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Molecular identification, description, and phylogenetic implications of the tadpoles of 11 species of Malagasy treefrogs, genus *Boophis*

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Abstract

Based on specimens identified by DNA barcoding, we describe the tadpoles of 11 species of treefrogs (*Boophis*) in the Malagasy family Mantellidae. All tadpoles belong to species of the stream-breeding clade within *Boophis*. Based on these and other published descriptions of *Boophis* tadpoles which develop in running water bodies, we tentatively distinguish three ecomorphological guilds for these larvae. Guild A, in which we describe the larvae of *B. boehmei*, *B. reticulatus*, *B. pyrrhus*, *B. tasymena*, and *B. viridis* which have few lotic adaptations, their oral disc width being 31–43% of body width, with a single row of 48–81 marginal papillae, and the first upper keratodont row having 58–144 keratodonts. Guild B, in which we describe the tadpoles of *B. albilabris*, *B. madagascariensis*, *B. luteus*, and of an undescribed species here named *B.* sp. aff. *elenae*, is intermediate, with an enlarged oral disc, an increasing number of keratodont rows and a lower height of the caudal fin. In these tadpoles, oral disc width is 43–63% of body width, they have one or two rows of 69–164 marginal papillae, and the first upper keratodont row has 164–238 keratodonts. Guild C contains tadpoles with a very large oral disc, living on submerged rocks and stones in stream sections of strong current. In this guild we describe the tadpoles of *B. marojezensis* and *B. sibilans*. Their oral disc width is 63–89% of body width, there are multiple rows of many marginal papillae, and the first upper keratodont row has many small keratodonts which are difficult to count, but consistently amount to over 200. In *B. marojezensis*, the dorsal gap in the marginal papillae rows, apparent in all other species, is closed. These larval morphologies show a rather good fit with recently published molecular phylogenetic data: species groups that were confirmed to be monophyletic in most cases have similar larval morphologies, and, in contrast, where species of the same group have disparate larval morphologies the monophyly of the group is questionable (e.g. the *B. majori* group). Nevertheless, some cases of convergent evolution are apparent, such as the highly specialized Guild C morphology, which may have evolved separately in the *B. albipunctatus group*, *B. mandraka* group, and in some species of the *B. majori* group.

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Introduction

Anuran amphibians are characterized by a unique type of larva, commonly named tadpole (Altig and McDiarmid 1999). Whereas adult frogs are carnivorous, most tadpoles are omnivorous and have a highly modified *bauplan*. Frogs in general are less variable in terms of morphology than in terms of reproductive biology. Many instances of partly or fully terrestrial reproduction are known, including direct development without a free-swimming larval stage, a mode that has evolved multiple times and mostly in tropical environments (Duellman and Trueb 1986). Aquatic tadpoles occur in a great variety of morphologies, and have adapted to a multitude of environments. Knowledge of the morphology and ecology of these larval stages is crucial to understand the ecological requirements of any particular frog species, an issue that becomes especially important in light of the delicate conservational status of amphibians as a whole (Stuart et al. 2004). Unfortunately, the identification of frog larvae is a complex task that involves either rearing of eggs obtained from a well-identified mating pair of frogs, or rearing of wild-collected tadpoles and tentative assignation of the metamorphosing juveniles to a species known to occur at the collecting locality. This latter method especially has caused a large number of misidentifications in the past and encounters major problems in megadiverse tropical anuran communities, because these often contain numerous sibling species which are hard to distinguish morphologically in their adult stage, and impossible to identify morphologically as juveniles.

The rainforests of Madagascar are known to harbour very species-rich amphibian communities (Blommers-Schlösser 1979a, 1979b; Blommers-Schlösser and Blanc 1991) which are characterized by numerous instances of sibling species (Glaw and Vences 2003). A group where morphologically similar but bioacoustically disparate sibling species are particularly common is the genus *Boophis*. These are treefrogs (Cadle 2003), part of the endemic mantellid radiation of Madagascar and the Comoros (Vences et al. 2003), and currently comprise more than 50 species (Glaw and Vences 2003; Vences and Glaw 2005). Many more species have been identified and are in the process of taxonomic description. Except for a few highland species, *Boophis* are strictly arboreal, and can be divided into two major clades which are characterized by either breeding in stagnant or running water (Vences et al. 2003). The stream-breeding clade is more speciose and represents a radiation mainly of the humid east of Madagascar (Vences et al. 2002). Tadpoles of 15 species of *Boophis* have been described by Blommers-Schlösser (1979b): *B. erythrodactylus*, *B. goudoti*, *B. granulosus*, *B. hillenii*, *B. idae*, *B. luteus*, *B. madagascariensis*, *B. majori*, *B. mandraka*, *B. microtympanum*, *B. rappiodes*, *B. tephraeomystax*, *B. williamsi*, and two species of uncertain identification, one assigned to the *B. luteus* group, a second one reported under the name *B. untersteini* which is presently a junior synonym of *B. goudoti*. A few additional larval morphologies have been reported since: *Boophis jaegeri* and *B. ankaratra* (Glaw and Vences 1992, 1994); *B. occidentalis* (Andreone et al. 2002); *B. laurenti* (Thomas et al. 2005); *B. rufioculis* (Grosjean et al. 2006). Most of the early tadpole identifications were made by assigning reared juveniles to species, and are therefore rather reliable at genus and species-group level, but require confirmation at species level. Although all *Boophis* tadpoles known so far have relatively generalized, exotrophic and benthic morphologies, conforming to the ranoid type (type IV of Orton 1953), some stream-breeding species have evolved obvious adaptations to the lotic environment, such as various degrees of enlargement of the oral disc, and an increase in the number of keratodont rows, of keratodonts and papillae

(Blommers-Schlösser 1979b). Such adaptations are known from various phenetic species groups of *Boophis*, such as the *B. rappiodes* group, *B. luteus* group, *B. albilabris* group, *B. mandraka* group, *B. majori* group, and *B. microtympanum* group, but since the monophyly of these species assemblages was uncertain until recently, the phylogenetic significance of these larval adaptations has not been analysed so far.

The advent of molecular techniques has led to an impressive acceleration of the understanding of phylogenetic relationships among organisms, among them mantellid frogs and the genus *Boophis* (e.g., Richards et al. 2000; Vences et al. 2002, 2003; Lehtinen and Nussbaum 2003; Lehtinen et al. 2004; Vences and Glaw 2005; Glaw and Vences 2006). In addition, DNA barcoding techniques allow a largely unequivocal and fast identification of larval stages, once a proper database for adults has been assembled (Hebert et al. 2003; Blaxter 2004), a method that has already been applied to some amphibians (Thomas et al. 2005; Vences et al. 2005). We here use this DNA barcoding approach to identify and describe the tadpoles of 11 species of *Boophis*, representing six species groups, and discuss their patterns of morphological evolution in relation to molecular phylogenies that have recently been published.

Material and methods

We collected tadpoles in the field from several streams in or near rainforest during the rainy season (December 2001 to January 2002), using a variety of large and small nets, adjusted to the specific conditions of each water body. General abiotic characteristics of the streams were recorded in as much detail as possible. Physico-chemical parameters of water bodies were assessed using portable devices in the field (temperature, depth, oxygen content, pH) or in the laboratory using standardized procedures. Tadpoles were euthanized by immersion in chlorobutanol solution, and, using a stereomicroscope, immediately in the field sorted into homogeneous series based on morphological characters. From each series one specimen was selected, and from this individual, a tissue sample from its tail musculature or fin was taken and preserved in 99% ethanol. This specimen is here named "DNA voucher". The drawings and morphological descriptions are based on this unequivocally identified specimen, whereas the additional tadpoles of a series are discussed under "Variation". In the tadpole drawings (Figures 1–11) the missing tissue pieces of the tail were completed by comparison with additional specimens of the series. After tissue collection, all specimens were preserved in 4% formalin. DNA vouchers have been deposited in the Zoologische Staatssammlung, Munich, Germany (ZSM). Further specimens of the series are so far uncatalogued and will be integrated in the collections of ZSM and of the Département de Biologie Animale, Université d'Antananarivo at a later stage; they are here reported with their field numbers of the first author (L.R.). Comparative specimens were examined from the herpetological collection of the Zoological Museum, Amsterdam, Netherlands (ZMA).

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 550 bp fragment was amplified using the primers 16Sa-L and 16Sb-H from Palumbi et al. (1991) and applying standard protocols, resolved on automated sequencers, and compared to a near-complete library 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 (except for *B.* sp. aff. *elenae*; see Discussion below), and not more similar to any

sequence from another species. DNA sequences were deposited in GenBank (accession numbers DQ792462–DQ792499; accession numbers of comparative adult specimens are included in the sequence sets AY847959–AY848683 and AJ315909–AJ315913).

All detailed tadpole descriptions in the following are based on one DNA voucher specimen, whereas variation is described based on further specimens of the same series, and DNA vouchers and specimens of additional series. Morphological terminology follows Altig and McDiarmid (1999); keratodont row formula (KRF) follows Dubois (1995) and developmental stages were determined according to Gosner (1960). Measurements were taken with a graduated ocular attached to a stereomicroscope. The landmarks are largely those shown in Altig and McDiarmid (1999, p 26, Figure 3.1); for others see Grosjean (2001). Drawings were made with the aid of a camera lucida.

The abbreviations used in the descriptions are the following: BH, maximum height of body; BL, body length; BW, maximum width of body; DG, maximum size of dorsal papilla gap; ED, maximum diameter of eye; MTH, maximum tail height; NN, internarial distance; NP, distance from centre of nares to anterior margin of eye; ODW, oral disc width; PP, interpupilar distance; RN, rostro-narial distance; SS, distance from tip of snout to opening of spiracle; TMH, tail muscle height; TMW, tail muscle width; TL, total length.

Results

Characteristics of study area and water bodies

Specimens analysed for this study came from four localities in central-eastern Madagascar, all close to Andasibe village: (1) a relatively fast-flowing stretch of Ranomena river next to Vohidrazana, within remnants of primary rainforest; (2) a small stream and dam next to the village Andasibe, within Analamazaotra Special Reserve; (3) a relatively slow-moving stretch of the Analamazaotra river around the bridge of the road leading to the village of Andasibe, at the border of Analamazaotra Special Reserve, surrounded by a mix of degraded vegetation, secondary forest and primary rainforest; (4) a stretch of Andranomanaponga river within Mantadia National Park, flowing through primary rainforest. A few additional specimens were collected from (5) a small stream at a place called Andranomena, located south-west of Moramanga. Water was clear and transparent at all sites except no. 3. The bottom was composed mainly of large granitic boulders and rocks at site no. 1, and of sand and debris at site nos 2–5. Geographic location and physico-chemical water parameters are summarized in Table I. In the following accounts, collecting localities 1–5 refer to the sites listed above and in Table I.

Species accounts

In the following accounts, we have grouped species according to phenetic species groups as recognized by Glaw and Vences (1994, 2006), in alphabetical order within groups and order of species groups according to their similarity and putative phylogenetic relationships.

***Boophis goudoti* group**

Boophis boehmei Glaw and Vences, 1992

(Figure 1)

The following description refers to one tadpole in developmental stage 25 (ZSM 534/2004, field number LR 145, TL 28.2 mm, BL 10.5 mm), from locality 2.

Table I. Study sites, their geographical coordinates, elevation, physico-chemical water parameters, and species and number of tadpole specimens recorded per site.

	(1) Vohidrazana	(2) Analamazaotra I	(3) Analamazaotra II	(4) Mantadia	(5) Andranomena
Water body	Ranomena river	Stream and small dam	Analamazaotra river	Andranomanaponga river	Stream
Geographical coordinates	18°57′58″S, 48°30′35″E	18°55′54″S, 48°25′44″E	18°56′50″S, 48°25′07″E	18°49′48″S, 48°25′56″E	19°01′30″S, 48°10′0″E
Elevation a.s.l. (m)	810	ca 900–1000	ca 900–1000	966	921
Temperature (°C) (surface)	18.0	17.0	18.5	17.9	17.7
Temperature (°C) (bottom)	15.1	16.9	15.1	15.1	17.0
Turbidity (NTU)	3.9	1.7	6.6	3.6	1.9
Water depth (cm)	20–100	15–30	20–120	15–100	20–35
pH	6.3	6.2	6.9	7	6.2
Dissolved O_2 ($mg\,l^{-1}$)	6.20	6.35	6.00	6.19	6.30
NO_2^- ($mg\,l^{-1}$)	0.16	0.02	0.00	0.02	0.02
NO_3^- ($mg\,l^{-1}$)	0.03	0.20	0.02	0.14	0.16
NH_4 ($mg\,l^{-1}$)	0.00	0.00	0.00	0.00	0.00
Conductivity ($mS\,cm^{-1}$)	0.11	0.20	0.24	0.13	0.19
Global mineralisation ($mg\,l^{-1}$)	0.05	0.11	0.13	0.07	0.10
Total hardness ($mmol\,l^{-1}$)	0.15	0.40	0.70	0.25	0.38
Carbonate hardness ($mmol\,l^{-1}$)	0.40	0.30	1.00	1.10	0.30
Boophis madagascariensis	–	–	–	–	6
B. marojezensis	9	–	–	–	–
B. reticulatus	2	–	–	–	–
B. tasymena	1	–	–	–	–
B. boehmei	–	7	–	–	–
B. sp. aff. *elenae*	–	–	6	–	–
B. luteus	8	2	21	2	1
B. viridis	–	–	26	–	–
B. pyrrhus	–	–	11	–	
B. albilabris	–	–	2	–	–
B. sibilans	–	1	–	7	–
Total no. of species	4	3	5	2	2

