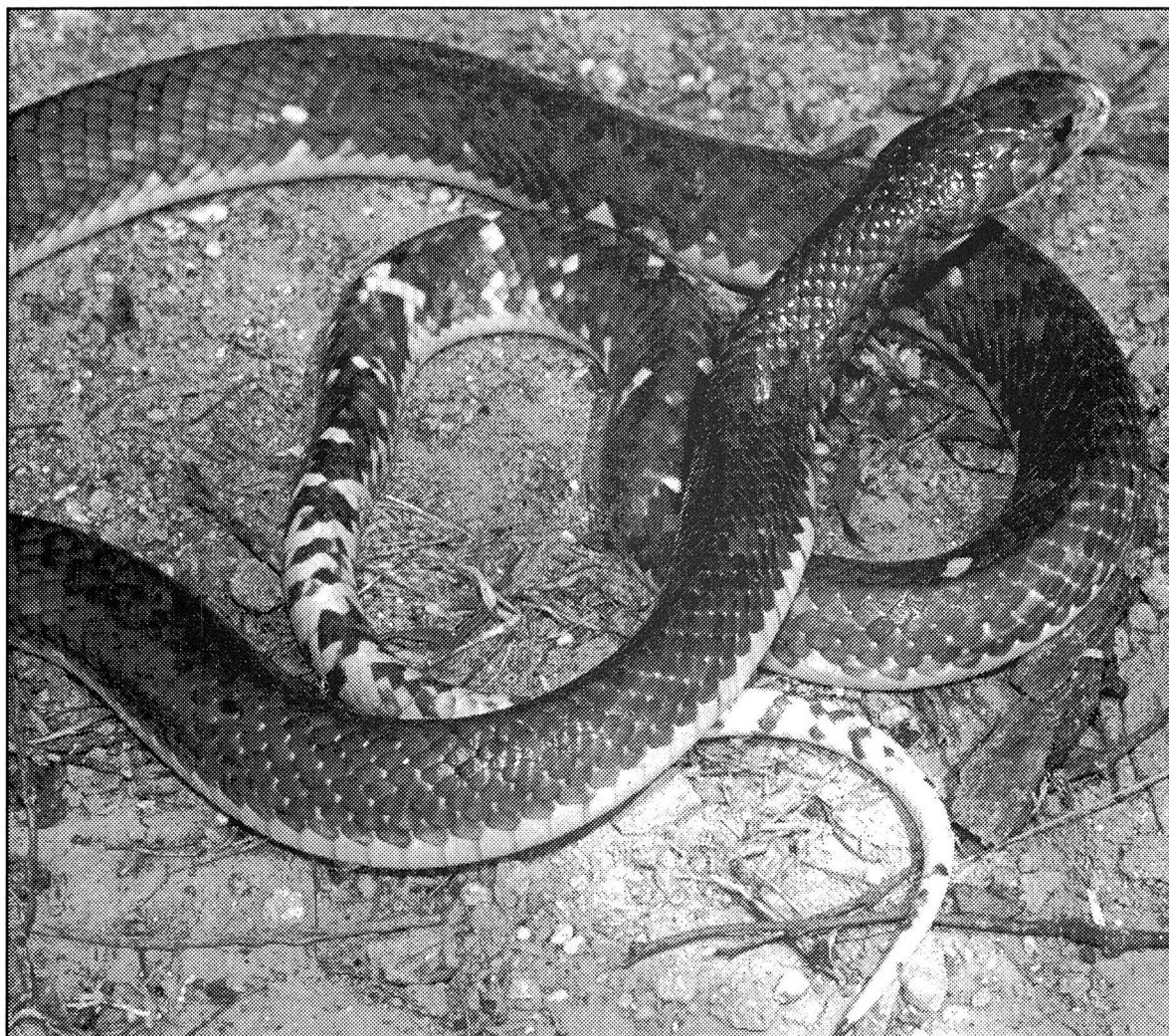


Volume 11, Number 4

October 2001

ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

A NEW SPECIES OF INDIGO SNAKE FROM NORTH-WESTERN VENEZUELA (SERPENTES: COLUBRIDAE: *DRYMARCHON*)

WOLFGANG WÜSTER¹, JOSÉ LUÍS YRAUSQUIN² AND ABRAHAM MIJARES-URRUTIA³

¹*School of Biological Sciences, University of Wales, Bangor, UK*

²*Departamento de Desarrollo Agrícola, Facultad de Agronomía, Universidad Francisco de Miranda, Venezuela*

³*CIEZA, Universidad Francisco de Miranda, Venezuela*

We describe a new species of snake of the genus *Drymarchon* from Falcón State, north-western Venezuela. The distinctive nature of this species, compared to the two other South American mainland taxa of *Drymarchon*, is supported by principal components analysis of scalation and colour pattern characters. The taxa *corais* and *melanurus*, hitherto considered conspecific, are found to be highly distinct, but homogeneous throughout their considerable ranges; consequently, we consider *melanurus* to be a full species, separate from *Drymarchon corais*.

Key words: *Drymarchon*, taxonomy, systematics, new species, multivariate morphometrics, South America

INTRODUCTION

The last two decades have seen a revival in interest in the alpha taxonomy of many groups of animals. This re-surgent interest can be traced to several factors, including the increasing awareness of the extreme rate of extinction caused by human activities, the development of new molecular (e.g. Avise, 1994) and numerical (e.g. Thorpe, 1976, 1987) methods for the investigation of species-level systematics, and a widespread shift from process-based species concepts (in particular, the biological species concept) towards historical concepts, such as the evolutionary and phylogenetic species concepts (Wiley, 1981; Cracraft, 1989; Frost & Hillis, 1990). In general, the current trend has been towards the recognition of clearly distinct taxa as separate species rather than subspecies, without undue concern for often untestable questions of reproductive compatibility.

During this paradigm shift, it has become apparent that the use of the biological species concept – which groups similar populations together on the basis of established or assumed reproductive compatibility – is likely to result in a serious underestimate of biological diversity and a misrepresentation of phylogeny (Cracraft, 1989). A number of studies have found that groups of populations formerly regarded as subspecies of a single species in reality represent divergent and independently evolving lineages, which should be given taxonomic recognition at the species level.

