

FOUR SPECIES OF BRAZILIAN POISON FROGS RELATED TO *EPIPEDOBATES PICTUS* (DENDROBATIDAE): TAXONOMY AND NATURAL HISTORY OBSERVATIONS

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ABSTRACT: We present morphological and natural history data on *Epipedobates pictus* and three additional taxa currently regarded as synonyms of the former: *Epipedobates braccatus*, *E. flavopictus*, and *E. hahneli*. Topotypes of the four species were examined. Morphological data on tadpoles and adults, in addition to distribution patterns and vocalizations, indicate that the four taxa represent distinct species. Two groups are evident within them: (1) the slender-bodied, Amazonian *E. hahneli* with small flash marks on the thighs and a low-finned tadpole, and (2) the robust bodied, almost extra-Amazonian *E. braccatus*, *E. flavopictus*, and *E. pictus* with large flash marks on the thighs and tadpoles with fins of moderate height.

Key words: Taxonomy; Amphibia; Dendrobatidae; *Epipedobates*; Vocalizations; Distribution; Tadpoles; Natural history

RECENTLY, Myers (1987) proposed the genus *Epipedobates* to accommodate certain species of *Dendrobates*, including those in the *pictus* group. Seven species comprising this group were reviewed by Silverstone (1976): *E. bolivianus*, *E. ingeri*, *E. parvulus*, *E. petersi*, *E. pictus*, *E. pulchripictus*, and *E. smaragdinus*. Vigle and Miyata (1980) described *E. erythromos* and suggested that this species is closely allied to *E. ingeri*. Myers and Burrowes (1987) tentatively included a new species, *E. andinus*, in the *pictus* group, suggesting a close relationship between this species and *E. erythromos*. Although the *pictus* group might not be a natural group (Silverstone, 1976), authors are conservatively adopting the scheme proposed by Silverstone (1976) while awaiting revisions of the species included therein.

Five taxa conservatively considered as *E. pictus* in the literature are reviewed here (see Frost, 1985). *Hylaplesia picta* was described by Bibron (in Tschudi, 1838) based on material from Santa Cruz de la Sierra, Bolivia. Later Steindachner (1864) briefly described specimens from two populations, one from Mato Grosso (probably São Vicente) and the other from Rio Ma-

more (Rondônia), Brazil and used Fitzinger's label names, *Dendrobates braccatus* and *Dendrobates eucnemis*, respectively, for these populations. Cope (1887) described additional specimens from Chapada dos Guimarães, Mato Grosso, Brazil, and also named them *Dendrobates braccatus*. Boulenger (1883) described *Dendrobates hahneli* from Yurimaguas, Peru, and A. Lutz (1925) described *Hylaplesia flavopicta* from Belo Horizonte, Minas Gerais, Brazil.

B. Lutz (1952) briefly reviewed the species above and considered the later four as subspecies of *Dendrobates pictus*. Following B. Lutz, Silverstone (1976) conservatively regarded all the above species as conspecific. Following these two authors, the species that occur throughout northern South America have been referred to under the name *Dendrobates pictus* in recent decades (e.g., Duellman, 1978; Heatwole et al., 1965; Lescure, 1976; Myers and Burrowes, 1987; Schlüter, 1980; Stebbins and Hendrickson, 1959; Vigle and Miyata, 1980). Haddad et al. (1988) and Myers (1987) cited *Epipedobates flavopictus* as a valid species, although they did not comment on this decision, and Caldwell and

Myers (1990) suggested that "the current name *Epipedobates pictus* is still being applied to two or more distinct species." The changes proposed here were anticipated in a popular account by Martins and Sazima (1989).

In this paper, we analyze museum specimens and present field data and observations on habitat and vocalizations of *E. braccatus*, *E. hahneli*, *E. flavopictus*, and *E. pictus*. We propose *E. eucnemis* as a junior synonym of *E. pictus*. Except for *E. eucnemis*, we analyzed specimens from the type localities to assure proper identification (Martins and Haddad, 1990).

MATERIALS AND METHODS

We measured snout-vent length (SVL), head width (HW), head length (HEL), thigh length (THL), and tibia length (TIL) of adults with a caliper. We took additional measurements of adults with an ocular micrometer: foot length (FL), hand length (HAL), eye diameter (ED), eye to nostril distance (EN), internarial distance (ID), and tympanum diameter (TD). In order to avoid damaging the material examined, sex was not determined, except for individuals carrying tadpoles. We also took measurements of tadpoles with an ocular micrometer. Gosner's (1960) table was used to identify tadpole stages. Tooth row formula notation of tadpoles follows Altig (1970). Specimens analyzed are listed in Appendix I.

We recorded vocalizations of *E. hahneli* and *E. pictus* with a Sony TCM 2 tape recorder and a Sony F-V10T microphone and those of *E. flavopictus* with a Uher 4000 Monitor tape recorder and a Uher M538 microphone. The recorded tapes were analyzed in a Voice Identification Series 700 sound spectrograph with a wide band filter (300 Hz).

SPECIES ACCOUNTS

Epipedobates braccatus (Steindachner, 1864)

Dendrobates braccatus Steindachner, 1864:258-259. Two syntypes: NHMW (Naturhistorisches Museum, Wien) 3818: 1-2, São Vicente, Mato Grosso, Brazil.

Dendrobates braccatus Cope, 1887:53-54. Holotype: ANSP (Academy of Natural Sciences, Philadelphia) 13414, Chupada (= Chapada dos Guimarães), Mato Grosso, Brazil.

Dendrobates pictus braccatus, B. Lutz, 1952:599-601, pl. II-IV, Figs. 2, 5, and 6. *Phyllobates pictus* (part.), Silverstone, 1976:38-42, Fig. 9E (only the syntypes of *Dendrobates braccatus* Steindachner, 1864, and the holotype of *Dendrobates braccatus* Cope, 1887).

Epipedobates braccatus, Martins and Sazima, 1989:34.

Description.—A small *Epipedobates* (18.3-21.8 mm SVL, sexes grouped) with slightly granular skin (Fig. 1). Small finger discs (Fig. 1), first finger longer than second. Measurements and mean ratios are given in Tables 1 and 2. In life, *E. braccatus* has a dark brown dorsum with pale brown marbling and yellowish spots (some specimens lack dorsal spots); black flanks; two yellowish white to yellow dorsolateral stripes extending from tip of snout to groin; whitish stripes on upper lips extending from below nares to axillae; dorsolateral stripes become orange to reddish orange flash marks that extend along the upper and lower surfaces of the thighs; orange to reddish orange flash marks are also present on the proximal half of the lower surface of tibiae and behind axillae; upper surfaces of limbs brown with darker irregular transverse stripes; belly brownish white with scattered small black spots concentrated in the ventrolateral region; chest and throat brown (specimens from Chapada dos Guimarães, MT, Brazil). Preserved specimens from Barra do Bugres, MT, have whitish spots on the dark brown dorsum and/or two dorsal stripes formed by the juxtaposition of spots. In preservative, all colors, except the darker, fade to brownish white.

