Zootaxa 2694: 1–25 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Description of ten tadpoles in the genus *Boophis* from Madagascar

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Abstract

We provide morphological descriptions of the tadpoles of ten species of Malagasy treefrogs of the genus *Boophis* (family Mantellidae). Based on individuals determined by DNA barcoding, the larvae of eight species are described for the first time: *B. anjanaharibeensis*, *B. axelmeyeri*, *B. elenae*, *B. englaenderi*, *B. luciae*, *B. rhodoscelis*, *B. roseipalmatus*, and *B. vittatus*. For two additional species, *B. andreonei* and *B. microtympanum*, we provide descriptions from other localities than the previously known larvae. All tadpoles described herein are stream-adapted, exotrophic, and of a relatively generalized morphology. In general, we found a morphological similarity of larvae belonging to phenetic species groups of *Boophis*, but more detailed analyses showed several differences between taxa that are known to be sister species or closely related to each other: *B. luciae* has a much higher number of oral papillae than *B. sibilans*, *B. roseipalmatus* has a slightly lower number of papillae and possibly a stronger caudal musculature than *B. madagascariensis*, and *B. elenae* has a distinctly lower number of oral papillae and keratodonts in the first upper keratodont row than *B. sandrae*. This indicates that tadpole characters might, in some cases, provide good taxonomic characters in *Boophis*, a genus in which adults of closely related species are often morphologically extremely similar.

Key words: Amphibia, Anura, Mantellidae, Larval morphology, *Boophis andreonei*, *Boophis anjanaharibeensis*, *Boophis axelmeyeri*, *Boophis elenae*, *Boophis englaenderi*, *Boophis luciae*, *Boophis microtympanum*, *Boophis rhodoscelis*, *Boophis roseipalmatus*, *Boophis vittatus*

Introduction

The rainforests of Madagascar are known to harbour species-rich amphibian communities (Blommers-Schlösser 1979a, 1979b; Blommers-Schlösser & Blanc 1991; Glaw and Vences 2003; Strauß *et al.* 2010). These communities, composed of only frogs as salamanders and caecilians are absent from Madagascar, are heavily affected by the current biodiversity crisis (Andreone 2008; Mittermeier & Gascon 2008). Knowledge on the taxonomy, distribution, behavior, ecology and life history of most species is insufficient, and baseline research in these fields is thus needed (Andreone 2008). Knowledge on the morphology and habitat of tadpoles helps understanding the ecological requirements and the natural history of frog species (Thomas *et al.* 2005). Also, surveys of tadpoles can provide information on the presence of a species, especially outside the reproductive season when adults might be difficult to find (e.g., Vences *et al.* 2008).

Within Malagasy frogs, the monophyletic Mantellidae is the largest family (Glaw & Vences 2007) and it is endemic to Madagascar and Mayotte (Blommers-Schlösser & Blanc 1991; Vences *et al.* 2003). Mantellids are divided in 3 sub-families (Boophinae, Laliostominae, and Mantellinae) and 11 genera (Glaw & Vences 2006; Glaw *et al.* 2006). The Boophinae contain a single genus, *Boophis* Tschudi consisting of 58 species of tree frogs. These are divided in ten different phenetic species groups: *B. albilabris* group, *B. albipunctatus* group, *B. goudoti* group, *B. luteus* group, *B. majori* group, *B. mandraka* group, *B. microtympanum* group, *B.*

Accepted by S. Carranza: 7 Oct. 2010; published: 2 Dec. 2010

rappiodes group, *B. tephraeomystax* group, *B. ulftunni* group (Glaw & Vences, 2007). In terms of larval morphology, *Boophis* is currently the best known group of Malagasy frogs (Schmidt *et al.* 2008). *Boophis* mostly have rather generalized tadpoles with well developed jaw sheaths and keratodonts (Randrianiaina *et al.* 2009), and the major variation of these tadpoles is along the axis of adaptations to weaker or stronger water current, by mainly enlargement of the oral disk with more keratodont rows and more marginal papillae (Schmidt *et al.* 2008). Exceptional morphologies occur in the larval stages of only a few species, especially in *Boophis picturatus* which is totally devoid of keratinized oral structures but has long papillae (Altig & McDiarmid 2006). As well, the form of both the upper and lower jaw sheath in *B. majori* is not known from any other *Boophis* species (Schmidt *et al.* 2008).

To complete the morphological knowledge on *Boophis* tadpoles, we here provide descriptions of the larvae of ten species of *Boophis*, eight of which were previously unknown, based on specimens identified by DNA barcoding.

Material and methods

Tadpoles were collected in the field, euthanised by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here named “DNA voucher”. All detailed tadpole descriptions and drawings are based on this DNA voucher (Table 1), whereas variation is described based on further specimens of the series as well as further DNA voucher specimens (Tables 2 to 7). After tissue collection, all specimens were preserved in 5% formalin. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). Other acronyms used are UADBA, Université d'Antananarivo, Département de Biologie Animale, and ZCMV and FGZC, field numbers of M. Vences and F. Glaw..

TABLE 1. Morphometric measurements (all in mm) of the DNA voucher specimens used for the descriptions of ten species of *Boophis*. For abbreviations, see Material and Methods.

Species	*B. andreonei*	*B. anjanaharibeensis*	*B. axelmeyeri*	*B. elenae*	*B. englaenderi*
ZSM number	ZSM 0623/2008	ZSM 0624/2008	ZSM 0629/2008	ZSM 0631/2008	ZSM 0623/2008
BL	13.6	8.9	10.7	6.3	11.8
BW	8.0	5.5	5.9	7.5	6.2
BH	6.2	3.7	5.1	3.1	4.5
ED	2.3	1.3	1.4	1.1	1.8
IOD	5.7	3.6	3.3	5.7	4.8
NS	0.3	0.2	0.3	0.2	0.4
IND	3.1	2.0	2.2	3.1	2.2
RN	2.5	1.5	1.5	1.1	2.2
NP	3.1	2.0	2.0	1.7	2.6
ODW	4.2	2.9	2.5	3.2	3.3
Length A_1	2.8	2.2	1.8	1.7	3.1
SP	2.8	1.6	1.8	0.7	2.1
SS	10.3	5.6	6.6	4.6	7.9
TAL	26.8	13.1	15.9	12.8	19.4
TMW	4.2	2.5	3.0	3.6	3.7
TMH	4.4	2.7	3.3	2.0	3.2
MTH	4.4	2.7	3.5	2.8	3.4

continued.

Species	*B. microtympanum*	*B. rhodoscelis*	*B. vittatus*	*B. roseipalmatus*	*B. luciae*
ZSM number	ZSM 0622/2008	ZSM 0630/2008	ZSM 0625/2008	ZSM 0628/2008	ZSM 0634/2008
BL	19.1	14.7	5.0	11.0	7.8
BW	12.3	8.2	2.3	6.7	4.1
BH	11.6	7.3	2.1	5.0	3.5
ED	2.3	2.2	0.7	1.6	1.1
IOD	6.7	5.6	1.9	4.2	3.2
NS	0.4	0.3	0.1	0.3	0.3
IND	2.8	2.6	1.1	2.8	1.4
RN	3.1	2.2	1.1	1.6	1.2
NP	4.0	2.9	1.0	2.3	1.7
ODW	5.2	3.2	1.9	3.2	3.3
Length A_1	4.9	3.1	0.7	2.2	1.8
SP	3.4	4.5	1.7	2.30	5.4
SS	12.3	9.0	3.6	7.3	---
TAL	38.4	21.9	---	18.4	13.0
TMW	5.4	5.2	1.3	3.1	2.7
TMH	7.2	4.3	1.3	3.2	2.2
MTH	7.2	4.3	---	3.3	2.7

Tadpoles were identified using a DNA barcoding approach based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Thomas *et al.* 2005). The ca. 550 bp fragment was amplified using primers 16Sar-L and 16Sbr-H from Palumbi *et al.* (1991) applying standard protocols, resolved on automated sequencers, and compared to a near-complete database of sequences of adult Malagasy frog species. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. Newly determined DNA sequences have been deposited in Genbank under accession numbers HM769902-HM769940; accession numbers of comparative adult specimens are included in the sequence sets AY847959-AY848683, AJ315909-AJ315913, FJ559069–FJ559372, EF682212, AF215336).

The molecular results identified the tadpoles examined here as belonging to *B. andreonei* Glaw & Vences, *B. anjanaharibeensis* Andreone, *B. axelmeyeri* Vences, Andreone & Vieites, *B. elenae* Andreone, *B. englaenderi* Glaw & Vences, *B. luciae* Glaw, Köhler, de la Riva, Vieites & Vences (corresponding to *B.* sp. aff. *sibilans* of Glaw & Vences 2007 and *B.* sp. 17 of Vieites *et al.* 2009; for a new *Boophis* taxonomy see Glaw *et al.* 2010), *B. microtympanum* (Boettger), *B. rhodoscelis* (Boulenger), *B. roseipalmatus* (corresponding to *B.* sp. aff. *madagascariensis* of Glaw & Vences 1994, to *B.* sp. aff. *madagascariensis* "North" of Glaw & Vences 2007, and to *B.* sp. 12 of Vieites *et al.* 2009), and *B. vittatus* Glaw, Vences, Andreone & Vallan. Of these taxa, the tadpoles of *B. andreonei* and *B. microtympanum* have been described before (Randrianiaina *et al.* 2009; Blommers-Schlösser 1979b) from Manongarivo and Ankaratra, respectively. We here add for these taxa descriptions from additional sites (Marojey and Ambohitantely). Tadpoles described herein are from the following localities:

B. axelmeyeri and *B. roseipalmatus*, belonging to *B. goudoti* group, were collected in Marojejy National Park. They were collected by R.-D. Randrianiaina on 19 February 2005 at a site locally named Camp Mantella (14°26.972' S 49°47.214' E, 327 m a. s. l.) in a stream crossing the track to the cascade.

Tadpoles of *B. anjanaharibeensis*, *B. andreonei*, and *B. englaenderi* belonging to the *B. luteus* group, were collected in Marojejy National Park. The first two were collected by R. D. Randrianiaina on 14 February 2005

at Camp Mantella (14°26.972' S 49°47.214' E, 327 m a. s. l.) in the Ambinanitelo river; specimens of the third species were collected by R. D. Randrianiaina on 18 February 2005 at Camp Marojejia site (14°26.070' S 49°45.638' E, 740 m a. s. l.) in a river upstream of a cascade close to the camping site. Tadpoles of *B. elenae*, equally belonging to the *B. luteus* group, were collected by R. D. Randrianiaina, L. Raharivololoniaina, F. Ranjanaharisoa and T. Razafindrabe on 23 February 2006 in the Ranomafana National Park at a site locally named Imaloka (21°14.032' S 47°27.055' E , 950 m a. s. l.).

Tadpoles of *B. vittatus*, belonging to the *B. majori* group, were collected by R. D. Randrianiaina on 15 February 2005 in Marojejy National Park at Camp Mantella site (14°26.972' S 49°47.214' E, 327 m a. s. l.) in the Ambinanitelo river.

Tadpoles of *B. microtympanum* were collected by R. D. Randrianiaina and L. Raharivololoniaina on 19 January 2006 in Ambohitantely Special Reserve (18°11.058' S 47°16.051' E, 1580 m a. s. l.) in a stream close to the ANGAP campsite. Tadpoles of *B. rhodoscelis* were collected by R. D. Randrianiaina and L. Raharivololoniaina on 20 February 2006 in a stream next to a ricefield, close to Vohiparara village (21°14.143' S 47°23.152' E, 1118 m a. s. l.).

Tadpoles of *B. luciae* were collected by R. D. Randrianiaina and L. Raharivololoniaina on 24 February 2006 in the Ranomafana National Park at a site locally named Talatakely (21°15.846' S 47°25.161' E, 966 m a. s. l.).

Developmental stages (DS) are described following Gosner (1960). Morphological measurements were taken by using a graduated ocular attached to a stereomicroscope, following landmarks, terminology and definitions of Altig & McDiarmid (1999). The formula of keratodont rows (= labial tooth rows; LTRF) is given according to Altig & McDiarmid (1999). Drawings and photographs of the preserved tadpoles are represented in Figures 1 to 10.

