus* is a yellowish snake with many small dark punctations, but never with clearly defined dark dorsal or tail band or blotches. *I. Imantodes cenchoa* has large dark saddles (Fig. 1A) whose centers are chestnut brown to almost red (both in life and after preservation). The dark markings in *I. gemmistratus* tend to be less pronounced than in *cenchoa* and are much narrower in longitudinal extent and often have white centers (Figs. 1B, 1C). The ground color of the latter species is

light brown to beige, with a distinct yellowish hue in most examples from the Pacific versant and many from the Atlantic as well. *Imantodes cenchoa* most frequently has a dark to medium brown ground color although some Atlantic lowland examples are light brown to beige.

The single unusual, essentially unicolor, yellowish hued *gemmistratus* (CRE 8261) from near Parrita is an exception to our initial statement since it might be mistaken for *inornatus*. In the latter narrow dark spots that may be lined up to form lines are always present, while the Parrita rarity is unspotted.

In juvenile *I. cenchoa* the centers of the dorsal blotches usually are nearly red and contrast to the black blotch outline. In one example (CRE 4607) the blotchs are solid black. Ontogenetically the blotch colors seem to change to the typical chestnut brown fround in most adults. Juvenile *I. gemmistratus* on the other hand, have dark brown blotches or bands, that appear to lighten in color during ontogeny. The white blotch centers found in some examples (Fig. 1C) are not present in any juveniles. These differences make it relatively easy to determine the identity of juvenile specimens (verified by examination of the vertebral scale row) without needing to undertake the arduous task of making segmental counts in most cases.

We have examined an unusual juvenile example (KU 80260) of *Imantodes* from Panamá thought to be an aberrant *gemmistratus* by Myers (1982: 15). This little snake has 255 ventrals, 155 subcaudals, 410 total segmental counts and 64 body blotches. In these features except the high number of blotches, the example resembles Panama *cenchoa* (Tab. 1). The blotch coloration (black-outlined, reddish blotches) and shape on the anterior part of the body conforms to the discription of Costa Rica juveniles as given above and for Panama juveniles described by Myers (op. cit.). The unique pattern of this example consists of a series of about 31 typical blotches on the anterior portion of the body. They are followed by about 15 blotches in which many are asymmetric (i.e. off-set on one or the other side) or are represented only on one side. A few of the latter barely cross over the midline onto the opposite side and would be included in a count such as Myers' (64 blotches "as counted from left side"). The final 16 blotches are small spots that represent fragmentation of 8 blotches. The total blotch positions in this example are 56, a high number but one found in other examples of *cenchoa*, when fragments of the posterior blotches are counted as two blotches. The number of dark tail blotches (50), and the tail length as a percentage of total length (28.1), as noted by Myers (op. cit.) for this example are typical of *cenchoa*. In *cenchoa* and *gemmistratus* the number of dark tail blotches is 22-53 and 28-42, respectively, and the relative tail length 26-34% and 24-28%, respectively. While Myers (op. cit.) states that the width of the vertebral scale rows (2.5 x laterals) in this example resemble *gemmistratus* our examination indicates that the rows near midbody approach 3 x laterals, which is near the lower limits of variation for *cenchoa*. We suspect this difference may be an artifact of measuring technique, since. Myers compared the width of the vertebral scales to the midlateral scales. Most other workers and we compared them to the upper lateral scales nearer the vertebral series. In any event Myers (p. 15) mentions 2.5 x laterals as the lowe limit of variation in vertebral scale width in Panama *cenchoa*.

In light of the above we regard KU 80260 as a juvenile *I. cenchoa* with characteristic scalation, proportions and color, but with an unusual amount of fragmentation of its dorsal body blotches, posteriorly.

DISTRIBUTIONAL PATTERNS

Geographic occurrence: – The following list contains Costa Rican records of unquestionable identity based upon examination of specimens or the literature and forms the basis for the distributional maps (Figs. 3-5).

