Description of tadpoles of five frog species in the subgenus *Brygoomantis* from Madagascar (Mantellidae: *Mantidactylus*)

HEIKE SCHMIDT¹, AXEL STRAUSS¹, FRANK GLAW², MEIKE TESCHKE³ & MIGUEL VENCES¹,⁴

¹Zoological Institute, Technical University of Braunschweig, Spielmannstr. 8, 38106 Braunschweig, Germany
²Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München, Germany
³Max-Planck Institute for Evolutionary Biology, Department of Evolutionary Genetics, 24306 Plön, Germany
⁴Corresponding author. E-mail m.vences@tu-bs.de

Abstract

We describe the larval stages of five frog species classified in the Madagascan subgenus *Brygoomantis* of the genus *Mantidactylus*, which were identified by DNA barcoding: *Mantidactylus alutus*, *Mantidactylus curtus*, and three taxonomically undescribed species here named *Mantidactylus* sp. aff. *biporus* "Ranomafana", *M*. sp. aff. *biporus* "Marojejy", and *M*. sp. aff. *curtus* "Ankaratra". The larvae of *M. alutus*, and of *M*. sp. aff. *curtus* "Ankaratra", had been described before, and we confirm and complement the previous studies. Our data confirm that *Brygoomantis* tadpoles are benthic, of a rather generalized body shape and oral disc morphology. All species for which tadpoles are known so far have a large dorsal gap of marginal papillae, a labial tooth row formula of 3-5 rows on the anterior labium of which only the first is continuous and the others have distinct medial gaps, and three rows of labial teeth on the posterior labium of which the first usually has a very small medial gap which however can sometimes be undetectable. Total number of marginal and submarginal papillae ranges from 50 to 103 and density of labial teeth (on the second upper row) from 19 to 76 per mm.

Key words: Amphibia, Anura, *Mantidactylus alutus*, *Mantidactylus curtus*, *Mantidactylus* sp. aff. *biporus*, *Mantidactylus* sp. aff. *curtus*, tadpole descriptions, DNA barcoding

Introduction

Madagascar harbours a fascinating variety of anuran amphibians that are still incompletely inventoried. Even less complete is the inventory of their larval forms, although these may be relevant to understand the adaptations in the endemic radiations of Malagasy frogs (e.g., Randrianiaina et al. 2007). Within the family Mantellidae, endemic to Madagascar, *Mantidactylus* Boulenger is one of the most species-rich lineages. The genus is subdivided into five subgenera (Glaw & Vences 2006). Species in one of these subgenera, *Brygoomantis* Dubois, were formerly known as the *Mantidactylus ulcerous* species group (Blommers-Schlösser 1979; Blommers-Schlösser & Blanc 1991). *Brygoomantis* are small to medium-sized frogs of usually brownish dorsal colour and inconspicuous appearance. These frogs are characterised by riparian to semi-aquatic habits, i.e., they are usually found along streams and many of them typically escape by diving into the water. They can be found throughout Madagascar along streams, occasionally occurring also in lentic waters like swamps, displaying diurnal and nocturnal activity (Blommers-Schlösser 1979; Blommers-Schlösser & Blanc 1991; Glaw & Vences 1994, 2007).

Some larvae assigned to species of *Brygoomantis* have been described by Arnoult & Razarihelisoa (1967) and Blommers-Schlösser (1979). However, due to the large number of cryptic, yet undescribed species in this subgenus (e.g., Glaw & Vences 2007), the exact assignment of the described tadpoles to species is in some cases questionable. In addition, some of these previous descriptions were based on series from different
localities which may represent more than one species. Recently, Knoll et al. (2007) provided data on the tadpoles of two described and two undescribed Brygoomantis species, based on specimens identified and matched to adults by DNA barcoding.

As a contribution to the goal of a complete and comparable set of larval descriptions of Malagasy frogs (e.g., Thomas et al. 2005; Raharivololoniaina et al. 2006; Vejarano et al. 2006; Randrianiaina et al. 2007; Knoll et al. 2007) we here present descriptions of the previously unknown tadpoles of three species, and re-descriptions of two additional species of Brygoomantis.

Materials and methods

Tadpoles were collected in the field, euthanised by immersion in chlorobutanol solution, and immediately sorted into series based on their morphology. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. These specimens are here named “DNA vouchers. Drawings and descriptions of the tadpoles in this paper are based only on the DNA vouchers. All specimens of each series were examined to assess morphological variability and to complete the structures missing because of tissue sampling in the DNA vouchers. After tissue collection, specimens were preserved in 4% formalin, or in 70% ethanol in the case of the series ZSM 123/2007. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). We give the ZSM catalogue number of voucher specimens as well as the field numbers (ZCMV; FGZC; FG/MV) applied to the same series.

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 circa 550 bp were 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 not more similar to any sequence from another species. DNA sequences were deposited in Genbank (accession numbers EU717879-EU717893; accession numbers of comparative adult specimens are included in the sequence sets AY847959-AY848683 and AJ315909-AJ315913).

Developmental stages are based on Gosner (1960). Morphological terminology follows Altig & McDiarmid (1999). Labial tooth row formulae are given according to Altig (1970) and Altig & McDiarmid (1999). A1-A5 is used to refer to the anterior (upper) labial tooth rows, P1-P3 for the posterior (lower) rows. Small and irregularly occurring gaps in rows of labial teeth were interpreted as oral deformities (see Drake et al. 2007). Measurements of body and tail were taken using a digital calliper (effective range: 0-150 mm; precision: 0.03 mm; repeatability: 0.1 mm). Drawings are mainly based on the preserved tadpoles. Pictures and measurements of the oral apparatus were taken using a Zeiss Stereo Discovery microscope with a mounted digital camera.

