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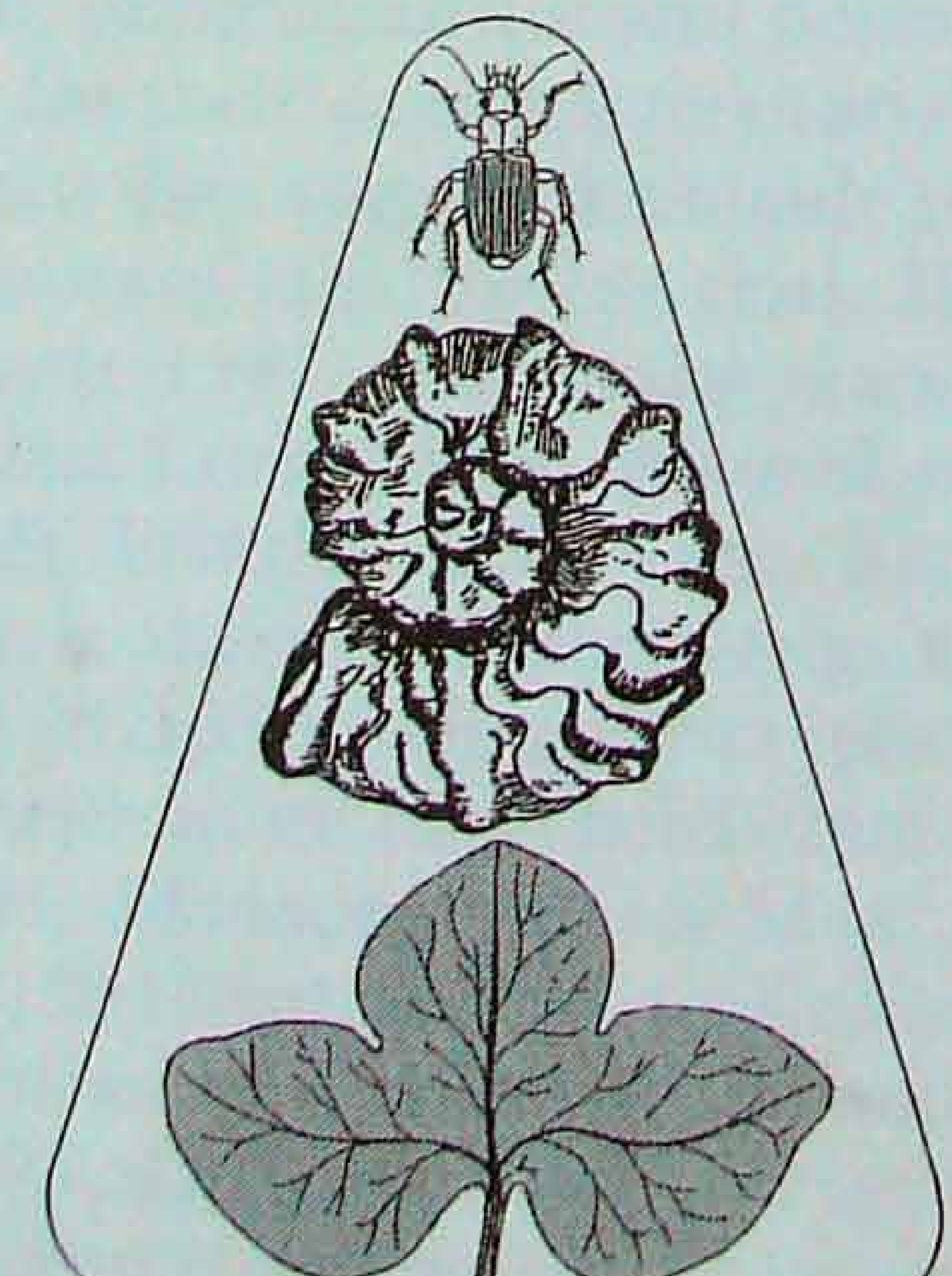

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A New Genus of Aposematic Poison Frog (Amphibia: Anura: Dendrobatidae) from the Upper Amazon Basin, with Notes on Its Reproductive Behaviour and Tadpole Morphology

Eine neue aposematische Giftfrosch-Gattung (Amphibia: Anura: Dendrobatidae) aus dem oberen Amazonas-Becken mit Anmerkungen zu deren Reproduktionsverhalten und Kaulquappenmorphologie

