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ORIGINAL ARTICLE

Shape variation in lentic and lotic tadpoles of *Melanophryniscus* (Anura: Bufonidae)

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The bufonid genus *Melanophryniscus* includes 26 species that are divided into three phenetic groups based on adult morphology. Larvae develop in environments such as temporary ponds, streams or phytotelms. We studied variation in external morphology related to lentic and lotic microhabitats, through landmark-based geometric morphometrics on body shape, and multivariate analysis on oral disc measurements. Results show a morphological continuum between species that inhabit lentic versus lotic water systems. Features both in body shape and oral disc coincide with previous characterizations of lentic and lotic tadpoles published elsewhere.

El género de bufónidos *Melanophryniscus* comprende 26 especies actualmente reunidas en tres grupos fenéticos distinguidos por la morfología de los adultos. En adición, las larvas se desarrollan alternativamente en variados ambientes, tales como charcos, arroyos temporarios y fitotelmata. Estudiamos la variación morfológica externa asociada a ambientes lóticos y lénticos, mediante morfometría geométrica de landmarks sobre la forma del cuerpo, y análisis multivariado de las medidas del disco oral. Los resultados muestran un continuo morfológico entre las especies que habitan sistemas lénticos vs. lóticos. Las características corporales y del disco oral coinciden con caracterizaciones previas de renacuajos lénticos y lóticos ya publicadas.

Keywords: anuran larvae; basal bufonids; body shape; geometric morphometrics; oral disc

Introduction

The genus *Melanophryniscus* is a group of basal bufonids distributed in northern Argentina, southern Bolivia, southern Brazil, Paraguay, and Uruguay (Frost 2011). Species are small to medium-sized, have typically diurnal habits, and breed in aquatic, temporary environments (Baldo & Basso 2004; Goldberg et al. 2006; Santos et al. 2010). Twenty-six species are described thus far (Frost 2011), and 23 of these are assigned to one of three phenetic groups (Caramaschi & Cruz 2002). The *M. stelzneri* group includes 11 species with tadpoles that develop in small temporary ponds (Bustos Singer & Gutierrez 1997; Lavilla & Vaira 1997), except for *M. krauczuki* larvae, which inhabit temporary streams that run over basaltic beds (Baldo & Basso 2004). The *M. moreirae* group includes three species with larvae that develop in temporary ponds (Bokermann 1967). The *M. tumifrons* group contains nine species with tadpoles that live in temporary streams (Santos et al. 2010; Baldo pers. obs.); only this latter group has a putative synapomorphy that involves the presence of a frontal swelling in adults (Baldo & Basso 2004).

Three species (i.e. *M. admirabilis*, *M. alipioi*, and *M. vilavelhensis*) are not assigned to any species group; the tadpoles of *M. admirabilis* live in ponds, whereas those of the other two live in phytotelms (Di-Bernardo et al. 2006; Langone et al. 2008; Steinbach-Padilha 2008).

In this paper, we study variation in external morphology in tadpoles of 15 species representing the three phenetic groups. At first glance, these larvae reveal a wide variation in body shape and oral disc configuration (Figure 1). The main goals of our study are (1) to survey shape variation and (2) to relate it with the environment where larvae develop and the intrageneric division of the genus.

Materials and methods

We selected tadpoles of 15 species of *Melanophryniscus* in stages 31–37 of Gosner (1960); the number of specimens per species was 2–24 (see Appendix). Studied species were: *M. stelzneri* group: *M. atroluteus* (N = 8–15), *M. klappenbachi* (N = 2), *M. krauczuki* (N = 6), *M. montevidensis* (N = 4), *M. paraguayensis* (N = 3), *M. rubriventris* (N = 4), and *M. stelzneri* cf. *spagazzinii*

