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On the geographic distribution of the false coral snake, *Rhinobothryum bovallii* (Serpentes: Dipsadidae), in Colombia – a biogeographical perspective

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Analyses of the geographical distributions of species are essential to understand their evolutionary processes relative to time and space, due to the fact that the spatial arrangements of these are basically a result of the vicariant formation of the taxa involved (Craw et al. 1999, Morrone 2001). The Neotropics, especially the rainforest region known as the Choco biogeographical province (see Dinnerstein et al. 1995 and Mittermeier et al. 1999 for a geographical and biological definition), represent an area of great interest for the development of studies in this respect due to its high degree of biodiversity, the endemism patterns of some groups, and the geological dynamics that gave rise to its current arrangement (Müller 1972, Hernández-Camacho et al. 1992a, b, Webb 1997). It is well known that the snake fauna of this ecoregion is one of the richest and most varied in the world (Dixon 1979, Pérez-Santos & Moreno 1988, Rengifo & Lundberg 1999, Castaño-Mora et al. 2004), presenting in general a high percentage of endemic species (for Colombia see Table 1), although there also exists a high representation of species that are shared with other ecoregions of South and Central America (Dixon 1979, Duellman 1990).

Rhinobothryum bovallii (Andersson, 1916) (Fig.1) is one of two known species of this genus (the other species is *R. lentiginosum* [Scopoli, 1785]). It inhabits the tropical lowland rainforests of the Choco region, ranging from Honduras, Costa Rica and Panamá in Central America, to Colombia and Ecuador in northern South America, but there are also records from the tropical rainforest on the eastern flank of the Serranía del Perijá in Venezuela (Peters 1960, Kornacker 1999, Savage 2002, Castaño-Mora et al. 2004, McCranie et al. 2006). Following the proposal on the biogeographical regionalisation for the Caribbean and Latin America by Morrone (2006), *R. bovallii* inhabits five out of the 70 biogeographical provinces recognized by this author, namely: province 15 (eastern Central America), 24 (Choco), 28 (Magdalena), 29 (Venezuelan Llanos), and province 32 (western Ecuador). However, for Colombia, Hernández-Camacho et al. (1992a) recognize that the provinces 24 and 28 proposed by Morrone (2006) correspond to a single unit called Chocó-Magdalena province, which is subdivided into 20 biogeographical districts (see Hernández-Camacho et al. 1992a for details). In this paper, I follow Hernández-Camacho et al.

Figure 1. An adult *Rhinobothryum bovallii* from the Río Manso Natural Reserve, municipality of Norcasia, department of Caldas, Colombia (Table 2), not collected. Lateral and dorsal views of the head in the bottom left corner.

Table 1. Snake species known only from the Choco region and western flank of the Western Cordillera in Colombia. * Species distributed below 1000 m a.s.l. (Choco tropical forest); ** species distributed above 1000 m a.s.l. (cloud rainforest).

Species	Reference
Atractus boulengerii Peracca, 1896*	Passos et al. (2009)
Atractus echidna Passos, Mueses-Cisneros, Lynch & Fernandes, 2009*	Passos et al. (2009)
Atractus iridescens Peracca, 1896*	Passos et al. (2009)
Atractus medusa Passos, Mueses-Cisneros, Lynch & Fernandes, 2009*	Passos et al. (2009)
Atractus melas Boulenger, 1908*	Passos et al. (2009)
Atractus typhon Passos, Mueses-Cisneros, Lynch & Fernandes, 2009*	Passos et al. (2009)
Bothrocophias myersi (Gutberlet & Campbell, 2001)*	Gutberlet & Campbell (2001), Castro et al. (2005)
Micrurus spurrelli (Boulenger, 1914)*	Campbell & Lamar (1989), Roze (1996), Castaño-Mora et al. (2004)
Synophis plectovertebralis Sheil & Grant, 2001**	Sheil & Grant (2001)
Tantilla nigra (Boulenger, 1914)*	Castaño-Mora et al. (2004)
Tantilla reticulata Cope, 1860*	Castaño-Mora et al. (2004)

Table 2. Locality records for *Rhinobothryum bovallii* in Colombia. The biogeographical characterization follows the proposal by Hernández-Camacho et al. (1992a).

