SALAMANDRA 51(2) | 91–102 | 30 June 2015 | ISSN 0036–3375

The tadpoles of four Central African *Phrynobatrachus* species

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Manuscript received: 1 April 2014
Accepted: 17 July 2014 by Stefan Lötters

Abstract. We describe the tadpoles of four Cameroonian *Phrynobatrachus* species, *P. auritus, P. chukuchuku, P. jimzimkusi,* and *P. manengoubensis*. While *P. auritus* is a widespread frog of Central African rainforests, the other three species are endemic to parts of the Cameroonian Volcanic Line. All tadpoles have the short and rotund body shape that is typical of *Phrynobatrachus*, with comparatively short tails and delicate jaw sheaths. We describe morphological characters suited to differentiate between these species, in particular labial tooth row formulae and the presence or absence of particular papillae, and summarize corresponding data for other described tadpoles of the genus. As far as is currently known, different reproductive modes, as well as morphology and biology of *Phrynobatrachus* tadpoles is not mirrored in the phylogenetic relationships of the respective species. We further point out profound morphological differences between *P. jimzimkusi* tadpoles from the type locality, Mt. Bamboutos, and Mt. Manengouba, and argue that the taxonomic status of the latter population should be verified.

Key words. Amphibia, Anura, larval morphology, Cameroon, DNA-barcoding, Phrynobatrachidae.

Introduction

The small to medium-sized species of the frog genus *Phrynobatrachus* Günther, 1862 are endemic to sub-Saharan Africa (Frétey 2008, Zimkus et al. 2010, Frost 2013). Currently, 87 species are recognized (Frost 2013), occurring from dry savannahs to rainforests and from lowland to montane habitats (e.g., Rödel 2000, Channing 2001, Channing & Howell 2006). New species are continuously added to this list; e.g., ten species in the last five years (Zimkus 2009, Rödel et al. 2009, 2010, 2012a, b, Blackburn 2010, Schick et al. 2010, Blackburn & Rödel 2011, Zimkus & Gvoždík 2013).

Some of the smaller species are very short-lived, with adults living for less than half a year, and they may reach enormous densities in places (Barbault 1972, Barbault & Trefaut Rodrigues 1978, 1979, Barbault & Pilorge 1980, Rödel et al. 2004). Most species reproduce in small and temporary waters, where they deposit a single layer of floating eggs (Wager 1986, Rödel 1998b, 2000). Other species have been observed to reproduce in small streams (Rödel 2003; Fig. 1), tree holes (Rödel 1998a), or have a terrestrial development (Rödel & Ernst 2002a). Some species attach their clutches to tree bark (Rödel et al. 2004), rock (Harper et al. 2010), or leaves (Amiet 1981, Ernst & Rödel 2002b). While most species abandon their clutches, at least one provides parental care (Amiet 1981). Most known tadpoles of the genus are developing as free-swimming and feeding larvae (e.g., Lamotte & Dzieduszycka 1958, van Dijk 1966, de Sá & Channing 2003). The tadpoles of *P. sandersoni* do not feed, but develop outside eggs on moist ground (Amiet 1981), whereas tadpoles of *P. tokba* remain within the eggs and only hatch after metamorphosis (Rödel & Ernst 2002a). Most known *Phrynobatrachus* tadpoles are very cryptic in colour and secretive in behaviour (e.g., Lambiris 1989, Rödel 2000, Channing & Howell 2006, Du Preez & Carruthers 2009), one however, is aposematically coloured (Rödel et al. 2009).

This large variability in habitat choice, reproduction strategy, and developmental mode promises an interesting opportunity to investigate the evolution of life-history traits in a group of closely related species (Zimkus et al. 2012), in particular as the phylogeny of *Phrynobatrachus* is now comparatively well known (Zimkus et al. 2010). Unfortunately, tadpoles have so far been described of only 15 out of 87 *Phrynobatrachus* species (Channing et al. 2012). Herein, we add tadpole descriptions for another three species from Cameroon and redescribe the tadpole of a fourth.

Material and methods

Sampling

Tadpoles were collected in Cameroon on Mt. Manengouba by M. Hirschfeld (November through December 2010), in the Ebo forest by M. Dahmen and M. Hirschfeld (August through October 2011), and on Mt. Oku by T.M. Doherty-Bone (August through September 2012). For exact locality details, see tadpole descriptions and Appendix.

Tadpoles were caught by hand or with dip nets. They were anaesthetized in either a tricaine methane sulphonate (MS222, Thomson & Joseph Ltd), or a chlorobutanol solution. For molecular analysis, a piece of tail muscle was cut off and preserved in ethanol (96%) from at least one individual for each set of morphologically distinct tadpoles from every locality. The remaining tadpoles were then fixed in formalin (8%) and later transferred into ethanol (75%). All vouchers have been inventoried at the Museum für Naturkunde Berlin (ZMB).

Identification

Species identity of tadpoles was verified by DNA-barcoding, i.e., comparing 16S ribosomal RNA sequences from tadpoles to known adults (Fig. 2). For molecular procedures applied, see Hirschfeld et al. (2012). All tadpoles could be unambiguously assigned to known species. The genetic divergence of tadpoles ranged from 0–0.2% to the respective adults (see Tabs 1–2 and Appendix).

Figure 1. *Phrynobatrachus jimzimkusi* with clutch attached to a small branch, in a medium-sized mountain stream at Mt. Manengouba, Cameroon (5.0098° N, 9.8569° E, 2,135 m a.s.l.).

Table 1. Intra- and interspecific genetic distances (uncorrected p) in the mitochondrial 16S ribosomal RNA (543bp) of *Phrynobatrachus* species, tadpoles compared to each other and to adult individuals (see Appendix and Tab. 2); SD – standard deviation, N – number of pairwise comparisons.

Species	Min	Max	Mean	SD	N
auritus	0.00	0.20	0.06	0.09	21
chukuchuku	0.00	0.00	0.00	0.00	3
jimzimkusi	0.00	0.00	0.00	0.00	6
manengoubensis	0.00	0.00	0.00	–	1
Interspecific comparisons	3.32	17.28	10.73	4.15	89

Table 2. Voucher numbers of adult *Phrynobatrachus* individuals, to which tadpoles were compared.