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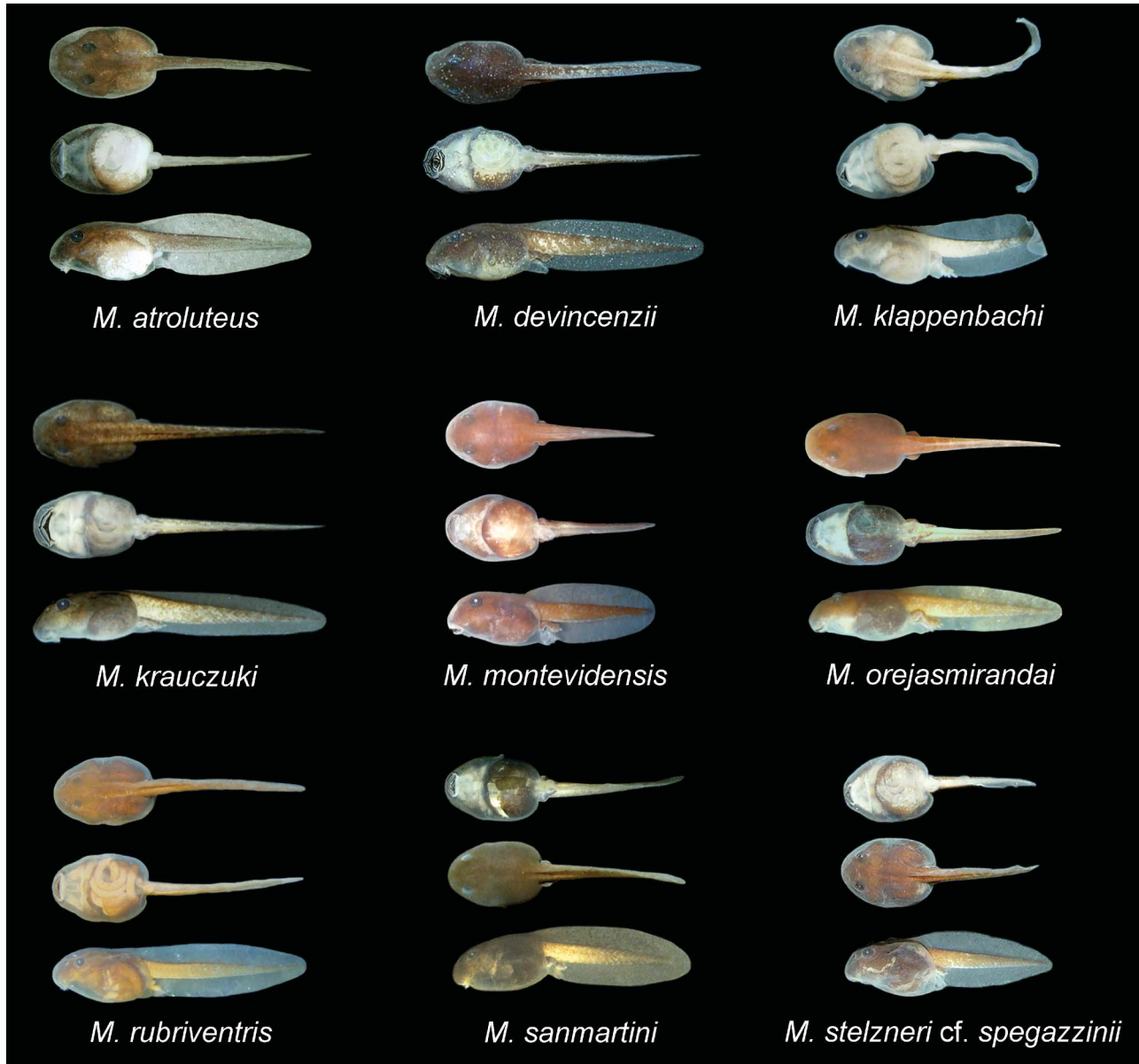


Figure 1. A sample of the *Melanophryniscus* species included in this study, showing variation in body and oral disc shape. Figures not to scale.

(N = 9); *M. moreirae* group: *M. sanmartini* (N = 5); *M. tumifrons* group: *M. devincenzii* (N = 23–24), *M. macrogranulosus* (N = 2), *M. orejasmirandai* (N = 5–8), *M. pachyrhynchus* (N = 17), *M. simplex* (N = 4), *M. cf. tumifrons* (N = 2), and an undescribed species from Santa Catarina, Brazil (*M. sp.*, N = 5).