In many long-recognized, widespread, polytypic species, conspecificity of the various subspecies has never been investigated, but has become fixed in the literature through a three-stage process. The three stages are an initial plethora of species described independently for various “forms” (usually in the 19th century), followed by largely evidence-free lumping into a single species,

followed by inertia, whereby later workers accepted the various populations as conspecific subspecies out of habit, without fresh evidence of conspecificity. These lumped, polytypic species were described by Good (1994) as consequences of the “inertial species concept”, where polytypic species are retained due to inertia and lack of study rather than positive evidence of conspecificity. The use of this “concept” has been particularly prevalent in easily identified, monotypic genera, and in well-defined, distinctive groups (e.g. Asiatic cobras – Wüster & Thorpe, 1991; *Echis carinatus* – see Wüster & McCarthy, 1996; bushmasters – Zamudio & Greene, 1997), where most researchers appear to have contented themselves with the casual identification of specimens as *Naja naja*, *Echis carinatus* or *Lachesis muta*, without further questioning the affinities of the individual populations involved.

Another likely example of this phenomenon is represented by the colubrid genus *Drymarchon*, a widespread group of large and conspicuously distinctive colubrid snakes from South America, Central America and south-eastern North America. The nomenclatural history of the genus corresponds to the three-stage scenario described above: six taxa were described as full species between 1827 and 1905. However, throughout most of the 20th century, *Drymarchon* has been considered monotypic (e.g. Amaral, 1929; Smith, 1941; McCranie, 1980), consisting of the single species *D. corais* (Boie, 1827). Only two authors questioned the monotypy of *Drymarchon*: (1) Roze (1959) described *Drymarchon margaritae* as a full species, but later regarded it as a subspecies of *D. corais* (Roze, 1964); this was followed by practically all later authors (e.g. Peters & Orejas-Miranda, 1970; Lancini, 1986; Lancini & Kornacker, 1989), with the exception of Roze (1966), who returned *margaritae* to full species status while simultaneously expressing doubt about this; (2) Collins (1991) raised the Florida indigo snake to the status of a full species, *Drymarchon couperi*, but without providing any

Correspondence: W. Wüster, School of Biological Sciences, University of Wales, Bangor, Gwynedd, LL57 2UW, Wales, UK. E-mail: w.wuster@bangor.ac.uk

TABLE 1. Morphological characters used for multivariate analysis of South American *Drymarchon*

-
1. Ventrals
 2. Subcaudals
 3. Anterior temporals
 4. Contact upper anterior temporal - posterior temporal(s) (0 = none, 0.5 = one side, 1 = both sides)
 5. Posterior temporals
 6. %VS position of reduction 19 to 17 rows
 7. %VS position of reduction 17 to 15 rows
 8. %CS position of reduction 10 to 8 rows
 9. %CS position of reduction 8 to 6 rows
 10. %CS position of reduction 6 to 4 rows
 11. Change of colour along dorsum (1 = darker at front, 0 = uniform, -1 = darker at back)
 12. Oblique black mark on side of neck (1 = present, 0 = absent)
 13. Presence of individual paler scales (1 = present, 0 = absent)
 14. Change of colour along ventral side (1 = darker at front, 0 = uniform, -1 = darker at back)
 15. Underside of tail pale or dark (1 = dark, 0 = pale)
 16. Presence of individual dark subcaudals (1 = present, 0 = absent)
 17. Presence of obvious dark edges on supralabials
-

evidence to support this action, which has not been widely followed. The monospecificity of the remainder of the genus has not been questioned, despite conspicuous qualitative differences in coloration (see illustrations in Mehrtens, 1987, for example), as well as scalation differences (Smith, 1941) between different subspecies.

On the mainland of South America, two well-differentiated subspecies of *Drymarchon corais* have been widely recognized: *Drymarchon corais corais* (Boie, 1827) is reported from east of the Andes, and *D. c. melanurus* (Duméril, Bibron & Duméril, 1854) from west of the Andes as well as northern Venezuela (Peters & Orejas-Miranda, 1970; Roze, 1966). The ranges of the two forms meet in northern Venezuela, albeit with an element of ecological separation: *D. c. corais* is reported from hot lowlands, whereas *D. c. melanurus* is reported to occur in higher, mesic areas in the west and north of the country (Roze, 1966; Lancini, 1986; Lancini & Kornacker, 1989; La Marca *et al.*, 1995). During work in Falcón State, Venezuela, the authors encountered specimens of the genus *Drymarchon* that could not be assigned to either of these two taxa. This prompted the present investigation of the population systematics of this genus in South America.

MATERIALS AND METHODS

In order to analyse the affinities of the new Venezuelan taxon in relation to the established taxa, we used multivariate analysis of characters of scalation and colour pattern. Compared to character-by-character approaches to morphological systematics, multivariate morphometrics has the advantage of comparing the generalised phenotypes of the animals concerned, resulting in a more robust assessment of patterns of morphological differentiation and the elucidation of relatively subtle patterns of geographic variation missed in conventional systematics (e.g., Wüster *et al.*, 1992). Furthermore, multivariate techniques such as principal

components analysis, which do not rely on *a priori* grouping of specimens, can reveal patterns of geographic variation unconstrained by prior assumptions of taxon membership. This avoids the circularity inherent in assigning each specimen to a predetermined taxon based on some aspect of morphology or appearance, and then comparing these taxa.

For this analysis, we used preserved material from a number of natural history collections, listed in the Acknowledgements. The assessment of the distinctiveness of the new form requires an appraisal of as much of the spectrum of geographic variation of the other relevant taxa as possible. We therefore examined specimens from most parts of the range of *D. corais corais* (Venezuela to southern Brazil) and *D. c. melanurus* (Mexico to Ecuador). The specimens used are listed in Appendix 1.

