Occasional Papers of the Museum of Natural Science, Louisiana State University

Volume 1 | Number 50 Article 1

4-15-1976

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NUMBER 50 15 APRIL 1976

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

LOUISIANA STATE UNIVERSITY

BATON ROUGE, LOUISIANA

REVISION OF THE SOUTH AMERICAN COLUBRID SNAKES OF THE *HELICOPS PASTAZAE* COMPLEX

By DOUGLAS A. ROSSMAN

HELICOPS PASTAZAE Shreve, which was described from the Río Pastaza drainage of southeastern Ecuador, is one of three currently recognized species (*pastazae*, *polylepis*, *yacu*) constituting what I refer to as the *polylepis* section of the genus. Members of this section are characterized by having spotted dorsum, nonglossy scales, and relatively large numbers of dorsal scale rows, ventrals, and subcaudals. *Helicops polylepis* Günther is a wide-ranging Amazon Basin form that primarily differs from the other species in having a very dark venter (with some light spots) and no intergenial scales. Its range abuts that of *H. pastazae* where the foothills of the Andes merge into the Amazonian lowlands but completely encompasses that of *H. yacu* Rossman and Dixon, which is presently known only from the vicinity of Iquitos, Perú. This last species differs from both *H. polylepis* and *H. pastazae* in having 27 dorsal scale rows, a very small eye, and more space between the dorsal spots.

Newly acquired material from the eastern Andean foothills in Ecuador reveals the existence of two distinct species (one undescribed) sharing what were previously thought to be diagnostic characteristics of *Helicops pastazae*, i.e., a premdominantly light venter, closely placed dorsal spots, and no more than 25 dorsal scale rows. These two taxa are referred to hereafter as the *pastazae* species complex. Other specimens establish the existence of *H. pastazae* (*sensu stricto*) in Perú, Colombia, and Venezuela, and reveal that

this species is far more variable in both pattern and scutellation than was previously recognized.

Most of the Ecuadorian specimens examined in this study were acquired by the late James A. Peters. In recognition of his numerous contributions to our understanding of the South American herpetofauna generally, and that of Ecuador in particular, I name the undescribed species in his honor.

Helicops petersi new species

Holotype.—USNM 196360, an adult ♂ from the east bank of the Mishualli River, 1 mile NE Tena, Napo-Pastaza Province, Ecuador, collected 31 October - 3 November 1958 by James A. Peters; original no. JAP 2758.

Paratypes.—USNM 196352-196359, 196362-196366, LSUMZ 29386, same locality as holotype; UIMNH 61042-61052, Napo, Tena; KU 112266, 148311, Napo, Santa Cecilia, 340 m; KU 121888, Napo, Río Aguarico, Puerto Libre, 570 m; USNM 198630, Napo, mouth of Río Guataracu; USNM 198631, Napo, Concepcion; USNM 198585, Pastaza, headwaters of Río Arajuno; UMMZ 90819 (2 specimens), Oriente, Río Cotopino, ca. 400 m; UMMZ 91565, Alpa-Yacu, 300 m.

Definition.—A moderately large (maximum recorded snout-vent length 504 mm) species of *Helicops* characterized by: a maximum of 21-23 dorsal scale rows (>21 only in a third of the females); scales in dorsal rows striated, not glossy, and bearing a broad median keel not reaching end of scale; single internasal usually in contact with rostral; a very large number of ventrals (♀♀ 137-150, ♂♂ 135-142); a large number of subcaudals (♀♀ 67-73, ♂♂ 85-91); the dorsum with 4 or 5 rows of alternating dark spots; the venter light with a lateral series of dark checks, the light ventral color rarely extending onto dorsum; the subcaudals entirely dark in adults.

Description of holotype.—Dorsal scales in 21-21-16 rows, with broad incomplete keels except for scales in row 1, which appear smooth; the complete scale row reduction formula

$$21\ \frac{3+4(110)}{-3(107)}\ 19\ \frac{-5(115)}{-5(115)}\ 17\ \frac{+10(131)}{}\ 18\ \frac{-10(137)}{-9(136)}\ 16;$$

ventrals 138½; subcaudals 91; anal divided. Supralabials 8, fourth entering orbit; infralabials 10, five in contact with anterior genials, which are longer than posterior genials (138.1%); 2 intergenials; nasal entire, with a subnarial crease present; loreal higher than long; preocular single; postoculars 2; anterior temporal single; posterior temporals 2 on left, 3 on right, keeled; single internasal narrowly in contact with rostral; muzzle 16.3%, frontal 24.2%, and parietal 31.5% of head length; frontal width 65.1% of its length; well-developed tubercles on anterior genials and first infralabials, smaller ones on adjacent scales. Snout-vent length 385 mm, tail length 188 (32.8% of total length); head 4.6% of snout-vent length; eye 10.7% of head length.

