

# On the systematics of the harlequin frogs (Amphibia: Bufonidae: *Atelopus*) from Amazonia. II: Redescription of *Atelopus pulcher* (BOULENGER, 1882) from the eastern Andean versant in Peru

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## Zusammenfassung

Zur Systematik der Harlekinfrösche (Amphibia: Bufonidae: *Atelopus*) aus Amazonien. II: Wiederbeschreibung von *Atelopus pulcher* (BOULENGER, 1882) vom östlichen Andenabhang in Peru.

Die Systematik der neotropischen Bufoniden-Gattung *Atelopus* ist kompliziert. Die Arten sind zum einen sehr merkmalsarm und können sich daher sehr ähnlich sehen; zugleich kann innerhalb mancher Arten die Merkmalsausprägung auch sehr variabel sein. *Atelopus spumarius* umschließt einen Artenkomplex, der im Amazonas-Becken sowie am Ost-Abhang der Anden und in der Guyana-Region vorkommt. In Peru können neben *A. spumarius* sensu stricto mindestens zwei weitere Arten unterschieden werden. Sie unterscheiden sich in der Lebendfärbung, Zeichnung, Adult-Größe, Hauttextur, Larvalmorphologie und im innerartlichen Kommunikationsverhalten (Winken mit dem Vorderfuß, Rufe). In dieser Arbeit wird *A. pulcher* vom östlichen Anden-Abhang (Departamentos Loreto und San Martín) aus der Synonymie von *A. spumarius* herausgenommen. Es werden gepulste Rufe sowie die Larve von *A. pulcher*, deren oberer Hornschnabel kürzer ist als der untere, beschrieben. Zudem wird ein alphataxonomischer Überblick über die Gattung *Atelopus* in Amazonien sowie den angrenzenden Gebieten gegeben.

Schlagwörter: Amphibia: Bufonidae: *Atelopus pulcher* bona sp.; *A. spumarius*-Artenkomplex, Alphataxonomie, Bioakustik, Larve, Peru.

## Abstract

Systematics of the Neotropical bufonid genus *Atelopus* are complicated. On the one hand, species are poor in characters and hence similar to each other; on the other hand, within some species characters are very variable. *Atelopus spumarius* comprises a complex of species, distributed in the Amazon basin as well as on the eastern versant of the Andes and in the Guianan region. In Peru, besides *A. spumarius* sensu stricto, at least two species can be distinguished. They differ in life colour, pattern, adult size, skin texture, larval morphology and intraspecific communication behaviour (forefoot waving, calls). In this paper, *A. pulcher* from the eastern Andean versant (Departamentos Loreto and San Martín) is removed from the synonymy of *A. spumarius*. Pulsed calls and the larva, which is characterised by having the upper beak shorter than the lower, of *A. pulcher* are described. In addition, an alphataxonomic overview of the genus *Atelopus* in Amazonia and adjacent areas is provided.

Key words: Amphibia: Bufonidae: *Atelopus pulcher* bona sp.; *A. spumarius* species complex, alphataxonomy, bioacoustics, larva, Peru.

## 1 Introduction

According to recent data, the wide-spread Amazonian *Atelopus spumarius* COPE, 1871 comprises a complex of species. Allocation of populations has been difficult and confusion about the use of scientific names has occurred. Revisionary action is needed (cf. COCROFT et al. 1990, LÖTTERS 1996). Unfortunately, many *Atelopus* populations are poor in external characters and we know that both interspecific variation can be limited and intraspecific variation can be considerable. As a result, alphataxonomic and phylogenetic relationships remain difficult. COLOMA et al. (2000) suggested to study morphological, osteological, behavioural and bioacoustical data as well as adult

Species/Art	Range/Verbreitung	Comment(s)/Kommentar(e)
<i>A. andinus</i>	Pre-cordilleras, E Peru (Deptos. San Martín and Loreto)	Recently elevated to the species level by LÖTTERS & DE LA RIVA (1998), originally described as a subspecies of <i>A. spumarius</i>
<i>A. boulengeri</i>	Andes and pre-cordilleras of SE Ecuador (Provs. Morona-Santiago and Loja), 900-2000 m	Thoroughly redescribed by PETERS (1973), placing <i>A. bicolor</i> as junior synonym
<i>A. erythropus</i>	Andes of SE Peru (Cordillera Carabaya, Depto. Puno), ca. 1800 m	Status of the single known individual uncertain (cf. LÖTTERS & DE LA RIVA 1998)
<i>A. flavescens</i>	Coastal French Guiana and adjacent Brazil (Estado Amapá), < 100 m	Type species of <i>Atelopis</i> ; thoroughly redescribed by LESCURE (1973) except intraspecific variation; possible junior synonyms are <i>A. spumarius barbotini</i> <sup>1</sup> (cf. KOK 2000) and <i>A. vermiculatus</i> (cf. LESCURE 1976); tadpole described by LESCURE (1981 b)
<i>A. franciscus</i>	Coastal French Guiana, < 50 m	Thoroughly described by LESCURE (1973), but because intraspecific variation in <i>A. flavescens</i> requires further studies, the status of the similar <i>A. franciscus</i> from the same general area needs to be reanalysed (R. BOISTEL, pers. comm.)
<i>A. hahlihelos</i>	Cordillera de Cutucú, E Ecuador (Prov. Morona-Santiago), ca. 1900 m	Thoroughly described by PETERS (1973)
<i>A. minutulus</i>	E versant of the Cordillera Oriental, Colombia (Depto. Meta), ca. 1500 m	Thoroughly described by RUÍZ-CARRANZA et al. (1988)
<i>A. nepiozomus</i>	Andes of SE Ecuador (Prov. Morona-Santiago), > 2000 m	Thoroughly described by PETERS (1973)
<i>A. palmatus</i>	E Andean versant of Ecuador (Provs. Napo and Pastaza), ca. 1000-1740 m	Thoroughly redescribed by PETERS (1973), but COLOMA (1997: 56) was unable to distinguish it from <i>A. planispina</i> , which probably is a senior synonym
<i>A. planispina</i>	Cordillera de Cutucú and Volcán Sumaco, E Ecuador (Provs. Morona-Santiago and Napo), ca. 500-3900 m	Thoroughly redescribed by PETERS (1973); see comment under <i>A. palmatus</i>
<i>A. pulcher</i>	E Andean versant, Peru (Depto. Loreto) and maybe ranging into adjacent Ecuador, ca. 600-900 m	See this paper

<i>A. seminiferus</i>	Upper Amazon basin, E Peru (Deptos. San Martín and/or Loreto)	The original description is poor; GRAY & CANNATELLA (1985) provided data on the holotype
<i>A. reticulatus</i>	Cordillera Azul, E Peru (Depto. Ucayali), ca. 1600 m	Thoroughly described by LÖTTERS et al. (2002)
<i>A. siranus</i>	Cordillera de Sira, E Peru (Depto. Huánuco)	Thoroughly described by LÖTTERS & HENZL (2000)
<i>A. spumarius</i> sensu lato	Almost entire Amazon basin into the Guianan region, < 100 m	See this paper; including <i>A. spumarius hoogmoedi</i> <sup>1</sup> ; two descriptions of different tadpoles are available (DUELLMAN & LYNCH 1969, GASCON 1989)
<i>A. spumarius</i> sensu stricto	Upper Amazon basin, E Peru (Depto. Loreto), probably ranging into adjacent Brazil, Colombia and Ecuador, < 50 m	See this paper
<i>A. tricolor</i>	E Andean versant of SE Peru (Depto. Cuzco) and adjacent NE Bolivia (Deptos. La Paz and Cochabamba), ca. 1250-2500 m	Thoroughly redescribed by LÖTTERS & DE LA RIVA (1998), placing <i>A. rugulosus</i> and <i>A. willimani</i> as junior synonyms; tadpole described by LAVILLA et al. (1997)

Table. 1. List of species of *Atelopus* currently recognized from the eastern versant of the Andes, the Amazon basin and the Guianan region.

