Distribution and natural history of the Ecuadorian Toad-headed Pitvipers of the genus *Bothrocophias*
(Squamata: Serpentes: Viperidae: Crotalinae)

Verbreitung und Naturgeschichte der ecuadorianischen Krötenkopf-Grubenottern der Gattung *Bothrocophias*
(Squama: Serpentes: Viperidae: Crotalinae)

**DIEGO F. CISNEROS-HEREDIA & MARIA OLGA BORJA & DANIEL PROANO & JEAN-MARC TOUZET**

**ABSTRACT**

Limited information is available for pitvipers of the genus *Bothrocophias*. This article presents information on the three species of *Bothrocophias* known to occur in Ecuador: *Bothrocophias campbelli* (Freire Lascano, 1991), *B. hyoprora* (Amaral, 1935) and *B. microphthalmus* (COPE, 1875), including geographical distribution, altitudinal range, provincial records, sympatric pitviper species, activity patterns, behavior, size, reproductive biology, diet, and longevity. *Bothrocophias campbelli* inhabits the northern, central and southern regions of the Pacific slopes of the Andes in Ecuador between 800 and 2000 m; *Bothrocophias hyoprora* occurs in the northern and southern Amazonastiefland and in the southern slopes of the Andes in Ecuador between 210 and 1500 m; and *B. microphthalmus* in the south-eastern slopes of the Andes in Ecuador between 210 and 1500 m. The relative clutch mass values in *B. microphthalmus* ranged from 0.22 (in *B. microphthalmus*) to 0.30 (in *B. hyoprora*).

**KEY WORDS**

Reptilia: Squamata: Serpentes: Viperidae: Crotalinae: *Bothrocophias campbelli*, *Bothrocophias hyoprora*, *Bothrocophias microphthalmus*; Ecuador; behavior, distribution; ecology, diet, natural history; reproductive biology; venomous snake
Snakes of the subfamily Crotalinae (family Viperidae), commonly known as pit-vipers, are widely distributed in America and the Old World; with seventeen species occurring in Ecuador (Campbell & Lamar 2004). Much attention has been focused on these venomous snakes because of their medical importance in comparison with other snake species.

Figure 1: Distribution in Ecuador of Bothrocophias campbelli (Freire Lascano, 1991) (■ □), B. hyoprora (Amaral 1935) (■ □), and B. microphthalmus (Cope 1876) (• ○). Examined material = (• • •); data from literature = (□ ○ □) (Orcés 1943, 1948; Schätti & Kramer 1993; Touzet 1986; Freire & Kuch 2000; Gutberlet & Campbell 2001; Campbell & Lamar 2004).

A symbol can represent more than one locality. Numbers correspond to the mainland Ecuadorian provinces: Esmeraldas (1), Manabí (2), Guayas (3), Los Ríos (4), El Oro (5), Carchi (6), Imbabura (7), Pichincha (8), Cotopaxi (9), Bolívar (10), Tungurahua (11), Chimborazo (12), Cañar (13), Azuay (14), Loja (15), Sucumbíos (16), Napo (17), Orellana (18), Pastaza (19), Morona-Santiago (20), Zamora-Chinchipe (21).

Continuous thick line: international border; thin dotted line: borders of provinces.


Ein Symbol kann mehr als einen Fundort darstellen. Die Numerierung bezieht sich auf die ecuadorianischen Festlandsprovinzen: Esmeraldas (1), Manabí (2), Guayas (3), Los Ríos (4), El Oro (5), Carchi (6), Imbabura (7), Pichincha (8), Cotopaxi (9), Bolívar (10), Tungurahua (11), Chimborazo (12), Cañar (13), Azuay (14), Loja (15), Sucumbíos (16), Napo (17), Orellana (18), Pastaza (19), Morona-Santiago (20), Zamora-Chinchipe (21).

Ununterbrochene starke Linie: Landesgrenzen von Ecuador; punktierte Linie: Provinzgrenzen.
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groups; yet our knowledge on most pit-vipers species still lacks basic biological data, and only limited information on their distribution and ecology is available (Campbell & Lamar 2004). Gutberlet & Campbell (2001) described the genus *Bothrocophias* to accommodate five species of terrestrial, stout-bodied pitvipers from northwestern South America. Three of these species are found in Ecuador (Campbell & Lamar 2004): *Bothrocophias campbelli* (Freire Lascano, 1991), *Bothrocophias hyopra* (Amaral, 1935), and *Bothrocophias microphthalmus* (Cope, 1875).