Based on initial observations and literature data, 17 morphological characters were selected and recorded from all available specimens (Table 1). In order to characterize the position of dorsal scale row reductions along the body and tail, the ventral scales were numbered according to the method of Dowling (1951), and the subcaudal scales starting from the first pair in contact along the ventral midline behind the vent (not including the tail spine). In *Drymarchon*, dorsal scale row reductions involve fusions of scale rows 3 and 4, 4 and 5, or 5 and 6. On the tail, the reductions generally involve the highest pair of rows on each side of the vertebral line. The position of each scale row reduction was noted as the number of the ventral or subcaudal pair directly above which it was situated. This was then converted to % ventral scale row count (%VS) or % caudal scale count (%CS), to compensate for differences in the numbers of ventral and subcaudal scales among different individuals.

In order to visualize the pattern of variation in morphology among the three taxa included in the study, we used principal components analysis (PCA), run on the

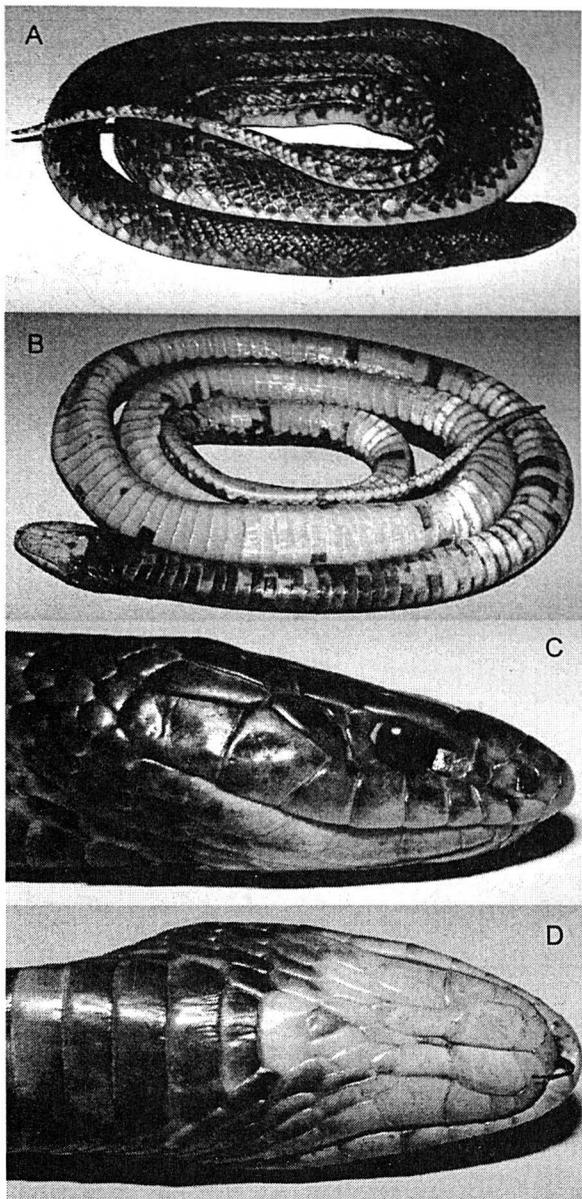


FIG. 1. A, dorsal side; B, ventral side of the holotype of *Drymarchon caudomaculatus* (EBRG 3412). Note the pale mottling, the dark throat, the isolated dark subcaudals and the lack of colour change along the body. C, lateral view; D, ventral view of the head of EBRG 3412.

data recorded from individual specimens. Before analysis, each character was converted to zero mean and unit standard deviation. Analyses were carried out both separately for the two sexes, and for specimens of the two sexes combined. Since sexual dimorphism among the characters studied did not confound the analysis, the results of the combined analysis are presented here. The ordination of individual specimens along the first two principal components was plotted out.

RESULTS

DRYMARCHON CAUDOMACULATUS SP. NOV.

Holotype. EBRG 3412, an adult female (Fig. 1). On the road to Los Tablones, 1 km from the junction with the

new Coro-Churuguara road, Municipio Colina, Estado Falcón, Venezuela. Found freshly road-killed at 9.20 am on 16.7.1997. The locality is situated approximately 1 km from the village of Las Dos Bocas (11°18'N, 69°24'W), in the eastern foothills of the Sierra de San Luis, at an altitude of approximately 110 m. The vegetation consists of semi-deciduous tropical forest, with a canopy height of approximately 5-10 m, and moderate anthropogenic intervention. Collected by W. Wüster and J.L. Yrausquin.

Diagnosis. *Drymarchon caudomaculatus* is easily distinguishable from the other two taxa of *Drymarchon* found on the South American mainland (see Table 2).

In their colour pattern, adults of *Drymarchon caudomaculatus* differ from *D. c. corais* in lacking any obvious change of hue along the dorsal side of the body, in having the anterior part of the venter more or less covered with dark pigment, in having scattered paler scales on the posterior body, and in having isolated dark subcaudals under an otherwise pale tail. Additionally, *D. caudomaculatus* has consistently lower subcaudal scale counts than any of the *D. c. corais* examined in this study or listed by Amaral (1929) (65 or fewer, vs. 66 or more in *D. c. corais*). In most specimens of *D. c. corais*, the dorsal scale row reductions are situated in a more posterior position and the caudal scale row positions in a more anterior position than in the new species. Almost all adult specimens of *D. c. corais* show a conspicuous change in body coloration along the dorsum, being dark anteriorly and pale posteriorly. This is contrary to the key to the subspecies of *Drymarchon corais* in Peters & Orejas Miranda (1970), which erroneously states *D. c. corais* to be uniformly black above. The extent of melanization in this form is in fact very variable (pers. obs.; compare photographs in Moonen *et al.* (1979) and Murphy (1997)). Finally, *D. c. corais* also lacks dark pigmentation of the throat area, and we have not seen specimens with isolated paler scales on the body.