Diagnosis.—*Epipedobates braccatus* is distinguished from *E. pictus* and *E. hahneli* by having a dark brown dorsum (instead of deep black), by the lack of blueish marbling on the belly, and by a more robust body. From *E. flavopictus* by having the upper surfaces of limbs brown with darker transverse stripes (instead of black

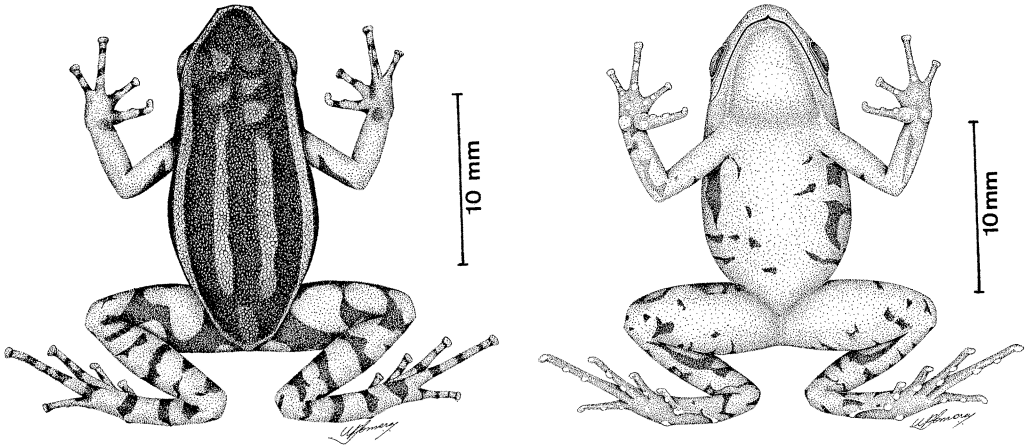


FIG. 1.—Dorsal and ventral views of *Epipedobates braccatus* (ZUEC 9143) from the type locality, Chapada dos Guimarães, Mato Grosso, Brazil.

with bright yellow spots), brownish white belly with scattered black spots (instead of yellowish white with black marbling), by relatively larger eyes and smaller tympana, and by smaller size. From *E. hahneli* also by more robust members, yellowish

white to yellow dorsolateral stripes (instead of white), and larger, orange to reddish orange flash marks on the groin (instead of yellow). From *E. pictus* also by having dark stripes on the upper surfaces of limbs and by smaller fingers and toes.

TABLE 1.—Measurements of four Brazilian species of *Epipedobates*: mean and standard deviation ($\bar{x} \pm SD$) and range (in parentheses).

	<i>E. braccatus</i> (n = 9)	<i>E. flavopictus</i> (n = 38)	<i>E. hahneli</i> (n = 64)	<i>E. pictus</i> (n = 6)
SVL	20.19 \pm 1.32 (18.3–21.8)	26.66 \pm 2.22 (21.4–30.5)	19.02 \pm 1.50 (15.3–23.0)	22.20 \pm 0.83 (21.3–23.1)
HW	6.26 \pm 0.46 (5.7–6.9)	8.03 \pm 0.72 (6.6–9.6)	5.76 \pm 0.41 (4.8–6.7)	6.38 \pm 0.17 (6.2–6.6)
HEL	6.60 \pm 0.47 (6.0–7.2)	8.70 \pm 0.63 (7.5–10.0)	6.35 \pm 0.41 (5.3–7.2)	7.03 \pm 0.14 (6.9–7.2)
THL	9.59 \pm 0.68 (8.9–10.9)	12.45 \pm 0.85 (10.3–13.9)	8.97 \pm 0.67 (7.1–10.4)	10.43 \pm 0.43 (10.0–11.0)
TIL	10.12 \pm 0.82 (9.3–11.6)	12.99 \pm 0.92 (10.8–14.6)	9.33 \pm 0.64 (7.5–10.7)	10.75 \pm 0.33 (10.2–11.0)
FL	9.07 \pm 0.67 (8.3–10.1)	11.90 \pm 0.89 (10.1–14.0)	8.78 \pm 0.64 (7.0–10.4)	10.62 \pm 0.28 (10.3–11.0)
HAL	5.59 \pm 0.61 (4.8–6.5)	7.08 \pm 0.44 (6.2–8.0)	5.32 \pm 0.34 (4.5–6.2)	6.38 \pm 0.10 (6.3–6.5)
ED	2.50 \pm 0.12 (2.3–2.7)	2.73 \pm 0.29 (2.3–3.4)	2.35 \pm 0.19 (2.1–3.1)	2.42 \pm 0.08 (2.3–2.5)
TD	1.16 \pm 0.15 (0.9–1.4)	1.44 \pm 0.26 (0.9–1.9)	1.15 \pm 0.10 (0.9–1.4)	1.12 \pm 0.04 (1.1–1.2)
EN	2.23 \pm 0.14 (2.1–2.5)	2.71 \pm 0.24 (2.2–3.2)	1.85 \pm 0.15 (1.6–2.3)	2.25 \pm 0.08 (2.1–2.3)
ID	2.52 \pm 0.22 (2.3–2.9)	3.08 \pm 0.28 (2.4–3.6)	2.45 \pm 0.17 (2.1–3.0)	2.62 \pm 0.12 (2.4–2.7)

TABLE 2.—Mean ratios and standard deviation ($\bar{x} \pm SD$) and range (in parentheses) of four Brazilian species of *Epipedobates*.

	<i>E. braccatus</i> (n = 9)	<i>E. flavopictus</i> (n = 38)	<i>E. hahnelt</i> (n = 64)	<i>E. pictus</i> (n = 6)
HW/SVL	0.31 ± 0.01 (0.30–0.32)	0.30 ± 0.02 (0.25–0.32)	0.30 ± 0.04 (0.27–0.33)	0.29 ± 0.01 (0.28–0.30)
HEL/SVL	0.33 ± 0.01 (0.30–0.34)	0.33 ± 0.01 (0.30–0.35)	0.33 ± 0.01 (0.30–0.36)	0.32 ± 0.01 (0.30–0.33)
THL/SVL	0.47 ± 0.01 (0.46–0.50)	0.47 ± 0.02 (0.43–0.50)	0.47 ± 0.06 (0.43–0.52)	0.47 ± 0.01 (0.46–0.48)
TIL/SVL	0.50 ± 0.02 (0.47–0.53)	0.49 ± 0.02 (0.44–0.53)	0.49 ± 0.02 (0.45–0.55)	0.49 ± 0.01 (0.47–0.51)
FL/SVL	0.45 ± 0.01 (0.43–0.46)	0.45 ± 0.03 (0.39–0.51)	0.46 ± 0.02 (0.45–0.52)	0.48 ± 0.01 (0.46–0.49)
HAL/SVL	0.28 ± 0.02 (0.25–0.31)	0.26 ± 0.01 (0.24–0.29)	0.28 ± 0.02 (0.24–0.37)	0.29 ± 0.01 (0.28–0.30)
TD/ED	0.46 ± 0.05 (0.38–0.52)	0.54 ± 0.06 (0.39–0.63)	0.49 ± 0.05 (0.38–0.61)	0.47 ± 0.02 (0.44–0.50)
EN/ED	0.90 ± 0.06 (0.81–1.00)	0.99 ± 0.09 (0.82–1.20)	0.79 ± 0.07 (0.55–0.92)	0.93 ± 0.05 (0.84–1.00)
ID/HW	0.40 ± 0.03 (0.35–0.44)	0.38 ± 0.04 (0.29–0.47)	0.43 ± 0.03 (0.39–0.58)	0.41 ± 0.02 (0.38–0.42)

Distribution.—*Epipedobates braccatus* is known from the type locality (Chapada dos Guimarães, MT, Brazil), from two nearby localities (Barra do Bugres and Cáceres, MT, Brazil), from Aquidauana, MS, Brazil, and from Santa Rita do Araguaia, GO, Brazil (Fig. 2).