In dorsal view (Figure 1a), body ovoid elongate, snout rounded. In lateral view (Figure 1b), body depressed, BW 111% of BH, snout rounded. Eyes of moderate size, ED 11.4% of BL, slightly bulging, not visible in ventral view, positioned and directed dorsolaterally, situated at about the anterior third of the body. Pineal ocellus present between eyes. Nares elliptical, moderately sized, rimmed, positioned dorsolaterally, directed anterodorsolaterally and equidistant from tip of snout to anterior edge of eyes, RN 100% of NP; NN 62% of PP. Spiracle sinistral, a short tube free at opening, well visible from dorsal view; spiracular opening oval, directed posteriorly, situated at the height of the longitudinal axis of caudal musculature and closer to end of body than to snout, SS 68% of BL. Vent tube short, dextral and opening at ventral edge of fin, its right wall displaced anterodorsally. Caudal musculature moderately developed, TMH 45% of BH and 68% of

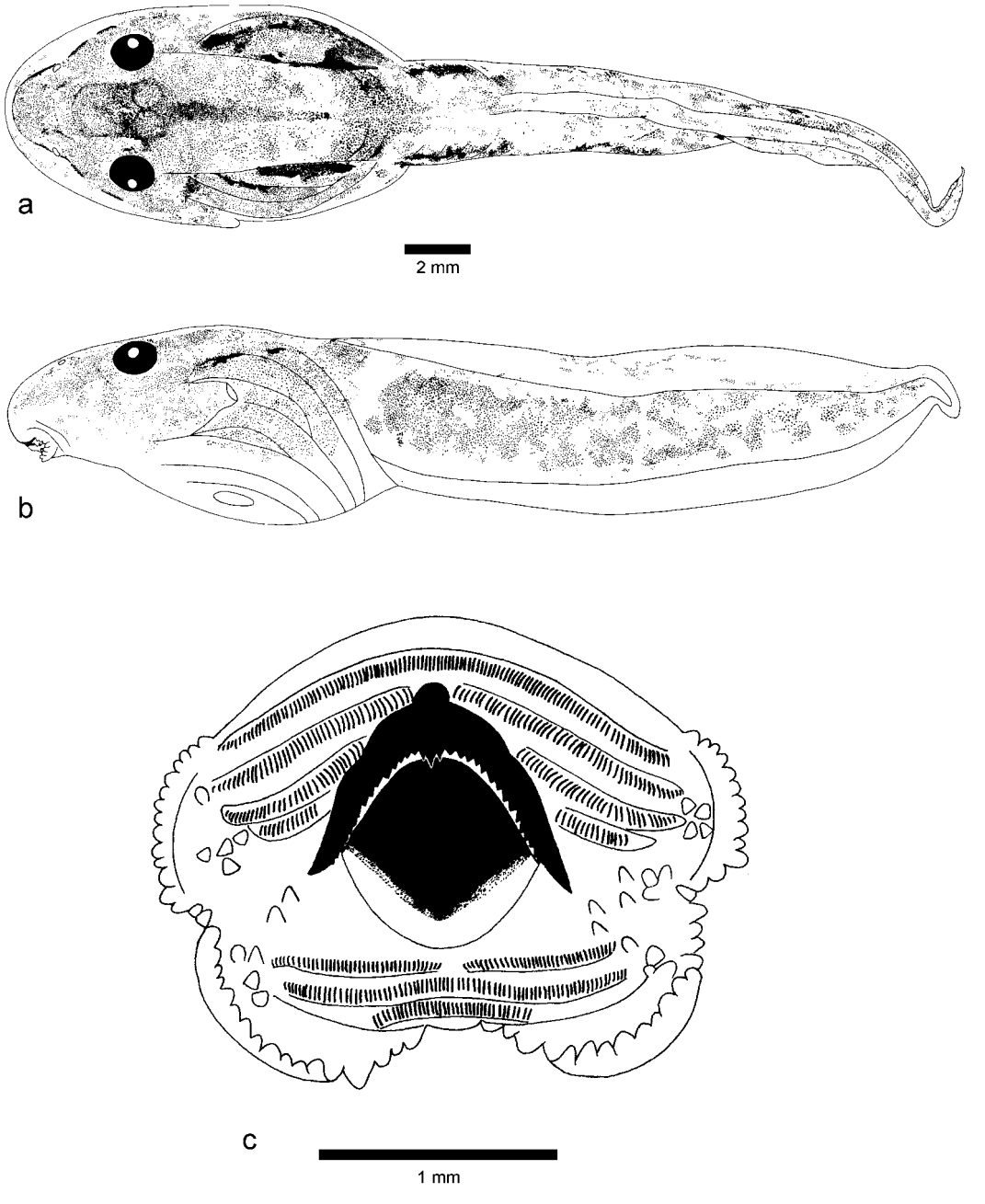

Figure 1. Drawings of the tadpole of *Boophis boehmei* (ZSM 534/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

MTH, TMW 47% of BW; its height three-fifths of total height at mid-length of tail. Caudal fins shallow anteriorly and deepest at about midway of tail, height of caudal fins decreasing progressively towards the nearly pointed tail tip, MTH 66% BH; dorsal fin beginning next to the dorsal tail–body junction.

Oral disc (Figure 1c) of moderate size, ODW 24% of BL and 40% of BW, positioned and directed ventrally, emarginate. A single row of marginal papillae interrupted by a large medial gap on the upper labium (DG 94% of ODW) and by a small medial gap on the lower labium; total number of marginal papillae about 64 (33 on the left side, 31 on the right side). A few submarginal papillae positioned on the lateral parts of the anterior and posterior labia. Papillae of moderate size, round or conical with rounded tip. No denticulate papillae. Keratodont row formula 1:3+3/1+1:2. The density of keratodonts on A1 is about 50 per mm (a total of ca 110). The length of interrupted anterior keratodont rows (A2, A3, and A4) decreases gradually towards the centre of the disc, length of P3 about one-third of P2. Both jaw sheaths coarsely serrated; upper jaw completely black with a large medial serration surrounded by smaller serrations on each side forming a slight convexity; lower jaw partially pigmented, V-shaped.

Coloration in preservative. Dorsally: body and tail musculature brownish, covered by scattered black spots. Some concentrated pigmentation forming dark patch between eyes. Laterally: intestinal coils well visible; caudal musculature mottled, dorsal fin slightly pigmented; ventral fin clear. Ventrally: the whole surface of ventral body transparent, branchial and cardial region translucent, easily visible through ventral surface.

Variation. TL and BL of seven tadpoles at stages 25–31, all from locality 2 (ZSM 533/2004–537/2004 and LR 147, LR 165) are 21.5–35.5 and 9.3–14.2 mm, respectively. The ratios vary in the following proportions: BW 102–122% of BH; ED 10.2–13.5% of BL; RN 94–115% of NP; NN 56–66% of PP; SS 58–71% of BL; TMH 45–63% of BH; TMH 58–86% of MTH; TMW 43–58% of BW; MTH 69–92% of BH; ODW 19–25% of BL; ODW 38–47% of BW. KRF of the seven tadpoles is 1:3+3/1+1:2.

Boophis reticulatus Blommers-Schlösser, 1979
(Figure 2)

The following description refers to one voucher specimen in developmental stage 41 (ZSM 525/2004, field number LR 68, TL 42.5 mm, BL 14.0 mm), from locality 1.

In dorsal view (Figure 2a), body ovoid elongate, snout rounded. In lateral view (Figure 2b), body depressed, BW 131% of BH, snout rounded. Eyes moderately large, ED 14.0% of BL, bulging, not visible in ventral view, positioned dorsolaterally but directed slightly more laterally than anterolaterally or dorsolaterally, situated at about the anterior quarter of the body. Nares elliptical, rimmed with a mediodorsal projection giving them a bean shape, moderately small, positioned dorsolaterally, directed anterodorsally and about equidistant between tip of snout and anterior edge of eyes, RN 106% of NP; NN 53% of PP. Spiracle sinistral, moderately sized, tubular, well visible from dorsal view, distal half free from body, spiracular opening orientated posterodorsally, closer to end of body than to snout, SS 65% of BL, situated at the height of the lower part of tail musculature. Vent tube moderately sized, short, dextral, opening dextral at ventral edge of fin, its right wall displaced anterodorsally, directed posterolaterally, linked to ventral tail fin except its tip. Tail long and tapered. Caudal musculature strong, TMH 64% of BH and 87% of MTH, TMW 46% of BW, at mid-length of tail its height is equal to half of total tail height, reaching tail tip. Caudal fins regular with straight edges, moderately weakly developed, their general appearance almost similar throughout tail musculature, point of maximum height attained in the second half of the tail, MTH 74% of

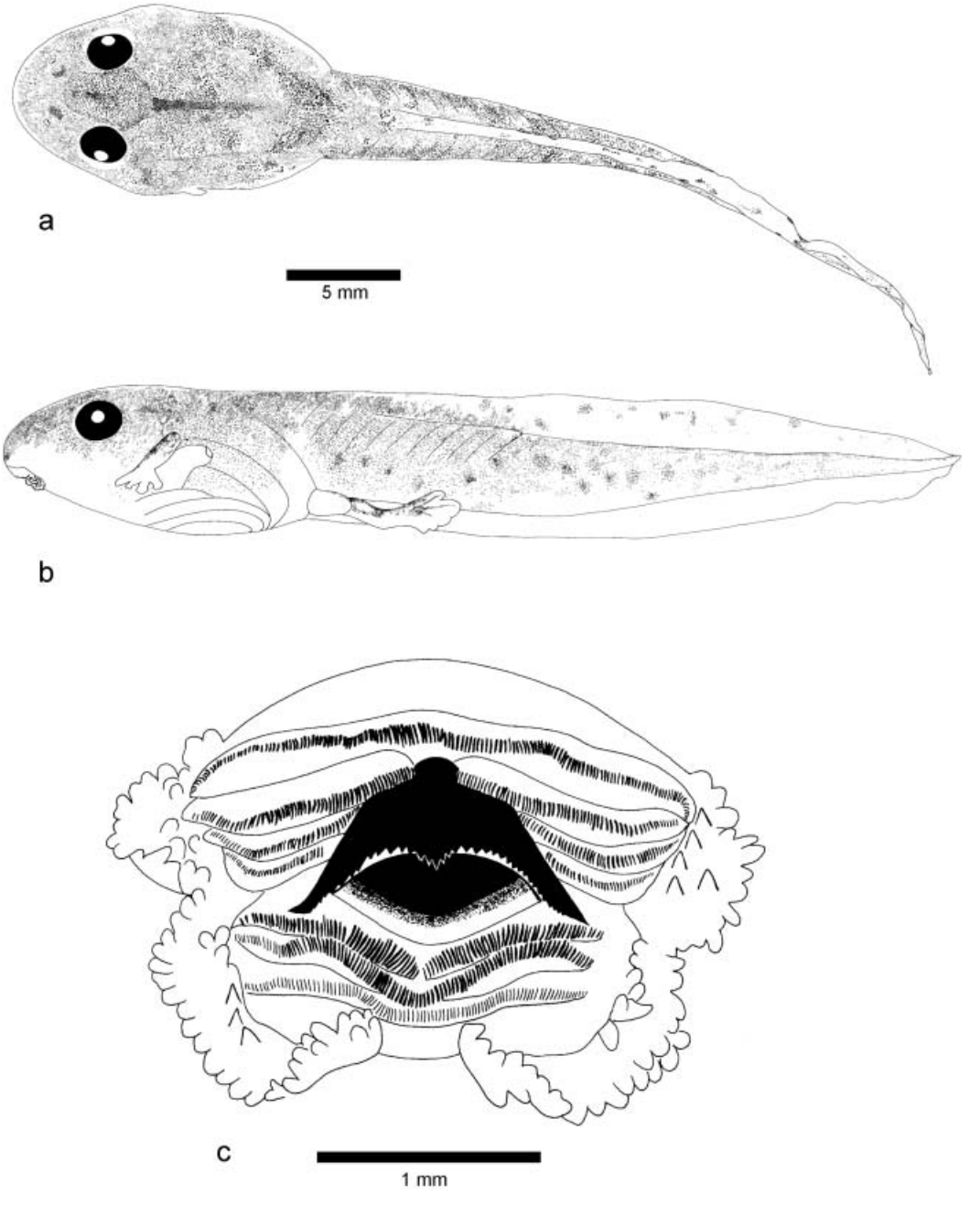

Figure 2. Drawings of the tadpole of *Boophis reticulatus* (ZSM 525/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

BH; dorsal fin originating at the dorsal tail–body junction and slightly taller than ventral fin at mid-length of tail; tail tip bluntly pointed, its state as reproduced in Figure 2 (caudal fins not reaching tail tip) probably being an artefact of preservation or damage during transport.

Oral disc (Figure 2c) of moderate size, ODW 21% of BL and 38% of BW, positioned and directed ventrally, emarginated. A single row of marginal papillae interrupted by a large median gap on the upper labium (DG 73% of ODW) and by a small medial gap on the lower labium; total number of marginal papillae about 81 (43 on the left side and 38 on the right side). A few submarginal papillae positioned in the lateral parts of anterior and posterior labia. Papillae moderately large, cylindrical with rounded or pointed tips. No denticulate papillae. Keratodont row formula 1:3+3/1+1:2. The density of keratodonts on A1 is about 55 per mm (a total of ca 144). The length of interrupted anterior keratodont rows (A2, A3, and A4) decreases gradually towards the centre of the disc, P1 and P2 are of about similar size, slightly longer than P3. Both jaw sheaths coarsely serrated; upper jaw completely black with a large medial serration surrounded by smaller serrations on each side forming a slight convexity; lower jaw partially pigmented, strong and V-shaped.

Coloration in preservative. Dorsally: whole body and caudal musculature dark brown and covered by scattered black dots; dark pigments concentrated dorsally forming dark patches slightly visible on the interorbital area and beside the nares; a dark line slightly visible mid-dorsally on body. Laterally: intestinal coils well visible; body and caudal musculature with scattered dark pigmentation; dorsal fin transparent with a few sparse black dots; ventral fin clear. Ventrally: branchial and cardial region opaque through ventral body wall; intestinal coils well visible.