Maxilla with 16 recurved teeth and, following a diastema, a pair of enlarged nonrecurved teeth. Eleven teeth lie anterior to the posterior end of the prefrontal process.

The *in situ* hemipenis extends to the level of the 13th subcaudal. It is nude to the level of the 5th subcaudal, has large spines thence to the level of the 8th subcaudal, and small spines or papillae thence to the apex. Both the hemipenis and the sulcus spermaticus are bifurcated.

The dorsum is dark olive brown with 5 rows of alternating irregular black spots. The spots are 2 scales long and 2 scales high, except in the vertrebral row, where they are only half as large; spots in the same row are separated by 1-1½ scale lengths. The top of the head is uniformly dark and the ventral surface from the chin to the back of the head is mottled cream and dark. The venter is cream medially, very dark brown to diffuse black laterally. The lateral dark pigmentation is irregular, and cream patches appear on a few scales in the first dorsal scale row. The subcaudals are charcoal throughout.

Variation.—Meristic and mensural variation is summarized in Tables 1 and 2. Females have more ventrals, fewer subcaudals, and a shorter tail than do males. Females also exhibit a slight tendency to have more dorsal scale rows. Coloration (Fig. 1) in the type series of *Helicops petersi* is fairly uniform, although some ontogenetic changes are apparent. Juveniles are lighter overall and have the subcaudals checkered rather than generally dark.

The venter is checkered in many specimens, but in others (including the holotype) the central section of each ventral is unpigmented. Some individuals have only 4 rows of dorsal spots, others may have 4 or 5. The paravertebral spots may be as large as 3 scales long and 4 scales high. In a few specimens the cream color of the venter extends onto dorsal scale row 1; in UIMNH 61046 it extends as high as row 3, although it is partly suffused with dark pigment.

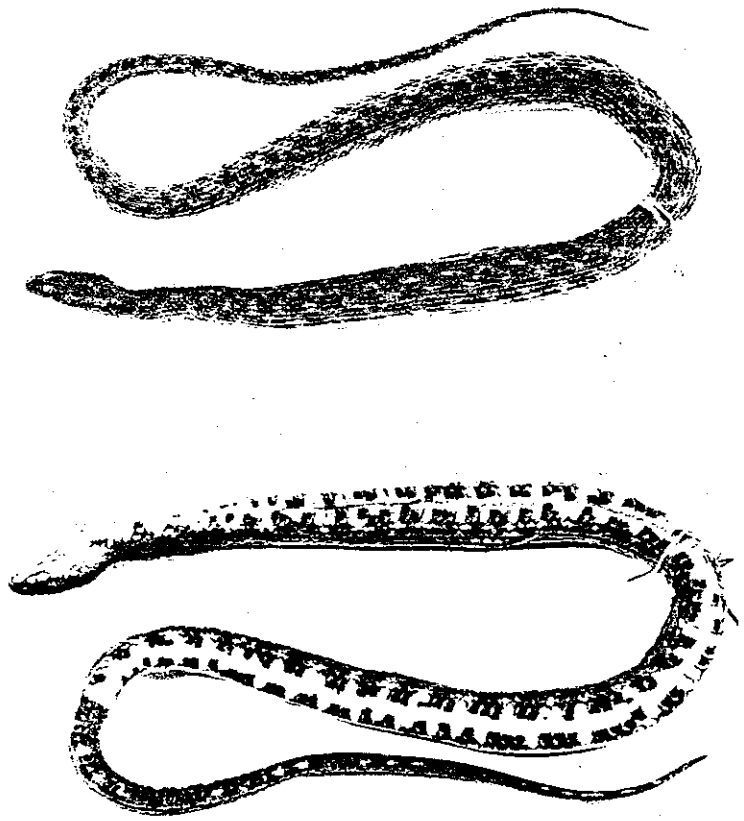

FIGURE 1. Dorsal and ventral views of a paratype of *Helicops petersi* (USNM 196358) from Tena, Ecuador.