Natural history.—Individuals of *E. braccatus* were found amidst leaf litter in gallery forests in the “cerrado” (savanna-like vegetation). On 8 December 1988, at Estação Ecológica Serra das Araras, MT, one male was found carrying seven tadpoles on its dorsum, near a rivulet in the “cerrado” (U. Caramaschi, personal communication).

Vocalization.—Unknown.

Tadpoles.—The following description is based on a series of seven tadpoles in stage 25 that were found while being carried by a male at Estação Ecológica Serra das Araras, MT, on 8 December 1988.

Head and body depressed (depth nearly two-thirds width), convex above and slightly flattened below (Fig. 3A); eyes and nostrils directed dorsolaterally from a dorsolateral position (Fig. 3A). Head-body length 3.6–4.2 mm ($\bar{x} = 3.9 \pm 0.2$ mm); total length 10.1–11.3 mm ($\bar{x} = 10.7 \pm 0.4$

mm); tail length 60–65% of total length; greatest depth of the medium-finned tail 16–19% of total length. In preservative, head and body dark brown above and below; tail brown with light brown fins sparsely speckled with brown. Oral disc directed ventrally; tooth row formula 2(2)/3, second anterior row broadly broken above the jaw sheath; jaw sheath keratinized, finely serrated; posterior jaw sheath V-shaped; oral disc laterally emarginate; anterior edges of anterior labia without papillae; lateral edges of anterior labia and edges of posterior labia with a single row of pointed papillae (Fig. 3A).

Comments.—The specimens here referred to as *E. braccatus* fit well the original description provided by Steindachner (1864). However, two specimens (ZUEC 9015 and 9017) from Chapada dos Guimarães, MT, have intermediate color patterns between *E. braccatus* and *E. pictus*. It is possible that both of these species occur and may hybridize at Chapada dos Guimarães. Additional data from this locality would help to solve this problem. Two specimens from the Rio das Mortes, MT (MZUSP 4271 and 6486), are intermediate between *E. braccatus* and *E. fla-*

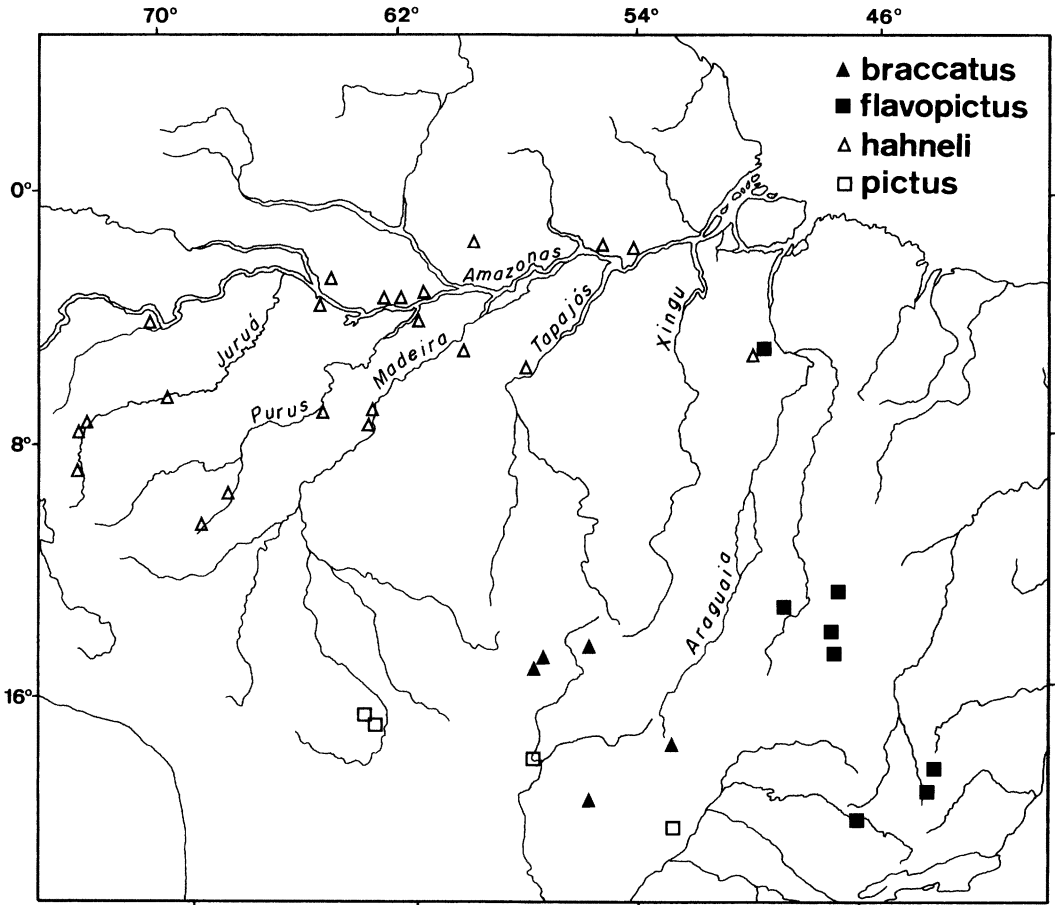


FIG. 2.—Map of central and northern South America showing localities of the four species of *Epipedobates*.

vopictus (additional localities where intermediate forms were found are in B. Lutz, 1952).

Epipedobates flavopictus
(A. Lutz, 1925)

Hylaplesia flavopicta A. Lutz, 1925:139. Syntypes: AL 853 and 854, USNM (National Museum of Natural History, Washington) 96986, Belo Horizonte, Minas Gerais, Brazil.

Dendrobates braccatus, Miranda-Ribeiro, 1926:179–180, text Fig. 96, pl. 20, Figs. 3a and b.

Dendrobates pictus flavopictus, B. Lutz, 1952:597–601, pl. I–IV, Figs. 1, 2, 5, and 6.

Dendrobates flavopictus, Cochran, 1955: 8–9, pl. 1, Figs. G and H.

Phyllobates pictus (part.), Silverstone, 1976:38–41, Figs. 3D and 9D (only the holotype of *Hylaplesia flavopicta* A. Lutz, 1925).

Epipedobates flavopictus, Myers, 1987: 303.

Epipedobates flavopictus, Haddad et al., 1988:12, Fig. 2c.

Epipedobates flavopictus, Martins and Sazima, 1989:34, Figs. on p. 36.