Variation. TL and BL of two tadpoles at stage 41 (ZSM 525/2004–526/2004) from locality 1 are 36.5–42.5 and 13.0–14.0 mm, respectively. The ratios vary in the following proportions: BW 124–131% of BH; ED 13.1–13.6% of BL; RN 106–121% of NP; NN 53–57% of PP; SS 63–65% of BL; TMH 64–65% of BH; TMH 64–71% of MTH; TMW 46–51% of BW; MTH 90–102% of BH; ODW 20–21% of BL; ODW 38–39% of BW. KRF of the two tadpoles is 1:3+3/1+1:2.

Boophis madagascariensis (Peters, 1874)
(Figure 3)

The following description is based on one tadpole in developmental stage 35 (ZSM 519/2004, field number LR 5, TL 34.7 mm, BL 13.7 mm), from locality 5.

In dorsal view (Figure 3a), body ovoid elongate, snout rounded. In lateral view (Figure 3b), body depressed, BW 117% of BH, snout rounded. Eyes of moderate size, ED 11.0% of BL, very slightly bulging, not visible in ventral view, positioned dorsolaterally but directed almost laterally, situated at about the anterior third of the body. Pineal ocellus in line with the anterior margin of eyes. Nares moderately sized, elliptical, rimmed with a flat mediodorsal projection giving them a bean shape, positioned dorsolaterally, directed anterolaterally and slightly dorsally, nearer to anterior edge of eyes than to snout, RN 109% of NP; NN 55% of PP. Spiracle sinistral, moderately sized, well visible from dorsal view, oval, its tip free from body; spiracular opening orientated posteriorly, closer to end of body than to snout, SS 66% of BL, situated at the height of the lower part of tail musculature. Vent tube moderately sized, short, dextral, opening dextral at ventral edge of fin, its right wall displaced anterodorsally, directed posteriorly. Caudal musculature moderately strong, TMH 54% of BH and 58% of MTH, TMW 49% of BW, at mid-length of tail its height is two-fifths of the total tail height, reaching tail tip. Caudal fins regular with straight edges, MTH 93% of BH; dorsal fin low, originating on tail muscle and wider than ventral fin; tail tip pointed.

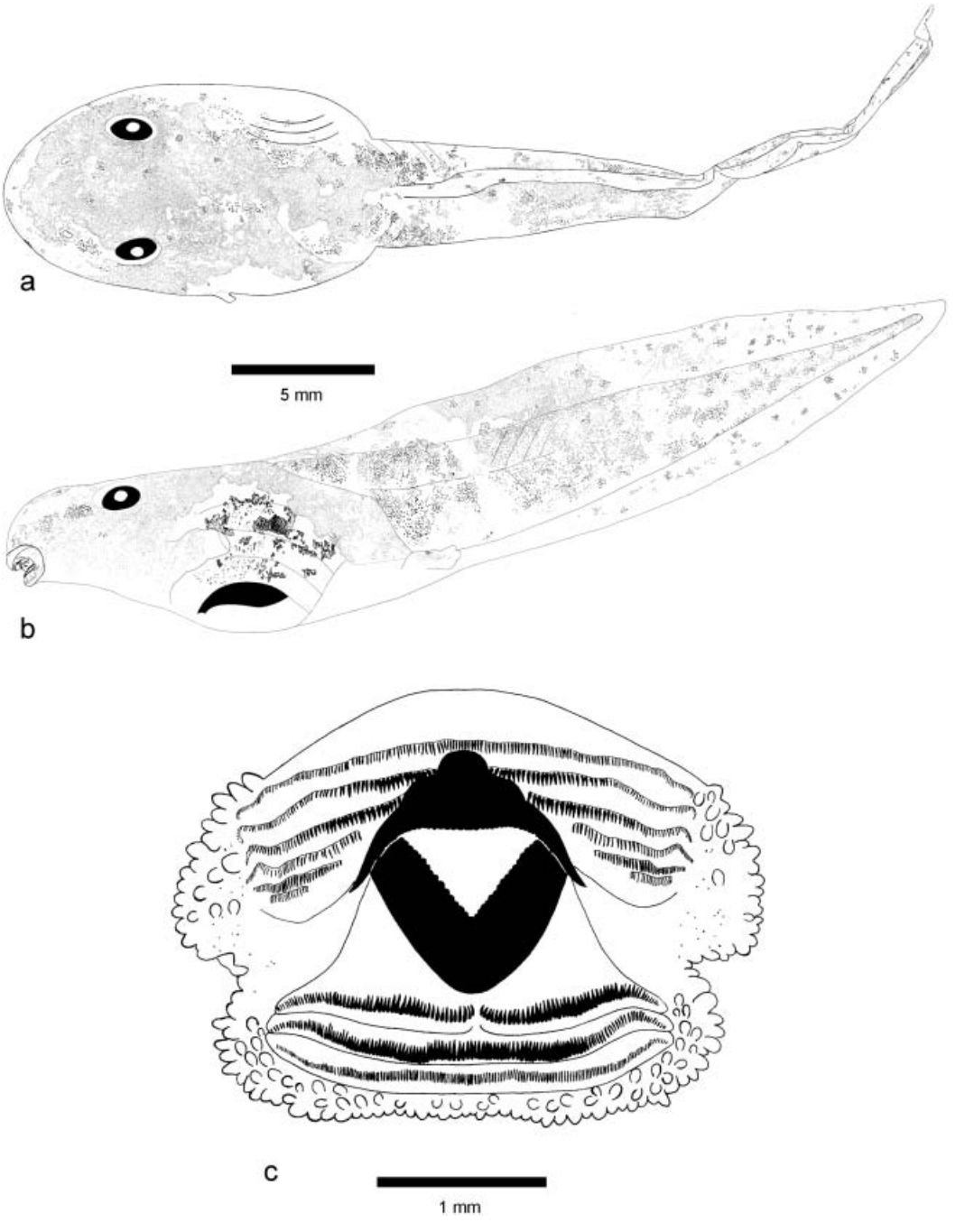

Figure 3. Drawings of the tadpole of *Boophis madagascariensis* (ZSM 519/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

Oral disc (Figure 3c) of moderate size, ODW 26% of BL and 43% of BW, positioned and directed anteroventrally, emarginated. A single row of marginal papillae interrupted by a large median gap on the upper labium (DG 81% of ODW) and without visible gap on the

lower labium; total number of marginal papillae about 95. Submarginal papillae present, some of them clustered at the corners of the disc but most localized on posterior labium and distributed in two rows. Papillae of moderate size, elongate with rounded tip. No denticulate papillae. Keratodont row formula 1:5+5/1+1:2. The density of keratodonts on A1 is about 60 per mm (a total of 164). The length of interrupted anterior keratodont rows (A2–A6) decreases gradually towards the centre of disc, P1 interrupted by a gap of less than 0.1 mm, keratodont rows of lower labium subequal in size. Both jaw sheaths completely dark pigmented; upper jaw a wide flattened, medially convex arch, finely serrated; lower jaw V-shaped, moderately finely serrated.

Coloration in preservative. Dorsally: body grey with sparse dark markings, caudal musculature with scattered dark pigmentation. Laterally: intestinal coils visible; fins translucent with sparse black dots. Ventrally: branchial and cardial region not visible through ventral body wall; intestinal coils obscure.

Variation. TL and BL of six tadpoles at stages 28–37, all from locality 5 (ZSM 517–520, and LR 4, LR 17) are 24.5–35.6 and 10.8–15.6 mm, respectively. The ratios vary in the following proportions: BW 117–157% of BH; ED 10.0–12.2% of BL; RN 109–207% of NP; NN 54–63% of PP; SS 61–69% of BL; TMH 54–71% of BH; TMH 58–84% of MTH; TMW 43–58% of BW; MTH 67–93% of BH; ODW 26–29% of BL; ODW 42–57% of BW. KRF of the six tadpoles varies from 1:4+4/1+1:2 to 1:5+5/1+1:2.

***Boophis albilabris* group**

Boophis albilabris (Boulenger, 1888)

(Figure 4)

The following description refers to one voucher specimen in developmental stage 33 (ZSM 588/2004, field number LR 236, TL 44.3 mm, BL 16.1 mm), from locality 3.

In dorsal view (Figure 4a), body elliptical, snout rounded. In lateral view (Figure 4b), body depressed, BW 116% of BH, snout rounded. Eyes moderately large, ED 13.0% of BL, bulging, not visible in ventral view, positioned dorsolaterally but directed anterolaterally and dorsolaterally, situated at about the anterior quarter of the body. Pineal ocellus placed anteriorly to margin of eyes. Nares round, moderately sized, rimmed, positioned dorsolaterally, directed anterolaterally and opening dorsolaterally, positioned nearer to tip of snout than to anterior edge of eyes, RN 86% of NP; NN 44% of PP. Spiracle sinistral, moderately small, slightly conical, slightly visible from dorsal view, free at tip, orientated posterodorsally; spiracular opening oval, situated closer to end of body than to tip of snout, SS 58% of BL, situated below the longitudinal axis of tail musculature. Vent tube short, dextral, opening dextral, its right wall displaced anterodorsally, directed posterolaterally, entirely linked to ventral tail fin. Caudal musculature moderately strong, TMH 55% of BH and 62% of MTH, TMW 51% of BW, at mid-length of tail its height about two-fifths of the total tail height, reaching tail tip. Caudal fins moderately developed, point of maximum height attained at the proximal third of the tail, MTH 89% of BH; dorsal fin convex, originating at the dorsal tail–body junction and taller than ventral fin at mid-length of tail, ventral fin originating immediately behind body; tail tip pointed.

Oral disc (Figure 4c) moderately large, ODW 25% of BL and 47% of BW, positioned and directed ventrally, emarginated. Oral disc surrounded by a single row of 69 (34 on the left side and 35 on the right side) marginal papillae interrupted by a large median

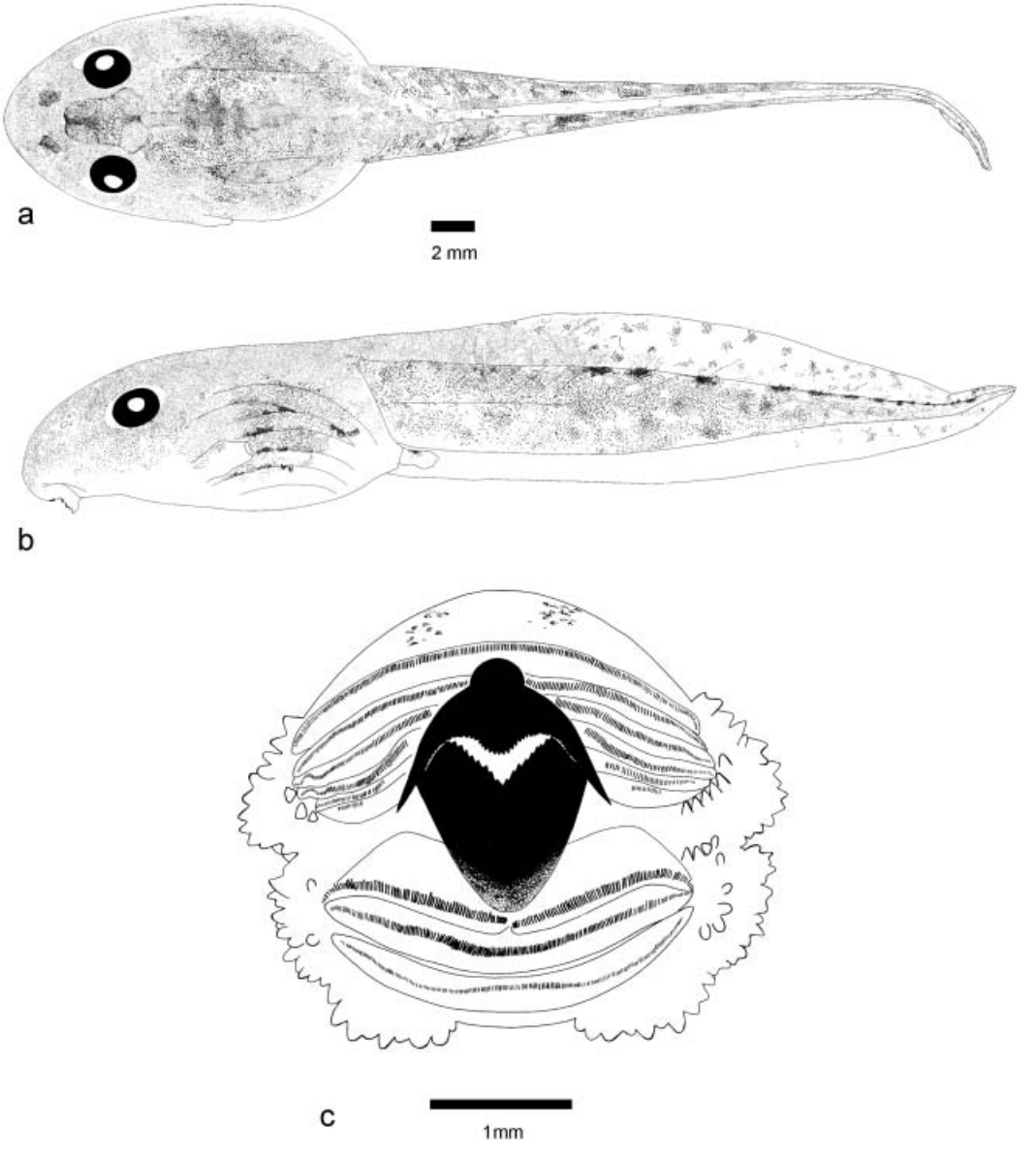

Figure 4. Drawings of the tadpole of *Boophis albilabris* (ZSM 588/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

gap on the upper labium (DG 71% of ODW), and by a small medial gap on the lower labium. A few submarginal papillae positioned on the lateral parts of the upper labium, and lateral and posterolateral parts of the lower labium. Papillae of moderate size, cylindrical with a rounded tip. No denticulate papillae. Keratodont row formula 1:5+5/1+1:2. Gap on P1 shorter than 0.1 mm; about 188 keratodonts on A1, the longest keratodont row of the oral disc (ca 61 per mm); P1 and P2 of about similar size, slightly longer than P3. Upper jaw completely black, moderately serrated, a large arch with a large median

convexity; lower jaw V-shaped, coarsely serrated, mostly coloured in black but its base less pigmented.