Auflistung der derzeit anerkannten *Atelopus*-Arten vom Osthang der Anden, dem Amazonas-Becken sowie der Guyana-Region.

<sup>1</sup> In a recent publication, LESCURE & MARTY (2000) refer to *A. spumarius barbotini* and *A. spumarius hoogmoedi* as valid names without discussion.

life colour pattern and tadpole characters to assess *Atelopus* systematics. In a recent contribution, LÖTTERS et al. (2002) supported the former authors and described a new species out of the *A. spumarius* complex from Amazonian Peru: *Atelopus reticulatus* LÖTTERS, HAAS, SCHICK & BÖHME, 2002. It is, besides morphological aspects, characterised by its specific communication behaviour, i.e. forefoot waving and pure tone calls. Ethological observations were made in captivity. Captive data on behaviour and reproduction also are available for a second Peruvian form out of the *A. spumarius* complex (cf. HAAS 1995). It originates from a site close to the type locality of *A. pulcher* (BOULENGER, 1882), currently a junior synonym of *A. spumarius* (e.g. FROST 1985). Specimens examined coincide with the type material of *A. pulcher* rather than with that of *A. spumarius*. The purpose of this paper is (i) to briefly review the alphataxonomy of the genus *Atelopus* in the Amazon basin and adjacent areas, especially the *A. spumarius* complex, and (ii) to redescribe *A. pulcher* including a description of vocalisations and of its tadpole.

## 2 Brief review of *Atelopus* alphataxonomy in the Amazon basin and adjacent areas

Table 1 lists all species currently recognized (including those, treated in this paper). The known geographic ranges of Peruvian species are shown in Figure 1. The taxonomic status of the following taxa appear to be sufficiently cleared: *Atelopus andinus* RIVERO, 1968; *A. boulengeri* PERRACA, 1904; *A. halihelos* PETERS, 1973; *A. minutulus* RUÍZ-CARRANZA & HERNÁNDEZ-CAMACHO & ARDILA, 1988; *A. nepiozomus* PETERS, 1973; *A. planispina* JIMÉNEZ DE LA ESPADA, 1875; *A. reticulatus*; *A. siranus* LÖTTERS & HENZL, 2000; *A. tricolor* BOULENGER, 1902. *Atelopus erythropus* BOULENGER, 1903 and *A. seminiferus* COPE, 1874 are not comprehensively described in comparison with modern standards (cf. COLOMA et al. 2000) but seem to be distinguishable species. The taxonomic status of *A. palmatus* ANDERSSON, 1945 remains to be clarified. *Atelopus flavescens* DUMÉRIL & BIBRON, 1841 and *A. franciscus* LESCURE, 1973 “1972” are relatively well defined but intraspecific variation in the former needs to be enlightened. KOK (2000) provided evidence that *A. flavescens* is a variable taxon. As a result, at present, validity of *A. franciscus* (as well as probably of the current junior synonym of *A. flavescens*, *A. vermiculatus* McDIARMID, 1973) remains to be confirmed (R. BOISTEL, pers. comm.). Three names listed in Table 1 have not been mentioned so far: *Atelopus pulcher*; *A. spumarius* sensu lato; *A. spumarius* sensu stricto. In the current context, they deserve detailed discussion.

*Atelopus spumarius* was originally described from the upper Amazon basin in Peru (Fig. 1). Several authors treated it as identical to the later-described *A. pulcher*, supposed to originate from a locality about 600 km southwest and more close to the Andean massif (Fig. 1). However, confusion occurred, because the original material of *A. spumarius* is lost (e.g. RIVERO 1968, PETERS 1973, FROST 1985). LESCURE (1981 a) designated a neotype for *A. spumarius*. Accordingly, *A. pulcher* was considered a junior synonym of *A. spumarius*. The latter, LESCURE (e.g. 1981 a) suggested to be a wide-spread species ranging from the Andean foothills of Colombia, Ecuador and Peru over the Amazon basin into the Guianan region (cf. FROST 1985). Two subspecies from the north-eastern portion of the range were named: *Atelopus spumarius barbotini* LESCURE, 1981 which has recently been shown to be more related to (or probably conspecific with) *A. flavescens* (KOK 2000); *Atelopus spumarius hoogmoedi* LESCURE 1974 “1973” (Fig. 2) which was synonymised with the nominotypical form by LESCURE & GASC (1986).

It is our opinion and that of other authors that *A. spumarius* sensu LESCURE & GASC (1986) consists of several species (cf. LÖTTERS 1996). COCROFT et al. (1990) provided bioacoustic evidence for a complex of species. GASCON (1989) described an *Atelopus* tadpole from the Manaus region which is strikingly different from an Ecuadorian larva assigned to *A. spumarius* by DUELLMAN & LYNCH (1969). The population studied by GASCON (1989), he assigned to *A. pulcher* and thus revalidated this name. However, according to LÖTTERS (1996), the validity of *A. pulcher* is not warranted. Allocations of tadpoles to either *A. spumarius* and *A. pulcher* have to be treated with care because adults have not been compared with type specimens or toptotypical material of both nominal species (see description of tadpole below). For a comprehensive revision of the *A. spumarius* complex, additional material and data are necessary, especially from areas currently appearing as collection gaps.

Our preliminary results suggest that *A. spumarius* sensu stricto is a relatively small species with snout-vent length  $25.2 \pm 1.94$  mm (range 23.0-29.7 mm) in six adult females (see Appendix for specimens examined) and of about 19.3 mm in adult males (cf. ASQUITH & ALTIG 1987: 32), small warts behind the eye, greenish yellow to yellow

dorsolateral bands, with reticulation or incorporated annuli, on a dark brown to black ground as well as partly reddish venter in life, soles and palms (for neotype illustration see LÖTTERS et al. 2002: Fig. 1; for illustration of living specimen see RODRÍGUEZ & DUELLMAN 1994: Plate 1). Collections of specimens are very limited. At present, *A. spumarius* sensu stricto seems to be restricted to the upper Amazon basin of Peru (Fig. 1) and apparently of adjacent Brazil and Colombia (e.g. LESCURE 1981 a, RODRÍGUEZ & DUELLMAN 1994) as well as probably of adjacent Ecuador (L.A. COLOMA, pers. comm.).

There are also populations in which individuals have larger adult size, smooth skin, more robust bodies and life colour pattern different to *A. spumarius* sensu stricto (cf. LESCURE 1981 a; Figs. 2-3). According to our current knowledge, these populations fall into two geographic groups, one from the central Amazon basin (probably, in part, in sympatry with *A. spumarius* sensu stricto) plus the Guianan region and another one from the lower eastern Andean versant of Peru and Ecuador. The former, we suggest to call *A. spumarius* sensu lato. Ventral sides of most populations included are yellowish or pinkish (versus partly reddish venter in life). The soles and palms are rarely red. Several species may be involved. One may be called *A. hoogmoedi* (SVL of female holotype 34.9 mm; Fig. 2), while others might have to be named as new to science. The tadpole described by GASCON (1989) and part of the vocalisations discussed by LESCURE (1981 a) and COCROFT et al. (1990) will have to be considered within this context.

Populations of the second mentioned group of individuals from the lower eastern Andean versant differ from *A. spumarius* sensu lato in pattern and/or colour in life (see below). As mentioned above, they are different from *A. spumarius* sensu stricto in adult

Fig. 1. Map of Peru with major river systems and areas above 3000 m above sea level showing known distributions of species of *Atelopus* from the Amazon basin and the eastern Andean versant. Legend: 1 = *Atelopus andinus*; 2 = *A. erythropus*; 3 = *A. seminiferus*; 4 = *A. siranus*; 5 = *A. tricolor*; 6 = *A. spumarius* sensu stricto; 7 = *A. pulcher*; 8 = *A. reticulatus*. Localities are as listed in the Appendix and correspond to unpublished data in the case of *A. spumarius* sensu stricto. Localities given by RIVERO (1968) and allocable to *A. pulcher* (see text) are not considered. Type localities are surrounded by squares.