Relationships.—The affinities of *Helicops petersi* are discussed together with those of *H. pastazae* in the concluding section of this paper.

HELICOPS PASTAZAE Shreve, 1934

Holotype.—MCZ 36993, a juvenile ♀ from the Pastaza River, between Canelos and the Marañón River, Ecuador [=Perú], collected in 1932 by C. Spencer.

Definition.—A large (maximum recorded snout-vent length 670 mm) species of *Helicops* characterized by: a maximum of 23-25[1] dorsal scale rows; scales in dorsal rows striated, not glossy, and bearing a broad median keel not reaching end of scale; single internasal usually separated from rostral by nasals; a large number of ventrals (♀♀ 130-145, ♂♂ 121-134); a very large number of subcaudals (♀♀ 72-97, ♂♂ 93-117); the dorsum with 4 or 5 rows of alternating dark spots, the paravertebral spots large and often fused transversely; the venter light with a series of dark crossbands or alternating checks, the light ventral color extending several rows onto the dorsum; the subcaudals similar in color pattern to the venter.

Variation.—Shreve's original description of the holotype is adequate, hence no redescription is presented here. Meristic and mensural variation is summarized in Tables 1 and 2. Reduction in the number of dorsal scale rows results from losses and fusions involving lateral rows 3-6. In some animals the vertebral row is also lost a short distance anterior to the vent. Ventral and subcaudal numbers and relative tail length exhibit both geographic variation and sexual dimorphism, the females having more ventrals than the males but a shorter tail and fewer subcaudals. The number of ventrals decreases progressively from south to north, a trend generally paralleled by tail length and subcaudal number although both characters also undergo a decrease southward from Ecuador to Peru. There is little sexual dimorphism in the maximum number of dorsal scale rows in Ecuadorian snakes but very pronounced dimorphism in this feature in the sample from southern Colombia, in which all the females have more than 23 rows whereas most of the males have a maximum of 23. None of the 4 Peruvian males examined had more than 23 rows, which suggests this population may fit the Colombian rather than the Ecuadorian pattern of variation. Three of the 4 Peruvian snakes (LSUMZ 29383-29385) have each supraocular scale divided into 2 subequal halves, an anomaly occurring nowhere else in the range of the species. Two specimens from Ecuador (KU 121335, USNM 196351) possess a divided internasal.

The dorsum is tan to gray brown with 4 or 5 rows of alternating irregular dark spots (margins more or less indistinct), the vertebral (if present) and paravertebral spots often fusing transversely to form large rectangular blotches 3½-5 scales long in Ecuador (Fig. 2), 2½ scales long in northern

[1] One adult ♀ *Helicops pastazae* (USNM 196361) has an irregular series of additions and reductions on the anterior ⅓ of its body with a maximum of 29 rows.

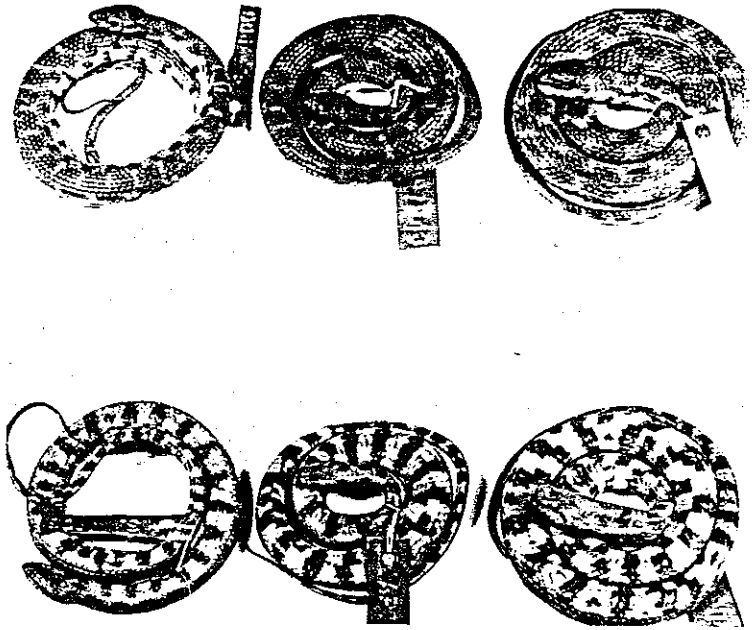

FIGURE 2. Dorsal and ventral views of three specimens of *Helicops pastazae* (USNM 196369, 196368, 196367) from Ecuador showing the color pattern prevalent in that region.