Coloration in preservative. Dorsally: body and tail musculature mottled with black stippling; dark pigmentation concentrated dorsally forming dark patches between eyes and next to nares. Laterally: intestinal coils well distinct; dorsal fin with scattered black dots; ventral fin generally clear except near tail tip; at about mid-tail many small dark patches visible along the upper tail musculature. Ventrally: whole surface of ventral body transparent; branchial and cardial organs translucent but slightly visible through ventral body wall.

Variation. TL and BL of two tadpoles at stages 33 and 41, from locality 3 (ZSM 588/2004–589/2004) are 43.5–44.3 and 15.5–16.1 mm, respectively. The ratios are: BW 116–140% of BH; ED 13.0–14.8% of BL; RN 86–113% of NP; NN 44–49% of PP; SS 58–70% of BL; TMH 55–70% of BH; TMH 62–63% of MTH; MTH 89–112% of BH; ODW 24–25% of BL; ODW 44–47% of BW. KRF of the two tadpoles varies from 1:4+4/1+1:2 to 1:5+5/1+1:2.

***Boophis majori* group**

Boophis pyrrhus Glaw, Vences, Andreone and Vallan, 2001

(Figure 5)

The following description refers to one specimen in developmental stage 31 (ZSM 580/2004, field number LR 231a, TL 41.3 mm, BL 15.0 mm), from locality 3.

In dorsal view (Figure 5a), body ovoid elongate, snout rounded. In lateral view (Figure 5b), body depressed, BW 117% of BH, snout rounded. Eyes of moderate size, ED 11.3% of BL, bulging, not visible in ventral view, positioned anterolaterally but directed anterolaterally and dorsolaterally. Nares round, moderately small, rimmed, positioned dorsally, directed anterolaterally, nearer to anterior edge of eyes than to tip of snout, RN 123% of NP; NN 40% of PP. Spiracle sinistral, moderately small, square, well visible from dorsal view, free at tip, orientated almost posteriorly; spiracular opening oval, situated closer to end of body than to tip of snout, SS 64% of BL, situated at the height of the longitudinal axis of tail musculature. Vent tube short, dextral, opening dextral, its right wall displaced anterodorsally, directed posterolateroventrally. Caudal musculature moderately developed, TMH 50% of BH and 60% of MTH, TMW 40% of BW, at mid-length of tail its height about two-fifths of the total tail height. Caudal fins moderately weakly developed, MTH 83% of BH; dorsal fin originating at the dorsal tail–body junction, ventral fin originating immediately behind body; tail tip nearly rounded.

Oral disc (Figure 5c) of moderate size, ODW 20% of BL and 37% of BW, positioned and directed ventrally, emarginated. A single row of marginal papillae interrupted by a large median gap on the upper labium (DG 53% of ODW), and by a very small medial gap on the lower labium. A few submarginal papillae positioned in the lateral parts of the upper and lower labia. Papillae stout, of moderate size, conical with a rounded tip. No denticulate papillae. Keratodont row formula 1:3+3/1+1:2. About 92 keratodonts on A1 (ca 54 per mm). P1 interrupted by a gap of less than 0.1 mm and slightly longer than P2; P3 about two-thirds of P2. Upper jaw completely black, a large arch with a slight median convexity, moderately coarsely serrated; lower jaw strong, V-shaped, coarsely serrated.

Coloration in preservative. Dorsally: the whole dorsum body and the caudal musculature with dark scattered pigmentation. Laterally: intestinal coils completely visible; lateral body

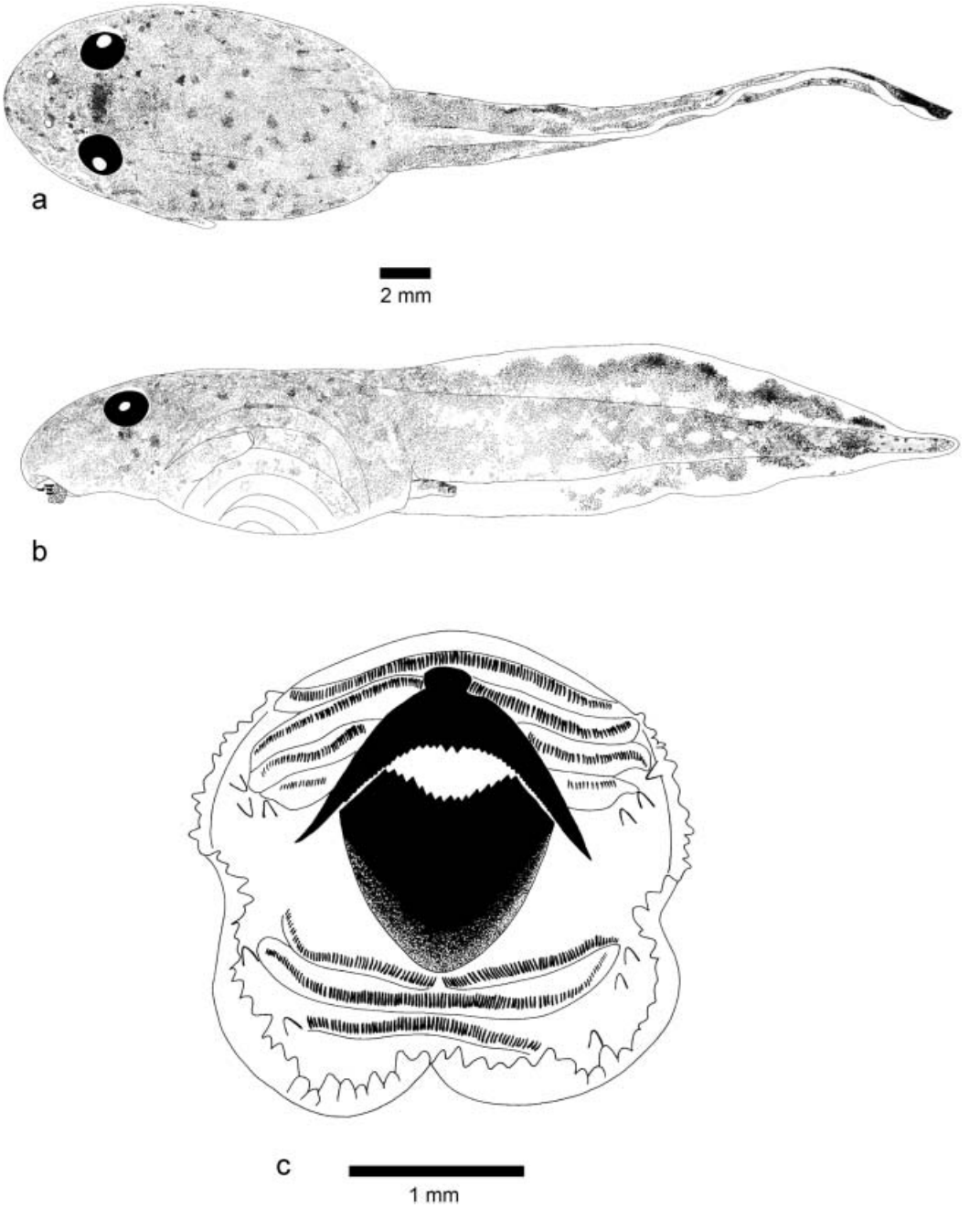

Figure 5. Drawings of the tadpole of *Boophis pyrrhus* (ZSM 580/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

and caudal musculature covered with sparse black dots; caudal fins moderately pigmented. Ventrally: the whole surface of ventral body transparent; branchial and cardial region visible through ventral body wall.

Variation. TL and BL of 11 tadpoles at stages 31–41 (ZSM 580/2004–587/2004, and LR 231c, LR 231d, LR 231i), all from locality 3, are 30.3–43.4 and 13.1–16.2 mm, respectively. The ratios vary in the following proportions: BW 111–133% of BH; ED 10.7–12.6% of BL; RN 113–155% of NP; NN 40–47% of PP; SS 59–67% of BL; TMH 50–59% of BH; TMH 46–58% of MTH; TMW 35–44% of BW; MTH 89–109% of BH; ODW 17–21% of BL; ODW 29–37% of BW. KRF of the 11 tadpoles is 1:3+3/1+1:2.

Boophis marojezensis Glaw and Vences, 1994
(Figure 6)

The following description is based on one tadpole in developmental stage 41 (ZSM 523/2004, field number LR 66, TL 26.5 mm, BL 10.0 mm), from locality 1. Hindlimbs of this specimen were largely used for tissue sampling and are therefore not shown in Figure 6.

In dorsal view (Figure 6a), body ovoid elongate, snout rounded. In lateral view (Figure 6b), body greatly depressed, BW 145% of BH, snout almost truncate. Eyes large, ED 16.0% of BL, slightly bulging, not visible in ventral view, positioned dorsolaterally but directed almost laterally, situated at about the anterior third of the body. Nares moderately small, round, rimmed with a very small and flat mediodorsal projection, positioned dorsally, directed anterolaterally and dorsally, much closer to anterior edge of eyes than to snout, RN 169% of NP; NN 44% of PP. Spiracle sinistral, narrow and long, slightly visible from dorsal view, its tip free from body; spiracular opening orientated posterodorsally, much closer to end of body than to snout, SS 76% of BL, situated at the height of the lower part of tail musculature. Vent tube small, short, medial, opening just before the beginning of ventral fin, opening medial, directed more posteriorly than posteroventrally, linked to caudal muscle. Caudal musculature strong, TMH 66% of BH and 59% of MTH, TMW 48% of BW, especially in the anterior half of the tail; height of caudal musculature almost half of total tail height at mid-length of tail, almost reaching tail tip. Caudal fins regular with straight edges, very shallow, MTH 111% of BH; dorsal fin originating next to body–tail junction, convex in its medial part; ventral fin beginning at the level of the ventral terminal of the body, following the caudal muscle; tail tip fine.

Oral disc (Figure 6c) enlarged, ODW 41% of BL and 63% of BW, positioned and directed ventrally, not emarginated. Several uninterrupted rows of marginal papillae around oral disc; no medial gaps in rows of marginal papillae on upper or lower labium. Papillae of internal row round and of moderate size, papillae of external rows small, elongate, and cylindrical. No denticulate papillae. Keratodont row formula 4:3+3/3. About 203 keratodonts on A3 (32–33 per mm). The length of interrupted anterior keratodont rows (A5, A6, and A7) decreases gradually towards the centre of the disc, keratodont rows of lower labium subequal in length. Upper jaw not serrated and weakly developed, median part straight, a black halo on its distal part; lower jaw more developed, narrow V-shaped, ribbed, composed of two parts connected by a less keratinized median area, coarsely serrated.

Coloration in preservative. Dorsally: part anterior to eyes covered with sparse black dots; dark pigmentations concentrated dorsally forming dark patches between eyes and beside nares; black colour on either side of lateral body obscuring intestine area; caudal musculature with scattered dark pigmentation. Laterally: intestinal coils invisible; caudal

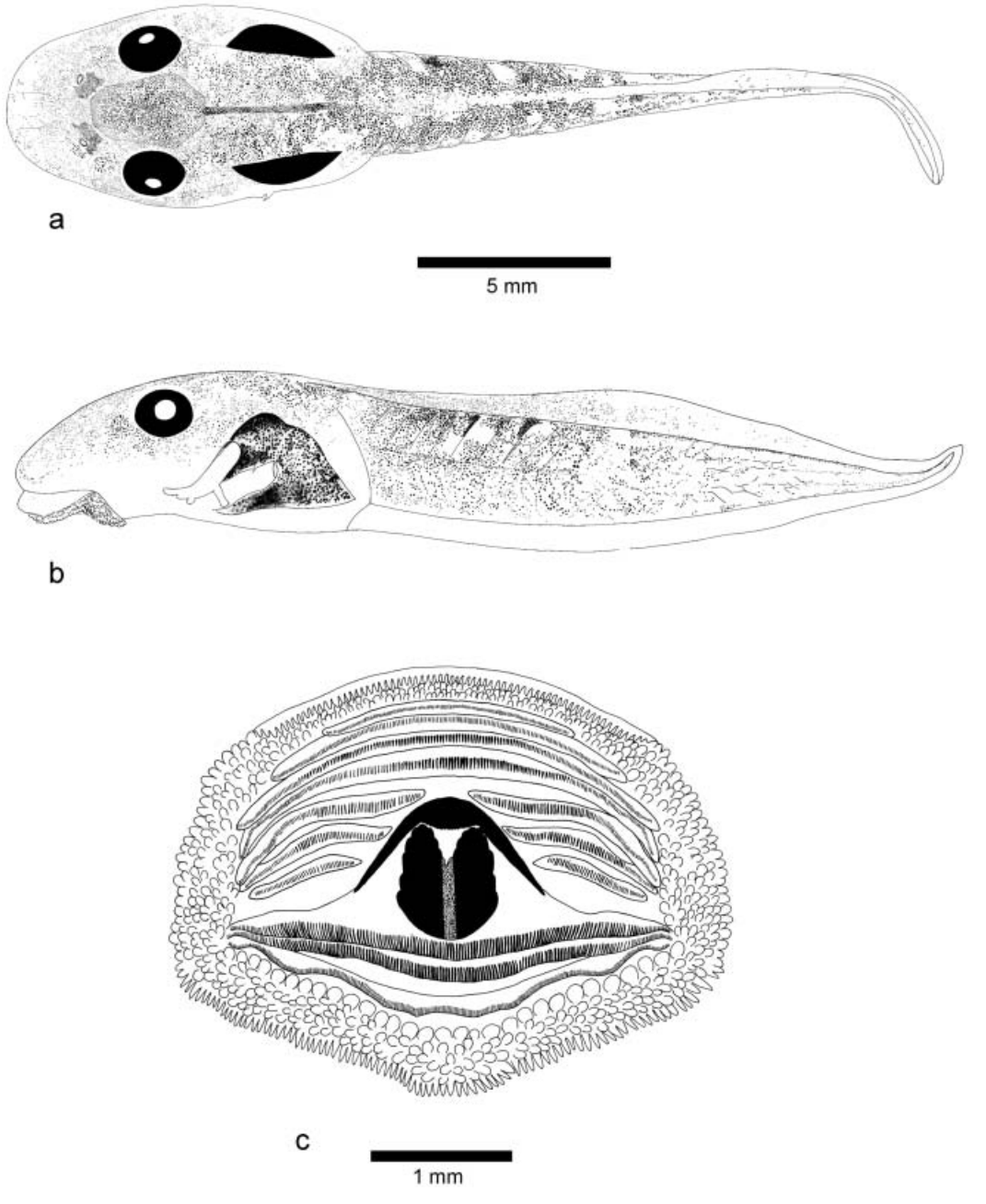

Figure 6. Drawings of the tadpole of *Boophis marojezensis* (ZSM 523/2004). (a) Dorsal view; (b) lateral view, note that the hindlimb has been removed from the specimen for better visibility of structures; (c) oral disc.

musculature with sparse black spots, showing some reticulations at its posterior end; dorsal fin with small black spots, ventral fin clear. Ventrally: branchial and cardial region translucent, well visible through ventral body wall; intestinal coils invisible.