Karte von Peru mit den Haupt-Flusssystemen und Bereichen über 3000 m NN sowie den bekannten Verbreitungen der *Atelopus*-Arten aus Amazonien und vom östlichen Andenabhang. Legende: 1 = *Atelopus andinus*; 2 = *A. erythropus*; 3 = *A. seminiferus*; 4 = *A. siranus*; 5 = *A. tricolor*; 6 = *A. spumarius* sensu stricto; 7 = *A. pulcher*; 8 = *A. reticulatus*. Fundorte sind wie im Appendix aufgeführt und, im Falle von *A. spumarius* sensu stricto, unpubliziert. Fundorte, die RIVERO (1968) angibt und *A. pulcher* zugeschrieben werden könnten (s. Text) werden nicht berücksichtigt. Typuslokalitäten sind mit Quadraten umrandet.

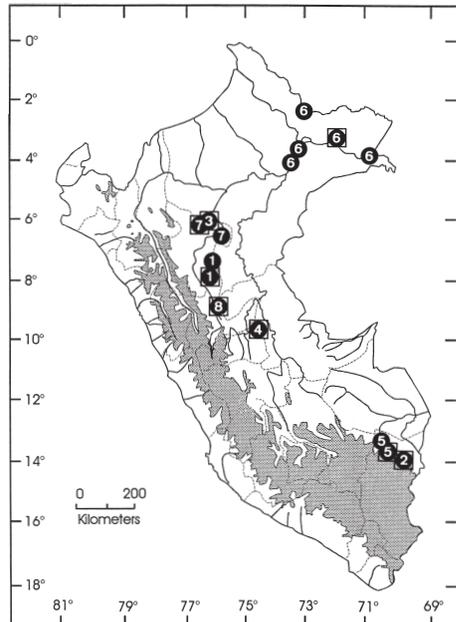




Fig. 2. Dorsal and ventral views of female holotype of *Atelopus spumarius hoogmoedi* (MNHNP A 522). Photo J. KÖHLER.

Dorsal- und Ventralansicht vom Holotypus von *Atelopus spumarius hoogmoedi*, Weibchen (MNHNP A 522). Foto J. KÖHLER.

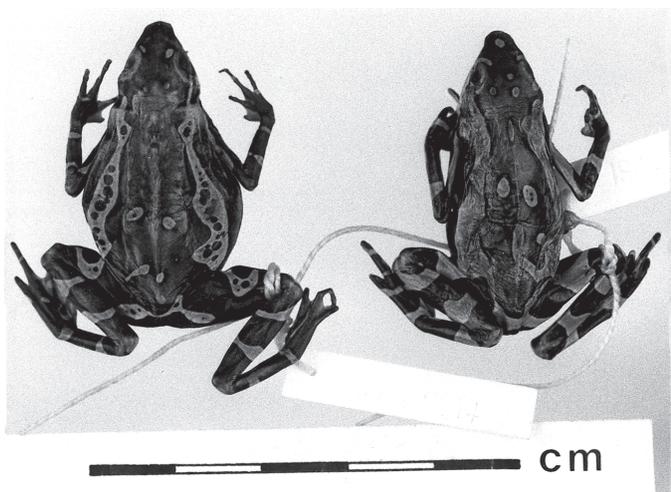


Fig. 3. Dorsal- and ventral views of two female types of *Atelopus pulcher*, with lectotype left (BM 1947.2.1480, 1947.2.1482). Photo J. KÖHLER.

Dorsal- und Ventralansicht von zwei Typen von *Atelopus pulcher* (Weibchen) mit dem Lectotypus links (BM 1947.2.1480, 1947.2.1482). Foto J. KÖHLER.

size and skin texture (cf. RIVERO 1968, PETERS 1973, LESCURE 1981 a). In our opinion they represent a distinct species. Comparisons with type specimens of *A. pulcher* (Fig. 3), which are supposed to originate from the Andean foothills of Peru (RIVERO 1968: 19; see Fig. 1), revealed that this name is applicable to those populations. Due to the lack of information on life history, tadpole morphology etc. for the many populations, we do not know how many species actually are involved and therefore use for the revalidation of *A. pulcher* only part of the original material (BM 1947.2.1480, 1947.2.1482) as well as specimens from a nearby Peruvian locality (KU 211676-683, 212530, ZFMK 48573, 50680-685, 76243-244) (cf. Fig. 1). To avoid further confusion, we designate BM 1947.2.1480 as a lectotype out of the five syntypes of *A. pulcher*. We are able to add reproductive data as well as descriptions of vocalisations and tadpoles, all obtained under laboratory conditions (based on ZFMK 76243-245; cf. HAAS 1995).

For a better understanding of the *A. spumarius* complex, material from additional localities should be considered, accompanied by life history, tadpole data etc. Moreover, information on osteology and DNA sequencing may help to enlighten the complex, too. Alphataxonomy shall focus on (i) the status of Ecuadorian and Peruvian populations similar to *A. pulcher*, (ii) a formal redescription of *A. spumarius* sensu stricto along with (iii) an analysis of the relationships of both *A. pulcher* and *A. spumarius* sensu stricto towards *A. spumarius* sensu lato.

### 3 Material and Methods

Material examined, as listed in the Appendix, is harboured at AMNH (American Museum of Natural History, New York), BM (British Museum, London), CBF (Colección Boliviana de Fauna, La Paz), KU (The University of Kansas, Natural History Museum, Lawrence), ICN (Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Santafé de Bogotá), MNHNP (Muséum

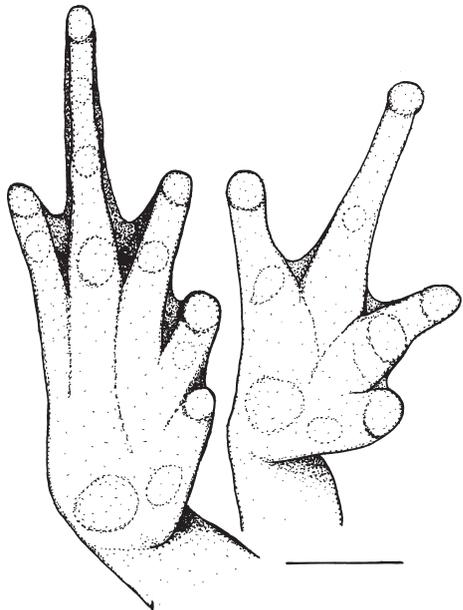


Fig. 4. Sole and palm of male *Atelopus pulcher* from the vicinity of Tarapoto (ZFMK 50682). Line equals 2.0 mm.

Fuß- und Handunterseite von einem *Atelopus pulcher* Männchen aus der Umgebung von Tarapoto (ZFMK 50682). Die Linie entspricht 2,0 mm.

national d'Histoire Naturelle, Paris), NHMW (Naturhistorisches Museum Wien) and ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn).

Description scheme for adults follows LÖTTERS et al. (2002). We describe the webbing formula in the manner of SAVAGE & HEYER (1969) as modified by MYERS & DUELLMAN (1982) and SAVAGE & HEYER (1997). Sex determination of adults was by external characters used by previous authors (e.g. PETERS 1973). Description scheme for tadpoles follows LÖTTERS (2001). Terminology of larval features is as proposed by ALTIG & JOHNSTON (1989); developmental stages are those of GOSNER (1960). Morphometric data to the nearest 0.1 mm were obtained by measuring both adult specimens and tadpoles with dial callipers, when necessary under a dissection microscope, by the senior author. Definitions of measurements for adults follow GRAY & CANNATELLA (1985) and COLOMA (1997); these are: SVL (snout-vent length), HDWD (head width), HLSQ (head length from the squamosal), EYDM (eye diameter), ITNA (internarial distance), EYNO (eye to nostril distance), SW (sacrum width at widest), TIBL (tibia length), FOOT (foot length), HAND (hand length), THBL (thumb length).