Abbreviations used in the descriptions are as follows: BL, body length (distance from the tip of the snout to the body-tail junction); BH, maximum body height; BW, maximum body width (at the widest point); TL, total length (sum of body length and tail length); TAL, tail length; ED, eye diameter; IOD, inter-orbital distance (measured between the centres of the pupils); IND, inter-narial distance (measured between the centres of the narial apertures); ESD, distance between eye and spiraculum (distance between the centre of the eye and the centre of the spiracular apertures); LTRF, labial tooth row formula; LTD, labial tooth density (number of teeth per millimetre in A2); LTN, number of all teeth in A2; PN, papillae number; TMH, tail muscle height (measured vertically from the junction of the body wall with the ventral margin of the tail muscle); TMW, tail muscle width (measured horizontally from the sinistral and the dextral junction of the body); MTH, maximum tail height (including fins and caudal musculature, taken at its maximal vertical extent); DF, height of dorsal fin at midlength of tail; TMHM, height of tail muscle at midlength of tail; VF, height of ventral fin at midlength of tail; ODW, oral disc width (maximum width of the oral disc).
Results

*Mantidactylus* sp. aff. *biporus* "Ranomafana"

**Series examined.** ZSM 123/2007. The 14 tadpoles of this series were collected in a rather shallow stream at a site locally known as Fompohonina in the Ranomafana National Park in eastern Madagascar (stream called Fompohonina III; depth about 7 cm, 21°15.907'S; 47°25.349'E, 1012 m a.s.l.) by A. Strauß, R.-D. Randrianiana and S. H. Ndriantsoa on 16 March 2007. The stream had a low downward slope of 16 cm per 10 m and its substrate was characterised by a high percentage of sand (58%) and leaves (40%), almost without vegetation. It was surrounded by primary rain forest with high canopy cover (> 70%). Water temperature was 18.9°C, pH was 8.9. The tadpoles were collected within or close to leaf agglomerations in the slower running parts of the stream.

**Taxonomic note.** The DNA sequence of the DNA voucher of this tadpole series agrees with DNA sequences (unpublished) from adult specimens belonging to an undescribed *Mantidactylus* from Ranomafana National Park (e.g., ZSM 667/2003), morphologically close to *Mantidactylus biporus* but differing distinctly in their DNA sequences, and also having a different advertisement call. For a photograph of an adult specimen, see Glaw & Vences (2007) on page 239, colour plate 5b.

**TABLE 1.** Measurements and morphological data of DNA voucher specimens from each species (Genbank accession numbers included in the series EU717879-EU717893). For abbreviations, see Materials and Methods. Each column refers to the individual specimen that was identified through DNA barcoding and for which species identity is thus reliable.
**TABLE 1.** (continued.)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dev. stage</td>
<td>26</td>
<td>40</td>
<td>37</td>
<td>42</td>
<td>28</td>
</tr>
<tr>
<td>BL (mm)</td>
<td>7</td>
<td>-</td>
<td>7.3</td>
<td>12.3</td>
<td>12.5</td>
</tr>
<tr>
<td>BH (mm)</td>
<td>3.1</td>
<td>4.6</td>
<td>7.2</td>
<td>4.9</td>
<td>4.7</td>
</tr>
<tr>
<td>BW (mm)</td>
<td>4.9</td>
<td>8.4</td>
<td>9.5</td>
<td>5</td>
<td>5.6</td>
</tr>
<tr>
<td>TL (mm)</td>
<td>-</td>
<td>45.4</td>
<td>36.8</td>
<td>39.5</td>
<td>37</td>
</tr>
<tr>
<td>TAL (mm)</td>
<td>-</td>
<td>29.5</td>
<td>29.5</td>
<td>27.0</td>
<td>24.5</td>
</tr>
<tr>
<td>ED (mm)</td>
<td>0.9</td>
<td>1.4</td>
<td>1.5</td>
<td>1.6</td>
<td>1.1</td>
</tr>
<tr>
<td>IOD (mm)</td>
<td>4.4</td>
<td>4.2</td>
<td>4.3</td>
<td>3.9</td>
<td>3.3</td>
</tr>
<tr>
<td>IND (mm)</td>
<td>1.2</td>
<td>2.2</td>
<td>2.2</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td>ESD (mm)</td>
<td>3</td>
<td>4.5</td>
<td>3.9</td>
<td>3.9</td>
<td>3.7</td>
</tr>
<tr>
<td>TMH (mm)</td>
<td>2.7</td>
<td>3.9</td>
<td>4.8</td>
<td>4.4</td>
<td>4.4</td>
</tr>
<tr>
<td>TMW (mm)</td>
<td>1.9</td>
<td>3.9</td>
<td>3.6</td>
<td>2.8</td>
<td>2.9</td>
</tr>
<tr>
<td>MTH (mm)</td>
<td>-</td>
<td>7.9</td>
<td>6.9</td>
<td>6.3</td>
<td>5.7</td>
</tr>
<tr>
<td>DF (mm)</td>
<td>-</td>
<td>1.2</td>
<td>1.6</td>
<td>1.1</td>
<td>1.5</td>
</tr>
<tr>
<td>TMHM (mm)</td>
<td>-</td>
<td>4.7</td>
<td>4.1</td>
<td>3.7</td>
<td>3.4</td>
</tr>
<tr>
<td>VF (mm)</td>
<td>-</td>
<td>1.5</td>
<td>1.1</td>
<td>0.8</td>
<td>1.5</td>
</tr>
<tr>
<td>ODW (mm)</td>
<td>2.5</td>
<td>5.3</td>
<td>5</td>
<td>3.8</td>
<td>4.1</td>
</tr>
<tr>
<td>LTRF</td>
<td>3(2–3)/3(1)</td>
<td>4(2–4)/3(1)</td>
<td>4(2–4)/3(1)</td>
<td>4(2–4)/3(1)</td>
<td>4(2–4)/3(1)</td>
</tr>
<tr>
<td>LTD</td>
<td>40</td>
<td>27</td>
<td>28</td>
<td>30</td>
<td>33</td>
</tr>
<tr>
<td>LTN</td>
<td>86</td>
<td>101</td>
<td>95</td>
<td>88</td>
<td>76</td>
</tr>
<tr>
<td>PN</td>
<td>59</td>
<td>103</td>
<td>94</td>
<td>76</td>
<td>78</td>
</tr>
</tbody>
</table>

