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

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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 resurgent 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. Asian 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; McRanie, 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...
Furthermore, multivariate techniques such as principal conventional systematics (e.g., Wüster
subtle patterns of geographic variation missed in con-
cal differentiation and the elucidation of relatively
in a more robust assessment of patterns of morphologi-
eralised phenotypes of the animals concerned, resulting
morphometrics has the advantage of comparing the gen-
numbers of ventral and subcaudal scales among dif-
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were compared according to the method of Dowling (1951), and
along the body and tail, the ventral scales were num-
characterize the position of dorsal scale row reductions
from all available specimens (Table 1). In order to char-
the subcaudal scales starting from the first pair in con-
tact along the ventral midline behind the vent (not
involve the highest pair of rows on each side of the ver-
and 5, or 5 and 6. On the tail, the reductions generally
including the tail spine). In Drymarchon, dorsal scale
reductions involve fusions of scale rows 3 and 4, 4
and 5, or 5 and 6. On the tail, the reductions generally
involves the highest pair of rows on each side of the ver-
D. c. corais 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 Venezue-
lan 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 morphologi-
cal differentiation and the elucidation of relatively subtle patterns of geographic variation missed in conven-
tional 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 geo-
graphic variation unconstrained by prior assumptions
of taxon membership. This avoids the circularity inher-
ent 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 Ac-
knowledgements. 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 char-
acterize the position of dorsal scale row reductions
along the body and tail, the ventral scales were num-
bered according to the method of Dowling (1951), and
the subcaudal scales starting from the first pair in con-
tact 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
involves the highest pair of rows on each side of the ver-
tebrae line. The position of each scale row reduction was
noted as the number of the ventral or subcaudal pair di-
rectly above which it was situated. This was then
converted to % ventral scale row count (%VS) or % cau-
dal scale count (%CS), to compensate for differences
in the numbers of ventral and subcaudal scales among dif-
ferent individuals.

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

<table>
<thead>
<tr>
<th>TABLE 1. Morphological characters used for multivariate analysis of South American Drymarchon</th>
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<tbody>
<tr>
<td>1. Ventrals</td>
</tr>
<tr>
<td>2. Subcaudals</td>
</tr>
<tr>
<td>3. Anterior temporals</td>
</tr>
<tr>
<td>4. Contact upper anterior temporal - posterior temporal(s) (0 = none, 0.5 = one side, 1 = both sides)</td>
</tr>
<tr>
<td>5. Posterior temporals</td>
</tr>
<tr>
<td>6. % VS position of reduction 19 to 17 rows</td>
</tr>
<tr>
<td>7. % VS position of reduction 17 to 15 rows</td>
</tr>
<tr>
<td>8. % CS position of reduction 10 to 8 rows</td>
</tr>
<tr>
<td>9. % CS position of reduction 8 to 6 rows</td>
</tr>
<tr>
<td>10. % CS position of reduction 6 to 4 rows</td>
</tr>
<tr>
<td>11. Change of colour along dorsum (1 = darker at front, 0 = uniform, -1 = darker at back)</td>
</tr>
<tr>
<td>12. Oblique black mark on side of neck (1 = present, 0 = absent)</td>
</tr>
<tr>
<td>13. Presence of individual paler scales (1 = present, 0 = absent)</td>
</tr>
<tr>
<td>14. Change of colour along ventral side (1 = darker at front, 0 = uniform, -1 = darker at back)</td>
</tr>
<tr>
<td>15. Underside of tail pale or dark (1 = dark, 0 = pale)</td>
</tr>
<tr>
<td>16. Presence of individual dark subcaudals (1 = present, 0 = absent)</td>
</tr>
<tr>
<td>17. Presence of obvious dark edges on supralabials</td>
</tr>
</tbody>
</table>
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 Luís, 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), and 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.
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 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


Head scalation. 8/8 supralabials, fourth and fifth enter orbit, seventh and eighth very large; 9/9 infralabials; 1/1 preoculares (very high); 2/2 postoculares; 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.

