

Advertisement calls of *Melanophrynniscus dorsalis* (MERTENS, 1933) and *M. montevidensis* (PHILIPPI, 1902), two parapatric species from southern Brazil and Uruguay, with comments on morphological variation in the *Melanophrynniscus stelzneri* group (Anura: Bufonidae)

AXEL KWET, RAÚL MANEYRO, ANNE ZILLIKENS & DIETRICH MEBS

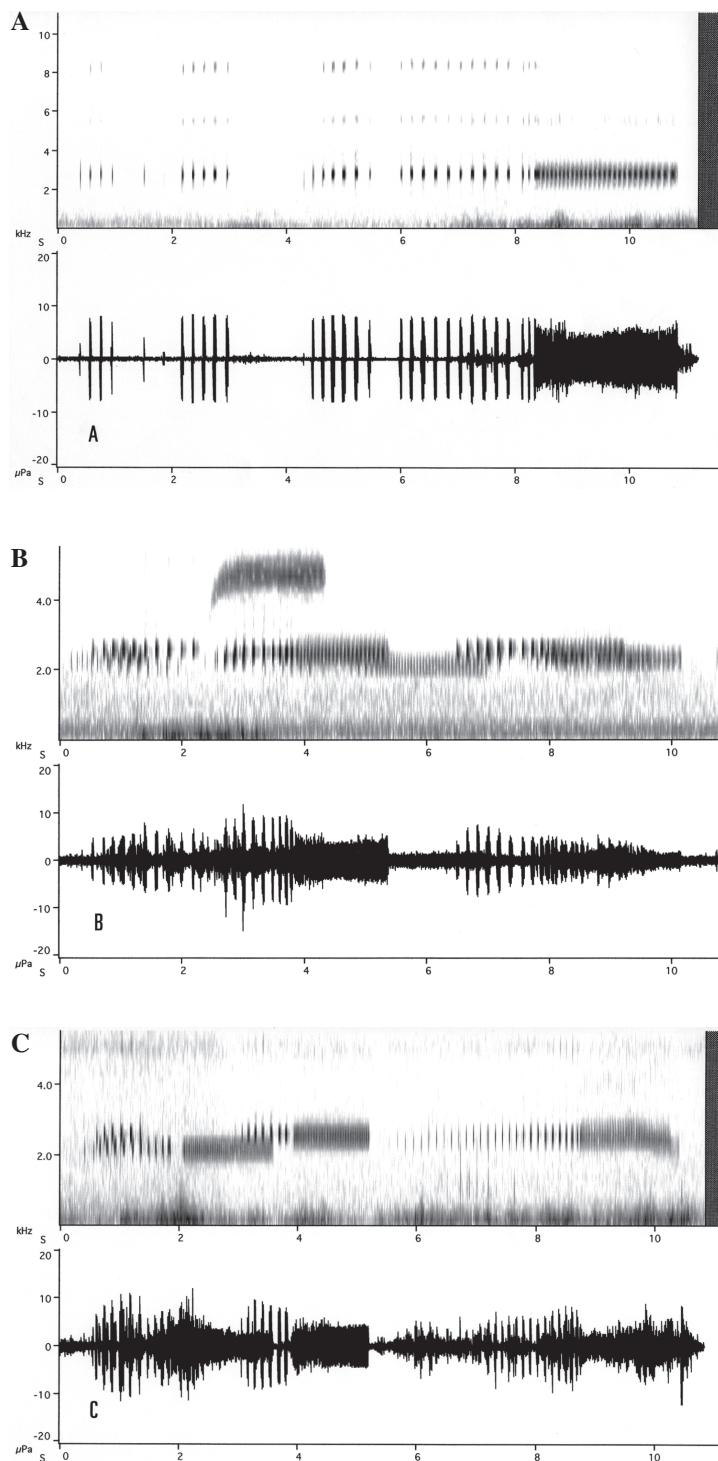
Abstract. The advertisement calls of *Melanophrynniscus montevidensis* and *M. dorsalis*, two red-bellied toads of the *M. stelzneri* group, are described for the first time. *Melanophrynniscus dorsalis* is endemic to the coastal zone of southern Brazil (southern Santa Catarina and northern Rio Grande do Sul), whereas *M. montevidensis* has a parapatric distribution in the coastal regions of Uruguay and extreme southern Rio Grande do Sul. The calls of both species are similar to the published calls of *M. atroluteus* and *M. stelzneri*. The advertisement call of *Melanophrynniscus dorsalis* differs from those of the other three species by a relatively high dominant frequency, long pulse duration and low pulse repetition rate. Although *Melanophrynniscus montevidensis* and *M. atroluteus* are bioacoustically not well distinguishable, they are considered distinct species because of geographical separation and morphological differences, such as colouration and skin structure. All taxa are closely related and show great intraspecific variation in advertisement call and body pattern. Remarks on the taxonomy of the *M. stelzneri* group are presented and a key for the identification of all known species is provided.

Key words. Anura: Bufonidae: *Melanophrynniscus dorsalis*, *Melanophrynniscus montevidensis*; advertisement call; Brazil; Rio Grande do Sul; Santa Catarina; Uruguay.

Introduction

Red-bellied toads of the genus *Melanophrynniscus* GALLARDO, 1961 are distributed in the southern parts of South America, ranging from Uruguay and southern Brazil (States of Rio Grande do Sul, Santa Catarina, Paraná, and Mato Grosso do Sul), across central and northern Argentina to Paraguay and central Bolivia. This genus is currently composed of 19 species which are arranged in three (CARAMASCHI & CRUZ 2002, CRUZ & CARAMASCHI 2003), or four (FROST 2002, LARSON et al. 2003) species groups based on external morphology (see Discussion). The *Melanophrynniscus moreirae* group consists of two species (*M. moreirae* [MIRANDA-RIBEIRO, 1920], *M. sanmartini* KLAPPENBACH, 1968), the *tumi-*

frons group of eight species (*M. cambaraensis* BRAUN & BRAUN, 1979, *M. devincenzi* KLAPPENBACH, 1968, *M. macrogranulosus* BRAUN, 1973, *M. orejasimirandai* PRIGIONI & LANGONE, 1987 “1986”, *M. pachyrhynus* [MIRANDA-RIBEIRO, 1920], *M. simplex* CARAMASCHI & CRUZ, 2002, *M. spectabilis* CARAMASCHI & CRUZ, 2002, *M. tumifrons* [BOULENGER, 1905]), the *rubriventris* group which is considered part of the *stelzneri* group by CARAMASCHI & CRUZ (2002) and CRUZ & CARAMASCHI (2003), of one species (the three subspecies of *M. rubriventris* [VELLARD, 1947] are now considered to be synonymous; see VAIRA 2002), and the *stelzneri* group of eight species (*M. atroluteus* [MIRANDA-RIBEIRO, 1920], *M. cupreuscapularis* CÉSPEDEZ & ALVAREZ, 2000 “1999”, *M. dorsalis* [MERTENS, 1933], *M. fulvogutta-*



Advertisement calls of *Melanophrynniscus dorsalis* and *M. montevidensis*

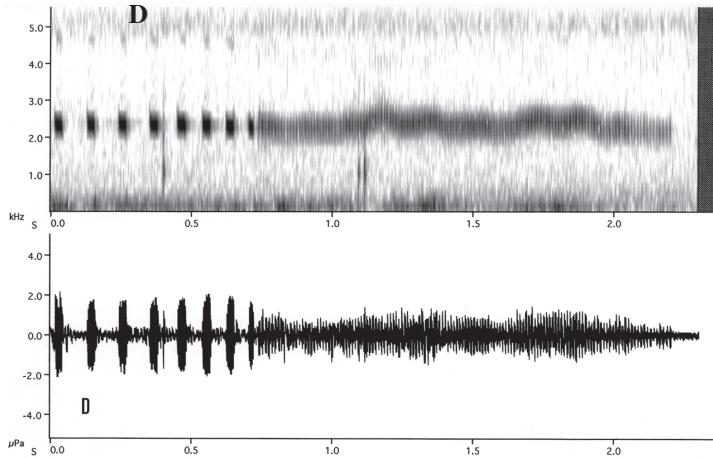


Fig. 1. Audiospectrograms (above) and oscillograms (below) of the advertisement calls of *Melanophrynniscus dorsalis*; (A) Laguna, Santa Catarina; (B) Torres, Rio Grande do Sul; (C, D) *Melanophrynniscus montevidensis*, La Paloma, Uruguay.

tus [MERTENS, 1937], *M. klappenbachi* PRIGGIO NI & LANGONE, 2000, *M. krauczuki* BALDO & BASSO, 2004, *M. montevidensis* [PHILIPPI, 1902], *M. stelzneri* [WEYENBERGH, 1875]). *Melanophrynniscus dorsalis* and *M. fulvoguttatus*, which have been treated until recently as subspecies of *M. stelzneri*, were elevated to species rank by CRUZ & CARAMASCHI (2003).

