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Where to grow in the Tsingy? Limestone rock pools as breeding habitats of the relict frog *Tsingymantis antitra* from Madagascar and description of its tadpole

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Abstract. The monotypic genus *Tsingymantis* is an isolated, microendemic anuran lineage from the karstic limestone area of Ankarana in northern Madagascar that probably separated from other mantellids about 40 million years ago. It was described only in 2006, and basic data on the natural history of this enigmatic frog is still wanting. Field surveys in the late rainy season (February–March 2007) revealed the previously unknown larvae of *Tsingymantis antitra,* developing in comparatively small rock pools. The pools had diameters of 20–170 cm and depths of 3–19 cm. Each of the five pools inhabited contained 1–2 (in one case 8) tadpoles and apparently, most of them contained only limited amounts of potential tadpole food. The larvae have an oral disc characterized by the presence of lateral emarginations, completely keratinised and strong jaw sheaths, and double rows of marginal papillae without a ventral gap, and with five rows of anterior and three rows of posterior labial keratodont rows, of which rows 4 and 1 are discontinuous, respectively. Despite a general similarity to generalized tadpoles as observed in *Aglyptodactylus* and *Laliostoma* (Mantellidae: Laliostominae), the strongly enlarged and keratinised jaw sheaths with strong serrations in the upper and lower jaw found in *Tsingymantis* are otherwise typical for oophagous tadpoles. Although no direct evidence exists, the combination of oral morphology and larval habitats could be an indication for oophagy or a predatory feeding mode in tadpoles of *Tsingymantis*. Our data also suggest that reproducing in small rock pools can be a successful long-term strategy in karstic habitats.

Key words. Amphibia, Mantellidae, *Tsingymantis*, *Aglyptodactylus*, *Laliostoma*, karst limestone, Ankarana National Park, tadpole morphology.

Introduction

Several parts of western and northern Madagascar are characterized by Mesozoic or Tertiary limestone of marine origin. Especially the Mesozoic formations form layers of about 400 m and due to continued erosion, give shape to some of the most spectacular Malagasy landscapes, the so-called Tsingy (Du Puy & Moat 2003). These deeply eroded karst areas are most famous in Bemaraha in western Madagascar, and in Ankarana in the north, where they present themselves as spectacular pinnacle-like formations and deep canyons and caves.

This unique landscape also allows for the survival of very particular faunae and florae. Although, for instance, the Tsingy de Bemaraha are located in the largely dry west, they are populated by numerous amphibians that are otherwise rare or absent from western Madagascar, such as endemic representatives of cophyline microhylids (genera *Plethodontohyla*, *Rhombophryne* and *Stumpffia*; see Bora et al. 2010). Also, the Ankarana massif harbours several endemic species, such as a probably cave-dwelling representative of *Stumpffia* (Köhler et al. 2010), and especially, *Tsingymantis antitra.* This large-sized frog is the sole known representative of its genus and represents a basal, enigmatic lineage within the family Mantellidae (Glaw et al. 2006, Kurabayashi et al. 2008).

The family Mantellidae is endemic to Madagascar and the Comoros (Glaw & Vences 2006), and its probably more than 250 species and candidate species (Vieites et al. 2009) comprise a wide variety of ecological, morphological and reproductive adaptations (Glaw & Vences 2007). Mantellids are subdivided into three subfamilies, Boophinae, Laliostominae, and Mantellinae. The Boophinae comprise a single, species-rich genus (*Boophis*) with pond-breeding and stream-breeding species, characterized by axillary amplexus and depositing their eggs directly in the water. The Laliostominae comprise the monotypic genus *Laliostoma* and the species-poor genus *Aglyptodactylus*, which all are pond-breeding species with axillary amplexus, depositing their eggs in the water, and are characterized by explosive breeding behaviour. The Mantellinae contain various genera with a wide variety of reproductive

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modes, including stream-dwelling tadpoles with numerous oral specializations, larval development in phytotelmata, pond breeding, or terrestrial and nidicolous development of non-feeding tadpoles. However, all mantellines (except a few taxa with reversed character states) are characterized by the absence of strong mating amplexus, absence of nuptial pads, oviposition outside the water, and the presence of femoral glands in males. Based on molecular phylogenetic results, *Tsingymantis* has been considered to be the most basal mantelline (Glaw et al. 2006), but other data sets rather supported its sister position to the Laliostominae (Kurabayashi et al. 2008). Based on the morphology of the single known male *Tsingymantis*, Raselimanana et al. (2007) hypothesized that this genus has a mosaic of reproduction-related characters, lacking the mantelline synapomorphy of femoral glands, but sharing with mantellines the synapomorphy of reduced nuptial pads.