Description.—A medium sized *Epipedobates* (21.4–30.5 mm SVL, sexes grouped) with slightly granular skin (Fig. 4). Finger and toe discs small (Fig. 4), first finger slightly longer than second. Measurements and mean ratios are given in Tables 1 and 2. In life, *E. flavopictus* has a deep black dorsum with bright yellow

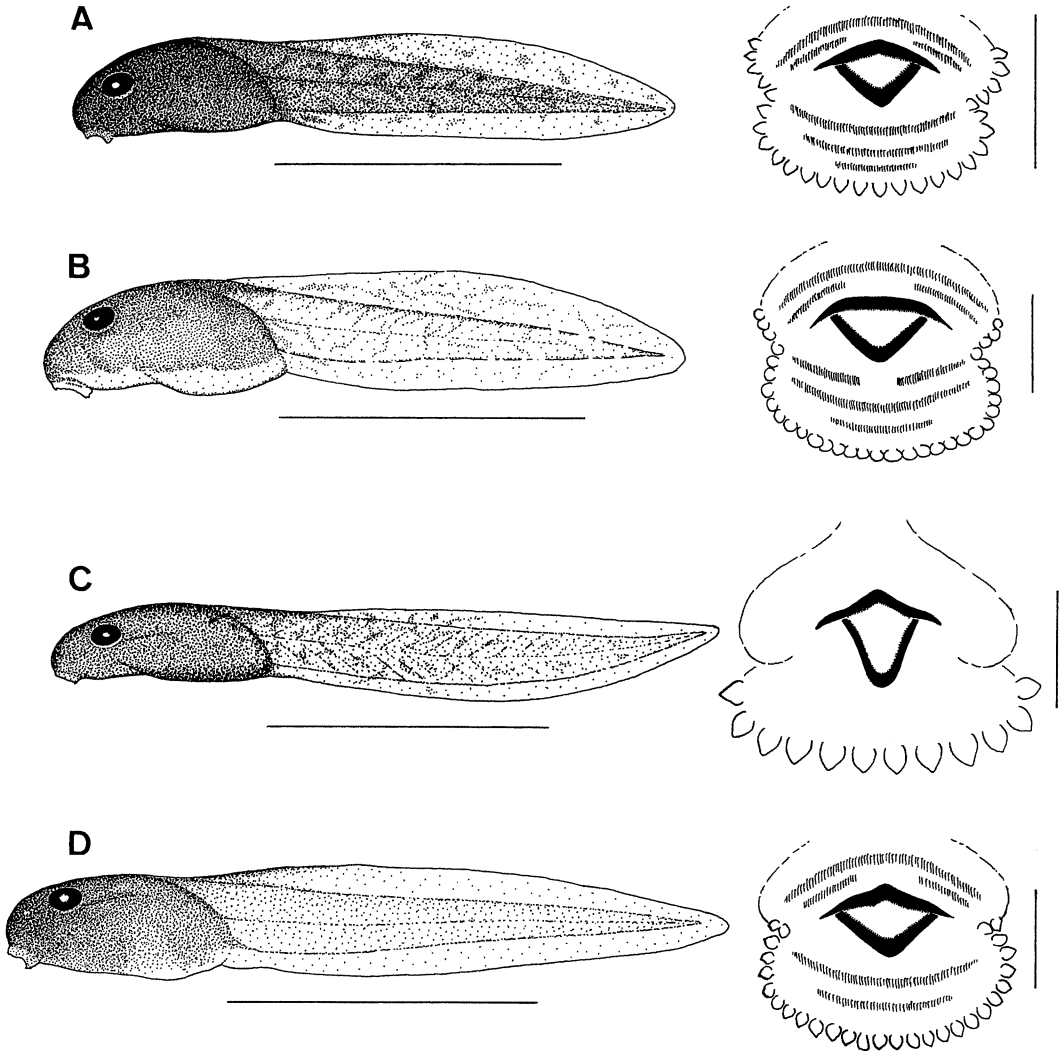


FIG. 3.—Lateral view and oral disc of tadpoles (stage 25) found on the dorsum of male *Epidobates*: (A) *E. braccatus* from Estação Ecológica Serra das Araras, MT, Brazil; (B) *E. flavopictus* from Santana do Riacho, MG, Brazil; (C) *E. hahneli* from Presidente Figueiredo, AM, Brazil; (D) *E. pictus* from Santa Cruz de la Sierra, Santa Cruz, Bolivia. Bars under tadpoles = 5 mm and beside oral discs = 0.5 mm.

round spots often arranged in two longitudinal rows; deep black flanks with sparse bright yellow round spots; two bright yellow dorsolateral stripes extending from tip of snout to groin; dorsolateral stripes become orange to red flash marks that extend along the anterior, superior, and posterior surfaces of the thighs; orange to red flash marks also on proximal half of the lower surfaces of tibiae and behind axillae; upper surfaces of limbs deep black with bright

yellow round and elongate spots; belly and throat yellowish white with black, scattered marbling (specimens from the Serra do Cipó, Santana do Riacho, MG, and the Serra dos Carajás, Paraopebas, PA, Brazil). In preservative, all except the darker colors fade to white.

Diagnosis.—*Epidobates flavopictus* is distinguished from the other three species reviewed here by the presence of yellow spots on the flanks and upper surfaces

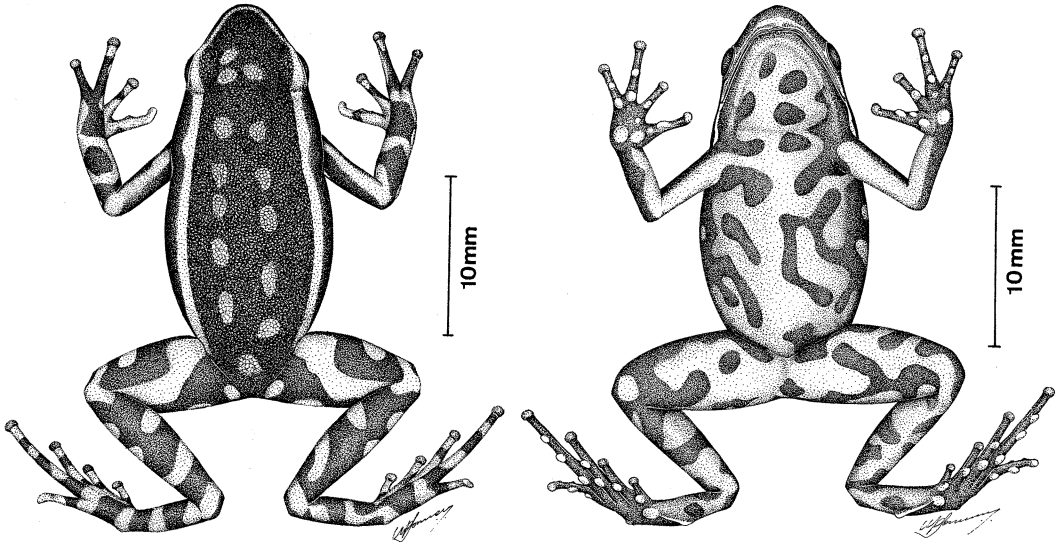


FIG. 4.—Dorsal and ventral views of *Epipedobates flavopictus* (ZUEC 3014) from Santana do Riacho, MG, Brazil.

of limbs, by relatively larger tympana, and by larger size. It is distinguished from *E. braccatus* also by having black dorsum and limbs (instead of dark brown) and by relatively smaller eyes; from *E. hahneli* also by larger flash marks on the groin, by having yellow dorsolateral stripes (instead of whitish), by the lack of blueish marbling on the belly, by the presence of yellow spots on the dorsum, and by relatively smaller eyes; from *E. pictus* also by having black dorsum and limbs (instead of dark brown), by the presence of spots on the dorsum, and by the lack of blueish marbling on the belly.