The remaining subspecies, *M. stelzneri spegazzini* GALLARDO, 1961, has never been collected since 1897 (LAVILLA & CEI 2001) and data are still lacking to re-evaluate its taxonomic status.

The *Melanophrynniscus stelzneri* group comprises small to mid-sized toads (snout vent-length 20-30 mm) which are character-

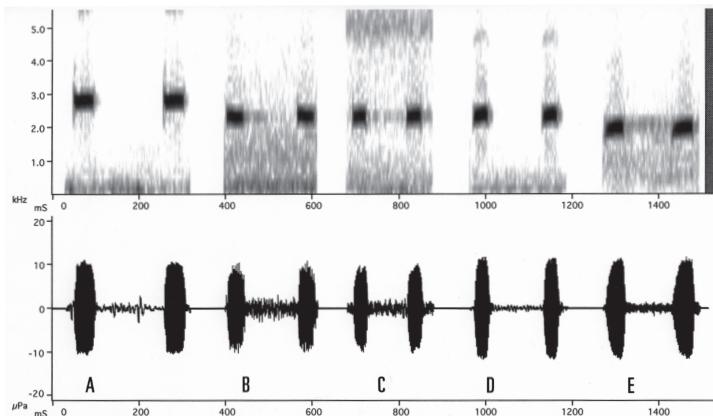


Fig. 2. Two pulses of type A call (audiospectrogram above, oscillogram below) of (A) *Melanophrynniscus dorsalis*, Laguna; (B) *Melanophrynniscus dorsalis*, Torres; (C) *Melanophrynniscus montevidensis*, La Paloma; (D) *Melanophrynniscus atroluteus*, Ausentes, Brazil; (E) *Melanophrynniscus stelzneri*, Argentina.

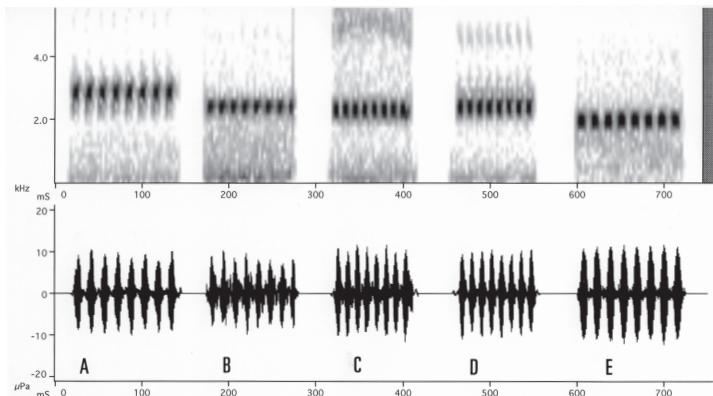


Fig. 3. Eight pulses of type B call (audiospectrogram above, oscillogram below) of (A) *Melanophrynniscus dorsalis*, Laguna; (B) *Melanophrynniscus dorsalis*, Torres; (C) *Melanophrynniscus montevidensis*, La Paloma; (D) *Melanophrynniscus atroluteus*, Ausentes, Brazil; (E) *Melanophrynniscus stelzneri*, Argentina.

ized by presenting small corneous spines, absence of a protuberance on the snout, and a predominantly black dorsal pattern usually with contrasting yellow spots (CRUZ & CARAMASCHI 2003). All species of the *M. stelzneri* group appear to have, as far as currently known, similar advertisement calls. The call of *M. stelzneri* was described by BARRIO

(1964) and STRANECK et al. (1993), the call of *M. atroluteus* by KWET & MIRANDA (2001) and BALDO & BASSO (2004), and the call of *M. krauczuki* by BALDO & BASSO (2004). The vocalization of all other members in this group has not yet been published.

The purpose of this paper is to describe the advertisement calls of *M. dorsalis* and *M. montevidensis*, two species we observed during field studies in southern Brazil and Uruguay. Moreover, we present new data on bioacoustic and morphological variation within the *stelzneri* group and provide a key to the identification of living specimens of the known species in this group.



Fig. 4. Amplexant pair of *Melanophrynniscus dorsalis*. Photo: A. KWET.

Material and Methods

Material collected during our field survey is deposited in the Museu de Ciências e Tecnologia da PUCRS, Porto Alegre (MCP), Staatliches Museum für Naturkunde Stuttgart (SMNS), and Sección Zoología Vertebrados, Facultad de Ciencias, UDELAR, Montevideo (ZVCB). Additional material examined (see Appendix) is housed in the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN).

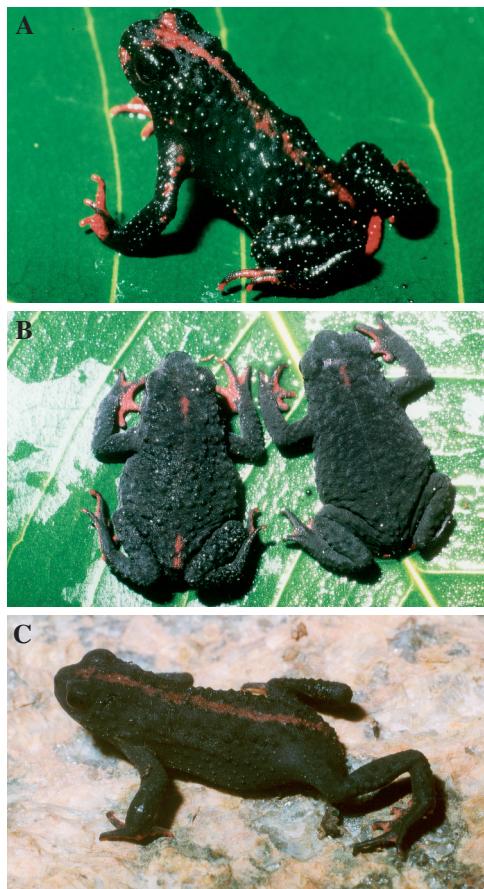


Fig. 5. Variation in dorsal body pattern in living *Melanophrynniscus dorsalis* from Brazil. (A) male with distinct red middorsal line from Torres, Rio Grande do Sul; (B) two males from Torres with weak middorsal line; (C) male with distinct middorsal line from Laguna, Santa Catarina. Photos: A. KWET.

Call recordings were made with a Sony WM-D6C tape recorder, a Sennheiser directional microphone system K6 with ME66 module on Sony Metal XR-90 metal tapes. Calls were analysed with the Macintosh-based signal analysis software Canary 1.2 (Cornell University) at a sampling frequency of 44.1 kHz.

Advertisement calls of *Melanophrynniscus dorsalis* were recorded on 25 October 2002, 16.00 h, at Itapeva (municipality of Torres), Rio Grande do Sul, 21 °C air temperature (tape AK 16A10, seven calls from two males, voucher specimens are in the series MCP 6446-47 and 6524-28); and on 2 November 2003, 16.45 h, at Laguna, Santa Ca-

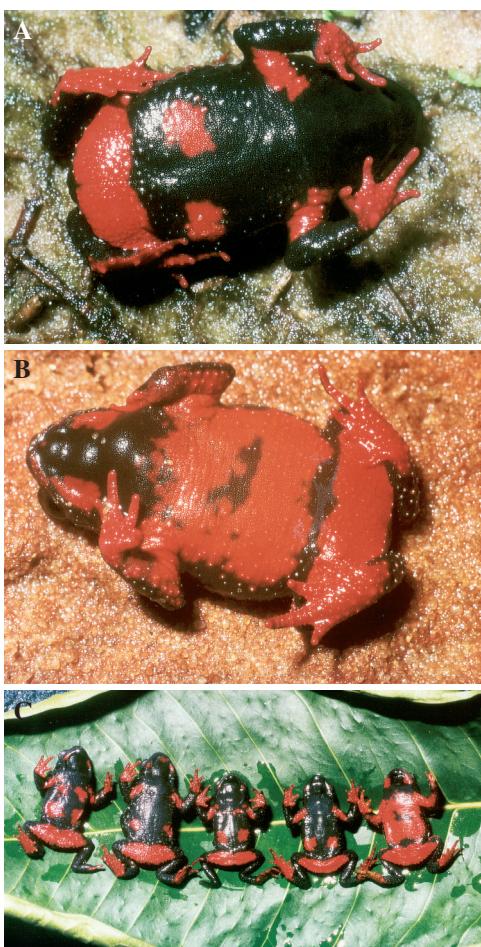


Fig. 6. Variation in ventral body pattern in living *Melanophrynniscus dorsalis* from Torres, Rio Grande do Sul. (A) male with predominantly black colouration; (B) male with predominantly red colouration; (C) series of five specimens. Photos: A. KWET.