Morphological characters of anuran larvae are known to be phylogenetically informative (Haas 2003). However, the tadpole of *Tsingymantis antitra* has so far remained unknown. The reproduction of this species is also of interest because limestone habitats in general are not rich in open and permanent water bodies, and therefore the possibility of derived and possibly water-independent reproductive modes needs to be considered in species specialized to a life in the Tsingy.

Based on own field surveys, we here report on the discovery of tadpoles and freshly metamorphed juveniles of *Tsingymantis antitra* in small rock pools in the Ankarana limestone area. Breeding habitats and tadpole morphology are described in detail and results are discussed with respect to their ecological and phylogenetic significance.

Material and methods

Tadpoles were collected in the field and euthanized by immersion in a chlorobutanol solution. A tissue sample from the tail musculature or fin of each tadpole was taken and preserved in 99% ethanol. All detailed morphological tadpole characterizations and drawings are based on one DNA voucher, whereas variation is described based on further DNA vouchers specimens. After tissue collection, all specimens were preserved in 5% formalin. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). Other numbers refer to field numbers of F. Glaw (FGZC) and R.-D. Randrianiaina (Tad).

Tadpoles were identified using a DNA barcoding approach based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Thomas et al. 2005). The ca. 550 bp fragment was amplified using primers 16Sar-L and 16Sbr-H from Palumbi et al. (1991) as per 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 if the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. DNA sequences from this study were deposited in GenBank (accession numbers JF828284–JF828294); for accession numbers of comparative adult specimens see Vieites et al. (2009).

The tadpoles here described were collected by P. Bora, H. Enting, F. Glaw, A. Knoll and J. Köhler on 28 February 2007 in the Ankarana National Park (14°26.972' S, 49°47.214' E, 327 m a.s.l.), on the trail to the Petit Tsingy and Grotte des Chauves-Souris, and catalogued as ZSM 2236/2007–2245/2007 (10 tadpoles; field numbers FGZC 1120–1125 and FGZC 1142, 1143, 1145, 1146).

Additional tadpoles used for comparison are: *Aglyptodactylus laticeps* collected by J. Glos at the CFPF Station in the Kirindy forest (20°03' S, 44°40' E, ca. 20 m a.s.l.); *Aglyptodactylus madagascariensis* and *Aglyptodactylus securifer,* collected by R.-D. Randrianiaina, M. Puente and F. Glaw, respectively on 19–21 February 2004 in the National Park of Montagne d'Ambre, in a brook crossing the track "Voie des milles arbres", (coordinates at stream not taken, but not far from 12°31'12" S, 49°10'32" E, 1050 m a.s.l.) and on 26 February 2004 in Ankarana; and *Laliostoma labrosum* collected by R.-D. Randrianiaina, M. Thomas, M. Puente and F. Glaw on 22 January 2004 between Ejeda and Ampanihy, 24°32'20" S, 44°38'55" E.

For detailed morphological examination, especially to determine developmental stages and assess characters of the oral disc, preserved tadpoles were stained slightly with methylene blue. Tadpoles were examined under water, and a few drops of methylene blue were applied to the oral disc, hind limb, spiracle, narial opening, and vent tube to facilitate a clearer view of their structures. Developmental stages follow Gosner (1960).

Morphological description, measurements and drawings are based on digital pictures of the preserved tadpoles taken with a stereomicroscope Zeiss Discovery V12 connected to a computer, following landmarks, terminology and definitions of Altig & McDiarmid (1999) and Randrianiaina et al. (2011), except that we predominantly use the term keratodonts instead of labial teeth. The formula of keratodonts (labial tooth row formula, LTRF) is given according to Altig & McDiarmid (1999). Detailed measurements of all tadpoles examined are given in the Appendix. 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).