The colour pattern of adult *D. caudomaculatus* differs from that of adult *D. c. melanurus* in lacking any obvious change of hue along the dorsal side of the body (posterior body and tail conspicuously darker in *D. c. melanurus*), in having the anterior part of the venter more or less covered with dark pigment (anterior part pale, posterior part dark in *D. c. melanurus*), in having scattered paler scales on the posterior body and isolated dark subcaudals under an otherwise pale tail (subcaudal surface uniformly dark in *D. c. melanurus*), in lacking the distinct black, oblique bars found on the side of the neck in *D. c. melanurus*, and in lacking distinct black supralabial edges. In its scalation, *D. caudomaculatus* displays consistently lower subcaudal scale counts (65 or fewer) than any *D. c. melanurus* examined in this study or by Amaral (1929) or Smith (1941) (71 or more). However, McCranie (1980) listed subcaudal scale counts as low as 59 for *D. c. melanurus*, without indicating the origin of the specimens concerned. The caudal scale row reductions are generally in a more anterior position in *D. c. melanurus* than in *D. caudomaculatus*.

TABLE 2 Range of variation of selected scalation and colour pattern characters in the three South American species of *Drymarchon*. * General colour pattern and ventral and subcaudal scale counts, were recorded from two additional live specimens.

	<i>D. caudomaculatus</i>	<i>D. corais</i>	<i>D. melanurus</i>
Sample size	2-4*	29	12
Ventrals	195-200	188-216	196-214
Subcaudals	61.5-64.5	66-81	71-93
%VS position of reduction from 19 to 17 rows	6.7-9.1	3.2-8.4	5.0-8.4
%VS position of reduction from 17 to 15 rows	66.0-77	70.5-94.8	59.8-78.0
%CS position of reduction from 10 to 8 rows	7.3-7.9	2.8-8.6	2.8-5.9
%CS position of reduction 8 to 6 rows	17.9-27.0	6.3-26.5	9.9-21.5
%CS position of reduction 6 to 4 rows	56.1-56.3	31.2-64.2	35.9-50.0
Change of colour along dorsum in adults	Uniform	Darker anteriorly, paler posteriorly	Paler anteriorly, darker posteriorly
Oblique black mark on side of neck	Absent	Absent	Present
Presence of individual paler or darker scales	Present	Absent	Absent
Change of colour along ventral side	Often dark or mottled anteriorly	Uniform	Darker posteriorly
Underside of tail	Pale	Pale	Dark
Presence of individual dark or pale subcaudals	Present or absent	Absent	Absent

Drymarchon caudomaculatus is easily distinguished from the remaining taxa of *Drymarchon*, which are not found on the South American mainland. *Drymarchon couperi* is uniformly blackish-blue above as an adult, and the antepenultimate supralabial is excluded from contact with the postoculars or temporals by a contact between the two adjoining labials below the eye. *Drymarchon corais unicolor* lacks the dark throat, has a darker posterior venter, 70 or more subcaudals, and often over 200 ventrals. Adult *D. c. rubidus* are black dorsally, lack a dark throat, have a dark posterior belly, black-edged supralabials, and more subcaudals (69 or more) than *D. caudomaculatus*. Adult *D. c. orizabensis* are black dorsally, all but the anterior third of the venter is black, and they have higher subcaudal counts (71-78). Adult *D. c. erebennus* are blackish above posteriorly, spotted anteriorly, and have dark diagonal markings on the sides of the neck. Additionally, this subspecies usually has 14 dorsal scale rows anterior to the vent.

Etymology. The term *caudomaculatus* refers to the spotted aspect of the tail of adult specimens.

DESCRIPTION OF HOLOTYPE

Body scalation. 197 ventrals, 61/62 subcaudals, all paired, anal entire. Dorsal scales smooth, with double apical pits, in 17 rows at midbody. Dorsal scale reduction formula: 21 4+5(6/8) 19 2+3(15/21) 17 2+3(129)/3+4(131) 15 7+8(195) 14 +8(196/196) 16. Caudal scale reduction formula: 12 3+4(3) 11 3+4(4)/4+5(4) 9 4+5(5) 8 3+4(10/12) 6 2+3(34/35) 4 1+2(61) 3.

Head scalation. 8/8 supralabials, fourth and fifth enter orbit, seventh and eighth very large; 9/9 infralabials; 1/1 preoculars (very high); 2/2 postoculars; 2/2 anterior temporals, upper very small; lower anterior temporal contacts parietal behind upper anterior temporal, excluding latter from contact with posterior temporals. 2/2 posterior temporals, lower long and narrow. Two pairs of chin shields, posterior pair separated by small scale.