Identification	Dominant frequency (kHz)	Other frequencies (kHz)	Call duration (s)	Pulse duration (ms)	Pulse interval (ms)	Pulses per call	Pulses per s
<i>M. dorsalis</i> (Laguna)							
– Type A	2.6-3.2	5.4-5.7	3.70 (3.5-4.1)	54.4 (30-65)	152.7 (130-190)	19 (18-20)	5-6
– Type B	2.6-3.2	5.4-5.7	2.37 (2.0-2.6)	7.3 (7.0-9.5)	7.1 (6.5-7.5)	161 (152-173)	62-74
<i>M. dorsalis</i> (Torres)							
– Type A	2.3-3.2	4.9-6.0	1.89 (1.0-2.3)	42.4 (20-50)	140.2 (80-170)	13 (6-18)	4-7
– Type B	2.3-3.2	4.9-6.0	1.50 (0.6-2.2)	7.1 (7.0-9.0)	6.9 (6.5-7.5)	112 (54-162)	74-78
<i>M. montevidensis</i>							
– Type A	2.1-2.8	4.4-4.5	1.98 (1.0-4.5)	31.3 (21-39)	103.5 (78-130)	17 (7-28)	8-10
– Type B	2.1-2.8	4.4-4.5	1.58 (1.2-2.0)	5.1 (4.5-6.0)	5.2 (5.0-6.0)	147 (100-192)	85-95
<i>M. atroluteus</i>							
– Type A	1.9-3.1	4.1-5.0 6.4-7.2	2.50 (1.8-3.2)	38.3 (21-43)	94.5 (85-100)	17.6 (11-26)	8-9
– Type B	1.9-3.1	4.1-5.0 6.4-7.2	1.10 (0.5-1.4)	5.5 (5.0-6.5)	5.3 (5.0-6.5)	87.6 (45-116)	85-95

Tab. 1. Call characteristics of *Melanophrynniscus dorsalis* from Laguna, Santa Catarina (20 °C; single male, n=3) and Torres, Rio Grande do Sul (21 °C; two males, n=7), Brazil; *M. montevidensis* from La Paloma, Uruguay (24 °C; two males, n=14); *M. atroluteus* from São José dos Ausentes, Rio Grande do Sul (21.5 °C; two males, n=10).

tarina, 20 °C air temperature (tape AK 18A5, three calls from one male, voucher specimen MCP 7660). *Melanophrynniscus montevidensis* was recorded on 25 October 2003, 16.50 h, at La Paloma, Uruguay, 24 °C air temperature (tape AK 18A1, 14 calls from two males, voucher specimens are in the series ZVCB 10625-10639 and SMNS 11807-11816). For comparison, we reanalysed tape recordings of the published calls of *Melanophrynniscus atroluteus* (KWET & MIRANDA 2001) from São José dos Ausentes, Rio Grande do Sul, and *Melanophrynniscus stelzneri* (STRANECK et al. 1993) from Córdoba, Argentina.

Measurements of snout-vent length (SVL) were made with digital calipers and rounded to 0.1 mm. Variation in ventral and dorsal body pattern was examined recording the size, shape and colour of blotches and mid-dorsal lines on dorsum and venter.

Results

Advertisement calls

The advertisement calls of *Melanophrynniscus dorsalis* and *M. montevidensis* are very similar to those of *M. atroluteus* and *M. stelzneri* (Table 1, Figs. 1-3). In all species, the typical vocalization is composed of two call types (here named A and B). Usually, it begins with the A type lasting about 1-5 s consisting of single notes, that are separated by relatively long time intervals. This call is usually followed by the B type, a 0.5-3 s lasting trill consisting of 100-200 notes with short time intervals. Due to high intraspecific bioacoustic variation, it is difficult for the human ear to distinguish between these four species, especially between *M. montevidensis* and *M. atroluteus* which have nearly identical calls. On average, the call of *M. stelzneri* has the lowest and *M. dorsalis* the

highest dominant frequency, and both calls present relatively low note repetition rates in comparison to those of *M. montevideensis* and *M. atroluteus*.

In *Melanophryniscus dorsalis*, A type calls had a variable duration of about 1-4 s, whereas B type calls were shorter on average lasting between 0.6 and 2.6 s (Table 1, Figs. 1A, B, 2A, B, 3A, B). The dominant frequency range in both call types was between 2.3 and 3.2 kHz presenting weak harmonic frequency bands between 4.9 and 6.0 kHz and between 7.8 and 8.4 kHz. Type A consisted of 6-20 unpulsed notes, each lasting 20-65 ms with time intervals of 80-170 ms (Figs. 2A, B). Sometimes small groups of 5-7 pulses were separated by 0.5-1 s lasting intervals (Fig. 1A). Type B consisted of 50-180 pulses, each pulse with a duration of 7-9.5 ms being separated by time intervals of 6.5-7.5 ms (Figs. 3A, B). The pulse rates were 4-7 pulses per s for type A and 60-80 pulses per s for type B (air temperature 20-21 °C). The call of *M. montevideensis* (Table 1, Figs. 1C, D, 2C, 3C) differed in its higher pulse rates (type A with 8-10 pulses per s, type B with 85-95 pulses per s) and shorter pulse duration and pulse intervals. Parts of these differences may be explained by the higher air temperature (24 °C) in the recording of *M. montevideensis* but the call of this species presented also on average a lower dominant frequency (2.1-2.8 kHz versus 2.3-3.2 kHz in *M. dorsalis*). In both species, certain specimens were able to change their calling frequency by up to 800 Hz within 100 ms. This considerable frequency modulation was observed especially in the B type call (Fig. 1D) and led to broadly overlapping spectral parameters between the species.

We recorded calling males of *Melanophryniscus dorsalis* and *M. montevideensis* in October and November. The habitats were similar in both species consisting of grassland or low dune vegetation on sandy soil in the coastal zones near the Atlantic Ocean. Males called from morning through afternoon and early night partially submerged in small temporary ponds. In a moist meadow in

La Paloma, Uruguay, we observed many *M. montevideensis* being active in plain sunshine. In Torres, Brazil, we heard about 20 males of *M. dorsalis* calling in the afternoon and we observed an amplexant pair which attached a clutch with 20-30 eggs to an aquatic plant, about five centimeters below the water surface (Fig. 4). In the laboratory, this pair spawned additional small clutches with a total amount of 105 black eggs, of 1.2-1.4 mm in diameter, which did not develop into tadpoles.

Inter- and intraspecific morphological variation

Regarding the dorsal body pattern of *Melanophryniscus dorsalis* and *M. montevideensis*, we found considerable variation within both species. In a series of *M. dorsalis* from Torres (MCP 233-266), 28 out of 36 specimens exhibited a complete or partly interrupted red middorsal line, whereas the remaining specimens presented only a trace of this stripe between and behind the eyes, or above the anus (Figs. 5A-C). In a second series collected recently (MCP 6524-28), only one of the five specimens had a distinct middorsal line. The great variation in dorsal pattern is further expressed by several *M. dorsalis* in the MCN collection presenting yellow spots on their flanks (e. g., MCN 12588). Such lateral blotches are typical for *M. montevideensis* which, on the other hand, never show a red middorsal line (Figs. 7A-C). However, we also collected many *M. montevideensis* with no lateral blotches at all, although the uniformly black dorsal pattern is considered to be the main character for the identification of *M. atroluteus* (Figs. 9A, C; see also LANGONE 1994, 2002). Sixteen out of 25 individuals (64 %) of *M. montevideensis* collected in La Paloma, Uruguay (ZVCB 10625-10639, SMNS 11807-11816), were uniformly black on dorsum. This was also the case in 25 % of the specimens from Perla de Rocha, 50 km NE from La Paloma (ZVCB 10432-10443), in 70 % of the specimens from Co-



Fig. 7. Variation in dorsal body pattern in living *Melanophryniscus montevidensis* from La Paloma, Uruguay. Specimen with (A) numerous yellow lateral spots; (B) few lateral spots; (C) without lateral spots. Photos: A. KWET.

ronilla (ZVCB 11019-11035), and in 13 % of those from Cabo Polonio (ZVCB 10994-11016).