The following abbreviations are used: A_1 (first upper keratodont row), A_2 (second upper keratodont row), A_{2gap} (medial gap in A_2), A_3 (third upper keratodont row), A_4 (fourth upper keratodont row), A_5 (fifth upper keratodont row), A_6 (sixth upper keratodont row), A_7 (seventh upper keratodont row), $A_{1-7\ den}$ (density of the keratodonts in rows A_{1-7}), $A_{1-7\ len}$ (length of A_{1-7}), $A_{1-7\ num}$ (number of keratodonts in A_{1-7}), BH (maximal body height), BL (body length), BW (maximal body width), DF (dorsal fin height at midtail), DG (size of the dorsal gap between marginal papillae), DMTH (distance of level of maximal tail height from the tail-body junction), ED (eye diameter), EH (eye height – measured from the lower curvature of the belly to the centre of the eye), HAB (height of the point where the axis of the tail myotomes connects with the body – measured from the lower curvature of the belly), IND (inter-narial distance – measured from the centre), IOD (inter-orbital distance – measured from the centre), JW (maximal jaw sheath width), MC (medial convexity of the upper sheath),

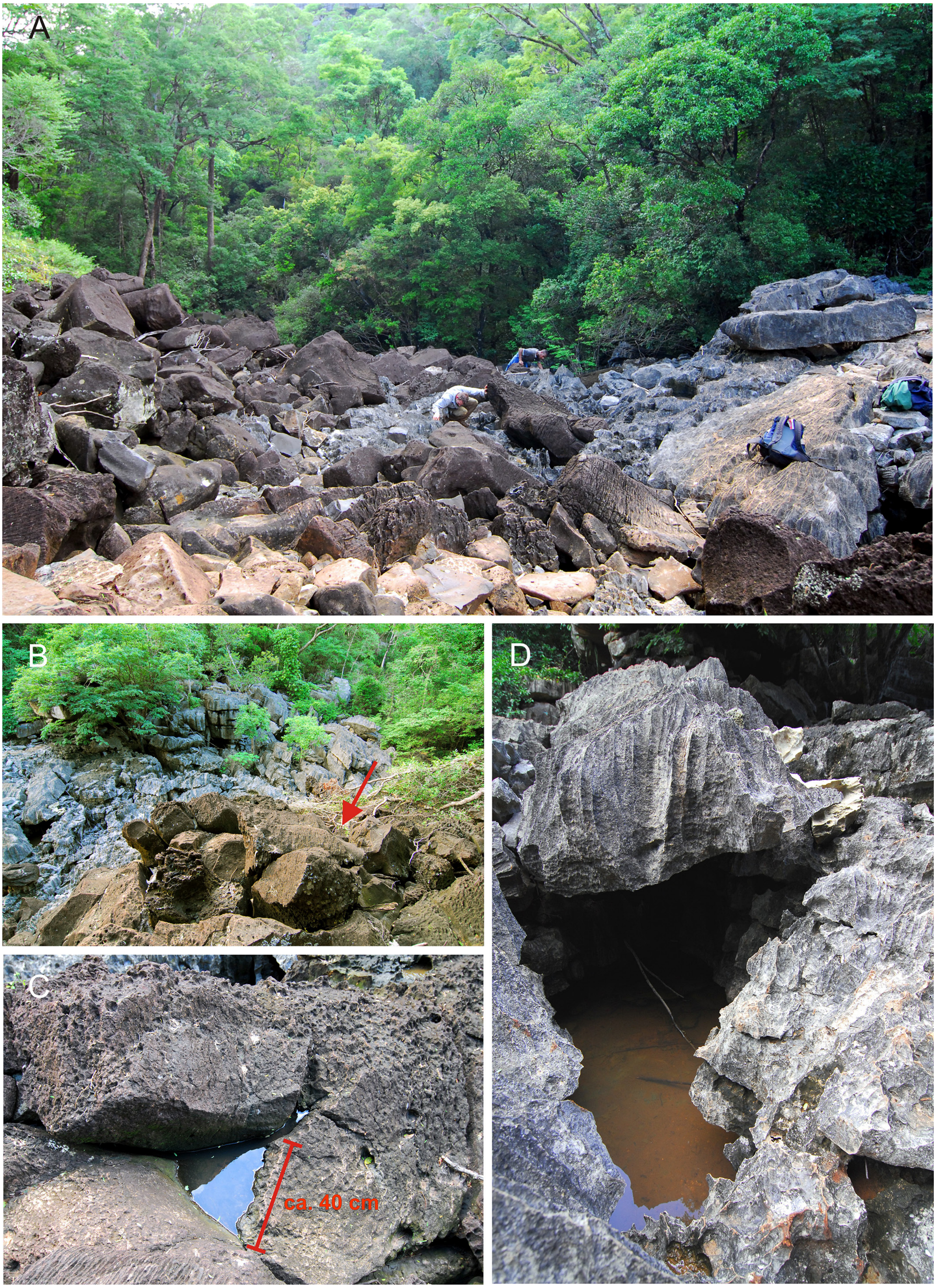

Figure 1. Habitat of *Tsingymantis antitra* in a dry riverbed of the Ankarana National Park, northern Madagascar: (A) overview of river bed at the type locality; (B) detail of limestone boulders in the riverbed with the arrow pointing out the location of Pool 1; (C) view of Pool 1, which contained at least eight tadpoles; (D) larger pool (Pool 2), which contained a single large tadpole (FGZC 1125 – ZSM 2241/2007).

MCL (length of the medial convexity of the upper sheath), MP (marginal papillae), MTH (maximal tail height), ND (naris diameter), NH (naris height – measured from the lower curvature of the belly to the centre of the naris), NP (naris–pupil distance), OD (oral disc), ODW (maximum oral disc width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), $P_{1–3\,den}$ (density of the keratodonts in rows $P_{1–3}$), $P_{1–3\,len}$ (length of the rows $P_{1–3}$), $P_{1–3\ num}$ (number of keratodonts in rows $P_{1–3}$), RN (rostro-narial distance), SBH (distance between snout and the level of maximal body height), SBW (distance between snout and the level of maximal body width), SE (snout–eye distance), SH (spiracle height – measured from the lower curvature of the belly to the centre of the spiracle), SL (spiracle length – distance between the visible edges), SMP (submarginal papillae), SS (snout–spiracle distance), SV (spiracle–vent distance), SVL (snout–vent length), TAL (tail length), TH (tail height at the beginning of the tail), THM (tail height at mid-tail), Thorn-pap (thorn-shaped papillae), TL (total length), TMH (tail muscle height at the beginning of the tail), TMHM (tail muscle height at mid-tail), TMW (tail muscle width at the beginning of the tail), LR (number of the lower rows of keratodonts), UR (number of the upper rows of keratodonts), VF (ventral fin height at mid-tail), VG (size of the ventral gap between marginal papillae), VL (vent tube length).

Results

Tadpole habitat and juveniles

Our expeditions to Ankarana in 2003 and 2004 led to the discovery of adult *Tsingymantis* females, but did not reveal any data on their reproductive mode or even potential waterbodies for their reproduction. During the next Ankarana trip in 2007, we discovered tadpoles and juveniles in and around small rock pools and afterwards systematically searched all available pools for further tadpoles. Beside a few (less than five) pools without any evidence of tadpole life, five water-filled rock pools inhabited by *Tsingymantis* tadpoles were found between 28 February and 2 March 2007. They are characterized as follows:

Pool 1: Triangular, largely sun-exposed pool (surface ca. 40 × 40 × 40 cm, maximum water depth 8 cm, but with a deep inaccessible water-filled cleft) in an otherwise dry riverbed with limestone boulders (Fig. 1B, C). Water temperature was 29.8°C (17:00 h). Eight tadpoles at similar developmental stages (6 of them collected) were found, together with large mosquito larvae.

