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TAXONOMIC STATUS OF MISCELLANEOUS NEOTROPICAL VIPERIDS, WITH THE DESCRIPTION OF A NEW GENUS

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Despite the contributions made to crotaline systematics over the last few decades (for example, Gloyd, 1940; Klauber, 1972; Campbell and Lamar, 1989; Gloyd and Conant, 1991), the systematic status of several taxa remains questionable. We herein attempt to resolve some of these problems. Terminology follows Klauber (1972); the method of counting scales is that of Dowling (1951).

We argue that recognition of certain Neotropical genera (*Bothriechis* and *Bothriopsis*) accurately reflects our knowledge of natural groups and adheres to modern systematic practice. Conversely, the evidence that the genus *Bothrops* as presently comprised is monophyletic is less compelling. The name *Bothrops*, contrary to the views of several recent authors (for example, Schätti *et al.*, 1990, and Shätti and Kramer, 1991), is masculine in gender (Smith and Larsen, 1974; Internat. Code Zool. Nomenclature, 1985, art. 30a, ii). The variation and generic allocation of *Bothrops albocarinatus* Shreve (1934) are discussed and its distribution is redefined to include south-central Colombia. We discuss the reasons for our distinction between *Bothrops asper* and *B. atrox* (Campbell and Lamar, 1989), and suggest that possibly several additional unrecognized species may be present in the *asper-atrox* complex. *Bothrops microphthalmus colombianus* Rendahl and Vestergren (1940) is elevated to specific status. *Bothrops roedingeri* Mertens (1942) and *Trigonocephalus xanthogrammus* Cope (1868) are placed, respectively, in the synonymies of *Bothrops pictus* (Tschudi,

1845) and *B. asper* (Garman, 1884). *Bothrops campbelli*, *B. osbornei*, and *Bothriechis mahnerti* are referred to the synonymy of previously described species, which are herein redescribed with amplified distributions. Finally, a new genus is proposed for three species of high-montane Middle American pitvipers that appear to form a natural group.

THE GENERA *BOTHRIECHIS*, *BOTHRIOPSIS*, AND *BOTHROPS*

The genus *Bothriechis* Peters (1860) was recognized by Campbell and Lamar (1989) for seven species of arboreal pitvipers, most of which are confined to wet montane habitats in southern México and Central America, but with one species ranging into northwestern South America in lowland as well as lower montane habitats. The generic arrangement recognizing both *Bothriechis* and *Bothriopsis*, as well as *Ophryacus*, was first proposed by Burger (1971) in an unpublished doctoral dissertation. Subsequently, Burger's identification keys to these genera were published by Pérez-Higareda *et al.* (1985).

Shätti *et al.* (1990) suggested that the genera *Bothriechis* and *Bothriopsis*, as recognized by Campbell and Lamar (1989), appeared to be artificial groups, and that *Bothrops* (*sensu* Burger, 1971) "probably represents a monophyletic group." Cadle (1992) voiced the opinion that he "preferred to err on the side of conservatism" and suggested that *Bothrops* (*sensu lato*) be retained. We hardly would agree that recognition of a paraphyletic taxon could be called conservative. We hypothesize that *Bothriechis* and *Bothriopsis* represent monophyletic groups, whereas the diverse, widespread genus *Bothrops* may be paraphyletic.

Shätti *et al.* (1990), on the basis of newly collected material, confirmed the suggestion of Campbell and Lamar (1989:172) that *Bothriopsis albocarinata* and *B. alticola* are conspecific, with *albocarinata* having priority, but they placed *albocarinata* in the genus *Bothriechis*. Shätti and Kramer (1991) also described *Bothriechis mahnerti*, which they mistakenly thought was a novel taxon, but what in actuality is *Bothriopsis punctata* (see discussion below of the taxonomic status of *Bothrops osbornei* and *Bothriechis mahnerti*). We take this opportunity to point out that the distribution of *Bothriopsis albocarinata* is not restricted to Ecuador as delimited by Shätti *et al.* (1990) and that this species ranges at least as far north as south-central Colombia (UV 10561). This specimen is noteworthy in that it is one of the largest known (649 mm snout-vent, 764 mm total length), is significantly

darker in overall pattern than typical specimens, and lacks distinctive pale keels on the dorsal scales. Two additional specimens from Pastaza, Ecuador (GNM 3765 from Chambira, Río Bobonaza, and GNM 3766 from the Río Conambo) are typical in most respects, except GNM 3765 possesses 23 dorsal scale rows at midbody rather than 19 to 21.

Shätti *et al.* (1991) suggested that five species, which they placed in the genus *Bothriechis*, were closely related: *schlegelii*, *bilineata*, *punctata*, *taeniata*, and *albocarinata*. The only evidence these authors gave for this purportedly close relationship was that all of these species have a prehensile tail. In lieu of additional evidence, a prehensile tail might be considered a homologous character uniting Middle American and South American groups of arboreal pitvipers. However, when the preponderance of evidence is considered (summarized by Campbell and Lamar, 1989), it appears more likely that a prehensile tail is convergent in these two groups.

Characters distinguishing *Bothriechis* from *Bothriopsis* given by Campbell and Lamar (1989) and cited by Shätti *et al.* (1990) include hemipenis shape (subcylindrical or tapered with papillate calyces as opposed to attenuated with a calyculate distal half), number of hemipenial spines (10 to 24 as opposed to 30 to 40), and subcaudal condition (entire as opposed to divided). Other characters defining these genera given by Burger (1971) and cited by Shätti et al. (1990) include the shape of the ectopterygoid (broad and slightly curved without truncate dorsolateral projections as opposed to lacking anterior dorsolateral projections) and palatine (triangular with apex near or posterior to mid-palatine in *Bothriechis* and variable in *Bothriopsis*), and the nature of scale ornamentation on the distal portion of the tail (first and second rows of scales on distal one-third of tail strongly keeled as opposed to unmodified). Shätti *et al.* (1990) questioned the validity of these characters, although they apparently did not examine skeletal material or even external features of comparative material. Paradoxically, after indicating support for the value of the hemipenis as a character to distinguish phylogenetic groups among New World pitvipers, Shätti *et al.* (1990:884) discussed some of the differences between *Bothriechis* and *Bothriopsis*, yet they chose to ignore these differences in their generic designations (Schätti *et al.*, 1990; Schätti and Kramer, 1991). Schätti *et al.* (1990:884) did not explain their rationale while casting aspersions on the observations of others by unfounded statements such as "likely due to a limited number of preparations in a

few species" and "is a poor character" and "differences . . . are at best gradual." Unfortunately, while these authors were eager to offer their taxonomic opinions, they were less forthcoming with any real evidence.

Crother *et al.* (1992) examined the phylogenetic relationships of the seven species of *Bothriechis* recognized by Campbell and Lamar (1989). Independent analyses of biochemical and morphological characters each yielded a single most parsimonious cladogram. The combined data yielded two equally parsimonious trees that had topologies similar to those trees derived independently by use of morphology and allozymes. Werman (1992), also using biochemical and anatomical characters, identified a monophyletic lineage containing Middle American pitvipers (*schlegelii*, *lateralis*, *nigroviridis*). Crother *et al.* (1992) and Werman (1992) independently identified the Mexican *Ophryacus undulatus* as the sister taxon of *Bothriechis*.

Recently, the issue of gender involving names of New World pitvipers has again become confused in the literature (Wilson and Meyer, 1985; Villa *et al.*, 1988; Schätti *et al.*, 1990; Schätti and Kramer, 1991). The gender of *Bothrops* is masculine (Internat. Code Zool. Nomenclature, 1985, chapter 7, article 30(a)ii; Smith and Larsen, 1974; Campbell, 1987; Campbell and Lamar, 1989; Lamar, 1990), whereas the gender of *Bothriopsis* is feminine (Internat. Code Zool. Nomenclature, 1985, Article 30, A.); *Bothriechis* is masculine for the same reasons. The genus *Porthidium*, although neuter, does not require a change in the name *hyoprora* (*contra* Schätti and Kramer, 1991), which is a noun in apposition.