Species	Voucher #	GenBank #	Source
auritus	CAS 207932	FJ769125	Zimkus (2009)
chukuchuku	MCZ A-138126	FJ769105	Zimkus (2009)
jimzimkusi	ZMB 80238	KJ626418	this study
manengoubensis	MCZ A-138047	FJ769108	Zimkus (2009)

Character assessment

Measurements were taken with a measuring ocular on a dissecting microscope (accuracy of ± 0.1 mm) by one person (TP). The following measurements were collected: EL (entire length = head–body length + tail length), BL (head–body length), TL (tail length), BH (body height at the level of spiracle insertion), BW (maximum body width), AW (width of tail axis at tail base), AH (maximum tail axis height), VF (maximum height of ventral fin), DF (maximum height of dorsal fin), TTH (maximum total tail height), ED (horizontal eye diameter), IOD (interocular distance; measured across centres of eyes), IND (internostril distance; measured across centres of nostrils), SND (snout–nostril distance; measured to centre of nostril opening), SED (snout–eye distance; measured to centre of eye), ODW (oral disc width), SL (spiracle length), and SSD (snout–spiracle distance). A summary of all measurements is provided in Tab. 3. The following relationships were calculated: BL/TL, BH/BL, BW/BL, SND/SED, IND/BL, ED/BL, IOD/IND, TL/EL, DF/VF, AH/DF, TH/BH, AW/BW, AH/BH, SL/BL, ODW/BW, and SSD/BL. The relation of head–body length to total length was usually not available for genotyped vouchers, as fin tips had been removed for tissue samples prior to measuring. These relations were calculated for non-genotyped, morphologically identical

Figure 2. Adult Cameroonian *Phrynobatrachus* and their breeding sites; a+b) *Phrynobatarchus auritus* (ZMB 80227), Ebo Forest, 4.348017° N, 10.23238° E, 315 m a.s.l.; c+d) *P. chukuchuku*, Kinkolong Swamp, Mt. Oku summit; e+f) *P. jimzimkusi* (not collected, Mt. Manengouba, near summit, 5.01795° N, 9.86525° E, 2,100 m a.s.l.); g+h) *P. manengoubensis* (ZMB 80247), Mt. Manengouba, near Nkikoh, 5.0929° N, 9.8177° E, 1,328 m a.s.l.

Table 3. Measurements (in mm) of *Phrynobatrachus* tadpoles; gen – genotyped; G – developmental stage (Gosner 1960); for other abbreviations see Material and methods.