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Alex Widmer, Zürich

With 4 figures

Mit 4 Abbildungen

Introduction

The neotropical poison frogs (Dendrobatidae) are a conspicuous group of almost 200 small, often colourful and poisonous species. Dendrobatids are also remarkable for their complex territorial, mating and parental care behaviour. Numerous data suggest the family to comprise a monophyletic unit of New World anurans (e.g. Vences et al. 2000). Several genus names have been erected (Frost 1985). For many years three of them were widely accepted, *Colostethus* Cope, 1866, *Dendrobates* Wagler, 1830, and *Phyllobates* Duméril & Bibron, 1841 (e.g., Savage 1968; Silverstone 1975, 1976). According to different authors (e.g. Vences et al. 2000), *Colostethus* is a paraphyletic group including the cryptically coloured, usually non-toxic dendrobatids with more basal behaviour. *Aromobates* Myers & Paolillo & Daly, 1991, *Mannophryne* La Marca, 1992, and *Nephelobates* La Marca, 1994 „1991" are related to *Colostethus* and also primitive. The names *Dendrobates* and *Phyllobates* as understood by Savage (1968) and Silverstone (1975, 1976) were applied to the aposematic taxa. Species of these genera are also characterised by more or less toxic skin secretions as well as derived behavioural traits. Myers et al. (1978) restricted *Phyllobates* only to some trans-Andean species allied to *Phyllobates bicolor* Duméril & Bibron, 1841. The remaining taxa formerly referred to this genus were transferred to *Dendrobates*. Subsequently, the latter genus was splitted when *Minyobates* Myers, 1987 [for several small species formerly allied to the *D. minutus* group of Silverstone (1975) and additional ones] and *Epipedobates* Myers, 1987 [for species referred to *Phyllobates* by Silver-

STONE (1976) and additional ones] were erected. *Epipedobates* was further divided when *Allobates* ZIMMERMANN & ZIMMERMANN, 1988 (for *Prostherapis femoralis* BOULENGER, 1884) and *Phobobates* ZIMMERMANN & ZIMMERMANN, 1988 [for *Dendrobates silverstonei* MYERS & DALY, 1979 and the *Phyllobates trivittatus* group of SILVERSTONE (1976)] were described. Apart from morphology, dendrobatid generic characteristics include skin toxin profiles, and behaviour (e.g., MYERS 1987; ZIMMERMANN & ZIMMERMANN 1988). Some of the recently described genera have been discussed controversially (e.g., MYERS et al. 1991) regardless of the lack of comprehensive phylogenetic studies.

Recently, infra-familial relationships of dendrobatid frogs have been accessed on the basis of mitochondrial DNA sequences (e.g. CLOUGH & SUMMERS 2000; VENCES et al. 2000). Independently, different authors roughly came to the following conclusions:

1. *Dendrobates* and *Phyllobates* are the most derived poison frog genera forming a clade;
2. *Epipedobates* is their more primitive sister group;
3. *Allobates* is a valid genus clustering with the more basal dendrobatids (*Colostethus* sensu lato);
4. of doubtful generic position are *Minyobates* and *Phobobates*, which should probably best be regarded as junior synonyms of *Dendrobates* and *Epipedobates*, respectively (cf. VENCES et al. 2000).

As a result, evolutionary relationships among the derived aposematic dendrobatid genera (and the validity of their proposed names) are generally well understood. These are also supported by other than only genetic characters (e.g. ZIMMERMANN & ZIMMERMANN 1988; MYERS et al. 1996).

When included in DNA sequence studies, a species originally described as *Phyllobates azureiventris* KNELLER & HENLE, 1985 (Figs. 1, 2) always appeared apart from the other genera in a position of its own [valid for all genes sequenced, i.e. 12S, 16S and cytochrome b (CLOUGH & SUMMERS 2000; VENCES et al. 2000; WIDMER et al. in press)]. The generic placement of this small aposematic dendrobatid from the eastern versant of the Andes of Peru has always been discussed controversially. In the original description, a close relationship with the trans-Andean genus *Phyllobates* sensu stricto was proposed (KNELLER & HENLE 1985). In contrast, MYERS & BURROWES (1987) suggested a possible relationship with the cis-Andean *pictus* group of *Epipedobates*. As a result, MYERS (1987) included *azureiventris* in *Epipedobates*. Morphologically, adult *Epipedobates* and *Phyllobates* are more or less identical and therefore external characters are probably not useful to allocate *azureiventris*. According to HENLE (1992), the generic placement remains to be resolved because the reproductive behaviour (as described by KNELLER 1987) shows characteristics of both *Phyllobates* and *Epipedobates*. LÖTTERS & KNELLER (2000) described the advertisement call of *azureiventris* and concluded that it was very similar to trill calls known in the species of *Phyllobates* sensu stricto and some *Epipedobates*. Genetic data suggest *azureiventris* to be a basal part of a sister clade to *Dendrobates* (including *Minyobates*) + *Phyllobates*, that also contains *Epipedobates* (in-