**Description.** Based on one tadpole from series ZSM 123/2007 (field number ZCMV 4051; Genbank accession number EU717892; Figure 1). Specimen in developmental stage 25 and in fairly good state of preservation (a small ventral part of tail excised for DNA analysis). BL 9.8 mm, TL 27.4 mm, for further measurements see Table 1. Colouration in preservative brown with a yellowish shade, pale brown with a few irregular dark brown spots on body and dorsal fin, not visible in ventral view. Belly and two-thirds of ventral caudal fin almost lacking these darker spots. In dorsal view body shape ovoid-elongated. In lateral view body appears elongated and depressed, BW 1.26 of BH. Body shape in lateral view flattening toward snout. Nostrils directed dorsolaterally, not protuberant, positioned closer to tip of snout than to eyes. IND 0.67 of IOD. Eyes positioned dorsally, moderately sized, ED 0.09 of BL, protuberant, not visible in ventral view. Snout rounded in lateral view, nearly rounded in dorsal view. Spiracle sinistral, closely attached to body wall at the end of spiracle, oriented posteriorly, not visible in dorsal view. Spiracular opening oval, inner wall free from body, slightly closer to tip of snout than to end of body. ESD 0.26 of BL. Intestinal spiral well visible in ventral view, not visible in dorsal and lateral view. Short, flattened vent tube, medial with lateral dextral displacement. Caudal musculature well-developed, TMH 0.88 of BH and 1.04 of MTH, gradually tapering from base to the round fin tip. Dorsal fin homogeneous and more pigmented than ventral fin, originating behind base of caudal musculature, slowly increasing in height. MTH 0.85 of BH. Ventral fin convex in its outline, ventral fin at maximum height even higher than dorsal fin, curved towards tail tip. Dorsal fin slightly convex. Oral disc small, generalized, ODW 0.32 of BL and 0.56 of BW, transversally elliptical, directed anteroventrally, laterally emarginated, not visible in dorsal view, but margins visible in lateral view. Large...
dorsal gap of marginal papillae, all papillae with a rounded tip. Lower and upper labium with two rows of papillae, some with pigmented cores. Total number of papillae 98. LTRF 4(2–4)/3 (with small gaps in rows A1, P2 and P3, here interpreted as deformities), about 76 teeth per mm and a total of 105 teeth in A2. Tooth row length decreases from A2 to A4. Large medial gap in second anterior tooth row and small medial gap in first anterior tooth row. Second and third posterior row are with one and three small medial gaps. Beak well developed, upper jaw sheath M-shaped and lower jaw sheath V-shaped. Both jaw sheaths gently serrated, with three parts having different colourations: base totally keratinised, black; medial part partially keratinised, brown; edge not keratinised, unpigmented.

**Variation.** The series ZSM 123/2007 consists of 14 specimens in stages 24–25. Proportions vary as follows: BW 1.03–1.47 of BH, IND 0.47–0.88 of IOD, ED 0.09–0.11 of BL, ESD 0.26–0.35 of BL, TMH 0.55–0.83 of BH, TMH 0.60–1.08 of MTH, MTH 0.72–0.95 of BH, ODW 0.29–0.47 of BL, ODW 0.51–0.79 of BW, TAL 1.88–2.41 of BL, BL 0.29–0.35 of TL, TAL 0.65–0.70 of TL. Tooth row formula variations are as follows: 5(2–5)/3; 5(2–5)/3(1); 4(2–4)/3; 4(2–4)/3(1). There was no obvious correlation between the number of tooth rows and developmental stages of the tadpoles. Gaps in rows P2 and P3, here interpreted as oral deformities, were encountered in several specimens. Numbers of labial teeth per mm in A2 vary from 67–88; numbers of papillae vary from 71–98. The intestinal spiral is always visible in ventral view. There are differences in lateral and dorsal view, in some specimens the intestinal spiral is visible in both views, in others only in lateral view.

**FIGURE 1.** Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. aff. *biporus* “Ranomafana (stage 25), series ZSM 123/2007; (a) oral disc, (b) dorsal view, (c) lateral view. Scale bars represent 1 mm.

*Mantidactylus* sp. aff. *biporus* “Marojejy

**Series examined.** ZSM 1592/2007 (1 specimen). The single tadpole was collected by R.-D. Randrianaiaina, F. Glaw and M. Vences on 17 February 2005 in a small stream inside primary forest in Marojejy National Park, close to a campsite locally known as Camp Simpona. Stream with yellowish water and a muddy bottom with leaf litter. Maximal width 40 cm, canopy along the stream opened 20%. Further data: O$_2$: 4.0 mg/l; NO$_3$: <0.1 mg/l; NO$_3$: 0 mg/l; PO$_4$: 0.1 mg/l; NH$_4$/N$_5$: 0 mg/l; Fe: 0.1 mg/l; carbonate hardness: 1; total hardness: 4; pH: 6.3; air temperature: 18.4°C; water temperature: 17.9°C.