Species	ZMB#	gen	G	BL	TL	EL	BW	BH	AH	VF	DF	TTH	AW	IOD	IND	SND	SED	ED	SSD	ODW
auritus	79648	yes	36	5.5	–	–	3.6	2.4	1.1	0.5	0.7	2.6	1.1	1.6	0.9	0.5	1.3	0.7	3.0	1.1
auritus	79648	no	37	5.8	9.5	15.3	3.8	2.9	1.2	0.6	1.1	2.9	1.1	1.5	1.0	0.5	1.4	0.8	3.4	0.7
auritus	79648	no	36	6.0	10.1	16.1	4.3	3.1	1.1	0.7	1.1	3.5	1.2	1.6	1.1	0.5	1.5	0.8	3.5	0.8
auritus	79649	yes	39	6.0	–	–	3.9	2.5	1.3	0.5	0.6	2.6	1.1	1.8	1.0	0.5	1.4	0.8	3.0	1.2
auritus	79649	no	38	6.1	–	–	4.1	3.0	1.3	0.9	1.2	3.3	1.2	1.5	1.0	0.4	1.3	0.9	3.5	0.6
auritus	79649	no	37	5.6	10.2	15.8	3.5	2.9	1.2	0.7	1.2	3.2	1.2	1.5	0.9	0.5	1.5	0.8	3.7	0.7
auritus	79649	no	37	6.1	10.6	16.7	4.4	3.0	1.3	0.9	1.3	3.4	1.2	1.6	1.0	0.5	1.5	0.8	3.3	0.7
auritus	79649	no	37	6.0	10.7	16.7	3.9	3.1	1.2	0.8	1.2	3.3	1.2	1.5	1.0	0.5	1.4	0.8	3.5	0.7
auritus	79649	no	37	5.8	10.2	16.0	4.0	3.0	1.2	0.7	1.2	3.2	1.3	1.4	0.9	0.5	1.3	0.8	3.4	0.7
auritus	79649	no	37	5.9	10.1	16.0	4.2	3.1	1.3	0.8	1.3	3.5	1.2	1.7	1.1	0.5	1.4	0.8	3.5	0.8
auritus	79650	yes	36	5.8	–	–	3.5	2.5	1.1	0.4	0.5	2.6	1.1	1.6	1.0	0.5	1.3	0.7	3.0	1.1
auritus	79651	no	37	6.4	11.9	18.3	4.5	3.1	1.4	–	1.2	–	1.4	1.5	1.1	0.6	1.8	0.8	3.6	0.8
auritus	79651	no	37	6.5	11.8	18.3	4.7	3.3	1.5	–	1.4	–	1.4	1.6	1.2	0.6	1.7	0.8	3.5	0.7
auritus	79651	no	36	6.3	–	–	4.4	3.0	1.3	–	1.2	–	1.2	1.5	1.1	0.5	1.5	0.8	3.4	0.7
auritus	79651	no	37	6.3	–	–	4.5	3.2	1.3	–	1.2	–	1.3	1.7	1.2	0.5	1.5	0.8	3.5	0.7
auritus	79651	no	36	6.3	–	–	4.1	3.1	1.3	–	1.3	–	1.3	1.6	1.1	0.5	1.4	0.8	3.4	0.6
auritus	79652	yes	35	5.9	–	–	4.0	2.5	1.2	–	0.5	2.7	1.2	1.8	1.0	0.5	1.5	0.7	3.0	1.4
auritus	79652	no	36	5.8	–	–	4.0	3.0	1.1	0.9	1.1	3.4	1.3	1.5	1.0	0.5	1.3	0.8	3.0	0.7
auritus	79653	yes	28	4.8	–	–	3.0	1.7	1.1	0.4	0.5	1.8	0.9	1.2	0.8	0.4	1.1	0.6	2.4	1.0
auritus	79654	yes	25	4.0	–	–	2.8	1.3	1.0	–	–	–	0.9	1.0	0.7	0.2	0.8	0.5	1.5	0.7
chukuchuku	79655	yes	37	7.2	11.9	19.1	5.2	4.1	1.2	1.1	1.0	3.8	1.2	2.3	1.1	0.4	1.4	0.8	3.8	1.2
chukuchuku	79656	yes	41	6.5	13.0	19.5	4.5	3.3	1.8	1.0	1.1	3.1	1.9	2.5	1.2	0.2	1.3	1.0	3.1	0.8
chukuchuku	79657	no	38	6.1	–	–	4.7	3.8	1.3	1.1	1.2	3.6	1.2	2.0	1.0	0.6	1.2	0.7	2.2	1.0
chukuchuku	79657	no	42	6.8	14.1	20.9	4.5	3.2	1.5	1.0	1.1	3.6	1.5	2.5	1.2	0.5	1.2	0.8	3.0	0.9
chukuchuku	79658	yes	34	6.0	–	–	4.1	3.3	1.2	1.0	0.9	3.0	1.1	1.9	0.9	0.4	1.2	0.7	2.7	1.1
jimzimkusi	79659	yes	37	8.0	–	–	4.9	3.7	1.7	1.0	1.3	4.0	1.3	1.9	1.3	0.5	1.8	0.7	3.5	1.2
jimzimkusi	79661	yes	25	4.2	–	–	2.8	2.3	1.0	0.5	0.9	2.4	0.8	1.2	0.9	0.3	0.8	0.4	–	0.8
jimzimkusi	79661	no	25	6.4	9.9	15.3	4.2	3.4	1.4	1.1	1.2	3.7	1.2	1.5	1.1	0.7	1.3	0.5	2.3	0.5
jimzimkusi	79661	no	25	4.8	7.2	12.0	3.3	2.4	1.0	0.7	0.9	2.6	1.0	1.1	0.7	0.5	1.1	0.4	2.2	0.4
jimzimkusi	79661	no	25	5.9	8.9	14.8	3.8	2.8	1.2	0.9	1.1	3.2	1.1	1.3	1.0	0.6	1.3	0.4	2.5	0.5
jimzimkusi	79662	no	25	4.9	8.1	13.0	3.7	2.8	1.1	0.6	0.8	2.5	1.0	1.4	1.0	0.3	1.0	0.4	2.3	0.5
jimzimkusi	79662	no	25	4.3	7.5	11.8	3.1	2.4	0.9	0.5	0.7	2.1	0.8	1.2	0.8	0.3	1.0	0.4	2.0	0.5
jimzimkusi	79662	no	25	4.5	7.6	12.1	3.3	2.8	1.1	0.6	0.8	2.5	0.9	1.3	0.8	0.3	0.9	0.4	2.2	0.6
jimzimkusi	79662	no	25	3.8	6.8	10.6	2.8	2.5	1.0	0.5	0.9	2.4	0.8	1.2	0.9	0.3	0.8	0.4	2.0	0.6
jimzimkusi	79662	no	25	3.7	6.9	10.6	2.9	2.4	1.1	0.6	0.8	2.5	0.8	1.2	0.8	0.3	0.9	0.4	2.1	0.6
manengoubensis	79664	yes	25	4.5	–	–	3.0	1.8	0.8	0.3	0.5	1.5	0.8	1.0	0.7	0.5	1.0	0.4	2.2	0.7
manengoubensis	79665	no	28	5.1	–	–	3.3	2.3	1.1	0.7	0.8	2.5	1.0	1.2	–	–	1.3	0.6	2.0	0.5

tadpoles of the respective series. Tadpole descriptions are predominately based upon the recommendations by Altig & McDiarmid (1999) and Altig (2007). Tadpole staging follows Gosner (1960), and labial tooth row formulae follow Rödel (2000).

Illustrations of genotyped representatives of each taxon were prepared, by one person (TP), with the help of a camera lucida mounted on a dissecting microscope. Drawings were scanned and processed with Adobe Photoshop CS6. Schematic sketches are based on the oral discs of genotyped individuals.

Results

Phrynobatrachus auritus Boulenger, 1900

The description is based on twenty tadpoles: ZMB 79648 (three tadpoles, Gosner stages 36 and 37, Bekob, Ebo Forest, Cameroon, 4.3575° N; 10.4168° E, 903 m a.s.l., 29 August 2011, secondary rainforest); ZMB 79649 (seven tadpoles, Gosner stages 37 to 39, Bekob, Ebo Forest, Cameroon, 4.3578° N; 10.4170° E, 921 m a.s.l., 1 September 2011, secondary rainforest); ZMB 79650 (one tadpole, Gosner stage 36, Bekob, Ebo Forest, Cameroon, 4.3569° N;

10.4165° E, 920 m a.s.l., 2 September 2011, secondary rainforest); ZMB 79651 (five tadpoles, Gosner stages 36 and 37, same data as ZMB 79650); ZMB 79652 (two tadpoles, Gosner stages 35 and 36, Ndogbanguengue, Ebo Forest, Cameroon, 4.4068° N; 10.1649° E, 100 m a.s.l., 20 September 2011, farmbush); ZMB 79653 (one tadpole, Gosner stage 28, Njuma, Ebo Forest, Cameroon, 4.3462° N; 10.2301° E, 264 m a.s.l., 10 October 2011, primary rainforest); and ZMB 79654 (one tadpole, Gosner stage 25, Bekob, Ebo Forest, Cameroon, 4.3578° N; 10.4170° E, 921 m a.s.l., 20 October 2011, secondary rainforest). All tadpoles were collected from shallow puddles and ponds, which in some cases were connected to streams after heavy rainfall.