Distribution.—*Epipedobates flavopictus* is known from southeastern (MG, GO, and TO), northern (PA), and northeastern (MA) Brazil (Fig. 2).

Natural history.—At Santana do Riacho, São Roque de Minas, and Alpinópolis, MG, *Epipedobates flavopictus* was heard

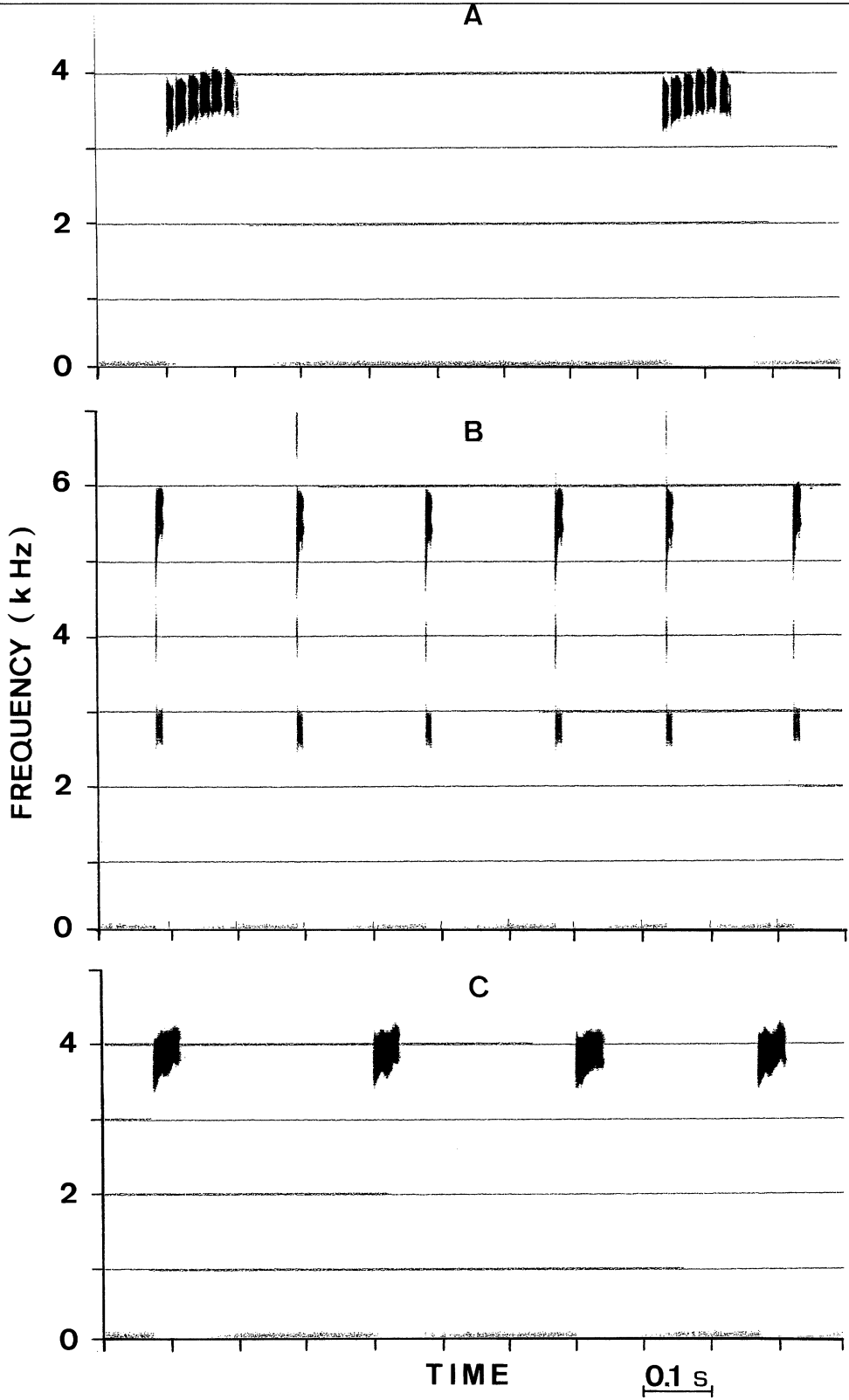
calling in rock crevices at creek margins in rupestrian fields. On 8 November 1989, at Santana do Riacho, a male found near a creek was carrying 18 tadpoles on its dorsum. At Paraopebas, PA, males and females were found in rock crevices, within the vegetation on a forest waterfall, and amidst leaf litter (apparently foraging) at the margins of this creek (no calling activity was observed); the creek is located in a ravine within “canga” fields (a rupestrian field vegetation on iron-rich soil: Morellato and Rosa, 1991).

Vocalization.—The advertisement call of *E. flavopictus* consists of frequency-modulated notes separated by about 480–630 ms in a narrow frequency range between 3.2–4.2 kHz (Fig. 5A). The duration of individual notes is about 110 ms. Each note is composed of six pulses.

Tadpoles.—The following description is based on a series of 10 tadpoles in stage

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FIG. 5.—Sonagrams of vocalizations of *Epipedobates*: (A) *E. flavopictus* from Santana do Riacho, MG, Brazil, air temperature 24 C, recording of Adão J. Cardoso (AJC) 13/07; (B) *E. hahneli* from Presidente Figueiredo, AM, Brazil, air temperature 28 C, recording of Marcio Martins (MRM) 08/07; (C) *E. pictus* from Santa Cruz de la Sierra, Santa Cruz, Bolivia, air temperature 22.5 C, recording MRM 08/06.



25 that were found while being carried by a male at Santana do Riacho, MG, on 8 November 1989.

Head and body depressed (depth nearly two-thirds width), convex above and slightly flattened below; eyes and nostrils directed dorsolaterally from a dorsolateral position (Fig. 3B). Head-body length 3.9–4.3 mm ($\bar{x} = 4.2 \pm 0.1$ mm); total length 10.4–11.6 mm ($\bar{x} = 11.0 \pm 0.3$ mm); tail length 60–64% of total length; greatest depth of the medium-finned tail 17–19% of total length. In preservative, head and body brown above and laterally; throat and belly cream; tail cream sparsely speckled with brown. Oral disc directed ventrally; tooth-row formula 2(2)/3(1), second anterior row broadly broken above jaw sheath; jaw sheath keratinized finely serrated; posterior jaw sheath V-shaped; oral disc laterally emarginate; anterior edge of upper labia without papillae; lateral edges of anterior labia and edges of posterior labia with a single row of round-tipped papillae (Fig. 3B). Color photographs of a free-living tadpole and a recently metamorphosed froglet are in Martins and Sazima (1989).

