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A NEW GENUS AND SPECIES OF TOAD (ANURA: BUFONIDAE) WITH AN EXTRAORDINARY STREAM-ADAPTED TADPOLE FROM NORTHERN HONDURAS

By

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In early June, 1980, at the end of the dry season, JRM and LDW travelled to the Cordillera de Nombre de Dios south of the port of La Ceiba, Atlántida, Honduras. Our objective was to sample the herpetofauna of the highest elevations in the region of Cerro Búfalo. While working in cloud forest in these steep mountains at 1760 m, we found a single apparently undescribed female bufonid. On the return trip, we collected a second specimen, a male, in highland rainforest at 940 m and a series of peculiar tadpoles which we suspected belonged to the same taxon.

In August of 1982 we returned to this area in the rainy season to try to link the strange tadpole and the undescribed toad. An additional adult male and numerous juveniles and tadpoles were collected. One of the tadpoles was in the process of metamorphosis and allowed its association with adults.

A third trip to the same area in August, 1984, netted one adult male and more juveniles and tadpoles, including a number of metamorphosing individuals.

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The larva of this new toad is a mountain stream inhabitant and appears to be the fourth example of a gastromyzophorous tadpole (Inger, 1966). This terminology describes the condition of a well-developed, extensive ventral suckorial disc anastomosed to the larval mouthparts, an adaptation for clinging to smooth rock surfaces in swift mountain streams. The condition has been reported in three genera of anurans belonging to two families and occurring in both hemispheres. The bufonid genus *Atelopus* occurs in humid forests in areas of some relief from Costa Rica southward to northern Bolivia (Frost, 1985). The ranid genus *Amolops* occurs in mountain streams from "Nepal, northeastern India, western and southern China to the Greater Sunda Is." (Frost, 1985: 452). The third is the ranid *Rana sauteri* from Taiwan (Kuramoto et al., 1984). However, the tadpole of *R. sauteri* differs noticeably from the other gastromyzophorous tadpoles in having a less well-developed abdominal disc.

The tadpole of the new toad bears a striking resemblance to those known for the species of *Atelopus*. The resemblance is so close that were it not for the known association of the tadpole and adult toad, it would be tempting to regard the tadpole as the larva of an undescribed species of *Atelopus*. In light of the distinctiveness of the Cerro Búfalo toads (see diagnosis and description below), we refer them to a new bufonid genus.

MATERIALS AND METHODS

Data on myology and osteology of the new genus were taken from a single male (KU 206733) that was first dissected and then alizarin-cleared and stained. Thigh musculature nomenclature and features used herein were described in detail by Grandison (1978) and jaw musculature by Starrett (1968). Bone terminology follows Trueb (1973) except for the shape of the terminal phalanges (after Lynch, 1971) and the nature of the occipital groove and orbitosphenoid, which follow McDiarmid (1971) and Cannatella (1986), respectively. Measurements taken were defined by Duellman (1970) and webbing formula by Myers and Duellman (1982). Tadpoles were staged according to Gosner's (1960) system. Data on other bufonid genera were taken from the literature with a few exceptions (see introduction to Comparisons section).

SYSTEMATICS

Atelophryniscus gen. n.

Type species. *Atelophryniscus chrysophorus* new species.

Diagnosis. A small bufonid distinguished from other genera in the family by the following combination of characters: (1) habitus bufoniform; (2) dorsal surface rugose, covered with scattered tubercles; (3) parotoid

glands distinct, subtriangular; (4) cranial crests low; (5) tympanic annulus present, concealed by skin; (6) columella present; (7) ostia pharyngea present; (8) single sinistral vocal slit present in adult males; (9) modal toe webbing formula I 1-1 II 1-2 III 1-2¹/₂ IV 3-1 V, subarticular tubercles small, flattened; (10) outer metatarsal tubercle small, ovoid; (11) inner tarsal fold present; (12) phalangeal formula of hands 2-2-3-3, feet 2-2-3-4-3; (13) adult males 33.6-37.4 mm ($n=2$) snout-vent length, single female 36.2 mm; (14) testes slender, cream colored, $\frac{1}{6}$ snout-vent length; (15) adductor longus muscle absent; (16) tensor fasciae latae short, arising from distal $\frac{1}{3}$ of ilium, inserting onto cruralis muscle at proximal $\frac{1}{4}$ of thigh; (17) iliacus externus muscle bulky, its origin at about mid-length of ilial shaft; (18) broad origin to dorsal portion of semitendinosus; (19) adductor mandibulae externus superficialis and posterior subexternus present, in S and E condition; (20) eight presacral vertebrae; (21) neural arches imbricate; (22) cervical not fused to second vertebra; (23) occipital condyles and cervical cotyles closely juxtaposed; (24) no intervertebral fusion; (25) pectoral girdle fully arciferal; (26) omosternum absent; (27) sacral-coccygeal articulation bicondylar; (28) coccyx with a very small posteriorly-directed transverse process on left side only, without expanded lateral edges; (29) terminal phalanges of hands expanded, moderately T-shaped, those of feet knobbed; (30) two centralia in hand; (31) frontoparietal bones not fused on midline; (32) frontoparietal fontanelle obscured by medial articulation of frontoparietals; (33) occipital groove open; (34) orbitosphenoid unossified; (35) otic ramus of squamosal extending over prootic; (36) palatine bone present, well-developed; (37) quadratojugal in bony contact with maxilla; (38) larvae gastromyzophorous.

