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A new cryptic species of poison frog from the Bolivian Yungas

(Anura: Dendrobatidae: *Epipedobates*)

Ein neuer kryptischer Giftfrosch aus den bolivianischen Yungas

(Anura: Dendrobatidae: *Epipedobates*)

STEFAN LÖTTERS & ANDREAS SCHMITZ & STEFFEN REICHLE

KURZFASSUNG

Wir beschreiben einen neuen Giftfrosch der Gattung *Epipedobates* aus den bolivianischen Yungas. Er ähnelt *E. hahneli* (BOULENGER, 1883) und *E. pictus* (BIBRON in TSCHUDI, 1838), unterscheidet sich von ihnen aber hinsichtlich des Farbmusters, Anzeigerufs und in der Basenabfolge des 16S rRNA Gens.

ABSTRACT

We describe a new poison frog of the genus *Epipedobates* from the Bolivian Yungas. It is similar to *E. hahneli* (BOULENGER, 1883) and *E. pictus* (BIBRON in TSCHUDI, 1838) but differs from these in color pattern, advertisement call and base composition of the 16S rRNA gene.

KEY WORDS

Amphibia: Anura: Dendrobatidae: *Epipedobates yungicola* spec. nov.; taxonomy; systematics; bioacoustics; RNA sequencing; Bolivia, Neotropics

INTRODUCTION

In recent years, numerous studies on systematics of neotropical poison frogs (Dendrobatidae) have become available. This includes higher taxa phylogeny (e.g. VENCES et al. 2003) as well as poison frog taxonomy at the species level (e.g. HADDAD & MARTINS 1994). Both increased efforts in the field and a broader methodical array allowed for new insights.

Nevertheless, the taxonomy of the cis-Andean members of *Epipedobates* MYERS, 1987 remains poorly understood. Several of the recognised species have been associated with *E. pictus* (BIBRON in TSCHUDI, 1838). In contrast to the previous view (e.g. SILVERSTONE 1976), *E. pictus* is not a wide-ranged variable species. Actually, several, in part cryptic species, more or less resembling *E. pictus,* can be distinguished when life colors, tadpole morphology, bioacoustics and/or molecular genetics are studied. At present, the following species (at least phenetically) related to *E. pictus* are widely accepted (HADDAD & MARTINS 1994; LÖTTERS et al. 1997; GONZALES et al. 1999; FROST 2004): (1) *Epipedobates pictus* sensu stricto from lowland to sub-Andean Bolivia and adjacent Brazil, (2) *E. bolivianus* (BOULENGER, 1902) from sub-Andean Bolivia, (3) *E. braccatus* (STEINDACHNER, 1864) and (4) *E. flavopictus* (A. LUTZ, 1925) from the central-eastern Brazilian highlands and south-eastern Bolivia, (5) *E. hahneli* (BOULENGER, 1883) from the Guianas, the Amazon basin and the adjacent Andean versant, (6) *E. rubriventris* LÖTTERS & DEBOLD & HENLE & GLAW & KNELLER, 1997 from sub-Andean Peru. In addition to these taxa, there is evidence for the existence of some unnamed species (e.g. HADDAD & MARTINS 1994; VENCES et al. 2003; own unpubl. data), while the status of a form originally named *E. pictus guayanensis* (HEATWOLE & SOLANO & HEATWOLE, 1965) from northern South America remains to be resolved (cf. SILVERSTONE 1976).