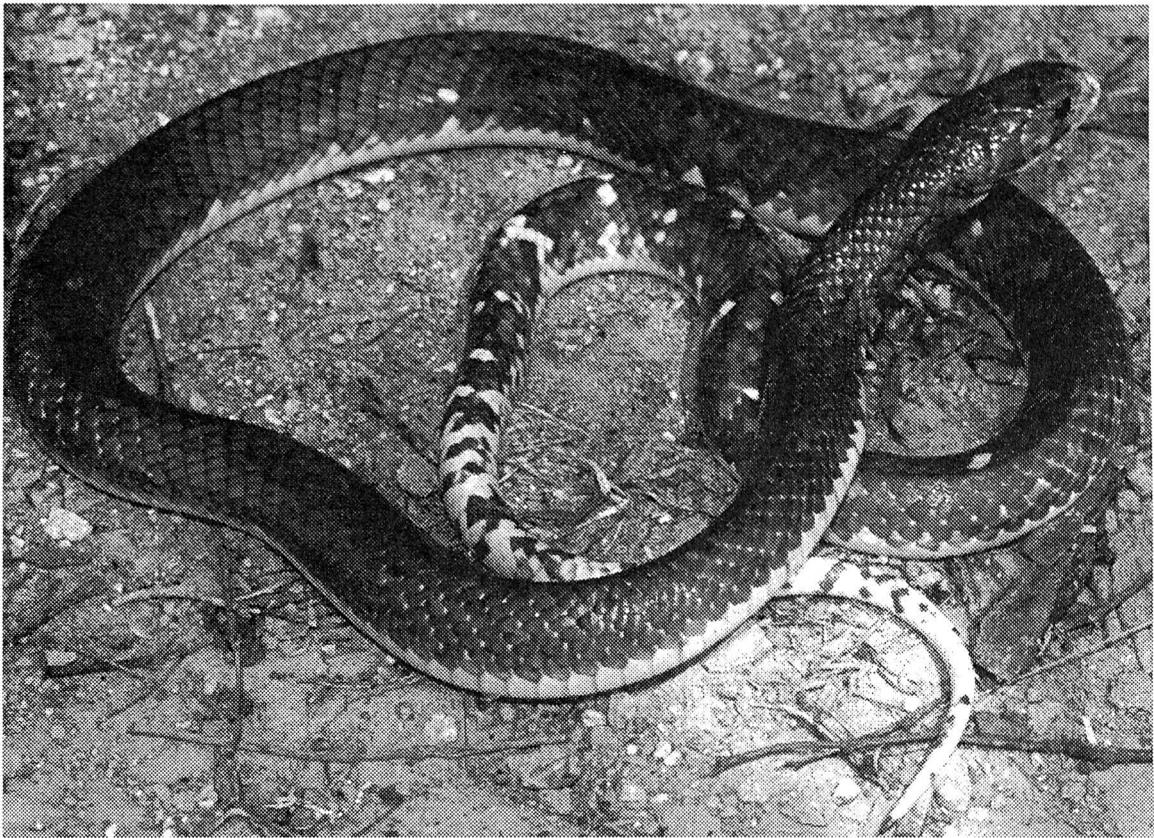


FIG. 2. Live specimen of *Drymarchon caudomaculatus*, a male with a total length of 1360 mm, from an unknown locality in Falcón State, Venezuela.

Posterior pair slightly longer but narrower than anterior pair. Rostral visible from above, broader than high. Internasals small, half the length of prefrontals. Frontal slightly broader (8.9 mm) than long (8.2 mm), straight anterior edge, narrower posteriorly, ends in obtuse angle, shorter than distance from rostral. Eye elongate, length 6.5 mm, height 4.6 mm, distance from edge of mouth 5.1 mm.

Dorsal pattern. Dorsum medium-brown throughout, without change along body. Extensive mottling with paler colours, becoming denser and more contrasting towards the posterior part of the body and the tail. Especially on the posterior body, some individual scales tend to be cream coloured, contrasting strongly with the ground colour. This is especially pronounced on the tail

Head pattern. Top of head of the same colour as dorsum, with cream marbling, especially along the parietal suture and along the sides. Rostral scale and anterior and central part of internasals cream. Chin shields, first 5 infralabials and other scales under head dirty white. Infralabials 6 and 7 white along edge of mouth, brown on lower part, infralabials 8 and 9 entirely brown. Posterior edges of supralabials slightly more densely pigmented, but no obvious dark edges.

Ventral pattern. Second preventral and first 24 ventrals largely covered in dark brown pigment, with some cream mottling; next 17 ventrals approximately half covered with dark pigment; dark and pale blotches occupy total width (anterior-posterior) of ventral. After

ventral 41, venter predominantly cream, with occasional dark spots occupying the entire width of their respective ventral, of variable lateral extent. Underside of tail predominantly cream, but 15 dark, isolated half-subcaudals (half of pair) out of a total of 123 are medium to dark brown.

Dimensions. Snout-vent length 1305 mm; tail length 257 mm; head length from snout to end of quadrate: 49.9 mm; head width across supraoculars: 18.0 mm.

VARIATION

Paratype. EBRG 3413, a female. Locality: Approximately 15 km (by road) SE of Coro, on the new Coro-Churuguara road, Municipio Colina, Estado Falcón, Venezuela (approximately 11°21' N and 69°35' W). Collected at an altitude of approximately 150 m, at 1730 h on 19.01.1993, while crossing the road. Generally similar to the holotype, with the following differences: 195 ventrals; 61 subcaudals, but the tail tip is missing, and the true subcaudal count is likely to have been about 2 or 3 scales higher. The upper anterior temporal is missing on the left, and does not contact the posterior temporal on the right, due to a contact between the lower anterior temporal and the parietal. Body scale row reduction: 23 4+5(4/4) 21 4+5(6/7) 19 3+4(12/14) 17 3+4(149/150) 15 +3(195/195)/7+8(195) 16. Tail scale row reduction formula: 10 3+4(5)/4+5(5) 8 3+4(16/18) 6 2+3(34/37) 4. Pattern: generally as in the holotype; however, this specimen displays far more scattered pale

TABLE 3. Eigenvector coefficients of the 17 characters along the first two principal components of the PCA. For details of characters, see Table 1.

	PC1	PC2
1. Ventrals	0.093	0.251
2. Subcaudals	0.215	0.115
3. Anterior temporals	-0.060	0.184
4. Contact ant.-post. temporals	0.185	0.213
5. Posterior temporals	0.097	-0.002
6. Reduction 19-17 rows	0.006	-0.319
7. Reduction 17-15 rows	-0.254	0.250
8. Reduction 10-8 rows	-0.220	-0.302
9. Reduction 8-6 rows	-0.165	-0.300
10. Reduction 6-4 rows	-0.258	-0.178
11. Dorsal colour change	-0.355	0.276
12. Oblique bars on neck	0.388	-0.194
13. Individual pale scales	-0.158	-0.428
14. Ventral colour change	-0.397	0.083
15. Underside of tail	0.388	-0.194
16. Dark subcaudals	-0.124	-0.355
17. Supralabial edges	0.259	-0.012

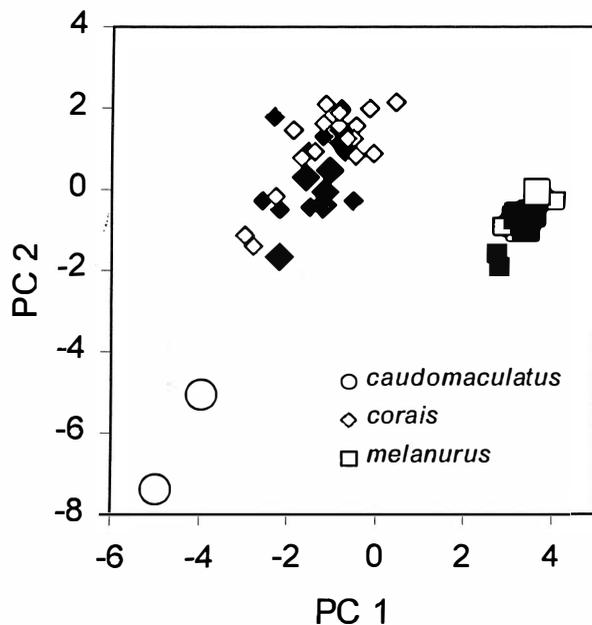


FIG. 3. Ordination of the specimens of the South American taxa of *Drymarchon* along the first two principal components of PCA 1. The distinctiveness of the three forms, and the very minor role played by sexual dimorphism, are obvious. The first and second principal components summarize 33.1% and 17.1% respectively, of the total variance of the data. Solid and hollow symbols denote male and female specimens, respectively, and enlarged symbols denote specimens from western Venezuela, where the distributions of the three taxa approach each other or overlap.

scales, and the throat and anterior part of the venter contains only isolated dark markings instead of a large mottled area.