Etymology. The generic name is derived from the Greek prefix *a-*, meaning "without," the Greek adjective *telo*, meaning "complete," the Greek noun *phryne*, meaning "toad," and the Greek diminutive suffix *-iscus*. The name is a reference to the resemblance of the tadpole to that of species of *Atelopus* and the resemblance of the adult to species of *Bufo*, as well as to the small size of the adults. The gender is masculine.

Atelophryniscus chrysophorus sp. n.

(Fig. 1)

Holotype. Adult male, University of Kansas Museum of Natural History (KU) 206730, from Quebrada de Oro (15° 38'N, 86° 47'W), elevation 880 m, tributary of Río Viejo, south slope of Cerro Búfalo, Cordillera de Nombre de Dios, Depto. Atlántida, Honduras, collected on 16 August 1982 by James R. McCranie, Kenneth L. Williams, and Larry David Wilson.

Paratypes. KU 206731, adult female, from south slope of Cerro Búfalo, elevation 1760 m, above the Quebrada de Oro, Cordillera de Nombre de Dios, Depto. Atlántida, Honduras, collected on 3 June 1980 by Gustavo A. Cruz



Fig. 1. Dorsal view of female paratype of *Atelophryniscus chrysophorus* (KU 206731).

Díaz, Mario R. Espinal, James R. McCranie, and Larry David Wilson; KU 206732, adult male, same data as holotype except elevation 785 m and collected on 16 August 1984.

Description of holotype. Snout-vent length (SVL) 33.6 mm; tibia length 16.7 mm, 49.7 per cent of SVL; hand length 10.6 mm, 31.5 per cent of SVL; foot length 15.3 mm, 45.5 per cent of SVL; head length 10.6 mm, 31.5 per cent of SVL; head width 11.3 mm, 33.6 per cent of SVL; snout in dorsal aspect broadly acuminate, in profile bluntly rounded; snout length 2.5 mm, 23.6 per cent of head length; distance from nostril to tip of snout 0.38 times less than distance between nostril and eye; loreal region slightly concave; nostrils protuberant, in line with anterior terminus of upper jaw, slightly below canthal ridge; diameter of eye 4.6 mm, 43.4 per cent of head length; width of eyelid

3.6 mm, 31.9 per cent of head width; pupil horizontally elliptical; palpebral membrane clear with a few silver flecks and a dusting of melanophores along upper and lower edges; internarial distance 2.9 mm, 25.7 per cent of head width; interorbital distance 4.1 mm, 36.3 per cent of head width; top of head flat, slightly concave between nostrils, almost smooth; skin co-ossified with skull; supraorbital crest low, pustulose, confluent with short parietal crest and low postocular crest; supratympanic crest short, bulbous, in contact with parotoid gland; upper surface of eyelids slightly pustulose; parotoid gland subtriangular, slightly larger than upper eyelid, extending posteriorly to level of axilla; tympanum concealed by skin; tongue lanceolate, barely free behind; single sinistral vocal slit, at the posterolateral edge of tongue, extending back to near angle of jaw; choanae subcylindrical, posterior to nostrils; prevomer edentate; ostia pharyngea present, posteromedial to angle of jaw.

Arms slender; fingers long, slender; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; fingers free of webbing; subarticular tubercles on hands small, subconical; supernumerary tubercles small, flattened; inner palmar tubercle round, slightly elevated; outer palmar tubercle large, round, flat, about twice size of inner palmar tubercle; prepollical protuberance present, with numerous tiny brown nuptial excrescences; inner tarsal fold present; toes long, slender; webbing formula I 1-1 II 1-2 III 1-2^{1/2} IV 3-1 V; length of toes from shortest to longest 1-2-5-3-4; phalangeal formula of foot 2-2-3-4-3; subarticular tubercles on toes small, flattened; supernumerary tubercles on foot few, small; outer metatarsal tubercle small, ovoid; inner metatarsal tubercle subtriangular, relatively small, about three times the size of the outer metatarsal tubercle.

Cloacal opening directed posteriorly at upper level of thighs. Anal sheath short. Skin of dorsum with moderate-sized scattered tubercles. Small scattered tubercles present on upper surfaces of forelimbs and hindlimbs. Skin of throat, chest, and belly pustulose.

Color (in life): dorsum pale lime green with olive brown blotching and rusty-red-tipped pustules; pale orange pustules outlining lower edge of pale lime green lateral stripe; lateral stripe bordered below by dark brown line grading to olive brown ventrally; side of head pale yellow, mottled with dark brown in front of and below eye; rusty-red dark brown-bordered bar extending from eye to posterior edge of lip; iris pale metallic green; limbs pale lime green dorsally with olive brown blotches; toe tips and outer edge of web orange; venter pale blue-green, mottled with dark chocolate brown.

Color (in preservative): dorsum pale gray with grayish brown blotching; pustules dull orange; venter cream, mottled with brown.