Description (Measurements are provided in Tab. 3). Body ovoid in dorsal view, snout rounded (Fig. 3b); body oval to slightly compressed in lateral view (Fig. 3a); head–body length 0.57 of tail length; body height 0.47 of head–body length; body width 0.67 of head–body length; maximum body width at slightly posterior to eyes; nostrils situated dorsolaterally, closer to snout-tip than to eyes (SND/SED = 0.35); distance snout–nostrils 0.17 of head–body length; eyes positioned dorsolaterally; eye diameter 0.15 of head–body length; interocular distance exceeds internostril distance by 1.53; tail 0.64 of total length; tail with well-developed fins; dorsal fin emerges at dorsal tail–body junction; dorsal fin considerably curved; ventral fin emerges at the ventral terminus of the body; narrower than tail axis and slightly curved to nearly parallel to tail axis; dorsal fin higher than ventral one; dorsal fin with its highest point at mid-length of tail (DF/VF = 1.47); fin tip slightly rounded to pointed; maximum tail height including fins barely surpasses body height (TTH/BH = 1.08); tail axis in dorsal view 0.30 of body width; maximum height of tail axis origin 0.51 of body height; tail axis height at its base almost equal to maximum height of dorsal fin (AH/DF = 1.04); vent tube dextral; spiracle sinistral, visible in dorsal view, its base slightly posterior to mid-body (SSD/BL = 0.55); spiracle tube length 0.12 of head–body length; mouth opens anteroventrally; oral disc small, its width less than a quarter of body width (ODW/BW = 0.21); one row of short and rounded papillae extending from slightly anterior to angles of mouth and completely surrounding lower lip, interrupted by wide rostral gap; lower lip with a second row of long and slender, filamentous papillae, width of the filamentous papillae row as wide as the widest row of posterior tooth rows; labial tooth row formula 1/1+1//3+3/1 (Fig. 3c); A2 with wide median gap; P4 about 1/3 shorter than P1–P3; keratinised parts of jaw sheaths narrow, slightly serrated; upper jaw widely U-shaped; lower jaw V-shaped.

Colouration in preservative. Body and tail axis irregularly speckled dark brown on yellowish ground; larger dark spots around eyes; dorsal fin predominantly translucent with some small brown spots; ventral fin translucent without darker spots; spiracle and vent tube translucent; intestines visible (Fig. 3a).

Phrynobatrachus chukuchuku Zimkus, 2009

The description is based on five tadpoles: ZMB 79655 (one tadpole, Gosner stage 37), ZMB 79657 (two tadpoles, Gosner stages 38 and 42), ZMB 79658 (one tadpole, Gosner stage 34, all collected at summit of Mt. Oku, Cameroon, 6.2016° N; 10.4594° E, 2,236 m a.s.l., 2 September 2012, slow-flowing runlet through sub-alpine meadow); ZMB 79656 (one tadpole, Gosner stage 41, Abu Forest, Ijim Ridge of Mount Oku, Cameroon, 6.2857° N; 10.3580° E, 2,162 m a.s.l., 24 August 2012, in pools of rocky fast-flowing stream at edge of montane forest).

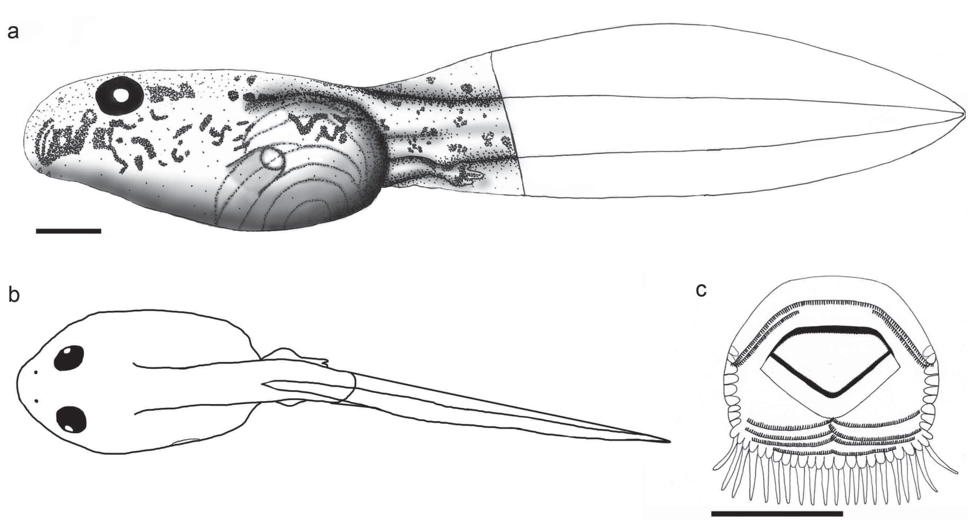

Figure 3. Lateral (a) and dorsal (b) views of *Phrynobatrachus auritus* (ZMB 79650, Gosner stage 36), and sketch of the oral disc (c); tail length and shape extrapolated from non-genotyped specimens; scale bars = 1 mm, sketch of dorsal view not true to scale.

Description (Measurements are provided in Tab. 3). Body ovoid with rounded snout in dorsal and lateral views (Fig. 4a, b); head–body length 0.53 of tail length; body height 0.54 of head–body length; body width 0.70 of head–body length; maximum body width at slightly posterior to spiracle insertion; nostrils situated dorsolaterally, closer to snout tip than to eyes (SND/SED = 0.34); distance snout–nostrils 0.17 of head–body length; eyes positioned dorsolaterally; eye diameter 0.12 of head–body length; interocular distance exceeds internostril distance by 2.07; tail 0.65 of total length, fins moderately developed; dorsal fin emerges at dorsal tail–body junction, slightly curved; ventral fin emerges at ventral terminus of body, narrower than tail axis; fin heights of dorsal and ventral fins nearly identical (DF/VF = 1.02); fin tip rounded; maximum tail height including fins lower than body height (TTH/BH = 0.92); tail axis slender in dorsal view, 0.30 of body width; maximum height of tail axis at tail base, 0.38 of total body height; tail axis height at tail base higher than maximum height of dorsal fin (AH/DF = 1.32); vent tube dextral; spiracle sinistral, barely visible in dorsal view, situated slightly anterior to mid-body (SSD = 0.45); spiracle tube length 0.11 of head–body length; mouth opens anteroventrally; oral disc small, its width less than ¼ of body width (ODW/BW = 0.22); one row of short and broad papillae with rounded tips extending caudally from one angle of mouth to the other, with wide rostral gap; groups of smaller papillae laterally to P3; no filamentous papillae present; labial tooth row formula 1/1+1//2+2/1, 1/1+1//1+1/2 or 1/1+1//1/1+1/1 (Fig. 4c); P3 slightly shorter than P1 and P2; keratinised part of jaw sheaths delicate, narrow, slightly serrated; upper jaw very widely U-shaped; lower jaw U-shaped with a median convexity.