Imantodes cenchoa: ALAJUELA: Montes del Aguacate; Aguas Claras de Grecia; Barranca de Río Sarapiquí, Isla Bonita; Esperanza; 5 km W La Fortuna; 8 km W and Quesada; El Venado de Grecia; CARTAGO: Azahar; Río Chitaria; Irazú; Moravia de Chirripó; Navarro; Finca Silvestre; Tres Equis. Turrialba; HEREDIA: La Selva; GUANACASTE: San Bosco; 2.2 km E Los Angeles; El Silencio; Tenorio; 2 km NW Tilarán; LIMON: Bambú; Fila Carbón; Cobal; Los Diamantes; 23 km NE Guápiles; Hamburgo; Río Jiménez; Pto. Limón; La Lola; 24 Millas de Santa María; Pandora; Reventazón; Sipurio; Siquirres; btwn. Suraya and

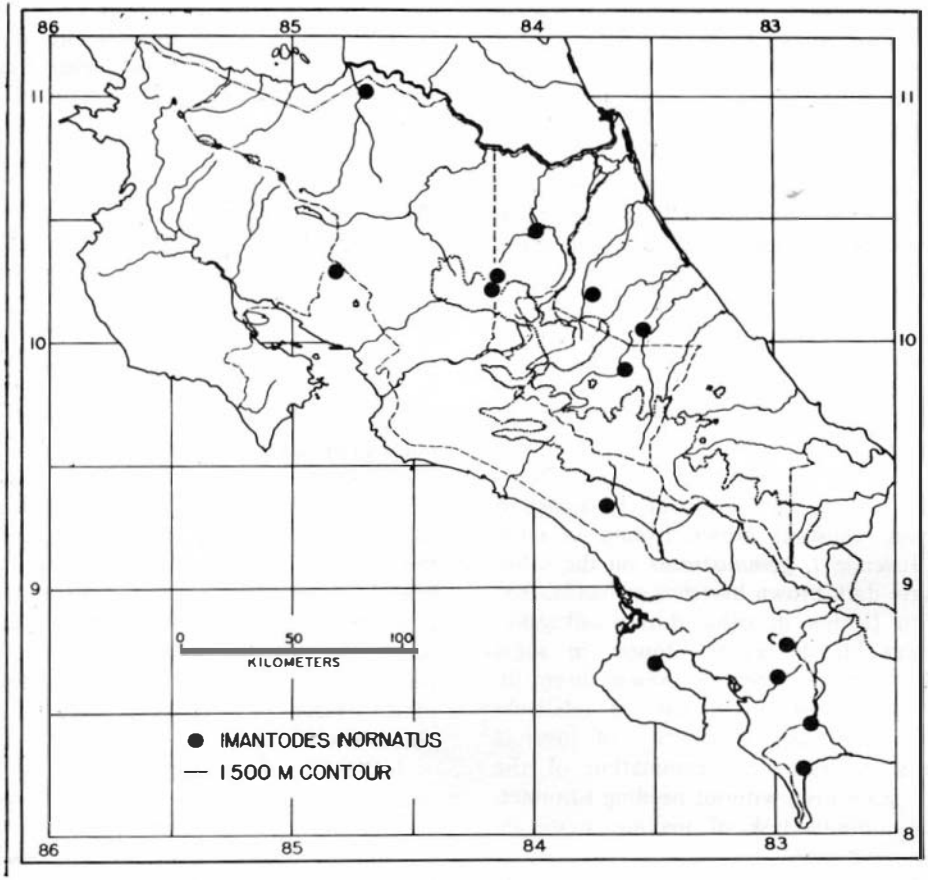


Fig. 5. Distribution of *Imantodes inornatus* in Costa Rica.

Río Yuani; Suretka; Tortuguero; Pto. Vargas; Waldeck; Zent; PUNTARENAS: Boruca; Isla de Caño; Río Claro at Golfito turnoff; Golfito; 0.5 E, 1.5 km SW and Monteverde; 4.8, 14.1 km NW Ciudad Neilly; 5 km SE Palmar Sur; 3,6, 8 km SW, 3 km SSW, 2, 3 km W, 3 km WSW Rincón de Osa; SAN JOSE: 0.5 km S and La Hondura; Río La Hondura; Moravia; La Palma; 1.4 km S Alto La Palma; San José.

Imantodes gemmistratus: ALAJUELA: Aeropuerto Internacional Juan Santamaría; Monte del Aguacate; Atenas; La Fosforera; Hda. Ojo de Agua; San Carlos; Hda. San Fernando; SanJosecito; btwn. San Miguel and Santo Domingo; San Rafael de San Ramón; CARTAGO: Cartago; Río Chitaria; Río Macho; Tres Ríos; Turrialba; HEREDIA: Barreal, Vara Blanca; GUANACASTE: Los Angeles; Cañas; Río Corobicí, 7 km NW Cañas; 1.6, 13, 20 km N, 48-80 km S Liberia; La Norma; La Pacífica; Río Sandillal, 3 km NW Cañas; Taboga; 3 km NW Tilarán; LIMON: Santa Clara; Los Diamantes; Pandora; Pocora; PUNTARENAS: Barranca; Corralitos; Coto Brus, Campo 2.5; 2 km E Jacó; Finca La Ligia, La Julieta; Quebrada Leona; Puntarenas; San Miguel de Barranca. SAN JOSE: Escazú; El Rodeo; Moravia; Pozo Azul; Quebrada Rodríguez, Santa Ana; San José; Barrios Las Americas and Dos Pinos, San José; Santa Ana.