The following abbreviations are used in the descriptions: A_1 (first upper keratodont row), A_2 (second upper keratodont row), A_{2gap} (medial gap in the second upper keratodont row), BL (body length), BH (body height), BW (maximum width of the body), DF (dorsal fin height), DG (dorsal gap of marginal papillae), ED (eye diameter), IOD (inter-orbital distance), JL (jaw sheath length), LTRF (lateral tooth row formula), MTH (maximal tail height), IND (inter-narial distance), NP (narial-pupil distance), NS (nare diameter), ODW (maximal oral disk width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), RN (Inter-narial distance), SBH (distance between snout and the point of the maximal height of the body), SBW (distance between snout and the point of the maximal width of the body), SP (spiracle length), SS (snout-spiracle distance), TAL (tail length), TH (tail height at the beginning of the tail), THM (tail height at mid-tail), TMH (tail muscle height at the beginning of the tail), TMHM (tail muscle height at mid-tail), TMW (tail muscle width), VF (ventral fin height), VG (ventral gap of marginal papillae), VL (vent tube length).

Results

Boophis andreonei Glaw & Vences

The following description refers to one tadpole in developmental stage 35 (ZSM 0623/2008, field number FGZC 2907, TL 40.5 mm, BL 13.6 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.6 % identical to a reference sequence of an adult specimen of *B. andreonei* (accession AY848450) from Tsaratanana.

In dorsal view, body elliptical, maximal width at midbody (SBW 51% of BL), rounded snout. In lateral view, body depressed (BW 123% of BH), maximal body height attained between the 1/2 and 3/4 of the body (SBH 71% of BL), rounded snout. Eyes large (ED 18% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the 3/10 and 4/10 of the body, wide distance between eyes (IOD 69% of BW). Moderately large elliptical nares (NS 3% BL), marked with marginal rim, positioned dorsally and oriented anterodorsally, situated nearer to eye than to snout (RN 72% of NP), very wide distance

between nares (IND 83% of IOD), black spot on the back of the nare present, ornamentation absent. Long sinistral spiracle (SP 21% of BL), directed posteriorly, visible from dorsal and ventral views and obvious from lateral view, inner wall free from body and aperture opens laterally instead of posteriorly, round opening, situated between the proximal 1/2 and 3/4 of the body (SS 69% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Very long medial vent tube (VL 16% of BL) with lateral displacement, attached to ventral fin. Tail of moderate length (TAL 184% of BL), maximal tail height higher than body height (MTH 102% of BH), tail height at midtail as high as body height and maximal tail height (THM 100% of BH and THM 97% of MTH), tail height at the beginning of the tail lower than body height (TH 84% of BH). Moderately developed caudal musculature (TMW 52% of BW, TMH 61% of BH and 60% of MTH, TMHM 45% of THM and 44 % of MTH). Tail muscle reaches tail tip. Very low fins (DF 73% of TMHM, VF 51% of TMHM), dorsal fin higher than ventral fin (DF 142% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses almost parallel to the margin of the tail muscle up to the proximal 1/4 where it increases up to maximal tail height, then declines up to the tail tip. Ventral fin originates on the ventral terminus of the body, progresses parallel to the margin of the tail muscle up to the maximal tail height, then decreases to the tip of the tail. Maximal tail height located between the proximal 1/2 and 3/4 of the tail, lateral tail vein visible on the proximal 1/2 of the tail, myosepta visible all along the tail, tail tip narrowly rounded.

Oral disk of moderate size (ODW 56% of BW), positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide dorsal gap (DG 56% of ODW), total number of marginal papillae 104. Twenty-two submarginal papillae (12 in the right and 10 in the left) positioned laterally. Moderately long conical papillae with protuberance, rounded tip, not visible from dorsal view, longest marginal and submarginal papillae measured 0.20 mm and 0.15 mm respectively. Jaw sheaths fully keratinized with rounded serrations, moderately wide (JL 41% of ODW) with very small medial convexity (MC 3% of JL). Lower jaw sheath U-shaped, partially hidden by the upper sheath. LTRF 6(4–6)/3(1). Single row of keratodonts per ridge. Wide A_1 (62% of ODW). Density of keratodonts on A_1 51/mm (total 143). Short,discernible keratodonts (0.18 mm). A_6 is smaller than the others, keratodonts are distinguishable but their size decreases towards the periphery. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body and tail brownish. Brownish spots of different forms distributed over the body, in particular between the eyes and around the nares. Dorsolaterally brownish body, ventrolaterally transparent, with some black round spots that are irregularly distributed. Laterally, the base of the tail musculature is whitish, with round brownish spots, some distributed irregularly in the caudal musculature and some forming stripes. Fins transparent. Ventrally, the intestine is visible.

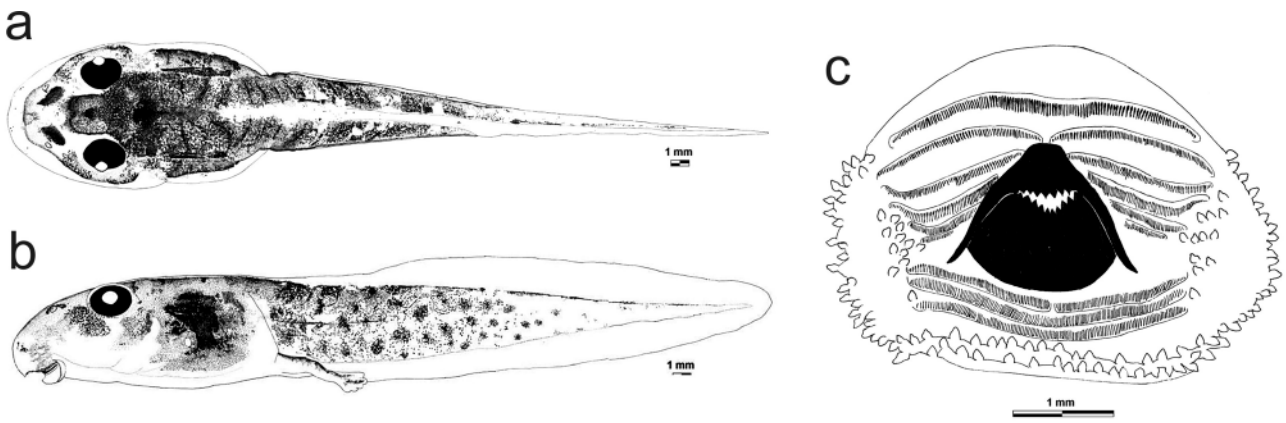

FIGURE 1. Drawings of preserved tadpole specimen of *Boophis andreonei* (ZSM 0623/2008) from Marojejy National Park (developmental stage 35). (a) dorsal view; (b) lateral view; (c) oral disk.

Variation. Described on the basis of 53 tadpoles at stages 24–41, among which are nine DNA voucher specimens (Table 2), all from Marojejy (FGZC 2234, 2239, 2246, 2247, 2904, 2907, 2910, 2919). All

specimens are in the UADBA collection. TL and BL 16–46 mm and 4–16 mm. BW 93–161% of BH; ED 12–19% of BL; RN 23–100% of NP; IND 35–61% of IOD; SS 46–81% of BL; TMH 48–100% of MTH; TMW 29–57% of BW; MTH 41–116% of BH; ODW 37–59% of BW. LTRF 5(2–5)/3, 3(2–3)/3, 4(2–4)/3.

TABLE 2. Morphometric measurements (all in mm) of additional DNA voucher specimens of *Boophis andreonei*, all from Marojejy National Park. For abbreviations, see Material and Methods.

Species	*B. andreonei*	*B. andreonei*	*B. andreonei*	*B. andreonei*	*B. andreonei*
Field number	FGZC 2234	FGZC 2239	FGZC 2246	FGZC 2247	FGZC 2904
BL	12.0	4.3	5.5	8.0	14.0
BW	8.0	4.3	4.0	5.0	10.0
BH	7.3	3.3	3.0	3.0	7.7
ED	2.0	1.2	1.3	1.2	2.7
RN	2.2	1.7	1.3	1.5	30.7
NP	3.0	1.7	1.8	2.0	3.8
IND	3.7	1.7	1.7	2.0	3.5
IOD	6.7	3.0	2.7	3.3	6.7
SS	8.7	2.2	2.0	5.7	7.3
TMH	4.7	2.2	1.7	2.3	4.7
TMW	4.7	2.0	1.2	1.8	5.0
MTH	4.7	2.2	1.7	2.3	7.0
BH	7.3	3.3	3.0	3.0	7.7
TAL	23.0	11.2	14.3	12.3	32.3
ODW	3.7	2.3	2.0	2.0	5.2

continued.

Species	*B. andreonei*	*B. andreonei*	*B. andreonei*	*B. andreonei*
Field number	FGZC 2910	FGZC 2910	FGZC 2919	FGZC 2919
BL	15.8	14.3	10.0	10.7
BW	8.5	8.7	5.2	6.7
BH	6.3	5.5	4.0	4.7
ED	2.5	2.3	1.5	1.5
RN	2.8	2.7	1.7	2.0
NP	3.5	3.3	2.2	2.5
IND	3.3	3.3	2.0	2.3
IOD	6.0	6.7	3.7	4.0
SS	10.0	11.3	5.5	7.7
TMH	4.5	4.7	3.2	3.0
TMW	4.8	5.0	2.5	2.3
MTH	7.2	5.0	4.5	3.2
BH	6.3	5.5	4.0	4.7
TAL	30.5	30.3	16.2	16.2
ODW	4.5	4.3	2.8	2.7

***Boophis anjanaharibeensis* Andreone**

The following description refers to one tadpole in developmental stage 25 (ZSM 0624/2008, field number FGZC 2245, TL 22 mm, BL 8.9 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 100 % identical to a reference sequence of an adult specimen of *B. anjanaharibeensis* (accession EF682212) from the same locality.

In dorsal view, body elliptical, maximal width attained between the proximal 1/4 and 1/2 of the body (SBW 48% BL), rounded snout. In lateral view, body depressed (BW 124% of BH), maximal body height attained at the proximal 3/4 of the body (SBH 75% of BL), rounded snout. Eyes large (ED 16% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the proximal 3/10 and 4/10 of the body, wide distance between eyes (IOD 72% of BW). Moderately large elliptical nares (NS 3% of BL), marked with marginal rim, positioned dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 69 % of NP), moderately wide distance between nares (IND 53% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 14% of BL), directed posterodorsally, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and aperture opens posteriorly, elliptical opening, situated between the proximal 1/2 and 3/4 of the body (SS 61% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Long medial vent tube (VL 13% of BL) with lateral displacement, attached to the ventral fin. Tail of moderate length (TAL 141% of BL), maximal tail height lower than body height (MTH 81% of BH), tail height at midtail lower than body height and maximal tail height (THM 70% of BH and THM 86% of MTH), tail height at the beginning of the tail lower than body height (TH 83% of BH). Moderately developed caudal musculature (TMW 65% of BW, TMH 67% of BH and 81% of MTH, TMHM 63% of THM and 54 % of MTH). Tail muscle reaches tail tip. Very low fins (DF 29% of TMHM, VF 26% of TMHM), dorsal fin higher than ventral fin (DF 112% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses to the maximal tail height, then declines up to the tail tip. Ventral fin originates on the ventral terminus of the body, progresses parallel to the margin of the tail muscle up to maximal tail height, then decreases to the tip of the tail. Maximal tail height between the proximal 1/4 and 1/2 of the tail, lateral tail vein visible on the proximal 1/2 of the tail, myosepta visible on the proximal 3/4 of the tail, tail tip narrowly rounded.