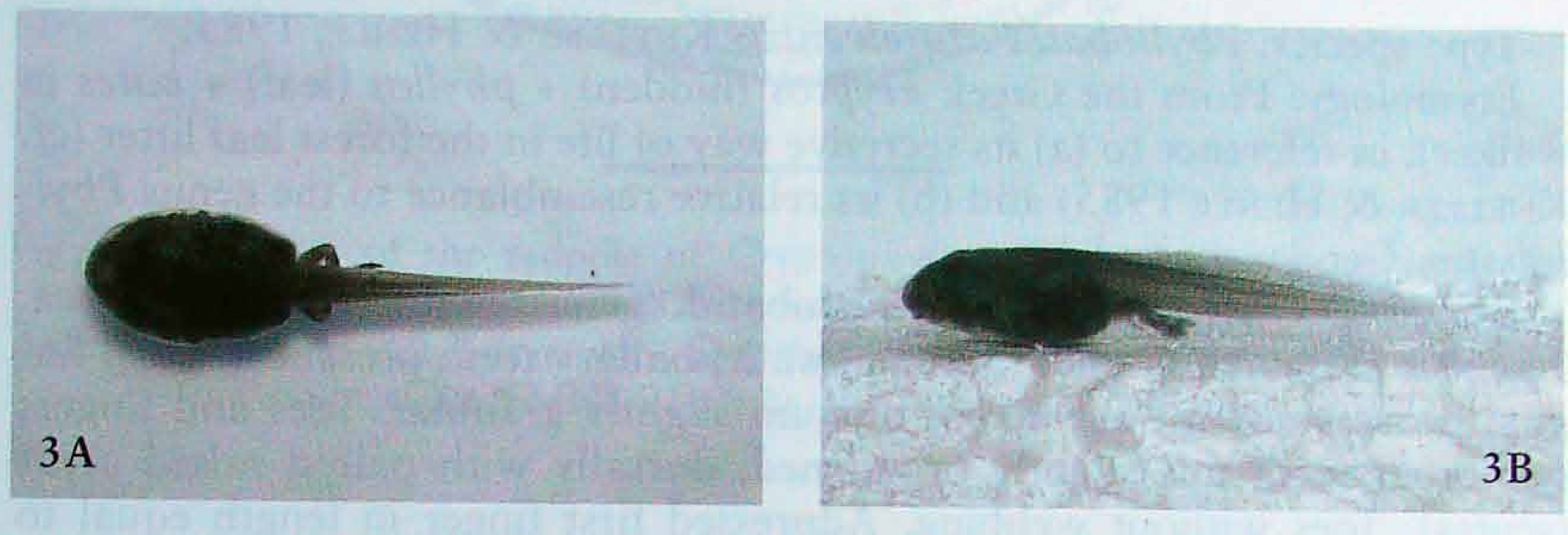

Fig. 1. *Cryptophyllobates azureiventris,* subadult specimen of 18 mm SVL. Note colour pattern with light labial line, light lateral line and light dorsolateral line ending on posterior back.

Abb. 1 *Cryptophyllobates azureiventris,* subadultes Tier von 18 mm Kopf-Rumpf-Länge. Beachte das Zeichnungsmuster mit leuchtender Labiallinie, leuchtendem Lateralstreifen und leuchtendem Dorsolateralstreifen, der auf dem Rücken ended.

Fig. 2. Captive male parent of *Cryptophyllobates azureiventris* carrying all tadpoles of one clutch together.

Abb. 2. Männliches Elterntier von *Cryptophyllobates azureiventris* in Gefangenschaft, das alle Larven eines Geleges gemeinsam transportiert.

Fig. 3. Tadpole of *Cryptophyllobates azureiventris* (SMNS 9282: 2), in stage 39, in life in dorsal (A) lateral view (B).

Abb. 3. Lebende Larve von *Cryptophyllobates azureiventris* (SMNS 9282: 2) im Entwicklungsstadium 39 in Dorsal- (A) und Lateralansicht (B).

cluding *Phobobates*) and, in one case, a species of currently classified as a *Colostethus*. But *azureiventris* was always placed separately from *Epipedobates* (Clough & Summers 2000; Vences et al. 2000). Clough & Summers (2000) also suggested that *azureiventris* may be basal not only to the *Epipedobates* lineages but to the entire *Epipedobates* + (*Phyllobates* + *Dendrobates*) clade. At least, recently Widmer et al. (in press), sequencing part of the mitochondrial cytochrome b gene of all known species of *Phyllobates* and *azureiventris,* demonstrated that the latter clearly is not a *Phyllobates.*

In summary, from a genetic point of view, it is apparent that *azureiventris* is more closely related to *Epipedobates* than to *Phyllobates*. We studied the reproductive behaviour of captive *azureiventris* and larval morphology. Our data demonstrate that the species is not a member of *Epipedobates,* from which it differs by at least one apomorphy. It shares more – but not all – characters with *Phyllobates* from which it appears genetically well separated. In our opinion, *azureiventris* forms a genus of its own. Because no name is available, we describe it as follows.