In both *M. dorsalis* and *M. montevidensis* the ventral pattern varies considerably. Living specimens show a conspicuous pattern of symmetrically arranged red, orange-red or yellow blotches on black ground. In preser-

vative, this colouration fades to a pale brown within some days. In living *M. dorsalis* all blotches are bright red, but never orange or yellow (Figs. 6A-C), whereas the ventral colouration of *M. montevidensis* varies from orange-red on the posterior half of belly and thighs, to orange or yellow on the anterior



Fig. 8. Variation in ventral body pattern in living *Melanophryniscus montevidensis* from La Paloma, Uruguay. (A), (B) specimens with many ventral spots; (C) specimen with only a few ventral spots. Photos: A. KWET.

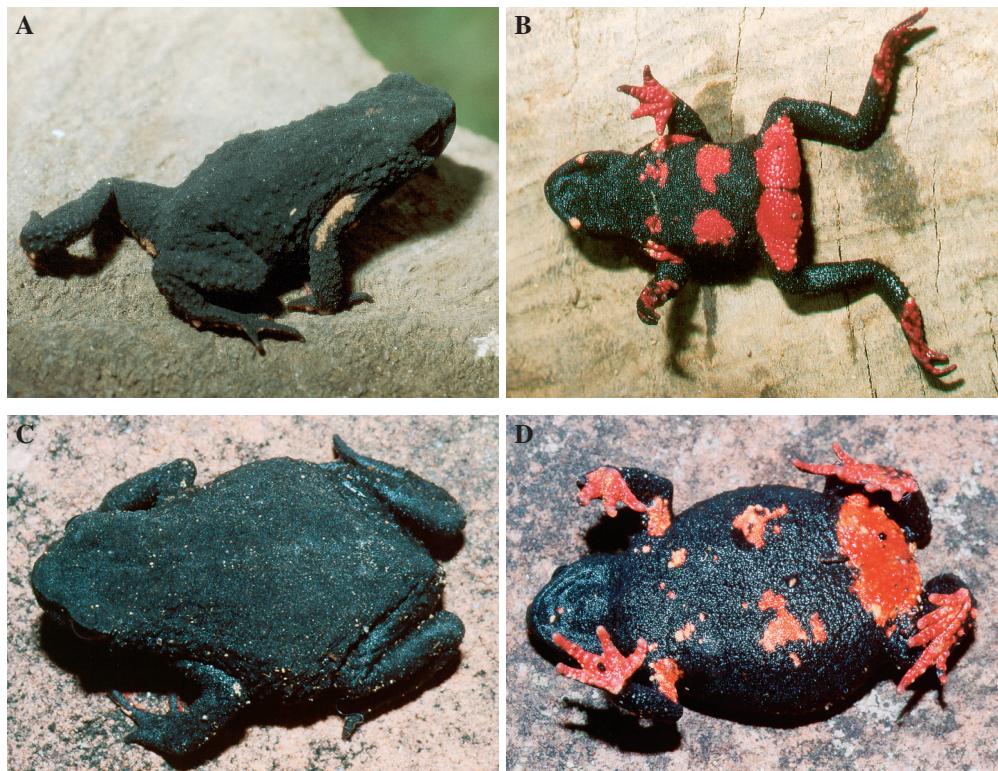


Fig. 9. *Melanophrynniscus atroluteus* from the Brazilian Araucaria plateau: (A) dorsal surface; (B) ventral surface. Photos: A. KWET. Specimen from São Borja, near the type locality: (C) dorsal surface; (D) ventral surface. Photos: M. DI-BERNARDO.

half of the belly and the throat (Figs. 8A-C). Due to this colouration, *M. montevidensis* is locally named “Sapito Bandera Española” (Spanish flag toadlet). There is also a considerable variation regarding size and shape of these blotches. In both species, most individuals are predominantly black on belly and throat, while in some specimens the red colouration predominates (Fig. 6B).

The ventral colouration of living *M. atroluteus* from the Brazilian type-locality in western Rio Grande do Sul and from Uruguay and Argentina is similar to that of *M. montevidensis* consisting of red, orange and yellow spots (Fig. 9D), but specimens from the Araucaria plateau of Rio Grande do Sul (São José

dos Ausentes) are almost exclusively red with yellow colouration only on throat (Fig. 9B). Additionally, there are differences when comparing the snout-vent length of adult specimens from the Araucaria plateau (SVL in males about 25 mm, in females 28 mm; KWET & MIRANDA 2001) with that of individuals from western Rio Grande do Sul, Argentina and Uruguay (SVL in males between 19 and 21 mm, in females between 22 and 25 mm; LANGONE 1994). For *M. dorsalis*, our own measurements revealed a SVL of 20-25 mm in males and 24-27 mm in females, for *M. montevidensis* 20-23 mm in males and 22-27 mm in females, and for *M. atroluteus* 18-24 mm in males and 22-26 mm in females.

Key to the species of the *Melanophrynniscus stelzneri* group

- 1 a.** Dorsum uniformly brown. *Melanophrynniscus krauczuki*
- 1 b.** Dorsum black. 2
- 2 a.** Dorsum black with many small and/or few large yellow spots; at least one pair of yellow blotches on the suprascapular region. 3
- 2 b.** Dorsum uniformly black or with red middorsal line, without yellow spots on middorsum or suprascapular region (however, yellow blotches may be present laterally). 6
- 3 a.** One yellow stripe between the eyes or 2-3 large yellow blotches forming a distinct interocular band. Dorsal and ventral surfaces with large and small, irregularly formed, yellow spots, sometimes with a black center (Figs. 10A, B). *Melanophrynniscus klappenbachi*
- 3 b.** Without distinct yellow interocular band. Dorsal surface with numerous small, or few mid-sized yellow spots without black center. 4
- 4 a.** Dorsum and venter with numerous small, irregularly arranged yellow spots; yellow blotches on suprascapular region not enlarged (Figs. 10C, D). Skin densely granular. *Melanophrynniscus fulvoguttatus*
- 4 b.** Dorsum and venter with larger, symmetrically arranged blotches; at least one pair of distinct yellow blotches on suprascapular region. Skin scarcely granular or nearly smooth. 5
- 5 a.** Dorsal surface uniformly black with a pair of distinct large, copper-coloured blotches on suprascapular region (Figs. 10E, F). *Melanophrynniscus cupreuscapsularis*
- 5 b.** Dorsal surface black with two large yellow blotches on suprascapular region and additional smaller and larger yellow spots on dorsum (Fig. 11). *Melanophrynniscus stelzneri*
- 6 a.** Dorsum usually with a distinct red (brown in preservative) middorsal line which is rarely absent but often interrupted or present only as a small trace behind the eyes and/or above anus. Without yellow lateral blotches and yellow line on posterior region of arms (sometimes there are few reddish spots). Ventral surface with red (not orange or yellow) blotches (Figs. 5, 6). *Melanophrynniscus dorsalis*
- 6 b.** Dorsum without red middorsal line; uniformly black, with or without yellow lateral spots. Distinct yellow stripe on posterior region of the arms. Ventral surface black, with red, orange and yellow spots (yellow colouration at least present on throat). 7
- 7 a.** Dorsum uniformly black, without yellow lateral blotches (Fig. 9). Skin texture warty and granular. Distribution in rocky habitats; does not occur in sandy areas on the coast. *Melanophrynniscus atroluteus*
- 7 b.** Dorsum usually with yellow lateral spots (Figs. 7, 8), but sometimes uniformly black. Skin texture less granular. Exclusively in sandy habitats on the coast. *Melanophrynniscus montevideensis*

Discussion

The seven species currently recognized in the *Melanophrynniscus stelzneri* group are *M. atroluteus*, *M. cupreuscacularis*, *M. dorsalis*, *M. fulvoguttatus*, *M. klappenbachi*, *M. krauczuki*, *M. montevideensis* and *M. stelzneri*. Due to clear differences in size, external morphology and colouration, we follow CÉSPEDEZ & ALVAREZ (1999) and LARSON et al. (2003) by not including *M. rubriventris* in the *stelzneri* group, although these authors do not provide specific reasons for considering *M. rubriventris* as a different group. LARSON et al. (2003) refer to LAVILLA & VAIRA (1997) and FROST (2002), who did not explicitly make these statements. However, *M. rubriventris* (Figs. 12A, B) is a medium sized species (snout-vent length 38–45 mm) with dark brown to blackish dorsal colouration and strongly glandular skin (large granules), whereas all members of the *stelzneri* group are morphologically similar being smaller than 30 mm and having small granules on a deep black dorsum, except the recently described *M. krauczuki*, which is brown. In life, all species present a conspicuous ventral pattern of variably shaped, bright red, orange or yellow spots on black ground. On dorsum, most species exhibit yellow spots and blotches varying in number and size, except *M. dorsalis* which has a red middorsal stripe and *M. atroluteus* which is uniformly black (this partly applies also to *M. montevideensis*). Members of the *Melanophrynniscus tumifrons* group are easily distinguished by the presence of a large protuberance on the snout (Fig. 13A).