Colouration in preservative. Body and tail axis dark brown, without any pattern; lateroventral part of posterior body nearly black; dorsal fin with some dark brown spots on translucent ground; ventral fin translucent without darker spots; spiracle and vent tube translucent (Fig. 4).

Phrynobatrachus jimzimkusi Zimkus, Gvoždík & Gonwouo, 2013

The description is based on ten tadpoles: ZMB 79659 (one tadpole, Gosner stage 37, Abdou, Mt. Manengouba, Cameroon, 5.0388° N; 9.8610° E, 1,996 m a.s.l., 5 November 2010, small runlet in montane savannah); ZMB 79661 (four tadpoles, Gosner stage 25, near summit of Mt. Manengouba, Cameroon, 5.0098° N; 9.8569° E, 2,135 m a.s.l., 7 November 2010, medium-sized river in gallery forest); ZMB 79662 (five tadpoles, Gosner stage 25, near Pola, Mt. Manengouba, Cameroon, 5.0577° N; 9.8275° E, 1,719 m a.s.l., 3 December 2010, medium-sized stream in farmbush).

Description (Measurements are provided in Tab. 3). Body ovoid with the snout rounded in dorsal view (Fig. 5b), elliptical in lateral view (Fig. 5a); head–body length 0.61 of tail length; body height 0.56 of head–body length; body width 0.70 of head–body length; maximum body width at level of spiracle insertion; nostrils situated laterally, closer to snout tip than to eyes (SND/SED = 0.37); distance snout–nostrils 0.19 of head–body length; eyes positioned dorsolaterally; eye diameter 0.09 of head–body length; interocular distance exceeds internostril distance by 1.44; tail 0.63 of total length with moderately developed fins; dorsal fin emerges at dorsal tail–body junction; dorsal fin slightly curved; ven-

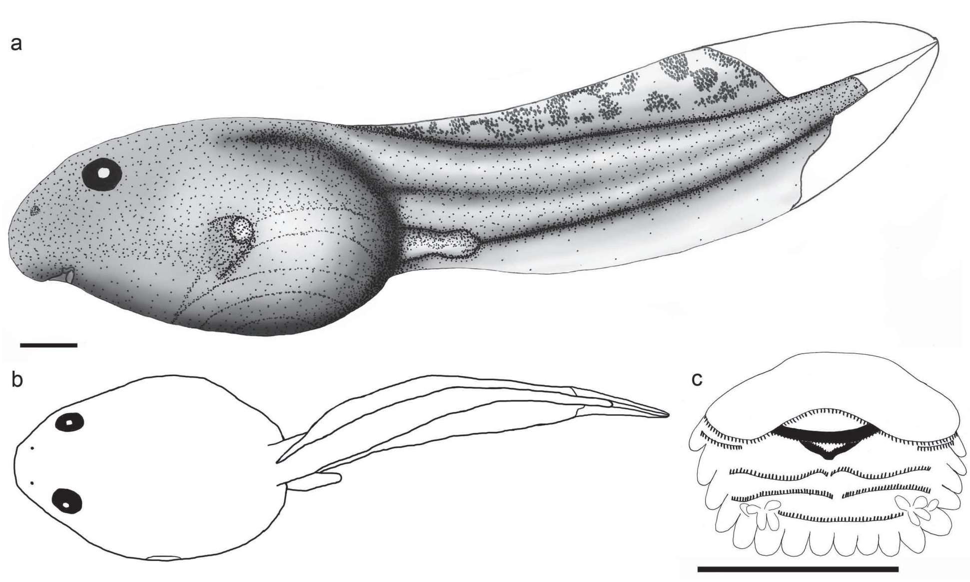

Figure 4. Lateral (a) and dorsal (b) views of *Phrynobatrachus chukuchuku* (ZMB 79658, Gosner stage 34), and sketch of the oral disc (c); tail length and shape extrapolated from non-genotyped specimens; scale bars = 1 mm, sketch of dorsal view not true to scale.

tral fin emerges at the ventral terminus of the body, narrower than tail axis and aligned nearly parallel to it; dorsal fin higher than ventral one (DF/VF = 1.34); fin tip slightly rounded; maximum tail height including fins nearly equals body height (TTH/BH = 1.01); tail axis slender in dorsal view, 0.28 of body width; maximum height of tail axis at its base 0.42 of body height; tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 1.23); vent tube dextral; spiracle sinistral, slightly conical, visible in dorsal view, situated slightly posterior to mid-body (SSD/BL = 0.46); spiracle tube length 0.17 of head–body length; mouth opens anteroventrally; oral disc small, its width less than 1/5 of body width (ODW/BW = 0.18); a row of short conical papillae with slightly pointed tips starting off anterior to angles of mouth and surrounding posterior lip, with a wide rostral gap; labial tooth row formulae 1//3 or 1/1+1//3 (Fig. 5c); keratinised parts of jaw sheaths delicate, narrow and slightly serrated; upper jaw widely rounded M-shaped; lower jaw U-shaped.

Colouration in preservative. Body on back and around eyes with dark speckles, dark brown spots on brownish ground; tail axis yellowish with some brown pattern on the upper part of the tail axis; dorsal and ventral fins translucent without any dark brown spots; spiracle and vent tube translucent; intestines well visible (Fig. 5).