Variation. TL and BL of nine tadpoles at stages 29–41 (ZSM 521/2004–524/2004, and LR 61, LR 62, LR 64, LR 65, LR 67), all from locality 1, are 22.1–27.2 and 8.1–10.7 mm, respectively. The ratios vary in the following proportions: BW 118–145% of BH; ED 14.9–16.8% of BL; RN 143–196% of NP; NN 42–49% of PP; SS 70–81% of BL; TMH 65–76% of BH; TMH 59–84% of MTH; TMW 48–67% of BW; MTH 86–111% of BH; ODW 36–47% of BL; ODW 63–86% of BW. KRF of the nine tadpoles is 4:3+3/3.

***Boophis albipunctatus* group**

Boophis sibilans Glaw and Thiesmeier, 1993

(Figure 7)

The following description is based on one tadpole in developmental stage 25 (ZSM 557/2004, field number LR 269, TL 25.2 mm, BL 9.0 mm), from locality 4.

In dorsal view (Figure 7a), body elliptical, snout rounded. In lateral view (Figure 7b), body depressed, BW 129% of BH, snout rounded. Eyes moderately large, ED 12.2% of BL, bulging, not visible in ventral view, positioned more dorsally than dorsolaterally but directed dorsolaterally, situated at about the anterior third of the body. Nares moderately sized, elliptical, rimmed with a flat mediodorsal projection, positioned dorsally, directed anterolaterally and opening almost dorsally, much closer to anterior edge of eyes than to snout, RN 148% of NP; NN 50% of PP. Spiracle sinistral, narrow and long, slightly visible from dorsal view, its tip free from body; spiracular opening orientated almost posteriorly, much closer to end of body than to snout, SS 72% of BL, situated below the lower part of tail musculature. Vent tube small, medial, directed posteriorly, linked to caudal muscle, opening posterolateral. Caudal musculature strong, TMH 77% of BH and 75% of MTH, TMW 59% of BW, at mid-length of tail height of caudal musculature almost half of total tail height, parallel in its proximal third then gradually tapering, almost reaching tail tip. Caudal fins moderately shallow, MTH 103% of BH; dorsal fin originating next to body–tail junction, shallow in its anterior part then becoming convex towards mid-tail, ventral fin beginning just behind body and reaching its maximum height more posteriorly than dorsal fin; tail tip rounded.

Oral disc (Figure 7c) enlarged, ODW 44% of BL and 89% of BW, positioned and directed ventrally, not emarginated. Several rows of marginal papillae around oral disc, interrupted by a large median gap on the upper labium (DG 53% of ODW); no gap on lower labium. Papillae small, conical with a more or less pointed tip. No denticulate papillae. Keratodont row formula 4:3+3/3. Keratodonts on continuous rows A1, A2, and A3 very small and difficult to count; estimation of keratodonts done on A4 with a total of about 208 (ca 70 per mm). The length of interrupted upper keratodont rows (A5, A6, and A7) decreases gradually towards the centre of the disc, keratodont rows of lower labium subequal in length. Upper jaw not serrated and weakly developed, black, median part straight; lower jaw more developed, V-shaped, ribbed, coarsely serrated, partially pigmented.

Coloration in preservative. Dorsally: body and tail musculature brownish with scattered dark pigmentation; either side of dorsal body black coloured with white stripes (the blood vessels); some dark pigment concentrated dorsally forming dark patches between eyes and beside nares; tail muscle barred black and white. Laterally: intestinal coils not visible through lateral body wall; spiracle not pigmented; caudal fins clear; lower part of caudal musculature less pigmented anteriorly; musculature junctions very distinct anteriorly.

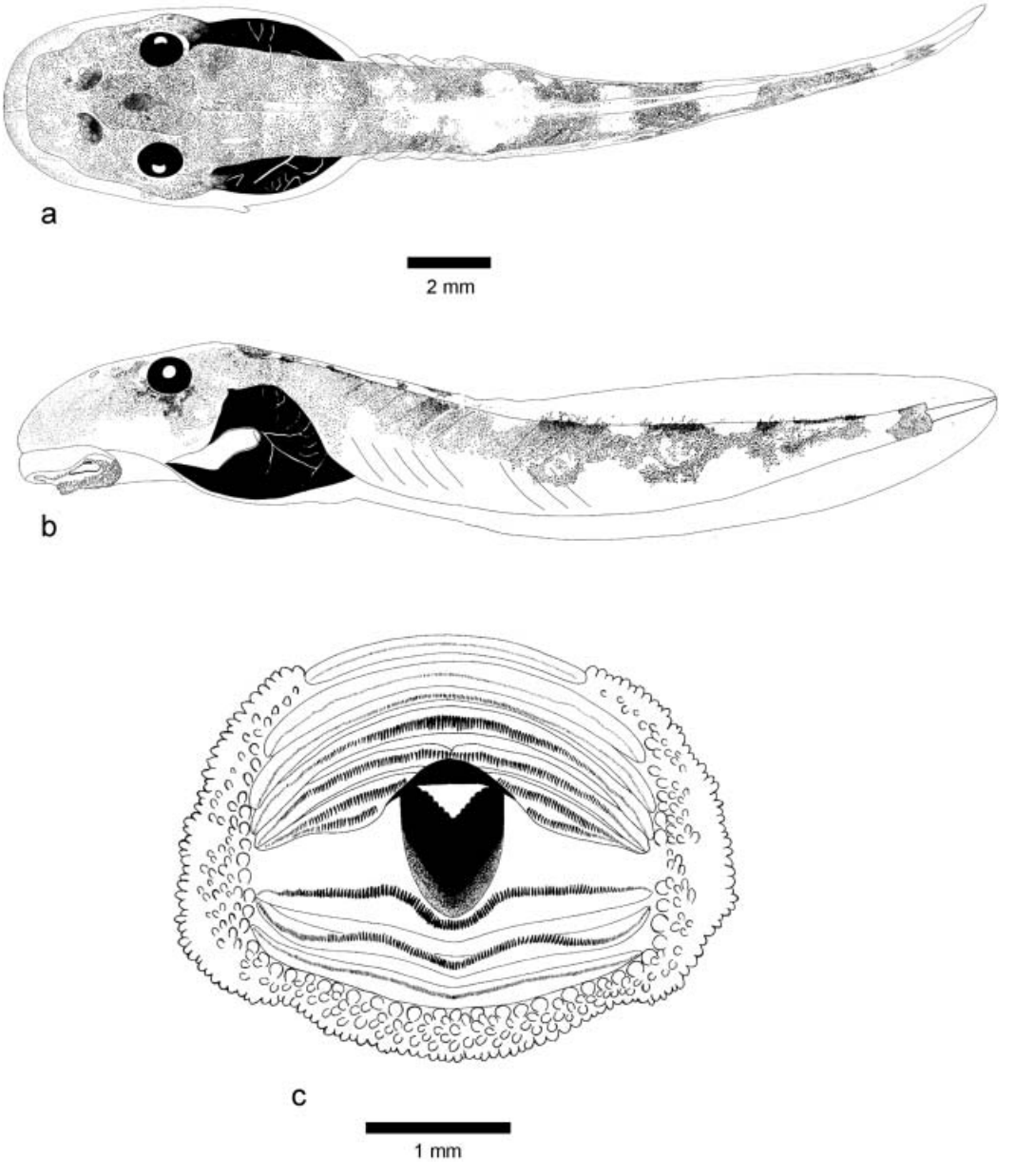

Figure 7. Drawings of the tadpole of *Boophis sibilans* (ZSM 557/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

Ventrally: opaque branchial and cardial organs slightly visible through ventral body wall; intestinal coils not visible.

Variation. TL and BL of eight tadpoles at stage 25 (ZSM 556/2004–560/2004, and LR 269a, LR 269c, LR 269f) from localities 2 and 4, are 19.1–25.2 and 6.9–9.0 mm, respectively. The ratios vary in the following proportions: BW 118–132% of BH; ED

11.8–13.0% of BL; RN 127–177% of NP; NN 46–53% of PP; SS 70–78% of BL; TMH 59–77% of BH; TMH 59–75% of MTH; TMW 54–61% of BW; MTH 97–113% of BH; ODW 44–53% of BL; ODW 88–96% of BW. KRF of the eight tadpoles is 4:3+3/3.

***Boophis luteus* group**

Boophis luteus (Boulenger, 1882)

(Figure 8)

The following description is based on one tadpole in developmental stage 33 (ZSM uncatalogued, field number LR 218, TL 33.1 mm, BL 13.1 mm), from locality 3.

In dorsal view (Figure 8a), body ovoid, snout rounded. In lateral view (Figure 8b), body depressed, BW 125% of BH, snout rounded. Eyes moderately large, ED 14.5% of BL, bulging, not visible in ventral view, positioned dorsolaterally but directed laterally, situated at about one-third of the body. Nares moderately sized, nearly oval, not rimmed, positioned and directed dorsally, closer to the anterior edge of eyes than to tip of snout, RN 133% of NP; NN 64% of PP. Spiracle sinistral, moderately small, slightly tubular, well visible from dorsal view, its tip free from body; spiracular opening oval, orientated posterodorsally, positioned at about three-quarters of body length, SS 76% of BL, and situated well below the longitudinal axis of tail musculature. Vent tube short, dextral, opening at ventral edge of fin, opening directed posterolaterally, linked to caudal muscle, its right wall displaced anteriorly. Caudal musculature moderately strong, TMH 54% of BH and 65% of MTH, TMW 48% of BW, height of caudal musculature about two-fifths of the total height at mid-tail, reaching tail tip. Caudal fins shallow anteriorly, deepest at about half of their length, their height decreasing progressively up to tail tip, MTH 82% of BH; dorsal fin originating well posterior to the dorsal tail–body junction, ventral fin starting just behind the body; tail tip obtuse.

Oral disc (Figure 8c) large, ODW 37% of BL and 63% of BW, positioned anteroventrally and directed ventrally, not emarginated. Oral disc bordered by one or two rows of marginal papillae interrupted by a large median gap on the upper labium (DG 94% of ODW), and by a small median gap on the lower labium. Submarginal papillae clustered in the corners of labia. Papillae of moderate size, cylindrical elongate with rounded tip. No denticulate papillae. Keratodont row formula 1:5+5/1+1:2. About 238 keratodonts on A1 (ca 63 per mm). The length of the interrupted anterior rows A2, A3, and A4 decreases towards centre of disc; keratodont rows of lower labium subequal in size. Both jaw sheaths serrated and fully black pigmented; upper jaw a wide flattened arch convex medially; lower jaw V-shaped.

Coloration in preservative. Dorsally: body and tail musculature dark pigmented; dark pigmentation concentrated dorsally forming obvious dark patches between eyes and immediately next to nares. Laterally: intestinal coils well visible; dorsal fin pigmented; ventral fin almost clear, musculature mottled. Ventrally: branchial and cardial organs apparent through the transparent surface of body.