Systematics

Cryptophyllobates gen. nov.

Type species: *Phyllobates azureiventris* KNELLER & HENLE, 1985.

Etymology: From the Greek *kryptos* (hidden) + *phyllos* (leaf) + *bates* (a walker), in reference to (a) its secretive way of life in the forest leaf litter (cf. KNELLER & HENLE 1985) and (b) its relative resemblance to the genus *Phyllobates.* Gender masculine.

Diagnosis: Medium-sized dendrobatid genus with adult SVL ca. 25–28 mm (females larger than males). Maxillary teeth present. Medial lingual process absent. Surface of dorsum slightly granular. Toes and fingers not broadened; tips slightly broadened, dorsally with paired raised areas (scutes). Toes without webbing. Adpressed first finger in length equal to second. Dermal flap above cloaca absent. Ground colour black with aposematic pattern: complete light labial, dorsolateral and lateral lines present with dorsolateral line ending on posterior back (Fig. 1); ventral side marbled. Light proximoventral calf spot lacking. Cephalic amplexus absent in mating. Advertisement call a trill. All larvae from one clutch carried together by the male parent (Fig. 2). Larval development in pools with more or less running water. Tadpoles with dextral vent tube and rounded tail fin, tail in length > 70 % of total length (Fig. 3 A, B). Labial tooth row formula (LTRF) 2 (2) / 3 (Fig. 4).

Allobates differs from *Cryptophyllobates* by having basal foot webbing and tadpoles with pointed tail and LTRF 2 (2) / 3 (1–2) (e.g. SILVERSTONE 1976; ZIMMERMANN & ZIMMERMANN 1988). *Epipedobates* (including *Phobobates*) shows cephalic amplexus in mating, lacks a complete light lateral line, dorsolateral line never ends on posterior back and several species develop a light proximoventral calf spot (e.g. MYERS 1987). From *Dendrobates* (including *Dendromedusa* GISTEL, 1848, *Hylaplesia* SCHLEGEL *in* BOIE, 1827 and *Minyobates*) the new genus can be distinguished by hand morphology [in *Dendrobates* the first finger is shorter than the second when adpressed and finger discs are expanded (e.g. SILVERSTONE 1975)], the presence of light dorsolateral and lateral lines as well as maxillary teeth (absent in *Dendrobates*). In the latter genus the tadpoles are carried singly or in small groups (usually not the whole clutch) either by a male or female parent. Larval development occurs in phytotelmata. *Phyllobates* always lacks a lateral line and, if present, the dorsolateral line ends in the groin, not on the posterior back (e.g. MYERS et al. 1978).

Cryptophyllobates differs from *Colostethus* (including *Prostherapis* COPE, 1868, *Hyloxales* JIMÉNEZ DE LA ESPADA, 1871 and *Phyllodromus*