The *Bothrops asper-atrox* Problem

The systematics of the *Bothrops asper-atrox* complex has been controversial for more than a century. Schätti and Kramer (1991:9) stated that "based on morphological evidence from Ecuadorian specimens at hand, we consider *Bothrops aspera* [*sic*] (Garman) and *B. atrox* (L.) to be conspecific." Unquestionably, the wide range of variation in nearly every external character renders difficult the task of separating these taxa. We have examined several hundred specimens during the course of related work in the Neotropics, and suggest that a multi-species complex may be involved, including cryptic species, discordant variation (both morphologically and biochemically), and multiple zones of contact. We suggested (Campbell and Lamar, 1989) that western

Venezuela may be an important area in the history of the *atrox-asper* complex, and recent investigations (Markezich and Taphorn, personal communication) do not refute the notion that secondary contact has occurred there.

There is reason to suspect that the genus *Bothrops* as currently recognized may be paraphyletic. There are few unifying characteristics among members of this group and the disparate morphologies would suggest the presence of a number of monophyletic species groups, some of which may be more closely related to *Bothriopsis* than to *Bothrops*.

The Taxonomic Status of *Bothrops microphthalmus colombianus*

Rendahl and Vestergren (1940) described *Bothrops microphthalmus colombianus* from two specimens from western Colombia. Why these authors thought the affinities of *colombianus* were with *B. microphthalmus* was not stated, but they noted (p. 15): "This new subspecies differs from typical *B. microphthalmus* in a higher number of scale rows, a different colouration and in a somewhat larger number of ventrals." We have examined three specimens of this rare snake, including the male holotype (NRM 23114), female paratype (NRM 33114), and an additional adult female (UTA R-25949). We have also examined several specimens of *microphthalmus* from Amazonian Perú (FMNH—see appendix) and find that *colombianus* differs from *microphthalmus* in other salient characters (Table 1).

Bothrops microphthalmus differs from *B. colombianus* in having a strongly proboscidiform snout (as opposed to blunt), in having a transverse suture above the eye that partially divides the supraocular scale, in having fewer ventrals (146 to 168 as opposed to 162 to 172), in having 21 to 23 midbody dorsal scale rows (as opposed to 25), and in being much smaller (adults usually less than 700 mm in total length, maximum known 941, as opposed to at least 1360 mm). The dorsal scales in *Bothrops colombianus* are strongly tuberculate and *Lachesis*-like, whereas in *B. microphthalmus* there is a keel present, but this is not raised into a tubercle.

These species are effectively isolated from each other by the higher elevations of the Andes. *Bothrops microphthalmus* is restricted to the Amazonian slopes of Colombia, Ecuador, Perú, and perhaps northern Bolivia (Nicéforo-María, 1975; Campbell and Lamar, 1989), and *B.*

FIG. 1.—*Bothrops colombianus*. Cerro Munchique, 1200 m., Cauca, Colombia. Photograph by Mats Höggren.

FIG. 2.—*Bothrops colombianus*. Variation in two juveniles from El Tambo, Cerro Munchique, 1500-2000 m., Cauca, Colombia. Photograph by Martin Carlson.

colombianus (Figs. 1-2) is known only from the Pacific versant of Colombia. The northernmost record for *B. colombianus* (Yarumal, Antioquia, Colombia) has been called into question (Nicéforo-María,

TABLE 1.—Variation of selected scale characteristics in *Bothrops colombianus* and *B. microphthalmus*. Slashes denote right/left. Adapted, in part, from Nicéforo-María (1975).

Species	Sex	Inter-supraoculars	Supra-labials	Infra-labials	Ventrals	Subcaudals	Midbody dorsal scale rows
			Bothrops colombianus				
NHRM 23114 (type)	♂	8	8/8	10/10	162	54*	25
NHRM 33114	♀	10	8/8	10/10	172	51	25
UTA R-25949	♀	6	9/9	10/10	169	53	25
MLS 1832	♀	7	8/8	——	172	51	25
			Bothrops microphthalmus				
FMNH 5580	♂	7	7/7	9/9	153	54	23
FMNH 40242	♂	6	7/8	10/9	155	56	21
FMNH 63740	♀	5	7/7	10/9	146	44	23
MLS 1632	♂	6	7/7	10/10	161	49	23
MLS 1633	♂	5	7/7	8/8	154	53	23
MLS 1634	♀	8	7/7	10/10	168	48	23
MLS 1635	♀	6	7/7	9/9	165	47	23
MLS 1636	♀	6	8/7	9/9	164	44	23

*Tip of tail missing, representing perhaps two or three subcaudals.

1964; S. Ayerbe, personal communication). The species probably occurs in northwestern Ecuador although we are unaware of specimens from that area. Little is known of its natural history, but it is said to be a sedentary forest dweller (S. Ayerbe, personal communication). Interestingly, there exists considerable anecdotal information suggesting that *B. colombianus* is an egg layer and egg brooder (S. Ayerbe, personal communication).

In view of the differences between these species, we propose that *Bothrops microphthalmus colombianus* Rendahl and Vestergren be considered a distinct species, *Bothrops colombianus.*

Taxonomic Status of *Bothrops roedingeri*

Bothrops roedingeri was described from two specimens by Mertens (1942) from Hacienda Huayuri, near Nazca, Departamento de Ica, Perú; this locality lies in the coastal desert region of western South America. In the original description of *B. roedingeri*, Mertens (1942) hypothesized that this species was most closely related to *B. ammodytoides*, a species occurring east of the Andes, more than 1500 kilometers to the southeast of the type locality of *B. roedingeri,* in subtropical savannas, steppes, and perhaps temperate broadleaf evergreen forest. As pointed out by Campbell and Lamar (1989), Mertens (1942) made no mention of *B. pictus* in his diagnosis of *B. roedingeri*, and *B. pictus* was curiously absent from the collection on which he reported. *Bothrops pictus* is a relatively widespread but poorly known species, with a distributional range that overlaps the range of *B. roedingeri* (Campbell and Lamar, 1989) in the desert coastal region of Perú. A comparison of the features reported for *B. roedingeri* (Mertens, 1942) with those given for *B. pictus* (Campbell and Lamar, 1989) reveals that the two species are practically indistinguishable. The only character purportedly separating the two taxa is the number of ventrals, 152 to 173 in *B. pictus* and 179 to 185 in *B. roedingeri* (Campbell and Lamar, 1989:222). However, these ranges of variation are based on small sample sizes and, on the basis of the meager material at hand, we suspect clinal variation in the number of ventrals in *B. pictus*, with a higher number in the south. We propose that *B. roedingeri* Mertens be relegated to the synonymy of *B. pictus* (Tschudi).

TAXONOMIC STATUS OF *BOTHROPS XANTHOGRAMMUS*

Bothrops xanthogrammus was described by Cope (1868) from Pallatanga, Departamento de Chimborazo, Ecuador. This locality lies at about 1500 meters on the Pacific versant. *Bothrops xanthogrammus* is known with certainty only from the type locality and the type material. Its purported existence in Colombia can be traced to the belief that *Bothrops quadriscutatus* Posada-Arango (1889*a*) is synonymous with *B. xanthogrammus* (Peters and Orejas-Miranda, 1970). Quintini (1927) and Milá de la Roca (1932) cited *B. xanthogrammus* for Venezuela based on spurious evidence. The specific status of *B. xanthogrammus* was challenged (Campbell and Lamar, 1989), although some investigators still consider it to be a valid species (Schätti and Kramer, 1991).

We have examined a syntype of *Bothrops xanthogrammus* (ANSP 9978) and find that this specimen is indistinguishable from *B. asper* Garman (1884), which also occurs in the region. A detailed description of the holotype is given by Campbell and Lamar (1989:226, figs. 247-248). The only character that purportedly separates this taxon from *B. asper* is the presence of smooth rather than keeled supracephalic scales. However, the head of ANSP 9978 is now missing, making verification of this feature impossible; nevertheless, smooth supracephalic scales may occur adventitiously as occasionally demonstrated in specimens of *B. asper* and *B. atrox* from widespread localities. Portions of a disarticulated skull of *B. xanthogrammus* (ANSP 9978) reveal no notable differences between *xanthogrammus* and *asper*. The frontals are 7.2 mm long and 4.7 mm wide, the supratemporal is 8.2 mm in length, both the left and right dentaries have 18 teeth, the left pterygoid has 17 teeth, and the left palatine bears three teeth.