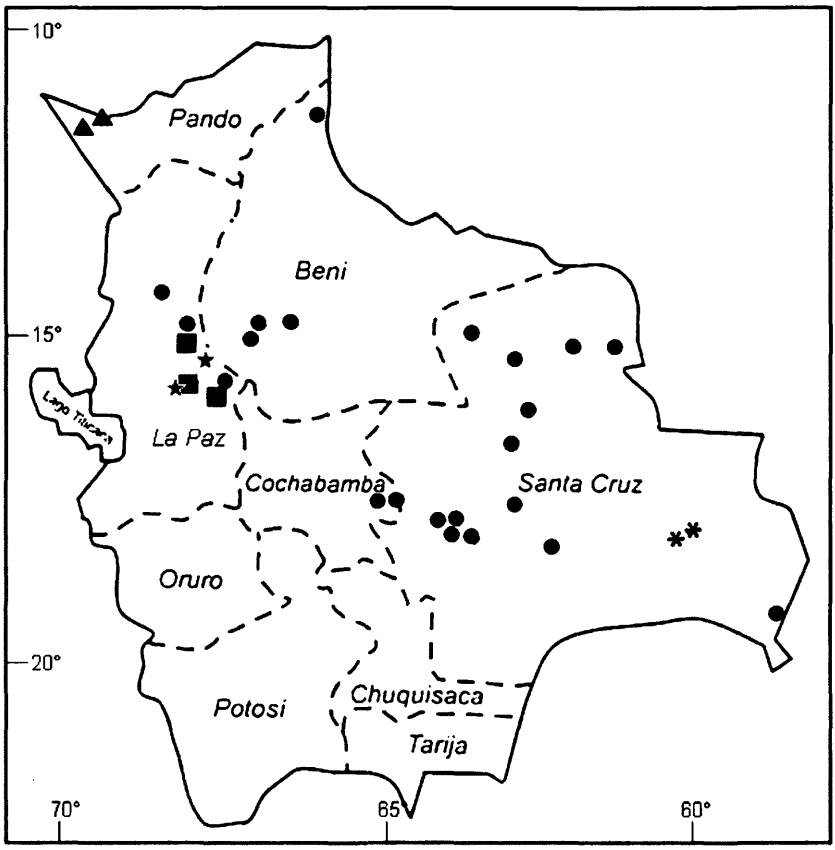

Fig. 1. Map of Bolivia with political units and known distributions of *Epipedobates* species (from data in GONZALES et al. 1999 and those in the present paper):
■ - *E. bolivianus*, ∗ - *E. flavopictus*, ▲ - *E. hahneli*, ● - *E. pictus* and ★ - *E. yungicola* spec. nov.

Abb. 1: Karte von Bolivien mit politischen Einheiten und den bekannten Verbreitungen von *Epipedobates*-Arten (nach Daten von GONZALES et al. 1999 und aus der vorliegenden Arbeit):
■ - *E. bolivianus*, ∗ - *E. flavopictus*, ▲ - *E. hahneli*, ● - *E. pictus* and ★ - *E. yungicola* spec. nov.

The purpose of this paper is to describe a new species of *Epipedobates* from sub-Andean Bolivia, i.e. the humid montane forest zone called Yungas, which is similar to *E. pictus* and *E. hahneli*. Like most other *Epipedobates* from Bolivia, it is only known from a relatively small geographic range (fig. 1).

MATERIALS AND METHODS

Specimens examined by the authors are deposited at BM (British Museum, London), CBF (Colección Boliviana de Fauna, La Paz), NKA (Museo de Ciencias Naturales "Noel Kempff Mercado", Santa Cruz de la Sierra), NMW (Naturhistorisches Museum, Vienna), ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn)