As the greatest constraint in conservation planning for either individual species or entire snake assemblages is the fundamental lack of basic biological information on most species (Dodd 1993), the aim of the present paper is to report updated information on the distribution and natural history of the Toad-headed Pitvipers of the genus *Bothrocophias* in Ecuador.

**MATERIALS AND METHODS**

Field data was collected at various localities in western and eastern Ecuador either by visual encounter surveys, opportunistic observations or from specimens collected by natives. Some snakes were maintained under captive conditions at the Vivarium de Quito, where records on captive-born offspring were obtained. Comparative data was obtained through examination of preserved specimens and from the literature. Measurements were taken with a meter stick and string. Body weight was recorded to the nearest 1 g using Ohaus® scales. All mean values are expressed as ± 95% confidence interval. Museum specimens were dissected to analyze their stomach contents and to determine their reproductive status. Stomachs were removed, opened, and the content separated and spread in dishes for identification. For each species we calculated mean and ranges for litter size and neonate size, as well as relative clutch mass. Information of activity and foraging modes was based on observations in the field and in captivity and on information from the literature. The following abbreviations are used throughout the text: FHGO (Fundación Herpetológica Gustavo Orcés’ collection, Quito); FHGO-alive (animals alive at the Vivarium of Quito); DFCH-USFQ (Diego F. Cisneros-Heredia’s collection housed at the Universidad San Francisco de Quito); USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.); TL (total length, from the tip of the snout to the tip of the tail); SVL (snout-vent length); RCM (relative clutch mass = total offspring mass / female total mass). Localities and their geographic coordinates and elevations were obtained from collector’s field notes and museum records, and revised according to the 2000 physical map of the Republic of Ecuador published by the Instituto Geográfico Militar and NIMA (2003). In order to classify the main types of habitats at the country level, we used the vegetation formations of Sierra (1999).

**SPECIES ACCOUNTS**

*Bothrocophias campbelli*  
(Freire Lascano, 1991)

Distribution and sympatry. – *Bothrocophias campbelli* has been reported to occur on the Pacific versant of the Andes of Ecuador at elevations between about 1,300 and 2,000 m (Gutberlet & Campbell 2001; Campbell & Lamar 2004), with records in the provinces of Imbabura, Pichincha, Cotopaxi, Chimborazo, and El Oro (Orcés 1948; Freire Lascano 1991; Campbell & Lamar 1992; Schätti & Kramer 1993; Freire & Kuch 2000). Five additional specimens are herein reported from the province of Pichincha and Imbabura (appendix 1, figure 1); two specimens from the province of Imbabura (FHGO 582, 787) represent the second known collecting locality from that province (previously
Bothrocophias hyoprora occurs at low elevations in equatorial forests of the Amazon basin in Colombia, eastern Ecuador, Peru, Bolivia, and western Brazil, from near sea level to at least 1000 m (Campbell & Lamar 2004). The species has been reported from all Amazonian provinces in Ecuador (Sucumbios, Napo, Orellana, Pastaza, Morona-Santiago and Zamora-Chinchipe; Orcés 1943, 1948; Touzet 1986; Schätti & Kramer 1993). Twenty-four specimens of B. hyoprora were studied (appendix 1, figure 1); and one specimen (FHGO-alive 2621) from the Nangaritza river valley represents the westernmost locality of the species.

Bothrocophias hyoprora is sympatric with seven species of pitvipers in the area of Makuma (or Macuma), Province of Morona-Santiago: Bothriopsis bilineata (Wied-Neuwied, 1821), Bothriopsis pulchra (Peters, 1862), Bothriopsis taeniata (Wagner, 1824), Bothrocophias microphthalmus (Cope, 1875) (see below for a discussion of this record), Bothrops atrox (Linnaeus, 1758), Bothrops brazili Hoge, 1954, and Lachesis muta (Linnaeus, 1766). The area of Makuma encompasses a zone between 600 to 800 m in the south-eastern slopes of the Andes of Ecuador. Out of 156 pitvipers collected in the area of Makuma between May 1993 and December 2002, 36% were Bothrops atrox, 24% Bothriopsis bilineata, 21% Bothrops brazili, 11% Bothrocophias hyoprora, 6% Bothriopsis taeniata, and 1% each, Bothriopsis pulchra, Bothrocophias microphthalmus, and Lachesis muta. Bothrocophias hyoprora is sympatric with at least four species of pitvipers at the Tiputini Biodiversity Station (TBS), Province of Orellana: Bothriopsis bilineata, Bothriopsis taeniata, Bothrops atrox, and Lachesis muta. TBS is located in the Amazonian lowlands between 250 to 300 m. Out of 60 pitvipers recorded at TBS between 1997 and 2003, 53% were Bothrops atrox, 30% Bothrocophias hyoprora, 10% Bothriopsis bilineata, 5% Lachesis muta and 2% Bothriopsis taeniata.