**Taxonomic note.** The DNA sequence of the single tadpole agrees most closely with DNA sequences from adult specimens of an undescribed *Mantidactylus* species from the same area (e.g., ZCMV 2017). These specimens bear superficial morphological similarities to *Mantidactylus biporus* but differ distinctly in their DNA sequences, and it is very likely that they represent a separate species.

**Description.** Based on the single tadpole available (ZSM 1592/2007; field number FGZC 2901; Genbank accession number EU717893; Figure 2). Tadpole in developmental stage 29 and in good state of preservation (a small part of ventral tail excised for DNA analysis). BL 9.8 mm, TL 27.4 mm, for further measurements see
Table 1. Colouration of the preserved tadpole pale brown with a slightly yellowish shade, dark brown with clearly visible edges at the end of body. Tadpole scattered with small, slightly darker irregular spots, including dorsal fin, especially posterior to body-tail junction in dorsal view. Belly and ventral caudal fin transparent with a slightly yellowish shade, almost lacking darker spots. In dorsal view body shape ovoid-rounded, head and body separated by a constriction of body wall at plane of spiracle. In lateral view body ovoid-depressed with a slightly elongated shape, slowly flattening from body-tail junction to snout, BW 1.06 of BH. Nostrils directed dorsolaterally, pointed, not protuberant, positioned closer to tip of snout than to eyes. IND 0.46 of IOD. Eyes positioned dorsally, orientated dorsolaterally, moderately sized, protuberant, and not visible in ventral view, ED 0.08 of BL. Snout rounded in dorsal and slightly rounded in lateral view. Spiracle sinistral, close to body, at the end inner wall free from body wall. Spiracular opening oval, oriented posteriorly, closer to tip of snout than to end of body, ESD 0.27 of BL. Intestinal spiral not visible in lateral view and very slightly visible in ventral view. Short, flattened vent tube, almost medial with lateral dextral displacement. Caudal musculature well developed, TMH 0.83 of BH and 0.92 of MTH, origin well visible in dorsal view and lower positioned (at the end of body in lateral and dorsal view), gradually tapering from base to tip. Dorsal fin originating on base of caudal musculature, increasing in height by one-third, MTH 0.9 of BH. Dorsal and ventral fin maintaining equal height to finely rounded tip. Fins to the end of caudal musculature nearly equally high, slightly convex in outline, margins not running parallel with margins of tail muscle. Oral disc small, generalized, ODW 0.38 of BL and 0.95 of BW, transversely ovoid, directed anteroventrally, laterally emarginated, not visible in dorsal view, but margins visible in lateral view. Large dorsal gap in marginal papillae. Lower labium with two rows of papillae (with pointed tip). All papillae from upper labium with a rounded tip. Some cores of papillae pigmented. Total number of papillae 91. LTRF 5(2–5)/3(1), about 19 teeth per mm and a total of 98 teeth in A2. Tooth row length decreases from A2 to A5. Large medial gap in second anterior tooth row. Only first posterior row with small medial gap. Beak well developed and black, both jaw sheaths gently serrated. Upper jaw sheath M-shaped, lower jaw sheath V-shaped.

FIGURE 2. Drawings of the preserved DNA voucher tadpole of Mantidactylus sp. aff. biporus “Marojejy (stage 29), series ZSM 1592/2007; (a) oral disc, (b) dorsal view, (c) lateral view. Scale bars represent 1 mm.

Mantidactylus curtus (Boulenger)

Series examined. ZSM 943/2004 (1 specimen). The single specimen was collected near Antoetra by M. Vences in the period of 18–22 January 2003 in a stream flowing through largely deforested highland grassland, with some bushes and isolated trees. The stream had a width of 1.5–3 m and included some small and shallow tributaries. Parts of the stream were of clear and fast-flowing water and rocky bottom whereas other parts, and especially the tributaries, were slow-moving, with the water largely covered by high grass tufts.
**Taxonomic note.** Tadpoles described by Arnoult & Razarihelisoa (1967) and Blommers-Schlösser (1979) as *Mantidactylus curtus* most likely belong at least partly to a different species (see section on *Mantidactylus* sp. aff. *curtus* "Ankaratra" below). The tadpole described here originates instead from a site in the general region corresponding to the type locality of *M. curtus* ("East Betsileo"), and its DNA sequence is close to specimens that we assign to this species (see Glaw & Vences 2007: page 237, figs. 1a and 1b).

