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Comparative larval morphology in Madagascan frogs of the genus *Mantella* (Amphibia: Mantellidae)

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Abstract

We describe and compare the tadpole morphology of nine species of frogs of the endemic Madagascan genus *Mantella* based upon specimens identified through DNA barcoding or captive bred. The tadpole morphology of *M. crocea/milotympanum*-hybrids, *M. madagascariensis*, *M. pulchra*, *M. viridis*, *M. baroni*, *M. bernhardi* and *M. betsileo* is described for the first time. In general, *Mantella* have small and generalized tadpoles with a uniform dark colouration. The oral disc is elliptical, emarginated, and positioned anteroventrally. In *M. laevigata* the oral disc is rounded, not emarginated, and positioned ventrally; eyes are positioned and directed dorsally, while in other species they are directed dorsolaterally. Labial tooth row formulas of *Mantella* tadpoles differ among some species, and in *M. aurantiaca* and *M. crocea/milotympanum* they also show intraspecific variation. Species identification is difficult when considering only morphometric variables. Tadpoles within each species group of the genus do not cluster together (except for some clustering of species belonging to the *M. madagascariensis* group), confirming that the larval morphology in closely related *Mantella* species is not suitable for determining phylogenetic relationships. *Mantella laevigata*, distinguished by tree-hole breeding and parental care, shows the most distinguished larval morphology.

Keywords: Anura, tadpole description, DNA barcoding, Madagascar, morphometry, ontogenetic variation

Introduction

The genus *Mantella* comprises attractive, small diurnal frogs which accumulate skin alkaloids, and are characterized by aposematic colouration (Daly *et al.* 1996; Vences *et al.* 1999). *Mantella* belongs to the Malagasy-Comoran endemic family Mantellidae. It is a well defined monophyletic group containing about 17 species that are morphologically poorly differentiated in their adult stage. Based on molecular phylogenetic analyses the genus is further subdivided into five monophyletic groups: the *M. cowani* group (comprising the species *M. cowani*, *M. baroni*, *M. haraldmeieri* and *M. nigricans*), *M. bernhardi* group (*M. bernhardi*), *M. madagascariensis* group (*M. aurantiaca*, *M. crocea*, *M. madagascariensis*, *M. milotympanum*, *M. pulchra*), *M. laevigata* group (*M. laevigata* and *M. manery*) and *M. betsileo* group (*M. betsileo*, *M. ebenaui*, *M. expectata*, *M. viridis*, *M.* aff. *viridis*) (Vences *et al.* 1999; Schaefer *et al.* 2002; Chiari *et al.* 2004; Vences *et al.* 2004; Rabemananjara *et al.* 2007). Snout-vent length (SVL) is 18–31 mm. *Mantella* are highly priced in the pet trade, particularly the more brilliantly coloured species, such that large numbers of specimens are exported from Madagascar every year (Behra 1993; Rabemananjara *et al.* 2008). Despite of their commercial interest and the fact that many publications are available on the husbandry of most of the species, it is surprising that

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detailed tadpole descriptions are only available for *M. aurantiaca* by Arnoult (1965), later summarised by Blommers-Schlösser & Blanc (1991), and *M. expectata* (Mercurio & Andreone 2005), while for two other species (*M. ebenaui* and *M. laevigata*) only rough descriptions have been published (Glaw & Vences 1994).

On the other hand, seen the very high number of known species of amphibians in Madagascar, it is not strange that for most of them the tadpole morphology and general larval ecology are not yet known. Notwithstanding, the knowledge of larval stages is a crucial step in the assessment of conservation priorities, and only the analysis of all life-history stages of a species results in a clear picture of the ecological requirements of a species. This is in particular true for anurans because tadpoles are known to be highly adapted in morphology and ecology to local ecological conditions (Mercurio & Andreone 2005; Candioti 2007).

This high level of adaptations to their environment was seen as a main factor causing the morphology of anuran larvae to reflect only poorly their phylogenetic relationships. However, several recent papers have shown that tadpole characters are phylogenetically informative (e.g. Maglia *et al.* 2001; Haas 2003; Grosjean *et al*. 2004). Due to the entirely different organisation of anuran larvae, the characters of tadpoles are complementary to those of adults and this set of new characters could help to resolve taxonomic and phylogenetic problems where adult characters alone have been inadequate (Grosjean 2005). Here we provide descriptions of the tadpole morphology of nine species of *Mantella*, six of them for the first time. Additionally we compare the external morphological characters and oral disc morphology between different species, as well as morphological measurements, as a contribution to an inventory of Malagasy anuran larval stages.

Materials and methods

Tadpoles were either collected in the field or reared after captive breeding. All animals were euthanized by immersion in chlorobutanol solution, and animals captured in the wild were immediately sorted into homogeneous series based on morphological characters. F1 hybrid tadpoles between *M. crocea* and *M. milotympanum* were obtained by captive breeding.

Tadpoles collected in the field were identified using the DNA barcoding approach, a rapid molecular technique that has shown reliable results in amphibian species identification (Vences *et al.* 2005a, b). We used a fragment of the mitochondrial 16S rRNA gene that is known to be sufficiently variable among species of amphibians (Vences *et al.* 2005a, b).

All specimens are deposited at the Zoologische Staatsammlung München (ZSM). Developmental stages are based on Gosner (1960). Morphological terminology, as well as the labial tooth row formula (LTRF) follows Altig & Mc Diarmid (1999). The measurements of total length (TL), tail length (TAL) and body length (BL) were taken with a calliper, and the other measurements were taken using a stereo microscope with measuring device and subsequently converted into millimetres. The following further abbreviations were used: BH (body height), BW (body width), TMW (tail muscle width), TMH (tail muscle height), MTH (maximum tail height), TMHM (height of the tail musculature at the midlength of the tail), ED (eye diameter), IOD (inter orbital distance), IND (internarial distance), ODW (oral disc width), TN (number of labial teeth/ mm in A2), PN (total number of papillae). A general description of *Mantella* tadpoles is given first, due to their great morphological similarity. Subsequently the species-specific characters are given separately for each species. Whenever possible only the results for Gosner stages 32–40 were compared. In these stages a developmental “climax is reached in tadpoles, indicating that they are the best suited for morphological interspecific comparisons (Grosjean 2005).

For the analysis of external morphological characters and oral disc morphology, a table was created using six characters of the external morphology and 23 characters of oral disc morphology. In the table, 0 represent an "absence" character state in a species and 1 indicates that the character state does apply to the species (table 1). When characters varied within a species, both character states were considered. This table with presence/ absence data was used to construct a similarity matrix of tadpoles of all species using Euclidean distances.

The similarity matrix was then submitted to Nonmetric Multidimensional Scaling (NMDS) (Guttman 1968; Borg & Lingoes 1987). This is an ordination analysis that produces a bidimensional diagram showing similarities among species. Tadpoles of *M. madagascariensis* and *M. baroni* were excluded from the analysis because of their very advanced Gosner stages and, accordingly, to their non-comparable oral disc morphology. A measure of 'stress' (mismatch between the rank order of distances in the data, and the rank order of distances in the ordination) was calculated. To ensure that the minimum stress function was reached, the NMDS analysis was repeated 10 times with a different position of samples in the initial configuration. The analysis was performed in 2 dimensions.

A second data set containing all morphometric measurements taken from each examined specimen, including number of labial teeth per mm and number of papillae, was divided into three subgroups, partitioned by Gosner stage (GS) (specimens belonging to GS 24–29 group 1, GS 30–39 group 2 and GS 40–44 group 3). A Principal Component Analysis (PCA) was performed for each group. All cases with one or more data missing were excluded from the analysis.

For GS group 3, the analysis was performed using only metric variables, i.e., all variables except TN and PN because these two values could not have been taken due to the very advanced stage of the tadpoles. All statistical analysis were performed using StatSoft, Inc. (2005), STATISTICA (data analysis software system), version 7.1.