Vocalisations were recorded in captivity using a Sony WM D6C walkman and a Sony ECM 957 microphone. For analysis, Avisoft, SASLab Pro (Berlin), was used. To exclude presumed echo effects in pulsed calls, signals subsequent to the first pulse of a call with an amplitude < 40 mV were not considered. Captive conditions were described by HAAS (1995).

#### 4 Systematics

*Atelopus pulcher* (BOULENGER, 1882)

(Figs. 3-10)

*Phryniscus pulcher* BOULENGER, 1882: 154. Lectotype designated herein: BM 1947.2.14.80 (formerly BM 1867.6.13.19); paralectotypes: BM 1947.2.14.81-83 (formerly BM 1867.6.13.20-22), USNM (United States National Museum, Washington) 193574 (formerly BM 1867.6.13.23), from "Chyavetas. E. Peru".

*Atelopus pulcher* – NIEDEN 1926: 80; RIVERO 1963: 107.

*Atelopus pulcher pulcher* – PETERS 1973: 41 (partim?); LESCURE 1974 "1973": 997.

*Atelopus spumarius* (non COPE, 1871) – RIVERO 1968: 19 (partim); LESCURE 1981 a: 894 (partim); HARDING 1983: 58 (partim); FROST 1985: 33 (partim); RODRÍGUEZ et al. 1993: 6 (partim); LÖTTERS 1996: 47 (partim).

*Atelopus spumarius spumarius* (non COPE, 1871) – HAAS 1995: 2.

*Atelopus spumarius pulcher* – HENLE 1992: 96.

Lectotype: BM 1947.2.14.80, an adult female from Chyavetas, eastern Peru, which is considered to be a misspelling for Chayahuitas (ca. 5°50'S, 76°10'W), Departamento Loreto, Peru (cf. RIVERO 1968: 19); leg. Mr. HIGGINS.

Paralectotypes: BM 1947.2.14.81-83, USNM 193574, same locality and collection data as for lectotype.

Diagnosis: A medium-sized to large *Atelopus* (SVL of seven adult females 32.0-35.1 mm and 13 adult males 25.2-29.3 mm) that can be distinguished from all other known species of the genus by the following combination of characters: (1) body slender (SW/SVL 0.23-0.34; n = 20), snout acuminate with tip gently rounded to slightly pointed;

(2) neural spines externally not or weakly visible; (3) hind limbs long, tibiotarsal articulation reaching at least to posterior corner of eye when leg adpressed forward along body (TIBL/SVL 0.43-0.49;  $n = 20$ ); (4) foot shorter than tibia (FOOT/TIBL 0.76-0.95;  $n = 20$ ); (5) tympanic membrane absent; (6) warts, spiculae or coni completely absent; (7) foot webbing formula I0 to I- — 0 to I-II0 to I- — 1 to 2III0 to I+ — 2- to 2+IV2+ to 3+ — 1 to 2V; (8) thumb short (THBL/HAND 0.37-0.44;  $n = 20$ ); (9) plantar and palmar surfaces almost smooth, with ill-defined subarticular tubercles on some phalanges; (10) in preservative and in life, dorsal body uniform brownish black with green dorsolateral band and irregular dorsal spotting or marks and similar pattern on limbs; ventral sides in life entirely reddish in females, cream with reddish postventral area in males (usually with brownish black markings in both sexes); sole and palm in life red (reddish pink or cream in preservative).

*Atelopus pulcher* is most similar to *A. spumarius* sensu lato. They can usually be distinguished by dorsal pattern (cf. Figs. 2-3; LESCURE 1981 a: Figs. 4-6) and colour in life (above usually orange, yellow or tan versus green in *A. pulcher* and below yellowish or pinkish in most *A. spumarius* sensu lato versus red); “morph C” of *A. spumarius hoogmoedi* (= here included in *A. spumarius* sensu lato) from French Guiana (cf. LESCURE 1981 a: 906) has a pattern similar to that of *A. pulcher* but is in life dorsally and ventrally yellowish versus above green and below red; green and red rarely occurs in *A. spumarius* sensu lato, either, but the pattern is different to *A. pulcher* (unpubl. observ.). Also, *A. spumarius* sensu stricto has similar colours (i.e. above greenish yellow to yellow and below red) but is smaller than *A. pulcher* (adult female SVL is  $25.2 \pm 1.94$  mm,  $n = 6$ , versus  $34.1 \pm 1.12$ ,  $n = 7$ , in *A. pulcher*) and possesses small warts behind the eye (absent in *A. pulcher*). Other species with more or less similar pattern and reddish venter (in part) and/or sole and palm are *A. reticulatus*, *A. siranus* and *A. tricolor* (including its junior synonyms *A. rugulosus* NOBLE, 1921 and *A. willimani* DONOSO-BARROS, 1969) — all known from the eastern versant of the Andes or outlying serranias in Peru. As adults, these three species are all smaller than *A. pulcher* (cf. LÖTTERS & HENZL 2000, LÖTTERS et al. 2002) and possess warty skin (versus smooth skin in *A. pulcher*). *Atelopus siranus* and *A. tricolor* lack green colour in life (present in *A. pulcher*), whereas *A. reticulatus* has yellowish green reticulation (versus green dorsolateral bands in *A. pulcher*). *Atelopus andinus* from Amazonian Peru is similar in adult size and pattern to *A. pulcher* (although it is tan in preservative rather than green) but *A. andinus* possesses warty versus smooth skin (cf. RIVERO 1968, LÖTTERS & DE LA RIVA 1998). The only other *Atelopus* described from eastern Peru are *A. erythropus* and *A. seminiferus*. The single known (adult?) specimen of the former is smaller than adult *A. pulcher* (SVL of *A. erythropus* holotype 20.4 mm), lacks dorsal pattern (at least in preservative), has a more blunt snout and small warts between eye and forearm (cf. LÖTTERS & DE LA RIVA 1998). Adult *A. seminiferus* are considerably larger than *A. pulcher* (SVL of *A. seminiferus* holotype 40.0 mm; GRAY & CANNATELLA 1985). In addition, specimens tentatively referred to *A. seminiferus* and examined by us (see Appendix) have tubercular skin and are overall dark brown to black. *Atelopus boulengeri*, *A. halihelos* and *A. nepiozomus* from Andean Ecuador differ from *A. pulcher* in life colour and pattern (*A. boulengeri* is brown with yellow sides and venter; *A. halihelos* is dorsally light brown, scattered with irregular dark brown spots and ventrally whitish; *A. halihelos* is above dark olive with brown spots or marbling and below orange and yellow); moreover, *A. boulengeri* (including its junior synonym *A. bicolor* NOBLE, 1921) is larger than *A. pulcher* (SVL of *A. boulengeri* > 40.0 mm) and *A. halihelos* and *A. nepiozomus* have dorsal and lateral warts (cf. PETERS 1973). *Atelopus*



Fig. 5. *Atelopus pulcher* from the vicinity of Tarapoto in amplexus (ZFMK 76243-244). Photo: W. HAAS.

*Atelopus pulcher* aus der Umgebung von Tarapoto im Amplexus (ZFMK 76243-244). Foto: W. HAAS.

