

The unexpectedly dull tadpole of Madagascar's largest frog, *Mantidactylus guttulatus*

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Submitted on 2016, 11th February; revised on 2016, 13th April; accepted on 2016, 9th July

Editor: Marco Sannolo

Abstract. The Madagascar-endemic mantellid genus *Mantidactylus* contains one subclade with two described frog species characterized by very large body sizes. This subclade is classified as the subgenus *Mantidactylus* and is widespread in eastern and northern Madagascar, but their reproductive biology and larval stages are still unknown. We here provide a detailed description of the larvae of one species in this subgenus, *M. guttulatus*, on the basis of genetic assignment (16S DNA barcoding). The tadpoles were collected in the dry season from shallow waters near a stream in the Mahajanga Province in northwestern Madagascar. Their body and tail shape is remarkably generalized as typical for stream-adapted tadpoles, and the oral disc and labial keratodont row formula (4(2-4)/3(1)) are similar to those of other lotic mantellid frog larvae with generalized mouthparts like those in the subgenus *Brygoomantis*. The well-separated positions of these subgenera in the mantellid phylogeny suggest extensive homoplasy in the evolution of larval mouthpart morphology within *Mantidactylus*.

Keywords. Amphibia, Madagascar, Mantellidae, *Mantidactylus*, generalized oral disc, tadpole morphology.

INTRODUCTION

Among Madagascar's native frogs, the family Mantellidae is the most diverse clade with 212 named species (Amphibiaweb, 2016) and numerous undescribed species (Vieites et al., 2009; Perl et al., 2014). Mantellids are endemic to Madagascar and the Comoros and include a fascinating diversity in ecomorphology and reproductive modes. The largest mantellids are classified in a well-supported subclade of the genus *Mantidactylus* (i.e., in the nominal subgenus *Mantidactylus*): *Mantidactylus guttulatus*, *M. grandideri*, and the candidate species *M. sp. aff. grandideri* "North", although their alpha-taxonomy is in need of revision (see comments under Materials and

Methods). With up to 120 mm snout-vent length *M. guttulatus* is the largest frog in Madagascar and is common in rainforest streams of the northern and eastern part of the island (Glaw and Vences, 2007).

Despite their size and local abundance, information on the reproduction of this frog species is scarce and basically limited to one report of a calling specimen (Vences et al., 2004). Because for decades no tadpoles could be assigned to *Mantidactylus guttulatus* or its close relatives, it was assumed that these species lack a larval phase or that the pre-metamorphic tadpoles develop in a nesting burrow (Glaw and Vences, 1994, 2007). Altig and McDiarmid (2006) described a tadpole with reduced oral structures from the Ranomafana region and tentatively

assigned it as belonging to *M. guttulatus*. Randrianiaina et al. (2011) provided molecular evidence for an assignment of these tadpoles to *M. majori* whose juveniles are morphologically similar to those of *M. guttulatus*.

During a survey in northwestern Madagascar, we obtained a small series of three *Mantidactylus* tadpoles that we initially identified by morphology as belonging into the subgenus *Brygoomantis*, despite being more elongated than other, syntopic *Brygoomantis* larvae. Molecular evidence demonstrated that these tadpoles instead belonged to *Mantidactylus guttulatus*, and we provide a detailed description of their morphology.

MATERIALS AND METHODS

Three tadpoles (field numbers ZCMV 13332, 13333 and 13334) were collected by R.D. Randrianiaina, F.M. Ratsoavina, A.S. Rasamison, A. Rakotoarison, D.R. Vieites, and M. Vences in the dry season on 29 June 2010. They were found in an opportunistic encounter survey near a large stream close to the Analamondrotra mobile phone pylon, between 56-57 km along the national road N°31 from Bealanana to Antsohihy (14.72602°S, 048.55497°E; 1175 m a.s.l.) in the Mahajanga Province.

Tadpoles were euthanized in a chlorobutanol solution shortly after collection. A tissue sample from the first third of the tail musculature of each tadpole was preserved in 99% ethanol. After tissue sampling, all specimens were preserved in 5% formalin and two of them were deposited in the Zoologische Staatssammlung München, Germany (ZSM; collection numbers ZSM 704/2010, ZSM 705/2010).

Tadpoles were identified by DNA barcoding based on a fragment of the mitochondrial 16S rRNA gene (Thomas et al., 2005). The fragment of about 550 bp was amplified with primers 16Sar-L and 16Sbr-H from Palumbi et al. (1991) and standard protocols resolved on automated sequencers were compared to a nearly complete database of sequences of adult Malagasy frog species. DNA sequences were deposited in GenBank (accession numbers KX023902, KX023903, KX023904).