Peru (Fig. 3), and 2-4 scales long in Colombia, which nearly encompasses the more consistent extremes occurring farther south. The blotches are separated by light interspaces 1-1½ scales long, and in a number of animals some of the scales in the interspaces have white edges.

The top of the head is uniformly dark in adults. In juveniles a broad light stripe encircles the muzzle, a pair of large light spots may occupy the angle of the jaw, and there is a prominent dark postocular stripe (Fig. 4). At all ages a narrow dark vertebral stripe extending to the nuchal blotch is usually readily apparent. The venter is cream colored with an irregular pattern of black checks, both the light and dark coloration extending onto the dorsum as high as the 3rd or 4th row. The light ventral color is increasingly obscured with gray-brown pigment in larger snakes.

Two individuals possess particularly noteworthy variant color patterns.

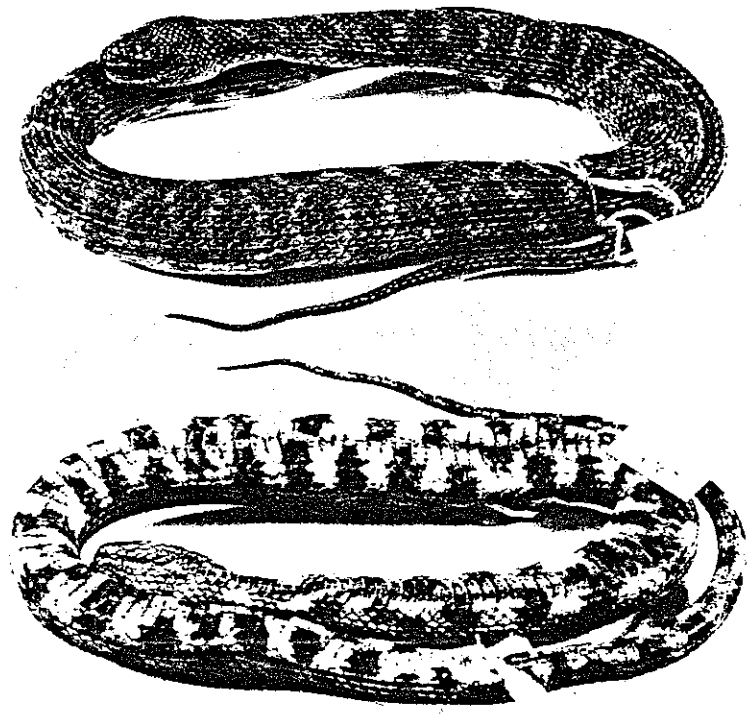

FIGURE 3. Dorsal and ventral views of a *Helicops pastazae* (LSUMZ 29385) from northwestern Peru.

The only Venezuelan specimen examined (MBUCV 3) has a considerable reduction in the amount of black pigment on the venter and lower sides (Fig. 5). The most extreme pattern variation occurs in a subadult male (USNM 196351) from Caveceras, Ecuador, which completely lacks black markings on the dorsum, and its dark ventral markings form an irregular broad median stripe (Fig. 6). James Peters and I originally thought that this animal represented an undescribed species, but it agrees well with males from adjacent populations of *Helicops pastazae* in all features save color pattern (its divided internasal is a condition shared with one other male from the region), and almost surely is a highly aberrant *H. pastazae*.

Specimens Examined.—COLOMBIA: Antioquia, Río Magdalena, Nare, ILS

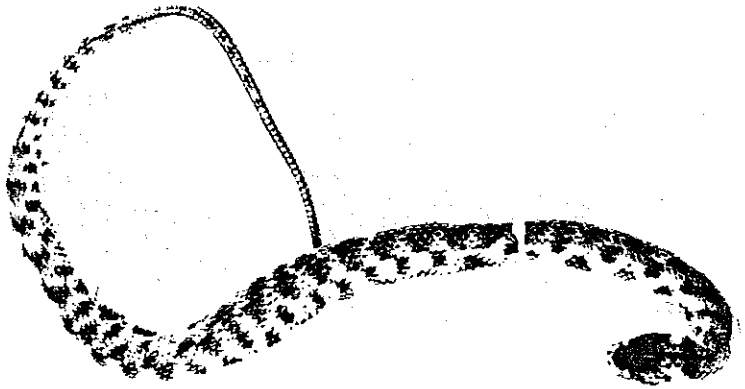

FIGURE 4. Dorsal view of a *Helicops pastazae* (AMNH 53920) from Iquitos, Perú, showing the juvenile head pattern.