Variation in the paratypes. The male paratype (KU 206732) has a snout-vent length of 37.4 mm, the female (KU 206731) 36.2 mm. Other measurements and ratios are as follows (data for male paratype listed first): tibia length 18.2 mm, 17.9 mm, 48.7, 49.4 per cent SVL; hand length 11.5 mm, 12.2 mm,

30.7, 33.7 per cent SVL; foot length 17.2 mm, 17.0 mm, 46.0, 47.0 per cent SVL; head length 12.3 mm, 11.6 mm, 32.9, 32.0 per cent SVL; head width 13.0 mm, 12.0 mm, 34.8, 33.1 per cent SVL; snout length 2.9 mm, 2.8 mm, 23.6, 24.1 per cent head length; diameter of eye 4.6 mm, 4.6 mm, 37.4, 39.7 per cent head length; width of eyelid 3.8 mm, 3.6 mm, 29.2, 30.0 per cent head width; internarial distance 3.4 mm, 3.0 mm, 26.2, 25.0 per cent head width; interorbital distance 4.5 mm, 4.5 mm, 34.6, 37.5 per cent head width.

The paratypes are similar morphologically to the holotype, except the female lacks nuptial excrescences and a vocal slit.

Color (in life) of female (KU 206731): middorsum dark lime green, flanked by pale lime green dorsolateral stripes; tubercles on dorsum brick red; flanks dark lime green with red-tipped tubercles; chin mottled with brick red and pale green; venter marbled with red-speckled gray and pale green; arms and legs pale lime green with dark brownish green bands and brick-red-tipped tubercles; iris lime green with some black reticulations.

Osteology. The premaxillae are separated medially, in contact anteromedially, slightly separated posteromedially. The pars palatina is edentate and there is a well-developed pointed posteromedially-oriented palatine process on each premaxilla. The quadratojugal is in bony contact with the maxilla. The otic ramus of the squamosal extends over the prootic.

The cervical cotyles are closely juxtaposed (Type II of Lynch, 1971). The neural arches are imbricate. There are eight presacral vertebrae. The widths of the moderately long transverse processes from narrowest to widest are 2-8-7-6-5-4-3. The transverse processes of the second presacral vertebra extend laterally, those of 3, 4, and 5 extend slightly to moderately posterolaterally, those of 6 and 7 extend laterally, and those of the eighth slightly anterolaterally. The sacral diapophyses are expanded. The sacral-coccygeal articulation is bicondylar. The coccyx bears a small, posteriorly-directed transverse process on the left side only, without expanded lateral edges. There is a well-developed dorsal crest extending about three-fourths of the length of the coccyx.

The pectoral girdle is fully arciferal and bears no omosternum. The sternum is bony and bears no xiphisternum. The clavicle is bony.

The terminal phalanges of the hands are expanded and moderately T-shaped, those of the feet are knobbed. There are two centralia in the hand.

Myology. The adductor longus muscle is absent in *Atelophryniscus*. The tensor fasciae latae muscle is short, arising from the ventral surface of the distal third of the ilium and inserting on the cruralis muscle at about the proximal fourth of the thigh. The iliacus externus muscle is bulky, its origin lies at about the midlength of the ilial shaft, its fibers arising mainly from the dorsal and dorsomedial surface of the bone, with some additional fibers given off from the lateroventral surface. There is a broad origin to the dorsal portion of the semitendinosus. There is no accessory head to the adductor magnus

muscle. Both the adductor mandibulae externus superficialis and posterior subexternus are present and in the S and E condition.

Description of the tadpole (Figs. 2 and 3). A typical tadpole (in lot number KU 206748) may be described as follows: developmental stage 37, body length 9.6 mm, total length 26.4 mm; body depressed, flattened ventrally, 1.5 times as wide as deep; snout broadly rounded in dorsal and lateral profiles; eyes moderately large, separated by distance equal to about three times diameter of eye, directed anterolaterally; nostrils small, considerably closer to eye than tip of snout; spiracle sinistral, directed posterodorsally, located low on body, at about three-fourths of body length; anal tube medial, long; caudal musculature deep at base, gradually tapering posteriorly to about midpoint where tapering noticeably increases, extending nearly to tip of rounded tail; dorsal fin slightly arched and deepest at about midpoint of tail; ventral fin not noticeably arched; fins not extending onto body.

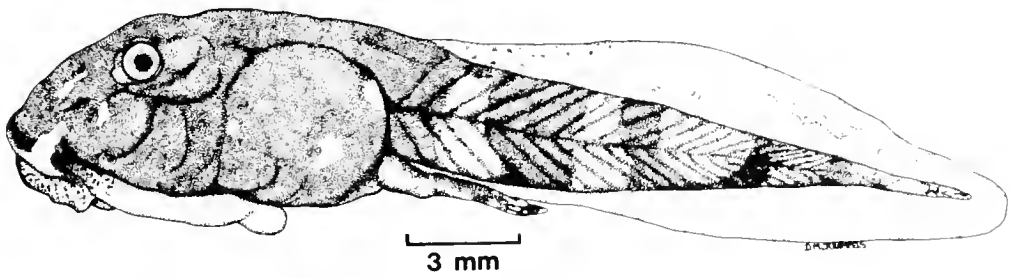


Fig. 2. Lateral view of the tadpole of *Atelophryniscus chrysophorus* (KU 206748) in Gosner stage 35.