We took photographs in dorsal and left lateral views, and a set of landmarks and semilandmarks was digitized on each of them. In dorsal view (Figure 2a) we defined 10 landmarks on the right half of the body: (1) most anterior point of the body; (2) naris location; (3) point on the body margin at the plane of the naris; (4) most medial point of the cornea; (5) most lateral

point of the cornea; (6) point of the body margin at the plane of the center of the eye; (7) point of the body margin at the plane of the end of the spiracular tube; (8) lateral point of the body–tail junction; (9) medial point of the body–tail junction; and (10) tail tip. Nine semilandmarks were included between landmarks 1 and 3, 3 and 6, 6 and 7 (#2 between each pair), and between landmarks 7 and 8 (#3). In lateral view (Figure 2b) we defined 15 landmarks according to Van Buskirk (2009): (1) most anterior point of the body; (2) naris; (3) most anterior point of the cornea; (4) most posterior point of the cornea; (5) maximum body height; (6) dorsal fin origin; (7) tail

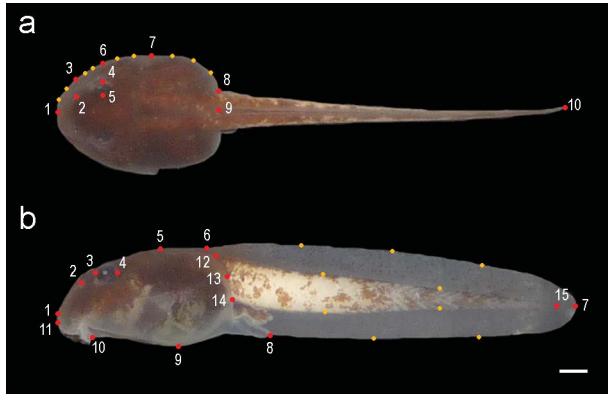


Figure 2. Landmarks and semilandmarks defined for geometric morphometric analysis, for (a) dorsal and (b) lateral views. See definition in text. Scale line = 1 mm.

tip; (8) most anterior point of the proctodeal tube–ventral fin junction; (9) maximum ventral curvature of the body; (10) most posterior point of the oral disc–body junction; (11) most anterior point of the oral disc–body junction; (12) most dorsal point of the caudal musculature–body junction; (13) most anterior point of the axis of the tail myotomes; (14) most ventral point of the caudal musculature–body junction; and (15) the caudal musculature tip. Nine semilandmarks were included between landmarks 7 and 8, 12 and 15, 14 and 15 (#2 between each pair), and between landmarks 6 and 7 (#3).

Some specimens were bent along the longitudinal or sagittal axes, and this inconvenience was solved with the option “unbend” of the software tpsUtil (Rohlf 2008). Landmark configurations were next rotated, translated, and scaled before being submitted to the software tpsRelw (Rohlf 2010) to perform a relative warp analysis. Shape variation was illustrated with thin-plate splines, which depict the shape change regarding a consensus (average) configuration.

We also carried out a linear morphometric analysis of the oral disc on 12 species: *M. atroluteus* (N = 8), *M. devincenzii* (N = 38), *M. krauczuki* (N = 6), *M. macrogramulosus* (N = 10), *M. montevidensis* (N = 14), *M. orejasmirandai* (N = 10), *M. pachyrhynchus* (N = 13), *M. rubriventris* (N = 4), *M. sanmartini* (N = 3), *M. simplex* (N = 10), *M. stelzneri* cf. *spagazzinii* (N = 9), and *M. sp.* (N = 10; see Appendix). The following measurements were taken: (1) oral disc width taken at the maximum transverse dimension of the relaxed disc; (2) width of dorsal gap in the marginal papillae; (3) width of ventral gap in the marginal papillae; and (4) body length (taken from the tip of the snout to the junction of the posterior body wall with the axis of the tail myotomes). We performed a multivariate variance analysis with the body length as a covariate (Statistica 6.0 2001).

Results

Body shape

The average *Melanophryniscus* tadpole calculated by geometric morphometric analysis is shown in Figure 3. The relative warp analysis shows an important shape variation among species. In dorsal view (Figure 4a), the first relative warp explained about 71% of the total variation; species could be arranged in a continuum between tadpoles of *M. pachyrhynchus* and those of *M. stelzneri* cf. *spagazzinii*. Deformation grids show that shape variation was mainly related with the body/tail proportion. Lentic tadpoles of the *M. stelzneri* group have the lowest scores on this warp, and this can be interpreted as a tail shorter than those of the remaining taxa; larvae of *M. krauczuki* were located among lotic tadpoles of *M. tumifrons* group, which have relatively longer tails. In lateral view (Figure 4b), the first two axes explained about 60% of the total variation, and the species were distributed in a continuum between *M. krauczuki* and *M. stelzneri* cf. *spagazzinii*. In this case, additionally to the body/tail proportion, deformation grids show that shape variation is related to body-tail height, eye and oral disc position, and the origin of the dorsal fin. Lentic tadpoles of the *M. tumifrons* group and *M. krauczuki* have a shallow body-tail shape, eyes more dorsally located, and a more ventral oral disc than those of lentic tadpoles. In dorsal and lateral views, tadpoles of species from both *M. stelzneri* and *M. tumifrons* groups, and tadpoles of *M. sanmartini* (*M. moreirae* group) overlap in morphospaces with shapes similar to the consensus shape.