1882; Caquetá, vicinity of Florencia, ILS 771-777, 779-780, 782-786, 788-790, 792-794, FMNH 69223; Caquetá, Puerto Boy, Río Caquetá, ILS 787, 791; Caquetá, Puerto Asís (Nicéforo-María, 1942, plate I, fig. 2); Meta, Villavicencio, UMMZ 126721; Norte de Santander, Río Pamplonita, N Cúcuta, ILS 757. ECUADOR: Río Pastaza between Canelos and Río Marañón, MCZ 36993 (holotype)—36996, UMMZ 107618, FMNH 35300; general region of upper Río Pastaza drainage, USNM 196367-196368; Río Pastaza, 500 m, UMMZ 88930-88933, 88935; Napo, headwaters of Río Arajuno, USNM 198628; Napo, mouth of Río Copataza, USNM 198629; Napo-Pastaza, Río Bobonaza about 2 km downstream from Caveceras, 655 m, USNM 196351; Pastaza, headwaters of Río Bobonaza, USNM 198583, 198591; Pastaza, Río Bobonaza just below Canelos, USNM 198584; Pastaza, Chichirota, USNM 198586, 198626; Pastaza, Río Bobonaza, Montalvo, USNM 198604-198605; Pastaza, Río Bobonaza, Sarayacu, USNM 198587-198589, 198594-198595; Pastaza, region of Sarayacu to Río Conambo, USNM 198592-198593, LSUMZ 29538; Pastaza, Río Bufeo, USNM 198590; Pastaza, Río Huiyayacu, USNM 198596-198597; Pastaza, Río Rutuno, USNM 198598-198600, 198617-198618; Pastaza, headwaters of Río Capahuari, USNM 198601-198602, 198610; Pastaza, Río Pindo, USNM 198603, 198611, 198613; Pastaza, Río Llushin, N Arapicos, USNM 198-606; Pastaza, Río Conambo, USNM 198607-198608; Pastaza, Río Villano, USNM 198609, 198612; Pastaza, Río Pucayacu, USNM 198614-198615;

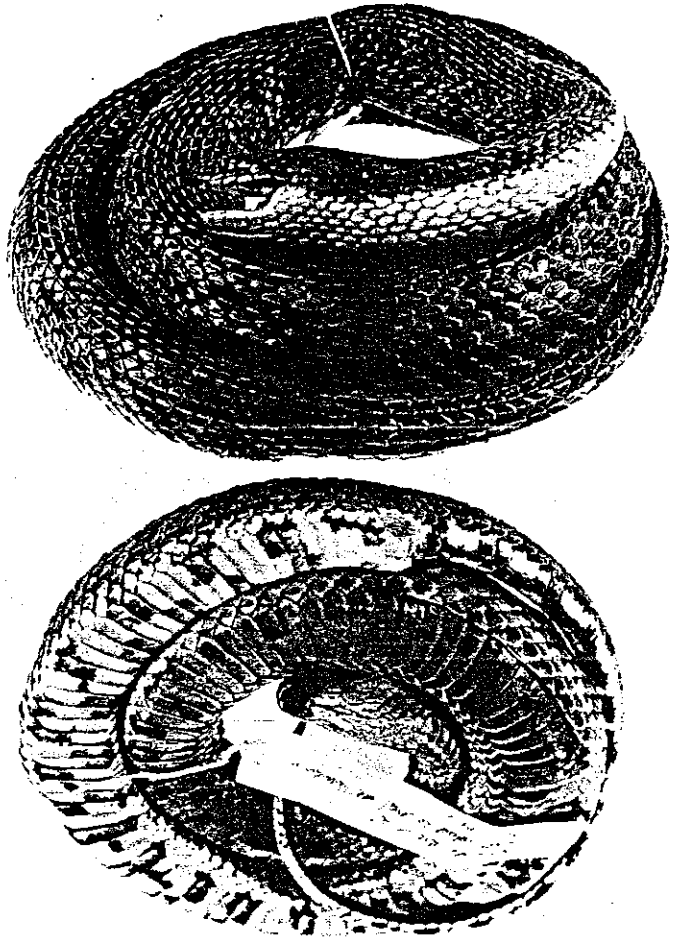

FIGURE 5. Dorsal and ventral views of a *Helicops pastazae* (MBUCV 3) from Maracaibo, Venezuela.