*palmatus* and *A. planispina* from Ecuador may resemble *A. pulcher* in life colour pattern (although still different.) But *A. palmatus* is smaller (adult female SVL < 31.5 mm) and *A. planispina* possesses well visible lateral warts (cf. PETERS 1973, LÖTTERS 1996). *Atelopus minutulus* from Colombia can be distinguished from *A. pulcher* by having dorsal reticulation and well visible lateral warts (cf. RUÍZ-CARRANZA et al. 1988). The Guianan forms *A. flavescens* (here provisionally included *A. spumarius barbotini* and *A. vermiculatus*) and *A. franciscus* differ from *A. pulcher* in life colour pattern (cf. LESCURE 1973) — both lack red ventral sides (they are pinkish to violet) and black and green dorsal sides (*A. flavescens* is uniform yellow to dark orange or yellowish, dark or black with orange to violet vermiculation; *A. franciscus* is uniform olive to dark brown).



Fig. 6. Ventral side of female (left) and male of *Atelopus pulcher* (same specimens as in Fig. 5). Photo: W. HAAS.

Ventralseite eines Weibchens (links) und Männchens von *Atelopus pulcher* (die selben Tiere wie in Fig. 5). Foto: W. HAAS.

Description of seven adult females and 13 adult males (if variation occurs, lectotype condition is given in parentheses): Body slender; neural spines externally not or weakly visible (weakly visible); head longer than broad; head length less than one third of SVL; snout acuminate with tip gently rounded to slightly pointed (gently rounded), dorsally depressed; in lateral aspect, upper jaw extending beyond lower;

	Females/Weibchen n = 7	Males/Männchen n = 13
SVL	34.07 ± 1.12 32.0-35.1	27.27 ± 1.07 25.2-29.3
SW	8.3 ± 0.66 7.6-8.9	6.53 ± 0.21 6.3-6.7
HDWD	9.1 ± 0.3 8.8-9.6	8.17 ± 0.52 7.4-9.2
HLSQ	9.66 ± 0.36 9.2-10.1	8.62 ± 0.43 8.1-9.5
EYDM	3.23 ± 0.1 3.1-3.3	2.9 ± 0.15 2.6-3.1
ITNA	2.7 ± 0.39 2.1-3.3	2.68 ± 0.15 2.5-2.9
EYNO	3.1 ± 0.24 2.7-3.3	2.6 ± 0.11 2.4-2.7
TIBL	15.47 ± 0.34 15.0-16.0	12.53 ± 0.54 11.9-13.8
FOOT	12.2 ± 2.6 11.9-12.4	10.6 ± 1.1 9.7-11.8
HAND	8.92 ± 0.41 8.4-9.4	7.12 ± 0.45 6.3-7.7
THBL	3.87 ± 0.2 3.6-4.1	3.12 ± 0.22 2.6-3.3
SW/SVL	0.24 ± 0.01 0.24-0.25	0.24 ± 0.01 0.23-0.25
HDWD/SVL	0.27 ± 0.01 0.26-0.28	0.30 ± 0.01 0.28-0.34
HDWD/HLSQ	0.95 ± 0.002 0.92-0.97	0.95 ± 0.04 0.88-0.99
HLSQ/SVL	0.28 ± 0.01 0.27-0.30	0.32 ± 0.01 0.30-0.34
TIBL/SVL	0.45 ± 0.02 0.44-0.48	0.46 ± 0.02 0.43-0.49
FOOT/TIBL	0.79 ± 0.03 0.76-0.81	0.85 ± 0.09 0.78-0.95
THBL/HAND	0.43 ± 0.03 0.39-0.49	0.44 ± 0.4 0.37-0.49

Table. 2. Measurements (in mm) and proportions of 20 specimens of *Atelopus pulcher*: mean ± standard deviation and range. Specimens examined are listed in the Appendix.

Maßangaben (in mm) und Proportionen von 20 Exemplaren von *Atelopus pulcher*: Mittelwert ± Standardabweichung und Spannweite. Die untersuchten Exemplare sind im Appendix aufgeführt.

nostril lateral, not visible from above; tongue about two to three times as long as wide, broadest anteriorly, free for half to two thirds of its length; canthus rostralis straight from nostril to tip of snout, slightly concave and longer from nostril to anterior corner of eye — most concave immediately anterior to eye; eye width larger than or equal in length to distance from nostril to anterior corner of eye (eye width in lectotype not measurable); loreal area barely concave; upper lip fleshy; immediate lateral postorbital area slightly convex, becoming straighter at temporal area; tympanic membrane absent; dorsal postorbital crest poorly developed. Tibia long, less than half SVL, tibiotarsal articulation extending to approximately posterior corner of eye or anterior to eye when hind limb adpressed forward along body (to approximately posterior corner of eye in lectotype); foot shorter than tibia; relative length of toes:  $I < II < III < IV < V$  ( $I < II < III < V < IV$  in lectotype); outer metatarsal tubercle not very prominent, inner metatarsal tubercle ill-defined, about half size of the outer tubercle; rest of sole smooth with ill-defined subarticular tubercles present at joints of phalanges of Toes II-V; foot webbing formula is  $I0$  to  $1^-$  —  $0$  to  $1-II0$  to  $1^-$  —  $1$  to  $2III0$  to  $1^+$  —  $2^-$  to  $2+IV2^+$  to  $3^+$  —  $1$  to  $2-V$  ( $II^-$  —  $0III^-$  —  $2III1^+$  —  $2+IV3^-$  —  $2V$  in lectotype). Forearm short, less than one third of SVL, proximally slightly wider than distally in males; relative length of fingers:  $I < II < IV < III$ ; palmar tubercle distinct, rounded; thenar tubercle smaller, less prominent and more ovoid; rest of palm smooth with ill-defined subarticular tubercles at joints of phalanges of Fingers II to IV; thumb relatively short, distance from tip to outer edge of palmar tubercle less than half hand length; keratinized nuptial pads present on thumbs in males. Skin of all dorsal surfaces of body including extremities completely smooth; skin on ventral surfaces, especially chest, belly and below cloacal region, slightly wrinkled.

In preservative, dorsal surfaces are completely brownish black, with a light to dark green (not evenly broad) dorsolateral band from behind the eye to groin, occasionally with small brownish black spots incorporated as in the lectotype (Fig. 3). Dorsum with irregular light to dark green spots or marks; limbs with light to dark green marbling, regular bands (as in the lectotype; Fig. 3) or irregular spots (occasionally with brownish black spots incorporated). Dorsal surfaces of hands and feet brownish black with irregular cream or light green markings at the outer portions; inner portions entirely cream, with small brownish black spots on Toe III and Finger II; Toes I-II and Finger I always entirely cream. Venter uniform reddish or cream (as in the lectotype) in females and entirely cream, occasionally with a reddish postventral area, in males, with (as in the lectotype; Fig. 3) or without brownish black spots and with (as in the lectotype; Fig. 3) or without transversal bands in the same colour; brownish area in cloacal region. Ventral surfaces of upper extremities cream, rest as dorsal sides. Sole and palm pink or cream (as in the lectotype), rarely with brownish black markings.

Colour in life was similar with reddish colours more bright and sole and palm are entirely red (Figs. 5-6). Green areas were paler peripherally. The iris was golden. For coloration of freshly metamorphosed specimens see below.

Measurements and proportions are provided in Table 2. Available measurements and proportions of female lectotype are: SVL 34.3; HDWD 8.9; HLSQ 9.2; ITNA 2.1; EYNO 2.7; TIBL 15.0; HAND 8.6; THBL 3.8; HDWD/SVL 0.26; HDWD/HLSQ 0.97; HLSQ/SVL 0.27; TIBL/SVL 0.44; THBL/HAND 0.44.

Sexual dimorphism is indicated by females being larger, without overlap with males in some morphometric characters (Table 2), and different ventral coloration. Females are entirely red, whereas only the postventral area is red in males; soles and palms are red in both sexes (Fig. 6). The function of ventral dichromatism in *A. pulcher* is unknown.