For species names in the subgenus *Mantidactylus*, we here follow the taxonomy suggested by Glaw and Vences (2007) who defined *M. guttulatus* as the species with a rather tubercular dorsum occurring mostly in northern Madagascar, and *M. grandidieri* as the species with smooth skin widespread in the southern and central east of the island. This differs from the definition of Altig and McDiarmid (2006) who applied the name *M. guttulatus* to populations from the southern central east. However, it is obvious that this taxonomy is in need of revision and it is likely that the available names (*Rana guttulata* Boulenger, 1881; *Mantidactylus grandidieri* Mocquard, 1895; and *Rana pigra* Mocquard, 1900, currently a synonym of *M. guttulatus*) will have to be applied in a different way to the biological entities in the subgenus than in current practice. In fact, the tadpoles described herein might turn out to belong to a yet undescribed species. Independent from this taxonomic conundrum, however, the subgenus *Mantidactylus* is well defined and

the molecular data leave no doubt that the tadpoles described herein belong into this clade.

A Canon DSLR with 100 mm 2.8L and MP-E 65 mm lenses mounted on an electronic-driven macro rail was used to obtain the digital images of the preserved specimens. A stack of 10-15 images was taken and merged with Helicon Pro software to achieve images with a wide depth of focus.

Morphological descriptions and measurements were done on the basis of digital and scaled images of preserved tadpoles. Terminology of morphological characters follows Altig and McDiarmid (1999). Gosner's (1960) classification was used to identify developmental stages. Structures of the oral apparatus were described according to Altig (1970), except for the term "keratodont," which is used for the keratinized structures on the labia of the oral disc and presented as the labial keratodont row formula (LKRF). Marginal papillae are considered separately for the region of the upper labium, the lateral region, and the region of the lower labium and the "marginal papillae row formula" (MPRF) is provided according to Schulze et al. (2015). All morphological landmarks and distances considered for the description are described and specified in Table 1. Comparing measurements, we consider them as "almost equal" if ratios of the measured values are 95-96% or 104-105%, "equal" if they are in the range 97-103%, as almost "in the middle" if they are in the range 45-46% or 54-55% and "in the middle" if they are in the range 47-53% (Randrianiaina et al., 2011).

RESULTS

Three tadpoles identified by 16S DNA barcoding as *Mantidactylus guttulatus* were collected within rainforest and close (ca. 20 m) to a large stream of 25 m width. The tadpoles were in a seepage area of a small, very shallow puddle (1-2 cm deep) with a slow steady flow of water. The 16S rDNA sequences of these tadpoles were 99% identical to a reference sequence of an adult *M. guttulatus* from the Tsaratanana Massif (GenBank accession no. FJ559237). The following description refers to one of these tadpoles in Gosner stage 26 (field number ZCMV 13332 / ZSM 704/2010, body length 9.5 mm, tail length 30.7 mm; Figs. 1, 2; Tab. 1). In dorsal view body elliptical, maximal body width attained almost at mid-body length, snout narrowly rounded. In lateral view, body depressed, maximal body height attained between the 3/5 and 4/5 of the body length, snout rounded. Eyes moderately large, not visible from ventral view, positioned high laterally and directed anterolaterally, situated between the 2/10 and 3/10 of the body length. Distance between eyes wide. Nares rounded and small, marked with a marginal rim, positioned moderately high dorsolaterally and directed anterolaterally, situated closer to snout than to eye and lower than eye. Distance between nares wide. Spiracle sinistrally positioned and short, directed posteriorly, visible from ventral view, invisible from dorsal

Table 1. Measurements of landmarks (in mm) and their ratios (in %) of the preserved tadpole specimen of *Mantidactylus guttulatus* (ZCMV 13332 / ZSM 704/2010) at Gosner stage 26: A₁ = first upper keratodont row; BH = maximal body height; BL = body length; BW = maximal body width; DF = dorsal fin height at region of mid-tail; DG = size of the gap of marginal papillae in the region of the upper labium; DMTH = distance of maximal tail height from the tail-body junction; ED = eye diameter; HAB = height of the point where the axis of the tail myotomes contacts the body, measured from the lower curve of the belly; IND = inter-narial distance, measured from the centre of the eyes; IOD = inter-orbital distance; JW = maximal width of keratinized upper jaw sheath; MTH = maximal tail height; NH = naris height, measured from the lower curve of the belly to the centre of the naris; NP = naris-pupil distance; ODW = maximum width of opened oral disc; RN = rostro-narial distance, measured from the centre of the nares; SBH = distance between snout and the point of maximal body height; SBW = distance between snout and the point of maximal body width; SE = snout-eye distance, measured to the centre of the pupil; SH = spiracle height; SL = spiracle length, measured from its visible edges; SS = snout-spiracle distance, measured from the centre of the spiracle opening; TAL = tail length, measured from medium point of body-tail junction; TH = tail height at the body-tail junction; THM = tail height at mid-tail; TL = total length; TMH = tail muscle height at the body-tail junction; TMHM = tail muscle height at mid-tail; TMW = tail muscle width at the body-tail junction; VF = ventral fin height at mid-tail.