Results

General morphology of tadpoles of the genus *Mantella* Boulenger

Tadpoles of *Mantella* species share a generally similar morphology, being identical in a variety of characters and divergent in only a few. For a brief morphological comparison of tadpoles of all *Mantella* species examined here, see figures 1–9. All Mantella tadpoles can be characterised by a quite uniform colouration. In dorsal view, body ovoid with rounded snout. In lateral view, body is elliptical and snout slopes gently until the oral region and then strongly bends (except in *M. laevigata* whose body is flattened in dorsolateral direction). The ratio BW/BL is very variable, this variability not only being inter- but also intraspecific, and extending between 37–89%. A similar variability is found in IND/IOD which spans between 44–94%. TAL/TL is stable and spans between 49–71%. The external nares are located dorsolaterally, approximately in the middle from snout tip to eyes. Eyes of moderate size, ED between 6–16% of BL, positioned dorsally, directed dorsolaterally. Spiracle sinistral, inner wall free from the body, with opening positioned laterally, directed posteriorly, visible in dorsal view. Tail fins low, both dorsal and ventral fins approximately of equal height. Caudal musculature well developed, not reaching the tip of the tail. Dorsal fin originates just before the body-tail junction and the ventral fin originates at the posterior ventral terminus of the body. Tail tip slightly rounded (except in *M. viridis* and *M. laevigata* which have pronounced rounded tail tips). Oral disc is elliptical, emarginated (except in *M. laevigata* where it is rounded and not emarginated), positioned anteroventrally. Mouth opens anteroventrally in *M. pulchra*, *M. betsileo* and *M. bernhardi* and ventrally in *M. aurantiaca*, *M. crocea/milotympanum*, *M. madagascariensis*, *M. viridis* and *M. laevigata*, with an uniserial row of marginal papillae in the lower labium and in the lateral side of upper labium (except in *M. viridis* and *M. bernhardi* that can have either one or two rows and *M. crocea/milotympanum* and *M. laevigata* which have two rows of papillae in the lower labium). Papillae are not pigmented, translucent and conical with rounded tips in *M. aurantiaca*, *M. madagascariensis*, *M. betsileo* and *M. viridis*, and rounded in *M. bernhardi*, *M. crocea/milotympanum*, *M. laevigata* and *M. pulchra*. Upper jaw sheath is concave (except in *M. viridis* in which it is M-shaped) and lower jaw sheath is V-shaped, both finely serrated (except in *M. viridis* and *M. laevigata* where both jaw sheaths have fewer large serrations) and fully black pigmented in more advanced developmental stages (except in *M. aurantiaca*). The size of the jaw sheath is variable; *M. aurantiaca*, *M. betsileo* and *M. bernhardi* have thin, *M. pulchra* and *M. crocea/milotympanum* have middle sized, and *M.*

laevigata and *M. viridis* have thick jaw sheaths. Labial tooth row formula of most species is 5(2–5)/3(1) (exceptions are *M. betsileo* 5(2–5)/3, *M. laevigata* 3(2–3)/3(1), in some individuals of *M. crocea/milotympanum* 5(2–5)/3(1–2) and in one individual of *M. aurantiaca* 6(2–6)/3(1)). Characters that differ from this general morphology are given for every species separately below.

TABLE 1. Morphological characters of tadpoles of the genus *Mantella*. Species abbreviations are as follows: aur = *M. aurantiaca*, croc/milo = *M. crocea/milotympanum*, mada = *M. madagascariensis*, pulc = *M. pulchra*, bets = *M. betsileo*, vir = *M. viridis*, exp = *M. expectata*, baro = *M. baroni*, laev = *M. laevigata*, bern = *M. bernhardi*.

Species	aur	croc/ milo	mada	pulc	bets	vir	exp*	baro	laev	bern
TAL/TL ≤ 65%	1	1	0	1	0	1	1	0	1	0
TAL/TL > 65%	0	0	1	0	1	0	0	1	0	1
Tail fully pigmented	1	1	0	1	0	1	1	0	0	1
Tail partially pigmented	0	0	1	0	1	0	0	1	1	0
Mouth opens anteroventrally	0	0	0	1	1	0	1	1	0	1
Mouth opens ventrally	1	1	1	0	0	1	0	0	1	0
Oral disc eliptical	1	1	1	1	1	1	1	–	0	1
Oral disc rounded	0	0	0	0	0	0	0	–	1	0
Emarginated	1	1	1	1	1	1	1	–	0	1
Not emarginated	0	0	0	0	0	0	0	–	1	0
Unis. row of marg. pap. in low. lab	1	0	1	1	1	1	1	–	0	1
2 rows of marg. pap. in low. lab	0	1	0	0	0	1	0	–	1	1
Papillae conical	1	0	1	0	1	1	1	–	0	0
Papillae rounded	0	1	0	1	0	0	0	–	1	1
Upper jaw sheath concave	1	1	1	1	1	0	1	–	1	1
Upper jaw sheath M-shape	0	0	0	0	0	1	0	–	0	0
Finely serrated	1	1	–	1	1	0	1	–	0	1
Fewer big serrations	0	0	–	0	0	1	0	–	1	0
Fully pigmented	0	0	–	1	1	1	1	–	1	0
Jaw sheaths thin	1	0	–	0	1	0	0	–	0	1
Jaw sheaths middle sized	0	1	–	1	0	0	1	–	0	0
Jaw sheaths thick	0	0	–	0	0	1	0	–	1	0
Tooth row formula 3(2–3)/3(1)	0	0	–	0	0	0	0	–	1	0
Tooth row formula 4(2–4)/3	0	0	–	0	0	0	0	–	0	0
Tooth row formula 4(2–4)/3(1)	0	0	–	0	0	0	0	–	0	0
Tooth row formula 5(2–5)/3	0	0	–	0	1	0	0	–	0	0
Tooth row formula 5(2–5)/3(1)	1	1	–	1	0	1	1	–	0	1
Tooth row formula 5(2–5)/3(1–2)	0	1	–	0	0	0	0	–	0	0
Tooth row formula 6(2–6)/3(1)	1	0	–	0	0	0	0	–	0	0

*taken from Mercurio & Andreone (2005)

The comparison of the characters used in the NMDS analysis is found in table 1 and the results are shown in figure 10.a. The NMDS analysis grouped *M. pulchra* and *M. expectata* very closely, and *M. bernhardi* a bit further apart. Similarly, *M. aurantiaca* and *M. crocea/milotympanum* were grouped together. All other species were scattered. The stress value obtained by this analysis was 0.056.

PCA performed separately for specimens in Gosner stage (GS) 24–29 (group 1), GS 30–39 (group 2) and GS 40–44 (group 3) showed slight grouping of specimens within each species. Factor loadings for PCA for all three groups are shown in table 2. For GS 24–29 (group 1; figure 10.b), only specimens of *M. laevigata* are separated, while specimens of *M. pulchra* and *M. bernhardi* overlap. For GS 30–39 (group 2; figure 10.c) specimens of *M. viridis* are clearly separated from other specimens (*M. pulchra*, *M. crocea/milotympanum*, *M. bernhardi* and *M. aurantiaca*). For GS 40–44 (group 3; figure 10.d) all specimens that belong to different species are separated from each other (except for a specimen of *M. pulchra* that is positioned very closely to one specimen of *M. crocea/milotympanum*).

TABLE 2. Factor loadings for PCA. GS group 1: Eigenvalue for factor 1 is 10.63 (70.86 % total variance), for factor 2 is 1.60 (10.66 % total variance), for factor 3 is 1.29 (8.61 % total variance). GS group 2. Eigenvalue for factor 1 is 8.38 (57.09 % total variance), for factor 2 is 2.29 (15.26 % total variance), for factor 3 is 1.16 (7.71 % total variance). GS group 3. Eigenvalue for factor 1 is 6.96 (53.50 % total variance), for factor 2 is 1.75 (13.45 % total variance), for factor 3 is 1.20 (9.23 % total variance).

Variable	Factor 1; GS 24–29	Factor 2; GS 24–29	Factor 3; GS 24–29	Factor 1; GS 30–39	Factor 2; GS 30–39	Factor 3; GS 30–39	Factor 1; GS 40–44	Factor 2; GS 40–44	Factor 3; GS 40–44
BL	–0.90	0.14	–0.25	–0.81	0.29	0.03	–0.86	–0.23	0.16
BH	–0.89	0.01	0.10	–0.86	–0.06	0.19	–0.70	–0.37	0.20
BW	–0.94	–0.29	0.14	–0.92	–0.13	0.01	–0.58	0.36	–0.46
TMH	–0.92	0.14	0.26	–0.89	0.02	–0.12	–0.56	0.05	–0.51
TMW	–0.77	–0.40	0.22	–0.91	0.04	–0.07	–0.74	0.56	0.19
MTH	–0.94	–0.15	0.07	–0.91	–0.16	0.12	–0.92	0.13	0.11
TMHM	–0.74	0.13	0.56	–0.74	0.07	0.28	–0.74	–0.11	0.23
ED	–0.95	0.24	0.02	–0.22	0.89	–0.08	–0.67	–0.45	0.24
IOD	–0.95	0.12	0.04	–0.88	0.09	–0.17	–0.26	0.72	0.58
IND	–0.95	–0.19	–0.04	–0.82	–0.25	–0.14	–0.62	–0.36	0.17
ODW	–0.88	–0.20	0.05	–0.69	–0.57	0.00	–0.79	–0.37	–0.18
TAL	–0.71	–0.23	–0.64	–0.71	0.42	–0.12	–0.86	0.29	–0.27
TL	–0.81	–0.10	–0.56	–0.81	0.41	–0.08	–0.93	0.17	–0.18
TN	–0.28	0.90	–0.18	0.44	0.79	0.09			
PN	–0.73	0.51	0.03	0.13	–0.07	–0.97			

Mantella aurantiaca Mocquard

The description is based on a tadpole in Gosner stage 30 from the series of tadpoles catalogued as ZSM 1478/2004 (11 tadpoles) obtained through captive breeding, from parental specimens without precise collecting locality, in 1996–1998 (see Glaw *et al.* 2000) (figure 1).