**Distribution:** We follow the proposition of RIVERO (1968: 19) that the type locality of *A. pulcher* as it is originally spelled (see above) is not known in Peru, but that likely it is a misspelling for “Chayahuitas ... near the margin of Río Puma [sic] (5°50'S, 76°10'W), and about 40 miles north of Balsapuerto”, Departamento Loreto. Presence of *A. pulcher* at Chayahuitas remains to be confirmed. Assuming its occurrence there and considering specimens from a nearby locality treated as conspecific in this paper, *A. pulcher* is distributed along the lower Andean versant in the upper Río Huallaga drainage, Departamentos San Martín and Loreto of Peru, at approximately 600-900 m above sea level (Fig. 1). There are populations resembling *A. pulcher* from the north-eastern Andean versant of Peru and adjacent Ecuador (cf. RIVERO 1968, PETERS 1973). In lack of additional material and detailed data, we cannot state about their taxonomic status and hence the exact geographic range of *A. pulcher* (see remarks below).

**Life history and vocalisation:** Three specimens, one female and two males, were kept in captivity for several months; the female and one male were preserved (ZFMK 76243-244). According to the observations made by WH, *A. pulcher* is a diurnal terrestrial species. COCROFT et al. (1990) described short calls for several species of the genus as calls with release function; this kind of vocalisation, in the same context, was occasionally given by captive *A. pulcher* males (no recordings available). In addition, they regularly produced another type of vocalisation, both when another *Atelopus* specimen could be seen or not. Forefoot waving, as known in other species of the genus including the similar *A. reticulatus* (LÖTTERS et al. 2002), was never observed. Vocalisations correspond to pulsed calls fide COCROFT et al. (1990). Five calls from one male, each consisting of a single note, recorded 25 July at 23°C were analysed (Fig. 7): mean note length was  $1.2 \pm 0.1$  s (range 1.1-1.3) with mean number of pulses per call  $35.4 \pm 9.2$  (range 25-47), i.e.  $28.8 \pm 5.5$  (range 22-35) pulses/s; dominant frequency was between 2034 Hz and 2824 Hz. Pulse structure and length was variable. In the five calls analysed, each the first and/or last pulse was prolonged (Fig. 8 bottom) with mean length  $24.5 \pm 5.6$  ms (range 18.5-34.7 ms,  $n = 7$ ), while the majority of pulses (Fig. 8 top) had mean length  $6.9 \pm 2.5$  ms (range 4.1-10.7,  $n = 10$ ).

Pulsed calls are known from numerous species of the genus and are currently interpreted to function in territorial behaviour and/or mate attraction (e.g. COCROFT et al. 1990). Among the species compared with *A. pulcher*, pulsed calls are known from *A. flavescens*, *A. franciscus*, *A. minutulus*, *A. reticulatus*, *A. tricolor* and populations referred to *A. spumarius* (LESCURE 1981 a, ASQUITH & ALTIG 1987, COCROFT 1990, LÖTTERS et al. 1999, 2002). COCROFT et al. (1990) suggested, vocalisations in the genus *Atelopus* are conservative. As a result, we found in part remarkable overlap among most the species mentioned concerning number of pulses per call, pulse/s and dominant frequency. However, note length varies considerably from longer or shorter to *A. pulcher*: *Atelopus flavescens* and *A. franciscus*  $> 1,3$  s; *A. minutulus*, *A. reticulatus* and *A. tricolor*  $< 0.5$  s (cf. LESCURE 1981 a, COCROFT et al. 1990, LÖTTERS et al. 1999, 2002). The populations referred to *A. spumarius* deserve detailed discussion. LESCURE (1981 a) described a pulsed call from Yubinetto, Peru, and ASQUITH & ALTIG (1987) from near Nauta, Peru (both localities are in the Departamento Loreto). In addition, pulsed calls were reported from localities in Brazil and French Guiana (LESCURE 1981 a, COCROFT et al. 1990). The calls from Peru are similar to each other. Although ASQUITH & ALTIG (1987) noted some discrepancies between them, we tentatively refer both to *A. spumarius* sensu stricto. Differences may be explained by intraspecific variation, higher temperature during recording in the vocalisation described by LESCURE (1981 a) and artificial conditions of ASQUITH & ALTIG (1987) who recorded a male in a transport

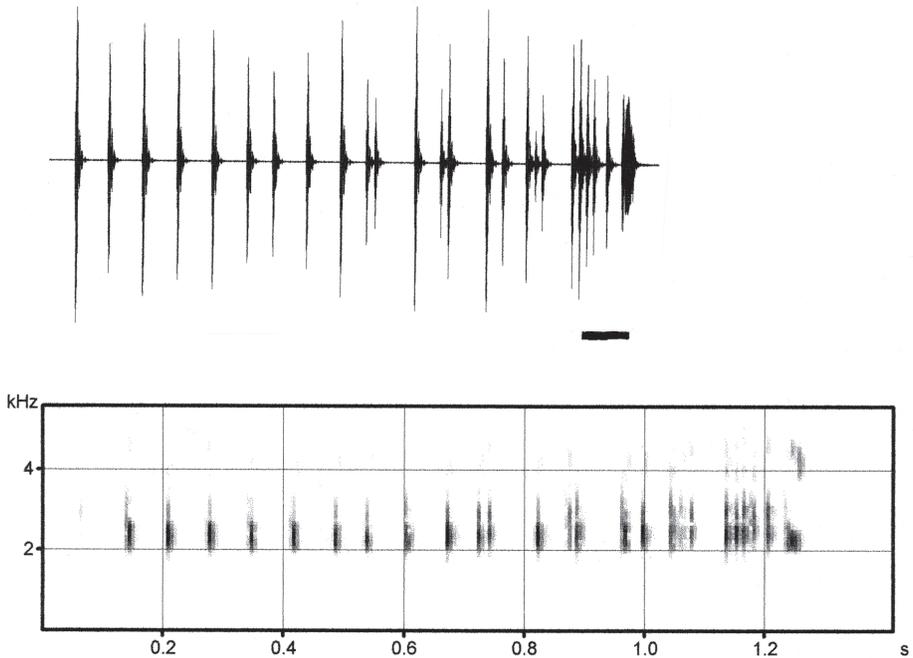


Fig. 7. Oscillogram and sound spectrogram of a pulsed call of *Atelopus pulcher* (temperature during recording: 23 °C; high-pass filter: 300 Hz). Time bar in oscillogram is 100 ms.

Oszillogramm und Klangspektrogramm eines gepulsten Rufes von *Atelopus pulcher* (Temperatur während der Aufnahme: 23 °C; Hochpassfilter: 300 Hz). Die Zeitmarke im Oszillogramm entspricht 100 ms.

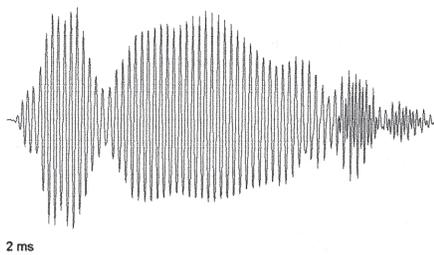
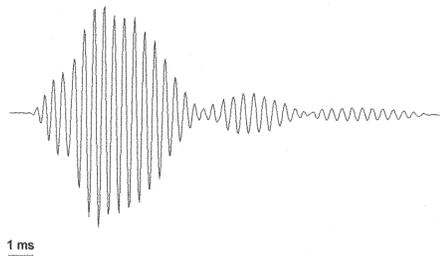


Fig. 8. Oscillograms of different pulsed calls of one male of *Atelopus pulcher* (temperature during recording: 23 °C; high-pass filter: 300 Hz).