Mouth ventral (Fig. 4), nearly as wide as body, followed by large suctorial disc with raised rim; suctorial disc border complete laterally and posteriorly; suctorial disc extending about three-fourths length of body, broadly rounded posteriorly; median portion of upper and lower lip bare, rest bordered by one row of small papillae, additional row present just inside outer row laterally on upper labium; lateral folds well-developed; two upper and three lower rows of denticles, all complete and about equal in length, extending to lateral edge

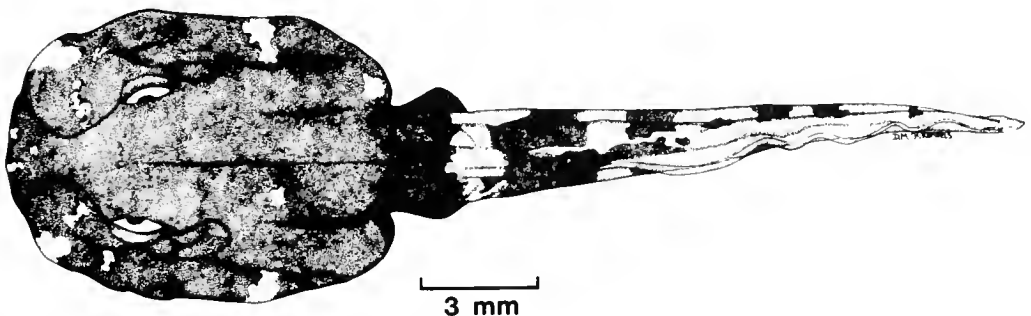


Fig. 3. Dorsal view of the tadpole of *Atelophryniscus chrysophorus* (KU 206748) in Gosner stage 35.

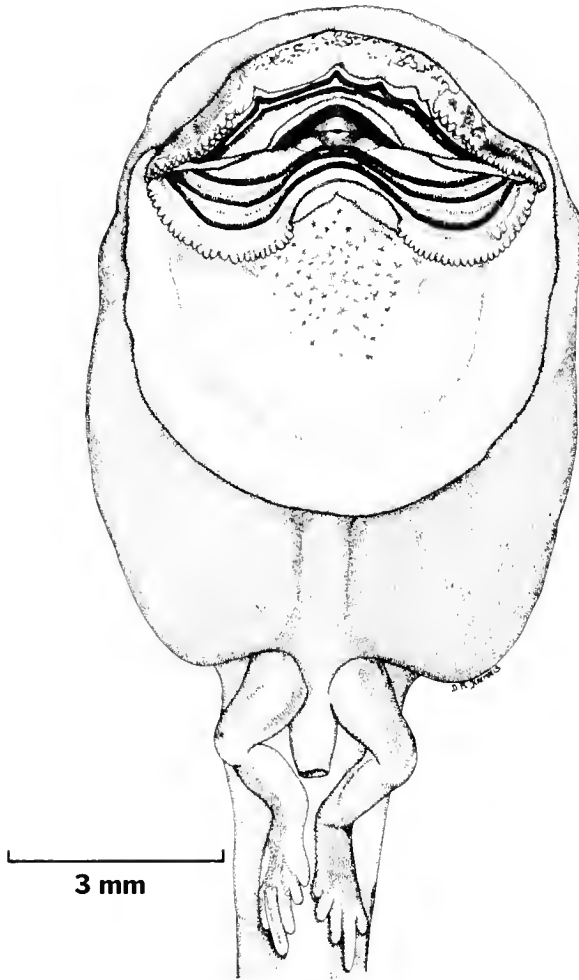


Fig. 4. Mouthparts and ventral suctorial disc of the tadpole of *Atelophryniscus chrysophorus* (KU 206748) in Gosner stage 35.

of mouth; beaks thin and without serrations, upper beak curved, slightly longer than V-shaped lower beak.

Color in life: body black with gold markings; caudal musculature black with pale yellow bands or spots; in preservative: body dark brown with tan markings slightly evident; caudal musculature brown with pale tan bands or spots; fins clear, lightly punctated with brown.

A tadpole in stage 42 (lot number KU 206748) has a body length of 10.8 mm and a total length of 25.4 mm. The beaks have disappeared and remnants of the second upper denticle row are all that remain. The suctorial disc has been partially resorbed and extends only slightly posterior to the axilla. Minute red tubercles are present on the dorsum and forelimbs, red tubercles on the hind limbs somewhat better developed. The webbing on the feet and the banding of the hind limbs is similar to recently-metamorphosed individuals.

A juvenile (lot number KU 206748) with a tail stub is 9.2 mm in snout-vent length; a juvenile (lot number KU 206748) with the tail completely resorbed

is 9.8 mm SVL. Color notes (in life) for these toadlets: olive green dorsum with red-tipped pustules; pale yellowish green lateral stripes; dorsal spots red, outlined with dark brown; bands on legs reddish brown, separated by pale yellowish green; venter turquoise blue, mottled with chocolate brown; iris metallic green.

Tadpoles in late stages of development, metamorphosing toadlets, and juvenile toads were collected (KU 206734–49). Uniformity of toe webbing, banding of the hind limbs, and red-tipped tubercles on the dorsum and hind limbs of all these specimens and the adults unquestionably confirm the link between the tadpoles and adults.