Melanophrynniscus dorsalis was originally described as a subspecies of *M. stelzneri* from Torres, Rio Grande do Sul, Brazil (MERTENS 1933). As main characteristics separating *M. stelzneri dorsalis* from the type form, MERTENS (1933) noted the more slender body, longer legs and different dorsal colouration without yellow points. CRUZ & CARAMASCHI (2003) considered *M. dorsalis* as a full species and provided an exact redescription of

preserved and, thus, faded specimens. Therefore, we emphasize here that the colouration in life (Figs. 5, 6) is deep black in this species (dark brown in preservative, as stated by CRUZ & CARAMASCHI 2003) and bright red (clear brown or pale yellow in CRUZ & CARAMASCHI 2003). According to MERTENS (1933) and CRUZ & CARAMASCHI (2003), most specimens have the name-bearing middorsal line but there are also specimens without this stripe. BRAUN (1978) mentioned that the distribution of *M. dorsalis* is restricted to the coastal range of southern Brazil, from Cidreira in northern Rio Grande do Sul to Laguna in southern Santa Catarina. CÉSPEDEZ (1997) cited *M. stelzneri dorsalis* for the Argentinean province Misiones but LAVILLA et al. (2002) mentioned that this material presumably belongs to *M. atroluteus*. Hence, *M. dorsalis* must be considered to be endemic to the coastal region of northern Rio Grande do Sul and southern Santa Catarina, as stated in GARCIA & VINCIPROVA (2003).

On the other hand, *Melanophrynniscus montevideensis* occurs in the coastal zones of the Río de la Plata and the southern Atlantic Ocean. For a long time, it has been considered to be endemic to Uruguay (LANGONE 1994), but recently TEDROS et al. (2001) expanded the known distribution of *M. montevideensis* from the Uruguayan departments of Canelones, Maldonado, Montevideo, Rocha and San José (NUÑEZ et al. 2004) to Alvorada, Barra do Chui, in the extreme south of Rio Grande do Sul. Up to date, there are neither records for *M. montevideensis* nor *M. dorsalis* from the central coast of Rio Grande do Sul and it seems that both taxa are parapatrically distributed.

The taxonomy in the *stelzneri* group is not yet adequately resolved. KLAPPENBACH (1968) described the overall morphological similarity between *M. montevideensis* and *M. atroluteus* stating the taxonomic priority of *M. montevideensis*. However, KLAPPENBACH (1968) also left the possibility of *M. atroluteus* being a subspecies of *M. stelzneri*. Accordingly, some following authors regarded

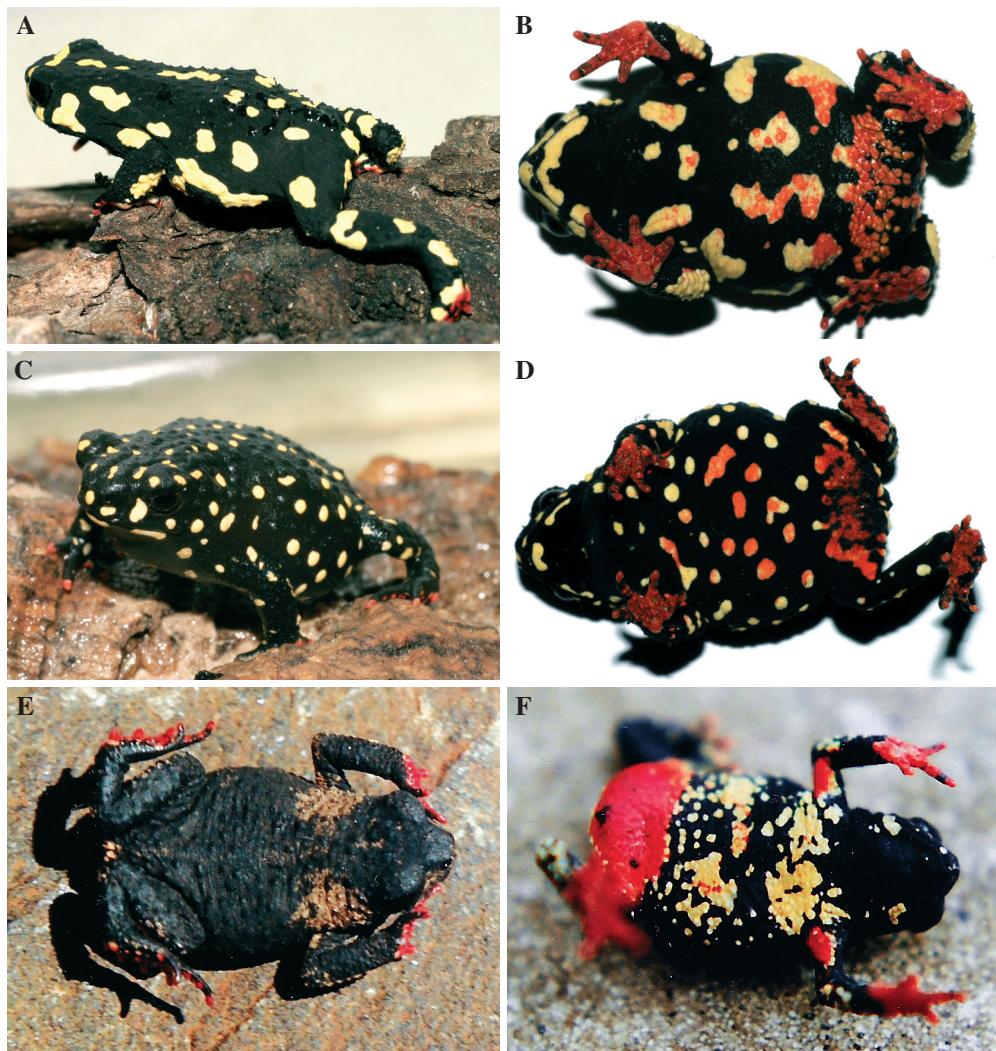


Fig. 10. *Melanophryniscus klappenbachi* (without locality; specimen from pet trade): (A) dorsal surface; (B) ventral surface. *Melanophryniscus fulvoguttatus* (without locality; specimen from pet trade): (C) dorsal surface; (D) ventral surface. Photos: T. EISENBERG. *Melanophryniscus cupreuscularis* from Argentina: (E) dorsal surface; (F) ventral surface. Photos: D. BALDO.

both taxa as synonymous, e. g., CEI (1980), FROST (1985) and LAVILLA (1992), whereas others, like BRAUN & BRAUN (1974, 1980), CEI (1987) and KOLENC (1987), considered them as valid subspecies of *M. stelzneri*. Based on

an unpublished revision, KLAPPENBACH & LANGONE (1992) elevated *M. montevidensis* and *M. atroluteus* to full species rank which was generally accepted (e. g., LANGONE 1994, MANEYRO et al. 1995, KWET & MIRANDA 2001,

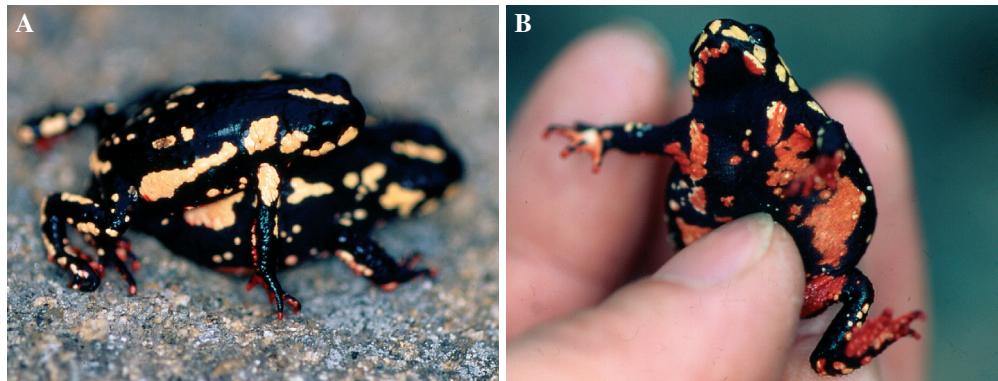


Fig. 11. *Melanophrynniscus stelzneri* from Argentina: (A) dorsal surface; (B) ventral surface. Photos: B. SCHLUMPERGER.