Taxonomic remarks. Frogs from the Bamenda-Banso Highlands, Mt. Manengouba and the Nigerian Obudo Plateau, previously known as *Phrynobatrachus steindachneri*, have been assigned to a new species, *P. jimzimkusi,* by Zimkus & Gvoždík (2013). The type locality of this new species was defined as being just below the summit of Mt. Bamboutos. Channing et al. (2012) described and figured a *P. steindachneri* tadpole, which was collected near the summit of Mt. Bamboutos (D. Blackburn pers. comm.). This tadpole thus very likely is the larvae of *P. jimzimkusi*. It differs from the tadpoles described herein by a different labial tooth row formula with more tooth rows in the lower and upper lips (Tab. 4; Figs 468–469 in Channing et al. 2012), differently shaped jaw sheaths, the presence of (a few) filamentous papillae on the lower lip (absent in our tadpoles), and possibly different larval habitats (Channing et al. 2012: "quiet side pools and swamps" versus streams). Samples of *P. jimzimkusi* from Mt. Manengouba form a distinct basal clade within this new species (see Fig. 1 in Zimkus & Gvoždík 2013). Given the remarkable morphological differences of tadpoles from Mt. Bamboutos and Mt. Manengouba and possibly different habitat preferences, it should be tested if these populations are indeed conspecific, or actually represent different taxa. Although the intraspecific sequence variation (12S and 16S genes) of *P. jimzimkusi* was low (0.94%, Zimkus & Gvoždík 2013), other frog populations of similar genetic divergence have been comprehensibly argued for and granted specific distinctiveness (see Portillo & Greenbaum 2014 for a recent example and papers cited therein). A distribution pattern within the Cameroon Volcanic Line, comparable to the populations of the *Phrynobatrachus steindachneri*-complex, is known from some chameleons that are morphologically distinguishable, yet very similar genetically (Barej et al. 2010). If both tadpole types indeed belonged to *P. jimzimkusi*, their differences might indicate different ecotypes. In contrast, the strong morphological differentiation may indicate further cryptic diversity that has not been uncovered by the methods applied thus far.

Phrynobatrachus manengoubensis (Angel, 1940)

The description is based on two tadpoles: ZMB 79664 (one tadpole, Gosner Stage 25) and ZMB 79665 (one tadpole,

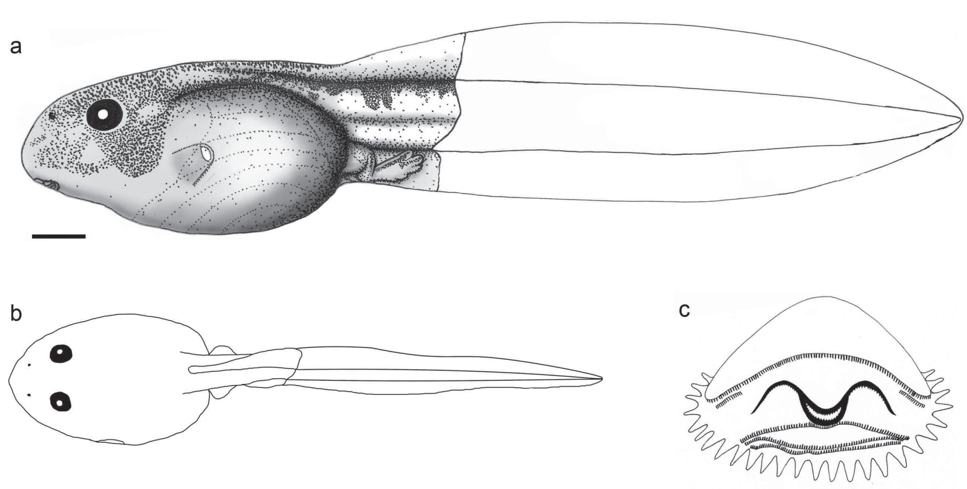

Figure 5. Lateral (a) and dorsal (b) views of *Phrynobatrachus jimzimkusi* (ZMB 79659, Gosner stage 37), and sketch of the oral disc (c); tail length and shape extrapolated from non-genotyped specimens; scale bars = 1 mm, sketch of dorsal view not true to scale.

Gosner stage 28), both from Abdou, Mt. Manengouba, Cameroon, 5.0388° N; 9.8610° E, 1,996 m a.s.l., 5 November 2010, small runlet in montane savannah. Proportions including total or tail lengths were not available for this species because the posterior parts of both individuals' tails were missing. The drawing of the tail (Fig. 6) combines both available specimens and was extrapolated from similarly sized congeners.

Description (Measurements are provided in Tab. 3). Body oval with nearly rounded snout in dorsal and lateral views (Figs. 6a, b); body height 0.42 of head–body length; body width 0.66 of head–body length; maximum body width at the level of the spiracle insertion; nostrils situated dorsolaterally, closer to snout tip than to eyes (SND/SED = 0.40); distance snout–nostrils 0.16 of head–body length; eyes positioned dorsolaterally; eye diameter 0.10 of head–body length; interocular distance exceeds internostril distance by 1.42; tail with moderately developed fins; dorsal fin emerges at dorsal tail–body junction; dorsal fin slightly curved; ventral fin emerges at the ventral terminus of the body, narrower than tail axis and slightly curved; dorsal fin higher than ventral fin (DF/VF = 1.20); maximum tail height including fins almost equal to head–body height (TTH/BH = 0.96; if the unknown last part of the tail is not higher than assumed, see caption of Fig. 6); tail axis in dorsal view 0.28 of body width; maximum height of tail axis at its base 0.41 of total body height; tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 1.33); vent tube dextral, positioned basicaudally; spiracle sinistral, barely visible in dorsal view, originating slightly anterior to mid-body (SSD/BL = 0.44); spiracle tube length 0.18 of head–body length; mouth opens anteroventrally; oral disc small, its width less than 1/5 body width (ODW/BW = 0.19); one row of long, slender papillae with rounded tips bordering lower labium; upper lip without papillae; labial tooth row formula 1//1+1/1 (Fig. 6c); P2 considerably shorter than P1; P1 with small gap; keratinised parts of jaw sheaths delicate, narrow and slightly serrated; upper jaw widely V- to M-shaped; lower jaw V- to U-shaped.