Etymology. The specific name *chrysochorus* is derived from the Greek noun *chrysus*, meaning “gold,” and the Greek suffix *-phora*, meaning “bearing.” The reference is to the gold markings on the dorsum of the otherwise black tadpole, to the name of the stream at the type locality, Quebrada de Oro (= “stream of gold”), and to the fact that the gold-spotted tadpole occurred in that stream.

Natural history. The type locality, Quebrada de Oro, is a mountain stream 3–4 m wide. The stream has variously-sized boulders in the areas of rapids, interspersed by broad, deep pools. The Quebrada de Oro flows into the Río Viejo, which joins the Río Cangrejal, a major river of the mid-northern coast of Honduras that flows through the port of La Ceiba on the Caribbean.

The vegetation of the area (at ca. 800 m) can be characterized as Subtropical Wet Forest (Holdridge, 1967) and less formally as highland rainforest. Trees of the forest include sweetgum (*Liquidambar*), *Cecropia*, *Ficus*, coralbean (*Erythrina*), oaks (*Quercus*), wild avocados (*Persea*), and *Miconia*. Some leguminous and rubiaceous trees and bactrid palms were also present. The undergrowth consisted of dumbcane (*Diefenbachia*), various small palms, *Solanum* sp., elephant ears, and other small aroids, *Piper* sp., *Selaginella* sp., and a few terrestrial bromeliads. Vines of the families Solenaceae, Apocynaceae, Curcubitaceae, and Bignoniaceae were present, as well as *Passiflora*, *Mikania*, *Vitis*, and *Smilax*. Vining aroids and ferns were seen, as were epiphytes, including Spanish moss and other small bromeliads, orchids, peperomias, ferns, aroids, mosses, and liverworts. No large, water-filled epiphytic bromeliads or tree ferns were seen.

At higher elevations the highland rainforest along the Quebrada de Oro gradually gives way to hardwood cloud forest (=Lower Montane Wet Forest formation of Holdridge, 1967). The stream begins at about 1500 m; above this point there is no contained water because of the steep slopes.

The adult female was found in a hole covered with vegetation at the base of a low embankment in undisturbed hardwood cloud forest at 1760 m. All other adults, juveniles, and tadpoles came from lower elevations (750–1090 m) in highland rainforest. The adult males came from within the forest along the stream during the day or at dusk and the juveniles were found hopping on

the banks of the stream during the day or at night. No *Atelophryniscus* were heard calling. The tadpoles usually inhabit the middle, fast-flowing portion of the stream, in relatively deep pools, where they cling to the surface of submerged boulders. When disturbed, they creep down the boulder, swim to the bottom, or swim to another boulder. Tadpoles sometimes occur in shallower areas where water moves rapidly over the rocks, or in side pools with slower moving water. None were found in stagnant side pools. Subaerial adhesion was occasionally observed in the *Atelophryniscus* tadpole, as has been recorded for the gastromyzophorous larvae of *Amolops* [Liu, 1950, (as *Staurois*); Wassersug and Heyer, 1983].

COMPARISONS

Information in this section was taken largely from Cannatella (1986), Grandison (1978, 1980a, 1981), Hoogmoed (1985), Inger (1966), Laurent (1986), McDiarmid (1971), Pillai and Yazdani (1973), Pregill (1981), Ruíz-C. and Hernández-C. (1976), Savage and Kluge (1961), Tihen (1960), and Trueb (1971), unless otherwise noted. Two colleagues (see Acknowledgments) also provided unpublished information on various New World genera.

New World Genera. Currently there are twelve genera of bufonids recognized in the New World (Frost, 1985; Hoogmoed, 1985; Cannatella, 1986; this paper). Cannatella (1986) divided ten of these genera into two groups. The atelopodines *Atelopus*, *Dendrophryniscus*, *Frostius*, *Melanophryniscus*, *Oreophrynella*, and *Osornophryne* have partial or full fusion of the epicoracoid cartilages, whereas *Bufo*, *Crepidophryne*, *Peltophryne*, and *Rhampophryne* have unfused epicoracoid cartilages (Cannatella, 1986). The recently-described *Andinophryne* (Hoogmoed, 1985) exhibits the atelopodine condition. *Atelophryniscus* displays the bufonine condition.

Atelophryniscus can be further distinguished from the "atelopodines" by the following combination of characters: tensor fasciae latae short (elongate in *Atelopus*, *Frostius*, and *Osornophryne*); adductor mandibulae in S+E condition (S in *Andinophryne*, *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Osornophryne*, E in *Oreophrynella*, unknown in *Frostius*); vocal slit present (absent in *Dendrophryniscus*, *Oreophrynella*, and *Osornophryne*); a columella (absent in *Atelopus* [except *flavescens* group], *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, and *Osornophryne*); frontoparietal fontanelle obscured by medial articulation of frontoparietals (no medial articulation in *Oreophrynella*); otic ramus of squamosal extending over prootic (not so in *Oreophrynella*, unknown in *Andinophryne*); 8 presacral vertebrae (normally 7 in *Atelopus*, 6 in *Osornophryne*, and 5 in *Oreophrynella*); no omosternum (present in *Andinophryne*); cervical not fused to second presacral vertebra (fused in *Atelopus* and *Oreophrynella*); sacrum not fused to coccyx (fused in *Dendrophryniscus*, *Oreophrynella*, and *Osorno-*

phryne); 2 centralia in hand (1 in *Atelopus*, *Dendrophryniscus*, *Frostius*, and *Osornophryne*, unknown in *Andinophryne*); fingers free of webbing (webbing well-developed in *Andinophryne* and *Osornophryne*); gastromyzophorous larvae (generalized oral disc in *Dendrophryniscus*, *Frostius*, and *Melanophryniscus*, unknown in *Andinophryne*, *Oreophrynella*, and *Osornophryne*).