Oral disc

Oral disc measurements are shown in Table 1. The MANCOVA reveals significant differences among all the species and all variables considered (Wilks' lambda = 0.234, $p < 0.000001$; oral disc width $F = 11.10$, $p < 0.000001$; dorsal gap width $F = 12.42$, $p < 0.000001$; ventral gap width $F = 9.70$, $p < 0.000001$).

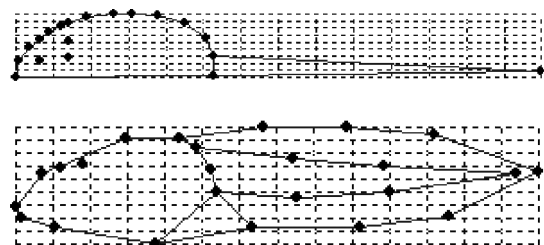


Figure 3. Consensus *Melanophryniscus* tadpole after rotation, translation, and scaling of landmarks configurations. Dorsal and lateral views.

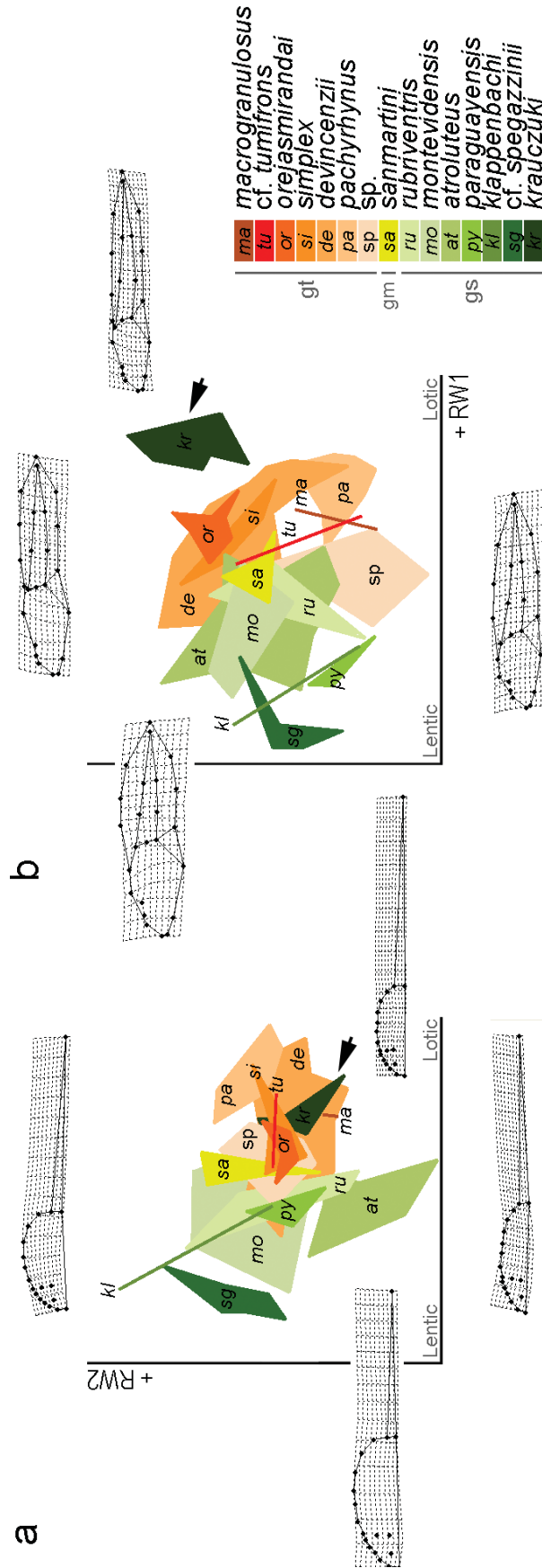


Figure 4. Relative warp analysis of *Melanophryniscus* tadpoles in (a) dorsal and (b) lateral views. Species are shaded according to their intrageneric phenetic group. Thin-plate splines depict shapes with minimum and maximum values along relative warps. gm, *M. moreirae* group; gt, *M. tumifrons* group; gs, *M. stelzneri* group. Note the position of lotic tadpoles of *M. krauczuki* (*M. stelzneri* group; arrow) among tadpoles of the *M. tumifrons* group.