**Description.** Based on the single voucher specimen (ZSM 0943/2004; field number FG/MV 2003.1757; Genbank accession number EU717879; Figure 3) in developmental stage 26, and in good state of preservation (a huge section from the dorsal tail has been excised for DNA analysis). BL 14.8 mm, TL 42.3 mm, for further measurements see Table 1. Colouration in preservative yellowish, transparent. A dark mid-dorsal yellowish line slightly visible through skin. Dark yellowish pigments concentrated dorsally besides eyes and at middle of body. Caudal fin dorsally covered to the tip with some irregular light brown patches and spots. Belly, caudal muscle and ventral fin almost uniformly transparent. In dorsal view, body shape ovoid to nearly rounded, snout elongated and flattened to tip. In lateral view, body depressed, BW 1.32 of BH, snout rounded. Nostrils elliptical and pointed to tip of snout, rimmed with a mediodorsal projection giving them a bean shape, not protuberant, positioned dorsolaterally. IND 0.38 of IOD. Nostrils, closer to tip of snout than to eyes. Eyes positioned dorsally, directed dorsolaterally, and moderately sized, ED 0.07 of BL, not protuberant. Spiracle sinistral, not visible in dorsal view, attached to body wall but its inner wall lifting up from body wall, closer to snout than to end of body, ESD 0.26 of BL. Spiracular opening oval, laterally positioned, oriented posteriorly. Intestinal spiral not visible in dorsal view, well visible in ventral and lateral views. Medial vent tube with lateral displacement, dextral. Caudal musculature rather strongly developed, upper origin well visible in dorsal view, TMH 0.76 of BH and 0.72 of MTH, fast tapering from approximately three-fourths of tail, almost reaching the tip. Dorsal fin originating at the end of first-quarter of caudal muscle, point of maximum height located after mid-tail, MTH 1.06 of BH. Margins of ventral and dextral fin slightly convex to finely rounded tail tip. Oral disc of moderate size, generalized, laterally emarginated, ODW 0.32 of BL and 0.56 of BW, transversely ovoid to nearly rounded, anteroventrally positioned, with robust dark coloured beaks, which slightly lost keratinisation. Oral disc margins not visible in dorsal view, but visible in lateral view. LTRF 5(2–5)/3(1), with additional gaps in rows A1 and P3, here interpreted as oral deformities. About 30 teeth per mm and a total of 115 teeth in A2. A5 very small, consisting of only 5 teeth on right side and 3 teeth on left of oral disc. Three small gaps in first anterior tooth row and large medial gap in second anterior tooth row. First and third posterior tooth rows with small medial gap.

![FIGURE 3. Drawings of the preserved DNA voucher tadpole of *Mantidactylus curtus* (stage 26), series ZSM 943/2004; (a) oral disc, (b) lateral view, (c) dorsal view. Scale bars represent 1 mm.](image)

Upper labium with large dorsal gap in marginal papillae, upper and lower labium with two rows of papillae. Papillae with a rounded tip (some pigmented), sporadically with pointed tip (total number of

54 · *Zootaxa* 1988 © 2009 Magnolia Press
papillae: 82). Upper jaw sheath M-shaped, lower jaw sheath V-shaped, both with almost equal-sized serrations.

*Mantidactylus* sp. aff. *curtus* "Ankaratra"

**Series examined.** Four tadpole series, ZSM 570/2008 (9 specimens; field number ZCMV 2601), ZSM 564/2008 (5 specimens; field number ZCMV 2607), ZSM 565/2008 (5 specimens; field number ZCMV 2609), ZSM 571/2008 (5 specimens; field number ZCMV 2615), all collected by R.D. Randrianiaina and D. R. Vieites on 14–15 February at Ambohimirandranana, Ankaratra Massif, Central Madagascar, in a mountain stream above the tree line, bordered by only isolated trees and bushes. The stream was of about 1 m width and rather fast-flowing. The collecting site was below a cascade. *Mantidactylus* sp. aff. *curtus* was one of the most common frogs along this stream.

**Taxonomic note.** Previous tadpole descriptions under the name *Mantidactylus curtus* by Arnoult & Razarihelisoa (1967) and Blommers-Schlösser (1979) likely refer to this species and not to *M. curtus*, because no specimens from near the *M. curtus* type locality were studied and genetic data indicate that the populations previously assigned to *M. curtus* are genetically highly divergent, with different areas and massifs in central Madagascar harbouring exclusive species of the complex (Andringitra: *M. bourgati*; Itremo and Antoetra areas: *M. curtus*; Ankaratra: *M. sp. aff. curtus* "Ankaratra"; Ambohitantely / Tampoketsa d'Ankazobe: *M. sp. aff. curtus* "Ambohitantely").

In the descriptions of Arnoult & Razarihelisoa (1967) an error in the drawings of mouthparts was detected (Blommers-Schlösser 1979). In the study of Blommers-Schlösser (1979), additional specimens from the locality Angavokely were also used for the descriptions. Because specimens from this site have not yet been studied genetically, it is at present uncertain if the description of Blommers-Schlösser (1979) may refer to a composite of species. We here provide a redescription of tadpoles of *M. sp. aff. curtus* “Ankaratra based on reliably identified specimens, all from the Ankaratra Massif.

**Description.** Based on the DNA voucher tadpole of the series ZSM 570/2008 (Genbank accession number EU717889; Figure 4). Tadpole in developmental stage 36, and in good state of preservation (a part of the ventral tail has been excised for DNA analysis). BL 17.0 mm, TL 46.2 mm, for further measurements see Table 1. Colouration of preserved tadpole dark to light brown with a slightly yellowish transparent shade. Head and body slightly separated by a constriction of body wall at plane of spiracle. Behind this separation, at the end of body, dark brown colouration in dorsal and lateral view. Next to each nostril, a dark brown coloured short line visible through transparent skin, not visible in ventral view. In dorsal and lateral view, large irregular brown spots, particularly concentrated on posterior fourth of tail. Belly and first two-thirds of ventral caudal fin lacking these darker spots. In dorsal view body shape elongated-elliptical. In lateral view, body depressed, BW 1.32 of BH. Body shape in lateral view without a distinct flattening toward snout. Nostrils rimmed with a mediadorsal projection giving them an arrow shape, not protuberant, positioned dorsolaterally, IND 0.63 of IOD. Nostrils closer to tip of snout than to eyes. Eyes positioned dorsally, directed dorsolaterally, ED 0.12 of BL, not protuberant. Spiracle sinistral, attached to body wall but its inner wall lifting up from body wall to tip. Spiracular opening oval, oriented posteriorly, slightly visible in dorsal view, upper margin situated under level of lower margin of eye, slightly closer to snout than to end of body, ESD 0.21 of BL. Intestinal spiral slightly visible in lateral view and well visible in ventral view, not visible in dorsal view. Medial vent tube with lateral displacement, dextral. Caudal musculature well developed, TMH 0.87 of BH and 0.71 of MTH. Dorsal fin originating at body-tail junction, vastly increasing in height at proximal quarter of tail, MTH 1.23 of BH, equal height throughout two-thirds of tail, slightly diminishing to finely rounded tip. Dorsal and ventral fin convex in outline, nearly equally sized. Oral disc small, generalized, laterally emarginated, ODW 0.33 of BL and 0.69 of BW, anteroventrally positioned, transversely rounded. Oral disc margins not visible in dorsal view, but visible in lateral view. Total number of papillae 91. LTRF 5(2–5)/3(1), about 30 teeth per mm in A2. Large medial gap in second anterior tooth row. Only the first posterior row with small medial gap.
Upper labium with large dorsal gap, upper and lower labium with two continuous rows of papillae. Papillae with a rounded tip, few of them pigmented, sporadically with a pointed tip. Dark coloured beak which slightly lost keratinisation to the border. Upper jaw sheath M-shaped, lower jaw sheath V-shaped, both with almost equal-sized serrations.