Cope (1868) referred to a "holotype" but stated that he had two specimens. Subsequently, Malnate (1971) indicated ANSP 9978 to be the holotype. This specimen and USNM 6717 were probably the two specimens used by Cope in his description (R. I. Crombie, personal communication). The USNM specimen cannot be located; thus ANSP 9978 must be regarded as the remaining syntype. A specimen from the type locality and resembling Cope's description of *B. xanthogrammus* is clearly *Bothrops asper* (Fig. 3).

We recommend that *B. xanthogrammus* (Cope, 1868) be placed in the synonymy of *B. asper* (Garman, 1884). An abbreviated history of the name is:

FIG. 3.—*Bothrops asper*. Pallatanga, Chimborazo, Ecuador. Photograph by Ulrich Kuch.

Trigonocephalus xanthogrammus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:110.

Lachesis xanthogrammus, Boulenger, 1896, Cat. snakes British Mus., 3:543.

Bothrops xanthogrammus, Amaral, 1930*b* [dated 1929], Mem. Inst. Butantan, 4:241.

Bothrops xantogrammus [*sic*], Hoge, 1966 [dated 1965], Mem. Inst. Butantan, 32:135.

Bothrops xanthogrammus, Peters and Orejas-Miranda, 1970, Bull. U.S. Nat. Mus. 297(1):55.

THE TAXONOMIC STATUS OF *BOTHROPS CAMPBELLI*

Studies dealing with geographic variation among Neotropical pitvipers are almost nonexistent, and many species are known only from scant reports, some of which were based on only a few specimens, or in which a series from a single locality was treated. Recent investigations in Ecuador have resulted in the descriptions of several species of pitvipers (Freire-Lascano, 1991; Schätti and Kramer, 1991), the redescription of another (Schätti *et al.*, 1990), and a novel generic arrangement (Schätti *et al.*, 1990). The species described as new by these authors are referable to two previously poorly known taxa, which merit redescription and discussion.

A specimen referable to *Bothrops pulcher* (Peters, 1863) recently was described as *Bothrops campbelli* (Fig. 4) by Freire-Lascano (1991). Inasmuch as *B. pulcher* is poorly represented in museum collections, we offer a description based on 22 specimens and a comparison with *B. campbelli*. Unfortunately, we were unable to examine type material of *B. pulcher*.

Diagnosis of Bothrops pulcher.— A moderately stout, terrestrial lancehead resembling *Bothrops asper* in some aspects of coloration and scutellation, but possessing larger snout scales (only two anterior and two posterior intercanthals, measured transversely) and fewer ventrals (139 to 174 as opposed to 161 to 240). *Bothrops pulcher* differs from *B. andianus* by possessing a banded body pattern lateral triangles in *andianus*), a faintly visible or nonexistent postocular stripe (well defined in *andianus*), and fewer intercanthals. *Bothrops pulcher* is more robust than *B. andianus*, with a comparatively shorter and broader head.

Description.— The rostral is approximately as high as wide, almost square, and contacted dorsally by one or two apical scales that divide the internasals. The canthal is slightly longer than wide and one and a half to two times as wide as the internasal. An anterior and posterior pair of enlarged intercanthals with low oblique keels are present. There are two to five postcanthals; two to seven intersupraoculars (usually four or fewer), with low keels; and 25 scale rows between the right and left rictus, all but lowest strongly keeled. The supraloreal is approximately twice as long as high; the infraloreal is nearly square; the one to three prefoveals are small and separate the posterior nasal from the lacunolabial; and the postfoveal broadly contacts the third supralabial and is not fused to lower preocular. The middle preocular is not fused to the supralacunal, and the lower preocular is about half the size of the middle preocular, with both scales entering the orbit. The subocular and postocular are usually entire and the oculabials are in one or two rows. There are seven to eight supralabials (second fused with prelacunal); eight to 10 infralabials, with the first three or four in contact with the chinshields; and three median gulars. Tiny tubercular mechanoreceptors (*sensu* Jackson and Sharawy, 1980) are scattered on the scale surfaces of head and chin, especially labials. The dorsal scales have raised, tubercular keels that do not reach the apices. Dorsal scales are arranged in 20 to 25 rows anteriorly, 20 to 25 rows at midbody, and 16 to 21 rows posteriorly. There are 139 to 174 ventrals, an

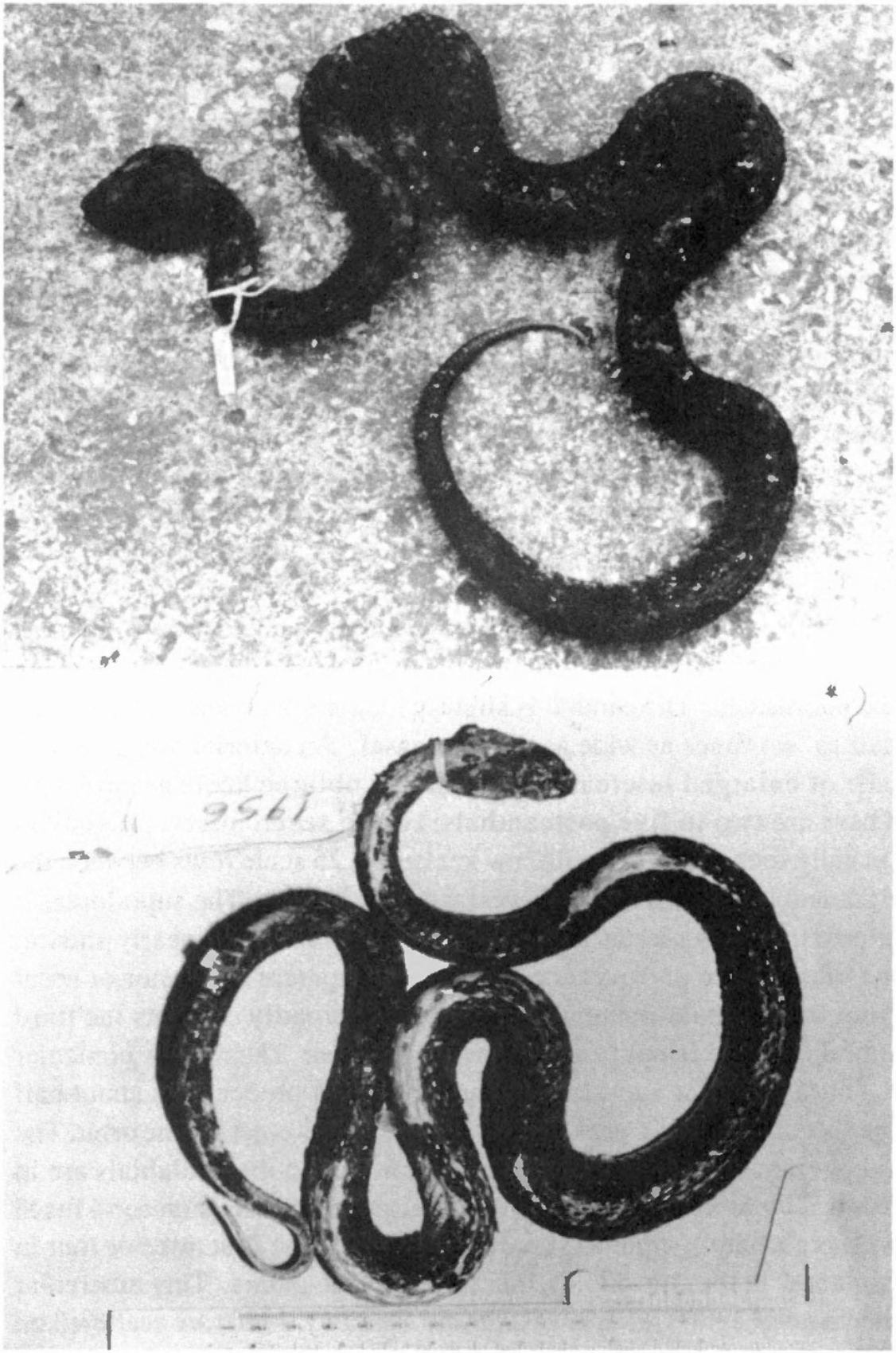

FIG. 4.—*Bothrops campbelli* [= *B. pulcher*]. Top: topotype (INHMT 2455), from Huagal-Sacramento, Cantón Pallatanga, 1500-2000 m., Chimborazo, Ecuador. Bottom: holotype (INHMT 1956). Photographs by Ulrich Kuch.

undivided anal, and 44 to 64 divided subcaudals. The terminal caudal scute is nearly straight, obtusely rounded, and equivalent in length to the preceding three to three and a half subcaudals, with dorsal capping scales extending to near the end and fusing with the terminal subcaudal distally.