Atelophryniscus can be distinguished from the "bufonines" (*Bufo* will be discussed separately) by the following combination of characters: tympanic annulus concealed by skin (tympanum absent in *Crepidophryne* and *Rhamphophryne*, present and visible in *Peltophryne*); adductor longus absent (present in *Peltophryne*); adductor mandibulae in S+E condition (E in *Crepidophryne*, unknown in *Rhamphophryne*); a columella (absent in *Crepidophryne* and *Rhamphophryne*); a well-developed palatine (reduced in *Crepidophryne*); a normal nasal region (extensively ossified and protruding in *Rhamphophryne*); no paired rostral bones (paired in *Peltophryne* [except *P. fluviatica*]); 8 presacral vertebrae (7 in some species of *Rhamphophryne*); coccyx without expanded lateral edges (present in *Crepidophryne*); phalangeal formula of manus 2-2-3-3, that of pes 2-2-3-4-3 (1-2-3-2 and 1-2-2-4-2, respectively, in *Crepidophryne*); tips of distal phalanges of manus modified T-shaped (simple or only slightly knobbed in *Crepidophryne*, *Peltophryne*, and *Rhamphophryne*); gastromyzophorous larvae (generalized oral disc in *Peltophryne*, unknown in *Crepidophryne* and *Rhamphophryne*).

The tadpoles of *Atelophryniscus* resemble those described for various species of *Atelopus* (Duellman and Lynch, 1969; Gray and Cannatella, 1985; Lescure, 1981; Lynch, 1986; Mebs, 1980; Starrett, 1967). Tadpoles of both genera have depressed bodies with flattened venters and an enlarged ventral mouth followed by a large suctorial disc with a raised rim extending $\frac{2}{3}$ to $\frac{4}{5}$ of the length of the body. They also have the typical bufonid condition of two upper and three lower denticle rows, a medial anal tube, and a sinistral spiracle. Color in life also is similar among the tadpoles of *Atelophryniscus* and those of some species of *Atelopus*. Duellman and Lynch (1969: 234) reported *A. certus* as "black with golden bronze flecks" and Gray and Cannatella (1985: 916) recorded "black with pale golden marks on dorsum of body and caudal musculature" for *A. peruensis*. Both approach the black body with gold markings and black caudal musculature with pale yellow bands and spots found in *Atelophryniscus*. Tadpoles of *Atelopus subornatus* and other species in Andean Columbia are boldly marked "cream and black" like those of *Atelophryniscus* (Lynch, 1986: 129). Differences between the two genera are in arrangement of the papillae (median half of upper and median third of lower lip bare in *Atelophryniscus*, complete on upper lip and a broad bare area on lower lip in *Atelopus* [Mebs, 1980, reported a complete row of papillae on lower lip in *A. cruciger*; Lescure, 1981, discredited this statement]) and the lateral folds of the mouth (well-developed in *Atelophryniscus*, absent in *Atelopus*). Differences also exist in the tadpole sizes. Of the tadpoles of

Atelopus species described, only that of *A. subornatus* is similar in size to that of *Atelophryniscus* (Lynch, 1986); the remaining species are considerably smaller. For example, the *Atelopus certus* tadpole in stage 36 has a mean body length of 6.8 mm and a mean total length of 14.0 mm and *A. pulcher* in stage 37 has a body length of 6.9 mm and a total length of 13.7 mm (Duellman and Lynch, 1969). A tadpole of *Atelophryniscus* in stage 37 has a body length of 9.6 mm and a total length of 26.4 mm.

Old World Genera. Frost (1985) recognized ten genera of bufonids in Africa and six in Asia, exclusive of the genus *Bufo*. Dubois (1987), using the features of reproduction and development (data taken from Grandison, 1978; Wake, 1980), divided the African genus *Nectophrynoides* into four genera by naming three new genera to accommodate the eight species previously placed in this genus (Frost, 1985). For convenience, these eight species are retained in the genus *Nectophrynoides*, in the following discussion. The African bufonids (exclusive of *Bufo*) were divided into two assemblages by Grandison (1981). The “*Nectophryne* line” contains the genera *Capensibufo*, *Didynamipus*, *Laurentophryne*, *Nectophryne*, *Nectophrynoides*, *Werneria*, and *Wolterstorffina*, whereas *Mertensophryne*, *Stephopaedes*, and possibly *Schismaderma* were thought to be related to the “*Bufo vertebralis* group.” No study comparable to those of Grandison (1978, 1980a, 1981) exists for the African genera *Mertensophryne*, *Schismaderma*, and *Stephopaedes* or for the Asian genera *Ansonia*, *Bufoides*, *Leptophryne*, *Pedostibes*, *Pelophryne*, and *Pseudobufo*.