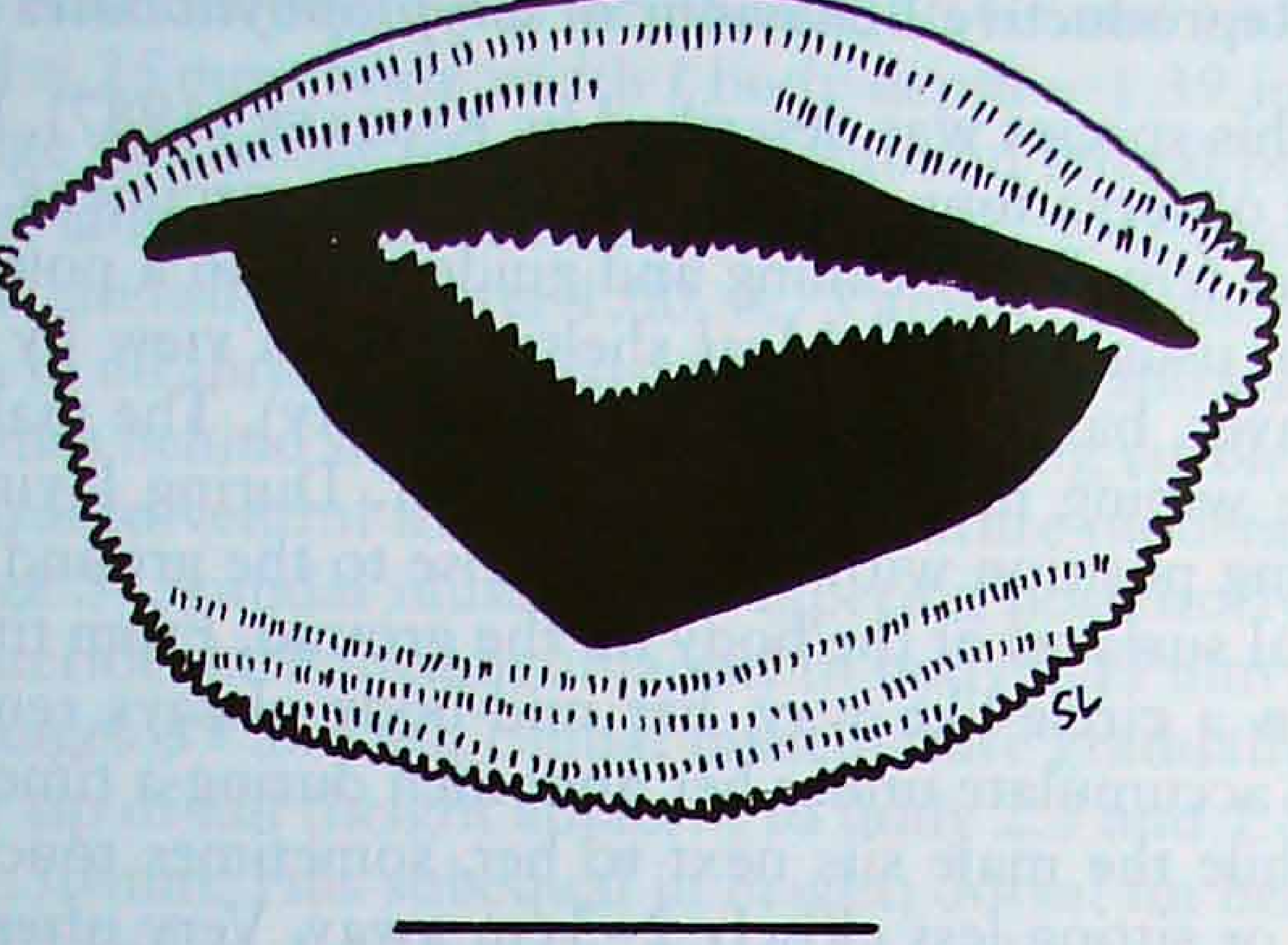

Fig. 4. Oral disc of the tadpole of *Cryptophyllobates azureiventris* in stage 39 (SMNS 9282: 2). Scale equals 1 mm.

Abb. 4. Mundfeld der Larve von *Cryptophyllobates azureiventris* Entwicklungsstadium 39 (SMNS 9282: 2). Die Linie entspricht 1 mm.

JIMÉNEZ DE LA ESPADA, 1871,) by having aposematic coloration with a dorsolateral line ending on the posterior back (usually absent but present in *C. nexipus* FROST, 1986), lacking webbing [present in many *Colostethus* (e.g. SILVERSTONE 1975; COLOMA 1995)], lacking a medial lingual process [as present in some *Colostethus* (GRANT et al. 1997)] and absence of cephalic amplexus [usually present in *Colostethus* (e.g. ZIMMERMANN & ZIMMERMANN 1988)]. From other cryptically coloured dendrobatids, *Cryptophyllobates* differs also by the following characters: from *Aromobates* by smaller size, from *Mannophryne* by absence of a collar pattern on the throat, from *Nephelobates* by lacking a dermal flap above the cloaca (MYERS et al. 1991; LA MARCA 1992, 1994).

Species included: *Phyllobates azureiventris* KNELLER & HENLE, 1985.

Distribution: Lower eastern versant of the Andes in the upper Amazon basin of Peru (Departamento San Martín) at elevations of ca. 700 m.

Taxonomic remarks: In DNA sequence studies by VENCES et al. (2000), *C. azureiventris* clustered with *Colostethus bocagei* (JIMÉNEZ DE LA ESPADA, 1871) from eastern Ecuador, although with relatively low bootstrap support. We negate that both species are representatives of the same genus for *C. bocagei* is dully coloured, lacking dorsolateral stripes at all, and possesses webbed feet (e.g. COLOMA 1995). *Colostethus nexipus* FROST, 1986 from the Amazonian versant of the Andes of Ecuador and Peru resembles *C. azureiventris* in having light labial, lateral dorsolateral lines (the latter ending on posterior back). But we suspect *C. nexipus* should not be included with *Cryptophyllobates,* because *C. nexipus* exhibits tarsal webbing and the first finger is shorter than the second (e.g. COLOMA 1995).