Pool 2: Large, partly shaded pool (170 × 150 cm, maximum water depth 19 cm) with fine sediment at its bottom in an otherwise dry riverbed with limestone boulders (Fig. 1D). Water temperature was 28.3°C (ca. 17:00 h). Only a single large tadpole was observed (collected). In this pool, our guide Angelin Razafimanantsoa (pers. comm.) had observed mating *Tsingymantis* on 7 February 2007.

Pool 3: Small, partly shaded pool (29 × 15 cm, maximum water depth 4 cm) in an otherwise dry riverbed with limestone boulders. Water temperature was 28.0°C (16:51 h). Two tadpoles at different developmental stages (both collected).

Pool 4: Small pool (23 × 11 cm, depth 6 cm) in eroded tsingy rock, partly shaded, with leaf litter on the bottom, in dry forest, at the edge of a trail. Water temperature was 28°C (after 17:00 h). One small tadpole (collected).

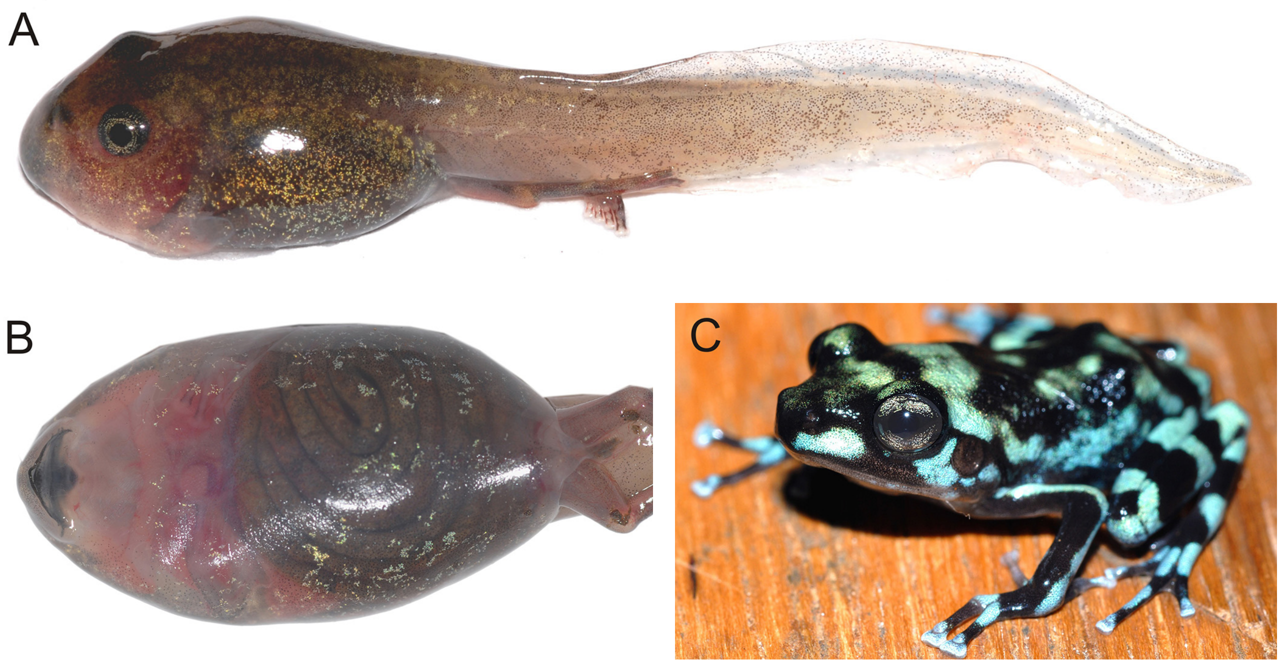

Figure 2. Tadpole (ZSM 2241/2007) and freshly metamorphed juvenile (ZSM 2115/2007) of *Tsingymantis antitra* in life: (A) complete view of tadpole, and (B) ventral view of tadpole body; (C) juvenile.