Pastaza, Río Siquino, USNM 198616; Pastaza, Río Oglan, USNM 198619-198625; Pastaza, Río Copataza, USNM 198627; Pastaza, Mera, 1140 m, KU 121335; Pastaza, Río Puyo, Puyo, 960 m, USNM 196361; Santiago-Zamora, no specific locality, UMMZ 82886, 82893; Santiago-Zamora, Río

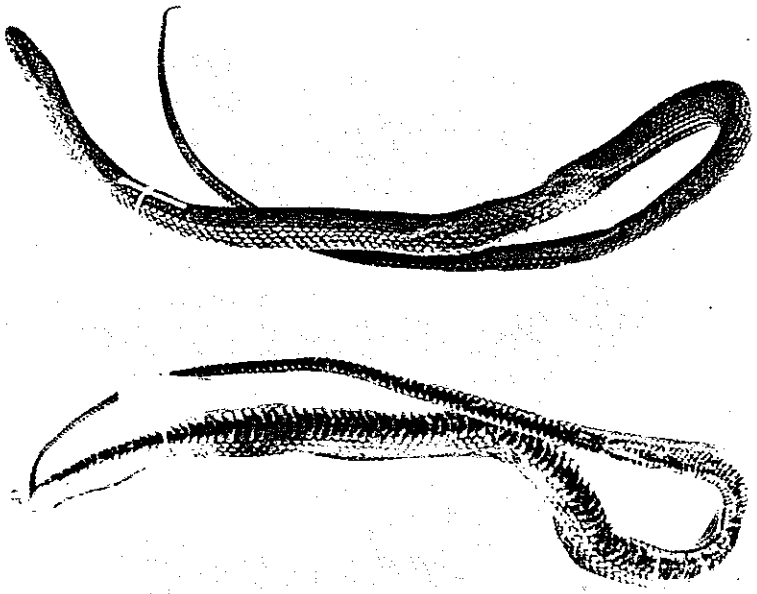

FIGURE 6. Dorsal and ventral views of a *Helicops pastazae* (USNM 196351) from Caveceras, Perú, showing its aberrant color pattern.

Llushin, USNM 196369; Zamora, Macuma, UIMNH 62858-62862. PERÚ: Amazonas, 20 km (by road) SW Chiriaco, 520 m, LSUMZ 29382-29385; Loreto, Río Itaya, Iquitos, AMNH 53920. VENEZUELA: Zulia, vicinity of Maracaibo, MBUCV 3.

DISTRIBUTION OF THE *PASTAZAE* COMPLEX

Members of the *pastazae* complex range northward along the eastern Andean foothills from the upper Marañón drainage in Perú to the vicinity of Maracaibo, Venezuela (Fig. 7). The known altitudinal range of the complex is 300-1140 m, but many of the localities are so inexpressly stated on the original data tags that we can reasonably expect the actual range to be somewhat greater. Although the range of *Helicops petersi*, which is confined to the Río Napo and its tributaries, lies within that of *H. pastazae*, the only locality from which specimens of both species have been taken is the headwaters of the Río Arajuno. The specimen from Iquitos (AMNH 53920) is