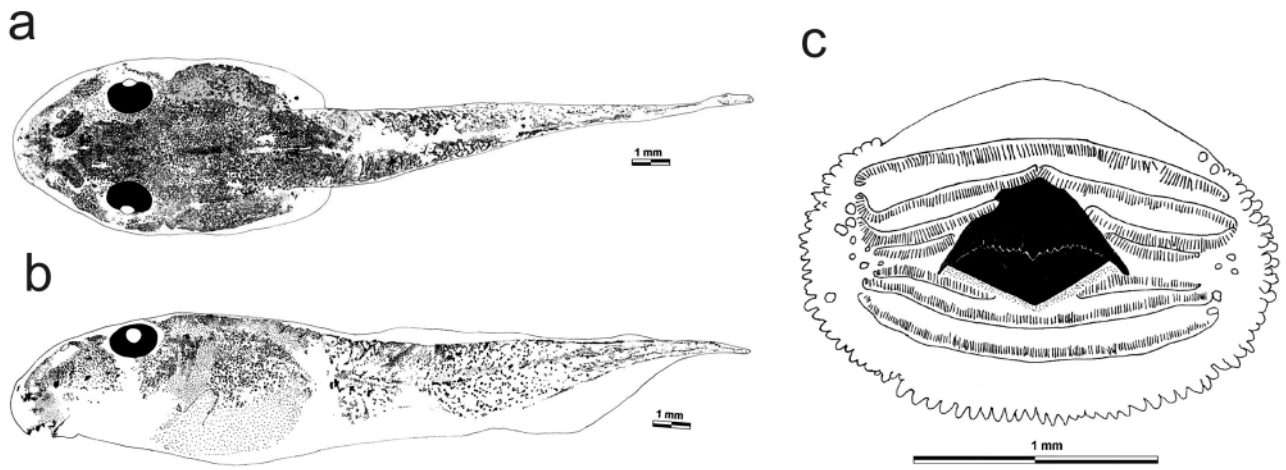

FIGURE 2. Drawings of preserved tadpole specimen of *Boophis anjanaharibeensis* (ZSM 0624/2008) from Marojejy National Park (developmental stage 25). (a) dorsal view; (b) lateral view; (c) oral disk.

Oral disk of moderate size (ODW 55% of BW), positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by moderately wide dorsal gap (DG 63% of ODW), ventral gap absent, total number of marginal papillae 85. Nineteen submarginal papillae (9 in the right and 10 in the left) positioned laterally. Moderately long conical papillae with protuberance, rounded tip, not visible from dorsal view, longest marginal and submarginal papillae measured 0.11 mm and 0.10 mm respectively. Jaw sheaths

fully keratinized with rounded serrations, moderately wide (JL 45% of ODW) with very small medial convexity (MC 5% of JL). Lower jaw sheath U-shaped, partially hidden by upper sheath. LTRF 5(4–5)/3(1). Single row of keratodonts per ridge. Very wide A_1 (75% of ODW). Density of keratodonts on A_1 110/mm (total 110). Short, discernible keratodonts (0.11 mm). A_5 is much smaller than the other rows. Moderate space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body and tail brownish caused by dark pigmentation of different forms that are distributed over the total body except at the margins. Dorsolaterally body is brownish, ventrolaterally body is translucent. Fins transparent. Ventrally, the intestinal coils are clearly visible.

Variation. TL and BL of one additional specimen (not a DNA voucher) at stage 25, from Marojejy National Park (FGZC 2245) are 19 mm and 7 mm, respectively. This specimen is deposited in the UADBA collection. BW 118% of BH; ED 14% of BL; RN 80% of NP; IND 61% of IOD; SS 69% of BL; TMH 100% of MTH; TMW 46% of BW; MTH 64% of BH; ODW 46% of BW. LTRF 5(2–5)/3(1).

Boophis axelmeyeri Vences, Andreone & Vieites

The following description refers to one tadpole in developmental stage 25 (ZSM 0629/2008; field number FGZC 2938, TL 26.6 mm, BL 10.7 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 99% identical to a reference sequence of an adult specimen of *B. axelmeyeri* (accession AF215336) from the same locality.

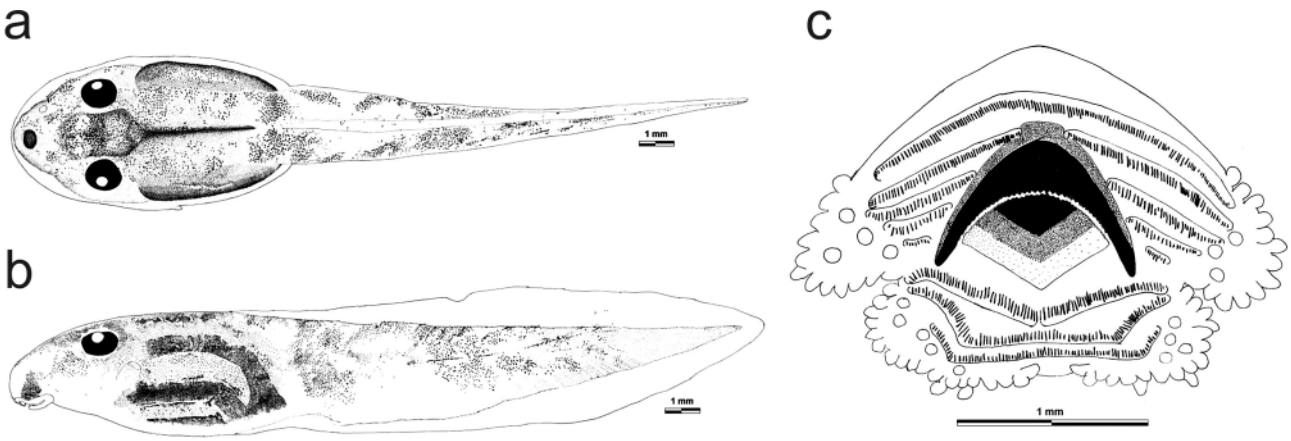

FIGURE 3. Drawings of preserved tadpole specimen of *Boophis axelmeyeri* (ZSM 0629/2008) from Marojejy National Park (developmental stage 25). (a) dorsal view; (b) lateral view; (c) oral disk.

In dorsal view, body elliptical, maximal width attained between the proximal 1/4 and 1/2 of the body (SBW 47% of BL), narrowly rounded snout. In lateral view, body depressed (BW 115% of BH) maximal body height attained between the proximal 1/2 and 3/4 of the body (SBH 62 % of BL), rounded snout. Eyes moderately large (ED 13% of BL), not visible from ventral view, positioned dorsally and oriented dorsolaterally, situated between the proximal 3/10 and 4/10 of the body, moderately wide distance between eyes (IOD 56% of BW). Moderately large oval nares (NS 3% BL), marked with marginal rim, positioned dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 75% of NP), wide distance between nares (IND 67% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 13% of BL), directed posteriorly, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 1/2 and 3/4 of the body (SS 62% of BL), located below the height of the point where the axis of the tail myotomes contact the body. Long dextral vent tube (VL 13% of BL), associated with ventral fin, inner wall present. Tail of moderate length (TAL 149% of BL), maximal tail height lower than body height (MTH 97% of BH), tail height at midtail equal to body

height and maximal tail height (THM 97% of BH and THM 100% of MTH), tail height at the beginning of the tail lower than body height (TH 86% of BH). Moderately developed caudal musculature (TMW 57% of BW, TMH 65% of BH and 67% of MTH, TMHM 49% of THM and MTH). Tail muscle reaches tail extremity. Very low fin type (DF 57% of TMHM, VF 49% of TMHM), dorsal fin higher than ventral fin (DF 117% VF). Dorsal fin originates on the dorsal body-tail junction, increases to reach maximal height and then declines abruptly until the caudal extremity. Ventral fin originates at the ventral terminus of the body, progress almost constant and decreases to the end of the tail to join the caudal extremity. Maximal tail height located in the mid-tail, lateral tail and myosepta visible on the proximal 3/4 of the tail, tail tip narrowly rounded.

Oral disk of moderate size (ODW 40% of BW), positioned ventrally and oriented antero-ventrally, emarginated, maximal width in the upper labium. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by small ventral gap (VG 10% of ODW) and a very wide dorsal gap (DG 81% of ODW), total number of marginal papillae 68 (32 right and 36 left). Sixteen submarginal papillae positioned laterally (9 right and 7 left). Moderately long conical papillae with rounded tips, not visible from dorsal view, longest marginal and submarginal papillae measured 0.10 mm and 0.13 mm, respectively. Jaw sheath fully keratinized with pointed serrations, moderately wide (JL 48% of ODW) with very small medial convexity (MC 4% of JL). Lower jaw sheath partially pigmented, V- shaped. LTRF 5(2–4)/3(1). Single row of keratodonts per ridge. Very large A_1 (92% of ODW). Density of keratodonts on A_1 73/mm (total 132). Very narrow gap in the first anterior interrupted row (A_{2gap} 11% of A_2). Short, discernible keratodonts (0.09 mm). Labial teeth distinguishable from one another. In most of the rows, the size decreases towards the peripheries. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, beige with brown spots dissipated dorsally and dorsolaterally. Laterally, intestinal coils well visible. Ventrally translucent, intestine well visible, regularly spiral shaped. Tail musculature whitish with brown spots. Fin transparent with some dots.

Variation. Based on 17 tadpoles at stages 25–32 from Marojejy National Park, including three DNA voucher specimens (FGZC 2931, 2932, 2933) (Table 5). All specimens are in the UADBA collection. TL and BL are 15–38 mm and 8–14 mm, respectively. BW 110–135% of BH; ED 12–16% of BL; RN 50–77% of NP; IND 52–65% of IOD; SS 33–66% of BL; TMH 61–92% of MTH; TMW 42–60% of BW; MTH 76–118% of BH; ODW 35–46% of BW; LTRF 4(2–4)/3(1), 5(2–5)/3(1).

Boophis elenae Andreone

The following description refers to one tadpole in developmental stage 25 (ZSM 0631/2008, field number ZCMV 2692, TL 19.1 mm, BL 6.3 mm; Table 1), from Ranomafana National Park. The 16S rDNA sequence of this specimen was 99.8 % identical to a reference sequence of an adult *B. elenae* (accession AY848469) from Antoetra.

In dorsal view, body elliptical, maximal width attained between the proximal 1/2 and 3/4 of the body (SBW 64% of BL), broadly rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained between the proximal 1/2 and 3/4 of the body (SBH 65% of BL), rounded snout. Eyes large (ED 19% of BL), not visible from ventral view, positioned dorsally and oriented dorsolaterally, situated between the proximal 4/10 and 5/10 of the body, wide distance between eyes (IOD 77% of BW). Moderately large elliptical nares (NS 4% of BL), marked with marginal rim, positioned dorsally and oriented anterodorsally, situated nearer to snout than to eye (RN 57% of NP), moderately wide distance between nares (IND 55% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 11% of BL), directed posterodorsally, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and aperture opens posteriorly, round opening, situated between the proximal 1/2 and 3/4 of the body (SS 69% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Long dextral vent tube (VL 14% of BL), attached to ventral fin, inner wall present. Tail of moderate length (TAL 161% of BL), maximal tail height lower than body height (MTH 75% of BH), tail height at midtail lower than body height and maximal tail height (THM

70% of BH and THM 93% of MTH), tail height at the beginning of the tail lower than body height (TH 83% of BH). Moderately developed caudal musculature (TMW 54% of BW, TMH 64% of BH and 85% of MTH, TMHM 61% of THM and 57% of MTH). Tail muscle reaches tail tip. Very low fins (DF 39% of TMHM, VF 27% of TMHM), dorsal fin higher than ventral fin (DF 145% of VF). Dorsal fin originates on the proximal 1/5 of the tail musculature, progresses parallel to the margin of the tail muscle up to the tip of the tail. Ventral fin originates on the ventral terminus of the body, progresses parallel to the margin of the tail muscle up to the tip of the tail. Maximal tail height located between the proximal 1/4 and 1/2 of the tail, lateral tail vein visible on the proximal 1/2 of the tail, myosepta visible on the proximal 3/4 of the tail, tail tip narrowly rounded.