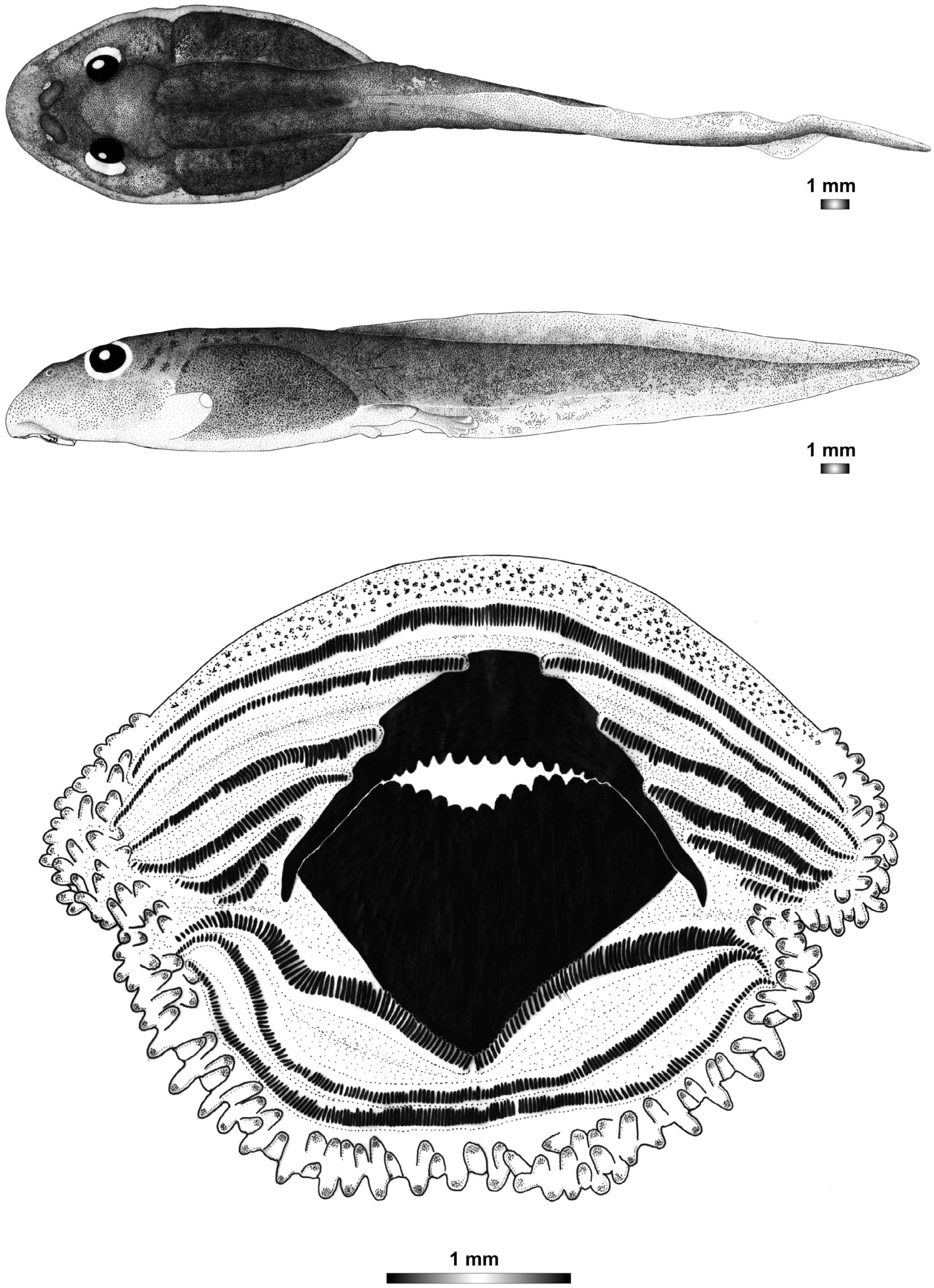

Figure 3. Drawings of dorsal and lateral views and of oral disc of the preserved DNA voucher tadpole of *Tsingymantis antitra* (FGZC 1121 – ZSM 2237/2007).