Variation. TL and BL of 28 tadpoles at stages 25–41 (LR 160, LR 189, LR 227f, LR 227g, LR 227h, LR 227i, LR 227j, LR 227l, LR 227m, LR 238, LR 238a, LR 267, LR 267a, LR 72, LR 73, LR 227e, LR 227k, LR 227n, LR 227q, LR 218, LR 227b, LR 24, LR 227o, LR 227p, LR 227a, LR 227c, LR 227d, LR 250), from localities 1–5, are 17.7–41.4 and 6.7–16.1 mm, respectively. The ratios vary in the following proportions: BW 121–145% of

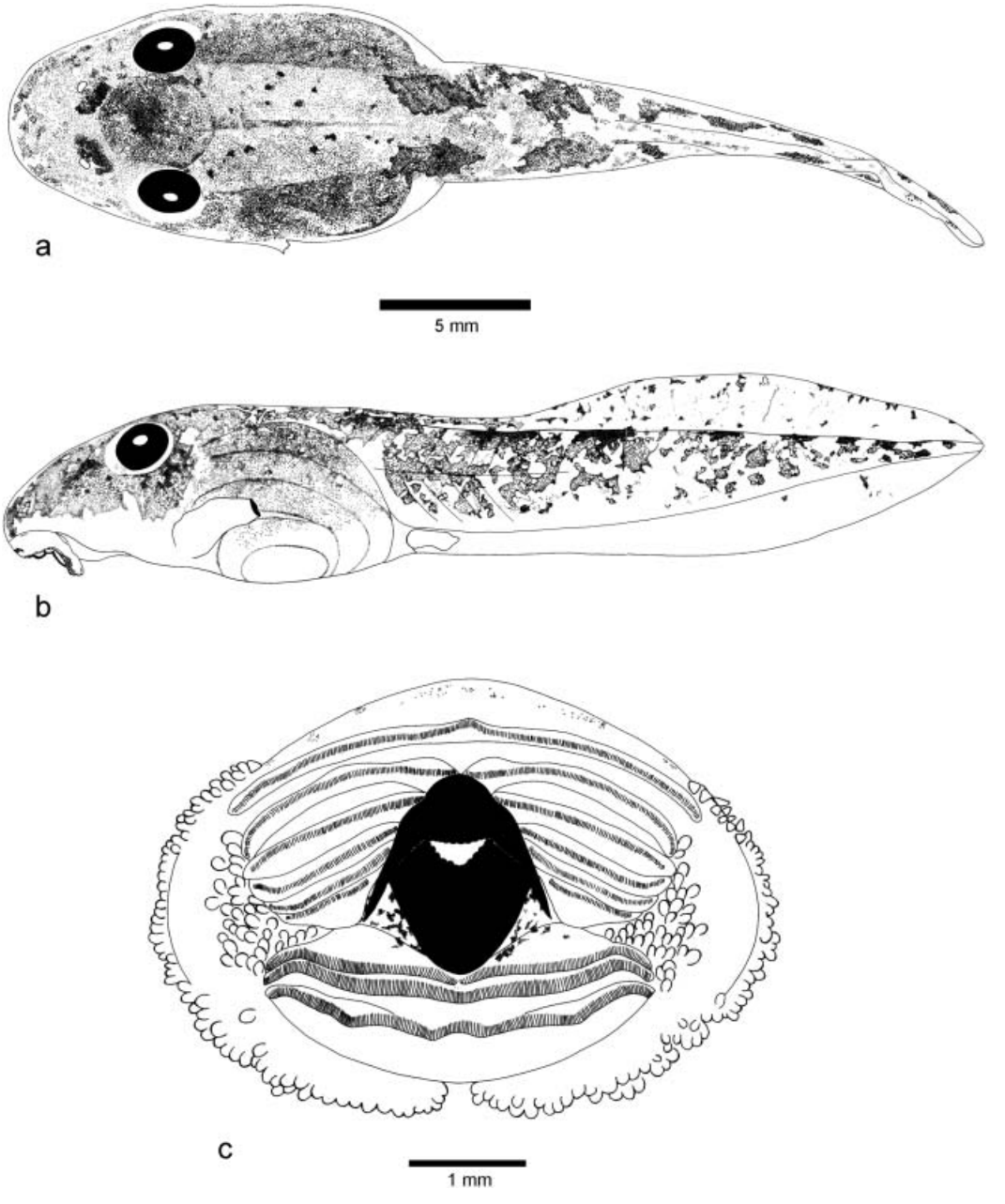

Figure 8. Drawings of the tadpole of *Boophis luteus* (ZSM uncatalogued). (a) Dorsal view; (b) lateral view; (c) oral disc.

BH; ED 10.0–16.7% of BL; RN 100–182% of NP; NN 40–64% of PP; SS 58–88% of BL; TMH 54–69% of BH; TMH 58–76% of MTH; TMW 42–65% of BW; MTH 84–113% of BH; ODW 26–44% of BL; ODW 49–75% of BW. KRF of the 28 tadpoles varies from 1:3+3/1+1:2 to 1:5+5/1+1:2.

Boophis* sp. aff. *elenae

(Figure 9)

This is an undescribed species of treefrog, similar to and sometimes sympatric with *Boophis elenae* Andreone, 1993. The following description is based on one tadpole in developmental stage 31 (ZSM uncatalogued, field number LR 214, TL 36.3, BL 14.6 mm), from locality 3.

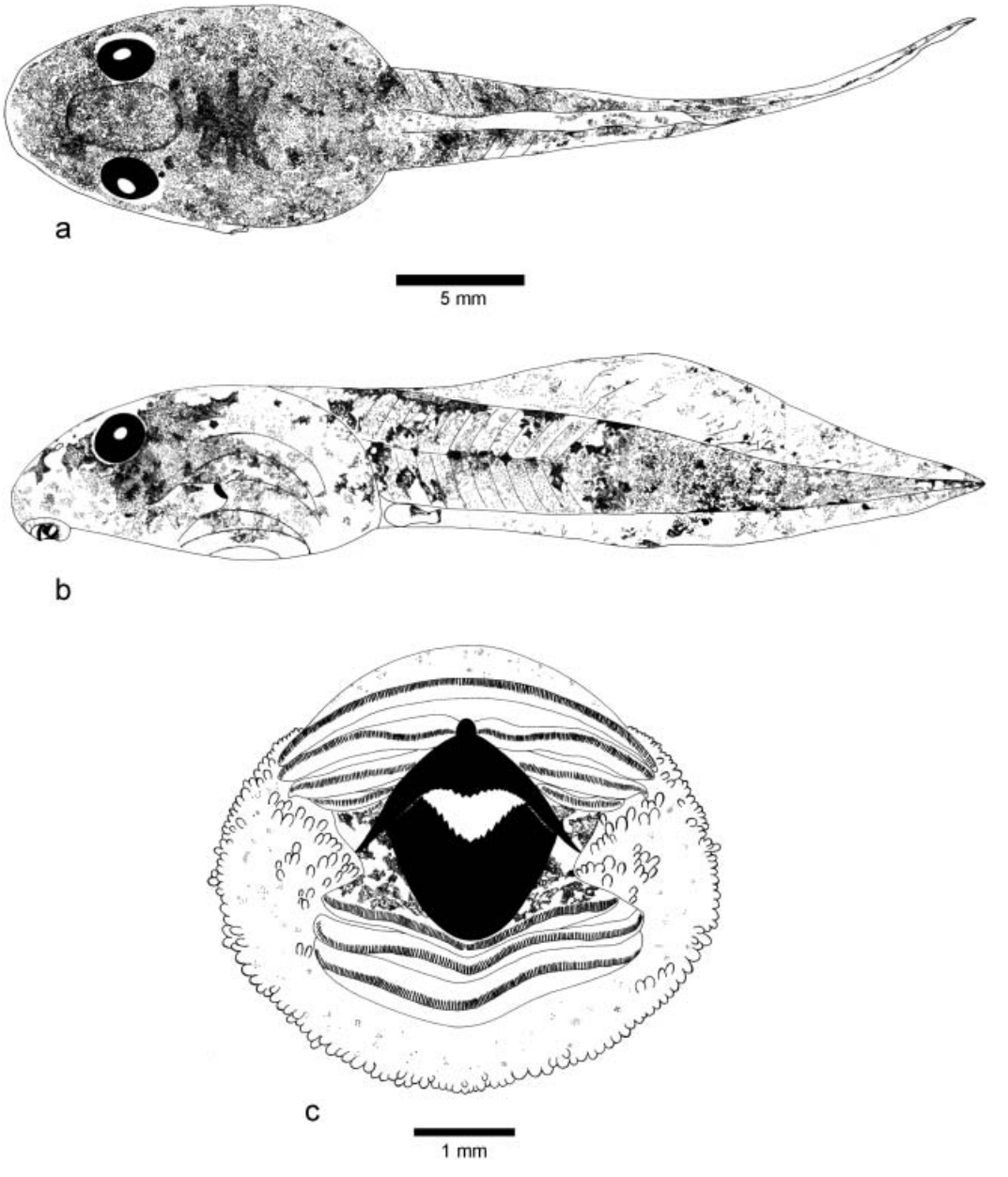

Figure 9. Drawings of the tadpole of *Boophis* sp. aff. *elenae* (ZSM uncatalogued). (a) Dorsal view; (b) lateral view; (c) oral disc.

In dorsal view (Figure 9a), body ovoid, snout rounded. In lateral view (Figure 9b), body depressed, BW 116% of BH, snout rounded. Eyes moderately large, ED 14% of BL, slightly bulging, not visible in ventral view, positioned dorsolaterally but directed laterally, situated at about the anterior third of the body. Nares small, oval, rimmed, positioned and directed dorsolaterally, much closer to the anterior edge of eyes than to tip of snout, RN 137% of NP; NN 58% of PP. Spiracle sinistral, moderately small, slightly conical, clearly visible from ventral view, its tip free from body; spiracular opening oval, orientated posterodorsally, much closer to end of body than to snout, SS 70% of BL and situated well below the longitudinal axis of tail musculature. Vent tube short, dextral, opening directed posterolaterally, its right wall displaced anteriorly. Caudal musculature strong, TMH 62% of both BH and MTH, TMW 51% of BW, height of caudal musculature about one-third of the total height at mid-tail, reaching tail tip. Caudal fins concave in their anterior parts, convex towards mid-tail then reducing gradually up to tail tip, MTH 100% of BH; dorsal fin originating well posterior to the dorsal tail–body junction, ventral fin starting just behind the body; tail tip pointed.

Oral disc (Figure 9c) moderately large, ODW 31% of BL and 56% of BW, positioned anteroventrally and directed ventrally, not emarginated. A total number of 164 marginal papillae disposed in two rows around the oral disc, interrupted by a large median gap on the upper labium (DG 67% of ODW); gap on the lower labium not distinct. Submarginal papillae clustered in the corners of labia. Papillae of moderate size, elongate with more or less rounded tip. No denticulate papillae. Keratodont row formula 1:3+3/1+1:2. About 194 keratodonts on A1 (ca 54 per mm). The length of the interrupted anterior rows A2, A3, and A4 decreases towards centre of disc; P2 and P3 subequal in size, P1 slightly shorter. Both jaw sheaths serrated and fully black pigmented; upper jaw with a large medial serration surrounded by smaller serrations on each side forming a slight convexity; lower jaw V-shaped.

Coloration in preservative. Dorsally: body and tail musculature dark brown with scattered black spots; some pigmentation forming a distinctive dark patch between eyes and also on mid-dorsal area of body. Laterally: body and caudal musculature covered by scattered dark pigmentation; musculature junctions obvious in the anterior half of tail musculature; intestinal coils completely visible; fins transparent with scattered pigmentation; dorsal fin showing some reticulations. Ventrally: whole surface of ventral body transparent; branchial and cardial organs visible through translucent ventral surface.

Variation. TL and BL of six tadpoles at stages 25–41 (LR 243, LR 228, LR 230, LR 214, LR 234, LR 249), all from locality 3, are 21.2–40.0 and 8.5–15.0 mm, respectively. The ratios vary in the following proportions: BW 116–157% of BH; ED 13.9–16.5% of BL; RN 87–143% of NP; NN 42–58% of PP; SS 69–78% of BL; TMH 50–67% of BH; TMH 53–69% of MTH; TMW 41–54% of BW; MTH 73–108% of BH; ODW 27–36% of BL; ODW 47–63% of BW. KRF of the six tadpoles varies from 1:3+3/1+1:2 to 1:5+5/1+1:2.

***Boophis rappiodes* group**

Boophis tasymena Vences and Glaw, 2002

(Figure 10)

The following description is based on one tadpole in developmental stage 25 (ZSM 527/2004, field number LR 96, TL 17.5 mm, BL 6.7 mm), from locality 1.

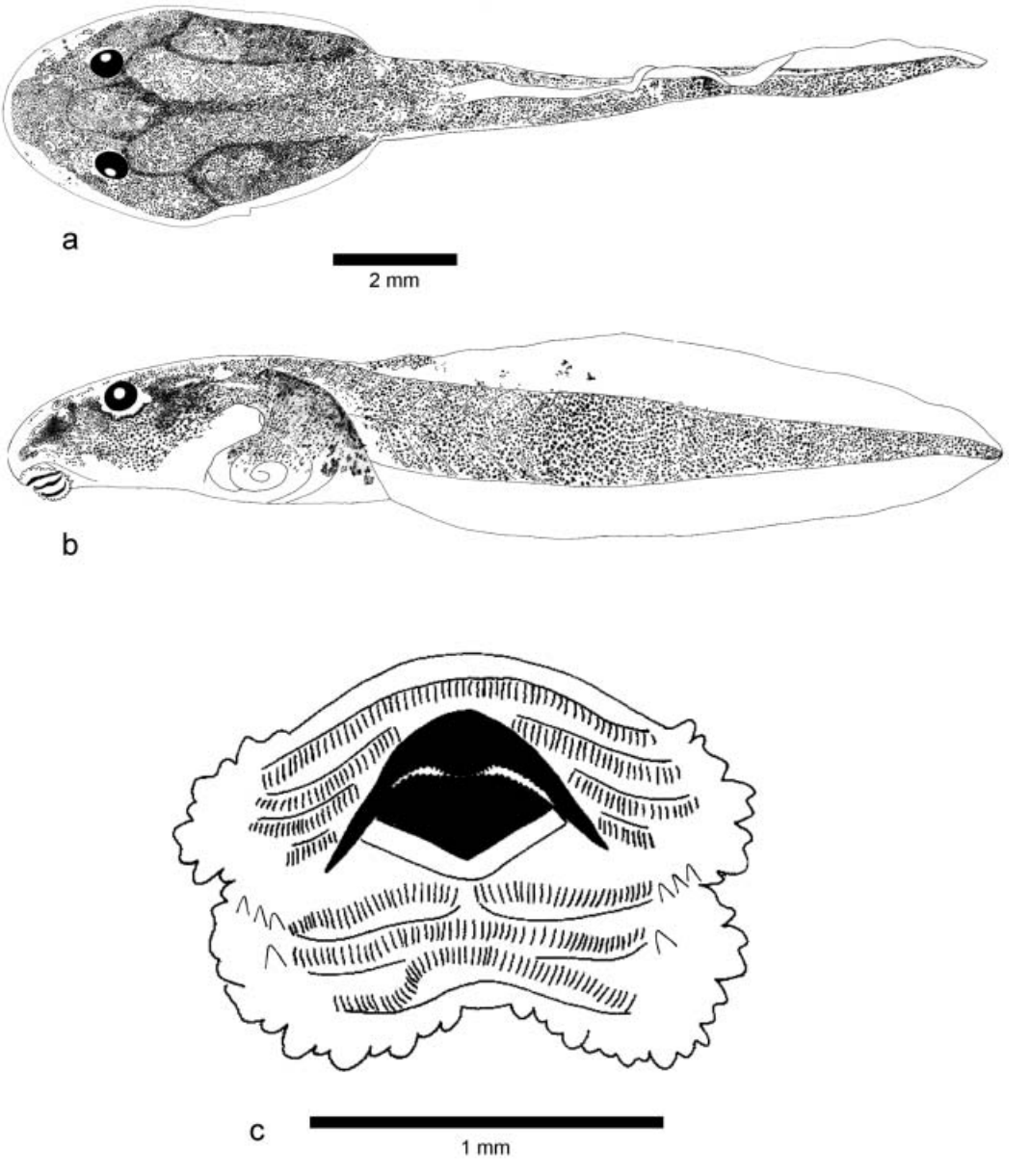

Figure 10. Drawings of the tadpole of *Boophis tasymena* (ZSM 527/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

In dorsal view (Figure 10a), body ovoid, snout rounded. In lateral view (Figure 10b), body greatly depressed, BW 156% of BH, snout rounded. Eyes of moderate size, ED 10.5% of BL, not visible in ventral view, positioned dorsolaterally, situated at about the anterior third of the body. Nares moderately sized, round, rimmed with a small flat mediodorsal projection, positioned quasi-dorsally and directed anterodorsolaterally, equidistant between tip of snout and anterior edge of eyes, RN 100% of NP; NN 60% of PP. Spiracle sinistral, moderately large, well visible from dorsal view, tubular, inner wall

free from body; spiracular opening oval, orientated more posteriorly than posterodorsally, closer to end of body than to snout, SS 69% of BL, situated at the height of the lower part of tail musculature. Vent tube moderately sized, short, dextral, opening directed posterolaterally, its right wall displaced anteriorly, entirely linked to ventral tail fin. Caudal musculature moderately developed, TMH 44% of BH and 42% of MTH, TMW 38% of BW, its height almost half of total height at mid-length of tail. Caudal fins regular with straight edges, MTH 104% of BH; dorsal fin originating next to body–tail junction, reduced in the anterior part and convex at about half of tail length; point of maximum tail height reached towards mid-tail; ventral fin moderately shallow; tail tip roughly rounded.