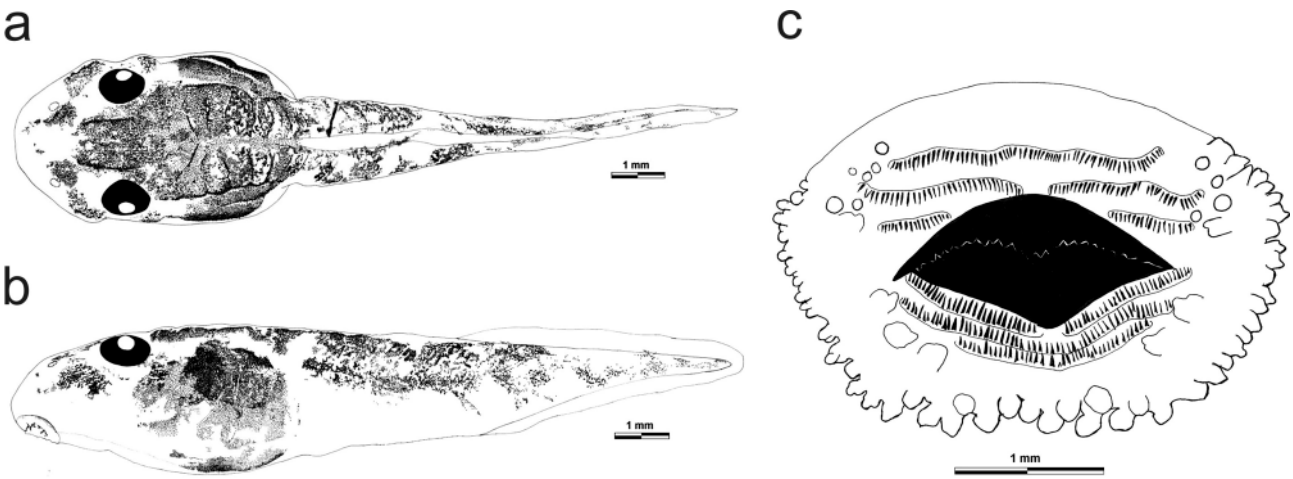

FIGURE 4. Drawings of preserved tadpole specimen of *Boophis elenae* (ZSM 0631/2008) from Ranomafana National Park (developmental stage 25). (a) dorsal view; (b) lateral view; (c) oral disk.

Small oral disk (ODW 27% of BW), positioned ventrally and oriented anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a very wide dorsal gap (DG 81% of ODW), total number of marginal papillae 56. Eighteen submarginal papillae positioned laterally (10 in the right and 8 in the left). Long conical papillae with protuberance, rounded tips, not visible from dorsal view, longest marginal and submarginal papillae measured 0.19 mm and 0.22 mm, respectively. Jaw sheaths fully keratinized with pointed serrations, moderately wide (JL 51% of ODW) with very small medial convexity (MC 3% of JL). Lower jaw sheath V- shaped. LTRF 3(2–3)/3(1). Single row of keratodonts per ridge. Moderately sized A_1 (53% of ODW). Density of keratodonts on A_1 49/mm (total 78). Very narrow gap in the first anterior interrupted row (A_{2gap} 4% of A_2). Short, discernible keratodonts (0.11 mm). Labial teeth distinguishable from one another. In most of the rows, the size decreases towards the peripheries. Narrow space between marginal papillae and keratodont rows.

Coloration in life. Body dorsum and flank with black pigmentation, ventral, gular and branchial regions whitish, abdominal surface silverish. Tail yellowish with many blotches.

Coloration in preservative. Dorsally, body covered by brown blotches that are condensed to form a dark region except in the beginning of the snout and in the anterior of the eyes. Dorsolaterally equal to dorsally. Ventrally, gular and branchial regions whitish, abdominal surface dark colored, intestine invisible.

Variation. Based on 128 tadpoles at stages 25–34, all from Ranomafana (ZCMV 2689, 2692, 2693, 3637, 3700, 3701), of which six are DNA voucher specimens (Table 3). All specimens are in the UADBA collections. TL and BL are 22–45 mm and 10–18 mm, respectively. BW 75–155% of BH; ED 13–21% of BL; RN 40–94% of NP; IND 43–90% of IOD; SS 41–94% of BL; TMH 69–157% of MTH; TMW 36–60% of BW; MTH 41–103% of BH; ODW 30–67% of BW; LTRF 3(2–3)/3(1), 2(2)/3(1).

TABLE 3. Morphometric measurements (all in mm) of additional DNA voucher specimens of *Boophis elenae* and *B. englaenderi*. For abbreviations, see Material and Methods.

Species	*B. elenae*	*B. elenae*	*B. elenae*	*B. elenae*	*B. elenae*	*B. englaenderi*	*B. englaenderi*
Field number	ZCMV 2693	ZCMV 2693	ZCMV 3637	ZCMV 3700	ZCMV 3701	FGZC 2258	FGZC 2272
BL	12.7	14.8	12.0	15.5	12.0	6.8	10.0
BW	8.3	9.0	4.0	9.7	9.7	3.7	4.8
BH	6.3	7.3	5.3	6.7	6.5	2.7	4.3
ED	2.2	2.3	1.8	2.3	2.3	1.0	1.3
RN	2.7	2.8	2.2	2.8	3.3	1.2	2.0
NP	3.3	3.8	2.8	3.8	4.0	1.7	2.5
IND	3.3	3.7	3.0	3.3	3.3	1.3	2.0
IOD	6.7	6.7	5.3	7.0	4.3	2.7	4.0
SS	9.3	10.5	8.3	11.2	11.3	4.8	7.3
TMH	4.0	4.7	3.7	5.0	4.7	2.2	3.0
TMW	3.0	4.3	3.0	4.7	4.0	1.8	2.8
MTH	4.0	4.7	3.8	5.0	4.7	2.2	3.0
BH	6.3	7.3	5.3	6.7	6.5	2.7	4.3
TAL	16.7	22.0	15.0	21.7	19.3	11.0	15.0
ODW	3.0	3.3	2.7	4.3	3.7	2.7	3.5

***Boophis englaenderi* Glaw & Vences**

The following description refers to one tadpole in developmental stage 41 (ZSM 0623/2008, field number FGZC 2244, TL 31.3 mm, BL 11.8 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.5 % identical to a reference sequence of an adult *B. englaenderi* (accession FJ559124) from Marojejy.

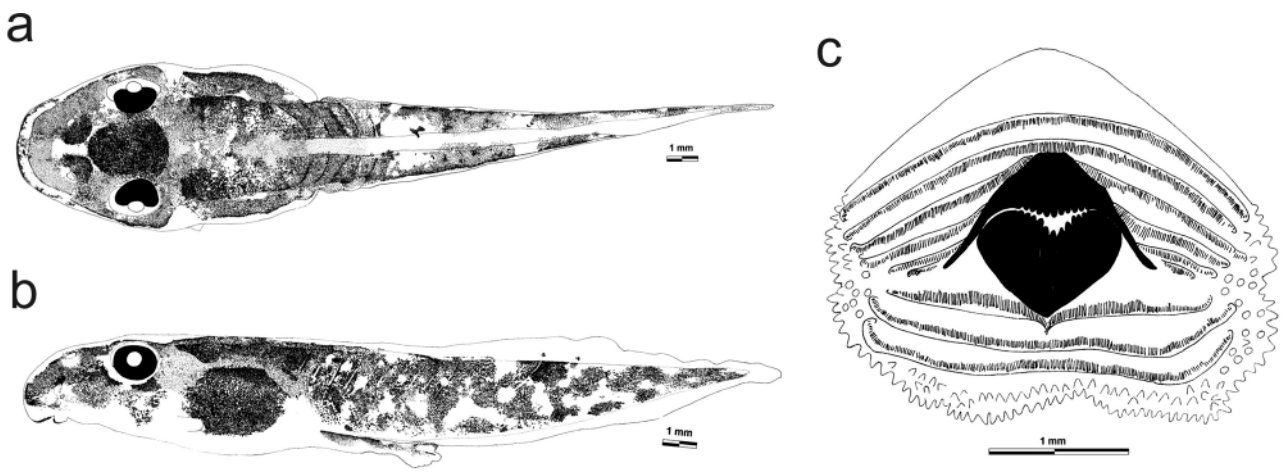

FIGURE 5. Drawings of preserved tadpole specimen of *Boophis englaenderi* (ZSM 0623/2008) from National Park of Marojejy (developmental stage 41). (a) dorsal view; (b) lateral view; (c) oral disk.

In dorsal view, body elliptical, maximal width attained between the proximal 1/2 and 3/4 of the body (SBW 60% of BL), almost aligned snout. In lateral view, body depressed (BW 133% of BH) maximal body height attained between the proximal 1/2 and 3/4 of the body (SBH 67 % of BL), rounded snout. Eyes large (ED 16% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the

proximal 3/10 and 4/10 of the body, wide distance between eyes (IOD 74% of BW). Moderately large elliptical nares (NS 4% of BL), marked with marginal rim, positioned dorsally and oriented anterodorsally, situated nearer to snout than to eye (RN 57% of NP), moderately wide distance between nares (IND 55% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 11% of BL), directed posteriorly, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and aperture opens posteriorly, elliptical opening, situated between the proximal 1/2 and 3/4 of the body (SS 69% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Short medial vent tube (VL 9% of BL), not attached to ventral fin. Tail of moderate length (TAL 155% of BL), maximal tail height lower than body height (MTH 90% of BH), tail height at midtail lower than body height and maximal tail height (THM 82% of BH and THM 92% of MTH), tail height at the beginning of the tail lower than body height (TH 88% of BH). Moderately developed caudal musculature (TMW 54% of BW, TMH 74% of BH and 85% of MTH, TMHM 66% of THM and 61 % of MTH). Tail muscle reaches tail tip. Very low fins (DF 34% of TMHM, VF 18% of TMHM), dorsal fin higher than ventral fin (DF 189% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, progresses parallel to the margin of the tail muscle up to the proximal 3/10 where it increases up to maximal tail height, then declines up to the tail tip. Ventral fin originates on the ventral terminus of the body, progresses parallel to the margin of the tail muscle up to maximal tail height, then decreases towards the tip of the tail. Maximal tail height between the proximal 1/4 and 1/2 of the tail, lateral tail vein visible on the 1/2 proximal of the tail, myosepta visible on the proximal 3/4 of the tail, tail tip narrowly rounded.

Oral disk of moderate size (ODW 56% of BW), positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a very wide dorsal gap (DG 85% of ODW), total number of marginal papillae 128. Thirty-three submarginal papillae positioned laterally. Moderately long conical papillae, rounded tips, not visible from dorsal view, longest marginal and submarginal papillae measured 0.12 mm and 0.09 mm, respectively. Jaw sheaths fully keratinized with rounded serrations, moderately wide (JL 46% of ODW) with very small medial convexity (MC 3% of JL). Lower jaw sheath U-shaped. LTRF 6(2–6)/3(1). Single row of keratodonts per ridge. Very wide A_1 (90% of ODW). Density of keratodonts on A_1 76/mm (total 236). Short, discernible keratodont (0.10 mm). Labial teeth are distinguishable from each other, their size decreases towards the periphery. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body and tail brownish, dark pigmentation of different forms distributed all over the body and tail, in particular around the eyes, above the nares, and on the intestine. Dorsolaterally body is brownish, ventrolaterally transparent, with black round spots that are irregularly distributed, except on the intestine. Tail musculature whitish with brownish round spots, some distributed irregularly in the caudal musculature and some form stripes. Fins translucent with some spots. Ventrally, the intestine is visible.

Variation. Based on 10 tadpoles at stages 25 all from Marojejy (FGZC 2258, 2272), of which two are DNA voucher specimens (Table 3). All the specimens are in the UADBA collection. TL and BL are 18–25 mm and 7–12 mm. BW 100–143% of BH; ED 9–16% of BL; RN 58–107% of NP; IND 47–52% of IOD; SS 50–79% of BL; TMH 100% of MTH; TMW 47–67% of BW; MTH 69–90% of BH; ODW 53–86% of BW; LTRF: 6(2–6)/3, 6(3–6)/3, 7(3–7)/3.

Boophis microtympanum (Boettger)

The following description refers to one tadpole in developmental stage 35 (ZSM 0622/2008, field number FGZC 2223, TL 57.6 mm, BL 19.1 mm; Table 1), from the Ambohitantely Special Reserve. The 16S rDNA sequence of this specimen was 99.4 % identical to a reference sequence of an adult of *B. microtympanum* (accession FJ559129) from the same locality.