and ZMB (Zoologisches Museum der Humboldt-Universität, Berlin) and include: *Epipedobates bolivianus* (5 specimens): Bolivia: BM 1947.2.13.89-90 (lecto- and paralectotype), San Carlos, Departamento La Paz; BM 1947.2.13.91 (paralectotype), San Ernesto, Departamento La Paz; CBF 3901, km 30, Caranavi-Yucumo road, Departamento La Paz; NKA 3707, Serrania Beu, Departamento La Paz; *Epipedobates flavopictus* (4 specimens): Bolivia: ZFMK 77442-44, Serranía de Santiago, Departamento Santa Cruz; Brazil: BM 1988.144, Proximo ao Retiro Zé Correia-fazenda Salto, Estado Minas Gerais; *Epipedobates hahneli* (10 specimens): Bolivia: ZFMK 66809-10, Cobija, Departamento Pando; Peru: BM 1947.2.15. 14-20 (lecto- and paralectotypes), Yurimaguas, Departamento Loreto; ZFMK 40742, Tarapoto, Departamento San Martín; *Epipedobates pictus* (51 specimens): Bolivia: ZFMK 72153, Estación Biológica del Beni, Departamento del Beni; ZFMK 66962-63, 66984, Parjacti-Cochabamba road, Departamento Cochabamba; La Paz; NKA 1190, 1539, 1400, 1510, Buenavista, Departamento Santa Cruz; NKA 2102-08, Concesión Forestal Oquiriquia, Río San Martín, Departamento Santa Cruz; ZFMK 66855-59, Parque Nacional Amboró, Campamento Mataracú, Departamento Santa Cruz; NKA 1028-1032, Proyecto Ríos Blanco y Negro, Departamento Santa Cruz; NKA 59-60, 98-100, Puerto Almacén, Departamento Santa Cruz; NKA 166, Puerto Rico, Departamento Santa Cruz; NKA 686, 692, 703-708, 710, 776-84, San Ramón, Departamento Santa Cruz; Brazil: NMW 19190: 3 (lectotype of *E. eucnemis*), Rio Mamoré, Estado Rondônia; *Epipedobates pictus guayanensis* (2 specimens): Guiana: ZMB 30019, Meamu Mouth; *Epipedobates rubriventris* (59 specimens): Peru: ZFMK 30037-52, 37892-907, 39854-69, 30053, 37908-11, 39870, 64838-42 (holo- and paratypes), Cordillera Azul, Departamento Ucayali.

The available specimens of the new species are adult males which were observed calling in the field. They were preserved in 70 % ethanol. The holotype was photographed in life before preservation. For genetic analysis, tissue of one toe of the holotype of the new and other species was stored in 98 % ethanol. The scheme of the description of the new species follows LÖTTERS et al. (1997). Measurements were taken with dial callipers to the nearest 0.1 mm; snout-vent-length is abbreviated SVL.

Before collecting the holotype, its advertisement calls were recorded in the field with a Sony® WM D6C walkman, a Sennheiser® Me 66 directional microphone on metal cassette tapes. Digitalisation and analysis was performed with Syntrillium® CoolEdit 2000® at FFT (Fast Fourier Transformation) 1028; a spectrogram was elaborated at FFT 256. Terminology of calls follows HEYER et al. (1990).

Genetic analyses, focusing on the sequence of a 491 bp section of the mitochondrial 16S rRNA gene, followed the methods applied by VENCES et al. (2003).

DESCRIPTION

Epipedobates yungicola spec. nov. (figs. 2, 3)

Holotype: CBF 3900 (field number SR 99-3), adult male, km 10 on road from Caranavi to Yolosa (15°53'17" S, 67°33' 09" W, ca. 600 m above sea level), Yungas de La Paz, Provincia Caranavi, Departamento La Paz, Bolivia, 2 October 1999, S. REICHLE leg.

Paratype: NKA 7908, adult male, same locality data as holotype, 29 October 2004, A. JOHN & S. REICHLE leg.

Diagnosis: A species related to *Epipedobates pictus* and allies (cf. SILVERSTONE 1976; HADDAD & MARTINS 1994) with (1) adult male SVL ca. 22.8-23.5 mm; (2) dorsal skin slightly granular; (3) Finger I > Finger II when adpressed; (4) toes and fingers lacking webbing; (5) maxillary teeth present; (6) tympanum visible; (7) in life black with irregular grey dorsal flecks, yellowish cream labial line and dorsolateral

Fig. 2. Holotype of *Epipedobates yungicola* spec. nov. in life (CBF 3900).
Abb. 2. Holotypus von *Epipedobates yungicola* spec. nov. im Leben (CBF 3900).