Activity patterns and behavior. – Individuals of B. campbelli observed in the surroundings of Mindo and at the Mashpi Protected Forest (18 km N of San Miguel de Los Bancos, on the road between Nanegalito-Pacto-Gualea-Mashpi-Pachijal, 1100 m) were active during the late afternoon and early evening, moving on the floor among the leaflitter, inside or on the borders of primary forest (pers. obs.).

Bothrocophias hyoprora (AMARAL, 1935)

Distribution and sympatry. – Bothrocophias hyoprora occurs at low elevations in equatorial forests of the Amazon basin in Colombia, eastern Ecuador, Peru, Bolivia, and western Brazil, from near sea level to at least 1000 m (Campbell & Lamar 2004). The species has been reported from all Amazonian provinces in Ecuador (Sucumbios, Napo, Orellana, Pastaza, Morona-Santiago and partially flooded forests; Orcés 1943, 1948; Touzet 1986; Schätti & Kramer 1993). Twenty-four specimens of B. hyoprora were studied (appendix 1, figure 1); and one specimen (FHGO-alive 2621) from the Nangaritza river valley represents the westernmost locality of the species.

Bothrocophias hyoprora is sympatric with seven species of pitvipers in the area of Makuma (or Macuma), Province of Morona-Santiago: Bothriopsis bilineata (Wied-Neuwied, 1821), Bothriopsis pulchra (Peters, 1862), Bothriopsis taeniata (Wagner, 1824), Bothrocophias microphthalmus (Cope, 1875) (see below for a discussion of this record), Bothrops atrox (Linnaeus, 1758), Bothrops brazili Hoge, 1954, and Lachesis muta (Linnaeus, 1766). The area of Makuma encompasses a zone between 600 to 800 m in the south-eastern slopes of the Andes of Ecuador. Out of 156 pitvipers collected in the area of Makuma between May 1993 and December 2002, 36% were Bothrops atrox, 24% Bothriopsis bilineata, 21% Bothrops brazili, 11% Bothrocophias hyoprora, 6% Bothriopsis taeniata, and 1% each, Bothriopsis pulchra, Bothrocophias microphthalmus, and Lachesis muta. Bothrocophias hyoprora is sympatric with at least four species of pitvipers at the Tiputini Biodiversity Station (TBS), Province of Orellana: Bothriopsis bilineata, Bothriopsis taeniata, Bothrops atrox, and Lachesis muta. TBS is located in the Amazonian lowlands between 250 to 300 m. Out of 60 pitvipers recorded at TBS between 1997 and 2003, 53% were Bothrops atrox, 30% Bothrocophias hyoprora, 10% Bothriopsis bilineata, 5% Lachesis muta and 2% Bothriopsis taeniata.

Activity patterns and behavior. – Individuals of Bothrocophias hyoprora observed at the Tiputini Biodiversity Station were active during the early and late evening, moving among the leaflitter in primary terra firme and partially flooded forest. One specimen was observed during the day (10:00 hr) inactive among dense vegetation 5 m from the border of an oxbow lake. One snake observed at the Jatun Sacha Biological Station was coiled up 2 m from a trail in secondary terra firme forest during late evening (19:00 hrs). One specimen from the Yasuni National Park was collected on primary terra firme forest, while inactive on the floor among leaf litter next to the roots of a Ceiba tree at 12:00 hr (F. Sorroza field notes 17 June 1996). Various specimens from the province of Morona-Santiago were found in cultivated areas or in trails near areas inhabited by human during the morning and noon or in open areas directly on the nude floor at 17:00 hr. The specimen from Shaime (FHGO-alive 2621) was collected during the day in primary forest.