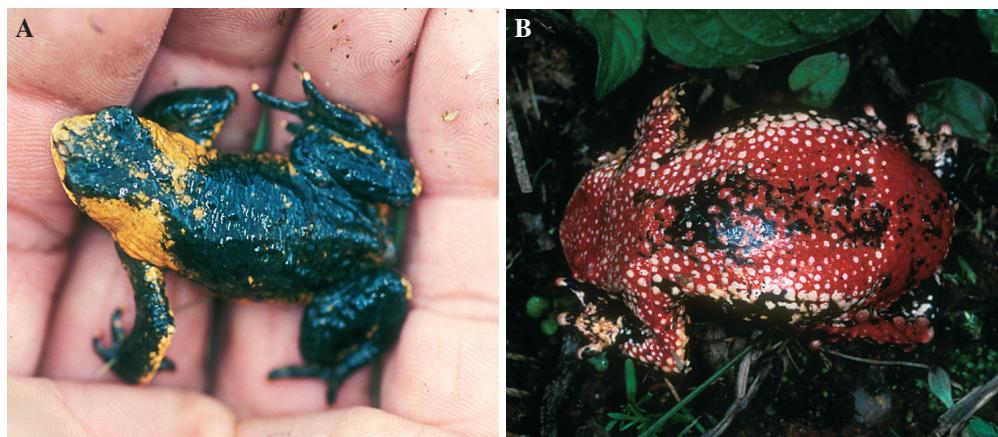


Fig. 12. *Melanophrynniscus rubriventris*, (A) dorsal surface; (B) ventral surface. Photos: B. SCHLUMPERGER.

LAVILLA & CEI 2001, MANEYRO & LANGONE 2001). To confirm this, KWET & MIRANDA (2001) suggested a comparison of the advertisement calls of both species. Whereas the bioacoustic data presented here support *Melanophrynniscus dorsalis* as a full species, as proposed by CRUZ & CARAMASCHI (2003), our data did not allow a differentiation between *M. montevideensis* and *M. atroluteus*, due to

the high intraspecific acoustic variation. Similarly, the dorsal colouration used by LANGONE (2002) as main character to distinguish *M. montevideensis* (with yellow spots on dorsal surface) from *M. atroluteus* (without yellow dorsal spots) is not sufficient because many specimens of *M. montevideensis* we collected were uniformly black on dorsum. This was also observed by KOLENC (1987). None-

theless, we maintain the specific status of both taxa pending further investigations. The two species seem to differ in morphological details (e. g., skin structure) and occur in different habitats which are well separated (*M. montevidensis* lives exclusively in sandy areas on the coast, whereas *M. atroluteus* occurs in rocky habitats in the interior).

Additionally, we stress the differences in snout-vent length and body colouration of populations of *M. atroluteus* from the Brazilian Planalto (KWET & MIRANDA 2001) and from the southwestern Rio Grande do Sul, adjacent Argentina and Uruguay (LANGONE 1994, 2002, ACHAVAL & OLMO 2003), including the Brazilian type-locality Itaqui (MIRANDA-RIBEIRO 1920). The latter population is represented by relatively small individuals with orange-red and yellow spots on the belly (*M. atroluteus* is described as having three yellow blotches on venter in the identification key by CÉSPEDEZ & ALVAREZ 1999, but usually these spots are orange in life; see Fig. 9D), whereas specimens from the Planalto are larger having a predominantly red ventral colouration. These differences suggest that *M. atroluteus* could be composed of two or more species. A general revision is needed which must also include the disjunct populations from the Sierras de la Ventana and de Tandil, Argentina, which are variably assigned to *M. montevidensis*, *M. atroluteus* or *M. stelzneri* (CEI 1980, KLAPPENBACH & LANGONE 1992, CABRERA 2001, CÉSPEDEZ & MOTTE 2001, LAVILLA & CEI 2001). VAIRA (2002), who studied different populations of *Melanophrynniscus rubriventris*, found an extremely high intraspecific variability in dorsal and ventral colouration and a broad overlap in most morphological parameters. Hence, he considered all subspecies of *M. rubriventris* as synonyms and stated that dorsal and ventral pattern may be inadequate for making delimitations between putative species or subspecies in the genus *Melanophrynniscus*. This statement, which is supported by our data on the body colouration of *M. dorsalis* and *M. montevidensis* to some

extent, seems to be also valid for bioacoustic characteristics, due to the great variation in frequency range, pulse duration, and pulse repetition rate. In order to resolve the taxonomic problems in this group, molecular techniques may be useful.

The species diversity within the genus *Melanophrynniscus* is much higher than currently acknowledged and there are several species to be described. Five taxa are currently known from Uruguay (KLAPPENBACH & LANGONE 1992, ACHAVAL & OLMO 2003, LANGONE 2003, NUÑEZ et al. 2004) and the status of some disjunct populations must be revised (e. g., *M. sanmartini*). Nine valid taxa are cited for Argentina (CÉSPEDEZ & ALVAREZ 1999, PRIGONI & LANGONE 2000, CÉSPEDEZ & MOTTE 2001, LAVILLA & CEI 2001), where at least three additional populations are taxonomically not yet resolved (CÉSPEDEZ & MOTTE 2001). Five species are known solely from the Argentinean province Misiones, three of which are undescribed (DIEGO BALDO, pers. comm.). Besides Misiones and Uruguay, the Brazilian state of Rio Grande do Sul is the focal point of distribution of the genus *Melanophrynniscus*. To date, there are seven species cited for this state (KWET 2001 and unpubl. data) and an undescribed species which might be the most spectacular species known so far in the genus *Melanophrynniscus* possessing a green dorsum and a black, bright red, green and yellow coloured venter was recently discovered in Rio Grande do Sul (Figs. 13B, C; DI-BERNARDO et al., pers. comm.). Furthermore, we stress the possibility that two specimens figured as *M. dorsalis* in FONTANA et al. (2003: 587) may belong to another undescribed taxon and at least four additional species of *Melanophrynniscus* are known from localities near the border to Rio Grande do Sul: *M. simplex* and *M. spectabilis*, two members of the *tumifrons* group recently described from Santa Catarina (CARAMASCHI & CRUZ 2002), and *M. sanmartini* and *M. devincenzi*, two Uruguayan species (ACHAVAL & OLMO 2003, LANGONE 2003). *Melanophrynniscus sanmartini*, described from

southern Uruguay, was recently found in commercial forest plantations in the north (NAYA & MANEYRO, 2001), only a few hundred meters from the Brazilian border. *Melanophryniscus devincenzi* is also distributed in this region, although the only citation of this species for Rio Grande do Sul (in a distribution map by CÉSPEDEZ & MOTTE 2001) must be considered to be erroneous and up to date there were no specimens collected. Nonetheless, an occurrence of all these taxa in Rio Grande do Sul is highly probable, due to geographical proximity and absence of barriers which would prevent the species' spreading.

Notes on the life history of *Melanophryniscus* are generally scarce. CEI (1980) provided notes on the life history of *M. stelzneri* and figured its aposematic behavior known as "Unkenreflex" (display of the bright colours of the ventral region as a defensive posture). We observed this behavior in both *M. dorsalis* (Fig. 14A) and *M. montevidensis*. The "Unkenreflex" is also typical among species of the *tumifrons* group (Fig. 14B). KOLENC (1987), PRIGONI & GARRIDO (1989), LANGONE (1994, 2002) and ACHAVAL & OLMO (2003) provided data on the life history of the Uruguayan species of *Melanophryniscus*, including *M. montevidensis*. GARRIDO-YRIGARAY (1989) described the larva of *M. montevidensis*, but very little is known about *M. dorsalis* (GARCIA & VINCIPROVA 2003). BRAUN (1978) collected active *M. dorsalis* in April, which were found crawling in dune vegetation near the ocean in the sunset. Our observations confirmed that both species live exclusively in open areas and sand-dunes near the Atlantic coast. They are mass-breeders and in the warm season, from October through March, hundreds of individuals appear simultaneously during or directly after heavy rainfalls. Males call from morning to early night, but their calling activity decreases quickly after one or two days without rain. However, in moist habitats individuals can be observed foraging in the sun and even in winter months it is possible to find active

specimens, although only after rainfall (KOLENC 1987, MANEYRO et al. 1995). *Melanophryniscus montevidensis* and *M. dorsalis* are frequently observed in the surroundings of small villages and urbanization close to the shore is considered to be a potential threat for both species (KOLENC 1987, MANEYRO et al. 1995, LANGONE 2002, GARCIA & VINCIPROVA 2003).