Colouration in preservative. Body and tail axis with dark brown spots on yellowish ground; dark marbling on tail axis, in particular in dorsal part; posterior part of body particularly dark; dorsal fin with dark irregular brown spots on translucent ground; ventral fin translucent without darker spots; spiracle and vent tube translucent (Fig. 6).

Discussion

According to Altig & McDiarmid (1999), *Phrynobatrachus* tadpoles are exotrophic, lentic and benthic; have tooth row formulae of 1//2, 1//3, 1//1+1/3, or 1/1+1//2; anteroventral mouth openings; uniserial marginal papillae with large dorsal (anterior) gaps; ventral papillae that are sometimes elongated; submarginal papillae on the lower lip; no or lateral disc emarginations; nares that are closer to the snout than to the eyes; medial vent tubes; dorsally positioned eyes; sinistral spiracles; upper jaws with wide, prominent medial convexity; lower jaw that are open U-shaped; low dorsal fins with pointed tips, emerging near the dorsal tail–body junction; oval to depressed bodies; dark colours; and are small to medium-sized at an advanced stage of development (20–35 mm; Gosner stage 36).

Since then, some more *Phrynobatrachus* tadpoles have been described (e.g., Rödel & Ernst 2002a, b, de Sá & Channing 2003, Pickersgill 2007, Channing et al. 2012), and *Phrynodon sandersoni,* with its aberrant reproductive mode (see Amiet 1981), was transferred to *Phrynobatrachus* (Scott 2005, Zimkus et al. 2010). Consequently, the known range of characters represented in tadpoles of this genus became much wider. Most newly

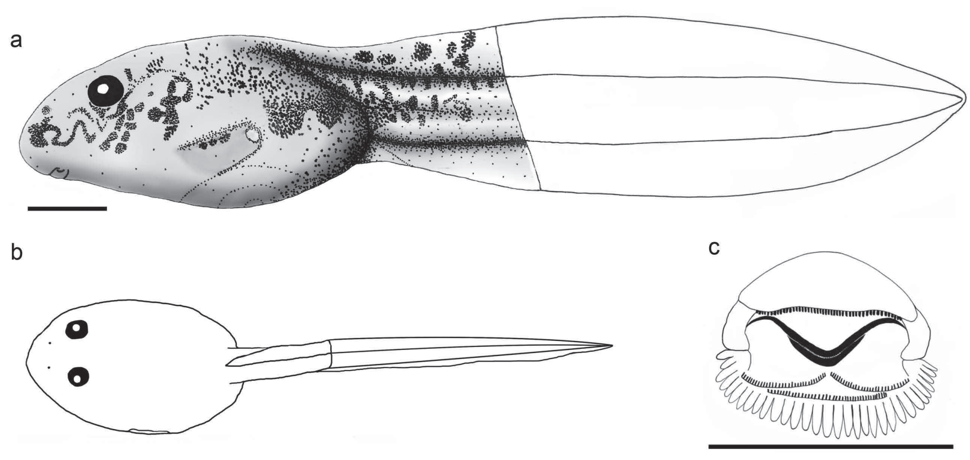

Figure 6. Lateral (a) and dorsal (b) views of *Phrynobatrachus manengoubensis* (ZMB 79664, Gosner stage 25), and sketch of the oral disc (c); tail length and shape extrapolated from both specimens and similar congeners (compare text); scale bars = 1 mm, sketch of dorsal view not true to scale.

Table 4. Summary of described *Phrynobatrachus* tadpoles; given are feeding mode (exotrophic versus endotrophic), tooth row formulae, presence or absence of filamentous papillae on lower lip, major clade within *Phrynobatrachus* (see Zimkus et al. 2010) and references. * = comprises several cryptic species (see Zimkus et al. 2010; † = not included in this paper, assigned to clade based on assumed relationships with other species); ** = described as tadpole of *P. steindachneri* by Channing et al. (2012), these authors mention three keratodont rows on the lower labium, however, their figure 469 shows four. The tadpole on which this description is based, was collected near the summit of Mt. Bamboutos (D. Blackburn pers. comm.), i.e., the type locality of the newly described species, *P. jimzimkusi* (Zimkus & Gvoždík 2013), which should therefore be expected to be conspecific with our tadpoles, however, compare the respective species description; § = Pickersgill 2007; // = indicates border between upper and lower labium; + = indicates gaps within teeth rows; this table is a modified and updated version of the table published by Rödel et al. (2009).

Species	Exotrophic	Keratodont formulae	Filamentous papillae	Breeding sites	Clade	Source
acridoides	yes	1//1+1/1; 1//1/1+1	yes	temporary savannah waters	C	Pickersgill 2007
auritus	yes	1/1+1//3+3/1	yes	forest ponds	C	this paper
*calcaratus**	yes	1/1+1//2+2/1; 1//3	no	temporary forest ponds; stagnant pools close to rivers	B	Schiøtz 1963, Rödel 2000
chukuchuku	yes	1/1+1//2+2/1; 1/1+1//1+1/2; 1/1+1//1/1+1/1	no	slow-flowing waters in montane grassland	C†	Zimkus 2009, this paper
francisci	yes	1/1+1//3+3; 1/1+1//3	yes	temporary savannah waters	C	Lamotte & Dzieduszycka 1958, Rödel 2000
guineensis	yes	1/1+1//2; 1/1+1//2+2	no	tree holes, snail shells in rainforest	C	Rödel 1998a, Rödel & Ernst 2002b
*jimzimkusi***	yes	1/4+4//4**	yes	small stagnant waters	C	Channing et al. 2012
jimzimkusi	yes	1//3; 1/1+1//3	no	mountain streams	C†	this paper
kreffti	yes	2//3; 1/1+1//4; 1/1+1//5	no	stagnant forest waters	A	Channing & Howell 2006, Pickersgill 2007
latifrons	yes	1/1+1//2+2; 1+1//2+2	yes	temporary savannah waters	C	Rödel 2000
*mababiensis**	yes	1//2; 0//1; 1//3; 2/2+2//4; 1/3+3//4; 1//1	yes	temporary savannah waters	B	Lambiris 1989, Channing 2001, de Sá & Channing 2003, Channing & Howell 2006, Pickersgill 2007
maculiventris	yes	1//1+1/1	yes	larger forest pond	B	Rödel et al. 2009
manengoubensis	yes	1//1+1/1	no	–	C	this paper
*natalensis**	yes	1//1+1/1; 1/1+1//2; 1/2+2//1+1/2; 1//2; 1/1+1//1+1/2	yes/no§	small to medium-sized stagnant waters in savannah and forest edges	C	Wager 1986, Lambiris 1989, Rödel 2000, Channing 2001, Channing & Howell 2006, Pickersgill 2007
pallidus	yes	1//1+1/1	yes	stagnant savannah waters (?)	B	Pickersgill 2007
parvulus	yes	1//2	yes	stagnant savannah waters	B	Pickersgill 2007
phyllophilus	yes	1/1+1//3	yes	puddles on swampy forest floor	C	Rödel & Ernst 2002b
*sandersoni**	no	none	no	moist terrestrial (?) microhabitat along forest creeks	A	Amiet 1981
tokba	no	none	no	moist leaves on forest floor	C	Rödel & Ernst 2002a