Fig. 3. Ventral view of holotype of *Epipedobates yungicola* spec. nov. (CBF 3900).
Abb. 3. Ventralansicht des Holotypus von *Epipedobates yungicola* spec. nov. (CBF 3900).

line from tip of snout via nostril and eye to groin, small red signal spots in axillary, thigh, lower femoral and calf regions, venter dark grey with bluish grey marbling, extremities bronze with irregular dark brown stipples, iris black with golden stipples; (8) advertisement call existing of rapidly repeated notes (each of two pulses) lasting ca. 31-34 ms at a dominant frequency > 3550 Hz and < 3750 Hz; (9) sequence of a 491 bp section of the mitochondrial 16S rRNA gene as listed below.

The new species is most similar to *E. pictus* and *E. hahneli* (see Comparisons).

Description of holotype: Body slender, head narrower than body; snout in dorsal and lateral views rounded; maxillary teeth present, vomerine teeth absent; choanae rounded; tongue twice as long as wide, free for about half its length; vocal slits and median subgular vocal sac present; nares slightly protuberant, almost not visible from dorsal; canthus rostralis convex from tip of snout to nostril, straight from nostril to eye; loreal region vertical; horizontal eye diameter larger than distance from nostril to anterior corner of eye; tympanum visible; skin slightly granular, most prominent on dorsum; foot webbing absent; relative length of toes: I < II < V < III < IV; metatarsal tubercles well developed, rounded, about the same size; rest of sole smooth; well developed subarticular tubercles at joints of all phalanges of foot; hand webbing absent; relative length of fingers: IV < II < I < III, Finger I > Finger II when adpressed; metacarpal tubercles well developed, rounded, outer about twice the size of inner; rest of palm smooth; well developed subarticular tubercles at joints of all phalanges of hand.

In preservative, the holotype is dorsally black, greyish on limbs, with white labial line from below nostril to arm insertion and white dorsolateral line from tip of snout above nostril and eye to groin; small pink signal spots in axillary, thigh, lower femoral and calf regions; ventrally greyish, with white marbling on posterior belly and limbs. In life, this specimen was black with irregular grey flecks on dorsum; labial and dorsolateral lines were yellowish cream; signal spots were red; ventrally it was dark grey with bluish grey marbling; extremities were bronze with irregular dark brown stipples; the iris was black with golden stipples.

Description of paratype: The paratype agrees well with the above description of the holotype.

Measurements (in mm) and ratios of holotype (and paratype): SVL, 23.5 (22.8); head length from tip of snout to angle of jaws, 6.2 (5.6); head width at angles of jaws, 6.9 (6.8); interorbital distance, 2.5 (2.4); distance between nares, 1.7 (1.5); distance from nostril to anterior corner of eye, 1.8 (1.6); horizontal eye diameter, 3.3 (3.2); tibia length, 11.7 (11.1); foot length from tip of longest toe to proximal outer metatarsal tubercle, 10.9 (10.1); hand length from tip of longest finger to proximal outer metacarpal tubercle, 6.3 (5.1); head length/SVL, 0.26 (0.25); head width/SVL, 0.29 (0.30); tibia length/SVL, 0.50 (0.44); distance from nostril to eye/eye diameter, 0.55 (0.50).

Distribution and ecology: *Epipedobates yungicola* is only known from two localities within a relatively small geographic range in the Yungas de La Paz, Bolivia (fig. 1). Apart from the type locality, it was found and recorded by JOHN (2003) at km 22 on the Caranavi-Yucumo road, Yungas de La Paz, Provincia Caranavi, Departamento La Paz (ca. 1,000 m above sea level). The entire area is composed of humid mountain rain forest. At the type locality, however, human influence has converted almost all forest to small scale banana plantations.

All specimens observed by the authors and JOHN (2003) were males, calling from exposed positions on the ground during the day. From the same general area, *E. bolivianus* and *E. pictus* have been reported (see GONZALES et al. 1999). The latter was found syntopically with *E. yungicola* along the Caranavi-Yucumo road.