Table 1. Oral disc measurements in 12 species of *Melanophryniscus*, with average values per habitat and phenetic group. Species are grouped according to the water body where larvae developed and the intrageneric phenetic groups. Mean and standard deviation values are shown in millimeters. The last three columns are measurements scaled to body length. Abbreviations: *at*, *M. atroluteus*; *de*, *M. devincenzii*; *gm*, *M. moreirae* group; *gs*, *M. stelzneri* group; *gt*, *M. tumifrons* group; *kr*, *M. krauczuki*; *ma*, *M. macrogranulosus*; *mo*, *M. montevidensis*; *or*, *M. orejasmirandai*; *pa*, *M. pachyrhynchus*; *ru*, *M. rubriventris*; *sa*, *M. sanmartini*; *sg*, *M. stelzneri* cf. *spagazzinii*; *si*, *M. simplex*; *sp.*, *M. sp.*

	N	Body length	Oral disc length	Dorsal gap	Ventral gap	od / bl	dg / bl	vg / bl
<i>sa</i>	3	5.90 (0.56)	1.72 (0.35)	1.42 (0.24)	0.68 (0.03)	0.29 (0.03)	0.24 (0.02)	0.12 (0.01)
gm average		5.90 (0.56)	1.72 (0.35)	1.42 (0.24)	0.68 (0.03)	0.29 (0.03)	0.24 (0.02)	0.12 (0.01)
<i>at</i>	7	5.99 (1.73)	1.71 (0.15)	1.46 (0.19)	0.91 (0.13)	0.30 (0.08)	0.26 (0.06)	0.16 (0.03)
<i>mo</i>	6	5.62 (0.57)	1.75 (0.15)	1.40 (0.13)	0.80 (0.15)	0.31 (0.01)	0.25 (0.01)	0.14 (0.03)
<i>ru</i>	4	5.50 (0.41)	1.79 (0.11)	1.43 (0.09)	1.03 (0.06)	0.33 (0.04)	0.26 (0.03)	0.19 (0.02)
<i>sg</i>	9	5.28 (0.50)	1.56 (0.11)	1.19 (0.12)	0.86 (0.20)	0.30 (0.03)	0.23 (0.02)	0.16 (0.04)
Lentic average		5.66 (0.75)	1.71 (0.18)	1.38 (0.15)	0.86 (0.12)	0.31 (0.04)	0.25 (0.03)	0.15 (0.03)
<i>kr</i>	6	6.25 (0.71)	2.58 (0.25)	2.33 (0.26)	1.49 (0.27)	0.41 (0.03)	0.37 (0.03)	0.24 (0.02)
gs average		5.71 (0.96)	1.85 (0.40)	1.53 (0.43)	1.00 (0.30)	0.33 (0.06)	0.27 (0.06)	0.18 (0.04)
<i>de</i>	30	6.83 (0.87)	2.25 (0.28)	1.96 (0.28)	1.22 (0.23)	0.33 (0.02)	0.29 (0.02)	0.18 (0.02)
<i>ma</i>	10	6.09 (0.44)	2.11 (0.22)	1.79 (0.19)	1.25 (0.16)	0.35 (0.03)	0.30 (0.03)	0.21 (0.03)
<i>or</i>	10	7.72 (0.83)	2.30 (0.38)	2.16 (0.37)	1.38 (0.30)	0.30 (0.02)	0.28 (0.03)	0.18 (0.03)
<i>pa</i>	12	6.73 (0.33)	2.18 (0.13)	1.85 (0.07)	0.98 (0.10)	0.32 (0.01)	0.27 (0.01)	0.15 (0.01)
<i>si</i>	10	6.20 (0.16)	2.02 (0.25)	1.75 (0.28)	1.08 (0.15)	0.33 (0.04)	0.28 (0.05)	0.17 (0.03)
<i>sp.</i>	9	5.91 (0.45)	1.80 (0.13)	1.55 (0.11)	0.85 (0.13)	0.30 (0.01)	0.26 (0.02)	0.14 (0.02)
gt average		6.54 (0.75)	2.14 (0.28)	1.85 (0.27)	1.13 (0.23)	0.33 (0.03)	0.28 (0.03)	0.17 (0.03)
Lotic average		6.53 (1.46)	2.18 (0.53)	1.91 (0.48)	1.18 (0.32)	0.33 (0.07)	0.29 (0.06)	0.18 (0.04)

Note: bl, body length; dg, dorsal gap; od, oral disc; vg, ventral gap.