Landmarks	mm	Ratio	%
BH	4.1	SBW - BL	57
BL	9.5	BW - BH	117
BW	4.8	SBW - BL	57
DF	0.9	ED - BL	11
DG	1.4	SE - BL	25
DMTH	7.5	IOD - BW	71
ED	1.0	ND - BL	3
EH	2.1	NH - BH	46
HAB	2.8	RN - NP	47
IND	2.3	IND - IOD	67
IOD	3.4	SL - BL	8
JW	1.2	SS - BL	53
MTH	4.8	SH - BH	34
NH	1.9	SH - HAB	50
NP	1.7	TAL - BL	213
ODW	2.5	MTH - BH	117
RN	0.8	THM - BH	117
SBH	6.5	THM - MTH	100
SBW	5.4	TH - BH	88
SE	2.4	TMW - BW	54
SH	1.4	TMH - BH	63
SL	0.8	- MTH	54
SS	5.0	TMHM - THM and MTH	60
TAL	20.3	DF - TMHM	31
TH	3.6	VF - TMHM	38
THM	4.8	DF - VF	82
TL	30.7	DMTH - TAL	37
TMH	2.6	HAB - BH	68
TMHM	2.9	ODW - BW	52
TMW	2.6	DG - ODW	56
VF	1.1	A1 - ODW	83
		JW - ODW	48

view and perceptible from lateral view; posterior third of inner wall free from body and formed that aperture is lateroposteriorly directed, its opening rounded, narrower than tube, situated between the 2/5 and 3/5 of the body length, located low on the body at the height of the hind

limb insertion. Long medial vent tube with dextral wall shorter than sinistral, causing a dextral directed opening, fully attached to ventral fin. Glands absent. Tail long, maximal tail height higher than body height, tail height at mid-tail higher than body height and as high as maxi-



Fig. 1. Images of the living tadpole specimen of *Mantidactylus guttulatus* (ZCMV 13332 / ZSM 704/2010) at Gosner stage 26; a-c), in dorsal, lateral and ventral view (scale bar = 10 mm).

mal tail height, tail height at body-tail junction lower than body height. Caudal musculature well developed. Tail muscle reaches tail tip. Tail fins very low, dorsal fin slightly lower than ventral fin at mid-tail, but slightly higher in posterior third. Dorsal fin originates slightly behind dorsal body-tail junction, with shallow, gradually rising until the anterior 1/3 of the tail where it increases brusquely to attain its maximal height behind mid-tail and then continues gradually until the posterior 3/4 of the tail where it descends abruptly towards the tail tip. Ventral fin originates at the ventral terminus of the body, rises meticulously until the anterior 1/4 of the tail, and then remains almost parallel to the ventral border of the tail muscle until close to the tail tip. Maximal tail height located behind mid-tail, lateral line vein and myosepta imperceptible, point where the axis of the tail myotomes contacts the body located in the upper half of the body height, axis of the tail myotomes parallel with the axis of body length. Tail tip narrowly rounded. Moderately wide generalized oral disc, positioned almost ventrally and directed anteroventrally, clearly laterally emarginated. Oral disc not visible from dorsal view, upper labium as a continuation of snout. Marginal papillae uniseriate and interrupted by a wide gap on the upper labium, gap on the lower labium absent, total number of mar-

ginal papillae 48 (MPRF: (1)/1/1). Sixteen submarginal papillae present (8 on each side of the jaw sheaths folds). LKRF 4(2-4)/3(1), A_1 keratodont row very long. Density of keratodonts varies from 20/mm to 71/mm, A_1 59/mm (total 118). Gap in the A_2 row narrow ($>1\%$ of A_2 row) and distinctly wider in A_3 and A_4 . Gap in the P_1 row less than the width of three keratodonts. Alignment of anterior and posterior rows regular and nearly of same length. Distal keratodonts of same length as those in the centre; prominent space between marginal papillae and keratodont rows. Jaw sheaths partially keratinized, only the half section close to the edge coloured black; with finely pointed serrations. Upper jaw sheath moderately wide and slightly arched, with a very shallow medial concavity. Lower jaw sheath V-shaped, partially keratinized and partially hidden by the upper jaw sheath when closed.