The head and body are brown to grayish brown (sometimes pinkish gray or tan in juveniles) dorsally, with or without about 20 brown, black-margined crossbands (four to seven dorsal scales in length) some of which may be disrupted at the vertebral line. Paler interspaces are one to four dorsal scales in length (half scale on tail), being longest middorsally and most pronounced posteriorly. The last caudal interspace sometimes forms a ventrocaudal stripe. There is a ventrolateral series of small black spots on the first two rows of dorsal scales and extending onto the adjacent ventrals. A dark brown postocular stripe encroaches most of the two posterior supralabials and passes the oral rictus, terminating on the first row of dorsals. This stripe frequently merges with the dorsal head color; it is subtended by a pale line, which is often most visible on (and beneath) the neck. Indistinct brown nuchal spots are occasionally evident. In some specimens, the sides of the head are pale, revealing a darker brown subocular spot with concentric black-and-white margins. Black-bordered brown or white spots occur on the chinshields and infralabials; otherwise the chin is yellow and finely stippled with brown or rust. The venter is yellow, tan, or reddish brown, evenly mottled and stippled with dark brown, except for the chin, throat, and subcaudal surface, all of which are more sparsely pigmented. The edges of the ventrals are encroached by ventrolateral black spots. This species reaches at least 906 mm total length.

Distribution.—This species occurs from lowlands to at least 2500 meters along the Pacific slopes of the Andes from the Departamento Valle del Cauca, Colombia, south to at least Provincia El Oro, Ecuador. There are unverified reports from the Colombian Chocó, and from the Amazonian versant of the Ecuadorian Andes (the latter locality is unlikely). The type locality, Quito, is unsuitable habitat, and we suspect the specimen came from a nearby but less elevated area.

Discussion.—Most specimens of *B. pulcher* in museums are from the northern extreme of the range, in the lowlands of the Departamento Valle del Cauca, Colombia. These specimens possess a lower number of ventrals (143 to 150), reduced tubercular dorsal keels, and a slightly

paler color than those from farther south. A female specimen from "south of [La] Chonta," El Oro Province, Ecuador (AMNH 22094), has the highest number of anterior rows of dorsal scales (25) and ventrals (174) known for this species. It also represents the southernmost known locality for *B. pulcher*. The type specimen of *Bothrops campbelli* is a large male (although Freire-Lascano, 1991, referred to it as "young"). Its scutellation (three preloreals, one supraloreal, one row of scales prevent contact with infraoculars, 12 scales surround each supraocular, keels most pronounced middorsally, 160 ventrals, undivided anal, 50/50 divided subcaudals, 7/7 supralabials, 9/9 infralabials, five intersupraoculars, 21/21/19 dorsal scale rows) falls within the range of variation known for *B. pulcher*. The "preloreals" are prefoveals.

Freire-Lascano described the color of *B. campbelli* as follows [translated from Spanish]: venter black speckled with yellow spots; dorsum and head entirely black; rostral normal, without postocular line; a postinfralabial line, of yellow color, and covering 14 scales; some infralabials and gulars with yellow spots dorsally. Again, nothing differs substantially from that which is known for *B. pulcher* although his specimen is rather dark, but this is a common occurrence in *Bothrops*. A small specimen from Las Pampas, Cotopaxi (see fig. 242 in Camp- bell and Lamar, 1989), is noticeably dark as a result of preservation. We observed a live adult from Las Pampas, and it was dark reddish gray dorsally; a juvenile (Fig. 5) from the same locality was pale gray and brown. A topotypic specimen (KU 218462) identified by Freire-Lascano as "*Bothrops osbornei*" is a typical juvenile *B. pulcher*. *Bothrops campbelli*, in scutellation, pattern, appearance, and distribution, is in strong agreement with *B. pulcher*. The name "serpiente boca de sapo," cited for *B. campbelli* is used in Las Pampas for *B. pulcher* (G. Onore, personal communication). Clearly, *Bothrops campbelli* Freire-Lascano (1991) is a subjective junior synonym of *Bothrops pulcher* (Peters). An abbreviated synonymy for *B. pulcher* is:

Trigonocephalus pulcher Peters, 1863, Monatsber. Preuss. Akad. Wiss. Berlin, p. 672. Quito, Ecuador (ZMB 3868, three syntypes).

Lachesis pulcher, Boulenger, 1896, Cat. snakes British Mus., 3:539.

Bothrops pulchra, Amaral, 1923, Proc. New England Zool. Club, 8:104; Peters, 1960, Bull. Mus. Comp. Zool., 122:510.

Bothrops pulcher, Peters and Orejas-Miranda, 1970, Bull. U.S. Nat. Mus., 297(1):54.

Bothrops pulcher, Campbell and Lamar, 1989, Venom. Rept. Latin America, pp. 185, 221.

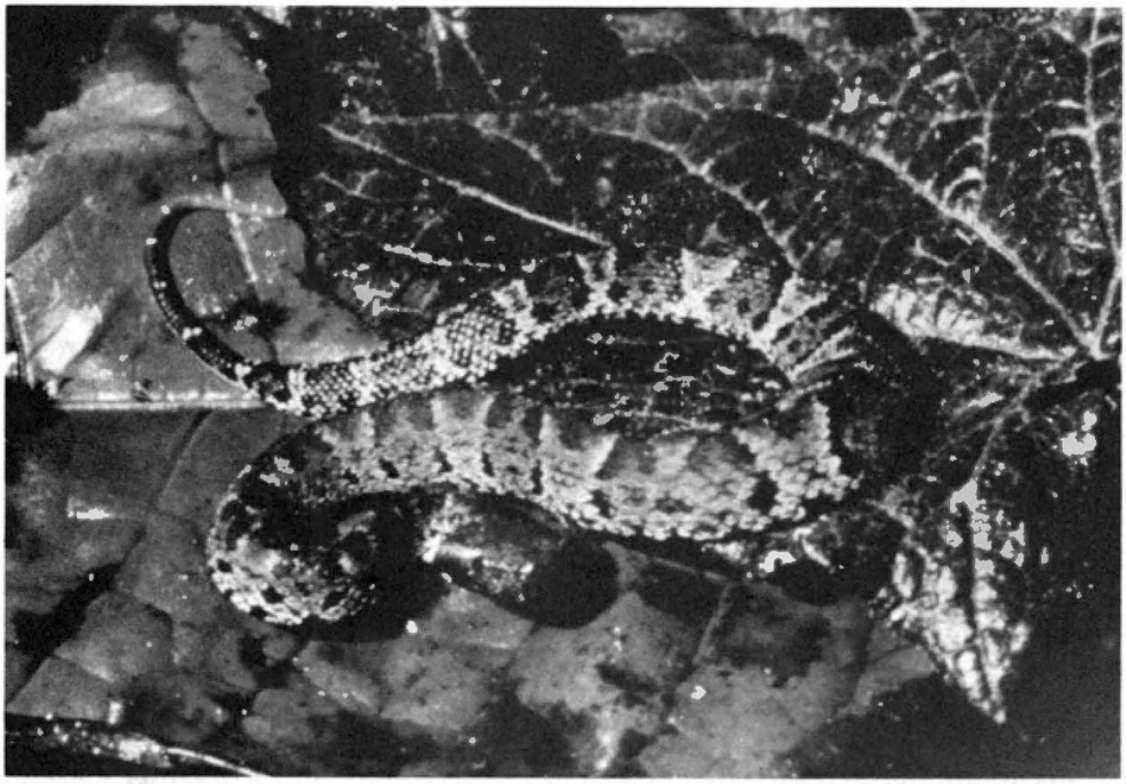

FIG. 5.—*Bothrops pulcher*. Juvenile from Las Pampas, Cotopaxi, Ecuador. Photograph by J. Anhalzer, courtesy Jean-Marc Touzet.