Stephopaedes was diagnosed on the basis of having larvae with a unique “crown” on the head (Channing, 1978). However, Grandison (1980b) demonstrated that the larvae of *Mertensophryne micranotis* have a similar “crown.” The genera *Bufoides* and *Schismaderma* are also poorly defined; thus, the data in the following discussion are incomplete for these genera.

Atelophryniscus can be distinguished from the Old World bufonids (*Bufo* will be discussed separately) in having cranial crests (no cranial crests in all genera, except *Bufoides*); parotoid glands (no parotoid glands in *Didynamipus*, *Laurentophryne*, *Nectophryne*, *Werneria*, *Wolterstorffina*, *Ansonia*, *Bufoides*, *Pelophryne*, and *Pseudobufo*, feebly developed in *Mertensophryne* and *Schismaderma*, a tendency toward a loss in *Nectophrynoides*); no adductor longus (present in *Capensibufo* and *Leptophryne*); a short tensor fasciae latae (elongate in *Didynamipus*, *Laurentophryne*, *Nectophryne*, *Werneria*, *Wolterstorffina*, *Leptophryne*, *Pelophryne*, and *Pseudobufo*); a columella (absent in *Didynamipus*, *Laurentophryne*, *Nectophryne*, *Werneria*, *Wolterstorffina*, *Mertensophryne*, and *Stephopaedes*, a tendency toward a loss in *Nectophrynoides*); quadratojugal well-developed and in bony contact with maxilla (reduced or vestigial in *Laurentophryne*, *Nectophryne*, *Wolterstorffina*, *Ansonia*, *Leptophryne*, *Pelophryne*, and *Pseudobufo*, absent in *Didynamipus*); a well-developed palatine (reduced in *Capensibufo*, *Didy-*

namipus, and *Laurentophryne*, absent in *Nectophryne* and *Pelophryne*); frontoparietal fontanelle obscured by medial articulation of frontoparietals (no medial articulation in *Capensibufo* and *Nectophryne*); 8 presacral vertebrae (7 in *Didynamipus*, *Laurentophryne*, *Mertensophryne*, and *Pelophryne*, 7 or 8 in *Nectophryne* and *Nectophrynoides*); cervical not fused to second vertebra (fused in *Leptophryne*); fully arciferal pectoral girdle (modified in *Didynamipus* and *Leptophryne*); no omosternum (present in *Capensibufo*, *Nectophrynoides*, and *Werneria*); sacral-coccygeal articulation bicondylar (fused in *Didynamipus*, *Laurentophryne*, *Nectophryne*, and *Pelophryne*, monocondylar or fused in *Wolterstorffina*, monocondylar in *Mertensophryne*); condyles of vertebrae ossified (not ossified in *Pseudobufo*); coccyx without expanded lateral edges (present in *Didynamipus* and *Pelophryne*); normal phalangeal formula of 2-2-3-3 and 2-2-3-4-3 (reduced in *Didynamipus* and *Mertensophryne*); terminal phalanges of hands expanded, moderately T-shaped (simple or knobbed in *Capensibufo*, *Didynamipus*, *Mertensophryne*, *Werneria*, and *Stephopaedes*); tips of digits not dilated into discs (dilated into discs in *Pedostibes*); non-aquatic adults (aquatic with fully-webbed feet in *Pseudobufo*); gastromyzophorous larvae (generalized oral disc in *Capensibufo*, *Schismaderma*, *Bufoides*, *Leptophryne*, and *Pedostibes*, vestigial in *Pelophryne*, funnel-shaped in *Nectophryne* and *Wolterstorffina*, an expanded oral disc not followed by a suctorial disc with a raised rim in *Werneria* and *Ansonia*, a "crown" on head in *Stephopaedes* and *Mertensophryne*, either aquatic with generalized oral disc, terrestrial non-feeders, or omitted in *Nectophrynoides*, unknown in *Didynamipus*, *Laurentophryne*, and *Pseudobufo*).

The Genus *Bufo*. As presently understood, there are 205 species in the genus *Bufo*, 92 of which occur in the New World (Frost, 1985; Hoogmoed, 1985). *Atelophryniscus* can be distinguished from *Bufo* by possession of modified T-shaped distal phalanges on the hand (simple or slightly knobbed in *Bufo* [Laurent, 1986; Tihen, 1960, 1962]) and gastromyzophorous tadpoles (larvae with generalized oral disc and no abdominal disc in *Bufo*). *Atelophryniscus* also lacks an adductor longus muscle, which is present in most *Bufo*. This muscle can be absent, however, in some species (Limeses, 1964; McDiarmid, 1971).