![Figure 4](image)

**FIGURE 4.** Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. aff. *curtus* Ankaratra (stage 36), series ZSM 570/2008; (a) oral disc, (b) dorsal view, (c) lateral view. Scale bars represent 1 mm.

**Variation.** To summarize variation we grouped specimens from all series based on their developmental stages. 12 specimens were in stages 25–30: stage 25 (1 specimen), 28 (2 specimen), 29 (3 specimens) and 30 (6 specimens). Proportions: BW 1.15–1.51 of BH, IND 0.42–0.62 of IOD, ED 0.07–0.13 of BL, ESD 0.21–0.28 of BL, TMH 0.72–0.97 of BH, TMH 0.68–0.85 of MTH, MTH 0.74–1.5 of BH, ODW 0.29–0.36 of BL, ODW 0.52–0.79 of BW, TAL 1.59–2.35 of BL, BL 0.30–0.39 of TL, TAL 0.61–0.70 of TL. LTRF: 5(2–5)/3(1); 4(2–4)/3(1). Labial teeth per mm in A2: 27–34. Numbers of papillae: 66–113.

11 additional tadpoles were in stages 31–38: stage 31 (1 specimen), 32 (2 specimens), 33 (4 specimens), 34 (2 specimens), 35 (1 specimen), 38 (1 specimen). Proportions: BW 1.24–1.60 of BH, IND 0.39–0.83 of IOD, ED 0.08–0.13 of BL, ESD 0.20–0.27 of BL, TMH 0.58–1.13 of BH, TMH 0.69–0.89 of MTH, MTH 0.74–1.45 of BH, ODW 0.25–0.35 of BL, ODW 0.46–0.80 of BW, TAL 1.56–2.49 of BL, BL 0.29–0.39 of TL, TAL 0.63–0.71 of TL. LTRF: 5(2–5)/3(1); 4(2–4)/3(1) (small non-medial gaps in some specimens in A1, here interpreted as oral deformities). There was no obvious correlation between the number of tooth rows and developmental stages of the tadpoles. Labial teeth per mm in A2: 24–31. Numbers of papillae: 76–100.

In earlier stages the skin is less brownish and often more transparent. Behind the separation at the end of the body, sometimes dark brown colouration in dorsal and lateral views and in other cases (not age-related) light brown in dorsal view.

**Mantidactylus alutus** (Peracca)

**Series examined.** ZSM 1482/2007 (1 specimen; field number FGZC 2212), ZSM 1490/2007 (6 specimens; field number FGZC 2221), ZSM 562/2008 (2 specimens; field number FGZC 2224), and ZSM 1492/2007 (9 specimens; field number FGZC 2225) all collected in an unspecified water body in a small forest near the main campsite, by L. Raharivololoinina and R.-D. Randrianiaina, at Ambohitantely Special Reserve on 18–19 January 2005. ZSM 945/2004 (1 specimen; FG/MV 2002.1759), ZSM 946/2004 (1 specimen; field number FG/MV 2002.1761), ZSM 947/2004 (1 specimen; field number FG/MV 2002.1762) and ZSM 949/2004 (1 specimen; field number FG/MV 2002.1764), all from a site near Antoetra, collected in the period of 18–22 January 2003 by M. Vences (for a habitat description, see section on *M. curtus* above).
Taxonomic note. Tadpoles of *M. alutus* were previously described by Boulenger (1918) and Blommers-Schlösser (1979). According to our mitochondrial DNA data, *M. alutus* is genetically homogeneous across its distribution range (Glaw & Vences 2007; see also sequences available from Genbank), and the previous descriptions thus are likely to be correctly assigned to this species. We here complement previous data with more details, and with information on additional populations. The data of Blommers-Schlösser (1979) referred to pooled samples from several localities (Angavokely, Antananarivo, Manjakatomp). We additionally provide morphological data referring to tadpoles from Ambohitantely and Antoetra (see table 1).