Other preserved material: MCNC 1019, Coro, Estado Falcón, Venezuela (11°25' N, 69°41' W), coll. 1959 by Erasmo Durán; MCNC 2251, Taratara, Estado Falcón, Venezuela (11°29' N, 69°30' W) coll. April 1962 by Erasmo Durán. In addition, two live specimens from unknown localities in Falcón State were observed in a private collection. The first was a male with a snout-vent length of 1134 mm and a tail length of 226 mm, 192 ventrals and 64.5 subcaudal pairs; the upper anterior temporals were in contact with the posterior temporals on both sides; the pattern was as described previously, with extensive pale mottling on the tail (Fig. 2). The second live specimen was another male with a snout-vent length of 1452 mm and a tail length of 280 mm, 200 ventrals and 64 subcaudals; the upper anterior temporals were in contact with the posterior temporals on both sides; the pattern was as described in the other specimen, although with relatively little pale mottling on the dorsum.

Three further road-killed specimens were recorded by one of us (JLY), but not collected due to their bad condition. The localities were Tocópero, Municipio Tocópero (11°30' N, 69°16' W), Sector Barrialito, Cumarebo, Municipio Zamora (11°28' N, 69°19' W), and an additional specimen from Coro, all in Falcón State, Venezuela.

It should be noted that no juvenile specimens of this form are known. In other *Drymarchon*, the juvenile pattern can differ substantially from the adult pattern.

MULTIVARIATE MORPHOMETRICS

The PCA ordination plot (Fig. 3) clearly shows the existence of three cohesive, highly distinct clusters. These correspond to the two widely recognized South American subspecies of *D. corais* (*D. c. corais* and *D. c. melanurus*) and *D. caudomaculatus*. The first principal component primarily separates *D. c. melanurus* from the remaining specimens. Separation along this axis is primarily related to variation in the patterns of colour change along the dorsum, the presence or absence of oblique black bars on the neck, and colour change along the ventral surface (Table 3). The second principal component separates the specimens of *D. caudomaculatus* from those of *corais* and *melanurus*. Separation of specimens along the second axis is mostly related to the presence of individual pale scales, and also the number of ventrals, the position of caudal scale reductions, and the presence or absence of dark edges along the supralabials (Table 3).

It can be seen that sexual dimorphism had minimal effect on the ordination of the specimens. Furthermore, it can also be seen that specimens from western Venezuela, where the distributions of the three taxa involved approach each other or overlap, show no tendency towards intergradation.

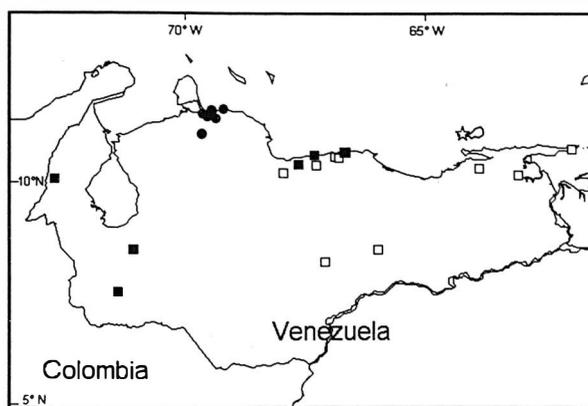


FIG. 4. Locality records of the four species of *Drymarchon* found in northern Venezuela. Records refer to specimens examined as part of this study, and locality records provided by Roze (1966). Circles represent *D. caudomaculatus*; hollow squares, *D. corais*; solid squares, *D. melanurus*; and the star, *D. margaritae*.

DISCUSSION

The results of the principal components analysis show clearly that three taxa of *Drymarchon* are found in mainland South America. Two correspond to the conventional subspecies *corais* and *melanurus*, and the third corresponds to the new taxon from Venezuela.

It is particularly notable that the two conventional subspecies, *Drymarchon corais corais* and *D. c. melanurus*, form cohesive clusters in the ordination, despite the geographically and ecologically diverse origins of the specimens involved. Furthermore, specimens from adjoining localities in northern and western Venezuela do not show any evidence of intergradation. Amaral (1929) suggested the existence of specimens intermediate between *corais* and *melanurus* in Colombia, but without providing further details; on the other hand, Pérez-Santos & Moreno (1988) indicate sympatry between the two forms in central and northern Colombia, but these records must be treated with scepticism (Cadle, 1992). It is also obvious that the new taxon is not morphologically intermediate between *D. c. corais* and *D. c. melanurus*. The hypothesis that it represents a hybrid population between the two subspecies can therefore be rejected.

The principal question is therefore the taxonomic level at which these taxa should be recognized. In recent years, there has been an increasing trend for diagnostically distinct populations to be recognized as full species, whereas the recognition of subspecies has become increasingly uncommon (Frost & Hillis, 1990). This use of the evolutionary species concept contrasts with the biological species concept, in which the potential or actual ability to interbreed is taken as a sign of conspecificity.