Advertisement call: Vocalizations produced by the holotype of *Epipedobates yungicola* (fig. 4) consisted of numerous rapidly repeated notes. Twenty such notes were analysed (recorded at a temperature of 27.8°C). These were each composed of two pulses, showing a slight upward frequency sweep from around 3550 to 3740 Hz. Dominant frequency was at about 3590-

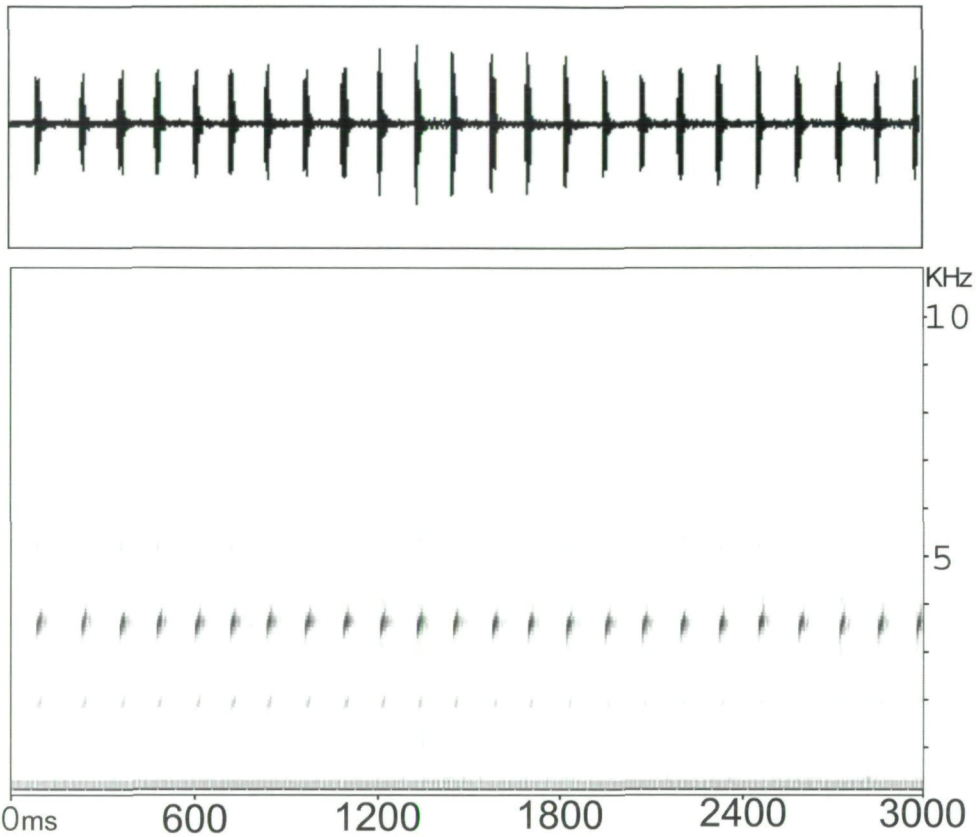

Fig. 4. Oscillogram (above) and sound spectrogram (below) of advertisement call of *Epipedobates yungicola* spec. nov. (CBF 3900). Temperature during recording 27.8°C.

Abb. 4: Oszillogramm (oben) und Klangspektrogramm (unten) des Anzeigerufes von *Epipedobates yungicola* spec. nov. (CBF 3900). Temperatur während der Aufnahme 27,8°C.

3719 Hz (mean 3660 ± 49 Hz). Note length ranged from 31 to 34 ms (mean 32.4 ± 0.9 ms), while note repetition rate was 4.5-5.0 notes/second (mean 4.7 ± 0.16 notes/second). The inter-note interval was 163-221 ms (mean 180.7 ± 11.9 ms). The data coincide with those given by JOHN (2003). The advertisement call of *E. yungicola* is not allocable to any of the known calls defined for dendrobatid frogs (cf. LÖTTERS et al. 2003).

