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

By DOUGLAS A. ROSSMAN

Helicops pastazae Shreve, which was described from the Rio 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 predomiantly 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 1946360, 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 1946352-1946359, 1946352-1946366, LSUMZ 29586, same locality as holotype; UIMNH 61042-61052, Napo, Tena; KU 112266, 149311, Napo, Santa Cecilia, 340 m; KU 121888, Napo, Río Aguarico, Pueblo Libre, 570 m; USNM 198630, Napo, mouth of Río Guatara; USNM 198631, Napo, Cuchipamba; USNM 198585, Pastaza, headwaters of Río Aranu: 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 304 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 (♀♀ 67-75, ♂♂ 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

\[
\begin{align*}
3+4(110) & \quad 19 \quad -5(115) \quad 17 \quad +1(131) \quad 18 \quad -10(137) \quad 16; \\
3(107) & \quad -5(115) \\
\end{align*}
\]

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 intergenals; nasal entire, with a subnarial crease present; loreal higher than long; preocular single; postoculars

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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 305 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 vertebral 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 creamy 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 pantoventral 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.
Definition.—A large (maximum recorded snout-vent length 670 mm) species of *Helicops* characterized by: a maximum of 23-25+ 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. Ventrals 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 Ecuadorean 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 supracaudal scale divided into 2 subcaudal halves, an anomaly occurring nowhere else in the range of the species. Two specimens from Ecuador (KU 121355, 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* pastaza (USNM 196361) has an irregular series of additions and reductions on the anterior ½ of its body with a maximum of 29 rows.
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 1-1 ½ 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 colocation extending onto the dorsum as high as the 3rd or 4th row. The light vental color is increasingly obscured with gray-brown pigment in larger snakes.

Two individuals possess particularly noteworthy variant color patterns.

Figure 2. Dorsal and ventral views of three specimens of *Helicops pastazae* (USNM 196369, 196360, 196367) from Ecuador showing the color pattern prevalent in that region.

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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 Cueva Mapocho, 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
1882; Caquetá, vicinity of Florencia, ILS 771-777, 779-780, 782-786, 788-790, 792-794, FMNH 60223; Caquetá, Puerto Boy, ILS 787, 791; Caquetá, Puerto Asís (Nicholls-María, 1942, plate I, fig. 2); Meta, Villavicencio, UMMZ 126721; Norte de Santander, Río Pamplona, N Córdoba, 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 196567-196368; Río Pastaza, 500 m, UMMZ 88930-88933, 88935; Napo, headwaters of Río Arinjuno, USNM 198628; Napo, mouth of Río Copataza, USNM 198629; Napo-Pastaza, Río Bobonaza about 2 km downstream from Cauca, 655 m, USNM 196351; Pastaza, headwaters of Río Bobonaza, USNM 198583, 198591; Pastaza, Río Bobonaza just below Canelos, USNM 198584; Pastaza, Chichiriviche, 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 Conamo, USNM 198592-198593; LSUMZ 29538; Pastaza, Río Bufo, USNM 198590; Pastaza, Río Huijayaca, 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, 198615; Pastaza, Río Lluishin, N Aracayos, USNM 198606-198608; Pastaza, Río Conamo, USNM 198607-198608; Pastaza, Río Villano, USNM 198609, 198612; Pastaza, Río Payacuca, USNM 198614-198615;
Distribution of the Pastaza Complex

Members of the *pastaza* complex range northward along the eastern Andean foothills from the upper Marañón drainage in Peru 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 peterisi*, which is confined to the Río Napo and its tributaries, lies within that of *H. pastaza*, the only locality from which specimens of both species have been taken is the headwaters of the Río Aracuana. The specimen from Iquitos (AMNH 53920) is unquestionably a *H. pastaza*, 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 Pastaza Complex

As can be ascertained from Table 2, *Helicops pastaza* and *H. peterisi* are similar in most proportional characters. *H. peterisi* 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 *polyplepis* section, *H. polyplepis* 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. polyplepis* 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. polyplepis* is intermediate in this respect between those two species and *H. petersi*. There is a continuous morphoclone in ventral number, the quantity increasing from *H. polyplepis* 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. polyplepis* 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. polyplepis* 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. polyplepis* and *H. petersi*. *Helicops yacu* and *H. polyplepis* 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. polyplepis* but separated by intergenial scales in the other three species.

Within the *polyplepis* section, *Helicops polyplepis* 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. polyplepis* do not. Interspecific variation in color pattern, sculation, 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 *polyplepis* 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 B. Duellman (Uni-

**Literature**

Nicéforo María, H.

Shreve, B.
<table>
<thead>
<tr>
<th>Character</th>
<th>H. pastazes</th>
<th>S. Colombie</th>
<th>Brador</th>
<th>N. Panam</th>
<th>H. petersoni</th>
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<tbody>
<tr>
<td>Maximum Dorsal Scale Rows</td>
<td>9-9</td>
<td>≥23(2)</td>
<td>≥23(15)</td>
<td>&gt;25(6)</td>
<td>≥21(0)</td>
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<tr>
<td>Ventrals</td>
<td>9-9</td>
<td>132.5(131-133.3)</td>
<td>138.5(131-133.3)</td>
<td>132.5(129-134)</td>
<td>138.5(133-142.1)</td>
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<td>Subcaudals</td>
<td>9-9</td>
<td>72.5(71-73)</td>
<td>80.2(78-81)</td>
<td>92.4(86-97)</td>
<td>69.4(67-73)</td>
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<tr>
<td>Tail as % of Total () length</td>
<td>9-9</td>
<td>29.2(28.6-29.8)</td>
<td>30.8(29.7-31.9)</td>
<td>30.6(28.9-32.6)</td>
<td>31.5(24.2-26.5)</td>
</tr>
</tbody>
</table>

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.
3 Omitted is an aberrant subadult male (ILS 791) from Puerto Boy that has only 115 ventrals.
4 Character state (number of specimens).
5 Mean (range of variation) number of specimens.

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**Table 2.** Individual and Interspecific Variation of Selected Characters. The characters are arranged in order of increasing number of specimens on which each measurement was based. The standard deviation is given in parentheses. The number of specimens is indicated in parentheses. The number of specimens is indicated in parentheses.

<table>
<thead>
<tr>
<th>Character</th>
<th>H. pastazes</th>
<th>S. Colombie</th>
<th>Brador</th>
<th>N. Panam</th>
<th>H. petersoni</th>
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<tr>
<td>Head % of Body Length</td>
<td>10.8(10.4-11.2)</td>
<td>11.1(10.9-11.3)</td>
<td>11.1(10.9-11.3)</td>
<td>10.8(10.4-11.2)</td>
<td>11.1(10.9-11.3)</td>
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<tr>
<td>Total Body Length</td>
<td>33.5(33.5-34.0)</td>
<td>37(35.7-38.4)</td>
<td>36(35.7-36.0)</td>
<td>37(35.7-36.0)</td>
<td>35.7(33.5-36.0)</td>
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<tr>
<td>Anterior Forked Tail</td>
<td>35.9(35.9-36.3)</td>
<td>35.9(35.9-36.3)</td>
<td>36.0(35.8-36.2)</td>
<td>35.9(35.9-36.3)</td>
<td>35.9(35.9-36.3)</td>
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