The three taxa of *Drymarchon* revealed here differ qualitatively, being unambiguously diagnosable in a number of features of colour pattern – and quantitatively in various scalation characters – often with little

or no overlap between the three forms (see Table 2). The distributions of the three forms approach each other in northern Venezuela (Fig. 4), very closely in the case of *D. c. corais* and *D. c. melanurus*, but there are no reliably documented zones of sympatry or intergradation between them. Consequently, we have no data on whether they are reproductively compatible. However, in view of the degree of differentiation of the three forms, and the homogeneity of two of them across a broad range, we believe that all three should be considered distinct evolutionary species: *Drymarchon corais*, *D. melanurus* and *D. caudomaculatus*.

The affinities of the remaining conventional subspecies of *Drymarchon* remain unresolved for the time being. There are no obvious reasons for believing that any of these forms is conspecific with *D. corais* sensu stricto. The taxon *margaritae* displays a unique combination of pattern characters, including a dorsal colour change similar to that of *D. corais* (dark anteriorly, paler markings posteriorly), but a ventral pattern change more akin to that of *D. melanurus* (darker posteriorly, compared to uniformly pale throughout in *D. corais*). The only known specimen has 76 subcaudals, compared to a documented maximum of 64.5 in *D. caudomaculatus*. In the light of these clear, categorical differences, and pending further studies, we consider this form to be a separate species, *D. margaritae*, as originally proposed by Roze (1959).

In North America, like Collins (1991), we regard *Drymarchon couperi* as a separate species from other *Drymarchon*, on account of apparently consistent differences in labial scalation (Smith, 1941). However, further studies are required to confirm the status of this taxon.

In Central America, Smith (1941) noted the existence of hybrid zones between *melanurus* on one hand and the taxa *erebennus*, *orizabensis* and *rubidus* on the other. Additionally, juveniles and some adults of *erebennus*, *rubidus* and *unicolor* display oblique dark bars on the sides of the neck, which appear to be homologous with the marks seen in *D. melanurus* (no *orizabensis* were examined). Although the sister taxon to *Drymarchon* is unresolved, these dark marks appear to be unique to these taxa, and can therefore be regarded as a synapomorphy for these populations. This makes the classification of the taxa *erebennus* Cope, 1860, *rubidus* Smith, 1941, *unicolor* Smith, 1941 and, presumably, *orizabensis* Dugès, 1905, as subspecies of *D. melanurus* (Duméril, Bibron & Duméril, 1854), a tenable provisional arrangement. Further studies of the complex as a whole are clearly urgently required, and molecular methods may make a significant contribution towards the illumination of the evolution and systematics of this group.

NATURAL HISTORY NOTES

Little is known of the biology of the new species. It appears to be diurnal, and the two specimens in which

time of capture is known were active in the early morning or late afternoon. Most known specimens originate from within 45 km of the city of Coro, Estado Falcón, Venezuela, to the east and south-east of the city (Fig. 4), but Mijares-Urrutia & Arends (2000) cite a specimen from El Paují (10°48' N, 69°37' W). The actual distribution of the species may be greater. Until very recently (Mijares-Urrutia & Arends, 2000), the herpetofauna of Falcón State has received much less attention from collectors than most other parts of Venezuela. For instance, Roze (1966) lists a record for only one single species of snake for the entire western half of the state, and many species common even in the surroundings of Coro (pers. obs.) have no records for the state. However, it is worth noting that no *Drymarchon* was included in a collection from south-eastern Falcón State (Shreve, 1947).

ACKNOWLEDGEMENTS

We wish to thank the curators and staff of the following collections for allowing us to examine specimens in their care, or themselves recording data for the authors: Natural History Museum (BM - London), Carnegie Museum of Natural History (CM - Pittsburgh), Zoological Museum of the University of Copenhagen (ZMUC - Denmark), Instituto Butantan (IB - São Paulo, Brazil), Muséum national d'Histoire naturelle (MHNP - Paris), Muséum d'Histoire naturelle de Genève (MHNG - Geneva), Naturhistoriska Riksmuseet (NRM - Stockholm), Estación Biológica de Rancho Grande, Ministerio del Ambiente y de los Recursos Naturales Renovables (EBRG - Maracay, Venezuela), and Museo de Ciencias Naturales de Caracas (MCNC - Venezuela). WW's visit to Venezuela was funded by a Research Career Development Fellowship from the Wellcome Trust.