Colouration in life uniformly dark brownish. Dorsally, body covered by homogeneous dark brown melanophoric pigments. Laterally, area below eyes, flank, and abdominal region densely reticulated. Ventrally, oral disc and gular region reticulated, branchial regions reddish and spotted, beating heart visible; venter transparent, regularly spiralled intestinal coils visible. Tail musculature yellowish coloured, and coarsely reticulated. Fins patched with dark small spots with fringing edges.

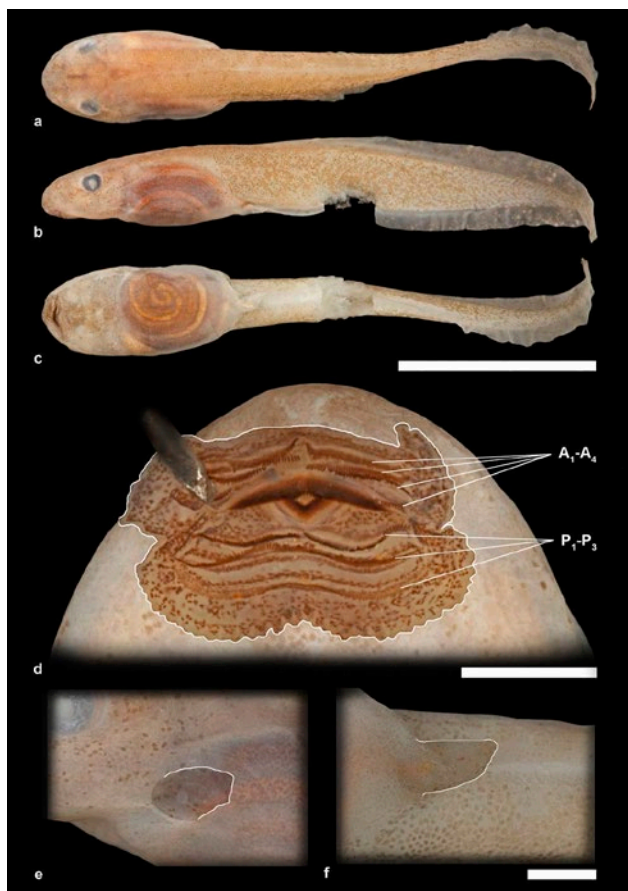


Fig. 2. Images of the preserved tadpole specimen of *Mantidactylus guttulatus* (ZCMV 13332 / ZSM 704/2010) at Gosner stage 26; a-c) in dorsal, lateral and ventral view (scale bar = 10 mm); d) wide open oral disc with anterior (A_1 - A_4) and posterior (P_1 - P_3) keratodont rows (white outline for better visibility, median gap in A_1 row caused by preparation, scale bar = 1 mm); e) spiracle and f) vent tube in closer view (white outline for better visibility, scale bar = 1 mm).

Colouration in preservative uniformly brownish coloured. Brown melanic pigment in layers deeper than the skin covered the dorsum and flank, leaving laterally a slightly transparent area. Some dark brown blotches scattered on the dorsum skin, condensed to form dark patches above the brain and the vertebral region. Laterally, area below eyes and flank covered by dark brown reticulations, leaving out a perceptible transparent spiracle on the body wall. Lower part of the flank spotted. Tail musculature overlaid by dark brown spots which condensed in some area to form reticulations. Fins covered by brown spots. Ventrally, oral disc, gular and branchial regions reticulated; venter pale and spotted, intestinal coils visible with regular spiral shaped.

In total, three tadpoles were captured, but due to a transportation problem, the second specimen (ZCMV

13333) was destroyed. The external morphology of the third voucher specimen (ZCMV 13334 / ZSM 705/2010; GS 25) from the same locality shows the same characters and an identical oral disc configuration as the described above.