Bothrops campbelli Freire-Lascano, 1991, Publ. Trab. Cient. Ecuador, Univ. Téc. Machala (Ecuador), p. 1 (unnumbered). Recinto, Huagal-Sacramento, Cantón Pallatanga, Provincia de Chimborazo, Ecuador; 1500 to 2000 meters elevation; Muestrario Herpetológico del Instituto Nacional de Higiene (Guayaquil, Ecuador), example no. 1956.

THE TAXONOMIC STATUS OF *BOTHROPS OSBORNEI* AND *BOTHRIECHIS MAHNERTI*

Specimens referable to *Bothriopsis punctata* (García) were described recently as *Bothrops osbornei* Freire-Lascano (1991) (Fig. 6), and *Bothriechis mahnerti* Schätti and Kramer 1991 (Fig. 7). Owing to its relative obscurity it seems worthwhile to redescribe and discuss *Bothriopsis punctata* (García).

Diagnosis.— A large, semiarboreal, forest pitviper; olive gray to yellowish in dorsal ground color, with 14 to 22 pairs of brown, pale-centered vertebral blotches, dorsally fused or not. These blotches are offset or fused with lateral blotches, creating a spotted, semibanded, or banded appearance. The top of head has symmetrical dark brown markings and there are 175 to 213 ventrals, 66 to 95 paired subcaudals, 22 to 29 midbody dorsal scale rows, and six to nine intersupraoculars. This species is similar to *Bothriopsis taeniata* (Wagler) in overall pat-

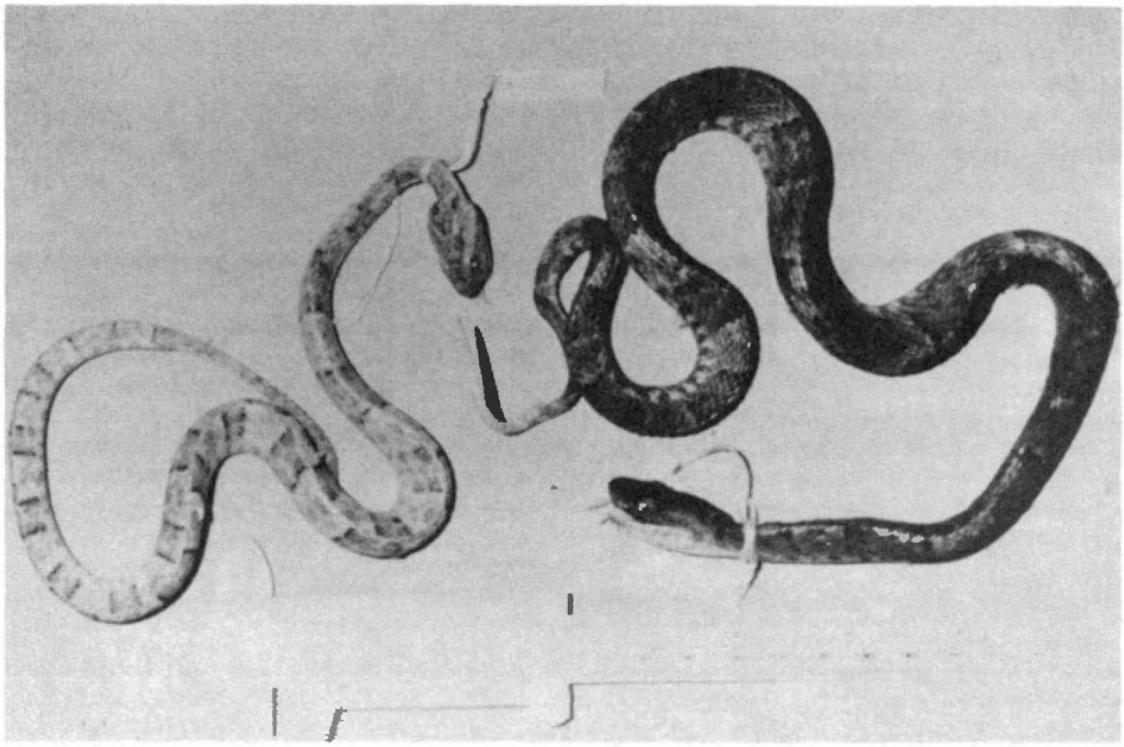

FIG. 6.—*Bothrops osbornei* [= *Bothriopsis punctata*]. Holotype (INHMT 1924) at left and paratype (INHMT 22340) at right. Photographs by Ulrich Kuch.

tern but the latter possesses more body bands, more ventrals, and mostly unpaired subcaudals. The ranges of the two species are separated by the Andes Mountains.

Description.—The rostral is about one and a half or more times higher than wide and contacts the internasal and first supralabial about equally. The internasals are large, in broad contact anteriorly, sometimes divided dorsally by a small apical scale, and overlap the *canthus rostralis*. The canthals are slightly longer and considerably wider than the internasals. There are two to three transverse rows of intercanthals, which usually contain some enlarged scales, but occasionally include granular scales. The supraoculars are two to two and a half times longer than wide, one-half to one-third the width of the cranium, and with the inner margin often quite irregular. There are six to nine keeled intersupraoculars and 24 to 28 scales between right and left rictus, all but the lowermost strongly keeled. The prenasal is higher and twice as long as the postnasal, with the posteroventral projection of the prenasal contacting the prefoveal, and separating the postnasal from the supralabials. There is a single prefoveal and subloreal, the latter separating the postnasal from the prelacunal. The loreal is irregularly quadrangular and slightly longer than high; the middle preocular enters the orbit broadly, is half as long and three-fourths as high as the upper

FIG. 7.—*Bothriechis mahnerti* [= *Bothriopsis punctata*]. Holotype (MHNG 2459.47) from Las Pampas, approximately 2000 m., Cotopaxi, Ecuador. Photograph by Giovanni Onore.

preocular; and the lower preocular is smaller, triangular in shape, and usually excluded from orbit. The middle and lower preocular are not fused to the supralacunal and infralacunal, respectively, the subocular is single, and there are two to three postoculars. The interoculabials are in one to two rows. There are six to nine supralabials, with the first pair in broad contact behind mental and the second fused with the prelacunal, and nine to 13 infralabials, with the anterior three pairs in contact with chinshields. There are four to five median gulars. The dorsal scales are distinctly keeled except for the paraventrals, which have low, incomplete, and slightly oblique keels. The paraventrals are greatly enlarged and the scales of the second row are slightly enlarged. There are 22 to 29 dorsal scale rows anteriorly, 22 to 29 scale rows at midbody, and 19 to 23 scale rows posteriorly. There are 175 to 213 ventrals; 67 to 95 divided subcaudals; and the terminal caudal spine is compressed laterally, equivalent in length to the two and a half to three and a half preceding subcaudals, with a blunt and slightly upturned end and six subtending scales, none of which is as differentiated dorsal capping scales.