Size. – Campbell & Lamar (2004) reported the TL of adult Bothrocophias hyoprora to range mainly between 40 - 50 cm, and the maximum TL of females as 83.0 cm and that of males as 53.6 cm. Fourteen
adult female specimens herein analyzed had a mean total length of 62.9 ± 4.8 cm (range 45.0 - 78.0 cm), and a mean weight of 200.7 ± 55.6 g (range 52.0 - 356.0 g). Seven males had a mean total length of 46.8 ± 10.9 cm (range 35.4 - 65.1 cm, therefore increasing the known maximum TL), and five had a mean weight of 67.2 ± 60.9 g (range 21.5 - 174.5 g). All these specimens came from the province of Morona-Santiago. The differences in size between males and females are statistically significant (one-way ANOVA, $F = 13.38, p < 0.01$), with females being larger and heavier than males.

Reproduction. - A female Bothrocophias hyoprora captured at the Centro Amazonas-Makuma, Province of Morona-Santiago, on 18 August 1999, gave birth to 13 young on 2 December 1999. The female measured 66.7 cm in TL and weighed 356 g before birth. The neonates had a mean length of 18.07 ± 0.39 cm (range 17.0 - 19.0 cm), mean weight of 6.4 ± 0.6 g (range 4.5 - 7.2 g, combined mass of all young = 82.9 g), and RCM of 0.30. Four were stillborn; the other eight snakes were maintained alive for 3 to 74 days. Another female B. hyoprora captured at the Centro Chuwints-Makuma, Province of Morona-Santiago, on 29 September 1998, gave birth to three stillborn young on 3 January 1999. All had deformities in the vertebral column, caudal region and on the head. The female measured 56.5 cm in TL.

Longevity. - Campbell & Lamar (2004) noted the unavailability of information on the longevity of Bothrocophias species, stating that "Bothrocophias are uncommon and have not been maintained frequently in captivity". One healthy specimen of B. hyoprora (FHGO-alive 2162) from the Centro Chuwints-Makuma, Province of Morona-Santiago, on 29 September 1998, gave birth to three stillborn young on 3 January 1999. All had deformities in the vertebral column, caudal region and on the head. The female measured 56.5 cm in TL.

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females can attain bigger sizes and weights than males, as in *B. hyoprora*; however more data is needed to support this hypothesis.

**Reproduction.** - The reproductive status of the two specimens from Namburgeri collected in April 1999 was analyzed. The 92.0 cm female contained 37 enlarged follicles (10 mm in diameter), while the 87.0 cm female contained 47 enlarged follicles (12 mm in diameter). A female *B. microphtalmus* captured at the Centro Kim-Makuma, province of Morona-Santiago, on 1 December 1998, gave birth to 13 young on 31 December 1998. The female measured 66.6 cm in total length and weighed 304 g before birth. The neonates had a mean length of 16.72 ± 0.85 cm (range 14.8 - 18.7 cm), mean weight of 4.2 ± 0.9 g (range 2.7 - 7.1 g, combined mass of all young = 54.7 g), and RCM of 0.22. Nine were stillborn; the other four young lived 24, 32, 55 and 930 days in captivity. The specimen that survived longest (FHGO 3194) increased its weight from initially 7.1 g to 11.5 g on 27 May 1999; it died on 18 July 2001.

**DISCUSSION**

New information presented in this paper along with data from the literature indicate that *Bothrocophias campbelli* occurs mainly inside or in the borders of primary and mature secondary forests in the northern, central and southern regions of the Pacific slopes of the Andes in Ecuador between 800-2000 m where it is found in the following vegetation formations: Foothill Evergreen forest, Low Montane Evergreen forest, and marginally into the Montane Cloud forest (FREIRE-LASCANO 1991; CAMPBELL & LAMAR 2004; this paper). *Bothrocophias hyoprora* occurs in a wide range of habitats, including primary forests, mature secondary forests, and cultivated areas, usually near wetlands (e.g. flooded forests, ponds, rivers, oxbow lakes), but also in terra firme forests with low hills; in the northern and southern Amazonian lowlands and low eastern slopes of the Andes in Ecuador between 210 - 1500 m. It inhabits the following vegetation formations: Lowland Evergreen Non-flooded forest, Lowland Evergreen Flooded forest by black-water rivers, Lowland Evergreen Flooded forest by white-water rivers, Foothill Evergreen forest, and Low Montane Evergreen forest (DIXON & SOINI 1986; DUELLMAN & MENDELSOHN 1995; CAMPBELL & LAMAR 2004; this paper). *Bothrocophias microphtalmus* occurs in primary and mature secondary forests in the south-eastern slopes of the Andes in Ecuador between 600 - 2350 m (it still remains unreported from the northern slopes, where it is expected to occur as it also inhabits south-eastern Andean Colombia). It occupies the following vegetation formations: Low Montane Evergreen forest, Montane Cloud forest, and Foothill Evergreen forest (CAMPBELL & LAMAR 2004; this paper).