Locality	Coordinates	Biogeographical unit	Data source
1. Department of Córdoba, municipality of Tierralta, La Plumilla village	8°1'59" N, 76°10'14" W	Chocó-Magdalena province, Sinú-San Jorge district	ICN 053929
2. Department of Boyacá, municipality of Puerto Romero (Las Quinchas)	5°50'35" N, 74°19'36"W	Chocó-Magdalena province, Lebrija district	ICN 054085
3. Department of Santader, municipality of Landázuri, 900 m a.s.l.	6°21'31" N, 73°53'58" W	Chocó-Magdalena province, Lebrija district	ICN 054086
4. Department of Cesar, municipality of San Alberto, Miramar village, 715 m a.s.l.	8°17'20" N, 73°24'59" W	Chocó-Magdalena province, Catatumbo district	ICN 054087
5. Department of Caldas, municipality of Samaná, Cañaveral village, 400 m a.s.l.	5°32'13" N, 74°54'31" W	Chocó-Magdalena province, Nechí district	MHUA-R 14142
6. Department of Antioquia, municipality of Mutatá, 140 m a.s.l.	7°14'50" N, 76°26'21" W	Chocó-Magdalena province, Sinú-San Jorge district	MHUA-R 14276
7. Department of Antioquia, municipality of Anorí, Primavera village	6°59'6" N, 75°5'22" W	Chocó-Magdalena province, Nechí district	MHUA-R 14559
8. Department of Antioquia, municipality of Maceo, Las Brisas village	6°32'48" N, 74°38'36" W	Chocó-Magdalena province, Nechí district	MHUA-R 14583
9. Department of Antioquia, municipality of Briceño, Capitan village	7°6'43" N, 75°33'15" W	Chocó-Magdalena province, Nechí district	MHUA-R 14703
10. Department of Caldas, municipality of La Victoria, El Llano village, 289 m a.s.l.	5°19'45" N, 74°50'57" W	Chocó-Magdalena province, Nechí district	MHUA-R 14785
11. Departament of Valle del Cauca, municipality of Buenaventura, Guamía village	3°43'54" N, 76°57'30" W	Chocó-Magdalena province, Alto Atrato-San Juan district	Vargas-Salinas & Bolaños-L (1999)
12. Department of Valle del Cauca, municipality of Buenaventura, San Cipriano, 115 m a.s.l.	3°50'03" N, 76°53'26" W	Chocó-Magdalena province, Alto Atrato-San Juan district	Pers. obs
13. Department of Caldas, municipality of Norcasia, San Roque village, Rio Manso Natural Reserve, 280 m a.s.l.	5°39'51" N, 74° 47'09" W	Chocó-Magdalena province, Nechí district	Pers. obs
14. Department of Chocó, municipality of Medio Atrato, San Martín de Purré village, 89 m a.s.l.	5°41'0" N, 76°40'0" W	Chocó-Magdalena province, Alto Atrato-San Juan district	Murillo (2005)