The head is greenish tan or gray dorsally. A dark brown or black postocular stripe is two scales wide, often paler medially, occasionally bordered narrowly in bright yellow or brown, and extends from the postoculars to, or slightly beyond, the rictus, crossing the dorsal part of the penultimate and posterodorsal half of the last supralabial. Similarly colored nuchal spots converge anteriorly and terminate separately over the occiput. The parietal stripes converge anteriorly, joining between the eyes into a "Y," and sometimes merging with the occipital marks to form an irregular ocellus. Dark pigment is scattered along various scale sutures, and is especially evident as narrow bars on supra- and infralabials. The supralabials are tan and the iris is gold, with or without bronze reticulations medially. The body is yellowish tan (especially in juveniles), greenish gray (especially large adults or specimens from northern part of range), or brown dorsally. There are 14 to 22 pairs of narrow dark brown crossbands, which are two to three dorsal scales in length. The crossbands are outlined and stippled with black, but otherwise are nearly as pale as the ground color. Individual crossbands of an individual pair are separated by interspaces of two to three dorsal scales, while pairs are separated from one another by interspaces of six to nine dorsal scales in length. Each crossband is constricted or interrupted midlaterally and middorsally, thus appearing as a chain of four rounded spots. The interspaces are outlined with yellow and sparsely stippled with black and brown.

The pairs of caudal crossbands are less distinctly outlined, with five to seven crossbands on the proximal two-thirds of the tail. The distal one-third of the tail is uniform pale pink, yellowish white, or soft gray, sometimes with faint bands near the tip. The tail is palest in juveniles, but often discernibly pale in adults. The throat is pale tan to yellow, immaculate or with fine dark brown or black stippling which increases posteriorly across the venter. A ventrolateral series of small dark spots (one and a half to two scales long), are spaced along paraventrals and edges of ventrals about one scale apart, and the posterior half of the belly of adults tends to be predominantly black (grayish tan in juveniles), either peppered with brown or irregularly spotted with yellow. There are ventrolateral dark spots that merge posteriorly with the dark venter in many specimens. The subcaudal surface becomes increasingly mottled with yellow posteriorly, and its distal one-third to two-fifths is usually immaculate yellow (especially in juveniles) to soft gray. Dark pigment increases overall in adults and in northern populations;

FIG. 8.—*Bothriopsis punctata* (UTA R-30284). Specimen from near Tumbés, Peru. Photograph by Gerald Marzec.

juveniles tend to be pale, with markings more distinctly delineated, especially on the dorsum of the head. Large females attain at least 1260 mm in total length, and there is anecdotal evidence of specimens approaching two meters (S. Ayerbe, personal communication).

Distribution.—Panamá south to near the Ecuador-Perú border, along the Pacific coast and adjacent Andean slopes, from near sea level to at least 2000 meters. The northernmost record is from Cañas, Darién, Panamá (type locality of *Bothrops leptura*). The species is uncommon in collections, and frequently misidentified as either *Bothrops asper* or *B. atrox*; thus its southern distributional limit was for many years considered to be in northwest Ecuador (Provincia Esmeraldas). However, the *Bothriechis mahnerti* type series extends the range southward through Pichincha to northern Cotopaxi, the *Bothrops osbornei* series is from Chimborazo, and a specimen (UTA R-30284) (Fig. 8) exists from a moist forest remnant near Tumbes, along the Ecuador-Perú border. The latter locality, while unusual for moist-forest species, is not without precedent: specimens of *Bothrops pulcher, Bothriechis schlegelii,*

and *Micrurus ancoralis* have been taken nearby. We suspect the population is relictual. Schätti and Kramer (1991) speculated that a specimen of *B. mahnerti* reportedly from Coca, Napo, in Amazonian Ecuador, has erroneous locality data. Most certainly either the record is in error or the specimen is referable to the superficially similar *Bothriopsis taeniata*, which does occur there.

Discussion.—Bothrops osbornei was described on the basis of four specimens. The scutellation of these specimens (182 to 198 ventrals, undivided anal, 66 to 69 divided subcaudals, 7/7 supralabials, 10 to 13 infralabials, seven intersupraoculars, 25/25 to 26/21 dorsal scale rows) falls within the range of variation cited herein for *Bothriopsis punctata*, although the subcaudals are at the lower extreme.

Freire-Lascano (1991) described the coloration of *Bothrops osbornei* as follows [translated from Spanish]: the dorsum consists of dark transverse bands over a pale brown (juveniles) or blackish gray (adults) ground color. Venter totally spotted with black . . . a dark postocular band that reaches the first [last] infralabial is present. Unfortunately, the color description is too rudimentary for close comparison with *B. punctata*; however no discrepancies are evident, and Freire-Lascano (1991) noted correctly the ontogenetic trend towards a darker ground color (see Fig. 6).

The legitimacy of the Freire-Lascano (1991) publication could be challenged under chapter 3, articles 8(d) and 9(3) of the International Code of Zoological Nomenclature, but the point is moot owing to the invalidity of his taxa and of *Bothriechis mahnerti*.

Shortly after Freire-Lascano's (1991) publication, Schätti and Kramer (1991) described *Bothriechis mahnerti* (Fig. 7) based on a series of six juvenile and subadult specimens (largest snake, 685 mm) from Las Pampas (Cotopaxi), and Santo Domingo de los Colorados (Pichincha). Variation in the *B. mahnerti* type series was cited as follows: ventrals 175 to 188; anal undivided; subcaudals 67 to 72 (divided); supralabials six to eight (second forming lacunolabial); infralabials nine to 12; intersupraoculars six to eight; midbody dorsal scale rows 25 to 27.

Schätti and Kramer's detailed color description can be compared with Freire-Lascano's (1991) abbreviated description of *Bothrops osbornei*, and there is no significant discrepancy. In comparison with known variation in *Bothriopsis punctata*, the *Bothriechis mahnerti* series includes the lowest number of ventrals (175). However, these

numbers are approached closely by those of other specimens, including some from the northern end of the range. The figure illustrating the holotype of *B. mahnerti* (Schätti and Kramer, 1991:fig. 1) shows the middle preocular to be fused with the supralacunal, an atypical condition. The same figure shows a single postocular, although the authors stated that two are present. The specimen from the Ecuador-Perú border area (UTA R-30284) possesses scutellational features that place it within the range cited for *Bothriechis mahnerti*—181 ventrals, anal undivided, 71 divided subcaudals, seven supralabials (second forming lacunolabial), nine to 10 infralabials, seven intersupraoculars, and 25 midbody dorsal scale rows. It is a juvenile female, nearly identical in size to the *B. mahnerti* holotype (366 mm as opposed to 368 mm), with an umbilical scar beginning on ventral 163.

Both *Bothrops osbornei* and *Bothriechis mahnerti* are indistinguishable from, and junior subjective synonyms of, *Bothriopsis punctata*. Schätti and Kramer (1991) apparently placed heavy reliance on the description by García (1896), and acknowledged, but failed to comprehend, the importance of the similarity of their taxon to *B. punctata*. Moreover, they noticed, but ignored, the darker color of the only nonjuvenile (a subadult female, MHNG 2250.21) in their series; this specimen is also from a locality to the north of other material examined by them. Schätti and Kramer called into question the identification of a specimen of "*punctatus*" [*sic*] figured by Campbell and Lamar (1989:fig. 157), citing its variance from García's description and its resemblance to *Bothriechis mahnerti*. They were correct on both points: García dealt inadequately with a single specimen of which the latter is a synonym. A juvenile snake from Valle, Colombia (Fig. 9), shows a darker overall pattern typical of specimens from the northern part of the range.