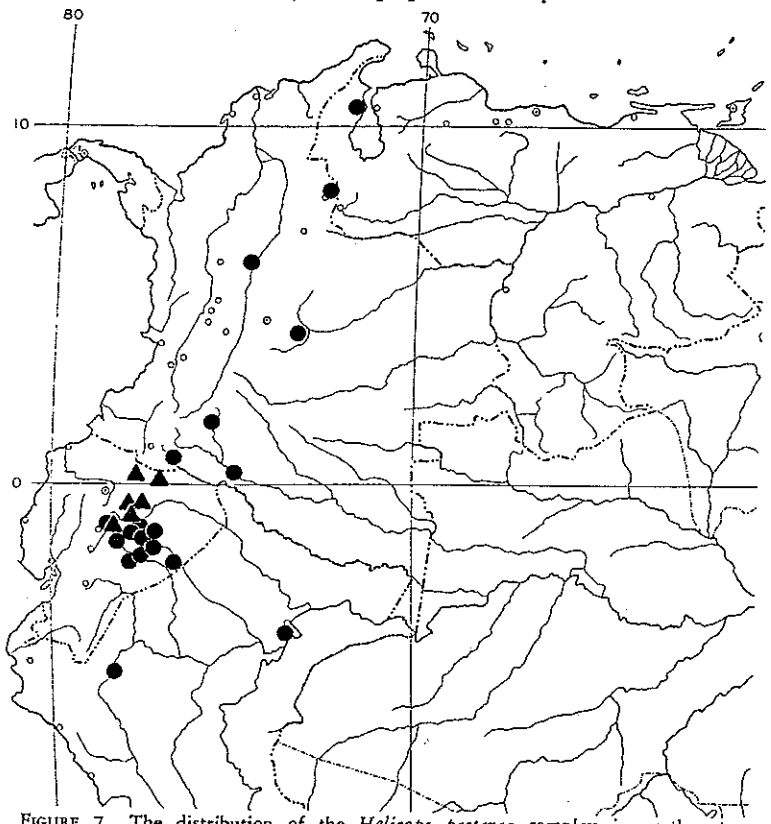

FIGURE 7. The distribution of the *Helicops pastazae* complex in northwestern South America. Solid dots represent *H. pastazae*, triangles *H. petersi*.

unquestionably a *H. pastazae*, agreeing well with the Ecuadorian material in meristic and mensural features, but the locality is far removed from the main range of the species and is at a lower elevation than is typical. Consequently I have some reservations as to whether the specimen actually represents an established population.

RELATIONSHIPS OF THE *PASTAZAE* COMPLEX

As can be ascertained from Table 2, *Helicops pastazae* and *H. petersi* are similar in most proportional characters. *H. petersi* does have a shorter tail

and fewer subcaudals than *H. pastazae* (Table 1); the most marked differences are in comparison with the Ecuadorian populations of the latter and suggest character displacement. On the basis of admittedly small samples, the other members of the *polylepis* section, *H. polylepis* and *H. yacu*, appear to have proportionately longer heads, shorter frontals, and shorter parietals than does the *pastazae* complex. *Helicops yacu* has a very small eye; that of *H. polylepis* is comparable in size to the eyes of *H. pastazae* and *H. petersi*. *Helicops yacu* shares with Ecuadorian *H. pastazae* the distinction of having the longest tail and most subcaudals of any *Helicops*; *H. polylepis* is intermediate in this respect between those two species and *H. petersi*. There is a continuous morphocline in ventral number, the quantity increasing from *H. polylepis* through *H. yacu* and *H. pastazae* to culminate in *H. petersi*, which has the most ventrals of any *Helicops*. *Helicops yacu* has a maximum of 27 dorsal scale rows, *H. polylepis* and *H. pastazae* 23-25, and *H. petersi* usually 21. The number of maxillary teeth averages about one less in *H. yacu* than in *H. polylepis* and *H. pastazae*, two less than in *H. petersi*. The nasals separate the internasal from the rostral in all available specimens of *H. yacu* and a substantial majority of *H. pastazae*, but fail to do so in most *H. polylepis* and *H. petersi*. *Helicops yacu* and *H. polylepis* have 11 or 12 infralabials on each side of the head; *H. petersi* usually has fewer than 11 on one or both sides, as does an occasional *H. pastazae*. The posterior genials are in contact with each other in *H. polylepis* but separated by intergenial scales in the other three species.

Within the *polylepis* section, *Helicops polylepis* is unique in having predominantly dark ventrals, *H. yacu* in having widely spaced dorsal spots, and *H. petersi* in having no nape stripe and no more than one row of light-colored scales adjacent to the venter. Juvenile *H. pastazae* and *H. yacu* have a light muzzle, juvenile *H. petersi* and *H. polylepis* do not. Interspecific variation in color pattern, scalation, and proportions shows few concordant trends and appears to be largely a mosaic that provides little assistance in determining affinities. An examination of cranial osteology, currently in progress, should shed further light on this problem and afford insight into the relationships of the *polylepis* section to the other species of *Helicops*.