Description. Based on the DNA voucher tadpole from series ZSM 1490/2007 (field number FGZC 2221; Genbank accession number EU717886; Figure 5). Specimen in developmental stage 40, and in good state of preservation (the whole right hindlimb has been excised for DNA analysis). BL 15.5 mm, TL 51.5 mm, for further measurements see Table 1. Colouration in preservative throughout brownish with a grey transparent shade through skin, and dark irregular spots in dorsal and lateral view, with light brown irregular spots, and dorsally with a lack of dark spots at mid-body. A dark brown coloured linear structure shines through the skin, dorsally, from each nare to the eyes, not visible in ventral view. Belly and two-thirds of ventral caudal fin almost lacking these darker spots. In dorsal view, body shape ovoid. In lateral view, body depressed-elongated and shape slightly flattening toward snout, BW 1.20 of BH. Nostrils directed dorsolaterally, rounded, slightly protuberant, positioned at equal distance between tip of the snout and eyes, IND 0.56 of IOD. Eyes positioned dorsally, orientated dorsolaterally, not protuberant, moderately sized, ED 0.12 of BL, not visible in ventral view. Snout nearly pointed in lateral view, rounded in dorsal view. Spiracle single, sinistral, attached to the body wall, with inner wall free from body wall at the tip. Spiracular opening oval, oriented posteriorly, situated closer to the end of the body than to the snout, ESD 0.33 of BL. Intestinal spiral well visible in ventral and lateral views, only a dark brown shadow of it visible in dorsal view. Flattened vent tube, right wall displaced dorsally. Caudal musculature strong developed, upper origin well visible in dorsal view, TMH 0.93 of BH and 0.78 of MTH, gradually tapering from base to slightly pointed caudal muscle tip. Dorsal fin originating behind base of caudal muscle, slowly increasing in height, MTH 1.17 of BH, slightly diminishing to tip. Dorsal and ventral fin slightly convex in outline, dorsal fin at its maximum height slightly higher than ventral fin. Oral disc small, generalized, ODW 0.34 of BL and 0.57 of BW. Transversely elliptical, directed anteroventrally, laterally emarginated, not visible in dorsal view, but margins visible in lateral view. Large dorsal gap of marginal papillae, lower labium with two continuous rows of papillae. Papillae with a rounded tip and some pointed. Total number of papillae 92, some of them pigmented. LTRF 4(2–4)/3(1), with an additional small gap in row P3, here interpreted as oral deformity. About 36 teeth per mm and a total of 104 teeth in A2. Tooth row lengths decrease from A1 to A4, with A4 consisting of 13 teeth only on the right side of the oral disc. Large medial gap in second anterior tooth row and a large dorsal gap. First and third posterior tooth rows with small medial gap.

FIGURE 5. Drawings of the preserved DNA voucher tadpole of *Mantidactylus alutus* (stage 40), series ZSM 1490/2007; (a) oral disc, (b) dorsal view, (c) lateral view. Scale bars represent 1 mm.
Beak well developed and dark brown, both jaw sheaths with serrations at their cutting edges, with three parts having different colourations: base, entirely keratinised, black; middle part, partially keratinised, brown; outer edges, not keratinised, unpigmented. Upper jaw sheath M-shaped, lower jaw sheath V-shaped.

**Variation.** To summarize variation we grouped specimens from all series based on their developmental stages. Seven tadpoles were in stages 25–28: stage 25 (3 specimens), 26 (1 specimen), 28 (3 specimens). Proportions: BW 1.03–1.56 of BH, IND 0.26–0.67 of IOD, ED 0.08–0.13 of BL, ESD 0.29–0.43 of BL, TMH 1.05–0.68 of BH, TMH 0.72–0.97 of MTH, MTH 0.97–1.31 of BH, ODW 0.28–0.37 of BL, ODW 0.51–0.73 of BW, TAL 1.58–2.19 of BL, BL 0.31–0.39 of TL, TAL 0.61–0.69 of TL. LTRF: 3(2–3)/3(1); 3(2–3)/3(1); 4(2–4)/3(1). Labial teeth per mm in A2: 24–41. Number of papillae: 59–105.

Thirteen additional tadpoles were in stages 31–40: stage 31 (2 specimens), 37 (3 specimens), 39 (2 specimens), 40 (6 specimens), Proportions: BW 1.14–1.83 of BH, IND 0.37–0.74 of IOD, ED 0.08–0.20 of BL, ESD 0.27–0.54 of BL, TMH 0.67–1.14 of BH, TMH 0.49–1.11 of MTH, MTH 0.89–1.72 of BH, ODW 0.29–0.68 of BL, ODW 0.48–0.62 of BW, TAL 1.58–2.49 of BL, BL 0.20–0.33 of TL, TAL 0.65–0.80 of TL. LTRF: 4(1–4)/3; 4(1–4)/3(1); 4(1–4)/3(1)/3(1); 4(2–4)/3; 4(2–4)/3(1)/3(1) (small non-medial gaps in some specimens in A1, here interpreted as oral deformities). Number of labial teeth per mm in A2: 27–43. Number of papillae: 75–121.

One tadpole was in developmental stage 42: Proportions: BW 1.02 of BH, IND 0.48 of IOD, ED 0.13 of BL, ESD 0.32 of BL, TMH 0.89 of BH, TMH 0.69 of MTH, MTH 0.29 of BH, ODW 0.31 of BL, ODW 0.74 of BW, TAL 2.20 of BL, BL 0.31 of TL, TAL 0.68 of TL. LTRF: 4(1–4)/3(1). Number of labial teeth per mm in A2: 30. Number of papillae: 76.

The tadpoles of *M. alutus* show a distinct correlation of the number of labial tooth rows and developmental stage: younger tadpoles (stages 25–26) had constantly three upper tooth rows, whereas in stages 28–40, an additional upper tooth row was visible in all specimens.

In earlier stages the skin is more transparent and less grey to more yellowish brown. A small gap in row P3 was observed in several specimens of earlier as well as advanced stages and is here interpreted as oral deformity.