Oszillogramme gepulster Rufe von einem Männchen von *Atelopus pulcher* (Temperatur während der Aufnahme: 23 °C; Hochpassfilter: 300 Hz).

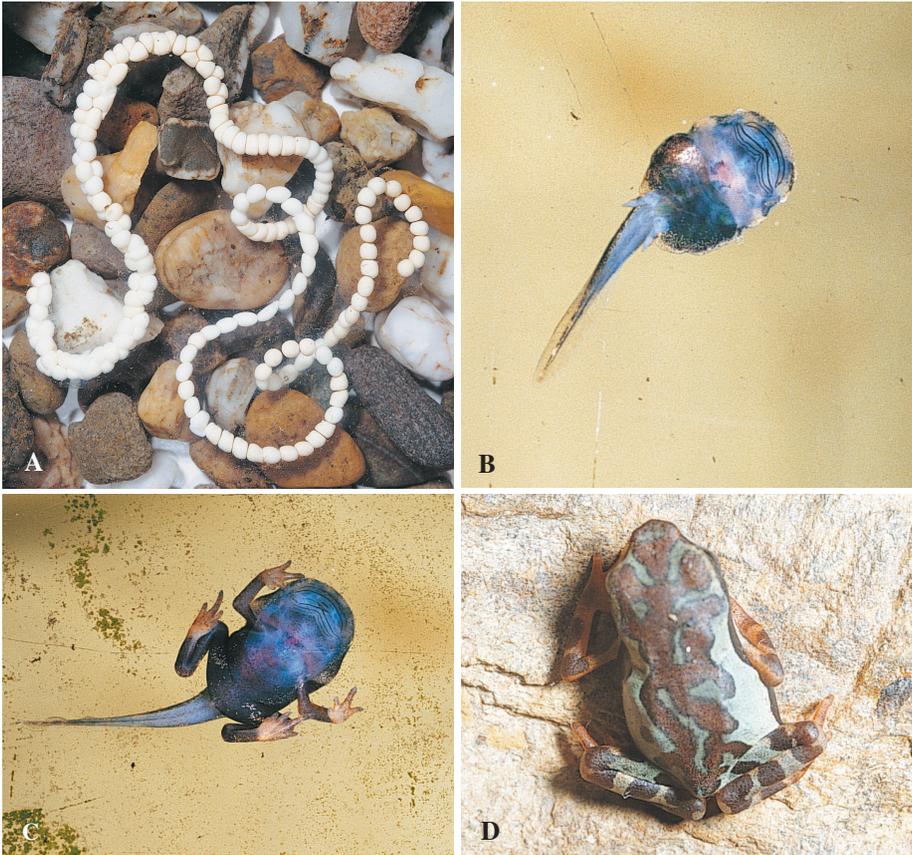


Fig. 9. Clutch (A), tadpoles (B-C) and recently metamorphosed individual (D) of *Atelopus pulcher*. Photo: W. HAAS.

Laich (A), Larven (B-C) und frisch metamorphosiertes Individuum (D) von *Atelopus pulcher*. Foto: W. HAAS.

bag. Following these authors, pulsed calls of *A. spumarius* sensu stricto are shorter (< 0.9 s) and have higher frequency range (> 3000 Hz) than those of *A. pulcher*. Brazilian and French Guianan populations of which pulsed calls are described, we refer to *A. spumarius* sensu lato. We can not see significant differences between pulsed calls of *A. pulcher* and those analysed from Mitaraca in French Guiana by LESCURE (1981 a). Pulsed calls described from 74 km east of Santarém, Brazil (Estado Pará), by COCROFT et al. (1990) show more pulses per call and per second (i.e. > 56 and > 39) than those of *A. pulcher*.

In August, the female and one male were found in axillary amplexus (Fig. 5). After two to three weeks, circa 600 unpigmented eggs were deposited in water. Eggs (ZFMK 76245), each circa 2.0-2.6 mm in diameter, were arranged in several strings. Arrangement of eggs was in a single chain or eggs were more clustered in a string-like fashion (cf. Fig. 9 A). Empty capsules or rami as observed in clutch of *A. subornatus* WERNER, 1899 by LYNCH (1986) were not observed. Larvae having total lengths of approxi-

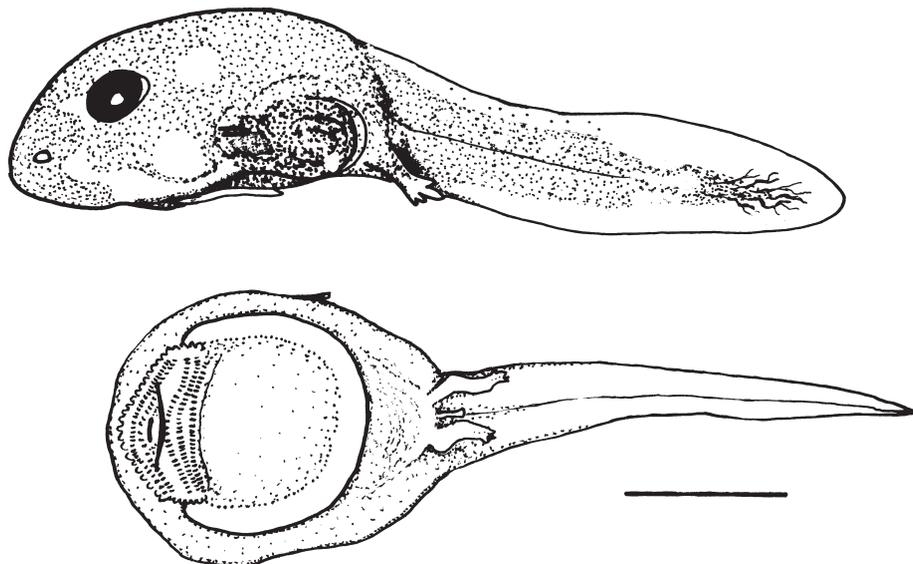


Fig. 10. Lateral and ventral views of captive-raised tadpole of *Atelopus pulcher* (out of ZFMK 76245) in Stage 35. Line equals 2.0 mm.

Lateral- und Ventralansicht einer in Gefangenschaft aufgezogenen Kaulquappe von *Atelopus pulcher* (aus ZFMK 76245) im Stadium 35. Die Linie entspricht 2,0 mm.

mately 4.0 mm hatched after six days and fed on algae (Fig. 9 B, C). At a temperature of 20-22 °C, metamorphosis was completed after about 58 days; froglets had SVLs of approximately 7.0 mm. The colour pattern resembled the adult colour pattern (Fig. 9 D). For additional information on reproduction and tadpole rearing see HAAS (1995).

**Tadpole:** Five larvae in different developmental stages have been preserved under ZFMK 76245: two in Stage 25 (4.1 and 4.9 mm total length), two in Stage 35 (9.7 and 10.9 mm total length), one in Stage 43 (14.5 mm total length).

The following description is based on an individual at Stage 35 (Fig. 10). Type IV tadpole of ORTON (1953), belonging to the gastromyzophorous ecomorphological guild as defined by ALTIG & JOHNSTON (1989). Total length 10.9 mm, body length 4.4 mm, body width 3.2 mm. Body elongately ovoid, flattened, about half as high as wide. Snout gently rounded in dorsal view and in profile; nostrils small, at about one-third the distance from eye to tip of snout, in lateral view below height of eye; eyes dorsal directed dorsolaterally, diameter 0.5 mm, interocular distance 0.9 mm. Spiracle sinistral, about two-thirds free, directed posterodorsally, originating at midpoint of body; diameter of opening about half the length of free tube; vent tube short, medial. Caudal musculature robust anteriorly, narrowing abruptly posterior to midlength of tail, terminating just anterior to end of rounded tail; dorsal fin highest at about two-thirds of tail; tail length about 60 % of total length; dorsal and ventral fin height ca. 0.9 mm at midlength of tail; dorsal fin beginning posterior to body, ventral fin beginning posterior to vent tube. Mouth ventral, surrounded by labia forming complete oral disc; complete row of marginal, blunt papillae anteriorly, no papillae

posteriorly; submarginal papillae present. Labial tooth row formula 2/3, rows complete, about equal in length; jaw sheaths serrate; upper beak narrow, about one third length of lower, U-shaped beak. Large belly sucker extending posteriorly from posterior labium for more than half the body length, forming a complete, round sucker without papillae.