<table>
<thead>
<tr>
<th>Sample size</th>
<th>D. caudomaculatus</th>
<th>D. corais</th>
<th>D. melanurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ventrals</td>
<td>195-200</td>
<td>188-216</td>
<td>196-214</td>
</tr>
<tr>
<td>Subcaudals</td>
<td>61.5-64.5</td>
<td>66-81</td>
<td>71-93</td>
</tr>
<tr>
<td>%VS position of reduction from 19 to 17 rows</td>
<td>6.7-9.1</td>
<td>3.2-8.4</td>
<td>5.0-8.4</td>
</tr>
<tr>
<td>%VS position of reduction from 17 to 15 rows</td>
<td>66.0-77</td>
<td>70.5-94.8</td>
<td>59.8-78.0</td>
</tr>
<tr>
<td>%CS position of reduction from 10 to 8 rows</td>
<td>7.3-7.9</td>
<td>2.8-8.6</td>
<td>2.8-5.9</td>
</tr>
<tr>
<td>%CS position of reduction 8 to 6 rows</td>
<td>17.9-27.0</td>
<td>6.3-26.5</td>
<td>9.9-21.5</td>
</tr>
<tr>
<td>%CS position of reduction 6 to 4 rows</td>
<td>56.1-56.3</td>
<td>31.2-64.2</td>
<td>35.9-50.0</td>
</tr>
</tbody>
</table>

| 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 |
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. Infraceralbials 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 prefrontal 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 hr 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

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

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

<table>
<thead>
<tr>
<th>Character</th>
<th>PC1</th>
<th>PC2</th>
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</thead>
<tbody>
<tr>
<td>Ventrals</td>
<td>0.093</td>
<td>0.251</td>
</tr>
<tr>
<td>Subcaudals</td>
<td>0.215</td>
<td>0.115</td>
</tr>
<tr>
<td>Anterior temporals</td>
<td>-0.060</td>
<td>0.184</td>
</tr>
<tr>
<td>Contact ant.-post. temporals</td>
<td>0.185</td>
<td>0.213</td>
</tr>
<tr>
<td>Posterior temporals</td>
<td>0.097</td>
<td>-0.002</td>
</tr>
<tr>
<td>Reduction 19-17 rows</td>
<td>0.006</td>
<td>-0.319</td>
</tr>
<tr>
<td>Reduction 17-15 rows</td>
<td>-0.254</td>
<td>0.250</td>
</tr>
<tr>
<td>Reduction 10-8 rows</td>
<td>-0.220</td>
<td>-0.302</td>
</tr>
<tr>
<td>Reduction 8-6 rows</td>
<td>-0.165</td>
<td>-0.300</td>
</tr>
<tr>
<td>Reduction 6-4 rows</td>
<td>-0.258</td>
<td>-0.178</td>
</tr>
<tr>
<td>Dorsal colour change</td>
<td>-0.355</td>
<td>0.276</td>
</tr>
<tr>
<td>Oblique bars on neck</td>
<td>0.388</td>
<td>-0.194</td>
</tr>
<tr>
<td>Individual pale scales</td>
<td>-0.158</td>
<td>-0.428</td>
</tr>
<tr>
<td>Ventral colour change</td>
<td>-0.397</td>
<td>0.083</td>
</tr>
<tr>
<td>Underside of tail</td>
<td>0.388</td>
<td>-0.194</td>
</tr>
<tr>
<td>Dark subcaudals</td>
<td>-0.124</td>
<td>-0.355</td>
</tr>
<tr>
<td>Supralabial edges</td>
<td>0.259</td>
<td>-0.012</td>
</tr>
</tbody>
</table>

**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.
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).

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REFERENCES


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: Cariri (IB r 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: Maruí (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 r 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 7929); Mérida: Mérida (BM 1905.5.31.64); Santa María de Caparo (CM 86900).