Oral disc (Figure 10c) of moderate size, ODW 25% of BL and 44% of BW, positioned and directed anteroventrally, emarginated. A single row of marginal papillae interrupted by a large median gap on the upper labium (DG 59% of ODW), and by a short gap on the lower labium; total number of marginal papillae about 48 (23 on the left side and 25 on the right side). No distinct submarginal papillae present. Papillae of moderate size, cylindrical elongate with rounded tip. No denticulate papillae. Keratodont row formula 1:3+3/1+1:2. About 58 keratodonts on A1 (55 per mm). The length of interrupted anterior keratodont rows decreases gradually towards the centre of the disc, P1 and P2 subequal in length, P3 shorter. Jaw sheaths moderately coarsely serrated; upper jaw as a large arch with a median convexity, totally coloured by black pigment; lower jaw V-shaped.

Coloration in preservative. Dorsally: body and tail musculature generally brownish, uniformly pigmented by black dots. Laterally: intestinal coils partially visible on the lower part of the body; dorsal fin faintly pigmented on the anterior part near its starting point; ventral fin clear; body and caudal musculature with black dots. Ventrally: region of the branchial and cardial organs somewhat obscure but still visible through the ventral surface of the body.

Variation. TL and BL of eight tadpoles at stage 25 (ZSM 527–532, LR 96c, LR 96f), all from locality 1, are 13.5–20.0 and 5.5–7.3 mm, respectively. The ratios vary in the following proportions: BW 113–156% of BH; ED 0.9–11.0% of BL; RN 60–120% of NP; NN 57–66% of PP; SS 60–73% of BL; TMH 41–59% of BH; TMH 34–54% of MTH; TMW 31–39% of BW; MTH 97–128% of BH; ODW 20–25% of BL; ODW 35–45% of BW. KRF of the eight tadpoles is 1:3+3/1+1:2.

Boophis viridis Blommers-Schlösser, 1979
(Figure 11)

The following description refers to one voucher specimen in developmental stage 36 (ZSM 574/2004, field number LR 222d, TL 30.5 mm, BL 11.5 mm), from locality 3.

In dorsal view (Figure 11a), body ovoid, snout rounded. In lateral view (Figure 11b), body depressed, BW 118% of BH, snout rounded. Eyes of moderate size, ED 10.0% of BL, slightly bulging, not visible in ventral view, positioned almost dorsally but directed anterolaterally and dorsolaterally, situated at about the anterior quarter of the body. Nares oval, of moderate size, rimmed, positioned dorsolaterally, directed anterolaterally and dorsolaterally, nearer to anterior edge of eyes than to tip of snout, RN 133% of NP; NN 49% of PP. Spiracle sinistral, small, conical, inner wall free and formed such that aperture opens laterally instead of posteriorly; closer to end of body than to snout, SS 67% of BL, situated a little below the longitudinal axis of tail musculature. Vent tube short, dextral, opening dextral, its right wall displaced anterodorsally, directed posterodorsally, linked to

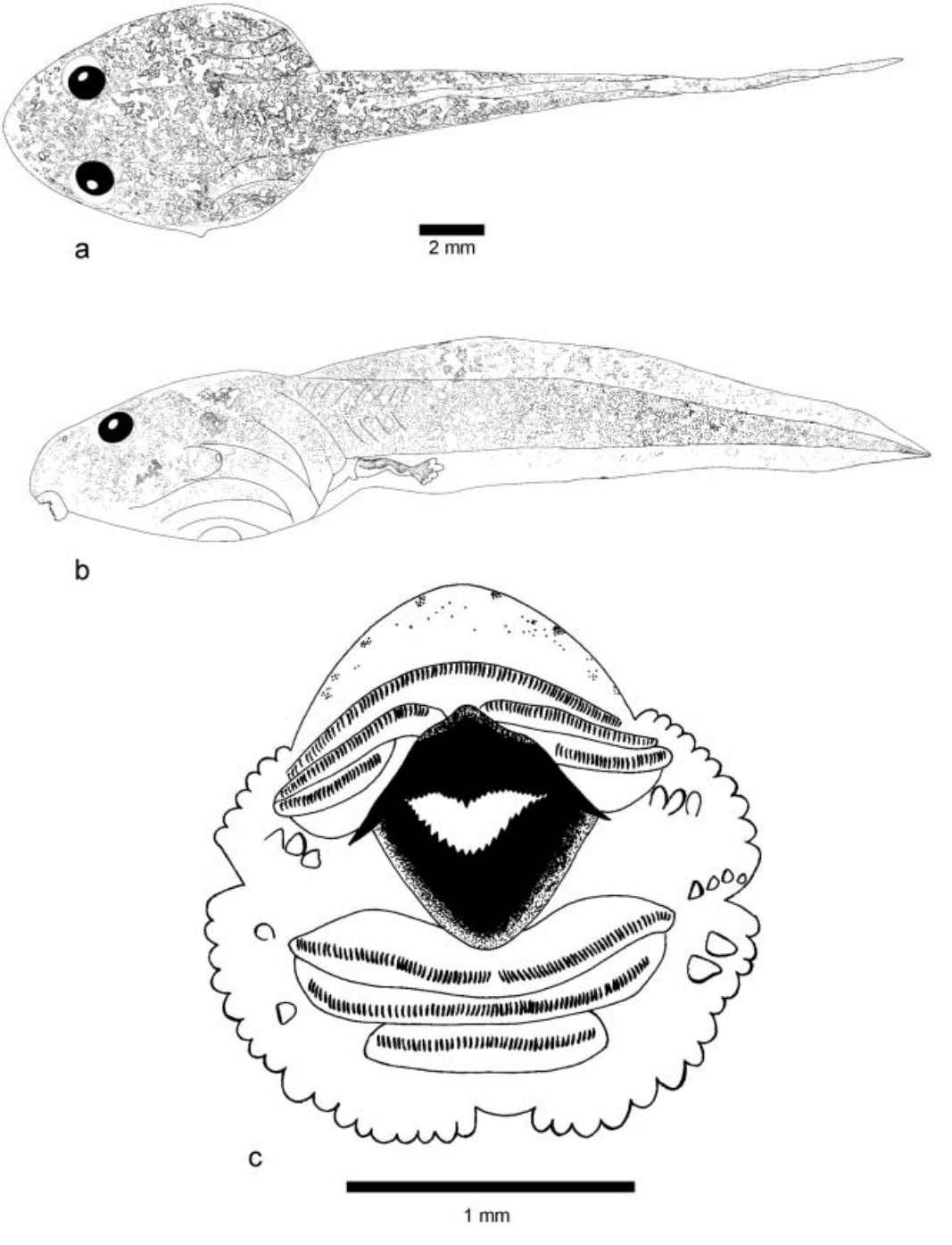

Figure 11. Drawings of the tadpole of *Boophis viridis* (ZSM 574/2004). (a) Dorsal view; (b) lateral view; (c) oral disc.

ventral tail fin except its tip. Tail relatively long. Caudal musculature moderately developed, TMH 50% of BH and 67% of MTH, TMW 37% of BW, at mid-length of tail its height about half of the total tail height, reaching almost to tail tip. Caudal fins moderately weakly developed, MTH 75% of BH; dorsal fin originating at the dorsal tail–body junction and slightly taller than ventral fin at mid-length of tail, ventral fin originating immediately behind body; tail tip pointed.

Oral disc (Figure 11c) moderately small, ODW 19% of BL and 31% of BW, positioned and directed anteroventrally, emarginated. Oral disc bordered by a single row of about 50 marginal papillae interrupted by a large median gap on the upper labium (DG 57% of ODW), and by a small medial gap on the lower labium. A few submarginal papillae positioned in the lateral parts of the anterior and posterior labia. Papillae moderately large, stout, conical with a rounded tip. No denticulate papillae. Keratodont row formula 1:2+2/1+1:2. P1 interrupted by less than 0.1 mm; P2 the longest keratodont row of the oral disc. About 79 keratodonts on A1 (ca 49 per mm); P1 and P2 of about similar length, P3 about two-thirds of P2. Upper jaw finely serrated, black with a larger medial serration surrounded by smaller serrations on each side forming a slight convexity; lower jaw black, moderately serrated, V-shaped.

Coloration in preservative. Dorsally: whole dorsum body and caudal musculature uniformly mottled; eyes partially sunk into orbital sockets; nares mixed with the markings and difficult to see. Laterally: intestinal coils well visible; musculature junctions slightly distinct in the anterior part of tail musculature; dorsal fin moderately mottled; ventral fin almost clear. Ventrally: branchial and cardial region slightly visible through ventral body wall; intestinal coils dextral, visible ventrally with regular spiral shape.

Variation. TL and BL of 26 tadpoles at stages 25–39 (ZSM 561/2004–574/2004, LR 221a, LR 221b, LR 221b2, LR 221b3, LR222c1, LR222c2, LR222c3, LR222c5, LR222c7, LR222c9, LR222c11, LR222c12), all from locality 3, are 18.3–33.5 and 7.3–12.5 mm, respectively. The ratios vary in the following proportions: BW 113–144% of BH; ED 10.0–13.2% of BL; RN 80–133% of NP; NN 41–54% of PP; SS 60–75% of BL; TMH 40–56% of BH; TMH 40–58% of MTH; TMW 30–41% of BW; MTH 75–118% of BH; ODW 17–25% of BL; ODW 27–42% of BW. KRF of the 26 tadpoles varies from 1:2+2/1+1:2 to 1:3+3/1+1:2.

Discussion

Identity of Boophis *tadpoles*

In this paper we identified tadpoles of 11 *Boophis* species using DNA barcoding, all from a single area around Andasibe village in central-eastern Madagascar, which is known to be a biodiversity hotspot (Lees et al. 1999) with a large number of species of frogs recorded in sympatry. The molecular identification of the tadpoles described herein was, despite this large diversity, unequivocal, since a large comparative database of homologous sequences from adult frogs collected at the same site exists (Vences et al. 2005) and could be used for comparison. In all cases, the larval DNA sequences were fully identical to those of adult frogs. The only exception is *Boophis* aff. *elenae*: although we have often heard the typical calls of this species at Andasibe, we have not yet been able to collect adults and, hence, to obtain DNA sequences from a well-identified specimen from this site. However, we have many such sequences from a second locality, Ranomafana, and our tadpole sequence from Andasibe clearly clusters with these, despite a considerable pairwise sequence divergence of

3.7%. In general, none of the species studied here belongs to a complex of sibling species among which instances of hybridization or haplotype sharing have been reported, which increases our confidence in the identity of the tadpoles.

Of the *Boophis* tadpoles described previous to the present paper, several can be considered as reliably identified. The tadpole of *B. laurenti* was identified by DNA barcoding (Thomas et al. 2005) and is extremely similar to that of *B. microtympanum* as described by Blommers-Schlösser (1979b) based on reared juveniles from the Ankaratra massif. This and the tadpole of the syntopic *B. williamsi* originate from montane habitats of low species diversity, and their large juveniles are very similar in colour and size to the adults, which is why we believe their identification is correct. Based on the large size of juveniles, which already bear characters of the morphology of the adults, we also consider the *B. goudoti* tadpoles described by Blommers-Schlösser (1979b) as likely to be correctly identified. The tadpole of *B. occidentalis*, described by Andreone et al. (2002), was reared from eggs deposited by a large aggregation of breeding adults, and its identification is therefore beyond doubt. The tadpole of *B. jaegeri* as described by Glaw and Vences (1994) was collected at the type locality of this species, Nosy Be, where only one additional stream-breeding *Boophis* occurs (*B. brachychir*). The *B. jaegeri* tadpole is similar in morphology to those of *B. luteus* and *B.* aff. *elenae* as described herein, which are its close relatives according to molecular data (Vences et al. 2002), and therefore it is likely to be correctly assigned. The *B. ankaratra* tadpole as described by Glaw and Vences (1994) originates from a montane site where it is the only bright green-coloured *Boophis* species, increasing the confidence in a correct assignation of the green juvenile that was reared through metamorphosis. Furthermore, we have recently identified further tadpoles of this species using DNA barcoding, and these specimens fully conform to the previous description. The tadpole of *Boophis mandraka*, described by Blommers-Schlösser (1979b) from the type locality of this species, agrees in morphology to that of a close relative of this species, *B. sambirano* Vences and Glaw, 2005, which is currently being described by R.-D. Randrianiaina; this makes it likely that the *B. mandraka* tadpole has also been correctly identified.