Imantodes inornatus: ALAJUELA; Isla Bonita; Los Chiles; CARTAGO: Tres Equis; HEREDIA: Cariblanco; La Selva; LIMON: Guápiles; El Tigre; PUNTARENAS: Las Cruces; Monteverde; Río Nuevo at Interamerican Highway; Rincón de Osa and 3 km SW; SAN JOSE: San Isidro de El General.

This seems an appropriate place to clear up the erroneous perpetuation by Myers (1982) of two transliterations of locality data asociated originally by Cope (1894a) with some syn-

types of the nominal form *Himantodes semi fasciatus.*

One of these errors relates to a syntype ot *H. semifaciatus* (AMNH 17358) attributed to "Sapurio", Talamanca. This specimen was doubtless collected by the famed ornithologist José M. Zeledón, who was a founder of the Museo Nacional de Costa Rica, or one of his associates when in the Baja Talamanca area of southeastern Costa Rica with William More Gabb in 1873-1874 (see Savage, 1970) or at a later date. No place called Sapurio exists in Costa Rica, but the Talamanca region administrative capital of the late 1800's was the village of Sipurio.

Another syntypic example of *H. semifasciatus* (AMNH 17314) was part of a series of Costa Rican forms sent to Cope by George K. Cherrie in 1894. Cherrie was employed as a zoologist and taxidermist by the Museo Nacional from 1890-1895 (Carriker, 1910; Gómez and Savage, 1983). Cope's 1893 and 1894 papers mention the receipt of other examples from Cherrie.

Cherrie worked under the direction of José M. Zeledón and visited many of the latter's favorite collectint sites. One of these is Pozo Azul de Pirrís (Carriker, 1910; Zavage, 1974). The handwritten labels of reptiles from this site sent to Cope by Cherrie seem to have been transliterated by Cope to "Paso Azul" (1893), 1894a) and "Pazo Azul" (1984b), but the fact that the type of *Leoptophis ultramarinus* from the latter site was collected by Zeledón leaves little doubt as to the locality in question. Savage (op. cit.) inadvertantly created another error regarding this place which is in the Cantón de Acosta, Provincia de San José (not Can ton Aguirre, Provincia de Puntarenas).

As an aside, it is interesting to note that Cherrie subsequently had a long career as an explorer and zoologist, most particularly in association with the American Museum of Natural History. Cherrie, of course, was the principal naturalist on the museum's Roosevelt-Rondon Expedition to Brazil (Roosevelt, 1914; Cherrie, 1930) and worked for the museum's ornithology department for a number of years.

Ecologic Occurrence. *Imantodes cenchoa* has a broad range throughout the lowland and premontane evergreen forest of Costa Rica, where it is found from near sea-level to 1500 m along the Atlantic versant. In the southwest Pacific portion of the country it is known only from lowland sites (2-550m), but occurs only in more upland areas (395-1500m) in Pacific northwestern Costa Rica. Its absence from the lowlands of northwestern Pacific crainage areas in best explained by the seasonal wet-dry climate and the resultant absence of evergreen forest in the region. On the Meseta Central where the climate supports a forest somewhat intermediate between the evergreen and deciduous formations *I. cenchoa* is found between 100-1500m.

Imantodes gemmistratus, on the other hand, is a common snake in the deciduous and transitional forests of Pacific Costa Rica and the Meseta Central, respectively. In the former area it is found from near sea-level to 500 m in elevation. The Meseta Central populations are continuous with the lowland ones and range onto the surrounding slopes up to 1936 m at the Paso Desengaño (Vara Blanca), but all other records for the species are from lower elevations.

The species is also found at scattered evergreen forest localities in the Atlantic lowlands and at two sites in the south-west Pacific area. On the Atlantic, *gemmistratus* generally occurs below 1000 m in elevation, but examples typical of the species occur in the gorge of the Río Reventazón in the vicinity of Cartago (1400-1500) and are related through snakes from intermediate localities (Turrialba 646 m and Río Chitaria 660 m) to Atlantic lowland populations.