In dorsal view, body elliptical, maximal width at midbody (SBW 50% of BL), broadly rounded snout. In lateral view, body depressed (BW 106% of BH), maximal body height attained between the proximal 1/2 and

3/4 of the body (SBH 64% of BL), pointed snout. Eyes of moderate size (ED 12% of BL), not visible from ventral view, positioned dorsally and oriented dorsolaterally, situated between the proximal 3/10 and 4/10 of the body, moderate distance between eyes (IOD 55% of BW). Small oval nares (NS 2% of BL), marked with marginal rim, positioned dorsally and oriented dorsolaterally, situated nearer to snout than to eye (RN 76% of NP), moderately wide distance between nares (IND 41% of IOD), black spot on the back of the nare present, ornamentation absent. Small sinistral spiracle (SP 7% of BL), directed posteriorly, visible from dorsal view, inner wall free from the body and its aperture opens laterally, situated between the proximal 1/2 and 3/4 of the body (SS 64% of BL), located at the level of the point where the axis of the tail myotomes contact the body. Very long medial vent tube (VL 17% of BL), separated by a web to the ventral fin. Tail of moderate length (TAL 164% of BL), maximal tail height lower than body height (MTH 93% of BH), tail height at midtail lower than body height and maximal tail height (THM 72% of BH and THM 77% of MTH), tail height at the beginning of the tail lower than body height (TH 91% of BH). Moderately developed caudal musculature (TMW 44% of BW, TMH 72% of BH and 77% of MTH, TMHM 56% of THM, TMHM 40% of MTH). Tail muscle reaches tail tip. Very low fins (DF 71% of TMHM, VF 46% of TMHM), dorsal fin higher than ventral fin (DF 155% of VF). Dorsal fin originates on the dorsal body-tail junction, increases to reach maximal height and then declines abruptly up to the tail tip. Ventral fin originates at the ventral terminus of the body, progresses almost constantly and decreases towards the tail tip. Maximal tail height located between the proximal 1/4 and 1/2 of the tail, lateral tail vein visible on the proximal 1/4 of the tail, myosepta visible all along the tail musculature, tail tip narrowly rounded.

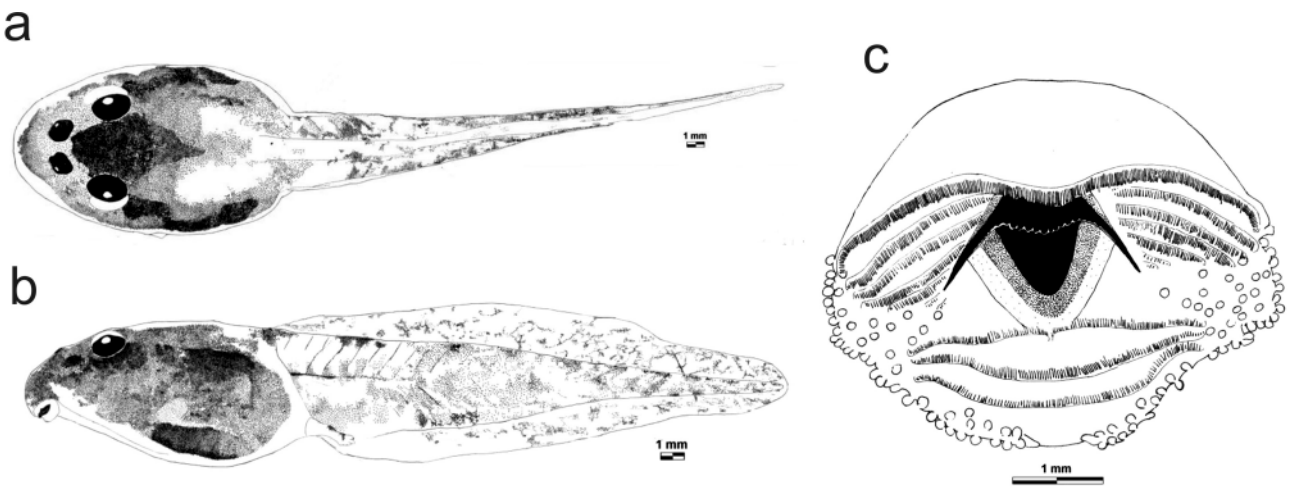

FIGURE 6. Drawings of preserved tadpole specimen of *Boophis microtympanum* (ZSM 0622/2008) from Ambohitantely Special Reserve (developmental stage 35). (a) dorsal view; (b) lateral view; (c) oral disk.

Oral disk of moderate size (ODW 43% of BW), positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a narrow ventral gap (VG 10% of ODW) and a very wide dorsal gap (DG 85% of ODW), total number of marginal papillae 70 (39 right and 31 left). Thirty-three submarginal papillae positioned laterally (13 in the right and 20 in the left). Moderate long conical papillae with rounded tip, not visible from dorsal view, longest marginal papillae measured 0.26 mm, and 0.13 mm for submarginal papillae. Upper jaw sheath finely serrated, dark color with a brownish basis, moderately wide (JL 44% of ODW) with very small medial convexity (MC 4% of JL). Lower jaw sheath broadly U-shaped, with three different colorations (1/3 in the margin black, 1/3 in the middle brown and 1/3 on the basis white) with pointed serration. LTRF 6(2–6)/3(1). Single row of keratodonts per ridge. Very large A_1 (95% of ODW). Density of keratodonts on A_1 59/mm (total 287). Very narrow gap in the first anterior interrupted row (A_{2gap} 7% of A_2). Short, discernible keratodonts (0.03 mm). Labial teeth distinguishable from one another. In most of the rows, the size decreases towards peripheries. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body brownish with brown and black pigment tasks of different forms which gather in some zones of the body and give dark patches. The dorsolateral part of body is equally colored as dorsally, and ventrolaterally equal to ventrally. Ventrally transparent, intestine visible, regularly spiral shaped. Tail musculature brownish with dark rounded spots dispersed irregularly in the caudal musculature, forming stripes. Fins transparent with dots and lines.

Variation. Based on 39 tadpoles at stages 25–41, from the Ambohitantely Special Reserve (FGZC 2216, 2223, 2226, 2227, 2230) and the Ankaratra massif (FGZC 2233), of which seven are DNA voucher specimens (two DNA vouchers in series FGZC 2226) (Table 4). All the specimens are in the UADBA collection**.** TL and BL are 26–68 mm and 10–26 mm, respectively. BW 95–153% of BH; ED 8–15% of BL; RN 37–111% of NP; IND 36–55% of IOD; SS 41–67% of BL; TMH 60–105% of MTH; TMW 29–65% of BW; MTH 53–126% of BH; ODW 18–41% of BL; ODW 35–72% of BW; LTRF 4(2–4)/3(1), 5(2–5)/3(1), 6(2–6)/3(1).

TABLE 4. Morphometric measurements (all in mm) of additional DNA voucher specimens of *Boophis microtympanum*. For abbreviations, see Material and Methods.

Species	*B. microtympanum*	*B. microtympanum*	*B. microtympanum*	*B. microtympanum*	*B. microtympanum*	*B. microtympanum*
Field number	FGZC 2216	FGZC 2226	FGZC 2226	FGZC 2227	FGZC 2230	FGZC 2233
BL	23.0	21.7	24.0	8.5	23.8	10.3
BW	12.7	12.7	13.2	6.7	13.0	8.7
BH	9.3	9.0	10.0	4.7	10.0	6.7
ED	2.7	2.3	2.7	1.3	3.3	1.5
RN	4.3	3.7	3.5	2.2	1.8	3.0
NP	4.8	4.7	4.8	2.3	4.8	3.3
IND	3.3	4.3	3.7	2.0	3.3	3.0
IOD	8.5	8.3	8.7	4.3	8.3	5.7
SS	14.3	13.3	13.3	4.2	0.0	4.3
TMH	7.7	6.3	9.0	3.0	7.7	5.3
TMW	7.3	5.7	6.3	2.3	8.3	5.0
MTH	7.7	6.3	9.0	3.0	12.7	6.3
BH	9.3	9.0	10.0	4.7	10.0	6.7
TAL	45.3	27.7	36.3	17.3	40.0	19.0
ODW	6.7	4.7	5.3	3.0	4.3	4.3

Boophis rhodoscelis (Boulenger)

The following description refers to one tadpole in developmental stage 33 (ZSM 0630/2008, field number ZCMV 2643, TL 40.5 mm, BL 14.7 mm; Table 1), from Vohiparara (near Ranomafana National Park). The 16S rDNA sequence of this specimen was 100 % identical to a reference sequence of an adult *B. rhodoscelis* (accession AY848618) from Ranomafana National Park.

In dorsal view, body elliptical, maximal width attained between the proximal 1/4 and 1/2 of the body (SBW 40% of BL), broadly rounded snout. In lateral view, body depressed (BW 127% of BH), maximal body height attained on the proximal 3/4 of the body (SBH 75% of BL), rounded snout. Eyes large (ED 14% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the proximal 3/10 and 4/10 of the body, wide distance between eyes (IOD 76% of BW). Moderately large elliptical nares (NS 2% of BL), marked with marginal rim, positioned dorsally and oriented anterodorsally, situated nearer to snout than to eye (RN 63% of NP), moderately wide distance between nares (IND 43% of IOD), black spot on

the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 12% of BL), directed posteriorly, visible from dorsal and ventral views and obvious from lateral view, inner wall free from body and aperture opens laterally instead of posteriorly, round opening, situated between the proximal 1/2 and 3/4 of the body (SS 55% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Short dextral vent tube (VL 9% of BL) attached to the ventral fin. Tail of moderate length (TAL 141% of BL), maximal tail height higher than body height (MTH 118% of BH), tail height at midtail higher than body height and lower maximal tail height (THM 109% of BH and THM 92% of MTH), tail height at the beginning of the tail lower than body height (TH 98% of BH). Weakly developed caudal musculature (TMW 51% of BW, TMH 70% of BH and 59% of MTH, TMHM 50% of THM and 46% of MTH). Tail muscle reaches tail tip. Very low fins (DF 63% of TMHM, VF 39% of TMHM), dorsal fin lower than ventral fin (DF 162% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses to the maximal tail height, and then declines up to the tail tip. Ventral fin originates on the ventral terminus of the body, increases up to the maximal tail height, and then decreases to the tip of the tail. Maximal tail height at mid-tail, lateral tail vein visible in the proximal 1/3 of the tail, myosepta visible all along the tail, tail tip narrowly rounded.

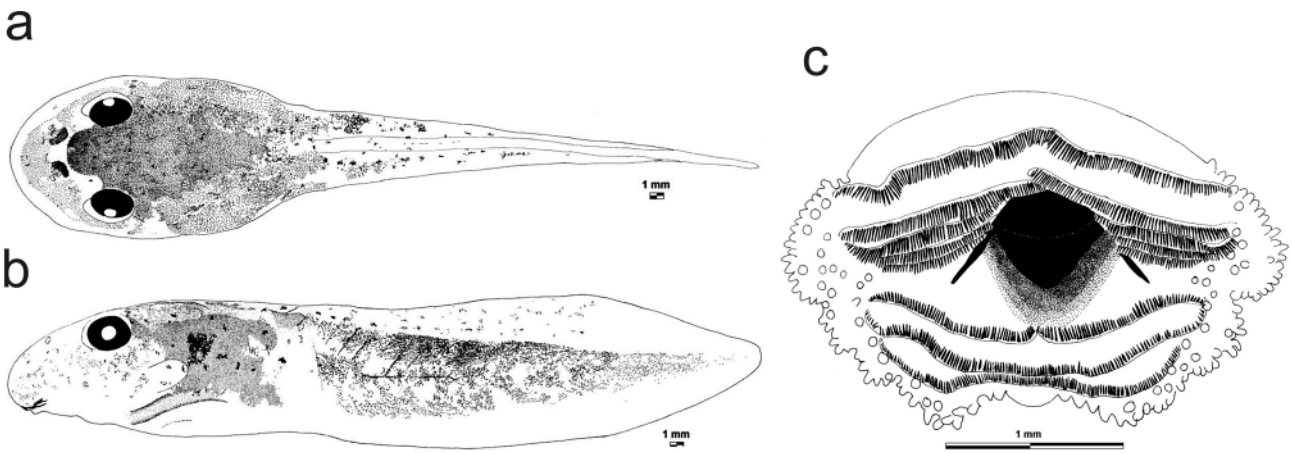

FIGURE 7. Drawings of preserved tadpole specimen of *Boophis rhodoscelis* (ZSM 0630/2008) from National Park of Ranomafana (developmental stage 33). (a) dorsal view; (b) lateral view; (c) oral disk.