Two other tadpole descriptions of Blommers-Schlösser (1979b), however, are equivocal. The larva of *B. majori* described by this author from the locality Mandraka almost certainly belongs instead to *B. marojezensis* which was described subsequent to Blommers-Schlösser's works (Glaw and Vences 1994). Indeed, adults from Mandraka collected by Blommers-Schlösser (1979b) were re-determined as *B. marojezensis* (Glaw et al. 2001), and the tadpole description conforms to that of *B. marojezensis* herein. More complex is the case of the *B. erythrodactylus* tadpole from the same locality, Mandraka (Blommers-Schlösser 1979b). This species clearly belongs in the *B. rappiodes* group according to molecular data, and is sister to *B. tasymena* (Vences et al. 2002; as *B.* sp. aff. *erythrodactylus*). Nevertheless, the tadpole described by Blommers-Schlösser (1979b) is highly different from that of *B. tasymena* and two other species of the *B. rappiodes* group (*B. rappiodes* and *B. viridis*; Blommers-Schlösser, 1979b and description herein), instead resembling those of *B. mandraka* and *B. ankaratra*, which are known from the same locality as well. Because of this indirect evidence we consider the identity of the tadpoles assigned by Blommers-Schlösser (1979b) to *B. erythrodactylus* as in need of confirmation.

Lotic tadpole adaptations and Boophis *phylogeny*

Our data, in combination with published tadpole descriptions of other *Boophis* species (Blommers-Schlösser 1979b; Glaw and Vences 1992, 1994; Andreone et al. 2002;

Grosjean et al. 2006), provide evidence for varying degrees of larval adaptation to running water in the stream-breeding clade of this genus. In the field we observed many times how species with large oral discs and strong caudal musculature were mainly distributed in fast-flowing parts of streams, and how these tadpoles attached to the surface of rocks and, later, of collecting bags or buckets with their oral discs. We are therefore convinced that these morphological features, large oral discs with high numbers of smaller papillae and keratodont rows, and stronger caudal musculature with reduced height of dorsal fins, are to be interpreted as adaptations to the current in the lotic environment of these tadpoles, conforming to Altig and Johnston (1989). More extreme evolution of these features is observed in the members of the gastromyzophorous guild such as the unrelated toadlets of the genus *Atelopus*, and the stream-breeding ranids of the genus *Amolops*, which have developed large ventral suctorial discs (Inger 1966; Lötters 1996).

For the purpose of generalization, we think that three guilds of lotic *Boophis* tadpoles can be distinguished, although intermediate adaptive states certainly exist and assignation is therefore certainly not unequivocal.

1. Guild A contains the more generalized lotic forms which can often be distinguished from pond-breeding *Boophis*, and many other mantellids belonging to the genus *Mantidactylus sensu lato*, by some enlargement of the oral disc. In the present study, *Boophis boehmei*, *B. reticulatus*, *B. pyrrhus*, *B. tasymena*, and *B. viridis* can be included in this guild. Their ODW is 31–43% of BW, there is a single row of 48–81 marginal papillae, and the first upper keratodont row has 58–144 keratodonts. According to the descriptions of Blommers-Schlösser (1979b), Glaw and Vences (1994) and Grosjean et al. (2006), *B. rappiodes*, *B. brachychir*, and *B. goudoti* can also be tentatively assigned to this guild.
2. Guild B contains intermediate forms, such as *Boophis luteus*, *B.* aff. *elenae*, and possibly *Boophis albilabris* and *B. madagascariensis*, although these latter species may also be included in Guild A. These species show a distinct enlargement of the caudal musculature, a reduction of the upper fin in its anterior part (especially in the two former species), and a rather large oral disc with an increase in the number of keratodont rows, although the size of the keratodont rows and the size and number of the oral papillae, and the horny beak, are not conspicuously modified. Their ODW is 43–63% of BW, they have one or two rows of 69–164 marginal papillae, and the first upper keratodont row has 164–238 keratodonts. The tadpoles of *B. microtympanum* and *B. laurenti* may also be assigned to this guild, although these montane larvae are deviant in being rather large, and in having high numbers of keratodont rows. According to the descriptions of Glaw and Vences (1994), the tadpole of *B. jaegeri* can also be assigned to this guild, as can possibly the larva of *B. occidentalis* which is similar to that of *B. albilabris* (Andreone et al. 2002).
3. Guild C contains the most highly modified tadpoles, with a very strong caudal muscle, a flat body ventrally, a large ventral suctorial oral disc, enlarged number of keratodont rows and high density of keratodonts, a large number of small oral papillae which in some cases tend to close the dorsal papilla gap, and often with a reduced size of the horny beak, reduction or absence of serrations on the upper beak, and a ''ribbed'' lower beak (one species with a less keratinized median area) characteristic of the stream-dwelling gastromyzophorous tadpoles of the genus *Meristogenys* (Inger 1966). The tadpoles of *Boophis marojezensis* and of *B. sibilans* clearly belong in this guild; their ODW is 63–89% of BW, there are multiple rows of many small marginal papillae, and the first upper keratodont row has many small keratodonts which are difficult to count,

but certainly are more than 200 (203–208 in the third or fourth upper keratodont row). The previously described larva of *B. mandraka* (Blommers-Schlösser 1979b) belongs in this guild as well, as probably does the tadpole of *B. ankaratra* that was briefly described by Glaw and Vences (1994). The montane specialist *B. williamsi* may also be assigned to this guild, although its large tadpoles do not show any obvious reduction of the horny beak (Blommers-Schlösser 1979b; and our own data).

Using these guild designations as a tentative yardstick to measure adaptations to fast-flowing waters in stream-breeding *Boophis*, several correlates of phylogenetic relationships are obvious, but in other cases convergence is to be invoked to explain morphological similarities (see Table II).

The species of Guild A belong in three *Boophis* species groups, the *B. goudoti* group (*B. boehmei*, *B. brachychir*, *B. reticulatus*, *B. goudoti*), the *B. rappiodes* group (*B. rappiodes*, *B. tasymena*, *B. viridis*), and the *B. majori* group (*B. pyrrhus*). Of these, the *B. goudoti* group seems to be phylogenetically fairly well-defined by molecular data (e.g. Vences et al. 2002), and although a tadpole of Guild B is included, Guild A larvae may be a common (though probably plesiomorphic) feature of all taxa in this group, which to a large extent are known to breed in slow-flowing or near-stagnant stretches of streams (Blommers-Schlösser 1979b; Glaw and Vences 1994). An evaluation of the pattern in the *B. rappiodes* group is complicated by the description of a Guild C larva in *B. erythrodactylus* (Blommers-Schlösser 1979b). After exclusion of the species of the *B. mandraka* group, the *B. rappiodes* group is highly likely to be monophyletic (Vences and Glaw 2005), and a Guild C larva in *B. erythrodactylus* would be a clear instance of convergent evolution. However, as discussed above, this record is in need of confirmation. Although several species of these small treefrogs often call along large and rather fast-flowing waters, their larvae may indeed be adapted to more slow-flowing sections of these streams. The discovery of a Guild A larva in a species of the *B. majori* group (*B. pyrrhus*) appears surprising, since the only other known tadpole of this group belongs in Guild C (*B. marojezensis*). However, in light of the fact that this species group is probably not monophyletic (Vences et al. 2002), larval morphology may help to reconcile phylogeny and classification.

The species of Guild B belong in four species groups, the *B. albilabris* group (*B. albilabris*, *B. occidentalis*), the *B. goudoti* group (*B. madagascariensis*), the *B. luteus* group (*B. jaegeri*, *B. luteus*, *B.* sp. aff. *elenae*), and the *B. microtympanum* group (*B. laurenti*, *B. microtympanum*). All these groups are likely to be monophyletic if the *B. albipunctatus* group is excluded from the *B. luteus* group (Glaw and Vences 2006). In the case of the *B. luteus* and *B. albilabris* groups, it is likely that most or all included species will have a Guild B morphology. The third species of the *B. microtympanum* group (*B. williamsi*) is here included in Guild C, but its morphological and genetic relationships to *B. laurenti* and *B. microtympanum* are well-supported, and it shows just a slightly more extreme expression of their montane larval morphology. Likewise, *B. madagascariensis* probably just shows a slightly more expressed adaptation to stream-life compared to other members of the *B. goudoti* species group, which have Guild A tadpoles.

The species of Guild C belong in four species groups, the *B. mandraka* group (*B. mandraka*), *B. majori* group (*B. marojezensis*), *B. albipunctatus* group (*B. ankaratra*, *B. sibilans*), and the *B. microtympanum* group (*B. williamsi*). Of these, the *B. mandraka* group is monophyletic (Vences and Glaw 2005). All species of this group were found along fast-flowing streams, and we consider it as likely that all of them have Guild C tadpoles. The *B. albipunctatus* group was recently split from the *B. luteus* group (Glaw and Vences 2006)

Table II. Summary of published tadpole descriptions in stream-breeding species of *Boophis* (all species except those of the *Boophis tephraeomystax* group) (the table lists descriptions according to the name used in the respective publication, grouped according to current classification in phenetic species groups; tadpole guilds are used as defined in the Discussion).

Species and species group	References of tadpole description	Identity/comment	Tadpole guild
Boophis albilabris group (two species; monophyletic)			
B. albilabris	This paper	DNA barcoding	B
B. albilabris	Blommers-Schlösser and Blanc (1991)	Assignation tentative	B
B. occidentalis	Andreone et al. (2002)	Reared from well-identified clutch	B
Boophis albipunctatus group (four species; probably monophyletic)			
B. ankaratra	Glaw and Vences (1994)	Rearing; confirmed by DNA barcoding	C
B. sibilans	This paper	DNA barcoding	C
B. goudoti group (eight species; probably monophyletic)			
B. boehmei	This paper	DNA barcoding	A
B. reticulatus	This paper	DNA barcoding	A
B. brachychir	Glaw and Vences (1994)	Rearing; probably correct	A
B. goudoti	Blommers-Schlösser (1979b)	Rearing; probably correct	A
B. madagascariensis	Blommers-Schlösser (1979b)	Rearing; probably correct	B
B. madagascariensis	This paper	DNA barcoding	B
B. rufioculis	Grosjean et al. (2006)	DNA barcoding	A
B. untersteini	Blommers-Schlösser (1979b)	Currently a synonym of *B. goudoti*; tadpoles may belong to *B. boehmei*, *B. burgeri*, or *B. rufioculis*	A
Boophis luteus group (eight species; probably monophyletic)			
B. jaegeri	Glaw and Vences (1994)	Rearing; probably correct	B
B. luteus	Blommers-Schlösser (1979b)	Rearing; probably correct	B
B. luteus	This paper	DNA barcoding	B
B. sp. aff. *elenae*	This paper	DNA barcoding	B
Boophis majori group (nine species; not monophyletic)			
B. majori	Blommers-Schlösser (1979b)	Almost certainly refers to *B. marojezensis*	C
B. marojezensis	This paper	DNA barcoding	C
B. pyrrhus	This paper	DNA barcoding	A
Boophis mandraka group (four species; monophyletic)			
B. mandraka	Blommers-Schlösser (1979b)	Rearing; probably correct	C
B. microtympanum group (four species; monophyletic)			
B. laurenti	Thomas et al. (2005)	DNA barcoding	B
B. microtympanum	Blommers-Schlösser (1979b)	Rearing; probably correct	B
B. williamsi	Blommers-Schlösser (1979b)	Rearing; probably correct	C
Boophis rappiodes group (five species, monophyletic)			
B. erythrodactylus	Blommers-Schlösser (1979b)	Rearing; possibly confusion with *B. ankaratra*; needs confirmation	C
B. rappiodes	Blommers-Schlösser (1979b)	Rearing; probably correct, but confusion with *B. bottae* possible	A
B. tasymena	This paper	DNA barcoding	A
B. viridis	This paper	DNA barcoding	A

based on molecular phylogenetic data, and may also be characterized by Guild C tadpoles in its entirety. The *B. majori* group is probably not monophyletic (see discussion of *B. pyrrhus* under Guild A above), and more data are necessary to understand relationships among species of this assemblage. Finally, for *B. williamsi*, see discussion under Guild B above.

As a conclusion, the distribution of larval morphologies among stream-breeding *Boophis* conforms rather well to current phylogenetic knowledge. Where species groups are known to be monophyletic, they appear to be characterized by a generally similar larval morphology, and where more than one larval morphology occurs in a species group, its non-monophyly has already been ascertained (like the *B. majori* group) (Table II). Hence, rapid and frequent adaptive shifts expressed in larval morphology seem to be uncommon in this genus of frogs. Nevertheless, it is highly probable that convergent adaptation to fast-flowing aquatic environments has taken place repeatedly. This is indicated by (1) the presence of Guild C morphologies in representatives of different species groups that do not have obvious phylogenetic relationships, and (2) the fact that several species of Guild C, although having apparently similar ecomorphological adaptations, show important morphological differences: for example, in Guild C, *B. ankaratra* and *B. mandraka* have a (plesiomorphic) dorsal gap in the rows of marginal papillae which is closed in *B. marojezensis*; and *B. williamsi* has no obvious reduction of the horny beak which is apparent in other species such as *B. marojezensis*. A precise analysis of these convergences requires a stable phylogeny on which morphological changes can be plotted, but unfortunately the available data so far are not conclusive with respect to the basal relationships among species groups (Vences et al. 2002, 2003; Vences and Glaw 2005). Obtaining more reliable phylogenies and completing the taxonomic inventory of *Boophis* larvae will allow further understanding of the importance of reproductive and larval traits as possible key innovations in the evolution of mantellid frogs.

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