Pool 5: Small pool in dry forest (29 × 25 cm, depth 3.5 cm) in a horizontal tsingy rock cleft, almost fully shaded and with a lot of leaf litter on the bottom, just one meter apart from Pool 4. Water temperature was 27.9°C (after 17:00 h). One tadpole (collected).

One juvenile (UADBA uncatalogued [FGZC 1126]) figured in Glaw & Vences (2007:228:Fig. 1b) was found close to Pool 1 (which contained eight tadpoles) on 28 February 2007. A second, slightly larger juvenile (ZSM 2115/2007 [FGZC 1127]), with a SVL of 17.9 mm (Fig. 2C), was found being active on boulders in the dry river bed (Fig. 1A) at night on 1 March 2007. Both froglets still had small remains of a tail when captured and thus must have finished metamorphosis very recently, suggesting that egg-laying of *Tsingymantis* might have occurred after the first heavy rains of the rainy season. Both juveniles were black with turquoise flecking. This conspicuous colouration, which is unique among Malagasy frogs and can be considered as aposematic, resembles the colouration of adult individuals of the Neotropical poison frog *Dendrobates auratus* (Dendrobatidae). The general colouration of juvenile *Tsingymantis* resembles that of adults (see Glaw & Vences 2007:228:Fig. 1a), however, the collected juveniles had brighter and more contrasting colours.

Tadpole description

The following description refers to one tadpole at developmental stage 38 (field number FGZC 1121 = ZSM 2237/2007, BL 15.8 mm, TL 34.2 mm) from Ankarana National Park. The 16S rDNA sequence of this specimen (accession number JF828288) was 99% identical to a reference sequence of a *Tsingymantis antitra* adult specimen (accession number AY848213) from the same locality.

In dorsal view, body elliptical, maximal body width at between $^3/_5$ and $^4/_5$ of the body length (SBW 64% of BL), snout narrowly rounded. In lateral view, body depressed (BW 136% of BH), maximal body height at between $^3/_5$ and $^4/_5$ of the body length (SBW 68% of BL), rounded snout. Eyes moderately large (ED 11% of BL), not visible in ventral view, positioned high dorsally (EH 78% of BH) and directed laterally, situated at between $^3/_{10}$ and $^4/_{10}$ of the body length (SE 32% of BL), distance between eyes moderately wide (IOD 49% of BW). Nares small, rounded (ND 3% of BL), with a marginal rim, positioned high dorsally (NH 72% of BH) and orientated anterolaterally, situated nearer to snout than to eye (RN 85% of NP) and lower than eye (NH 92% of EH), moderately wide distance between nares (IND 54% of IOD), dark spot posterior to the nares absent, ornamentation absent. Moderately long sinistral spiracle (SL 14% of BL), directed posteriorly, visible in ventral view, invisible in dorsal view and perceptible in lateral view; inner wall free from body and its elliptical aperture opens posteriorly, situated at between $^3/_5$ and $^4/_5$ of the body length (SS 62% of BL), located low on the body (SH 38% of BH) at the height of the hind limb insertion (SH 59% of HAB). Long dextral vent tube (VL 16% of BL), attached to ventral fin, inner wall present. No glands. Tail short (TAL 157% of BL), maximal tail height lower than body height (MTH 86% of BH), tail height at mid-tail lower than body height and as high as maximal tail height (THM 85% of BH and THM 99% of MTH), tail height at the beginning of the tail lower than body height (TH 75% of BH). Caudal musculature moderately developed (TMW 38% of BW, TMH 50% of BH and 58% of MTH, TMHM 38% of THM and MTH), extends to tail tip. Fins very low (DF 98% of TMHM, VF 78% of MTHM); dorsal fin higher than ventral fin (DF 144% of VF) at mid-tail. Dorsal fin begins at the dorsal body-tail junction, increases to its maximal height anterior to mid-tail and then descends slightly towards the tail tip. Ventral fin begins at the ventral terminus of the body, increases to its maximal height, and then decreases towards the tail tip. Maximal tail height at between $^2/_5$ and $^3/_5$ of the tail length (DMTH 46% of TAL), lateral tail vein and myosepta visible on the anterior $^1/_4$ of the tail musculature; the point where the axis of the tail myotomes connects with the body located in the upper half of the body (HAB 70% of BH), axis of the tail myotomes parallel with the long axis of the body. Tail tip narrow, rounded. Moderately wide, generalized oral disc (ODW 50% of BW), positioned and directed ventrally, emarginated, maximal width on the upper labium. Oral disc not visible from dorsal view, upper labium is a continuation of snout. Double rows of marginal papillae interrupted by a wide gap on the upper labium (DG 72% of ODW), gap on the lower labium absent, total number of marginal papillae 157. Twenty-three submarginal papillae (12 on the right and 11 on the left), laterally on the lower and upper labia. Short and moderately large conical papillae with rounded tips, with the longest marginal papillae measuring 0.17 mm, and 0.14 mm for submarginal papillae; papillae not visible in dorsal view.