In preservative, dorsum and sides of body uniform brown with regular whitish markings (on each side one spot of about the diameter of the eye dorsolaterally behind the eye and each one of about the same size lateral to this spot; flecking anterior to eye), edges of body translucent with numerous scattered brown spots; eyes black; hind limbs proximally brown, distally tan; caudal musculature brown with irregular whitish markings and reticulated pattern at the very end; both fins transparent with minute brown spots on anterior upper fin only; oral disc and belly sucker translucent; venter tan to translucent.

In life (Fig. 9 B, C), tadpoles were dark brown with orange-cream markings.

Several *Atelopus* larvae have been described. They can be allocated to two functional types, in one of which tadpoles have larger oral suckers and elongated tails (cf. LÖTTERS 2001). This larva type is usually found in Andean highlands whereas the tadpole of *A. pulcher* is more similar to other lowland species. Among them, *A. pulcher* larvae as described here resemble those assigned to *A. spumarius* by DUELLMAN & LYNCH (1969) and those assigned to *A. pulcher* by GASCON (1989) as well as those of *A. balios* PETERS, 1973 (COLOMA & LÖTTERS 1996), *A. varius* (LICHTENSTEIN & MARTENS, 1856) (LÖTTERS 1996), *A. tricolor* (LAVILLA et al. 1997), *A. elegans* (BOULENGER, 1882) (VÉLEZ-RODRÍGUEZ & RUÍZ-CARRANZA 1997), *A. zeteki* DUNN, 1933 (LINDQUIST & HETHERINGTON 1998) and *A. mindoensis* PETERS, 1973 (LÖTTERS 2001) in having symmetrical or asymmetrical light marks in life. Tadpoles of *A. pulcher* as treated above strikingly differ from all these larvae, except those allocated to *A. pulcher* by GASCON (1989), by having the upper beak considerably shorter than the lower (cf. Fig. 10). Other features of these tadpoles include, in part, a posteriorly well rounded suctorial disc, nostrils clearly below the level of the eye in lateral view and presence of submarginal papillae.

Tadpoles from Ecuador assigned to *A. spumarius* by DUELLMAN & LYNCH (1969) differ from those referred to *A. pulcher* here by having a significantly longer upper beak and having the oral disc posteriorly less well rounded. Among the two tadpoles, the position of the nostril in lateral view is very similar and the colour pattern appears to be very similar as well. Species allocation of the Ecuadorian larva remains to be done (see above); at least, we consider the species of DUELLMAN & LYNCH (1969) not to be *A. pulcher*. Larvae from central Amazonian Brazil assigned to *A. pulcher* by GASCON (1989) resemble those described here in having the upper beak considerably shorter than the lower. These are the only two *Atelopus* tadpoles from which this unusual character is known. The two larvae differ in position of the nostril in lateral view, however (located at about the height of the eye in larvae from Amazonian Brazil versus clearly below the level of the eye in the material treated in this paper). Moreover, the white flecks seem to be more scattered in the tadpole of GASCON (1989), following the description and illustrations by him. We continue our doubt that the species of GASCON (1989) is *A. pulcher*. We have not been able to study adults from the locality where GASCON (1989) collected tadpoles but suspect that *A. pulcher* does not occur in central Amazonian Brazil. From the general area *A. spumarius* sensu lato is known.

Remarks: As mentioned, we are uncertain about the taxonomic status of additional populations similar to *A. pulcher* from the Andean versant of Peru and Ecuador (cf. RIVERO 1968, PETERS 1973). We have examined a limited number of specimens from

Ecuador only (AMNH A 16695-712, 33913-915, BM 1970.68-69, 1970.117-118) and lack detailed information on communication and reproduction behaviour or tadpole morphology etc. An unpublished principal components analysis of morphometric data suggests that Ecuadorian populations may not be conspecific with *A. pulcher* (L.A. COLOMA, S. LÖTTERS & collaborators).

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### Appendix: Material Examined

*Atelopus andinus*: PERU: San Martín: upper Río Biabo valley, AMNH A 42657 (paratype), A 43200 (holotype); Loreto: Río Pisquí, AMNH A 43545 (paratype); border area of San Martín-Loreto: Río Cachiyacu (Tocachi), AMNH A 42914, A 43296-927 (paratypes). *Atelopus erythropus*: PERU: Puno: Santo Domingo, Cordillera Carabaya, BM 1947.2.14.65 (holotype). *Atelopus minutulus*: COLOMBIA: Meta: km 13-15 on Guayabetal-Manzanares road, ICN 13709 (holotype), 4851-853, 5028, 7085-891, 12898 (paratypes). *Atelopus pulcher*: PERU: San Martín: vicinity of Tarapoto, KU 211676-683, 212530, ZFMK 48573, 50680-685, 76243-244, 76245 (last mentioned are captive-raised clutch and tadpoles); Chyavetas (= Loreto: Chayahuitas?), BM 1947.2.14.80 (lectotype designated herein), 1947.2.14.82 (paralectotype). *Atelopus reticulatus*: PERU: Ucayali: Cordillera Azul, circa 3 km by road after Divisoria on the Tingo María-Pucallpa road, ZFMK 76246-247 (para- and holotype). *Atelopus* cf. *seminiferus*: PERU: Piura: Cerro Chinguela region, KU 196633-42. *Atelopus* sp. (aff. *A. pulcher*): ECUADOR: Morona-Santiago: Chancha, Normandía, AMNH A 16695-712; Cordillera de Cutucú, AMNH 33913-915; Pastaza: Río Villani, Villano, BM 1970.68-69, 1970.117-118. *Atelopus spumarius* sensu lato: BRAZIL: Amapá: Serra do Navio, ZFMK 54384-385; Pará: Sudam Floral Reserve, 74 km north-east of Santarém, KU 129954-960; COLOMBIA: Amazonas: Igara Parana, BM 1905.1.31.10-11; FRENCH GUIANA: Haut Maroni, Monts Atachi-Bacca, MNHNP A 522 (holotype of *A. pulcher hoogmoedi*), A515, A518, A519-521 (paratypes of *A. pulcher hoogmoedi*); SURINAME: Brownsberg, AMNH 7749, KU 206405-406. *Atelopus spumarius* sensu stricto: PERU: Loreto: Colonia, Río Ampiyacu, MNHNP 1979/8382 (neotype); 3 km north-east of Pebas, AMNH A 103-31-35. *Atelopus siranus*: PERU: Huánuco: Serranía de Sira, NHMW 33906:1 (paratype), NHMW 33906:2 (holotype). *Atelopus tricolor*: PERU: Cuzco: Marcapata valley, BM 1947.2.14.57-59 (paralectotypes), ZFMK 28103 (lectotype); 4 km south-west of Santa Isabel, Río Cosñipata, KU 162988; Puno: vicinity of Juliaca, AMNH 6097 (holotype of *A. rugulosus*); BOLIVIA: La Paz: 17 km from Carrasco, Serranía de Bellavista, CBF 285-288; Río Ñeques, circa km 10 on Charazani-Apolo road, Yungas de La Paz, CBF 2502; Pilon-Lajas, CBF 2487; Cochabamba: Río Ronco, Chapare, CBF 892; “old” road from Villa Tunari to Cochabamba, Chapare, ZFMK 69919-920.

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