Table 2. Bonferroni's test results after MANCOVA on three oral disc measurements (oral disc, dorsal gap, and ventral gap widths, in that order within each cell), with body length as covariate. *P* values of each species pair comparison are replaced with (*) and (-) when differences are significant or non significant, respectively ($\alpha = 0.05$). Species are grouped according to the water body where larvae developed and the intrageneric phenetic groups. Abbreviations as in Table 1.

Lotic	gt	<i>de</i>	---										
		<i>pa</i>	-**	--*									
		<i>ma</i>	-*-	---	--*								
		<i>si</i>	***	*--	---								
		<i>sp.</i>	***	*_*	**_	*_*	---						
		<i>kr</i>	---	***	***	**_	---	***	***				
Lentic	gs	<i>sg</i>	***	***	**_	***	**_	_*_	***				
		<i>ru</i>	***	**_	**_	_*_	---	---	***	---	---		
		<i>at</i>	***	***	**_	***	---	---	***	---	---		
		<i>mo</i>	***	***	**_	***	_*_	---	---	***	---	---	
		<i>sa</i>	***	***	**_	*_*	---	---	***	---	---	---	
gm		<i>or</i>	<i>de</i>	<i>pa</i>	<i>ma</i>	<i>si</i>	<i>sp.</i>	<i>kr</i>	<i>sg</i>	<i>ru</i>	<i>at</i>	<i>mo</i>	
		gt						gs					
		Lotic							Lentic				

The output of the Bonferroni's post hoc test is summarized in Table 2. The main results show that in general, species from lotic and lentic environments differ significantly in their oral features. All lentic species of the *M. stelzneri* group are similar to each other. Lotic species of the *M. tumifrons* group are more variable, and tadpoles of *M. simplex* and the unnamed species from Brazil are more similar to lentic larvae. *Melanophryniscus krauczuki* differs from every other species but lotic tadpoles of *M. orejasmirandai* (*M. tumifrons* group). *Melanophryniscus sanmartini* (*M. moreirae* group) is similar to all lentic species of the *M. stelzneri* group and *M. simplex* and

M. sp. from Brazil. Oral disc width and the gaps in the papillar margin are in general larger in lotic than in lentic species (see Table 1).

Discussion

Results show a morphological continuum between species that inhabit lentic versus lotic water systems in both body shape and oral disc features. Lentic tadpoles of the *M. stelzneri* group have a tall, globular body, a proportionately short tail with fins taller than the body, dorsolateral eyes, and a subterminal oral

disc. These features are most evident in *M. klappenbachi* and *M. stelzneri* cf. *spgazzinii*, which stand at one end of the morphological continuum (Figure 4). Tadpoles of the *M. tumifrons* group, all from lotic habitats, have a more depressed body, a proportionately long tail with low fins, dorsal fin originating more posteriorly, more dorsal eyes, and a large, ventral oral disc with wide gaps in the marginal papillae. These features are most evident in *M. devincenzii*, *M. orejasmirandai*, and *M. pachyrhynchus*, placed at the opposite extreme of the morphological continuum (Figure 4). Some tadpoles of both species groups (e.g. *M. rubriventris* and the unnamed species from Brazil) have intermediate features. *Melanophryniscus krauczuki* is currently assigned to the *M. stelzneri* group, but its larval morphology resembles that of larvae of the *M. tumifrons* group as a striking relationship with lotic environments. Tadpoles of *M. sanmartini*, the sole species representing the *M. moreirae* group, have intermediate features in both body shape and oral disc, characteristic of typical pond-type larvae.