Molecular genetics: The sequence of the 491 bp fragment of the mitochondrial DNA of the 16S rRNA gene of the holotype of *Epipedobates yungicola* (GenBank Accession Number AY263239; http://www.ncbi.nlm.nih.gov/) is:

1 cccagtgact ttgttcaacg gccgcggtat cctaaccgtg cgaaggtagc gtaatcactt
61 gttctttaaa tgaggactag tatgaatggc cccacgaggg ctgcactgtc tccttttct
121 aatcaatgaa actaatctcc ccgtgaagaa gcgggaataa ccctataaga cgagaagacc
181 ctatggagct ttaaacaatt gaaacatttg ctttttctt gacctcttcc gagctcttta
241 tcttacttaa gcattcttat ttctagtttt aggttggggt gaccacggag caaaacttaa
301 cctccatgaa gaaatgaata tatttttaag ccacaaacta ccctttaag catcaacaaa
361 ttgaccttca ttgacccaat atattgatca acgaaccaag ttaccctagg gataacagcg
421 caatctactt caagagctca tatcgacaag taggtttacg acctcgatgt tggatcaggg
481 tatcctagtg g

Remarks: After examination of the lectotype, we agree with previous authors (e.g. HADDAD & MARTINS 1994) that *Epipedobates eucnemis* (STEINDACHNER, 1864) from Brazil as a junior synonym of *E. pictus*.

We have not been able to study the type material of *E. pictus guayanensis*. From referable specimens from Guiana and according to the original description (HEATWOLE et al. 1965), this form is similar to *E. pictus* (see Comparisons), although we suspect it to represent a distinct species rather than a disjunct northern population of the latter.

Etymology: The specific name means "inhabitant of the yungas" and refers to the eco-geographic region in which the new species occurs.

COMPARISONS

Epipedobates yungicola is morphologically similar to *E. pictus* and *E. hahneli*, both known from Bolivia (fig. 1). In adult male SVL, it matches both species, including large individuals of *E. hahneli*. This latter poison frog apparently comprises a complex of species (cf. HADDAD & MARTINS 1994; LÖTTERS et al. 1997). Populations examined by HADDAD & MARTINS (1994) and us, including Bolivian and topotypic specimens from Peru (see Material and Methods), are similar to the new species in having (in life) black dorsal surfaces with irregular grey flecks and yellowish cream lines. However, they lack teeth (versus present in *E. yungicola*), have small yellowish orange (versus red in *E. yungicola*) signal spots in axillary, thigh and calf regions excluding (versus including in *E. yungicola*) lower femoral region.

Epipedobates pictus (sensu HADDAD & MARTINS 1994), including specimens found by us near the type locality, shares the presence of teeth and (in life) reddish signal spots with the new species. However, *E. pictus* has bright yellow (versus yellowish cream in *E. yungicola*) dorsolateral lines and always lacks dorsal spots (versus grey dorsal spots present in *E. yungicola*). The red thigh signal is usually larger in *E. pictus* than in *E. yungicola*, extending onto the upper femur (cf. HADDAD & MARTINS 1994: 292). A lower femoral signal spot is absent in *E. pictus* (versus present in *E. yungicola*). Characters of the colour pattern mentioned to distinguish the new species and *E. pictus* are also applicable to distinguish it and the form *guayanensis*. Moreover, according to SILVERSTONE (1976, by implication), the latter lacks teeth (versus present in *E. yungicola*).

Epipedobates bolivianus from the same general area as the new species (cf. GONZALES et al. 1999) lacks teeth (versus present in *E. yungicola*), has yellowish (versus red in *E. yungicola*) axillary and thigh signal spots and lacks lower femoral and calf spots (versus present in *E. yungicola*).

Other *Epipedobates* resembling *E. pictus* (see Introduction) differ from *E. yungicola* by the presence of yellowish dorsal markings (*E. braccatus*, *E. flavopictus*) or reddish venter (*E. rubriventris*) (HADDAD & MARTINS 1994; LÖTTERS et al. 1997).