Inasmuch as Schätti and Kramer (1991) cited no specimens of *B. punctata* as having been examined by them nor, for that matter, did they provide the rationale behind their counting and descriptive methods, it appears that they were unfamiliar with *B. punctata*. Schätti and Kramer (1991:14) further stated: "There is but a single species of arboreal pitvipers [*sic*] from west of the Andes resembling *Bothriechis mahnerti*, i.e. *B. peruvianus* (Boulenger)." They apparently based this conjecture on the fact that the specimen figured in Campbell and Lamar (1989) shows pronounced dorsal crossbars. There are similarities between the two, as both are members of the genus *Bothriopsis*, but *B.*

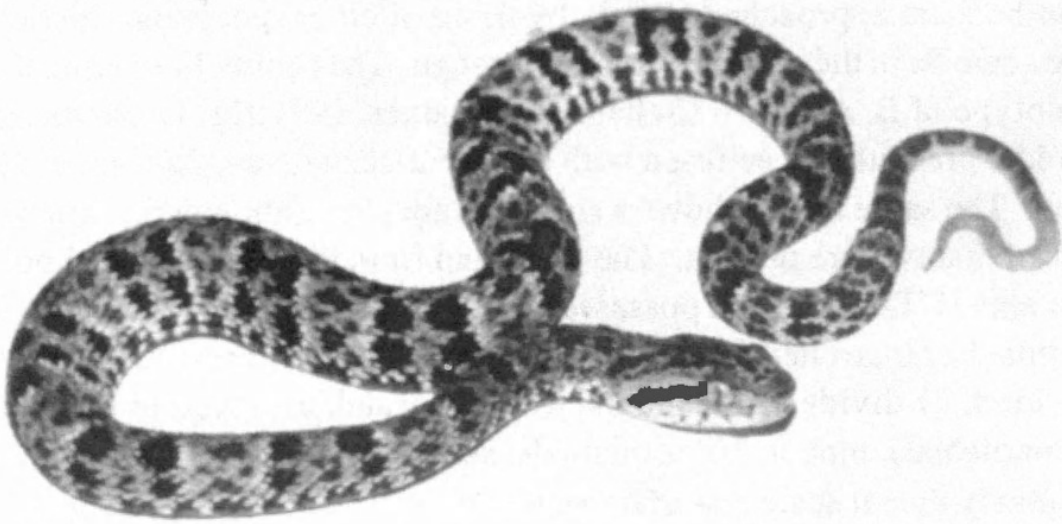

FIG. 9.—*Bothriopsis punctata*. Juvenile from Valle, Colombia. Photograph by Fernando Castro, courtesy of Santiago Ayerbe.

peruviana does not occur west of the Andes (Campbell and Lamar, 1989) and it is arguably closer to *Bothriopsis albocarinata* (Shreve), an Amazonian species recently redescribed by the same authors (Schätti *et al.*, 1990). That *B. campbelli*, *B. osbornei*, and *B. mahnerti* were described is illustrative of the need for caution owing to our lack of knowledge regarding geographic, individual, and ontogenetic variation in Neotropical snakes.

Although the type description of *Lachesis punctatus* García, 1896, is brief and the author failed to designate a type specimen, the color illustration is clearly representative, albeit of a spotted rather than banded specimen. On the basis of a specimen from eastern Panamá, Amaral (1923) described the species as *Bothrops leptura*. Nicéforo-María (1929*a*, 1929*b*) pointed to the priority of *Lachesis punctatus* and discussed some of the problems associated with García's (1896) nomenclature. Subsequently, Amaral (1930*a*) recognized the priority of *Lachesis monticelli* Peracca, 1910, although he refused to accept García's taxon. Recent investigators (Dunn, 1944; Peters, 1960; Peters and Orejas-Miranda, 1970; Campbell and Lamar, 1989) have recognized *Lachesis punctatus* García. The species *Thanatophis montanus* Posada-Arango (1889*a*), subsequently placed by the same author in the genus *Thanatos* (Posada-Arango, 1889*b*), has been considered by most workers to be synonymous with *Bothriopsis taeniata*, owing to the undivided condition of the subcaudals. However, the type locality of *T. montanus* in the mountains of Antioquia (Colombia) lies within the range of *B. punctata*. We regard the status of *Thanatophis montanus*

Posada-Arango (1889*a*) as unresolved. The abbreviated synonymy for *Bothriopsis punctata* is:

Lachesis punctatus García, 1896; Los ofídios venenosos del Cauca, p. 30, pl. 8 (las montañas del Dagua =mountains of Dagua River, Valle del Cauca, Colombia). No type specimen designated.

Lachesis monticelli Peracca 1910, Ann. Mus. Zool. Anat. Comp. Univ. Napoli, 3(12): 2 ("America tropicale?"). Holotype: UNZM, a female, destroyed during World War II.

Bothrops leptura Amaral, 1923, Proc. New England Zool. Club, 8:102 (USNM 50110; "Cana, eastern Panama" [= Cañas, Darién, Panamá).

Bothrops monticelli, Amaral, 1930*a* [1929], Mem. Inst. Butantan, 4:59.

Bothrops punctatus, Dunn, 1944, Caldasia, 3:215.

Bothrops osbornei Freire-Lascano, 1991, Univ. Técnica de Machala (Ecuador), p. 2 (unnumbered); example no. 1924 [Muestrario Herpetológico del Instituto Nacional de Higiene, Guayaquil, Ecuador]; Sacramento—Cantón Pallatanga, Provincia del Chimborazo [Ecuador]. The type is a juvenile female.

Bothriechis mahnerti Schätti and Kramer, 1991, Rev. Suisse Zool., 98:10 (MHNG 2459.47; Las Pampas, N Cotopaxi [Ecuador]). The holotype is a subadult male.

The Genus *Porthidium* (*sensu lato*)

The morphologically and ecologically diverse pitviper fauna of Middle America has only recently begun to be treated in an adequate systematic fashion. Exclusive of the rattlesnakes, bushmaster, and members of the genus *Agkistrodon*, New World species of pitvipers traditionally have been placed collectively in the genus *Bothrops* (see Hoge, 1966, and Peters and Orejas-Miranda, 1970) or in *Trimeresurus* (Smith, 1941). More recently, generic partitioning of this wide array of pitvipers has occurred (Burger, 1971, 1985; Campbell and Lamar, 1989). The monophyletic clade of Middle American arboreal pitvipers were placed in *Bothriechis* (Burger, 1971; Campbell and Lamar, 1989; Crother *et al.*, 1992; Werman, 1992), and the well differentiated sister taxon of *Bothriechis* was recognized as the monotypic *Ophryacus undulatus* (Campbell and Lamar, 1989; Crother *et al.*, 1992; Werman, 1992).

Campbell and Lamar (1989) pointed out that *Porthidium*, as recognized by them, contained several distinct lineages, the relationships of which were unknown. One of these lineages contains the hog-nosed pitvipers, and because the type species of *Porthidium* Cope (1871) is *Trigonocephalus lansbergii* Schlegel (1841), the name *Porthidium* has

priority for this group. The genus *Atropoides* was proposed recently (Werman, 1992) to accommodate the lineage containing the jumping pitvipers (*nummifer*, *olmec*, and *picadoi*).

Three species (*barbouri*, *godmani*, and *tzotzilorum*) were placed in the "montane pitviper" lineage of *Porthidium* by Campbell and Lamar (1989). These species appear to be closely related to each other (Campbell, 1985, 1988), but their relationship to other groups of pitvipers remains unclear. Preliminary biochemical evidence suggests that they may constitute a basal clade of New World pitvipers (Campbell and Whitmore, 1989; Werman, 1992). These distinctive snakes occur in montane habitats at relatively high elevations (1500 to more than 3000 meters) from southern México (Guerrero) through Central America to Panamá. They do not appear to be closely related to either the hog-nosed or jumping pitvipers. We propose for these snakes a new generic name as follows:

Cerrophidion, new genus

Type species.— *Bothriechis Godmanni* Günther, 1863, by present designation. [The spelling provided by Günther, 1895:190, pl. 57, fig. A, should be followed by indication.]

Diagnosis and definition.— Small, moderately stout, terrestrial pitvipers lacking a strongly prehensile tail, rarely exceeding 700 mm in total length, having a pattern of dorsal blotches often fused into a zigzag pattern and of smaller lateral blotches, and a ground color of some shade of brown, gray, or orange.

The snout is not elevated and the rostral scale is broader than high; scales in the frontal and parietal areas are enlarged (sometimes into plates) and often irregular (Fig. 10). The number of intersupraocular scales varies from one in some *C. barbouri* to seven in some *C. godmani*. There are 120 to 148 ventrals, 22 to 36 undivided subcaudals, and 17 to 25 dorsal scale rows at midbody. These snakes also are characterized by having a hyoid skeleton with relatively long branchials (second ceratobranchials according to some authors), and in having the basal portion of the pterygoid as long as, or longer than, the ectopterygoid (Burger, 1971).