In body morphology, our results agree with the characterization of ecomorphological guilds presented by Altig & Johnston (1989; updated in McDiarmid & Altig 1999). Several more recent studies also found similar morphological traits. For instance, lotic benthic tadpoles of Australian hylids and myobatrachids (Van Buskirk 2009), suctorial tadpoles of *Ansonia*, *Exerodonta*, *Hyloscirtus*, and *Telmatobius* (Inger 1992; Canseco-Márquez et al. 2003; Lötters et al. 2005; Matsui et al. 2005; Aguilar et al. 2007), gastromyzophorous tadpoles of *Atelopus*, *Rhinella*, *Sabahphrynus*, *Amolops*, *Huia*, *Meristogenys*, and *Rana* (Inger et al. 2001; Coloma 2002; Boistel et al. 2005; Matsui et al., 2006; Ngo et al., 2006; Shimada et al. 2007; Stuart 2008; Aguayo et al. 2009) exhibit these features associated with living in flowing water.

A functional explanation related to locomotion is assumed for many body features. For instance, long and deep tails have been proposed to enhance speed and maneuverability during swimming (e.g. Hoff & Wassersug 2000; Van Buskirk & McCollum 2000a; Arendt 2010; Kupferberg et al. 2011), and a depressed body with muscular tail and low fins originating posteriorly provide the streamlined shape desirable in an environment with permanent risk of drift (e.g. Wassersug & Heyer 1983; Inger 1992; Richards 2002). On the other hand, phenotype manipulation studies show that morphology can be plastic enough so that performance does not decline in response to even very wide shape variations, and the origin of variations may be then related to other ecological aspects (Van Buskirk & McCollum 2000b).

Richards (2002) studied habitat selection in tadpoles of a rainforest stream in Australia, and reported

species restricted to fast-flowing riffles and species confined to slow-flowing pools and runs. His experiments with flow regimes suggest that the inability of pool species to resist high flow rates and turbulences has a morphological and behavioral correlate, whereas the absence of riffle species in pools remains unexplained. Similarly, three species of *Melanophryniscus* coexist in syntopy in the Southern Cone Mesopotamian Savanna Ecoregion in Misiones, Argentina, characterized by a high diversity of reproductive sites, with pools and small streams very close to each other. In spite of this, *M. atroluteus* breeds exclusively in ponds and *M. devincenzii* and *M. krauczuki* reproduce in streams, so that tadpoles of the first species are never found in environments typical of the other two, and vice versa. Although this could be simply due to choice and fidelity to breeding sites of the adults, it still offers the opportunity to further explore larval morphological plasticity and functional constraints in these closely related species.

Regarding the oral configurations, several lotic tadpoles have large, ventral oral discs that are often used in substrate adhesion. Rows of teeth and marginal papillae are usually numerous and complete (e.g. *Hyloscirtus* tadpoles as compared with other cophomantines, and *Telmatobius atahualpai* as compared with other *Telmatobius*; Lötters et al. 2005; Aguilar et al. 2007). Among Australian hylids and myobatrachids, stream species have arched anterior tooth rows, a narrow oral disc and a thinner lower jaw sheath than pond larvae (Van Buskirk 2009). The oral disc of *Melanophryniscus* tadpoles shows an interesting morphological variation. Tadpoles from lotic habitats have in general larger discs, but unlike other lotic species, the gaps in marginal papillae are also larger than in pond species. In spite of these variations, phylogenetic constraints appear to have shaped the oral disc in this genus, which otherwise shows an oral disc typical of bufonids. First, the labial tooth row formula 2/3 is present in most bufonid species regardless of the habitat where the larvae develop (e.g. most lentic *Rhinella*, suctorial *Ansonia*, and gastromyzophorous *Atelopus*; Inger 1960; Duellman & Lynch 1969; Vera Candioti 2007). Reduced labial tooth rows appear in most species of the *R. granulosa* group (2/2, e.g. Borteiro et al. 2006), arboreal tadpoles (e.g. a short P3 in *Mertensophryne taitana* and LTRF 2/2 in *M. anotis* and *M. micranotis*; Müller et al. 2005), and in some endotrophic species (e.g. 1/0 in *Pelophryne signata*; Leong & Teo 2009). Conversely, labial tooth row formulae larger than 2/3 have not been reported in the family. Second, the ventral gap in marginal papillae has been proposed as a synapomorphy of Bufonidae (Haas 2003; Frost et al. 2006),

and is secondarily lost in a few taxa, in this case, not in an evident ecomorphological relationship (e.g. *Ansonia*, *Leptophryne*, *R. scitula*, and *Werneria*; Inger 1960, 1985; McDiarmid & Altig 1999; Caramaschi & Niemeyer 2003).