Comments.—Although the poor condition of the type specimens of *Hylaplesia flavopicta* make comparison difficult, the specimens that we analyzed agree well with the original description by A. Lutz (1925). The specimens of *E. flavopictus* from Paraopebas, PA, are somewhat distinctive compared to specimens of *E. flavopictus* collected near the type locality. The former specimens have larger eyes and red marks on the thighs and tibiae instead of orange as found in specimens from MG and GO. Field data on reproductive biology, especially vocalizations, are needed to ascertain the specific status of the population from Paraopebas.

Epipedobates hahneli
(Boulenger, 1883)

Dendrobates hahneli Boulenger, 1883:636, pl. 57, Fig. 4. Seven syntypes: BM 1947.2.15.14–20, Yurimaguas, Rio Huallaga, (Loreto), Peru.

Dendrobates pictus hahneli, B. Lutz, 1952: 600–601, pl. II–IV, Figs. 1, 3, 4.

Dendrobates pictus, (part.), Silverstone, 1976:38–42, Figs. 3, 9 (only the syntypes of *Dendrobates hahneli* Boulenger, 1883).

Epipedobates hahneli, Martins and Sazima, 1989:34, top Figs. on p. 38 (wrong caption as *E. pictus*).

Description.—A small *Epipedobates* (15.3–23.0 mm SVL, sexes grouped) with slightly granular skin (Fig. 6). Small finger and toe discs (Fig. 6), first finger slightly longer than second. Measurements and mean ratios are given in Tables 1 and 2. In life, *E. hahneli* has a black dorsum with pale grayish or greenish marbling; two white dorsolateral stripes extending from tip of snout to groin; white stripe on the upper lip extending from below the eye to the axillae; dorsolateral stripes become a small yellow flash mark on groin; yellow flash marks also on the proximal half of lower surfaces of tibiae and behind axillae; upper surfaces of limbs brown with scattered black marbling; belly and ventral surfaces of limbs black with light blue marbling; chest and throat black with pale marbling on the margin of throat (specimens from Presidente Figueiredo, AM, Paraopebas, PA, and Rio Branco, AC). Specimens from Rio Tejo, Cruzeiro do Sul, AC, do not have dorsolateral and upper lip stripes. In preservative, all except the darker colors fade to white.

Diagnosis.—*Epipedobates hahneli* is distinguished from the other three species reviewed here by having slender body and limbs, white dorsolateral stripes (instead of yellowish or yellow), and smaller, yellow flash marks on the groin (instead of orange or reddish orange). It is distinguished from *E. braccatus* also by having a black dorsum (instead of dark brown), by the lack of light spots on the dorsum (however, some *E. braccatus* lack dorsal spots), and by the presence of blueish marbling on the belly; from *E. flavopictus* also by the lack of yellow spots on the dorsum, upper surfaces of limbs, and flanks, by the presence of blueish marbling on the belly, by relatively larger eyes and smaller tympana, and by smaller size; from *E. pictus* also by having a black dorsum (instead of dark brown) and by slightly smaller size.

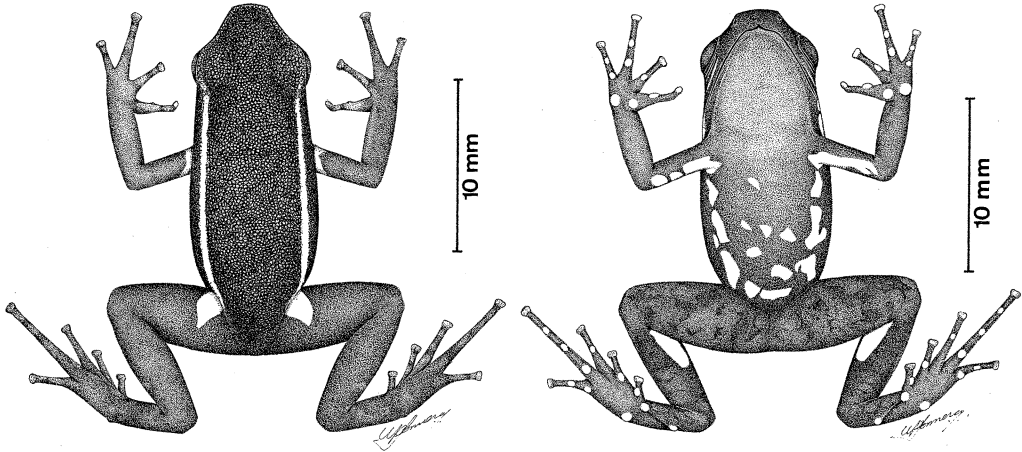


FIG. 6.—Dorsal and ventral views of *Epipedobates hahneli* (ZUEC 9049) from Presidente Figueiredo, AM, Brazil.

Distribution.—*Epipedobates hahneli* is known from the lowlands of Amazonian Brazil and adjacent areas (Fig. 2).

Natural history.—At Paraopebas, PA, and Presidente Figueiredo, AM, *E. hahneli* was found amidst leaf litter at margins of forest creeks. At Paraopebas, males were not calling during the field work (July 1988). At Presidente Figueiredo, males were heard calling in two of three field trips (December 1986 and April 1987). Males called within leaf litter and from low (up to 30 cm) perches (on small vines, fallen logs, and branches). On 24 April 1987, two males were found carrying tadpoles: one on a fallen tree over a creek had eight small tadpoles on the dorsum and the other was amidst leaf litter about 40 m from a creek, and had two larger tadpoles on the dorsum. On the same day, a male marked on the previous day was found a few centimeters from the site of marking; a detailed investigation within the leaf litter revealed that this male was guarding a clutch of eight eggs deposited on a large dead leaf beneath several others. On one occasion, a female followed a male that emitted three-note calls (courtship call?) intermittently, but a heavy storm interrupted the observations.

Vocalization.—The advertisement call of *E. hahneli* consisted of notes separated by about 150–300 ms (\bar{x} = 190 ms; SD = 40; n = 10) in a wide frequency range

from 2.5–7.0 kHz (Fig. 5B). The duration of individual notes was about 15 ms.

Tadpoles.—The following description is based on a series of eight tadpoles in stage 25 that were found while being carried by a male at Presidente Figueiredo, AM, on 24 April 1987.

Head and body highly depressed (width nearly two times depth), slightly convex above and flattened below (Fig. 3C); eyes and nostrils directed dorsolaterally from a dorsolateral position. Head-body length 3.2–3.9 mm (\bar{x} = 3.7 ± 0.2 mm); total length 10.5–12.2 mm (\bar{x} = 11.8 ± 0.6 mm); tail length 67–70% of total length; greatest depth of the low-finned tail 13–15% of total length. In preservative, head and body brown, turning slightly paler on throat and belly; tail cream, sparsely speckled with brown. Oral disc directed ventrally; labial teeth not yet keratinized; jaw sheath shallowly keratinized, finely serrated; posterior jaw sheath U-shaped; oral disc laterally emarginate; edges of anterior labia without papillae; posterior labia with a single row of slightly pointed papillae (Fig. 3C).