The hemipenes bear 12 to 40 large spines on the proximal third of each lobe; the remainder of the lobe is covered by calyces that have spinulate or papillate micro-ornamentation. Below the level of the

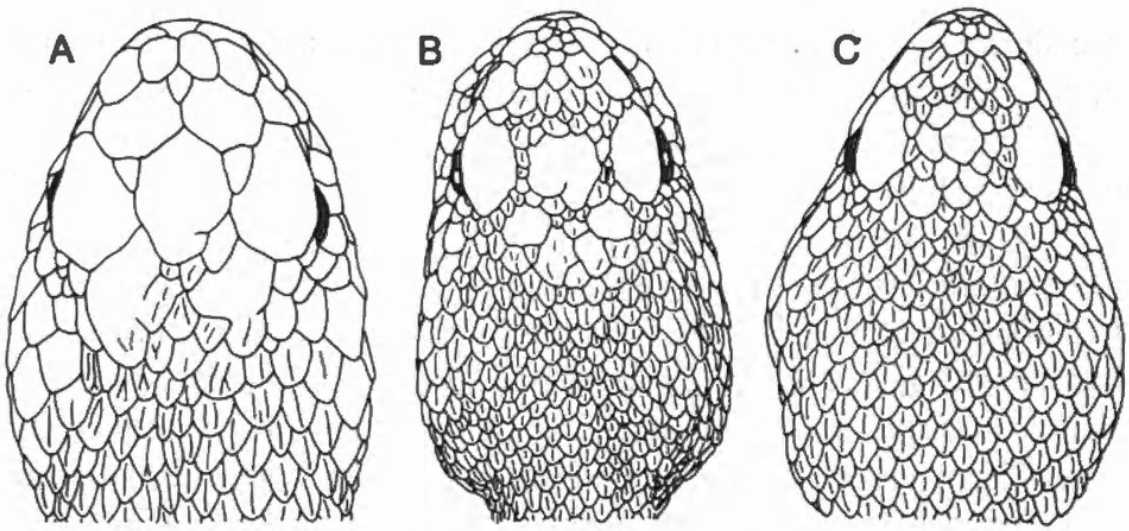

FIG. 10.—Variation in the dorsal head scales in members of the genus *Cerrophidion*. (A) *Cerrophidion barbouri*—0.8 km. N Puerto del Gallo, Guerrero, México, 2896 m.; UTA R-4450 (from Campbell, 1985:14, fig. 5B). (B) *Cerrophidion tzotzilorum*—10.9 km. ESE San Cristóbal de Las Casas, Chiapas, México, 2320 m.; UTA R-9641—holotype (from Campbell, 1985:50, fig. 2B). (C) *Cerrophidion godmani*—San Jorge Muxbal, Guatemala, Guatemala, ca. 1850 m.; UTA R-6185 (from Campbell and Solórzano, 1992:236, fig. 9B).

crotch, the organ is mostly naked, except for a few small spines that are concentrated on the lateral surfaces.

Pitvipers occurring in the Neotropics with which these snakes have sometimes been allied include species in the genus *Bothrops*, members of which differ from *Cerrophidion* in attaining a larger size, almost always more than a meter in total length, in usually having a higher number of ventrals and subcaudals, and in having divided subcaudals. Members of the genus *Bothriechis* usually have a green ground color, are arboreal with a strongly prehensile tail and attenuate, laterally compressed body, and usually have a higher number of ventrals (137 to 175) and subcaudals (42 to 72). The monotypic *Ophryacus undulatus* has scales over the eyes raised into a "horn," the supraocular region and crown are covered by small, keeled scales with 10 to 20 intersupraoculars between the elongated supraocular spines, and there are more ventrals (157 to 171) and usually more subcaudals (37 to 57), which are divided. In species of *Atropoides*, the body is exceedingly robust; the intersupraoculars are scalelike and more numerous (seven to 12), and are not enlarged into plates; and the supraoculars are reduced in size and longitudinally narrow or fragmented into small scales. Species of *Porthidium* (*sensu stricto*) differ from *Cerrophidion* in having a distinctly elevated canthus with a rostral that is higher than

broad; in having hemipenial lobes that terminate in a naked apical disc, in the center of which is a large papilla; and in usually having a pattern consisting of a pale middorsal line that is offset laterally by small, staggered blotches.

Other genera of New World pitvipers may be distinguished from *Cerrophidion* by the following features. The rattlesnakes (genera *Crotalus* and *Sistrurus*) have a rattle on the tip of the tail; *Agkistrodon* has a pattern of broad crossbands and larger supracephalic plates, usually arranged in a nine-plate, colubridlike pattern; *Lachesis* reaches a huge size (more than three meters), lays eggs, has the second supralabial fused with the prelacunal, and the distal subcaudals are divided into four or five rows of small spinelike scales; and *Bothriopsis* is arboreal with an attenuate body and strongly prehensile tail, a higher number of ventrals (153 to 254), and usually more subcaudals (41 to 91), most of which are usually divided.

Content.—The genus *Cerrophidion* contains three species: *barbouri* restricted to the Sierra Madre del Sur in Guerrero, México; *tzotzilorum* occurring in the highlands of Chiapas, México; and *godmani* disjunctly distributed from the highlands of southeastern Oaxaca, México, through Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica to western Panamá.

Etymology.—Derived from the Spanish *Cerro*, meaning mountain in allusion to the habitat of these snakes, and from the Greek *ophidion*, meaning a small snake.

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Appendix 1

Selected localities and referred specimens. For museum acronyms see Leviton *et al.* (1985).

Bothriopsis albocarinata.—Colombia. *Putumayo*: 35 km. from Mocoa, on road between Verde and Yolo (UV 10561). Ecuador. *Loja/Zamora-Chinchipe*: 5 km. E Loja, 9200 feet (holotype of *Bothrops alticola*, BM 1946.1.19.26). *Pastaza*: Río Pastaza (holotype of *Bothrops albocarinata*, MCZ 36989); Chambira, Río Bobonaza (GNM 3765); Río Conambo (GNM 3766). *Tungurahua*: Río Negro, 1260 m. (KU 121347-48). See Schätti *et al.* (1990) for additional specimens from Ecuador.

Bothrops asper.—Ecuador. *Chimborazo*: Pallatanga (syntypes of *B. xanthogrammus*, ANSP 9978 and USNM 6717—the latter specimen is now lost).

Bothrops microphthalmus.—Colombia. *Boyacá*: Miraflores (Puente de Rusa), 1432 m. (ICN 1533). Peru. *Madre de Dios*, Candama (FMNH 40242). *Huánuco*: valley of the Chinchao, Buena Vista (FMNH 5580); no specific locality (FMNH 63740).

Bothrops pictus.—Peru. *Ancash*: Chimbote (FMNH 5662-64). *Arequipa*: Majes Valley (FMNH 3991, Univ. Arequipa no. 7). *Ica*: Hacienda Huayuri (holotype and paratype of *Bothrops roedingeri*. SMF 6017-18). *Lima*: Chosica (MCZ 45716); Lima (MCZ 3573); "mountain uplands" (lectotype and paralectotype, MHNN 6-7, designated by Schätti, 1986).

Bothrops pulcher.—Colombia. *Valle del Cauca*: km. 13 on road from Buenaventura to Río Calima (FMNH 165586); road from Buenaventura to Río Calima (FMNH 165587-93); Río Calima, 7 km. from lumber camp (Campamento "Cartón de Colombia") (FMNH 165594-96); Río Raposo, Virology Field Station (USNM 151708, 154051)—not examined; Caimancito, south of Buenaventura, on bank of Río Cajambre (UTA R-21689). Ecuador: *Cotopaxi*: Las Pampas (Basel Museum Field Series-unnumbered). *Chimborazo*: Pallatanga (no. 1956, holotype of *B. campbelli*—Muestrario Herpetológico del Instituto Nacional de Higiene-Guayaquil), KU 218462 (topotype). *El Oro*: south of [La] Chonta, AMNH 22094.