Notes on the Reproductive Behaviour of *Cryptophyllobates azureiventris*

Breeding of this species was described by Kneller (1987). Following this author and our observations on topotypic captive specimens, *C. azureiventris* males attract females by calling and guide them to a potential terrestrial breeding site, usually a dead leaf sheltered from view by some kind of cover (other leaves, bark, coconut shell in captivity). The male initiates egg laying by some wiping movements of the feet. During laying, the female takes a crouching position with the head close to the ground and all of the posterior ventral surfaces of the body on the ground. From time to time she turns slightly in a circle-like way, her mid-body always remaining at the same site. Eggs accumulate under her abdomen during a time of about 1–2 hours. Meanwhile the male sits next to her, sometimes touching her back with one hand or sitting less closely 2–3 cm away. Very often the male has left when the female is still laying 12–18 eggs altogether. He returns after the female has left and remains with the eggs for almost the entire period to hatching, which occurs after about 14 days. He always carries all larvae capable of wriggling onto his back (Fig. 2); an occasional leftover larva is neglected after the others have been transported. In captivity larvae remain on the male's back for one to three days before they are released in a body of water. Not always the entire lot of tadpoles leaves the back at the same time. Then they are carried along for some more time and the male may appear to carry only a small group out of all hatchlings. However, no additional larvae (except for an occasional neglected one) were ever found at the egg deposition site in those cases.

The reproductive behaviour of *C. azureiventris* is different from that of *Epipedobates* (with cephalic amplexus), but very reminiscent of that of *Allobates* and *Phyllobates*. In both genera there is no amplexus. *Allobates femoralis* males carry all tadpoles together (Weygoldt 1980, Zimmermann & Zimmermann 1988). *Phyllobates* males carry smaller numbers of tadpoles (Zimmermann & Zimmermann 1988, Roithmair 1994). However, our own limited observations on captive *P. bicolor* and *P. vittatus* indicate that the whole number of tadpoles from one clutch is carried, too. Sperm release in *Cryptophyllobates*, like in *Dendrobates*, appears to happen before the female starts laying eggs (as most likely in the other dendrobatid genera lacking amplexus, too).

Description of Tadpole of *Cryptophyllobates azureiventris*

Three captive-bred tadpoles, obtained from topotypic specimens, in developmental stages 37, 39 and 40 (Gosner 1960) were available. They are preserved in 4 % formalin for permanent conservation at Staatliches Museum für Naturkunde Stuttgart (SMNS 9282: 1–3). The examination methods and description scheme principally follow Donnelly et al. (1990), added by characters of Altig & McDiarmid (1999).

Characters in order of developmental stages mentioned. Total length 26.1, 27.0 and 26.1 mm, tail length 18.50, 20.50 and 19.33 mm (70.9, 76.0

and 74.1 % of total length). Body depth 5.50, 6.67 and 5 mm; body width 7.67, 9.33 and 6.25 mm (body width / body depth = 1.39 in stages 37 and 39, 1.25 in stage 40); snout rounded in dorsal and lateral profiles. Nostrils dorsal, directed laterally; internarial distance 2.83, 2.42 and 2.08 mm. Eye dorsal, directed laterally; diameter 1.00, 0.75 and 0.67 mm; interorbital distance 2.50 mm in all three individuals. Single sinistral spiracle; opening 9.0, 9.25 and 7.75 mm behind snout, inner wall of opening visible as slight ridge. Vent tube dextral to ventral fin. Caudal musculature moderately robust anteriorly; in stage 37, caudal musculature tapering posteriorly to near tip of tail only at posterior third (height adjacent to body 2.17 mm and at mid-tail 2.08 mm); in stages 39 and 40, caudal musculature gradually tapering posteriorly to near tip of tail (height adjacent to body 2.5 and 1.83 mm, at mid-tail 1.67 and 1.50 mm. Fins subequal in height; dorsal fin height at mid-tail 1.25 in stage 37 and in 1.42 mm in stages 39 and 40, not extending onto body; ventral fin height at mid-tail 0.83, 0.50 and 0.78 mm. Tip of fin rounded (Fig. 3 A, B).

Mouth directed ventrally. Oral disc emarginate; oral disc width 2.58, 3.08 and 3 mm. Labial teeth in two anterior and three posterior rows. Anterior rows equal in length, extending to marginal papillae; second row with median gap. First and second posterior rows equal in length, slightly longer than third. LTRF 2 (2) / 3. Upper jaw sheath forming a broad arch with lateral processes; lower jaw sheath V-shaped, more robust than upper one. Jaw sheaths well serrated. One complete row of marginal papillae at border of posterior lip, extending onto lateral margin of anterior lip; no row of lateral submarginal papillae (Fig. 4).