DISCUSSION

For decades, searches for the tadpole of *Mantidactylus guttulatus* and its relatives in the subgenus *Mantidactylus* have been unsuccessful, and scientists eventually hypothesized a nidicolous developmental mode for this species with a nest hidden very deep in the soil or even direct development (e.g., Glaw and Vences, 2007). During our tadpole surveys in many streams in Ranomafana National Park mainly during the rainy seasons between 2006 and 2009, no tadpole assignable to this subgenus was encountered (Strauß et al., 2013), even at sites where many adults were present. One possible explanation for the absence might be a shifted onset of their reproductive season. Contrary to many other species that start their reproductive efforts at the beginning of the warm-rainy season, the reproduction period of these frogs might peak at the end of each rainy season towards the beginning of the cool-dry season. The avoidance of reproductive competition with co-occurring species would be one benefit of this shift. An indication for this hypothesis is the early developmental stage of these tadpoles which suggests that they hatched in May. On the other hand, the single report of a calling individual from February (Vences et al., 2004) indicates that some reproductive activity occurs during the peak of the warm-rainy season.

The noticeable fact that the tadpoles were found in very shallow water and, moreover, in the seepage area of a small water body could be seen as an indication of fossorial habits. However, morphological adaptations for fossoriality like a prominent tubular spiracle or particularly small eyes present in other fossorial tadpoles e.g. *Otophryne robusta* (Wassersug and Pyburn, 1987), *Leptobranchella mjobergi* (Haas et al., 2006) or *Micrixalus herrei* (Senevirathne et al., 2016) are absent in *Mantidactylus guttulatus*. Due to small sample size and the close vicinity of a large stream from which the tadpoles could have been washed away during a heavy rainfall this enigma requires further studies. Also, because we did not hypothesize these tadpoles would belong to *M. guttulatus* when encountering them in the wild we undertook no special efforts to further investigate the seepage area in which they occurred. For instance, we cannot exclude that upstream the seepage would originate from some kind of cavity, more suitable for such a large frog to deposit its eggs.

Mantidactylus guttulatus tadpoles show the typical morphology of stream-adapted, Orton (1953) Type IV tadpoles with a large and muscular tail and low fins. According to Altig and Johnston (1989) they can be classified as lotic-benthic and thus assigned to the ecomorphological guild Section I, Guild 7. The tadpoles of *M. guttulatus* are similar to those of the subgenus *Brygoomantis* (Schmidt et al., 2009) which are considered as rather generalized lotic tadpoles. They share an oral disc with a large dorsal gap of marginal papillae, and a LKRF of 3-5 keratodont rows on the anterior labium with only the first being continuous and the others are interrupted by medial gaps, and three keratodont rows on the posterior labium of which the first usually has a very small medial gap. Instead, the larvae of several other subgenera have highly specialized mouthparts, such as funnel-shaped structures (*Chonomantis*), poorly developed and reduced keratinized parts (*Ochthomantis*, *Hylobatrachus*) or a reduced number of keratodont rows in combination with unpigmented jaw sheaths (*Maitsomantis*) (Glaw and Vences, 1994; Vejarano et al., 2006; Grosjean et al., 2011; Randrianiaina et al., 2011). The well resolved phylogeny of Wollenberg et al. (2011) suggests that the subgenera with generalized mouthparts (*Mantidactylus* and *Brygoomantis*) are not sister clades. While the subgenus *Mantidactylus* branches off from the basal node of the *Mantidactylus* clade, *Brygoomantis* is a sister clade to *Chonomantis* (Wollenberg et al., 2011). If these relationships are confirmed, it suggests extensive homoplasy in the evolution of tadpole mouthparts — either multiple independent evolution of specialized mouthparts, or reversal towards generalized mouthparts in the *Brygoomantis* clade.

It is surprising that a frog like *Mantidactylus guttulatus*, whose reproductive mode has intrigued researchers for decades, has such a dull tadpole as described herein. The reproductive behaviour and the unusual microhabitat of the species still remains a mystery. Where the species deposits its eggs and whether it displays any kind of pre-hatching parental care requires being elucidated by future studies.

ACKNOWLEDGEMENTS

We are grateful to F. M. Ratsoavina, A. S. Rasamison, A. Rakotoarison, and D. R. Vieites for assisting during fieldwork for this study. This study was carried out in the framework of a cooperation accord between the Département de Biologie Animale of the University of Antananarivo, Madagascar and the Technical University of Braunschweig. Permission for collection was granted by the Ministère des Eaux et Forêts, Service de la Gestion

Faune et Flore; Autorisation de Recherche 064/070/10/MEF/SG/DGF/DCB.SAP/SLRSE, delivered 25 March 2010; including the export permit 135N-EAO07/MG10, delivered 8 July 2010. Financial support was granted by the Volkswagen Foundation to MV, RDR, and AS, and by the Deutscher Akademischer Austauschdienst to RDR.

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