Appendix

M. atroluteus: Brazil: Rio Grande do Sul: Garruchos: MCP 858-69, São Borja: MCP 6127-29, 7538-39, São José dos Ausentes: MCP 4607-09, São Nicolau: MCP 599, Tenente Portela: MCP 3158. Argentina: Entre Ríos: SMNS 8591, Misiones: MCP 612-13, 618, 636-41. *M. dorsalis*: Brazil: Rio Grande do Sul: Torres: MCN 7818-7913, 8409, 10072-79, 12588, 13293, MCP 233-66, 319-20, 6446-47, 6524-28; Santa Catarina: Laguna: MCP 7660. *M. fulvoguttatus*: Paraguay: SMNS 11789, 11924. *M. klappenbachii*: without locality: SMNS 11923:1-5. *M. cf. klappenbachii*: Paraguay: Cordillera: San Bernardino: SMNS 11652:1-10. *M. montevidensis*: Uruguay: Rocha: Cabo Polonio ZVCB 10994-11016; Coronilla: ZVCB 11019-35; La Paloma: SMNS 11807-11816, ZVCB 10625-10639; Perla de Rocha: ZVCB 10432-10443. *M. rubriventris*: Argentina: Jujuy: SMNS 8592; Salta: SMNS 8428:1-2. *M. stelzneri*: Argentina: Sierra de Córdoba: SMNS 1880:1-3, SMNS 7094-7115.

Acknowledgements

We thank MARCOS DI-BERNARDO and WOLF ENGELS for their valuable support and ANDREAS SCHLÜTER, DIEGO BALDO and ARLEY CAMARGO for critical comments on the manuscript. We are indebted to TOBIAS EISENBERG, BORIS SCHLUMPERGER and DIEGO BALDO for providing photographs. MIRCO SOLÉ provided measurements of some specimens. We thank MARIANA BEHEREGARAY and ANDRÉS CANAVERO for valuable help during our fieldwork. AK and AZ received financial support by German Federal Ministry of Education and Research (BMBF project 01LB0205 and DLR project BRA 02/008). RM was partially supported by a grant from PEDECIBA Biología and had a doctoral fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

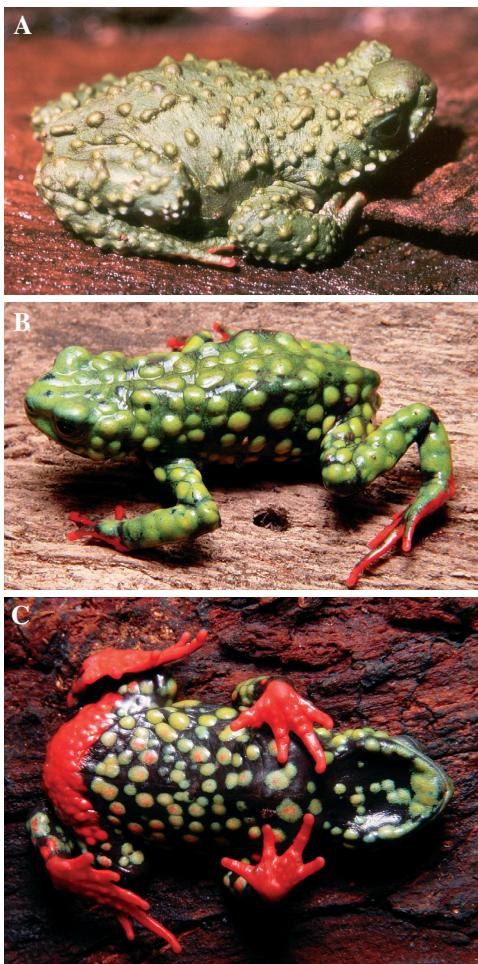


Fig. 13. (A) *Melanophryniscus cambaraensis*, a member of the *tumifrons* group. Photo: A. KWET. Undescribed species of *Melanophryniscus* from Rio Grande do Sul, MCP 7923, a female, (B) dorsal surface; (C) ventral surface. Photos: M. DI-BERNARDO.

References

- ACHAVAL, F. & A. OLMO (2003): Anfibios y reptiles del Uruguay. 2. edition. – Montevideo, Uruguay (Graphis Impresora), 136 pp.
- BALDO & BASSO (2004): A new species of *Melanophryniscus* GALLARDO, 1961 (Anura: Bufonidae), with comments on the species of the genus reported for Misiones, Northeastern Argentina. – J. Herpetol., **38**(3): 393-403.
- BARRIO, A. (1964): Peculiaridades del canto nupcial de *Melanophryniscus stelzneri* (WEYENBERGH) (Anura, Brachycephalidae). – Physis, **24**(68): 435-437.
- BRAUN, P.C. (1978): Ocorrência de *Melanophryniscus stelzneri dorsalis* (MERTENS, 1933) no estado de Santa Catarina, Brasil (Anura, Bufonidae). – Iheringia, Sér. Zool., **51**: 39-41.
- BRAUN, P.C. & C.A.S. BRAUN (1974): Fauna da fronteira Brasil-Uruguay. Lista dos anfíbios dos departamentos de Artigas, Rivera e Cerro Largo. – Iheringia, Sér. Zool., **45**: 34-49.
- BRAUN, P.C. & C.A.S. BRAUN (1980): Lista prévia dos anfíbios do estado do Rio Grande do Sul, Brasil. – Iheringia, Sér. Zool., **56**: 121-146.
- CABRERA, M.R. (2001): Sobre la distribución geográfica de *Melanophryniscus s. stelzneri* (WEYENBERGH) (Anura, Bufonidae). – Cuad. Herp., **15**: 137-139.
- CARAMASCHI, U. & C.A.G. CRUZ (2002): Taxonomic status of *Atelopus pachyrhynchos* MIRANDA-

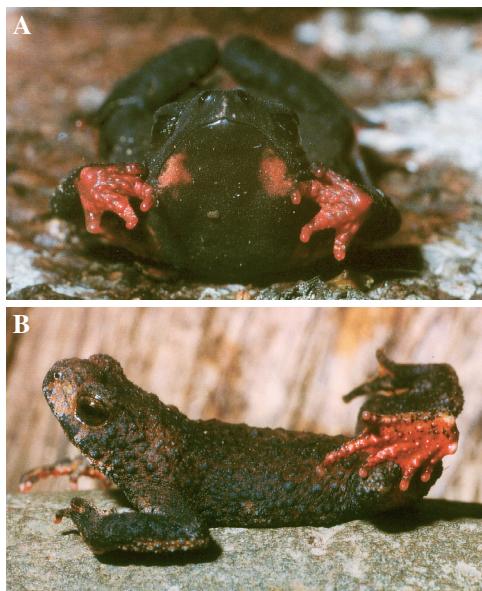


Fig. 14. “Unkenreflex” in (A) *Melanophryniscus dorsalis*; (B) *Melanophryniscus pachyrhynchos*. Photos: A. KWET.