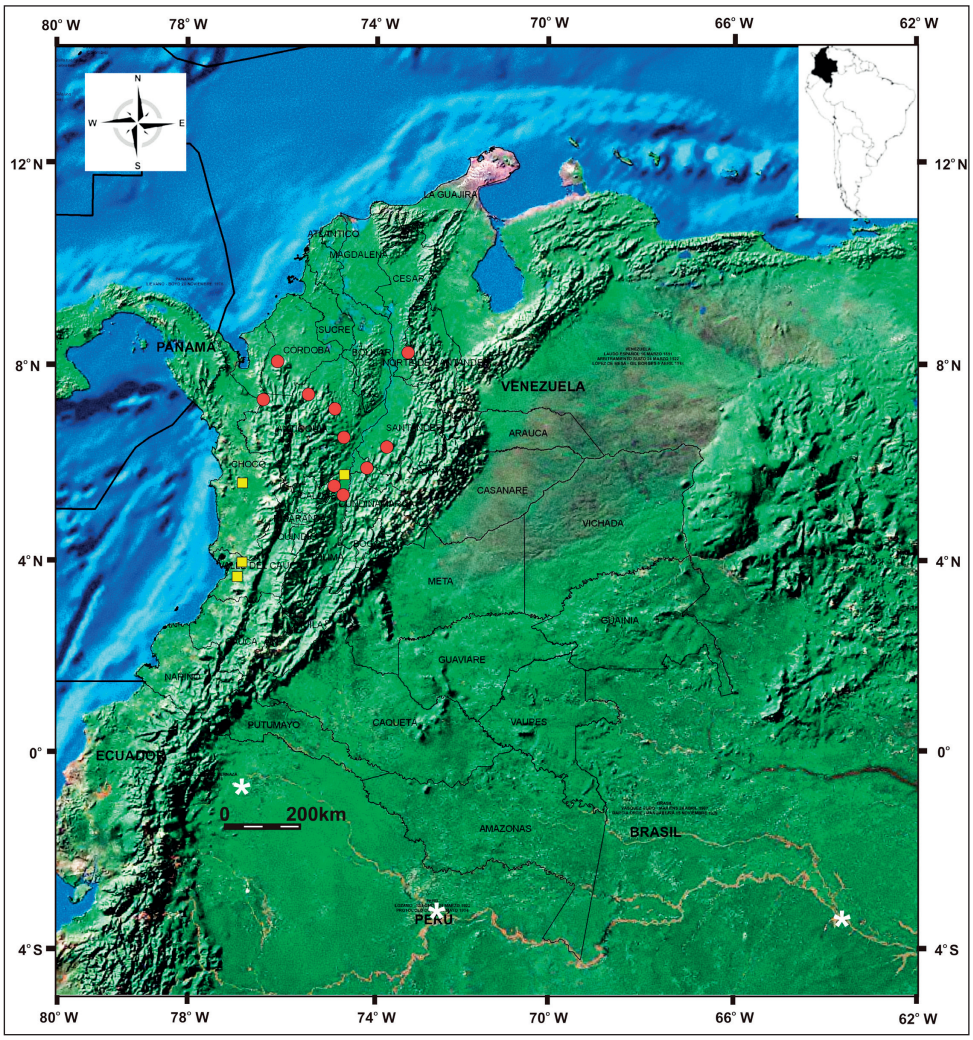

Figure 2. Map showing the known records of *Rhinobothryum bovallii* in Colombia, and distribution of *R. lentiginosum* (white asterisks) in the northwestern Amazonian forest. For *R. bovallii*, red circles represent data from specimens in collections, and yellow squares are data from literature and personal observations (see Table 2). Locality data for *R. lentiginosum* are from Ecuador (Ortega-Andrade 2010), Peru (Dixon & Soini 1977), and Brazil (Martins & Oliveira 1998). Map obtained from SIG-OT (Sistema de información geográfica para el ordenamiento territorial, Colombia).

(1992a) to characterize biogeographically the distribution of *R. bovallii* in Colombia, because these authors have developed the most comprehensive biogeographical analysis of this country yet.

According to Pérez-Santos & Moreno (1988), *R. bovallii* can also be found in the plains of the Caribbean and the Andean region of Colombia up to 2250 m a.s.l., but this asseveration is unconvincing (and maybe completely wrong), due to the lack of voucher specimens that would corroborate these records. Unfortunately, a checklist of Colombian snakes (and even reptiles), interpreting the distributional patterns for each species, is as yet lacking.

I present herein updated information on the geographical distribution of *R. bovallii* in Colombia, discussing in a biogeographical context its occurrence in the tropical lowland forests of the Choco region and the Magdalena river valley of this country, and exploring historical hypotheses to explain the allopatric distribution with respect to its sister species, *R. lentiginosum*. The data presented are extracted from: (1) bibliographical compilations where the specific locations of sightings are identified, (2) revision of the virtual herpetological collections of the ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá) and MHUA (Museo Herpetológico Universidad de Antioquia, Medellín, Colombia), and (3) own field observations (Tab. 2, Fig. 2).