Comments.—Although the analyzed cotype (MZUSP 15874) of *Dendrobates hahneli* is in poor condition, making comparison difficult, the specimens analyzed here conform well to the original description of *Dendrobates hahneli* Boulenger (1883), except for the flash marks that are

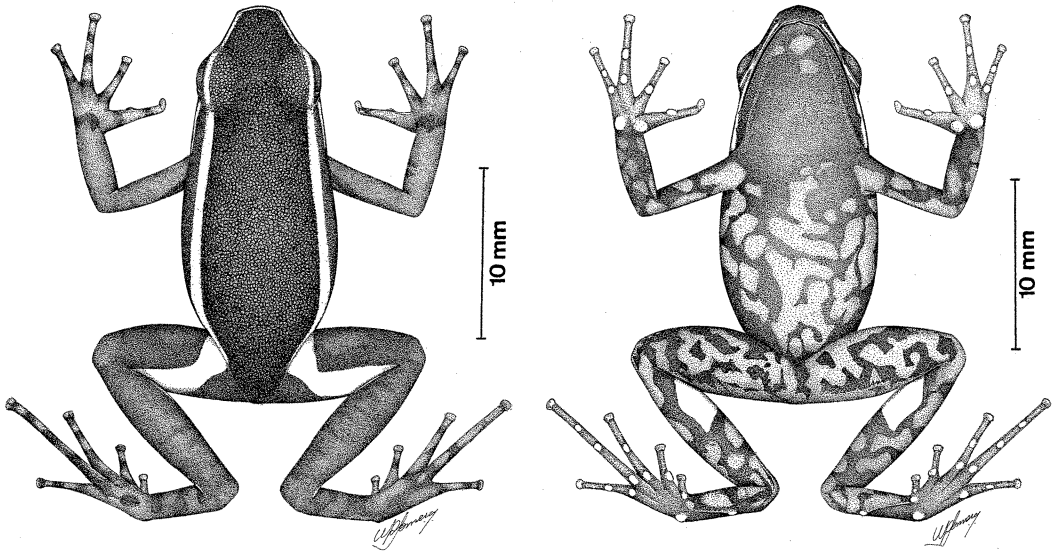


FIG. 7.—Dorsal and ventral views of *Epipedobates pictus* (ZUEC 9055) from the type locality, Santa Cruz de la Sierra, Santa Cruz, Bolivia.

reddish orange in the original description instead of yellow as in our specimens. A. Schlüter (personal communication) photographed and W. Hödl (personal communication) filmed specimens of a species similar to ours from Panguana, Peru, with reddish orange flash marks. The differences in the calls of specimens from Panguana (Schlüter, 1980) from those described here (e.g., note duration and note repetition rate) indicate that they may be two species. However, we prefer to refer our specimens to *E. hahneli* based on the original description until additional specimens from the type locality are examined. The tadpoles of *E. hahneli* described herein are similar to those described by Lescure (1976) under the name *Phyllobates pictus*, except for the higher number of papillae on the posterior labia in Lescure's description.

Epipedobates pictus
(Bibron in Tschudi, 1838)

Hylaplesia picta Bibron in Tschudi, 1838: 28,71. Two syntypes MNHNP (Museum National d'Histoire Naturelle, Paris) 4910, Santa Cruz (de la Sierra), Santa Cruz, Bolivia.

Dendrobates eucnemis Steindachner, 1864:258, pl. XIII, Fig. 2, 2a, 2b. Type locality: Rio Mamoré, Rondônia, Brasil.

Dendrobates pictus eucnemis, B. Lutz, 1952:600–601, pl. II, Fig. 8.

Dendrobates pictus pictus, B. Lutz, 1952: 599–600, pls. III and IV, Fig. 4.

Phyllobates pictus (part.), Silverstone, 1976:38–42 (only the syntypes of *Hylaplesia picta* Bibron in Tschudi, 1838 and *Dendrobates eucnemis* Steindachner, 1864).

Epipedobates pictus, Myers, 1987:302–303.

Epipedobates pictus, Martins and Sazima, 1989:34.

Epipedobates pictus (part.?), De la Riva, 1990:270 (at least the specimen in Fig. 14).

Description.—A small *Epipedobates* (21.3–23.1 mm SVL, sexes grouped) with slightly granular skin (Fig. 7). Small finger and toe discs (Fig. 7), first finger longer than second. Measurements and mean ratios are given in Tables 1 and 2. In life, *E. pictus* has a dark brown dorsum with two golden yellow dorsolateral stripes; deep black flanks; a yellowish white stripe on

the upper lip extending to the axilla; dorsolateral stripes become red orange flash marks that extend along the posterior surface of thighs; red orange flash marks also present on the proximal half of the lower surface of tibiae and behind the axillae; upper surfaces of limbs brown; belly and ventral surfaces of limbs black with blueish white marbling (more blueish on limbs); chest and throat black with pale marbling on the margin of throat (specimen from Santa Cruz de la Sierra, Bolivia). In preservative, all except the darker colors fade to white.

Diagnosis.—*Epipedobates pictus* is distinguished from *E. braccatus* by the lack of spots on the dorsum (however, some individuals of *E. braccatus* lack dorsal spots) and transversal dark stripes on the upper surfaces of limbs, by the presence of blueish marbling on the belly, and by longer fingers and toes. It is distinguished from *E. flavopictus* by having a dark brown dorsum (instead of black), by the lack of spots on the dorsum, upper surfaces of limbs, and flanks, by the presence of blueish marbling on the belly, by relatively smaller tympana, and by the smaller size; from *E. hahneli* by larger flash marks on the groin, by having a dark brown dorsum (instead of black), and by slightly larger size.

Distribution.—*Epipedobates pictus* is known from the type locality, Santa Cruz de la Sierra, in eastern Bolivia, and Corumbá and Xavantina, MS, in southwestern Brazil (Fig. 2).

Natural history.—At Santa Cruz de la Sierra, males of *E. pictus* were heard calling among dead tree branches on the leaf litter of the Rio Pirai gallery forest on 24 January 1989 (during a light rain). One male collected at the margins of a small forest creek with sandy banks was carrying 14 tadpoles on its dorsum.

Vocalization.—The advertisement call of *E. pictus* consists of frequency modulated notes separated by about 220–280 ms (\bar{x} = 258 ms; SD = 22; n = 6) in a narrow frequency range between 3.4–4.3 kHz (Fig. 5C). The duration of individual notes is about 50 ms.

Tadpoles.—The following description is based on a series of 14 tadpoles in stage 25 that were found while being carried by a male at Santa Cruz de la Sierra, Bolivia, on 24 January 1989.

Head and body depressed (depth nearly two-thirds width), convex above and slightly flattened below; eyes and nostrils directed dorsolaterally from a dorsolateral position (Fig. 3D). Head–body length 4.0–4.4 mm (\bar{x} = 4.2 \pm 0.1 mm); total length 11.2–12.2 mm (\bar{x} = 11.9 \pm 0.3 mm); tail length 63–65% of total length; greatest depth of medium-finned tail 16–19% of total length. In preservative, head and body cream, finely dotted with dark brown above and below, except on belly; tail cream with sparse dark brown dots, except on ventral fin. Oral disc directed anteroventrally; tooth-row formula 2(2)/2, second anterior row broadly broken above the jaw sheath; jaw sheath keratinized, finely serrated; posterior jaw sheath V-shaped; oral disc laterally emarginate; edges of anterior labia without papillae; edges of posterior labia with a single row of slightly pointed papillae (Fig. 3D).