The examined specimen had the following measurements: BL 5.7 mm, BH 2.5 mm, BW 3.3 mm, TMH 1.1 mm, TMW 1.2 mm, MTH 2.1 mm, TMHM 0.9 mm, ED 0.6 mm, IOD 1.6 mm, IND 1.3 mm, ODW 1.7 mm, TAL 11.3 mm, TL 17.1 mm, TN 90, PN 40. The mouth opens ventrally. The papillae are conical, uniserial in the lower labium and in the lateral side of upper labium. The jaw sheath is thin, not fully pigmented and finely serrated. The labial tooth row formula is 5(2–5)/3(1). TAL/TL is 67%. Variation (tables 3, 5–7): Average ratio TAL/TL is ≤ 65% and in one specimen LTRF 6(2–6)/3(1) is found.

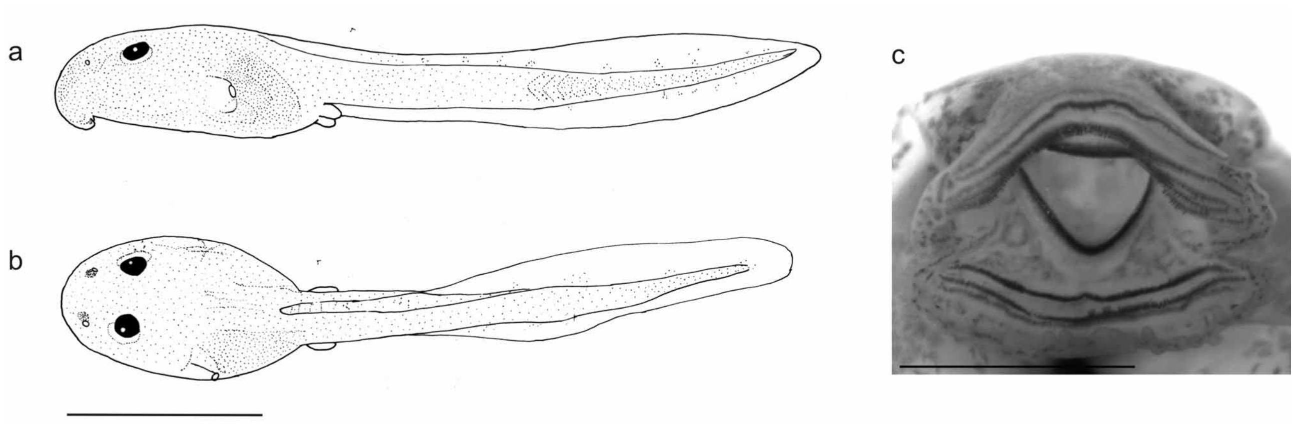

FIGURE 1. Drawings of the preserved tadpole specimen (GS 30) of *Mantella aurantiaca* (ZSM 1478/2004) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

TABLE 3. Measurements of tadpoles in GS 24–30 given as means and standard deviation for each species. All measurements given in millimetres. For abbreviations see table 1 and chapter Materials and methods.

Species	Nr. specimens	BL	BH	BW	TMH	TMW	MTH	TMHM	ED	IOD	IND	ODW	TAL	TL	TN	PN
aur	2	5.7± 0.0	2.4± 0.2	3.1± 0.3	1.0± 0.1	1.1± 0.1	1.8± 0.3	0.8± 0.2	0.6± 0.0	1.6± 0.1	1.3± 0.1	1.6± 0.11	10.4± 1.3	16.3± 1.1	85± 7.1	37.5± 3.5
bern	3	5.6± 0.9	2.7± 0.3	3.6± 0.4	1.3± 0.1	1.3± 0.1	2.5± 0.5	1.0± 0.0	0.5± 0.0	1.5± 0.0	1.2± 0.1	1.4± 0.1	8.0± 2.2	13.5± 2.9	70± 1.5	33.7± 2.5
croc/ milo	2	4.4± 0.7	2.3± 0.1	2.8± 0.1	1.0± 0.3	1.1± 0.1	2.0± 0.5	0.7± 0.0	0.4± 0.1	1.2± 0.3	0.7±	1.4± 0.0	7.0± 1.9	11.4± 2.7		
laev	4	4.9± 0.6	2.4± 0.2	3.6± 0.5	1.0± 0.1	1.2± 0.4	2.3± 0.3	0.7± 0.1	0.4± 0.1	1.3± 0.3	1.2± 0.1	1.5± 0.2	8.9± 1.6	13.9± 2.2	54± 1.7	23.3± 5.0
pulc	6	7.1± 0.6	3.5± 0.5	5.3± 0.5	1.9± 0.2	1.9± 0.2	3.5± 0.4	1.2± 0.3	0.8± 0.1	2.4± 0.2	1.5± 0.1	1.9± 0.1	11.6± 1.8	18.5± 2.1	71 3.6	37.7± 8.5

Mantella baroni Boulenger

The description is based on a tadpole in Gosner stage 42 from the series of tadpoles catalogued as ZSM 1418/2004 (figure 2) (2 tadpoles). Tadpoles were captive bred in 1996–1998 (see Glaw *et al.* 2000). The examined specimen had the following measurements: BL 7.1 mm, BH 3.7 mm, BW 5.7 mm, TMH 1.8 mm, TMW 1.9 mm, MTH 2.7 mm, TMHM 1.2 mm, ED 1.1 mm, IOD 2.6 mm, IND 1.7 mm, ODW 1.6 mm, TAL 14.8 mm, TL 21.9 mm. The mouth opens anteroventrally. Since all of the tadpoles are already in advanced Gosner stages, the description of the mouth part could not be accomplished. TAL/TL is 68%.

Other tadpoles from the series examined are catalogued as ZSM 1419/2004 (3 tadpoles). All tadpoles were obtained through captive breeding, from parental specimens without precise collecting locality. Variation of all tadpoles is shown in table 6 and 7.

Mantella bernhardi Vences, Glaw, Peyrieras, Böhme & Busse

The description is based on a tadpole in Gosner stage 35 from the series of 7 tadpoles catalogued as ZSM 835/2004, collected by M. Vences on 10 February 2004 in small puddles in a swampy area near a lowland rainforest stream, in Vevembe forest (22°47.686' S, 47°11.228' E, 581 m above sea level) (figure 3). DNA sequence from mitochondrial 16S rRNA gene is deposited in Genbank (accession number FJ830851). The examined specimen had the following measurements: BL 9.2 mm, BH 4.7 mm, BW 5.5 mm, TMH 2.0 mm, TMW 2.3 mm, MTH 4.3 mm, TMHM 1.6 mm, ED 0.9 mm, IOD 2.3 mm, IND 1.6 mm, ODW 2.0 mm, TAL 17.7 mm, TL 26.9 mm, TN 78, PN 47. The mouth opens anteroventrally. The papillae are rounded, uniserial in the lower labium and in the lateral side of upper labium. The jaw sheath is thin, fully pigmented and finely serrated. TAL/TL is 66%. The labial tooth row formula is 5(2–5)/3(1). Variation is shown in tables 3–5, and 7.