The advertisement call of *E. yungicola* is similar to those of *E. pictus* and *E. hahneli* (cf. data in LÖTTERS & KNELLER 2000). However, vocalisations in these two poison frogs are unpulsed (versus pulsed in *E. yungicola*) and their lower dominant frequency range is higher (= 3750 Hz) than the upper range in *E. yungicola* (< 3750 Hz). The note length in *E. yungicola* is clearly longer than in Amazonian (including Bolivian) populations or clearly shorter than in a sub-Andean population (i.e. from Peru) of the *E. hahneli* complex (temperature of *E. hahneli* recordings varied from 24.0-28.0°C; cf. LÖTTERS & KNELLER 2000). In contrast, note length and number of notes per second overlap with the lower range known in *E. pictus*. Vocalization parameters in the latter mentioned species show great variation (cf. HADDAD & MARTINS 1994; DE LA RIVA et al. 1996), probably related to its large geographic range (see fig. 1) or, more likely, the presence of unidentified additional cryptic species. Recordings of *E. pictus* from near its type locality exhibit a note length of about 40-50 ms with 2.8-2.9 notes per second (according to HADDAD & MARTINS 1994

Table 1 (this and opposite Page): Summary of the uncorrected p-distances for the 16S rRNA data set of dendrobatid frogs; values ≤ 1.8 % are in bold (see text). For origin of specimens and GenBank numbers see VENCES et al. (2003).

Tab. 1 (diese und gegenüberliegende Seite): Zusammenfassende Darstellung über die unkorrigierten p-Distanzen der 16S rRNA Daten von Dendrobatiden; Werte ≤ 1,8% in Fettschrift (siehe Text). Zur Herkunft und den GenBank-Nummern der Exemplare siehe VENCES et al. (2003).

	Taxon	1	2	3	4	5	6	7
1	*Allobates* cf. *femoralis* (BOULENGER, 1883)	-						
2	*Cryptophyllobates azureiventris* (KNELLER & HENLE, 1985)	0.1458	-					
3	*Dendrobates auratus* (GIRARD, 1855)	0.1220	0.1254	-				
4	*Dendrobates imitator* SCHULTE, 1986	0.1165	0.1315	0.0868	-			
5	*Epipedobates anthonyi* (NOBLE, 1921)	0.1494	0.1305	0.1046	0.1113	-		
6	*Epipedobates bassleri* (MELIN, 1941)	0.1322	0.1452	0.1086	0.1090	0.0874	-	
7	*Epipedobates bilinguis* (JUNGFER, 1989)	0.1347	0.1370	0.1111	0.1092	0.0876	0.0213	-
8	*Epipedobates flavopictus*	0.1220	0.1295	0.0944	0.0946	0.0895	**0.0149**	**0.0129**
9	*Epipedobates hahneli* (I)	0.1448	0.1646	0.1257	0.1164	0.0940	0.0194	0.0229
10	*Epipedobates hahneli* (II)	0.1370	0.1437	0.1137	0.1029	0.0891	0.0189	0.0192
11	*Epipedobates hahneli* (III)	0.1519	0.1735	0.1285	0.1271	0.0968	0.0302	0.0307
12	*Epipedobates parvulus* (BOULENGER, 1882)	0.1220	0.1315	0.1042	0.0965	0.0981	0.0256	0.0193
13	*Epipedobates pictus* (I)	0.1322	0.1295	0.0966	0.1028	0.0916	0.0297	0.0277
14	*Epipedobates pictus* (II)	0.1359	0.1301	0.0994	0.1057	0.0916	0.0297	0.0277
15	*Epipedobates silverstonei* (MYERS & DALY, 1978)	0.1333	0.1489	0.1180	0.1139	0.1007	0.0201	0.0225
16	*Epipedobates* cf. *tricolor* (BOULENGER, 1899)	0.1437	0.1255	0.0963	0.1025	**0.0042**	0.0873	0.0875
17	*Epipedobates trivittatus* (SPIX, 1824)	0.1289	0.1299	0.1011	0.1015	0.0855	**0.0170**	**0.0150**
18	*Epipedobates yungicola* spec. nov.	0.1382	0.1358	0.1110	0.1136	0.0863	0.0250	0.0206

[recorded at 22.5°C] or own unpublished data [recorded at 23.0°C and 26.5°C]), thus differing from *E. yungicola*.