Oral disk of moderate size (ODW 48% of BW), positioned and oriented ventrally, emarginated, maximal width in the upper labium. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by moderately wide dorsal gap (DG 67% of ODW), and a very narrow ventral gap, total number of marginal papillae 105 (52 in the right and 53 in the left). Thirty-nine submarginal papillae (20 in the right and 19 in the left) positioned laterally. Moderately long conical papillae with protuberance, rounded tip, not visible from dorsal view, longest marginal and submarginal papillae measured 0.14 mm and 0.10 mm, respectively. Upper jaw sheaths fully keratinized with rounded serrations, moderately wide (JL 41% of ODW) with very small medial convexity (MC 5% of JL). Lower jaw sheath wide V-shaped, with three colors, black in the 1/3 of the margin, brown in the median 1/3, and white in the 1/3 of the base. LTRF 5(2–5)/3(1). Single row of keratodonts per ridge. Moderately sized A_1 row (57% of ODW). Density of keratodonts on A_1 70/mm (total 160). Short, discernible keratodont (0.13 mm). Keratodont size variable, generally smaller at the margins. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body brownish, except in front of the snout, tail is whitish, with brown spots of different shapes. Dorsolaterally similar to dorsal view, snout and the area below the eye and the spiracle are transparent. Ventrolaterally similar to ventral view. Laterally, the caudal musculature is brown with many different shaped spots that are concentrated in some areas. The striations are well visible in the proximal 1/3 of the tail. Fins generally transparent, dorsal fin with some spots and fine striations. In ventral view the body is translucent, intestinal coils is well visible.

Variation. TL and BL of one additional non-voucher specimen at stage 32, from Vohiparara (ZCMV 2643) are 40 mm and 15 mm, respectively. This specimen is deposited in the UADBA collection. BW 115% of BH; ED 14% of BL; RN 70% of NP; IND 40% of IOD; SS 66% of BL; TMH 100% of MTH; TMW 49% of BW; MTH 68% of BH; ODW 45% of BW. LTRF 5(2–5)/3(1).

***Boophis vittatus* Glaw, Vences, Andreone & Vallan**

The following description refers to one tadpole in developmental stage 25 (ZSM 0625/2008; field number FGZC 2276, TL 18.6 mm, BL 5.0 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of an adult *B. vittatus* adult specimen (accession FJ559158) from the same locality.

In dorsal view, body elliptical, maximal width between the proximal 1/2 and 3/4 of the body (SBW 70% of BL), snout rounded. In lateral view, body depressed (BW 112% of BH), maximal body height between the proximal 1/2 and 3/4 of the body (SBH 74% of BL), snout pointed. Eyes positioned dorsally and oriented dorsolaterally, small sized (ED 8% of BL), not visible from ventral view, situated between the proximal 4/10 and 5/10 of the body, very wide distance between eyes (IOD 81% of BW). Small rounded nares (NS 1.4% of BL), prominent with marginal rim, positioned dorsally and oriented dorsolaterally, situated nearer to eye than to snout (RN 123% of NP), moderately wide distance between nares (IND 55% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 14% of BL), oriented posteriorly, visible from dorsal and lateral views, obvious from lateral view, inner wall free from the body and its aperture opens laterally, situated between the proximal 1/2 and 3/4 of the body (SS 75% of BL), located at the level of the point where the axis of the tail myotomes contact the body. Short dextral vent tube (VL 10% of BL), attached to the ventral fin, inner wall absent. Tail height at the beginning of the tail lower than body height (TH 89% of BH). Tail muscle width at the beginning of the tail 57% of body width. Dorsal fin originates on the dorsal body-tail junction and ventral fin originates at the ventral terminus of the body.

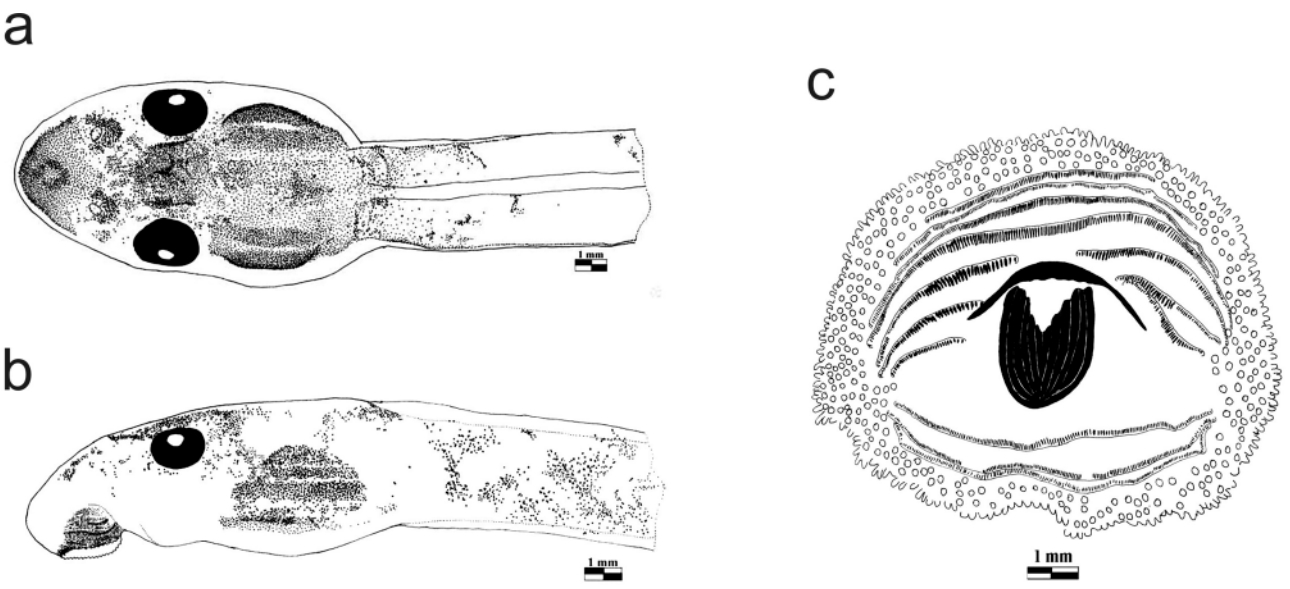

FIGURE 8. Drawings of preserved tadpole specimen of *Boophis vittatus* (ZSM 0625/2008) from Marojejy National Park (developmental stage 25). (a) dorsal view; (b) lateral view; (c) oral disk. Tail of the specimen is missing due to tissue sampling for DNA barcoding.

Very large oral disk (ODW 83% of BW) positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, dorsal and ventral gap absent. Complete marginal (113) and submarginal (184) papillae. Small rounded papillae, not visible from dorsal view, longest marginal papillae measured 0.06 mm,

and 0.05 mm for submarginal papillae. Jaw sheath completely keratinized, moderately wide (JL 40% of ODW), medial convexity absent. Lower jaw sheath U-shaped and ‘‘ribbed’’ (giving the appearance of vertical bars). LTRF 8(5–8)/3. Single row of keratodonts per ridge. Short A_1 (32% of ODW). Density of keratodonts on A_1 13/mm (total 85). Short, discernible keratodonts (0.07 mm). Labial teeth on A_1 and A_7 much smaller than on the other rows.

Coloration in preservative. Dorsally, body and tail whitish, with brown and black pigment tasks of different forms distributed irregularly. Dorsolaterally, similar to dorsally, ventrolaterally similar to ventrally. Fins transparent. Ventrally transparent, intestine visible, regular spiral shaped.

Variation. Based on ten additional tadpoles, of which three are voucher specimens (Table 6). TL and BL at stages 25, from the MarojejyNational Park (FGZC 2237, 2251 and 2276), are 8–19 mm and 5–7 mm, respectively. All the specimens are deposited in the UADBA collection. BW 115–128% of BH; ED 11–15% of BL; RN 67–150% of NP; IND 44–57% of IOD; SS 70–85% of BL; TMH 88–100% of MTH; TMW 53–67% of BW; MTH 69–86% of BH; ODW 30–43% of BL; ODW 67–93% of BW. LTRF 6(4–6)/3, 7(3–7)/3, 7(5–7)/3.

Boophis roseipalmatus

The following description refers to one tadpole in developmental stage 30 (ZSM 628/2008, field number FGZC 2935, TL 29.4 mm, BL 11.0 mm; Table 1), from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.8 % identical to a reference sequence of an adult *Boophis roseipalmatus* (accession AY848577) from Montagne d’Ambre.

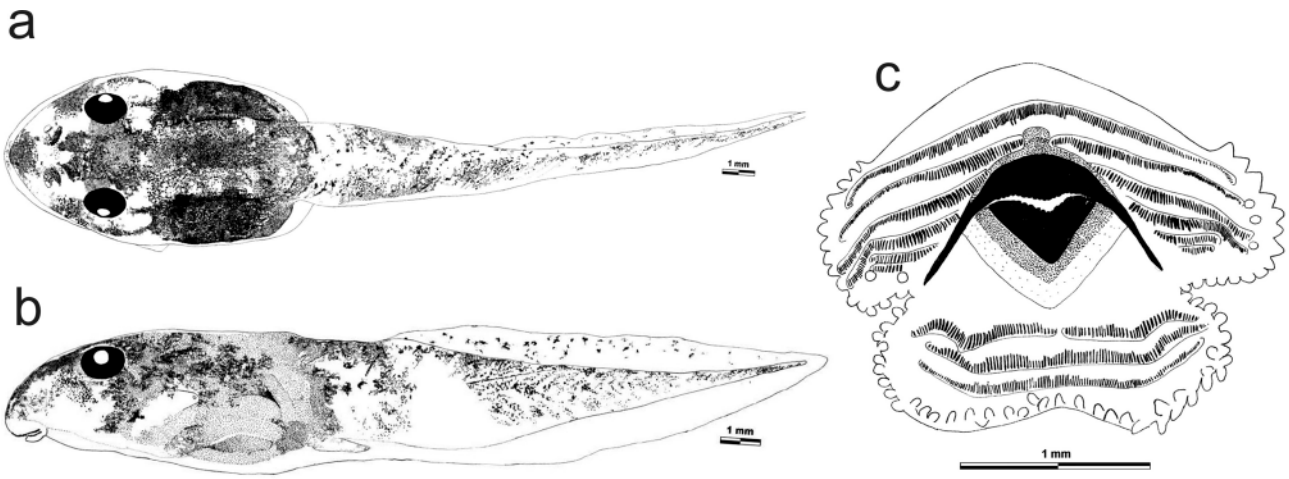

FIGURE 9. Drawings of preserved tadpole specimen of *Boophis roseipalmatus* Glaw, Köhler, de la Riva, Vieites & Vences (ZSM 0628/2008) from Marojejy National Park (developmental stage 30). (a) dorsal view; (b) lateral view; (c) oral disk.

In dorsal view, body elliptical, maximal width between the proximal 1/4 and 1/2 of the body (SBW 45% of BL), rounded snout. In lateral view, body depressed (BW 129% of BH), maximal body height between the proximal 1/2 and 3/4 of the body (SBH 71% of BL), rounded snout. Eyes large (ED 14% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the proximal 3/10 and 4/10 of the body, wide distance between eyes (IOD 67% of BW). Moderately large elliptical nares (NS 4% of BL), marked with marginal rim, positioned dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 61% of NP), moderately wide distance between nares (IND 47% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 12% of BL), directed posteriorly, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and aperture opens posteriorly, elliptical opening, situated between the proximal 1/2 and 3/4 of the body (SS 60% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Long dextral

vent tube (VL 10% of BL) attached to the ventral fin. Tail of moderate length (TAL 153% of BL), maximal tail height as high as body height (MTH 100% of BH), tail height at midtail lower than body height and maximal tail height (THM 91% of BH and THM 91% of MTH), tail height at the beginning of the tail lower than body height (TH 89% of BH). Moderately developed caudal musculature (TMW 49% of BW, TMH 69% of BH and 69% of MTH, TMHM 48% of THM and 44 % of MTH). Tail muscle reaches tail tip. Very low fins (DF 51% of TMHM, VF 57% of TMHM), dorsal fin lower than ventral fin (DF 90% of VF). Dorsal fin originates on the proximal 1/4 of the tail, progresses to attain the maximal tail height, and then declines up to the tail tip. Ventral fin originates on the ventral terminus of the body, increases up to the maximal tail height, then decreases to the tip of the tail. Maximal tail height located between the proximal 1/4 and 1/2 of the tail, lateral tail vein visible on the proximal 1/2 of the tail, myosepta visible all along the tail, tail tip narrowly rounded.