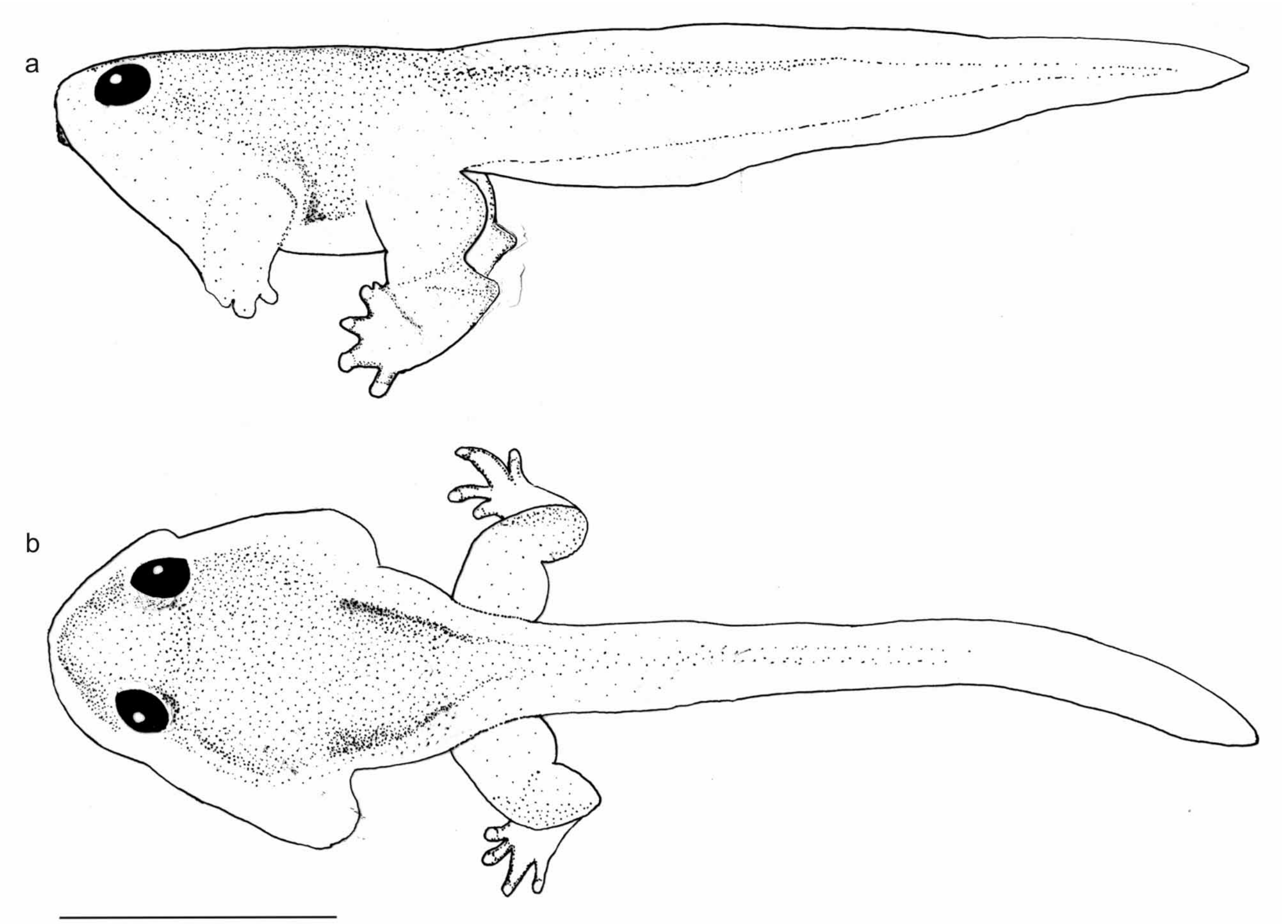

FIGURE 2. Drawings of the preserved tadpole specimen (GS 42) of *Mantella baroni* (ZSM 1418/2004) in (a) lateral (b) dorsal view. Scale bar represents 5 mm.

TABLE 4. Measurements of tadpoles in GS 31–35 given as means and standard deviation for each species. All measurements given in millimetres. For abbreviations see table 1 and chapter Materials and methods.

Species	Nr. specimens	BL	BH	BW	TMH	TMW	MTH	TMHM	ED	IOD	IND	ODW	TAL	TL	TN	PN
bern	8	8.7± 0.8	3.5± 0.4	5.2± 0.4	1.7± 0.1	2.2± 0.3	3.4± 0.1	1.5± 0.2	0.9± 0.0	2.3± 0.1	1.6± 0.1	2.0± 0.1	14.5± 1.9	23.2± 1.1	72± 5.7	44.±5 6.4
croc/ milo	1	7.2	3.3	4.4	1.5	1.5	2.2	1.0	1.0	2.1		1.9	10.1	17.7		
laev	1	7.9	4.4	4.2	1.8	2.3	3.9	1.2	0.7	2.2	1.2	2.2	12.5	20.4	58	33
pulc	1	8.2	3.7	5.6	1.9	2.1	3.6	1.4	0.9	2.6	1.7	2.2	13.6	21.8	70	36
vir	7	7.3± 0.3	3.2± 0.2	4.6± 0.3	1.6± 0.1	1.8± 0.2	2.9± 0.2	1.2 ± 0.3	0.8± 0.1	2.2± 0.1	1.6± 0.1	2.2± 0.3	13.3± 1.1	20.6± 1.1	63.4± 8.5	65.6± 15.3

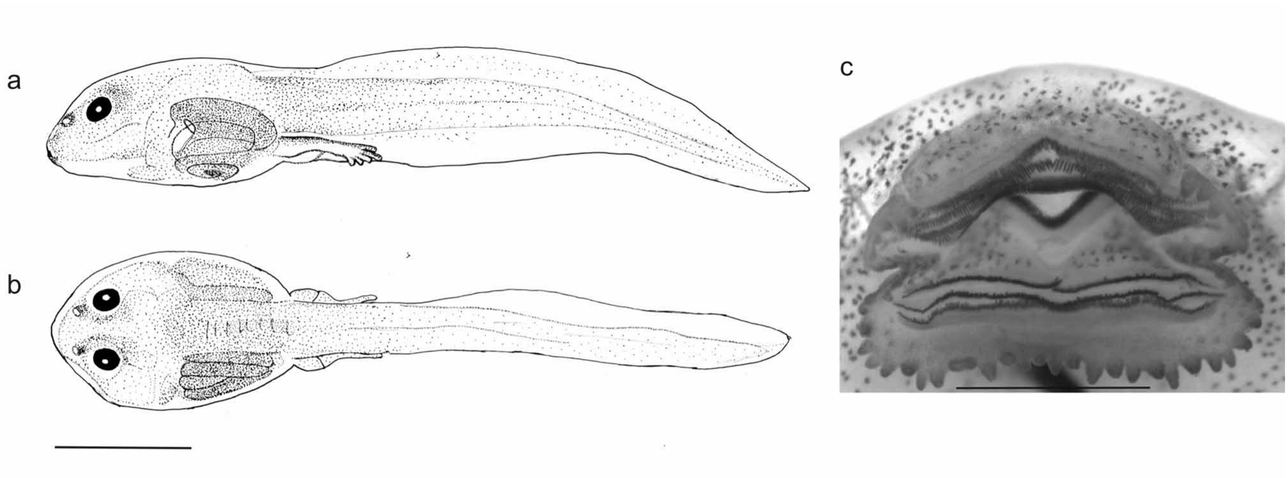

FIGURE 3. Drawings of the preserved tadpole specimen (GS 35) of *Mantella bernhardi* (ZSM 835/2004) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

TABLE 5. Measurements of tadpoles in GS 36–40 given as means and standard deviation for each species. All measurements given in millimetres. For abbreviations see table 1 and chapter Materials and methods.

Species	Nr. specimens	BL	BH	BW	TMH	TMW	MTH	TMHM	ED	IOD	IND	ODW	TAL	TL	TN	PN
aur	8	7.0± 0.7	2.7± 0.2	3.6± 0.4	1.4± 0.2	1.5± 0.1	2.0± 0.5	1.0± 0.1	1.0± 0.1	2.0± 0.2	1.4± 0.1	1.6± 0.2	13.1± 1.1	20.1± 1.6	86± 10.5	51.8± 6.4
bern	2	9.0± 0.3	4.5± 0.3	5.5± 0.0	2.0± 0.1	2.4± 0.1	2.3± 0.1	1.8± 0.2	1.0± 0.1	2.5 0.2	1.7± 0.1	2.1± 0.1	18.1± 0.7	27.1± 0.4	78± 0.0	46.5± 0.7
croc/ milo	2	7.0± 0.4	3.2± 0.1	4.6± 0.7	1.9± 0.1	2.4± 0.2	3.5± 0.4	1.7± 0.1	1.0± 0.1	2.3± 0.3	1.6± 0.1	2.0± 0.1	13.8± 2.2	20.7± 2.1	72± 5.7	56± 2.8
laev	1	9.7	4.7	5.4	1.8	2.1	2.3	1.3	1.2	2.5	1.7		12.3	21.9	56	46

TABLE 6. Measurements of tadpoles in GS 41–44 given as means and standard deviation for each species. All measurements given in millimetres. For abbreviations see table 1 and chapter Materials and methods.

Species	Nr. specimens	BL	BH	BW	TMH	TMW	MTH	TMHM	ED	IOD	IND	ODW	TAL	TL	TN	PN
aur	1	6.9	2.6	3.9	1.2	1.5		0.9	1.1	2.5	1.3	1.6	12.9	20.2	92	59
bar	5	7.6± 0.9	3.4± 0.4	5.5± 0.3	1.8± 0.1	1.2± 0.2	2.7± 0.4	1.4± 0.3	0.9± 0.2	2.8± 0.2	1.5± 0.1	1.5± 0.1	15.4± 1.4	23.0± 1.5	68	70
bets	5	10.0± 0.4	4.8± 0.2	5.8± 1.2	2.3± 0.5	2.2± 0.1	3.6± 0.6	2.0 ± 0.6	1.3± 0.1	2.6± 0.2	1.9± 0.4	2.5± 0.3	19.7± 0.5	29.6± 0.6		
croc/milo	6	8.7± 0.5	3.9± 0.4	4.5± 0.3	1.9± 0.2	2.3± 0.4	2.0± 1.0	1.5± 0.7	1.2± 0.2	3.4± 0.2	1.6± 0.1	1.7± 0.2	12.8± 3.5	21.6± 3.2	63± 4.4	35.5± 0.7
mada	2	10.1± 1.0	4.6± 0.1	7.0± 0.4	2.2± 0.1	3.1± 0.2	4.6± 0.5	2.1± 0.6	1.2± 0.1	3.8± 0.1	1.8± 0.0	2.2± 0.0	24.1± 1.4	34.2± 2.3		
pulc	1	8.8	3.1	4.8	1.7	2.0	2.4	1.6	1.4	3.0	1.5	0.8	12.1	21.1		
vir	2	7.8± 0.7	3.1± 0.4	3.8± 0.5	1.5± 0.4	1.7± 0.2	1.8± 0.0	1.2± 0.1	1.1± 0.0	2.9± 0.3	1.4± 0.1		8.9± 2.2	16.8± 3.1		

Mantella betsileo (Grandidier)

The description is based on a tadpole in Gosner stage 41 catalogued as ZSM 616/2003 (figure 4) (5 tadpoles), collected as embryos in the field from a clutch of a couple of *M. betsileo* in the Forêt de Kirindy/CFPF, and reared in the Kirindy field station, by J. Glos in January 1999. The examined specimen had the following measurements: BL 9.4 mm, BH 4.1 mm, BW 5.8 mm, TMH 3.0 mm, TMW 2.3 mm, MTH 2.6 mm, TMHM 1.8 mm, ED 1.3 mm, IOD 2.5 mm, IND 1.5 mm, ODW 2.4 mm, TAL 19.7 mm, TL 29.1 mm, TN 62, PN 35. The mouth opens anteroventrally. The papillae are conical, uniserial in the lower labium and in the lateral side of upper labium. The jaw sheath is thin, fully pigmented and finely serrated. TAL/TL is 68%. The labial tooth row formula is 5(2–5)/3. Variation is shown in tables 6 and 7.