We used available 16S rRNA sequences of species of the genus *Epipedobates* (cf. VENCES et al. 2003) to compare them with the sequence gained from the holotype of *E. yungicola*. The complete data matrix (16 samples; 591 bp including gaps; not shown) included the in-group species as listed as *Epipedobates* in table 1. The matrix for the uncorrected p-distances for all nucleotide sites is also presented in this table.

When applying both Most Parsimony and Bayesian analyses (cf. VENCES et al. 2003) to the resulting data set, we received overall coinciding topologies, strongly supporting the same terminal clades (trees not shown). All analyses suggest *E. yungicola* to be part of a well supported clade of cis-Andean species of *Epipedobates*.

Regarding the uncorrected p-distances (table 1), it becomes clear that the cis-Andean species of *Epipedobates* [i.e. all except *E. anthonyi* (NOBLE, 1921) and *E.* cf. *tricolor* (BOULENGER, 1899)] are rather close to each other with comparatively low genetic variation. *Epipedobates yungicola* is separated from *E. pictus* by a genetic difference of 1.8 % and *E. hahneli* by at least 2 % (table 1). These values support its spe-

Table 1 (continued): Summary of the uncorrected p-distances for the 16S rRNA data set of dendrobatid frogs; values ≤ 1.8 % are in bold (see text). For origin of specimens and GenBank numbers see VENCES et al. (2003).

Tab. 1 (Fortsetzung): Zusammenfassende Darstellung über die unkorrigierten p-Distanzen der 16S rRNA Daten von Dendrobatiden; Werte ≤ 1,8% in Fettschrift (siehe Text). Zur Herkunft und den GenBank-Nummern der Exemplare siehe VENCES et al. (2003).

	8	9	10	11	12	13	14	15	16	17
8	-									
9	**0.0162**	-								
10	**0.0138**	**0.0000**	-							
11	0.0264	**0.0149**	**0.0148**	-						
12	**0.0138**	0.0301	0.0254	0.0412	-					
13	**0.0138**	0.0327	0.0300	0.0443	0.0237	-				
14	**0.0142**	0.0327	0.0299	0.0443	0.0244	**0.0000**	-			
15	**0.0152**	0.0240	0.0204	0.0350	0.0261	0.0306	0.0305	-		
16	0.0825	0.0943	0.0869	0.0935	0.0904	0.0848	0.0872	0.0984	-	
17	**0.0119**	0.0190	**0.0162**	0.0294	0.0218	0.0218	0.0223	0.0219	0.0813	-
18	**0.0115**	0.0247	0.0209	0.0362	0.0228	**0.0182**	**0.0182**	0.0249	0.0861	**0.0136**

cific distinctness, since the level of genetic difference is even lower among other *Epipedobates* that are well identifiable as distinct species on the basis of morphology and bioacoustics (e.g. SILVERSTONE 1976; LÖTTERS & KNELLER 2000), as for instance among *E. bilinguis* JUNGFER, 1989 and *E. trivittatus* (SPIX, 1824) or *E. bassleri* (MELIN, 1941) and *E. flavopictus* (see table 1).

Comparing all available p-distances, *E. yungicola* is most close to *E. flavopictus* and *E. trivittatus* (1.2 and 1.4 %; table 1). On the basis of morphology (differences in SVL, color pattern, presence/absence of teeth etc.) and advertisement call parameters (e.g. note length), the new species is clearly distinct from both (cf. SILVERSTONE 1976; HADDAD & MARTINS 1994; LÖTTERS & KNELLER 2000). Thus, the possibility that *E. yungicola* may be conspecific with one of these has to be negated. In addition, a direct comparison of the sequences of *E. flavopictus*, *E. trivittatus* and *E. yungicola*, including all sequenced base pairs (an unambiguous alignment of the highly variable loop regions of the 16S rRNA gene is only possible in very closely related species – these regions [77 bp] were consequently not used for the overall phylogeny), raises the true genetic differences between them to about 3.1 % - 4.6 %.

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