Perspectives on the distribution patterns of many amphibians and reptiles previously only known from the

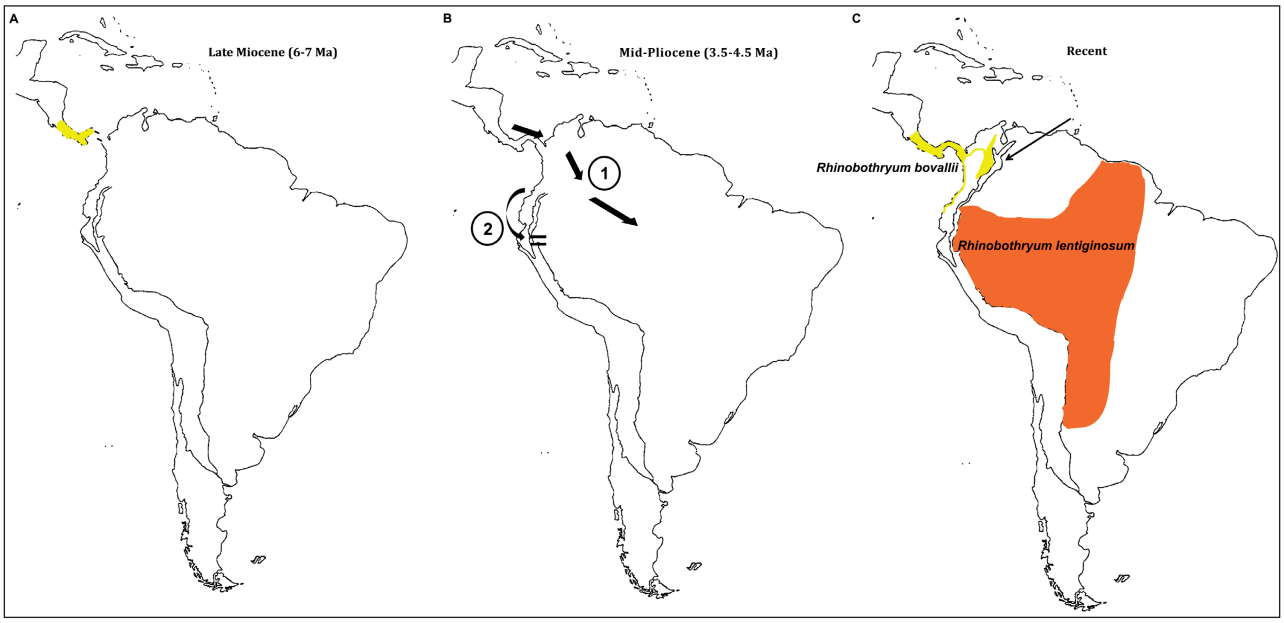

Figure 3. Schematic maps showing the hypothetical dispersal of the genus *Rhinobothryum* from Central to South America. A) Distribution of *Rhinobothryum* before closure of the Isthmus of Panama during the late Miocene; B) Possible dispersal routes in South America after the closure of the Isthmus of Panama, where (1) indicates the crossing in the northern Andes and (2) the Huancabamba Deflection pass. C) Allopatric distribution between *Rhinobothryum bovallii* and *R. lentiginosum* caused by the uplift of the northern Andes and Huancabamba Deflection during the upper Pliocene. The arrow points out the Eastern Cordillera of Colombia.

Choco region of Colombia recently changed when new finds of its characteristic species were recorded from other regions, such as the middle Magdalena river valley. This corroborates the proposal by Hernández-Camacho et al. (1992a) on the biotic affinity between these areas (see Castaño-Mora et al. 2004 for reptiles). The geographical distribution of *R. bovallii* in Colombia follows a pattern similar to that of other species distributed in these areas (Choco and Magdalena lowland rainforests), forming an arc in a southwest-north-southeast direction, bounded by the Western and Central Cordilleras of the Andes (Fig. 2). The report of individual ICN 054086 from 900 m a.s.l. (Tab. 2) indicates that *R. bovallii* not only inhabits tropical rainforests, but also forests whose vegetation represents a transition to sub-Andean Colombian forests (range between 800–1200 to 2000 m a.s.l. sensu Hernández-Camacho et al. 1992a). To the west of the country (Choco biogeographical province), it is evident that information on the distribution of this species (Fig. 2) is deficient, which can be explained by the few intensive sampling efforts at different locations, taking into account that *R. bovallii* is a rarely-seen snake (Savage 2002, Köhler 2003, pers. obs.).