TABLE 7. Mean values and standard deviation of different morphometric ratios for each species of *Mantella* for different Gosner stages. For abbreviations see table 1 and chapter Materials and methods.

GS	Nr. specimens	Species	BW/ BL	TAL/ TL	ED/ BL	ODW/ BL	ODW/ BW	IND/ IOD	IOD/ BL
24–30	2	aur	0.54± 0.05	0.64± 0.04	0.10± 0.00	0.28± 0.02	0.52± 0.01	0.78± 0.08	0.29± 0.01
36–40	8	aur	0.52± 0.03	0.65± 0.03	0.14± 0.01	0.23± 0.01	0.44± 0.04	0.70± 0.08	0.29± 0.02
41–44	1	aur	0.56	0.64	0.15	0.24	0.42	0.53	0.36
41–44	5	baro	0.73± 0.12	0.67± 0.04	0.12± 0.03	0.19± 0.03	0.26± 0.02	0.53± 0.07	0.37± 0.06
24–30	3	bern	0.65± 0.04	0.58± 0.04	0.10± 0.02	0.26± 0.03	0.40± 0.03	0.79± 0.02	0.27± 0.04
31–35	2	bern	0.61± 0.11	0.63± 0.05	0.10± 0.01	0.24± 0.03	0.39± 0.02	0.71± 0.02	0.27± 0.02
36–40	2	bern	0.61± 0.02	0.67± 0.02	0.11± 0.01	0.23± 0.02	0.37± 0.02	0.68± 0.01	0.28± 0.03
41–44	5	bets	0.59± 0.12	0.66± 0.01	0.13± 0.01	0.25± 0.03	0.45± 0.16	0.71± 0.13	0.26± 0.01
24–30	3	croc/milo	0.65± 0.08	0.61± 0.03	0.09± 0.04	0.32± 0.06	0.49± 0.03	0.46	0.29± 0.10
31–35	2	croc/milo	0.61	0.57	0.15	0.26	0.43		0.29
36–40	2	croc/milo	0.66± 0.07	0.67± 0.04	0.14± 0.01	0.29± 0.00	0.44± 0.04	0.68± 0.05	0.33± 0.03
41–44	6	croc/milo	0.52± 0.02	0.58± 0.07	0.14± 0.02	0.20± 0.03	0.37± 0.05	0.48± 0.04	0.39± 0.02
24–30	4	laev	0.74± 0.10	0.64± 0.03	0.08± 0.01	0.31± 0.04	0.41± 0.02	0.64± 0.43	0.26± 0.05
31–35	1	laev	0.53	0.61	0.09	0.27	0.52	0.82	0.28
36–40	1	laev	0.56	0.56	0.12			0.69	0.26
41–44	2	mad	0.70± 0.10	0.71± 0.01	0.12± 0.03	0.22± 0.03	0.31± 0.01	0.47± 0.02	0.37± 0.02
24–30	6	pulc	0.75± 0.04	0.62± 0.04	0.11± 0.01	0.27± 0.03	0.36± 0.03	0.64± 0.03	0.34± 0.02
31–35	1	pulc	0.69	0.62	0.11	0.27	0.39	0.65	0.32
41–44	1	pulc	0.55	0.58	0.16	0.09	0.16	0.50	0.34
31–35	7	vir	0.63± 0.04	0.65± 0.02	0.10± 0.01	0.30± 0.04	0.47± 0.05	0.73± 0.04	0.30± 0.01
41–44	2	vir	0.49± 0.01	0.53± 0.04	0.14± 0.01			0.48± 0.01	0.37± 0.00

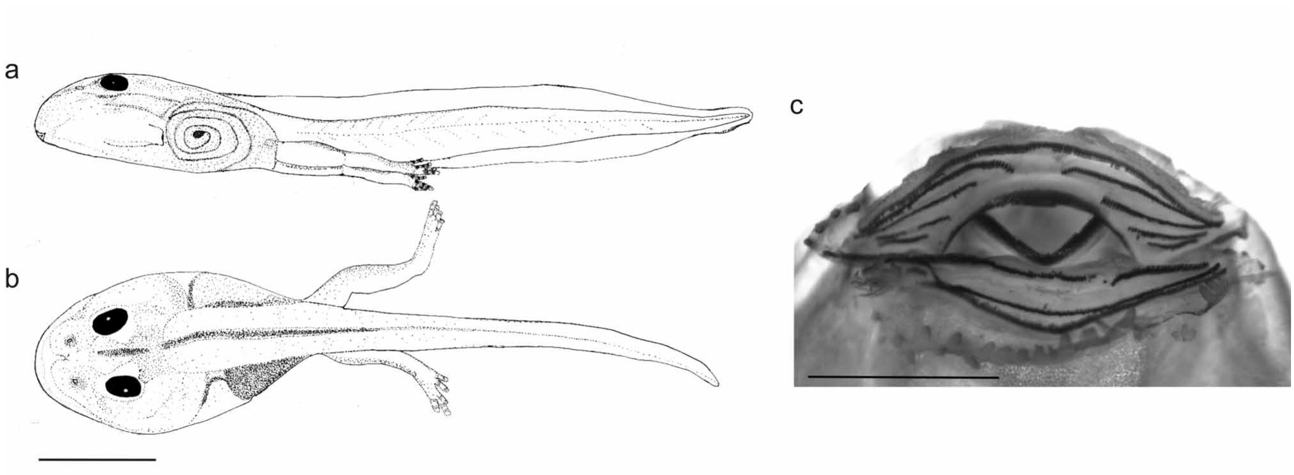

FIGURE 4. Drawings of the preserved tadpole specimen (GS 41) of *Mantella betsileo* (ZSM 616/2003) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

Mantella crocea Pintak & Böhme × *M. milotympanum* Staniszewski (F1 hybrid)

The description is based on a tadpole in Gosner stage 36 catalogued as ZSM 1414/2004 (figure 5). Tadpoles from this series are hybrids obtained through captive breeding, from parental specimens collected in 1996–1998 without precise locality (see Glaw *et al.* 2000). The examined specimen had the following measurements: BL 7.2 mm, BH 3.1 mm, BW 5.1 mm, TMH 2.0 mm, TMW 2.6 mm, MTH 3.2 mm, TMHM 1.8 mm, ED 1.0 mm, IOD 2.6 mm, IND 1.7 mm, ODW 2.1 mm, TAL 15.4 mm, TL 22.2 mm, TN 76, PN 54. The mouth opens ventrally. The papillae are rounded, biserial in the lower labium. The jaw sheath is middle sized, partially pigmented and finely serrated. The labial tooth row formula is 5(2–5)/3(1). TAL/TL is 69%. Other tadpoles from the series examined are catalogued as ZSM 1400–1405/2004 and 1408–1415/2004 (altogether 11 tadpoles). Variation is shown in tables 3–7. In some individuals LTRF is 5(2–5)/3(1–2).