In preservative, dorsal body dark tan, laterally turning into dark greyish, ventral body surface translucent with scattered brown pigmentation (least at mid of and posterior venter); gut partly visible through skin of venter. Spiracle and vent tubes transparent. Caudal musculature tan with minute dark brown stipples (at anterior dorsal side of caudal musculature, for almost one half of entire tail length, stipples very dense). Fins transparent with dorsal fin scattered brownish except outer margin of posterior two thirds. White blotches present only on lower fin of specimen in developmental stage 40. Life coloration was similar, dorsally (especially dorsolaterally) and around eye with greenish bronze lichenous marks; the iris was black (Fig. 3 A, B).

Tadpole morphology has been of limited use in dendrobatid frog systematics. SILVERSTONE (1975; 1976) figured larvae, provided measurements of several species of different genera and incorporated tadpole characters in genus definitions. MYERS (1987) also listed some larval features when defining genera. A comprehensive synopsis of *Phyllobates* larvae was provided by DONNELLY et al. (1990). These tadpoles are uniform in having depressed body, single sinistral spiracle, low-finned tail not extending onto body and rounded tip, LTRF 2 (2) / 3, serrated jaw sheaths and rounded papillae on posterior and lateral margins of oral disc (DONNELLY et al. 1990). The tadpole of *C. azureiventris* thus clearly resembles *Phyllobates* larvae. But the same characters as mentioned seem to be more general among the Dendrobatidae, since they are also shared by several tadpoles of *Colostethus* (e.g. Coloma 1995) and *Epipedobates* (e.g. SILVERSTONE 1976; MYERS 1987), although these are described in less detail. Nevertheless, as evident from the drawings and measurements in SILVERSTONE (1976), proportions of tail length / body length and maximum tail height / body length as well as the anterior extension of the upper fin and shape of tip of fin seem more variable in *Epipedobates* spp. and in the majority of them outside of *Phyllobates* and *Cryptophyllobates*. The most similar larva of *Epipedobates* seems to be that of *E. smaragdinus* (SILVERSTONE, 1976) from eastern Peru. The differences between *Cryptophyllobates* and *Phyllobates* tadpoles include a considerably larger tail in *C. azureiventris* [in stages 37–40 tail length / total length > 70 % versus ca. 56–64 % in larvae of *Phyllobates* spp. between stages 25 and 41 (based on data provided by DONNELLY et al. 1990; see also MYERS et al. 1978)], a more posterior position of the spiracle opening [9 mm behind snout in stage 37 versus ca. 6.9 mm in a *P. lugubris* tadpole of the same stage (Donnelly et al. 1990)] and a larger oral disc width [2.58 in stage 37 versus ca. 2.25 mm in a *P. lugubris* tadpole of the same stage (Donnelly et al. 1990)]. Other morphometric differences we assume to lie within the variation of the different species.

Systematic Discussion

Currently, there are eight valid dendrobatid frog genera. Unfortunately, these are not uniformly defined and plesimorphic characters are probably too heavily involved (comp. MYERS et al. 1991; MYERS 1987). *Cryptophyllobates* most closely resembles *Epipedobates* and *Phyllobates*. From the former it differs by at least one apomorphy, i.e. the lack of cephalic amplexus during mating. The latter character is also absent in the derived *Phyllobates* + *Dendrobates* clade and the more primitive *Allobates*. This suggests that cephalic amplexus has been lost at least twice in dendrobatid evolution (e.g. VENCES et al. 2000). If *Cryptophyllobates* was basal to *Epipedobates* (cf. CLOUGH & SUMMERS 2000; VENCES et al. 2000), cephalic amplexus would have independently disappeared one more time. If *Cryptophyllobates* was basal to the entire *Epipedobates* + (*Phyllobates* + *Dendrobates*) clade as alternatively proposed by CLOUGH & SUMMERS (2000), it would probably be related to *Allobates*. In contrast to the „higher“ dendrobatids, both these genera exhibit a light lateral line (which may be interpreted as a plesiomorphic character). However, the tadpole of *Cryptophyllobates* resembles larvae of *Epipedobates* (although not all) and especially *Phyllobates* more (although probably characterised by limited synapomorphies only); further, *Cryptophyllobates* lacks foot webbing (a derived character lacking in *Allobates*). *Allobates* spp. are often said to be slightly aposematic (e.g. VENCES et al. 2000) which is not the case in *Cryptophyllobates* [but neither in *A. zaparo* (SILVERSTONE, 1976)]. Moreover, due to its bright colour pattern, we suspect that the latter produces relatively potent skin toxins (in *Allobates* found in traces only), as do the „higher“ dendrobatids (e.g. DALY et al. 1978). But different to the genetic data (cf. CLOUGH & SUMMERS 2000;

Vences et al. 2000), behavioural and tadpole data do not cogently support the position of *C. azureiventris* as basal to the *Epipedobates* lineage. From these data it seems more likely that *Cryptophyllobates* is related to the more derived trans-Andean *Phyllobates* lineage (although genetically still distant; Widmer et al. in press). This genus is characterised by the apomorphic presence of steroidal alkaloids of the batrachotoxin class (Myers et al. 1978). We lack information on the presence or absence of skin substances in *C. azureiventris* (currently no data are available; J.W. Daly in litt. 16.08.2000). But, despite the limited usability of alkaloid profiles in dendrobatid systematics (Myers et al. 1996), an analysis may help to enlighten the phylogenetic position of *Cryptophyllobates* towards the other relevant genera.