**Discussion**

For two species of tadpoles described herein, those of *Mantidactylus alutus* and *M. sp. aff. curtus* "Ankaratra", previous morphological data are available from the work of Blommers-Schlösser (1979). For *M. alutus*, a comparison reveals only slight differences to the previous description, both regarding morphometric values and oral disc characters. Similarly, for *M. sp. aff. curtus*, the comparison with tadpoles described by Blommers-Schlösser (1979) under the name *M. curtus* reveal no relevant differences.

With the present contribution, we add descriptions of three additional and previously unknown *Brygoomantis* larvae to the existing descriptions, and provide more precise data on two further species. Considering the descriptions of Arnoult & Razarihelisoa (1967), Blommers-Schlösser (1979), Thomas *et al.* (2005), and Knoll *et al.* (2007), at present the tadpoles of ten *Mantidactylus* species assigned to the subgenus *Brygoomantis* are reliably known. Of these, five refer to described species and five to yet undescribed or unrecognized species: *Mantidactylus alutus*, *M. betsileanus*, *M. biporus*, *M. curtus*, *M. madecassus*, *M. sp. aff. biporus* "Marojejy", *M. sp. aff. biporus" RANOMAFANA", *M. sp. aff. betsileanus" very slow calls", *M. sp. aff. betsileanus" Vohidrazana", *M. sp. aff. curtus" Ankaratra". In addition, Blommers-Schlösser (1979) provided data on an undescribed species from Foulpointe and Fenerive on the east coast of Madagascar (as *M. ulcerosus*), and Glaw & Vences (1994) provide a very brief statement on the LTRF of the larvae of *M. ulcerosus* from the type locality Nosy Be.

All these larvae are benthic tadpoles (Altig & Johnston 1989) of a rather generalized body shape and oral disc morphology, with a large dorsal gap of marginal papillae, and a LTRF of 3–5 keratodont rows on the anterior labium of which only the first is continuous and the others have distinct medial gaps, being positioned...
at either side of the upper jaw sheath, and three keratodont rows on the posterior labium of which the first usually has a very small medial gap which however can sometimes be undetectable. Total number of marginal and submarginal papillae ranges from 50 to 103 and keratodont density on A2 ranges from 19 to 76. Compared to data from a second species-rich group of mantelline frogs, the genus Boophis, Brygoomantis tadpoles show very little variability. The number of marginal and submarginal papillae, for example, can vary from 56 up to several hundreds in Boophis (Raharivololoniaina et al. 2006; Randrianiaina et al. in press).

An interesting pattern was found in the presence or absence of gaps in rows of labial teeth in the specimens studied here. There are two different kinds of gap to be considered: those which are likely to be part of the typical morphology of the tadpoles but sometimes are absent or unrecognizable, and those that likely represent oral deformities. As an example for the first category, we count the medial gaps in A2 and in P1. Especially the small central gap in P1 is usually present in most mantellid tadpoles, but sometimes is not clearly recognizable and thus not counted in the LTRF. Whether presence or absence of this gap is more influenced by phylogenetic or ontogenetic factors remains unexplored.

Oral deformities can occur in remarkable frequencies in some tadpole populations (Drake et al. 2007). In several species studied here, we regularly observed small (usually non-medial) gaps in rows A1, P2 and P3 which we interpret as deformities. According to Drake et al. (2007), such deformities can be related to infection with Batrachochytrium dendrobatidis; this fungus, however, appears to be absent from Madagascar (Andreone et al. 2008), and we have verified this absence in several of the populations studied here (e.g., Mantidactylus sp. aff. curtus "Ankaratra" and M. alutus from Ankaratra and Ambohitantely). The origin of these anomalies thus remains unclarified as well.

Although Brygoomantis tadpoles are generalized, with some intraspecific variability, there are constant subtle differences between tadpoles of different species. Knoll et al. (2007) found morphological differences in the general body shape, colouration, and density of labial teeth also between closely related species in the Mantidactylus betsileanus complex. Of the tadpoles studied here, those of M. sp. aff. curtus are remarkable for their relatively large size and their dense black markings on the posterior part of the tail which are missing for example in the sympatric M. alutus. Unfortunately, only a single tadpole of the closely related M. curtus is available for comparison, which seems to lack this pattern.

Of the unknown larval stages in Brygoomantis, several belong to species that are phylogenetically close to other species of which the tadpoles have by now been described. For instance, relationships of Mantidactylus pauliani are likely with M. madecassus, of M. bourgati with M. curtus, and of several undescribed forms with either M. betsileanus, M. biporus, M. curtus, or M. ulcerosus. The most deviant species are a cluster of small frogs that include M. tricinctus and several allied undescribed species (see accounts in Glaw & Vences 2007), with adults sharing some characters otherwise typical to the subgenus Ochthomantis, such as yellow flanks spots. So far, tadpoles are not known for any of these species, and their discovery should thus be a priority to understand the evolutionary significance of the generalized tadpoles of the subgenus Brygoomantis compared to the highly derived tadpoles in the related subgenera Chonomantis, Hylobatrachus, and Ochthomantis (see Blommers-Schlösser 1979).

Acknowledgements

We are grateful to Julian Glos, Serge Ndriantsoa, Liliane Raharivololoniaina, Roger-Daniel Randrianiaina, and Hiobiarilanto Rasolonjatovo for their help in the field. This work was carried out in the framework of cooperation between the author's institutions and the Université d'Antananarivo (Département de Biologie Animale) and the Association Nationale pour la Gestion des Aires Protégées ANGAP. Financial support was provided by the Deutsche Forschungsgemeinschaft (grant VE247/2-1) to MV and AS, and by the Volkswagen Foundation to MV and FG.
References