Comments.—De la Riva (1990) reported the occurrence of *Epipedobates pictus* at several localities in Bolivia and figured an individual from Santa Cruz that perfectly fits the live specimens that we examined from this same locality. However, some of the specimens cited by De la Riva (1990) may be *E. hahneli*, especially those from Amazonian lowlands adjacent to Rondônia and Acre, Brazil, where *E. hahneli* is known to occur; in fact, it will not be surprising to find these two species in sympatry in these regions. We did not examine specimens from the Rio Mamoré (type locality of *Dendrobates eucnemis*), but the syntype illustrated in Steindachner (1864, pl. XIII, 2, 2a, 2b) is quite similar to what we regard here as *E. pictus*, especially the long flash mark on the thighs and the ventral pattern. Silverstone (1976) illustrated a tadpole of *Phyllobates pictus* from Bolivia that is similar to those described here, except for the higher extension of the row of papillae on the anterior labia and the presence of a third row of

labial teeth on the posterior labia in the former.

DISCUSSION

Two groups are evident within the four species reviewed here: (1) *Epipedobates hahneli*, a slender-bodied Amazonian species with small flash marks on the thighs and a strongly depressed and low-finned tadpole, and (2) *E. pictus*, *E. braccatus*, and *E. flavopictus*, robust-bodied nearly extra-Amazonian species with large flash marks on the thighs and a slightly depressed and medium-finned tadpole.

Studies based only on morphological data seem to be of little value when dealing with dendrobatids; these studies often resulted in a large number of confusing and probably erroneous synonymies (e.g., B. Lutz, 1952; Silverstone, 1976). Data on habitat, vocalization, and color in life, besides morphology, like those presented here and by C. Myers and colleagues in several papers (e.g., Caldwell and Myers, 1990; Myers and Burrowes, 1987; Myers and Daly, 1979) are more useful to assure proper identifications. Furthermore, analysis of specimens from type localities is highly recommended (Martins and Haddad, 1990).

RESUMO

Apresentamos dados morfológicos e de história natural de *Epipedobates pictus* e mais três espécies correntemente consideradas como sinônimos daquela: *Epipedobates braccatus*, *Epipedobates flavopictus* e *Epipedobates hahneli*. Topótipos e/ou material tipo das quatro espécies foram examinados. Dados morfológicos de girinos e adultos, além dos padrões de distribuição, indicam que os quatro taxons aqui considerados representam espécies distintas. Dois grupos são evidentes entre estas espécies: (1) *E. hahneli*, amazônico, com corpo delicado, pequenas manchas coloridas nas coxas e girinos com nadadeiras pouco desenvolvidas, e (2) *E. braccatus*, *E. flavopictus*, e *E. pictus*, praticamente extra-amazônicos, com corpo robusto, grandes manchas coloridas nas coxas e girinos com nadadeiras moderadamente desenvolvidas. A relação destas es-

pécies com as outras correntemente colocadas no grupo de *E. pictus*, incluindo *E. hahneli*, é de difícil análise no presente estágio de conhecimento e merece revisões futuras.

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- Epipedobates braccatus*.—Santa Rita do Araguaia, GO: MZUSP 66691, 66726. Aquidauana, MS: ZUEC 9014. Águas Quentes, MT: ZUEC 5347-5350. Barra do Bugres, MT: MN 10096-10098. Cáceres, MT: ZUEC 9142-9143, 9145-9146, 9148. Chapada dos Guimarães, MT (type locality): MZUSP 37482; ZUEC 9147. Jangada, MT: ZUEC 9144.
- Epipedobates flavopictus*.—Chapada dos Veadeiros, Alto Paraíso de Goiás, GO: MN 2711. Formosa, GO: ZUEC 3917. Rio Miguel, GO: MN 726, 7091-7095. Serra Dourada, GO: ZUEC 7501. Serra Negra, GO: MZUSP 69221-69222. Amaro Leite, MA: MN 2955, 10099-10102, one specimen without number. Alpinópolis, MG: ZUEC 3824-3825, 4448-4452, 8329. Belo Horizonte, MG (type locality): AL 853-854 (Syn-types); MN 10108-10109; MZUSP 295. Jaboticatubas, MG: MZUSP 10971. Santana do Riacho, MG: ZUEC 2068, 2194-2195, 2521, 3012-3018, 3020, 3342, 3641-3642, 3899, 9013. São Roque de Minas, MG: ZUEC 4456. Serra dos Carajás, Paraopebas, PA: ZUEC 6269, 6283, 9020-9035. Paranã, TO: MN 2995.
- Epipedobates hahneli*.—Brasileia, AC: ZUEC 5790. Cruzeiro do Sul, AC: ZUEC 5021. Restauração, Médio Rio Tejo, AC: ZUEC 8462-8464, 8484. Rio Branco, AC: ZUEC 5599. Taumaturo, Rio Tejo, AC: ZUEC 8452, 8504-8506. Alvarães, AM: MZUSP 51122. Beruri, AM: MZUSP 55666-55671. Eirunepé, AM: AL without number. Humaitá, AM: JJ 25 specimens without numbers. Igarapé Puruzinho, Rio Madeira, AM: MZUSP 51338, 51494-51497. Itacoai, tributary of Rio Javari, AM: AL without number. Lago Amanã, AM: MZUSP 58091. Lago Badajós, AM: MZUSP 53622-53623. Lago Miuiá, AM: MZUSP 30747. Mucuripe, Rio Purus, AM: MZUSP 51186. Paranã-Amanã, AM: MZUSP 58121-58125. São Leopoldo do Rio Amazonas, AM: INPA 1066. Terra Preta, Boca do Manacapuru, AM: MZUSP 42198. Rio Uatumã, Presidente Figueiredo, AM: INPA 724-725, 732, 890, 892-895, 898, 901, 903-907, 936-937, 939-941, 966-970, 983-985, 1007-1010, 1028-1031. Jacareacanga, left bank of Rio Tapajós, PA: AL without number. Rio Cuminá-Miri, PA: MZUSP 30768. Serra dos Carajás, Paraopebas, PA: ZUEC 9037-9051. Monte Alegre, PA: AL without number. Yurimaguas, Loreto, Peru: MZUSP 15874.
- Epipedobates pictus*.—Buena Vista, Santa Cruz, Bolivia: MN without number. Santa Cruz de la Sierra, Santa Cruz, Bolivia (type locality): ZUEC 9052-9057. Xavantina, MS: MN 10105. Corumbá, MT: ZUEC 3498-3499, 9018-9019.

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APPENDIX I

Specimens Examined

Museum abbreviations for the specimens analyzed are: AL (Coleção Adolpho Lutz, deposited at Museu Nacional, Rio de Janeiro, Brazil), INPA (Coleção de