DISCUSSION

Cannatella (1986: 202), as noted above, separated the New World bufonid genera into two subgroups. He did so with reservations, however, treating the "atelopodine" genera "as a monophyletic unit, primarily to point out areas where further work is needed." That his reservations were warranted is further indicated by the recognition of *Andinophryne* and *Atelophryniscus*. *Andinophryne* has partial fusion of the epicoracoid cartilages and lacks cranial crests

(Hoogmoed, 1985), both “atelopodine” features, but has parotoid glands, a “bufonine” feature. *Atelophryniscus* shares several “bufonine” traits but has a gastromyzophorous tadpole, a characteristic shared with *Atelopus*. The naturalness of the Cannatella arrangement is further compromised by confusion concerning the placement of *Rhamphophryne*. Cannatella (1986: 201) associated this genus with *Crepidophryne* and *Peltophryne* on the basis of sharing “fully arciferal pectoral girdles and the presence of cranial crests and parotoid glands. . . .” Hoogmoed (1985: 258), however, scored the girdle condition in *Rhamphophryne* as A_1 , following the terminology of McDiarmid (1971: 45), who described this condition as “anteriorly firmisternal, posteriorly arciferal.” Hoogmoed’s decision was apparently based on Trueb’s (1971: 16) description of *Rhamphophryne*, which stated: “The pectoral girdle is arciferal but tends to have a broad epicoracoid bridge.” As such, Hoogmoed (1985) associated *Rhamphophryne* with the “atelopodines” in spite of its possession of cranial crests and parotoid glands. The monophyletic nature of this genus also has been questioned by Cannatella (1986: 200), who noted that the “extensively ossified and protruding nasal region is the only unique derived feature of the genus.”

Another complication in assessing bufonid generic relationships is the lack of understanding about the huge and undoubtedly polyphyletic *Bufo*. Although usually considered to be characterized as having an adductor longus muscle (e.g., Hoogmoed, 1985: 258; Laurent, 1986: 702; Tihen, 1960: 232), one New World species, *B. ockendeni* (= *B. veraguensis*) is known to lack it (Limeses, 1964). This species also lacks a tympanum (Savage, 1969). *B. veraguensis* was placed in the same group with *B. fissipes* and *B. quechua* by Gallardo, 1961: 5), who noted that the tympanum is “not visible” in these two taxa. Three other species placed in this group by Gallardo (1961, 1967) have “visible” tympana. Duellman and Toft (1979: 62) described a new species, *B. nesiotetes*, indicating that it “presumably” belongs to the *veraguensis* group. *Bufo nesiotetes* has a “large, distinct” tympanum (although their drawing of the lateral view of the head of the holotype does not match the description), unlike some of the other members of this group. Unlike the “typical” New World *Bufo*, *B. nesiotetes* and *B. fissipes* lack cranial crests. All members of the *veraguensis* group occur in montane habitats in Perú and Bolivia. Six Central American and southern Mexican montane species (*B. bocourti*, *B. fastidiosus*, *B. holdridgei*, *B. periglenes*, *B. peripatetes*, and *B. tacanensis*) and two South American species (*B. cophotis* and *B. variegatus*) lack both a tympanum and a columella (Boulenger, 1900; Martin, 1972; Savage, 1972; Smith, 1952; pers. observ.). Some individuals of the Mexican *B. occidentalis* have the tympanum concealed by skin (Duellman, 1961). Unlike other *Bufo*, members of the *B. haematiticus* group have an omosternum (Trueb, 1971). Finally, *Bufo nesiotetes* has few, large, unpigmented eggs which, as noted by Duellman and Toft (1979: 63), makes it “an unlikely candidate for the usual

mode of reproduction in *Bufo*—strings of small pigmented eggs in water.” They further indicated that “it is possible that *B. nesiotetes* lays terrestrial eggs undergoing direct development.”

Absence of data regarding aspects of reproduction and/or reproductive behavior for many New World genera (including many of the montane species of “*Bufo*” discussed above) makes it difficult to assess the phylogenetic relevance of these features of bufonid biology. Finally, the scant effort to search for the relationships between New and Old World genera of bufonids renders suspect any arrangement based only on genera from one hemisphere or the other. Further discussion of the problems presented by our poor state of knowledge of New World bufonids is in Hoogmoed (1985: 261–262).

Given the existence of these problems, it is futile at this juncture to attempt a phylogenetic analysis of relationships within any generic segment of the family Bufonidae. We limit our comments on the relationships of *Atelophryniscus*, therefore, to consideration of its probable closest relative. *Atelophryniscus* appears to be a derivative of some group of *Bufo*, agreeing with this taxon in possessing a number of primitive features (including, in addition to the “bufonine” features [we consider the presence of parotoid glands primitive, following Grandison, 1981, not derived as suggested by Cannatella, 1986] a short tensor fasciae latae, S+E adductor mandibulae, 8 presacral vertebrae, palatine bone well-developed, 2-2-3-3 phalangeal formula, coccyx without expanded lateral edges, 2 centralia in hand). The principal distinction between these two genera is in the possession of a gastromyzophorous tadpole by *Atelophryniscus*. The resemblance between this tadpole and those of *Atelopus* might be considered as an argument for a relationship between this genus and *Atelophryniscus*. We consider the resemblance to represent convergence resulting from adaptation to similar environments. Mountain-stream tadpoles typically exhibit adaptation for life in rapidly-flowing streams by having a depressed body, muscular tail with low fins, and either suctorial mouthparts or a suctorial abdominal disc. Suctorial mouthparts are known in a variety of mountain-stream-breeding anurans. As noted above, only a few species of anurans are known to possess the gastromyzophorous condition. We thus consider the resemblance of *Atelophryniscus* and *Atelopus* to result from the superimposition of stream-adapted features (including the suctorial abdominal disc) on the standard bufonid tadpole morphology ($2/3$ tooth rows, median anal tube, and sinistral spiracle).

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