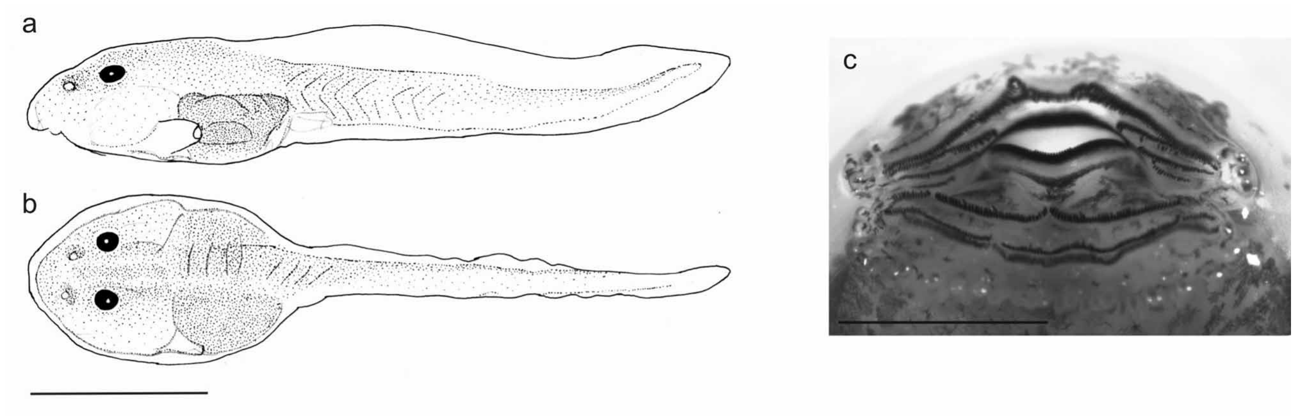

FIGURE 5. Drawings of the preserved tadpole specimen (GS 36) of *Mantella crocea/milotympanum* (ZSM 1414/2004) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

Mantella laevigata Methuen & Hewitt

The description is based on a tadpole in Gosner stage 25 catalogued as ZSM 1447/2004 (figure 6), obtained through captive breeding, from parental specimens without precise collecting locality, in 1996–1998 (see

Glaw *et al.* 2000). The examined specimen had the following measurements: BL 5.2 mm, BH 2.2 mm, BW 3.6 mm, TMH 0.9 mm, TMW 0.8 mm, MTH 2.2 mm, TMHM 0.7 mm, ED 0.4 mm, IOD 1.4 mm, IND 1.1 mm, ODW 1.6 mm, TAL 9.5 mm, TL 14.7 mm. Oral disc morphology is based on a tadpole in Gosner stage 38 catalogued as 1502/2004. Mouth part is not yet fully developed. Body is dorsolaterally flattened, with eyes positioned and directed dorsally. TAL/TL is 65%. The mouth opens ventrally. The mouth part is not emarginated. The papillae are rounded, biserial in the lower labium and in the lateral side of upper labium. The jaw sheath is thick, fully pigmented and with fewer big serrations. The labial tooth row formula is 3(2–3)/3(1).

Other tadpoles examined are catalogued as ZSM 1442–1444/2004, 1502/2004 and 1524/2004 (6 tadpoles). All tadpoles were obtained through captive breeding. Variation is shown in tables 3–5, and 7.

M. laevigata tadpoles examined in this study appear to have unusual oral disc development. The development starts at Gosner stage 25 with the formation of papillae and the first tooth rows. In contrast to the other *Mantella* species, the mouth parts are already considerably degraded at stage 39, with teeth falling out which is possibly a result of earlier metamorphosis, or may be an artefact during captive rearing. Due to a small sample size and lack of specimens captured in the nature, we cannot generalize that this is the case with all *M. laevigata* tadpoles.

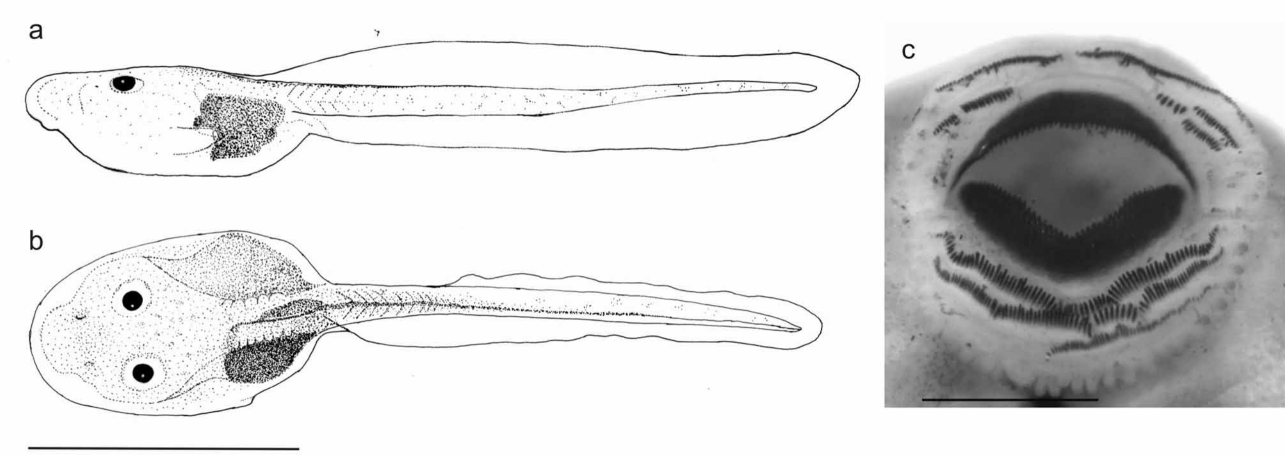

FIGURE 6. Drawings of the preserved tadpole specimen (GS 25) of *Mantella laevigata* (ZSM 1447/2004) in (a) lateral and (b) dorsal view, and (c) photography of its oral disc (ZSM 1502/2004; GS 38). Scale bar represents 5 mm, and 1 mm, respectively.

Mantella madagascariensis (Grandidier)

The description is based on two tadpoles in Gosner stages 41 and 42, catalogued as ZSM 1425/2004 (figure 7), obtained through captive breeding, from parental specimens without precise collecting locality, in 1996–1998 (see Glaw *et al.* 2000). The examined specimen had the following measurements: BL 9.4 mm, BH 4.6 mm, BW 7.3 mm, TMH 2.3 mm, TMW 3.3 mm, MTH 5.0 mm, TMHM 2.5 mm, ED 1.3 mm, IOD 3.7 mm, IND 1.8 mm, ODW 2.2 mm, TAL 23.1 mm, TL 32.5 mm. The mouth opens ventrally. The papillae are conical, uniserial in the lower labium and in the lateral side of upper labium. TAL/TL is 71%.

Variation is shown in tables 6 and 7. Since both of the tadpoles are already in advanced Gosner stage, a full description of the mouth part could not be accomplished.

Mantella pulchra Parker

The description is based on a tadpole in Gosner stage 28 from the series of tadpoles catalogued as ZSM 1/

2008 (figure 8) (7 tadpoles), collected at An'Ala forest, on 8 February 2006 by L. Raharivololoniaina and R. D. Randrianiaina. DNA sequence from mitochondrial 16S rRNA gene is deposited in Genbank (accession number FJ830849). The examined specimen had the following measurements: BL 7.1 mm, BH 3.9 mm, BW 5.3 mm, TMH 2.0 mm, TMW 2.0 mm, MTH 3.9 mm, TMHM 1.3 mm, ED 0.8 mm, IOD 2.4 mm, IND 1.6 mm, ODW 1.9 mm, TAL 13.1 mm, TL 20.2 mm, TN 74, PN 50. The mouth opens anteroventrally. The papillae are rounded, uniserial in the lower labium and in the lateral side of upper labium. The jaw sheath is middle sized, fully pigmented and finely serrated. TAL/TL is 65%. The labial tooth row formula is 5(2–5)/3(1). Variation is shown in tables 3–4, and 6–7.

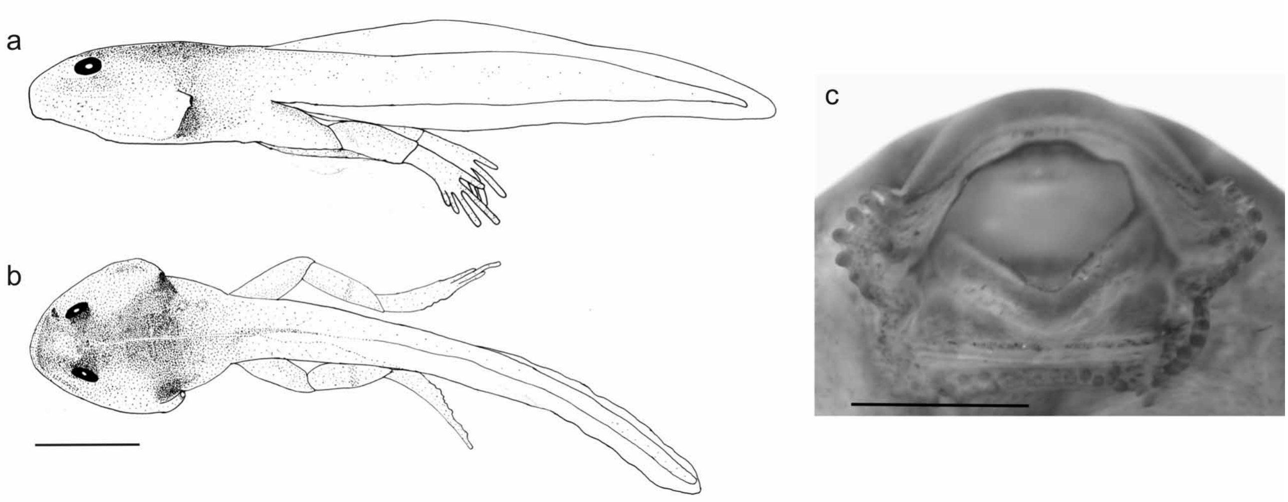

FIGURE 7. Drawings of the preserved tadpole specimen (GS 41) of *Mantella madagascariensis* (ZSM 1425/2004) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