- RIBEIRO, 1920, redescription of *Melanophryniscus tumifrons* (BOULENGER, 1905), and descriptions of two new species of *Melanophryniscus* from the state of Santa Catarina, Brazil (Amphibia, Anura, Bufonidae). – Arq. Mus. Nac., Rio de Janeiro, **60**: 303-314.
- CEI, J.M. (1980): Amphibians of Argentina. – Monitore zool. ital. (N.S.), Monogr. **2**: 1-609.
- CEI, J.M. (1987): Additional notes to Amphibians of Argentina: an update, 1980-1986. – Monitore zool. ital. (N.S.), Monogr. **21**: 209-272.
- CÉSPEDEZ, J.A. (1997): *Melanophryniscus stelzneri dorsalis*. First record. – Herpetol. Rev. **28**(2): 93.
- CÉSPEDEZ, J.A. & B.B. ALVAREZ (1999): Una nueva especie de *Melanophryniscus* (Anura: Bufonidae) del grupo *stelzneri* de Corrientes, Argentina. – Facena, **15**: 57-67.
- CÉSPEDEZ, J.A. & M. MOTTE (2001): Distribución de sapos del género *Melanophryniscus* (GAL-LARDO, 1961) en Argentina y Paraguay (Anura: Bufonidae). – Bol. Asoc. Herpetol. Esp., **12**(2): 71-76.
- CRUZ, C.A.G. & U. CARAMASCHI (2003): Taxonomic status of *Melanophryniscus stelzneri dorsalis* (MERTENS, 1933) and *Melanophryniscus stelzneri fulvoguttatus* (MERTENS, 1937) (Amphibia, Anura, Bufonidae). – Bol. Mus. Nac., N.S., Zool., Rio de Janeiro, **500**: 1-11.
- FONTANA, C.S., G.A. BENCKE & R.E. REIS (2003): Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul. – Porto Alegre, Brazil (Edipucrs), 632 pp.
- FROST, D.R. (ed.) (1985): Amphibian Species of the World – a taxonomic and geographical reference. – Lawrence, Kansas (Allen Press), 732 pp.
- FROST, D.R. (2002): Amphibian Species of the World: An online reference. V2.21 (inquiry: 15 July 2002). – [http://research.amnh.org/herpetology/amphibia/index.html].
- GARRIDO-Y RIGARAY, R.R. (1989): Descripción de la larva de *Melanophryniscus stelzneri montevidensis* (PHILIPPI, 1902) (Anura: Bufonidae). – Bol. Soc. Zool. Uruguay, 2^a época, **5**: 7-8.
- GARCIA & VINCIPROVA (2003): Anfibios. – pp. 147-164 in FONTANA, C.S., G.A. BENCKE & R.E. REIS (eds.): Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul. – Porto Alegre, Brazil (Edipucrs).
- KLAPPENBACH, M.A. (1968): Notas herpetológicas, IV. El género *Melanophryniscus* (Amphibia, Salientia) en el Uruguay, con descripción de dos nuevas especies. – Com. Zool. Mus. Hist. Nat. Montevideo, **9**(118): 1-12.
- KLAPPENBACH, M.A. & J.A. LANGONE (1992): Lista sistemática y sinonímica de los anfibios del Uruguay con comentarios y notas sobre su distribución. – An. Mus. Nac. Hist. Nat. Montevideo (2^a Serie), **8**: 163-222.
- KOLENC, F. (1987): Anuros del género *Melanophryniscus* en la República Oriental del Uruguay. – Aquamar, Madrid, **5**(30): 16-21.
- KWET, A. (2001): Frösche im brasilianischen Araukarienwald. Anurengemeinschaft des Araukarienwaldes von Rio Grande do Sul: Diversität, Reproduktion und Ressourcenaufteilung. – Münster (Natur und Tier-Verlag), 192 pp.
- KWET, A. & T. MIRANDA (2001): Zur Biologie und Taxonomie der Schwarzkröte *Melanophryniscus atroluteus* (MIRANDA-RIBEIRO, 1925). – Herpetofauna, **23**(134): 19-27.
- LANGONE, J.A. (1994): Ranas y sapos del Uruguay (Reconocimiento y aspectos biológicos). – Museo D. A. Larrañaga, Montevideo, Serie de Divulgación, **5**: 1-123.
- LANGONE, J.A. (2002): *Melanophryniscus*, interesantes sapitos uruguayos. – Doc. Divulgación Mus. Nac. Hist. Nat. Antropol., **4**: 1-13.
- LANGONE, J.A. (2003): Diversidad de la Biota Uruguaya: Amphibia. – An. Mus. Nac. Hist. Nat. Antropol. (2^a Serie), **10**(3): 1-12.
- LARSON, P.M., R.O. DE SÁ & D. ARRIETA (2003): Chondrocranial, hyobranchial and internal oral morphology in larvae of the basal bufonid genus *Melanophryniscus* (Amphibia: Anura). – Acta Zoologica, **84**: 145-154.
- LAVILLA, E.O. (1992): Tipos portadores de nombre y localidades tipo de anfibios de Argentina. – Acta zool. lilloana, **42**(1): 61-101.
- LAVILLA, E.O. & M. VAIRA (1997): The larva of *Melanophryniscus rubriventris rubriventris* (VELLARD, 1947) (Anura, Bufonidae). – Alytes, **15**: 19-25.
- LAVILLA, E.O. & J.M. CEI (2001): Amphibians of Argentina. A second update, 1987-2000. – Museo Regionale Scienze Naturali, Torino, Monogr. **28**: 1-178.
- LAVILLA, E.O., J.S. BARRIONUEVO & J.D. BALDO (2002): Los anfibios insuficientemente conocidos en Argentina. Una reevaluación. – Cuad. Herp., **16**: 99-118.
- MANEYRO, R., F. FORNI & M. SANTOS (1995): Anfibios del Departamento de Rocha. – Serie Divulgación Técnica, Probides, **1**: 1-24.
- MANEYRO, R. & J.A. LANGONE (2001): Categorización de los anfibios del Uruguay. – Cuad. Herp., **15**(2): 107-118.

- MERTENS, R. (1933): Über zwei südamerikanische Froschlurche der Gattungen *Dendrophryniscus* und *Gastrotheca*. – Zool. Anz., **102**: 257-260.
- MIRANDA-RIBEIRO, A. (1920): Os brachycephalídeos do Museu Paulista (com três espécies novas). – Revta Mus. paul., **12**: 307-315.
- NAYA, D. & R. MANEYRO (2001): *Melanophrynyicus sanmartini* KLAPPENBACH, 1968 (Anura, Bufonidae). – Cuad. Herp., **15**: 89-90.
- NUÑEZ, D., R. MANEYRO, J. LANGONE & R.O. DE SÁ (2004): Distribución geográfica de la fauna de anfibios del Uruguay. – Smithsonian Herpetological Information Service, **134**: 1-34.
- PRIGIONI, C.M. & R.R. GARRIDO (1989): Algunas observaciones sobre la reproducción de *Melanophrynyicus stelzneri montevidensis* (Anura, Bufonidae). – Bol. Soc. Zool. Uruguay (2^a época), **5**: 13-14.
- PRIGIONI, C.M. & J.A. LANGONE (2000): Una nueva especie de *Melanophrynyicus* GALLARDO, 1961, de Argentina y Paraguay (Amphibia, Anura, Bufonidae). – Com. Zool. Mus. Hist. Nat. Montevideo, **195**: 1-12.
- STRANECK, R., E. VARELA DE OLMEDO & G.R. CARIZO (1993): Catálogo de voces de anfibios Argentinos. Parte 1. – Buenos Aires, Argentina (Librería L.O.L.A.), 130 pp.
- TEDROS, M., F. KOLENC & C. BORTEIRO (2001): *Melanophrynyicus montevidensis* (PHILIPPI, 1902) (Anura, Bufonidae). Novedades zoogeográficas. – Cuad. Herp., **15**: 143.
- VAIRA, M. (2002): Variación de la coloración en poblaciones Argentinas de *Melanophrynyicus rubriventris* (VELLARD, 1947). – Cuad. Herp., **16**: 151-163.

Manuscript received: 27 April 2004

Authors' addresses: AXEL KWET, Staatliches Museum für Naturkunde, Zoologie, Rosenstein 1, D-70191 Stuttgart, Germany, E-Mail: kwet.smns@naturkundemuseum-bw.de; RAÚL MANEYRO, Sección Zoología Vertebrados, Facultad de Ciencias, Iguá 4225, CP: 11400, Montevideo, Uruguay, present address: Programa de Pós-Graduação em Zoologia, Laboratório de Herpetologia, Museu de Ciências e Tecnologia & Faculdade de Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga 6681, 90619-900 Porto Alegre, RS, Brasil, E-Mail: rmaneyro@fcien.edu.uy; ANNE ZILLIKENS, Zoologisches Institut, Auf der Morgenstelle 28, D-72076 Tübingen, Germany, E-Mail: anne.zillikens@uni-tuebingen.de; DIETRICH MEBS, Zentrum der Rechtsmedizin, University of Frankfurt, Kennedyallee 104, D-60596 Frankfurt, Germany, E-Mail: mebs@em.uni-frankfurt.de.