Acknowledgements

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Summary

A new genus of dendrobatid frog is erected for the species originally described as *Phyllobates azureiventris* Kneller & Henle, 1985. In addition, traits of its reproductive behaviour and its tadpole are described, distinguishing it from other genera. The new genus most closely resembles *Epipedobates* sensu lato and *Phyllobates* sensu stricto. However, its phylogenetic position remains unclear.

Resumen

Se designa un nuevo género de dendrobátido para la especie originalmente descrita como *Phyllobates azureiventris* Kneller & Henle, 1985. Además, se describen rasgos de su comportamiento reproductor y de la larva, que lo distinguen de otros géneros. El nuevo género se parece a *Epipedobates* sensu lato y a *Phyllobates* sensu stricto. No obstante, su posición filogenética está aún sin aclarar.

Zusammenfassung

Die neotropischen Frösche der Familie Dendrobatidae zeigen eine Vielzahl an Merkmalen, die sie als monophyletische Gruppe kennzeichnen. Innerhalb der Familie lassen sich aber auch viele für die Gruppe plesiomorphe bzw. apomorphe Merkmale feststellen. Zu den zuerst genannten zählt etwa die kryptische graubraune Färbung einiger Arten, während apomorphe Arten leuchtende aposematiche Farben aufweisen, die gewöhnlich mit dem Vorhandensein von giftigen Hautalkaloiden einhergehen. Aus diesem Grund werden auch manche Arten von der indigenen Bevölkerung genutzt, was ihnen den deutschen Namen Pfeilgiftfrösche eingebracht hat. Allen Arten gemein ist, nebst typischen morphologischen Merkmalen, ein komplexes Territorial-, Fortpflanzungs- und Brutpflegeverhalten, das innerhalb der Familie wiederum als ursprünglich und abgeleitet eingestuft werden kann. Verschiedene, in jüngerer Zeit unabhängig durchgeführte DNA-Sequenzierungen bestätigen die stammesgeschichtliche Einheit der Familie. Gegensätzlich sieht es dagegen bei der phylogenetischen Stellung der einzelnen Gattungen sowie der Validität der ver-

schiedenen Gattungsnamen aus. Derzeit werden folgende acht Taxa anerkannt, die durch morphologische und vor allem ethologische Merkmale definiert werden: *Dendrobates* (Synonyme: *Dendromedusa, Hylaplesia, Minyobates*), *Epipedobates* (Synonym: *Phobobates*) und *Phyllobates* für die stark abgeleiteten aposematisch-toxischen Arten sowie *Allobates, Aromobates, Colostethus* (Synonyme: *Hyloxalus, Phyllodromus, Prostherapis*), *Mannophryne* und *Nephelobates* für die restlichen Arten. Während bei der Phylogenie dieser basalen Dendrobatiden noch großer Forschungsbedarf besteht, gelten die Beziehungen von *Dendrobates* und *Phyllobates,* als höchst entwickelte Gruppen, mit *Epipedobates* als etwas primitivere Schwestergruppe vor allem auch genetisch als sehr gesichert.

Eine Art, die ursprünglich als *Phyllobates azureiventris* KNELLER & HENLE, 1985 vom Osthang der peruanischen Anden beschrieben wurde, fällt genetisch aus dem Rahmen. Sie weicht von der ansonsten rein trans-andinen Gattung *Phyllobates* (deren fünf Arten einen eigenen Kladus bilden) ab. Sie ist am ehesten als Teil eines Kladus, der hauptsächlich aus *Epipedobates* besteht, aber separat (basal) von *Epipedobates* selbst, zu bewerten. Merkmale des Fortpflanzungsverhaltens (speziell das Fehlen des Kopfamplexus) sowie die Morphologie der Kaulquappen sprechen jedoch eindeutig dafür, daß *azureiventris* nicht zu *Epipedobates* gehört. Wir stellen deshalb *azureiventris* in eine eigene Gattung, die hier beschrieben wird. Ihre genaue phylogenetische Stellung bleibt jedoch unklar.

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