At present, no phylogeny of Colubridae *sensu lato*, or even Colubroidea or Caenophidia, has adequately clarified the phylogenetic relationships of *Rhinobothryum* with other groups of Neotropical colubrids, and *R. bovallii* has never been included in a molecular analysis. However, *R. lentiginosum* was included by Vidal et al. (2010) in a molecular analysis of the Dipsadidae, which showed it to be phylogenetically more closely related to species of the subfamily Natricinae (following the classification by Pyron et al. 2011) (which are of Nearctic origin) than to representatives of Central and South America. This result supports the proposal by Duellman (1990) who suggested an Old-Northern origin for *R. lentiginosum*. Supposing the model of Duellman (1990), *Rhinobothryum* would have reached South America via the Isthmus of Panama, probably shortly after the connection between the two areas was established in the mid-Pliocene (3.5-4.5 Ma, Hernández-Camacho et al. 1992b) (Fig. 3). Evidence for this hypothesis might be derived from the disjunctive distribution of *R. bovallii* and *R. lentiginosum*, which suggests a process of allopatric speciation. The latter species is distributed in the Amazonian lowland rainforests from Colombia and Venezuela to Paraguay (Figs. 2, 3) (Peters & Orejas-Miranda 1970, Dixon & Soini 1977, Cunha & Nascimento 1993, Martins & Oliveira 1998), while *R. bovallii* is native to the west of the Andes in northwestern South America, with an isolated record from northwestern Venezuela. This gives rise to the question as to how and when could the divergence between the two species have occurred.

In the mid-Pliocene (3.5–4.5 Ma), the Colombian Andes (Western, Central and Eastern Cordilleras) had a configuration that was very different from the present situation, since elevations were fairly low, no more than 40% of their modern values of 4000 m on average (Gregory-Wodzicki 2000). These topographical conditions probably allowed that a species of the tropical lowland rainfor-

ests proper with a vertical distribution to about 1000 m in altitude, such as *R. bovallii*, could cross these only slightly raised mountains, resulting in its dispersal to the east and south of Ecuador. This colonisation event could have occurred in the mid-Pliocene, before the northern Andes reached their modern elevations shortly after (around 2.7 Ma; Gregory-Wodzicki 2000) and as a result environmentally impeded the spread of *Rhinobothryum* to east of the Andes. Apart from this possibility, there are indications that a lowland rainforest corridor could have existed between the Chocoan and Amazonian forests through the Huancabamba Deflection during the last major interglacial period (Harrington 1962), as was also suggested by Dixon (1979) to explain the recent geographical connection in genera like *Chironius*, *Leptophis* and *Liophis* east and west of the Andes. However, the possibility that Amazonian forests were colonised by *Rhinobothryum* through the Huancabamba Deflection is less likely, because no records of this genus are known from southwestern Ecuador or northwestern Peru, which suggests *Rhinobothryum* is absent in that area. Nevertheless, both upper Pliocene uplift events (the rise of the northern Andes and closure of the Huancabamba Deflection) could be identified as those forming the possible barriers that led to the divergence between *R. bovallii* and *R. lentiginosum* (Fig. 3), as they isolated the populations of *Rhinobothryum* east and west of the Andes. To phylogeographically test the hypothesis proposed herein, it is evident that it requires a detailed phylogenetical study of several populations of both species.

Due to the fact that *R. bovallii* is rarely observed (Savage 2002, Köhler 2003) the species remains poorly known and it could in fact be endangered in several regions. The records presented here (Tab. 2) might therefore be relevant for the conservation of this species throughout its area of occurrence.

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