The genus *Melanophryniscus* represents an excellent model for the study of the evolution of rheophilous living mode in anuran tadpoles. It is a diverse group whose species exhibit wide morphological and ecological variations. Furthermore, geographic distributions in several species broadly overlap, and microsympatry areas are known at least in four of them; interspecific matings are frequent and hybrid larvae, froglets, and adult specimens are viable (Baldo & Basso 2004). All this offers an interesting opportunity to address comparative research on lentic, lotic, and hybrid larvae and explore several other sources of variation. For instance, numerous studies find correlations between internal morphology and habitat in many species from lotic systems (e.g. Wassersug 1980; Wassersug & Heyer 1988; Haas & Richards 1998; Aguayo et al. 2009), and studies of the buccal cavity and musculoskeletal anatomy in *Melanophryniscus* species are very scarce (Echeverría 1992; Haas 2003; Larson et al. 2003). Likewise, information on developmental and morpho-functional aspects is not available within the genus, and several studies of unrelated lotic species show heterochronic patterns of development of limbs and lungs (e.g. Wassersug & Heyer 1983; Haas & Richards 1998). Variation at a generic level can be then compared with data of other highly modified bufonids (e.g. suctorial and gastromyzophorous tadpoles) and with representatives of other families that have converged in similar living modes (e.g. gastromyzophorous ranids and suctorial hylids). The basal position of *Melanophryniscus* within Bufonidae is widely supported (e.g. Frost et al. 2006; Pramuk 2006), but intrageneric relationships are not yet elucidated. In our results, excepting the case of *M. krauczuki*, we found a general agreement of larval morphological variation and the assignment of species to phenetic groups. Once the phylogeny of this group is resolved, results can be reinterpreted considering the contribution of common ancestry in determining the structure of interspecific variation.

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Appendix. Examined material

- *M. atroluteus* (N = 15): Ñu Pyahú, (27° 29' 25" S, 55° 40' 06" W), Dpto. Candelaria, Misiones Province, Argentina.
- *M. devincenzii* (N = 38): Ñu Pyahú, (27° 29' 25" S, 55° 40' 06" W), Dpto. Candelaria, Misiones Province, Argentina; Dpto. Rivera, Uruguay.

- *M. klappenbachi* (N = 2): Club Sixty (27° 25' 17"S, 58° 56' 20"W), Dpto. San Fernando; Chaco Province, Argentina.
- *M. krauczuki* (N = 6): Ñu Pyahú, (27° 29' 25"S, 55° 40' 06"W), Dpto. Candelaria, Misiones Province, Argentina.
- *M. macrogranulosus* (N = 10): Morro da Gruta (29° 24' 22.4"S, 49° 51' 05.1"W), Fourth District of Porto Colônia, Rio Grande do Sul State, Brazil.
- *M. montevidensis* (N = 14): Cabo Polonio and Valizas, Dpto Rocha, Uruguay.
- *M. orejasmirandai* (N = 10): Sierra de Animas, Dpto. Maldonado, Uruguay.
- *M. pachyrhynus* (N = 17): Cuchilla del Mangrullo, Dpto. Cerro Largo, Uruguay.
- *M. paraguayensis* (N = 3): Urbanización Surubu'í (25° 11' 12"S, 57° 30' 50"W), Dpto. Central, Paraguay.
- *M. rubriventris* (N = 4): Abra de Cañas, Parque Nacional Calilegua, Dpto. Ledesma, Jujuy Province, Argentina.
- *M. sanmartini* (N = 5): Salto del Penitente (34° 22' 00"S, 55° 03' 00"W), Dpto. Lavalleja, Uruguay.
- *M. simplex* (N = 10): São Francisco de Paula, near Aratinga RS486 (Rota do Sol) (29° 19' 12.6"S, 50° 12' 13.3"W), Rio Grande do Sul State; Brazil.
- *M. cf. tumifrons* (N = 2): Municipio de Gravataí, near Campus Palavra da Vida, Rio Grande do Sul State, Brazil.
- *M. stelzneri* cf. *spgazzinii* (N = 9): Sierras La Brava (37° 53' 06"S, 57° 59' 13"W), Pdo. Balcarce, Buenos Aires Province, Argentina.
- *M. sp.* (N = 10): General Carneiro, Santa Catarina State, Brazil.