described tadpoles still fall within the above character definitions (e.g., Pickersgill 2007), but non-feeding tadpoles, both hatching and non-hatching, with longer tails and reduced mouth parts have become known in addition (Amiet 1981, Rödel & Ernst 2002a), and aposematically coloured tadpoles were discovered in one case (Rödel et al. 2009). We herein describe tadpoles of another three species, redescribe the tadpoles of a fourth, and for the first time report *Phrynobatrachus* tadpoles from lotic waters.

In general, the tadpoles of this genus exhibit an astonishingly wide range of morphologies and biologies (compare "Introduction" and Tab. 4). The large number of different tooth row formulae within some species (Tab. 4) is, however, most likely due to the fact that these taxa apparently comprise various cryptic species (Zimkus et al. 2010, 2013). Such variation is also a pressing argument for re-investigating the status of *P. jimzimkusi* populations from different Cameroonian mountains, i.e., Mts. Bamboutos and Manengouba.

Although most resemble each other with regard to small size (usually < 20 mm), body shape (ovoid to oval with short tails and narrow fins), colouration (cryptically brownish, with one exception, Rödel et al. 2009), and jaw morphology (keratinised parts very delicate and narrow), the various tooth row formulae, shape and arrangement of marginal and filamentous papillae, as well as their different breeding sites, appear to allow the identification of many *Phrynobatrachus* tadpoles (Tab. 4). It would thus be obvious to assume that the morphological and/or biological variability in *Phrynobatrachus* tadpoles may be mirrored by their phylogeny. However, this, at least thus far, clearly is not the case (see the assignment of the different species to the three major clades as revealed by Zimkus et al. 2010, Tab. 4), and different reproductive modes appear to have evolved repeatedly (Zimkus et al. 2012). However, we still lack data on tadpole morphology for most species of this genus, and no data on their reproductive biologies are available. We need to learn more about the biology of this genus in order to really understand the evolution of its astonishingly rich spectrum of biological adaptations, as well as the tadpoles' impact on the ecology of the respective freshwaters.

Acknowledgements

The Cameroonian Ministry of Forestry and Wildlife (MINFOF) issued research, collection and export permits. Field work was funded by scholarships from the Federal State of Berlin (Elsa-Neumann-Stipendium; MH) and the German Academic Exchange Service (DAAD; MH), the "Wilhelm-Peters-Fonds" of the German Society of Herpetology (DGHT; MD, M-OR), the European Association of Zoos' & Aquaria's Amphibian Conservation Fund (TMD-B), the Mohammed bin Zayed Conservation Fund (TMD-B), and the Royal Zoological Society of Scotland (TMD-B). Barcoding of tadpoles was financially supported by the Förderverein des Museums für Naturkunde Berlin. We thank Lissa Mapouyat for assistance in the laboratory. We are indebted to our field assistants for their help!

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Appendix

Catalogue numbers (ZMB – Museum für Naturkunde Berlin) and GenBank accession codes (543 bp of 16S rRNA), as well as localities of *Phrynobatrachus* tadpoles studied herein. N – number of tadpoles.

Species	ZMB#	N	GenBank	Country	Region	Site	Latitude	Longitude	Altitude [m a.s.l.]
auritus	79648	3	KJ626406	Cameroon	Ebo Forest	Bekob	4.3575°N	10.4168°E	903
auritus	79649	7	KJ626407	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921
auritus	79650	1	KJ626408	Cameroon	Ebo Forest	Bekob	4.3569°N	10.4165°E	920
auritus	79651	5	–	Cameroon	Ebo Forest	Bekob	4.3569°N	10.4165°E	920
auritus	79652	2	KJ626409	Cameroon	Ebo Forest	Ndogbanguengue	4.4068°N	10.1649°E	100
auritus	79653	1	KJ626410	Cameroon	Ebo Forest	Njuma	4.3462°N	10.2301°E	264
auritus	79654	1	KJ626411	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921
chukuchuku	79655	1	KJ626412	Cameroon	Mt. Oku	summit	6.2000°N	10.5185°E	3011
chukuchuku	79656	1	KJ626413	Cameroon	Mt. Oku	Abu Forest	6.2857°N	10.3580°E	2162
chukuchuku	79657	2	–	Cameroon	Mt. Oku	summit	6.2000°N	10.5185°E	3011
chukuchuku	79658	1	–	Cameroon	Mt. Oku	summit	6.2000°N	10.5185°E	3011
jimzimkusi	79659	1	KJ626414	Cameroon	Mt. Manengouba	Abdou	5.0388°N	9.8610°E	1996
jimzimkusi	79661	4	KJ626415	Cameroon	Mt. Manengouba	near summit	9.8569°N	5.0098°E	2135
jimzimkusi	79662	5	KJ626416	Cameroon	Mt. Manengouba	near Pola	9.8275°E	5.0577°E	1719
manengoubensis	79664	1	KJ626417	Cameroon	Mt. Manengouba	Abdou	5.0388°N	9.8610°E	1996
manengoubensis	79665	1	–	Cameroon	Mt. Manengouba	Abdou	5.0388°N	9.8610°E	1996