*Bothrocophias myersi* GUTBERLET & CAMPBELL, 2001 was described from south-western Colombia, and the above authors mentioned the possibility that this species could inhabit the Ecuadorian Chocó region. Although destruction of the natural habitats in that area is extensive, especially by the illegal activities of timber companies, some undisturbed areas still remain. However, no specimens of *B. myersi* have yet been obtained from the area.

Pitvipers of the genus *Bothrocophias* prey upon rodents (FREIRE & KUCH 2000 for *Bothrocophias campbelli*; NICÉFORO-MARÍA 1938; CARRILLO DE ESPINOZA 1983; DUELLMAN & MENDELSOHN 1995 for *B. hyoprora*), *Atractus* snakes (D. SALAZAR pers. comm. for *B. campbelli*), gymnophthalmid lizards (CARRILLO DE ESPINOZA 1983; CAMPBELL & LAMAR 2004 for *B. hyoprora*), teiid lizards and hylid tree frogs (PRADO & HOGE 1948 for *B. microphtalmus*), and caecilians (ZUFFI 2004 for *B. campbelli*). The report presented herein of *Bothrocophias microphtalmus* preying upon mouse opossums is the first record of predation on marsupials. Although mouse opossums are considered as mainly arboreal mammals, members of the genus *Marmosops* occupy both arboreal and terrestrial levels during their foraging activities (EMMONS & FEER 1999). Specifically, *Marmosops noctivagus* uses the floor...
and the lower vegetation in the forest in areas with dense understory, especially near wetlands in primary or secondary forest (EMMONS & FEER 1999); therefore it is accessible as a prey for the terrestrial B. microphthalmus.

The data presented here and in the available literature (KUCH & FREIRE 1995; FREIRE & KUCH 2000; CAMPBELL & LAMAR 2004) indicate that Bothrocophias pitvipers can produce up to 47 enlarged follicles and known litter sizes range from three to 36. Reproductive B. hyoprora females had a mean TL of 63.0 cm (56.5 - 66.7 mm, n = 3), and offspring TL ranged between 17.0 - 19.0 cm (NEILL 1966; this paper). Reproductive B. microphthalmus females had a mean TL of 83.5 cm (66.6 - 92.0 cm, n = 4), and offspring TL ranged between 14.8 - 20.3 cm (KUCH & FREIRE 1995; this paper). The only report on B. campbelli indicates a reproductive female TL of 105.7 cm (FREIRE & KUCH 2000). Enlarged ovarian follicles were reported in April for B. campbelli by FREIRE & KUCH (2000), juveniles in December for B. microphthalmus and from August to September for B. hyoprora (this paper). The RCM values in Bothrocophias ranged from 0.22 (in B. microphthalmus) to 0.30 (in B. hyoprora). Although the sample is small, Bothrocophias RCM values are similar to those reported for other viviparous vipers (SIEGEL & FITCH 1984). When comparing B. hyoprora and B. microphthalmus, RCM values suggest that these species follow SIEGEL et al.'s (1986) hypothesis about RCM tending to decrease with increasing body size in viviparous snakes; however the small sample size prevents further conclusions and future studies should look at this interesting tendency.

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RESUMEN

Limitada información se ha publicado sobre las serpientes venenosas del género Bothrophiad. Este artículo presenta información para las tres especies de Bothrophiad que habitan en Ecuador: Bothrophiad campbelli (FREIRE LASCANO, 1991), B. hyopora (AMARAL, 1935), y B. microphthalmus (COPE, 1875); incluyendo datos sobre su distribución geográfica, rango altitudinal, registros provinciales, especies en simpatria, patrones de actividad, comportamiento, tamaño, biología reproductiva, dieta y longevidad. Bothrophiad campbelli habita las regiones norte, central y sur de la vertiente Pacífica de Ecuador entre 800 y 2000 m, B. hyopora habita las regiones norte y sur de las tierras bajas de la Amazonía y vertientes bajas de la Cordillera Oriental entre 210 y 1500 m; y B. microphthalmus habita en las vertientes sureste de la Cordillera Oriental entre 600 y 2350 m. Se reporta la segunda localidad conocida para B. campbelli en la provincia de Imbabura y la localidad mas occidental de B. hyopora en el valle del Río Nangaritza. Se confirma la simpatría de B. hyopora y B. microphthalmus en el área de Makuma, provincia de Morona-Santiago, incrementando el rango de distribución vertical de B. microphthalmus hasta al menos 600 m. La Raposa Chica de Vientre Blanco Marmosops noctivagus es reportada por primera vez como presa de B. microphthalmus. Se reporta nueva información sobre la biología reproductiva de Bothrophiad, incluyendo el tamaño de la camada y los neonatos de B. hyopora y B. microphthalmus.