Oral disk of moderate size (ODW 47% of BW), positioned and oriented ventrally, emarginated, maximal width in the upper labium. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by moderately wide dorsal gap (DG 65% of ODW), ventral gap absent, total number of marginal papillae 72. Nine submarginal papillae (3 in the right and 6 in the left) positioned laterally. Moderately long conical papillae, rounded tip, not visible from dorsal view, longest marginal and submarginal papillae measured 0.10 mm. Upper jaw sheaths fully keratinized with rounded serrations, wide (JL 61% of ODW) with very small medial convexity (MC 1% of JL). Lower jaw V-shaped; with three different colors, the 1/3 of the margin is black, the 1/3 in the middle is brown and the 1/3 of the basis is white. LTRF 6(2–6)/3(1). Single row of keratodonts per ridge. Very wide A_1 (76% of ODW). Density of keratodonts on A_1 79/mm (total 188). Short, discernible keratodonts (0.10 mm). Keratodont size variable, generally smaller at the margins. Narrow space between marginal papillae and keratodont rows.

Coloration in preservative. Dorsally, body and tail brownish, with irregularly distributed pigmentation of different forms. Dark spot on the nostril and in the front of the eyes. Dorsolaterally, coloration is equal to dorsal coloration, ventrolaterally, coloration is equal to ventral coloration, and the area below the eye is transparent. The muscle is white with many differently shaped spots that are irregularly distributed. The density of the spots decreases towards the tail tip. Fins generally transparent, dorsal fin with some spots. Ventrally the body is transparent and the intestinal coil is visible.

TABLE 5. Morphometric measurements (all in mm) of additional DNA voucher specimens of *Boophis axelmeyeri* and *B. roseipalmatus*. For abbreviations, see Material and Methods.

Species	*B. axelmeyeri*	*B. axelmeyeri*	*B.axelmeyeri*	*B. roseipalmatus*	*B. roseipalmatus*	*B. roseipalmatus*
Field number	FGZC 2933	FGZC 2931	FGZC 2932	FGZC 2939	FGZC 2943	FGZC 2947
BL	12.7	12.7	14.0	12.2	13.0	10.5
BW	7.2	7.0	8.0	6.7	8.0	8.2
BH	5.5	5.7	6.2	5.3	6.2	6.3
ED	1.8	1.5	2.0	1.8	1.8	1.8
RN	1.7	2.0	1.7	1.7	2.0	1.8
NP	2.3	2.7	2.5	2.0	2.5	2.5
IND	2.7	2.8	2.8	2.2	2.5	2.3
IOD	4.7	5.0	4.8	4.5	5.3	5.0
SS	6.5	8.3	6.7	5.7	8.7	5.2
TMH	4.5	4.0	4.7	3.3	4.0	3.5
TMW	3.7	3.7	4.2	3.3	3.3	3.0
MTH	6.2	4.3	6.7	5.3	4.0	3.5
BH	5.5	5.7	6.2	5.3	6.2	6.3
TAL	21.8	22.0	24.3	19.0	21.0	23.0
ODW	2.7	2.5	3.2	3.2	3.3	3.0

Variation. Based on 18 tadpoles at stages 25–36, from Marojejy National Park (FGZC 2935, 2939, 2943 and 2947), of which three are voucher specimens (Table 5). All the specimens are deposited in the UADBA collection. TL and BL are 24–36 mm and 9–15 mm, respectively. BW 81–139% of BH; ED 11–17% of BL; RN 60–100% of NP; IND 31–48% of IOD; SS 42–72% of BL; TMH 56–145% of MTH; TMW 36–56% of BW; MTH 55–113% of BH; ODW 37–72% of BW. LTRF 4(2–4)/3(1), 5(2–5)/3(1), 6(2–6)/3(1).

***Boophis luciae* Glaw, Köhler, de la Riva, Vieites & Vences**

The following description refers to one tadpole in developmental stage 25 (ZSM 0634/2008, field number ZCMV 3686, TL 20.8 mm, BL 7.8 mm; Table 1), from Ranomafana National Park. The 16S rDNA sequence of this specimen was 97.7% identical to a reference sequence of an adult *Boophis luciae*. (accession AJ315913) from Vohidrazana.

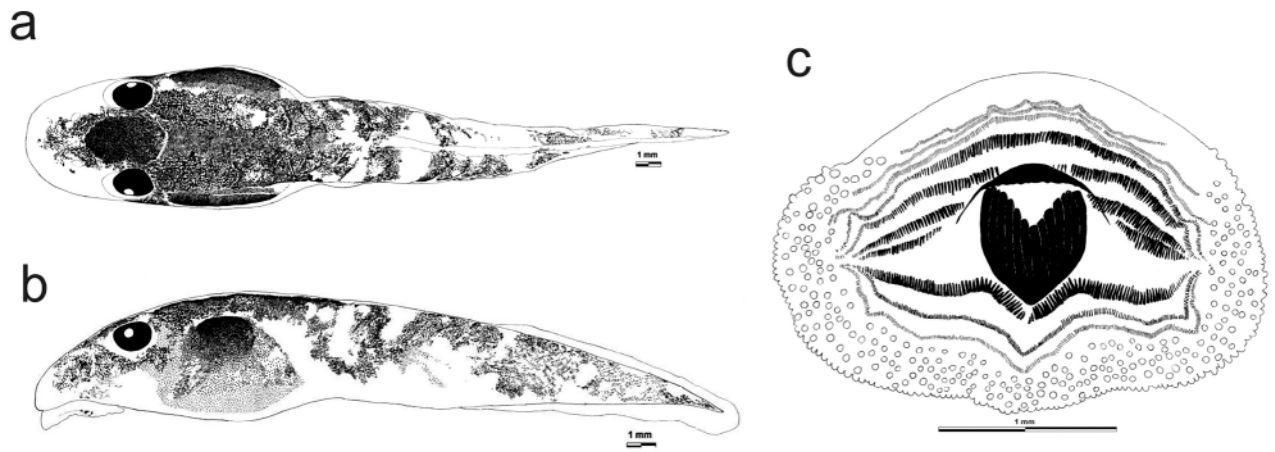

FIGURE 10. Drawings of preserved tadpole specimen of *Boophis luciae* (ZSM 0634/2008) from Ranomafana National Park (developmental stage 25). (a) dorsal view; (b) lateral view; (c) oral disk.

In dorsal view, body ovoid, maximal width between the proximal 1/2 and 3/4 of the body (SBW 60% of BL), wide rounded snout. In lateral view, body depressed (BW 115% of BH), maximal body height between the proximal 1/2 and 3/4 of the body (SBH 68 % of BL), rounded snout. Eyes large (ED 14% of BL), not visible from ventral view, positioned dorsally and oriented laterally, situated between the proximal 3/10 and 4/10 of the body, wide distance between eyes (IOD 75% of BW). Large elliptical nares (NS 5% of BL), marked with marginal rim, positioned dorsally and oriented anterodorsally, situated nearer to eye than to snout (RN 128 % of NP), moderately wide distance between nares (IND 45% of IOD), black spot on the back of the nare present, ornamentation absent. Moderately long sinistral spiracle (SP 11% of BL), directed posterodorsally, visible from dorsal and ventral views and perceptible from lateral view, inner wall free from body and aperture opens laterally instead of posteriorly, round opening, situated between the proximal 1/2 and 3/4 of the body (SS 66% of BL), located below the level of the point where the axis of the tail myotomes contact the body. Long medial vent tube (VL 10% of BL), not attached to the ventral fin. Tail of moderate length (TAL 162% of BL), maximal tail height lower than body height (MTH 84% of BH), tail height at midtail lower than body height and maximal tail height (THM 67% of BH and 79% of MTH), tail height at the beginning of the tail lower than body height (TH 82% of BH). Moderately developed caudal musculature (TMW 59% of BW, TMH 70% of BH and 83% of MTH, TMHM 100% of THM and 79% of MTH). Tail muscle reaches tail tip. Very low fins. Dorsal and ventral fins originate on the midtail, progresses almost parallel to the margin of the tail muscle up to the tail tip. Lateral tail vein visible on the proximal 1/2 of the tail, myosepta visible all along the tail, tail tip narrowly rounded.

Very wide oral disk (ODW 80% of BW), positioned and oriented ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by moderately wide dorsal gap (DG 54% of ODW), total number of

marginal papillae 129. Two hundred and thirty submarginal papillae positioned laterally and ventrally. Small conical papillae with protuberance, rounded tip, not visible from dorsal view, longest marginal and submarginal papillae measured 0.08 mm and 0.09 mm, respectively. Jaw sheaths fully keratinized with rounded serrations, narrow (JL 31% of ODW), medial convexity absent. Lower jaw sheath U-shaped, and ribbed (giving the appearance of vertical bars). LTRF 7(5–7)/3(1). Single row of keratodonts per ridge. Wide A_1 (60% of ODW). Density of keratodonts on A_1 119/mm (total 208). Short, discernible keratodont (0.14 mm). The keratodonts in the rows A_1, A_2, and A_3 are small and of equal size. For the others, the size decreases towards the margins.

Coloration in preservative. Dorsally, body and tail brownish, not uniform. The region between the eyes and parts of the intestine are very dark. Dorsolaterally same color as dorsally and ventrolaterally, the part below the eye is almost whitish and the snout is transparent with a brown spot, intestine is dark. Caudal musculature is whitish with some dark round spots of different sizes. Pigmented stripes along the tail, tail fins are whitish. Ventrally, intestinal coil is not visible.

Variation. Based on six tadpoles at stages 25–37, all from Ranomafana National Park (ZCMV 3619, 3631) of which two are DNA voucher specimens (Table 6). All the specimens are deposited in the UADBA collection. TL and BL are 23–29 mm and 7–13 mm, respectively. BW 94–107% of BH; ED 9–13% of BL; RN 46–83% of NP; IND 45–61% of IOD; SS 54–63% of BL; TMH 95–100% of MTH; TMW 50–71% of BW; MTH 61–77% of BH; ODW 42–79% of BW; LTRF 7(5–7)/3.

TABLE 6. Morphometric measurements (all in mm) of additional DNA voucher specimens of *Boophis vittatus* and *B. luciae*. For abbreviations, see Material and Methods.

Species	*B. vittatus*	*B. vittatus*	*B. vittatus*	*B. vittatus*	*B. luciae*	*B. luciae*
Field number	FGZC 2237	FGZC 2251	FGZC 2276	FGZC 2276	ZCMV 3619	ZCMV 3631
BL	6.8	5.7	6.3	5.0	6.7	12.3
BW	3.3	2.5	2.5	2.5	4.7	6.3
BH	2.7	2.2	2.0	2.0	4.7	6.5
ED	1.0	0.7	0.7	0.7	1.3	1.7
RN	1.8	1.0	1.2	1.3	1.8	1.0
NP	1.7	1.5	1.0	1.2	2.3	2.2
IND	1.3	1.3	1.0	1.0	2.0	2.7
IOD	3.0	2.0	2.0	2.0	4.0	4.3
SS	4.8	4.0	---	---	3.7	7.0
TMH	2.0	1.3	1.5	1.3	3.3	4.0
TMW	2.2	1.3	1.3	1.3	3.3	3.3
MTH	2.0	---	1.5	1.5	3.5	4.0
BH	2.7	2.2	2.0	2.0	4.7	6.5
TAL	11.8	---	9.7	8.3	18.0	15.3
ODW	2.3	2.2	2.3	2.2	3.7	2.7

Discussion

Data presented herein confirm that, in general, tadpoles of species classified in the same species group of *Boophis* have relatively similar morphologies. This is true for tadpoles described herein belonging to the *B. luteus* group (*B. andreonei*, *B. anjanaharibeensis*, *B. elenae* which all agree with other tadpoles in the same group), and in the *B. albipunctatus* group (*B. luciae* which largely agrees with *B. sibilans*). However, in the *B. microtympanum* group, the tadpoles of *B. rhodoscelis* are quite different from the more specialized tadpoles of *B. microtympanum*.