REFERENCES

- Amaral, A. do (1929). Estudos sobre ofídios neotrópicos. XXI. Revisão do gênero *Drymarchon* Fitzinger. *Memórias do Instituto Butantan* **4**, 323-330.
- Avise, J. C. (1994). *Molecular Markers, Natural History and Evolution*. New York: Chapman & Hall.
- Cadle, J. E. (1992). On Colombian snakes. *Herpetologica* **48**, 134-143.
- Collins, J. T. (1991). Viewpoint: a new taxonomic arrangement for some North American amphibians and reptiles. *Herpetological Review* **22**, 42-43.
- Cracraft, J. (1989). Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In *Speciation and its consequences*, 28-59. Otte, D. & Endler, J.A. (Eds.). Sunderland, Mass: Sinauer Associates.
- Dowling, H. G. (1951). A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* **1**, 97-99.
- Frost, D. R. & Hillis, D. M. (1990). Species in concept and practice: herpetological applications. *Herpetologica* **46**, 87-104.
- Good, D. A. (1994). Species limits in the genus *Gerrhonotus* (Squamata: Anguillidae). *Herpetological Monographs* **7**, 180-202.
- La Marca, E., Soriano, P.J. & Casado, R. (1995). Geographic Distribution. *Drymarchon corais melanurus*. *Herpetological Review* **26**, 109.
- Lancini, V. A. R. (1986). *Serpientes de Venezuela*. Caracas: Ernesto Armitano.
- Lancini, V. A. R. & Kornacker, P. M. (1989). *Die Schlangen von Venezuela*. Caracas: Ernesto Armitano.
- McCranie, J. R. (1980). *Drymarchon Fitzinger - Indigo snake*. *Catalogue of the American Amphibians and Reptiles* **267**, 1-4.
- Mehrtens, D. M. (1987). *Living Snakes of the World in Colour*. New York: Sterling Publishing Company.
- Mijares-Urrutia, A. & Arends, A. (2000). Herpetofauna of Estado Falcón, Northwestern Venezuela: a checklist with geographical and ecological data. *Smithsonian Herpetological Information Service* **123**, 1-30.
- Moonen, J., Eriks, W. & van Deursen, K. (1979). *Surinaamse Slangen in Kleur*. Paramaribo: Kersten & Co.
- Murphy, J. C. (1997). *Amphibians and Reptiles of Trinidad & Tobago*. Malabar, Florida: Krieger Publishing Co.
- Pérez-Santos, C. & Moreno, A. G. (1988). *Ofidios de Colombia*. Torino: Museo Regionale di Scienze Naturali.
- Peters, J. A. & Orejas-Miranda, B. (1970). Catalogue of the Neotropical Squamata. Part I. Snakes. *Bulletin of the United States National Museum* **297**, 1-347.
- Roze, J. A. (1959). Una nueva especie del género *Drymarchon* (Serpientes: Colubridae) de la Isla de Margarita, Venezuela. *Novedades Científicas - Contribuciones Ocasionales del Museo de Historia Natural La Salle* **25**, 1-4.
- Roze, J. A. (1964). La herpetología de la Isla de Margarita, Venezuela. *Memorias de la Sociedad de Ciencias Naturales La Salle* **24**, 209-241.
- Roze, J. A. (1966). *La Taxonomía y Zoogeografía de los Ofidios de Venezuela*. Caracas: Editora Biblioteca, Universidad Central de Venezuela.
- Shreve, B. (1947). On Venezuelan reptiles and amphibians collected by Dr. H.G. Kugler. *Bulletin of the Museum of Comparative Zoology* **99**, 519-535.
- Smith, H. M. (1941). A review of the subspecies of the indigo snake (*Drymarchon corais*). *Journal of the Washington Academy of Science* **31**, 466-481.
- Thorpe, R. S. (1976). Biometric analysis of geographic variation and racial affinities. *Biological Reviews* **51**, 407-452.
- Thorpe, R. S. (1987). Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Bolletino di Zoologia* **54**, 3-11.
- Wiley, E. O. (1981). *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. New York: John Wiley & Sons.
- Wüster, W. & McCarthy, C. J. (1996). Venomous snake systematics: implications for snakebite treatment and

toxinology. In *Envenomings and their Treatments*, 13-23. Bon, C. & Goyffon, M. (Eds.). Lyon: Fondation Mérieux.

- Wüster, W., Otsuka, S. Thorpe, R. S. & Malhotra, A. (1992). Morphological variation in Russell's viper in Burma and Thailand. *Herpetological Journal* **2**, 99-101
- Wüster, W. & Thorpe, R. S. (1991). Asiatic cobras: systematics and snakebite. *Experientia* **47**, 205-209.
- Zamudio, K. R. & Greene, H. W. (1997). Phylogeography of the bushmaster (*Lachesis muta*: Viperidae): implications for neotropical biogeography, systematics and conservation. *Biological Journal of the Linnean Society* **62**, 421-442.

Accepted: 8.6.01

APPENDIX 1

Material examined (specimens marked with *asterisks were not included in PCAs due to missing characters):

Drymarchon caudomaculatus

VENEZUELA: Falcón: 15 km SE Coro, on Coro-Churuguara Road (EBRG 3413); Las Dos Bocas (EBRG 3412); Coro (MCNC 1019*); Taratara (MCNC 2251*).

Drymarchon corais

BOLIVIA: "Bolivia" (BM 94.5.4.3); BRAZIL: Amazonas: Boca do Tefé (MHNP 1900-460); Bahia: Cabuçu, Santo Amaro (IB 23027); Mato Grosso: Barracão Queimado (IB 22567); Nobres (IB 54995); Pará: Caripe (BM rr 1964.1521); Ilha de Marajó (BM 1923.11.9.108-110); São Paulo: Fernandópolis: Usina

Hidroelétrica Agua Vermelha (IB 41744, 41918, 41929, 41937, 41950, 42173, 42216, 42030, 42229, 42232); Sergipe: Maruim (ZMUC r 60271); FRENCH GUYANA: Cayenne (MHNP 3332*, 3369); GUYANA: Demerara (BM 55.8.28.19); "Demerara River" (BM 1929.7.13.12); Dora Mission, 30 mi. North of Linden (BM 1977.308); PARAGUAY: Alto Paraguay: Primavera (BM 1956.1.16.36); SURINAME: "Suriname" (ZMUC r 60270); Paramaribo (BM 1946.4.4.15); Zanderij (BM 1946.4.4.14); TRINIDAD AND TOBAGO: "Trinidad" (BM rr 1964.1522, 1900.11.8.1); Hollis Dam Road: (BM 1964.1986); VENEZUELA: "La Morrocoy" (IB 25704); Aragua: Pie del Cerro, La Victoria (CM s 7420); Bolívar: Camarata (BM 1976.236); Carabobo: Valencia (ZMUC r 60317); Guárico: Paso del Caballo (IB 25707).

Drymarchon melanurus

BELIZE: Stann Creek (BM 91.3.4.4); COLOMBIA: Cauca: Buenaventura (NRM KVS 1964.820084887); Chocó: Condoto: Piña Lisa (BM 1914.5.21.37); COSTA RICA: Cartago (BM 71.1a.22.7); ECUADOR: Esmeraldas: Paramba (BM 1901.2.29.106); Loja: Catamayo Valley 30 km SW of Loja (BM 1935.11.3.73); Hacienda Juanes, 20 km W of Loja (BM 1935.11.3.74); GUATEMALA: Alta Verapaz: San Cristóbal Verapaz: Baleú (BM 1967.287); "Guatemala" (BM 1967.289); HONDURAS: ISLAS DE LA BAHÍA: Isla Borraca (BM 1938.10.4.90); MEXICO: "Yucatán" (BM 80.7.13.14); Tabasco: Teapa (BM 93.4.26.31); NICARAGUA: San Juan del Norte (NRM 517*); VENEZUELA: Distrito Federal: Camuri (MHNG 1363.35), Puerto La Cruz (CM s 7292); Mérida: Mérida (BM 1905.5.31.64); Santa María de Caparo (CM 86900)