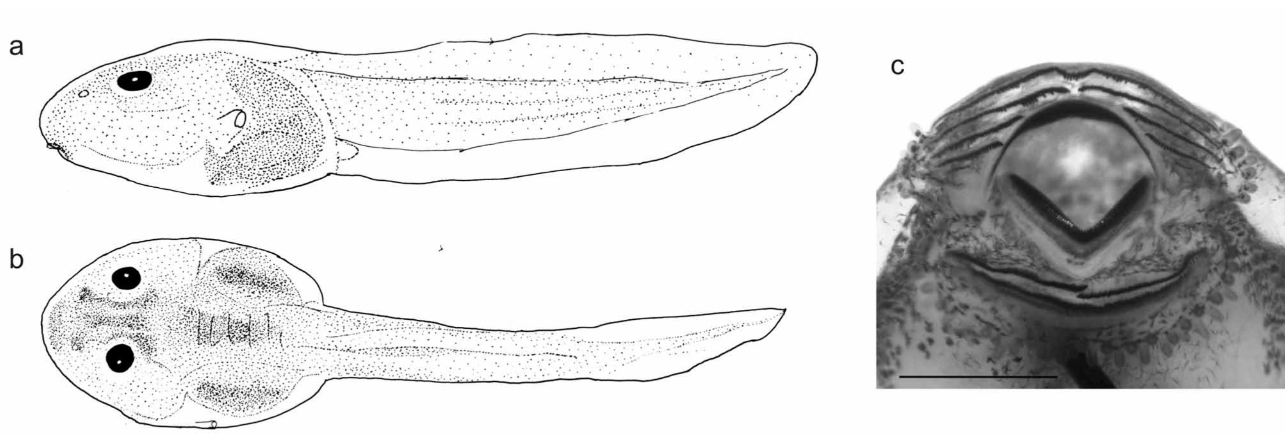

FIGURE 8. Drawings of the preserved tadpole specimen (GS 28) of *Mantella pulchra* (ZSM 1/2008) in (a) lateral and (b) dorsal view. Scale bar represents 5 mm, and 1 mm, respectively.

Mantella viridis Pintak & Böhme

The description is based on a tadpole in Gosner stage 34 from the series of tadpoles catalogued as ZSM 797/2004 (figure 9) (3 tadpoles). DNA sequence from mitochondrial 16S rRNA gene is deposited in Genbank (accession number FJ830850). The examined specimen had the following measurements: BL 7.5 mm, BH 3.1 mm, BW 4.6 mm, TMH 1.8 mm, TMW 2.2 mm, MTH 3.2 mm, TMHM 1.4 mm, ED 0.9 mm, IOD 2.3 mm, IND 1.8 mm, ODW 2.0 mm, TAL 11.5 mm, TL 19.1 mm, TN 76, PN 63. The mouth opens ventrally. The papillae are rounded, biserial in the lower labium and in the lateral side of upper labium. The jaw sheath is thick, fully pigmented and with fewer big serrations. The upper jaw sheath has M-shape. TAL/TL is 60%. The labial tooth row formula is 5(2–5)/3(1).

Other tadpoles from the series are catalogued as ZSM 796/2004 (1 tadpole), 798/2004 (3 tadpoles) and ZSM 1574/2004 (2 tadpoles). Tadpoles from series ZSM 796/2004 and 798/2004 were collected by RDR in the field on 20 February 2003 in Montagne des Français, in Madagascar, while tadpoles from the series ZSM 1574/2004 are obtained through captive breeding, from parental specimens without precise collecting locality, in 1996. Variation is shown in tables 4 and 6–7. Some specimens have an uniserial row of marginal papillae.

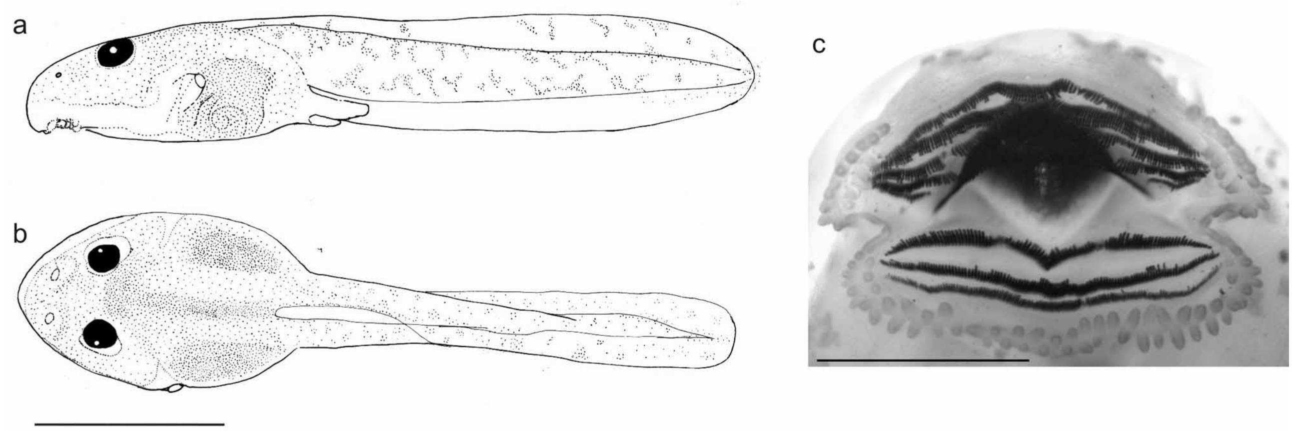

FIGURE 9. Drawings of the preserved tadpole specimen (GS 34) of *Mantella viridis* (ZSM 797/2004) in (a) lateral and (b) dorsal view, and (c) photograph of its oral disc. Scale bar represents 5 mm, and 1 mm, respectively.

Discussion

Mantella have tadpoles of the generalized type (Cannatella 1999), i.e. they do not have any morphological characters showing a high degree of specialization to a specific type of habitat or behaviour, e.g. the specialized funnel-shaped mouth observed in the subgenus *Chonomantis* (genus *Mantidactylus*) (Vences & Glaw 2004), reduced keratinized structures in *Boophis picturatus* as a possible adaptation to sand feeding (Altig & McDiarmid 2006), or the very prominent oral disc typical for the suctorial stream-living tadpoles in *B. schuboeae* and *B. ankaratra* (Glos *et al.* 2007).

The comparison of the previous description of *M. aurantiaca* with the specimens examined here shows some minor dissimilarities. The papillae of the specimens examined here are uniserial in contrast to the original description of Arnoult (1965), and the labial tooth row formula is variable (5(2–5)/3(1) or 6(2–6)/3(1)). The partial description of *M. laevigata* tadpoles (Glaw & Vences 1992, 1994; Glaw *et al.* 2000) fits the description provided in this study. Tadpoles that were previously described as *M. betsileo* tadpoles are today known to belong to *M. ebenaui* (Glaw & Vences 2007). A rough description given for *M. ebenaui* tadpoles is very similar to that of *M. betsileo*, and only a detailed examination of the former could probably show some differences.

We here described F1 hybrid tadpoles between *M. crocea* and *M. milotympanum* for two reasons: (1) tadpoles of both species were never collected in the field and (2) genetic analyses revealed that these two species are very closely related and might be just colour morphs of a single species (Chiari *et al.* 2004). Their taxonomy is in need of further study (Jovanovic *et al.* 2007).

In our comparison we noticed that there is some difference between the tadpoles of different species of *Mantella* when comparing various morphological characters. However, when considering all morphometric measurements, species identification remains difficult. Some morphometric ratios are very variable both intraspecifically as well as interspecifically, such as BW/BL, while some others (e.g. TAL/TL) are stable both intra- and interspecifically and show little variation. Also, LTRF is stable in some species (e.g. *M. betsileo*, *M.*

laevigata, *M. pulchra*, *M. viridis*, *M. expectata*) (Mercurio & Andreone 2005) and variable in other (*M. crocea/milotympanum* and *M. aurantiaca*). There is no apparent ontogenetic change of morphology that could be found consistently in all species, i.e. the ratios of morphological measurements do not change in a predictable manner with increasing developmental stage. Solely, a slight increasing trend is found for ED/BL in all species, and for IOD/BL in *M. aurantiaca*, *M. bernhardi*, *M. crocea/milotympanum* and *M. viridis*, and a slight trend of decrease in BW/BL in *M. bernhardi*, *M. viridis* and *M. pulchra*.