ACKNOWLEDGMENTS

For the loan of specimens and for other courtesies, I am indebted to the following curators: Richard G. Zweifel and Charles W. Myers (American Museum of Natural History—AMNH); Hymen Marx (Field Museum of National History—FMNH); Hermano Nicéforo María (Instituto de La Salle—ILS); William E. Duellman (University of Kansas Museum of Natural History—KU); Janis A. Roze (Museo de Biologia, Universidad Central de Venezuela—MBUCV); Ernest E. Williams (Museum of Comparative Zoology—MCZ); Donald F. Hoffmeister (University of Illinois Museum of Natural History—UIMNH); Arnold G. Kluge (University of Michigan Museum of Zoology—UMMZ); and the late James A. Peters and George R. Zug (National Museum of Natural History—USNM). I am also grateful to J. Harvey Roberts and H. M. Turner for their photographic assistance.

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TABLE 1. GEOGRAPHIC AND SEXUAL VARIATION OF SELECTED CHARACTERS IN THE *HELICOPS PASTAZAE* COMPLEX

		H. pastazae				*H. petersi*
Character		*N. Colombia*[1]	*S. Colombia*[2]	*Ecuador*	*N. Peru*	
Maximum Dorsal Scale Rows	♂♂	———	>23(2)[3]	>23(15)	>23(0)	>21(0)
		———	23(10)	23(15)	23(4)	21(14)
	♀♀	>23(2)	>23(11)	>23(28)	———	>21(7)
		23(1)	23(0)	23(12)	———	21(14)
Ventrals	♂♂	———	126.3(121-131)12[4]	128.5(121-133)30	132.5(129-134)4	138.5(135-142)13
	♀♀	131.0(130-132)3	135.5(133-141)11	138.8(135-145)40	———	143.6(137-150)21
Subcaudals	♂♂	———	100.4(93-108)9	108.8(105-117)25	102.5(102-104)4	88.3(85-91)12
	♀♀	72.5(72-73)2	80.2(78-84)9	92.1(86-97)31	———	69.4(67-73)17
Tail as % of Total length	♂♂	———	35.7(33.9-38.0)9	37.3(35.7-40.0)26	35.7(35.2-36.0)4	32.2(30.4-33.9)11
	♀♀	29.2(28.6-29.8)2	29.8(28.7-31.9)9	30.6(28.9-32.6)30	———	25.5(24.5-26.5)17

[1] Includes a specimen (MBUCV 3) from the vicinity of Maracaibo, Venezuela.
[2] Includes a specimen (ILS 1882) from the Magdalena valley that agrees with the southern Colombia population in all respects. Omitted is an aberrant subadult male (ILS 791) from Puerto Boy that has only 115 ventrals.
[3] Character state (number of specimens).
[4] Mean (range of variation) number of specimens.

TABLE 2. INDIVIDUAL AND INTERSPECIFIC VARIATION OF SELECTED CHARACTERS IN THE *HELICOPS PASTAZAE* COMPLEX

Character	*H. pastazae*	*H. petersi*
Head as % of Body length[1]	4.9(4.5-5.3)24[2]	4.9(4.4-5.5)19
Eye as % of Head length[1]	10.5(8.8-13.0)23	11.5(9.7-13.7)24
Muzzle as % of Head length[1]	17.1(15.3-20.1)23	16.1(14.6-17.0)22
Frontal as % of Head length[1]	23.9(20.6-26.5)25	24.5(21.1-27.9)23
Parietal as % of Head length[1]	30.1(27.4-34.2)25	31.0(27.2-33.9)23
Frontal width as % of Frontal length	59.4(52.3-71.1)31	61.0(53.8-66.7)22
Anterior genial as % of Posterior genial	134.1(93.3-159.6)30	132.0(107.1-200.0)24
Internasal contacts Rostral	19(19.8%)[3]	28[4](82.4%)
vs. Nasals in contact	77(80.2%)	6 (17.6%)
Supralabials: 8/8	70(76.9%)	35(100%)
8/9	14(15.4%)	
9/9	6(6.6%)	
9/10	1(1.1%)	
Infralabials: 9/10	1(1.0%)	2(5.9%)
10/10	7(7.1%)	9(26.5%)
9-10/11	12(12.2%)	13(38.2%)
11/11	43(43.9%)	9(26.5%)
10-11/12	21(21.4%)	1(2.9%)
12/12	10(10.2%)	
11-12/13	4(4.1%)	
Maxillary Teeth	15.5(14-17)+2,n=18	16.6(16-17)+2,n=10

[1] Because of marked ontogenetic changes in cephalic proportions, no data from specimens less than 270 mm in snout-vent length are included.
[2] Mean (range of variation) number of specimens.
[3] Number of specimens (percentage of total sample).
[4] One additional specimen could not be satisfactorily assigned to either character state.