Imantodes inornatus is an exclusively Atlantic evergreen forest form nearly restricted to the Atlantic and southwest Pacific lowlands in Costa Rica. Three records indicate a penetration locally into the premontane zone in the Cordillera de Tilarán (Monteverde, 1450 m) the north slope of the Cordillera Central (Cariblanco, 830 m) and in extreme southwestern Costa Rica (Las Cruces. 1200 m).

Sympatric Occurrences. As may be expected from the previous discussion of distribution, *Imantodes cenchoa* co-occurs with the other species of the genus at some localities in Costa Rica. There are no known instances of *I. gemmistratus* and *I. inornatus* being found at the same site. Documented sympatry or virtual sympatry is provided by the listing below:

I. cenchoa	Locality	I. gemmistratus
CRE 3261	Guanacaste: 2.2 km E Los Angeles de Tilarán	
	Los Angeles de Tilarán	UMMZ 131406
AMNH 17274	Alajuela: Montes del Aguacate	AMNH 17316 / 17330-31
NHMW 25472.1	San José: San José	numerous examples: AMNH, MCZ, NHMW, UMMZ, UCR
ZMH R01980		
KU 34032	Cartago: Turrialba	KU 35508-09
KU 35635-36		
UCR 2142-43	Cartago: Río Chitaria	UCR 6276
KU 25680	Limón: Los Diamantes	KU 13496
KU 25700		
FMNH 101245		
UMMZ 131409	Alajuela: San Carlos	UMMZ 131409Z
FMNH 103121	Alajuela; Isla Bonita	KU 25158
numerous examples CRE, UCR	Heredia; La Selva	numerous examples; CRE, UCR
CRE 2931	Cartago; Tres Equis	UCR 3413
CRE 851, 4461, 4588, 4607, 8056	Puntarenas: Monteverde	CRE 7201
numerous examples: CRE	Puntarenas: Rincón de Osa	LACM 114142-43

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RESUMEN

Imantodes inornatus e *Imantodes cenchoa* se encuentran en Costa Rica y recientemente se ha adelantado una hipótesis en el sentido que *I. cenchoa* es una amalgama de dos especies: *I. cenchoa* e *I. gemmistratus*. El análisis de los datos de escamación y coloración de los ejemplares de Costa Rica confirma que este complejo está compuesto por dos especies, una de las

cuales es obviamente *I. cenchoa*, de amplia distribución, que en Costa Rica se encuentra en las tierras bajas del Pacífico sudoccidental, en la Meseta Central, en las bajuras del Atlántico y en las estribaciones de las cordilleras y en la vertiente de los montes del Pacífico norte. No se le encuentra en las bajuras del Pacífico noroccidental. Una segunda especie ocurre en las bajuras del Pacífico noroccidental y en simpatría con *cenchoa* en la Meseta Central y en varias localidades de las bajuras del Atlántico y del Pacífico Sudoccidental. La segunda forma es alopátrica con *gemmistratus* de Panamá y difiere consistentemente de esta última con respecto a la escamación. Una revisión de los demás ejemplares centroamericanos y mexicanos asignados a *I. gemmistratus* (localidad tipo: El Salvador: Sonsonate: cerca del Volcán Izalco) indica que los ejemplares costarricenses son coespecíficos con ellas. La especie aparentemente está compuesta por tres subpoblaciones alopátricas a lo largo de la vertiente del Pacífico: El Salvador-Honduras; Nicaragua-Costa Rica; y Panamá. Existe, además, una cuarta subpoblación, más o menos alopátrica, en la vertiente atlántica de Costa Rica.

Es problemático el estatus sistemático de las poblaciones alopátricas del este de México y de la Península de Yucatán, asignadas recientemente por varios autores a *gemmistratus*. Otras poblaciones del Istmo de Tehuantepec y del oeste de México parecen candidatos más probables de ser coespecíficos con *gemmistratus*, aunque esto no se puede resolver con los datos que existen en la actualidad. Debe hacerse mención a una variación singular de un solo color de la vertiente del Pacífico de Costa Rica. *Imantodes inornatus* y *cenchoa* están restringidas (limitadas) a los hábitats del bosque perennifolio, mientras que *gemmistratus* es más abundante en los bosques caducifolios a lo largo de las costas occidentales de Centro América y México. Esta última especie se encuentra ocasionalmente en los bosques perennifolios en la vertiente atlántica de Costa Rica y en el centro de Panamá. Se sabe que *cenchoa* y *gemmistratus* son simpátricas en varios lugares de Costa Rica pero no así *I. inornatus* y la segunda especie. A menudo se captura a *I. cenchoa* y a *inornatus* juntas.

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