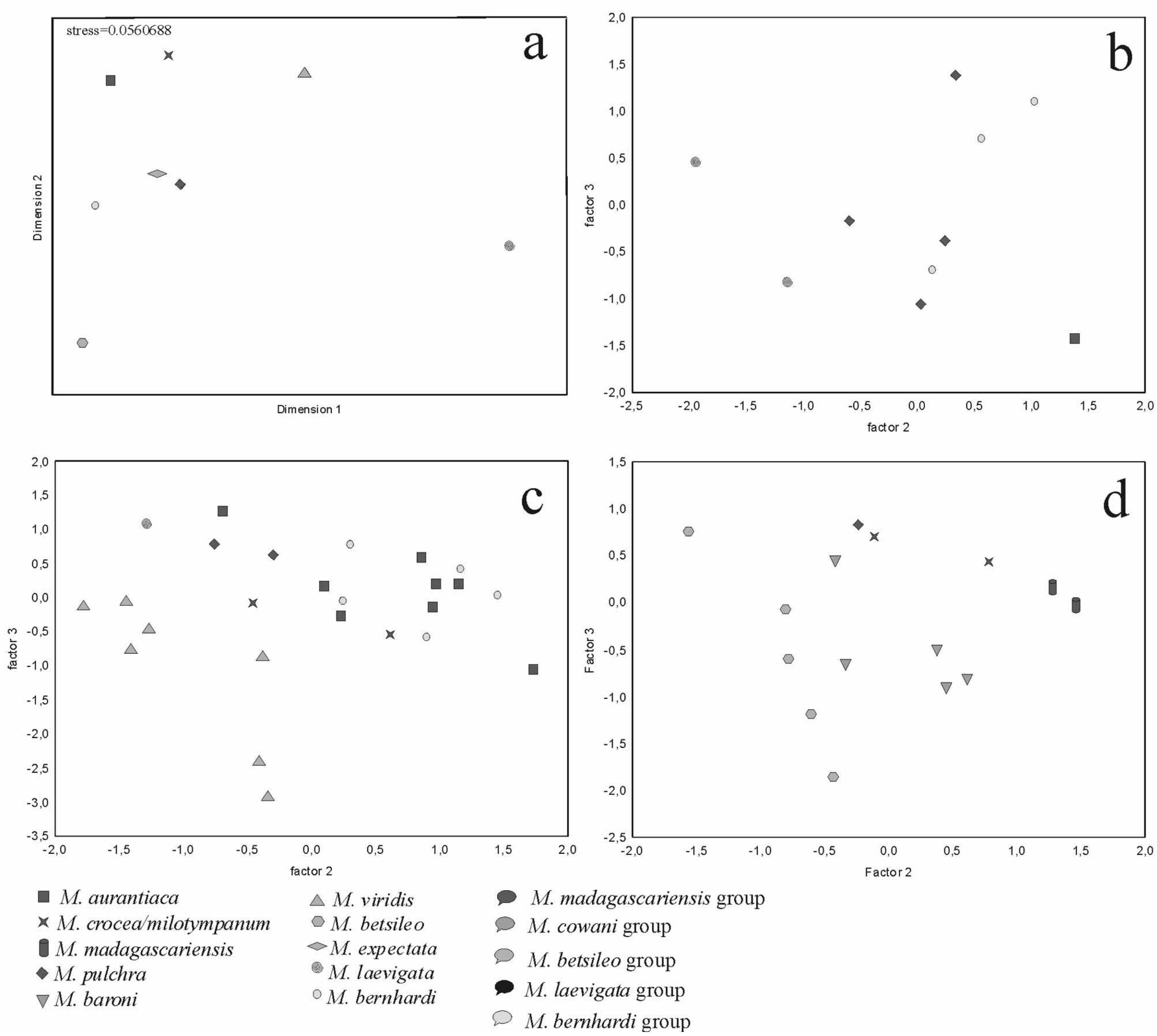

FIGURE 10. Graphical results obtained by statistical analysis; (a) NMDS analysis performed without *M. baroni* and *M. madagacariensis*; (b) PCA analysis for GS group 1 (includes tadpoles between GS 24–29); (c) PCA analysis for GS group 2 (includes tadpoles between GS 30–39); (d) PCA analysis for GS group 3 (group 3 includes tadpoles between GS 41–44). Each species is represented with its own symbol and each colour represents one *Mantella* species group.

Phylogenetic relatedness might be reflected in morphological similarities, i.e. it could be assumed that closely related species of *Mantella* have more similar tadpoles. The example of *M. crocea/milotympanum* and *M. aurantiaca* shows that this is not a general rule. Both species are very closely related and have morphologically very similar adults (Chiari *et al.* 2004). However, tadpole morphology of these two species does not show such an obvious pattern.

In the NMDS analysis (figure 10.a) based on the absence/presence of various morphological characters (performed without *M. madagascariensis* and *M. baroni* due to their very advanced Gosner stage) only two species are grouped closely together, namely *M. pulchra* and *M. expectata*. This similarity in morphology does not reflect phylogenetic relatedness as both species belong to different species groups. *M. laevigata* tadpoles, that are most deviant from all other *Mantella* tadpoles when inspected visually, showed also in the NMDS the highest dissimilarities to all other species. This is also in agreement with molecular phylogenetic data that place *M. laevigata* together with *M. manery* as a basal group of genus *Mantella* (Chiari *et al.* 2004; Rabemananjara *et al.* 2007). Tadpoles of this species have eyes positioned dorsally, a non-emarginated oral disc and strong jaw sheaths, in contrast to all other *Mantella* tadpoles (except *M. viridis* that also has strong jaw sheaths). Due to the early Gosner stage of the voucher specimen of *M. laevigata*, however, the possibility remains that these differences may be not so obvious in more advanced stages. As well, the unusual shape of the mouth part could be a consequence of an inappropriately applied fixation procedure (e.g. inappropriate handling of specimens, inadequate storage etc). Although it cannot be excluded that the flattened body shape is also a consequence of an inappropriate fixation procedure, it is together with the dorsal eyes likely an adaptation to the specific habitat niche (Glaw & Vences 1994). While other *Mantella* tadpoles are free living in slow running streams, wetlands or ponds, tadpoles from *M. laevigata* live in phytotelmata (Heying 2001).

Until today, very little is known about natural breeding habitats of *Mantella* species, and in this context most of the tadpoles described here were reared in captivity, without any previous encounters of these tadpoles in the nature. The only tadpoles collected in the field belong to *M. bernhardi*, *M. pulchra*, *M. betsileo*, *M. viridis* and *M. ebenaui* (previously assigned to *M. betsileo*), and to *M. laevigata*.

Tadpoles of *M. madagascariensis* were never recorded in nature but are presumed to have similar requirements like other species of the *M. madagascariensis* group (swamps). Tadpoles of *M. baroni*, as well as tadpoles of all other species in the *M. cowani* group were also never found in nature due to unknown reasons. In Ranomafana National Park in Madagascar, intensive searches were performed several times (January–February 2007 and 2008) and tadpoles were collected from many streams where adult individuals of *M. baroni* were common but none of the tadpoles of this species were found. In this case, we presume that some systematic omission has happened. The possibility of searching in the wrong period of the year can most certainly be excluded because the animals were calling at the researched sites, as well as the possibility of direct development (when bred in captivity, they do have tadpoles).

The PCA showed species specific morphological separation of *Mantella* tadpoles, and it is more pronounced in tadpoles of more advanced Gosner stages (keeping in mind that for different stages different species were used). Since PC factor 1 for all three GS groups was mainly contributed by size related variables, it was therefore omitted from the interpretation. In the analysis for GS group 3, we can see that PC factor 2 (mainly IOD) very clearly separates specimens of *M. betsileo* from other species. Both IOD (2.38–2.86 mm) values as well as IOD/BL (0.24–0.28) are very stable, while in other species both of these values are very variable (in most of the species IOD being greater than in *M. betsileo*).

Intraspecific morphological variability of *Mantella* tadpoles as it was found in our study can be a result of several influences, such as genetic background and environmental factors. Intraspecific variability in tadpoles reared in captivity can be caused by genetic factors. The origin of many of the specimens used in our study is unknown as they were obtained through the pet trade, but the same individuals have been used for genetic analyses (e.g. Schaefer *et al.* 2002) and it is unlikely that any of them had a genetically divergent background, e.g., originating from geographically distant populations. On the other hand, specimens collected in the field can show morphological variability either as a result of genetic variability or the ability to exhibit phenotypic plasticity. Taken in consideration general variability in *Mantella* tadpoles, we can examine the argument of Wilbur & Collins (1973) who have proposed that amphibian larvae might respond adaptively to changes in their environment. Phenotypically plastic responses to environmental change are typically compartmentalized by the type of environmental cues that cause the induction. In amphibian larvae for example, it can be influenced by temperature (Harkey & Semlitsch 1988; Newman 1998), but different types of environmentally induced responses might very well be related to each other. Additionally, factors that account for differences in growth rate and size at metamorphosis, are shown to have effects on the oral structure in *R. temporaria* larvae (Vences *et al*. 2002). In our study we observed relatively high variability by PCA between the specimens of *M. bernhardi*, *M. aurantiaca* and *M. pulchra*.

Tadpoles of the genus *Mantella* do not appear to bear many useful characters for determining phylogeny. Also *Mantella* adults appear morphologically very homogeneous, both in terms of morphology and ecology. Likewise, there is no great divergence in tadpole morphology, although some differences exist. We thus may hypothesize that ecological factors in *Mantella* species have stronger influence on tadpole morphology than does the phylogeny.

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