Las serpientes Bothrophiad pueden producir hasta 47 foliculos agrandados y el rango conocido del tamaño de las camadas incluye entre 3 a 36 individuos. Foliculos agrandados en el ovario han sido reportados en Abril para B. campbelli, y juveniles en Diciembre para B. microphthalmus y entre Agosto y Septiembre para B. hyopora. Los valores de la masa relativa de la puesta en Bothrophiad varían entre 0.22 (en B. microphthalmus) hasta 0.30 (en B. hyopora).
APPENDIX 1 – Ecuadorian Bothrocophias specimens examined

Bothrocophias campbelli - Province of Pichincha: FHGO 109 from Alluriquin (00°19'48"S, 78°59'27"W, ca. 800 m), collected on 25 December 1990; FHGO 334 from Alluriquin (00°19'48"S, 78°59'27"W, ca. 800 m), collected on 25 January 1991; FHGO 1227 from Mindo (00°02'S, 78°46'12"W, 1200 m), collected on 23 July 1995. Province of Imbabura: FHGO 582 from Chontal Alto, Garcia Moreno (00°17'12"N, 78°43'W, 1530 m), collected on 13 November 1992; FHGO 787 from Chontal Alto, Garcia Moreno (00°17'12"N, 78°43'W, 1530 m), collected on March 1993.

Bothrocophias hyoprora - Province of Zamora-Chinchipe: FHGO-alive 2621 from Destacamento Militar Shaime (1040 m), collected on 13 September 2003. Province of Sucumbios: FHGO 1315 from Tarapoa (00°08'W, 76°24', 310 m) collected on 26 June 1995; FHGO 922 from Zancudococha (00° 25'S, 75°30'W, 220 m) collected on 6 June 1994. Province of Orellana: DFCH-USFQ (3 unnumbered specimens) from Tiputini Biodiversity Station (0°37'05"S, 76°10'19"W, 250-300 m) collected between February 1998 and August 2000; FHGO 2465 from Parque Nacional Yasuni, carretera Pompeya Sur – Iro (300 m) collected on 17 June 1996. Province of Morona-Santiago: FHGO 178 from 4 km NE of Anduash (02°42'S, 77°45'W, 420 m) collected on 10 March 1996; FHGO 938, 1028, 1270, 2903 from Centro Amazonas-Makuma (02°08'S, 77°42'W, 600 m) collected between June 1993 and January 1999; USNM 165316 from "Maguma" (=Makuma); FHGO 2284-6, 2366, 2951 from Centro Chuwints-Makuma (01°59'S, 77°51'W, 600 m); FHGO 1174, 1029, 2488, 2895, 3574 from Centro Kiim-Makuma (03°00'S, 78°03'W, 600 m).

Bothrocophias microphthalmus - Province of Morona-Santiago FHGO 2680 from Centro Wisui-Makuma (02°08'S, 77°43'W, 600 m) collected on 27 March 1994; FHGO 2454 from Centro Kiim-Makuma (03°00'S, 78°03'W, 600 m) collected in December 1999. Province of Pastaza: USNM 165303 from near Puyo. Province of Morona-Santiago: FHGO 1663 from Pananza/San Miguel de Conchay (1000 m) collected on 12 October 1997. Province of Tungurahua: FHGO 3614 from El Topo (1200 m) collected on 28 August 1997. Province of Zamora-Chinchipe: FHGO 2027 from La Pituca, Cuenca del Rio Curintza (04°09'5'S, 78°59'W, 1835 m) collected on 22 June 1998; FHGO 2300 from La Pituca, Cuenca del Rio Curintza (04°09'S, 78°58'W, 1820 m) collected on 30 October 1998; FHGO 669, 670 from Nacacuntza (03°59'S, 78°49'W, ca. 1400 m) collected in December 1991; FHGO 2451, 2566 from Numbami, Cuenca del Rio Jambue (04°09'S, 78°55'W, ca. 1500 m) collected on 30 April 1999.

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