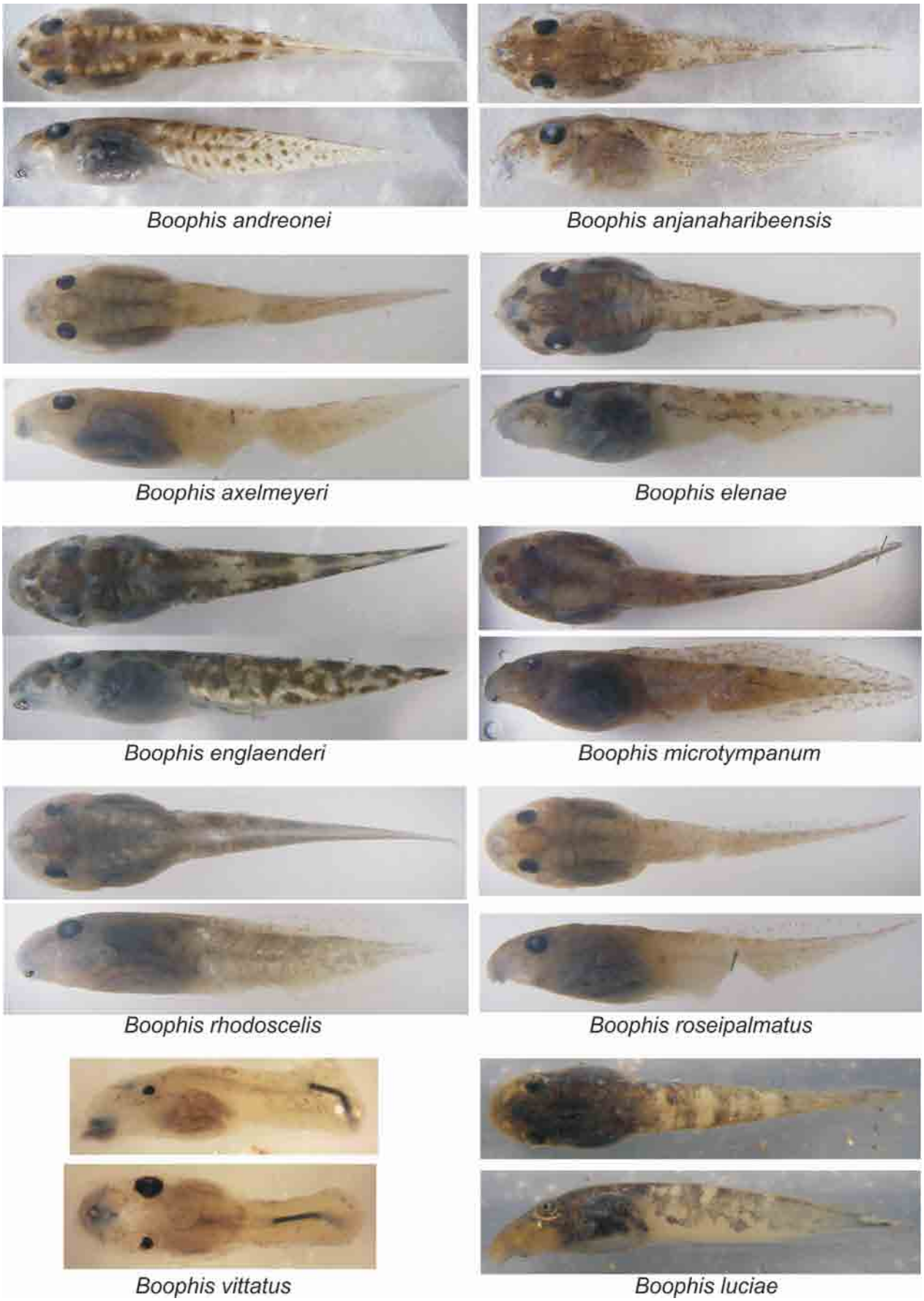

FIGURE 11. Photographs of preserved DNA voucher specimen tadpoles (as in Figs. 1–10) in lateral and dorsal views. Not to scale.

Two species for which larval morphological data are provided herein have been studied before in this respect: *Boophis microtympanum* by Blommers-Schlösser (1979b) and *B. andreonei* by Randrianiaina *et al.* (2009). For *B. microtympanum*, the previously published descriptions in general agree with our data but were not very detailed, so that the possibility of comparison is limited. For *B. andreonei*, the previous description refers to a tadpole in developmental stage 25 from the site Maromalo in Manongarivo Special Reserve (close to the type locality of the species, Benavony). In general, the tadpoles from Marojejy agree with those from Manongarivo (e.g., in LTRF, ventral position and non-emarginated shape of oral disk). Differences are found in the lower numbers of marginal and submarginal papillae in Manongarivo (65 vs. 99, and 14 vs. 24), and lower numbers of keratodonts in A_1 (108 vs. 143). This might be explained by the lower development stage of the Manongarivo specimen (25 vs. 37).

The tadpole of *Boophis luciae* can be compared with the previously described tadpole of *B. sibilans* (see Raharivololoniaina *et al.* 2006). Both descriptions refer to specimens in stage 25. These two tadpoles closely agree in most morphological characters such as LTRF, position and form of oral disk, body proportions, and number of keratodonts in A_1 . Differences are observed in the number of oral papillae (130 vs. 303) and keratodont density on A_1 (70/mm vs. 119/mm). These differences might partly be caused by different analysis methods (a digital measuring device and high-quality stereo microscope used only in the description of *B luciae* herein). However, it is unlikely that the difference in the number of papillae is only a counting error, and might indicate a stronger adaptation to strong currents in *B. luciae*, as the presence of high numbers of papillae is most common in tadpoles that attach to rocky surfaces in fast-moving streams (Altig & McDiarmid 1999).

TABLE 7. Comparison of morphological and ecological key characters of the tadpoles of ten species of *Boophis* as described herein. Ranges of ratios in this table are based on all DNA voucher specimens but not on additional specimens in the same series. LTRF, numbers of papillae and keratodonts are based only on the specimens used for description (see Table 1), LTRF variation on all other DNA voucher specimens.

Species	*B. andreonei*	*B. anjanaharibeensis*	*B. axelmeyeri*	*B. elenae*	*B. englaenderi*
Species group	*B. luteus*	*B. luteus*	*B. goudoti*	*B. luteus*	*B. luteus*
Breeding habitat	Stream	Stream	Stream	Stream	Stream
BL (mm)	4.30–15.8	8.9	10.6–14	11.7–15.5	6.8–12
TAL/BL (%)	154–261	142	149–174	125–161	144–161
BW/BH (%)	109–167	124	115–130	75–149	112–138
TMH/BH (%)	56–79	67	65–82	63–75	69–81
TMH/MTH (%)	66–142	81	67–124	107–133	106–118
TMW/BW (%)	29–58	65	51–52	36–75	50–61
MTH/BH (%)	55–113	82	97–112	63–75	69–88
ODW/BW (%)	40–55	55	37–40	36–67	52–73
OD orientation	Ventral	Ventral	Ventral	Ventral	Ventral
LTRF	6(5–6)/3(1)	5(4–5)/3(1)	4(3–4)/3(1)	3(2–3)/3(1)	6(4–6)/(3)
LTRF variations	3(2–3)/3(1) 4(3–4)/3(1) 5(4–5)/3(1)	5(4–5)/3(1)	4(3–4)/3(1) 5(4–5)/3(1)	2(1–2)/3(1) 3(2–3)/3(1)	6(5–6)/(3) 6(4–6)/(3) 7(5–7)/(3)
Number of keratodonts in A_1	143	108	132	78	236
Marginal papilae rows	Single	Single	Single	Single	Double
Marginal papillae	99	85	68	56	128
Submarginal papilae	24	19	16	18	33

continued.

Species	*B. microtympanum*	*B. rhodoscelis*	*B. vittatus*	*B. roseipalmatus*	*B. luciae*
Species group	*B. microtympanum*	*B. microtympanum*	*B. majori*	*B. goudoti*	*B. albipunctatus*
Breeding habitat	Brook	Brook	Brook	Brook	Brook
BL (mm)	8.5–23.8	15.3	4.9–6.8	10.5–13	6.7–12.3
TAL/BL (%)	128–204	141	130–173	153–219	124–270
BW/BH (%)	106–143	127	115–129	125–130	98–115
TMH/BH (%)	62–80	70	62–79	55–69	62–71
TMH/MTH (%)	67–129	59	92–110	69–120	83–120
TMW/BW (%)	35–64	51	53–65	37–50	53–71
MTH/BH (%)	64–127	118	75– 86	55–100	62–84
ODW/BW (%)	33–53	48	68–87	37–48	42–80
OD orientation	Ventral	Ventral	Ventral	Ventral	Ventral
LTRF	6(5–6)/3(1)	5(4–5)/3(1)	7(4–7)/(3)	6(5–6)/3(1)	7(3–7)/(3)
LTRF variations	4(3–4)/3(1) 5(4–5)/3(1) 6(5–6)/3(1)	5(4–5)/3(1)	7(5–7)/(3) 6(3–6)/(3) 7(3–7)/(3)	4(3–4)/3(1) 5(4–5)/3(1) 6(5–6)/3(1)	7(3–7)/(3)
Number of keratodonts in A_1	287	160	85	188	208
Marginal papilae rows	Single	Single	Single	Single	Single
Marginal papillae	70	105	113	72	230
Submarginal papilae	38	39	184	9	129

Tadpoles of *Boophis roseipalmatus* from Marojejy (described in this study) and its sister species, *B. madagascariensis* from Andasibe (tadpoles described by Rakotoarison *et al.* 2006), are similar in some characters: emargination and absence of ventral gap in oral disk, identical keratodont formulae, and similar numbers of keratodonts on A_1 (150 vs. 164). However, they appear to differ by some essential characters, such as a possibly slightly stronger caudal musculature (and reduced fins) (TMH/MTH ratio 69–120 vs. 100), ventral vs. antero-ventral orientation of the oral disk, and slightly lower numbers of oral papillae (81 vs. 95) in *B. roseipalmatus*. While one of the major differences (caudal fin) may be caused by a different state of preservation of the examined specimens, others could represent real differences between these species, although their general similarity in the tadpole stage is obvious.

Tadpoles of *Boophis elenae* from Ranomafana National Park (described in this study) and of *B. sandrae* from Andasibe (described by Rakotoarison *et al.* 2006 as candidate species *B.* sp. aff. *elenae*) have some common morphological features, such as a ventral orientation and lack of emargination of the oral disk and general body proportions. However, there seems to be a difference in the keratodont formula, with *B. elenae* having two (vs. three) interrupted anterior keratodont rows and a lower number of oral papillae (74 vs. 164) and keratodonts on A_1 (78 vs. 194). Although these differences may partly be influenced by different developmental stages (25 vs. 31) it is likely that they do represent real differences. In fact, despite their morphological similarity as adults (see Glaw & Vences 2007), *B. elenae* and *B. sandrae* are actually no sister species (Vieites *et al.* 2009), and *B. sandrae* is more closely related to *B. anjanaharibeensis* which by external morphology (coloration) can be distinguished rather easily in the adult stage (Glaw & Vences 2007).

However, in all of these comparisons, it needs to be taken into account that the detailed data on numbers of papillae and keratodonts have only been assessed for a single individual per species or population. Since these variables seem to be valuable to distinguish tadpoles, additional morphometric studies are needed to assess their variability and thereby their taxonomic value.

Acknowledgements

This study was carried out in the framework of a cooperation accord between the Département de Biologie Animale of the University of Antananarivo, Madagascar and the Technical University of Braunschweig. We are grateful to the staff of Madagascar National Parks in Marojejy, Ambohitantely, and Ranomafana, as well as of Valbio biological station in Ranomafana, for their help and support. Liliane Raharivololoniaina, Frank Glaw, and Tokihery Razafindrabe contributed to field work. Financial support was granted by the Volkswagen Foundation to HR, MV and RDR, by the Deutsche Forschungsgemeinschaft (grant VE247/2-1) to MV, JG and AS, and by the Deutscher Akademischer Austauschdienst to RDR.

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