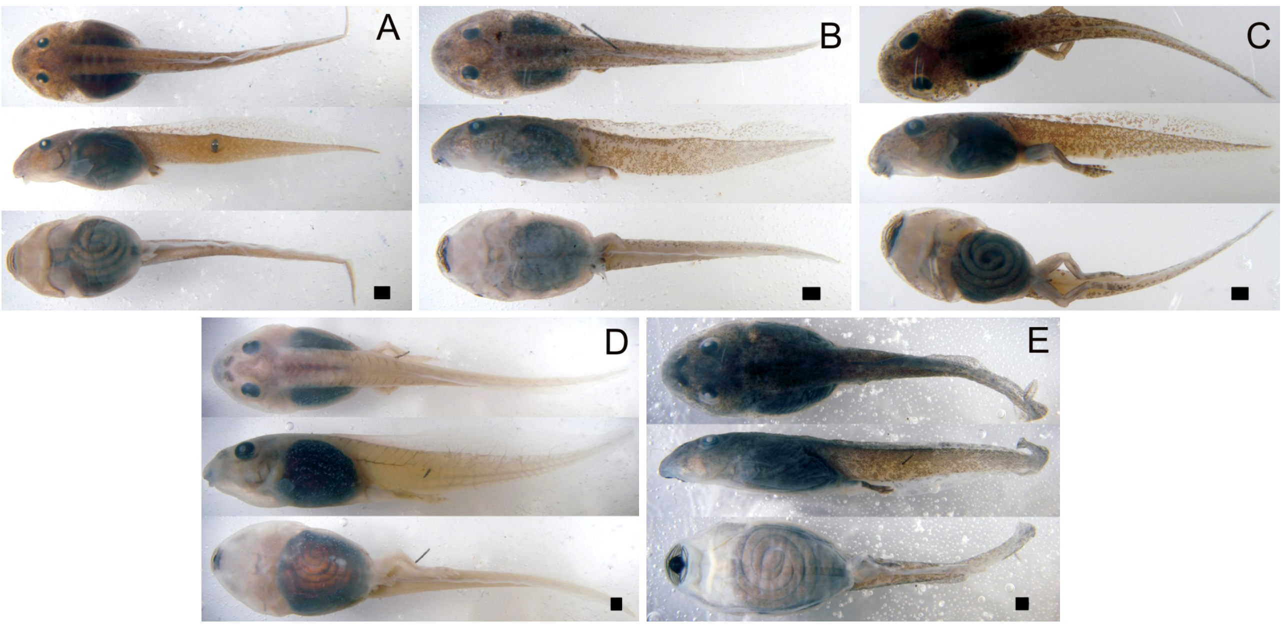

Figure 4. Colouration in preservative of tadpoles in dorsal, lateral and ventral views: (A) *Aglyptodactylus laticeps* (uncataloged); (B) *Aglyptodactylus madagascariensis* (Tad 2004-65 – ZSM 290/2008); (C) *Aglyptodactylus securifer* (Tad 2004-82 – ZSM 305/2008); (D) *Laliostoma labrosum* (Tad 2004-8 – ZSM 573/2008) (E) *Tsingymantis antitra* (FGZC 1121 – ZSM 2237/2007). Scale bars each represent 1 mm.

LTRF 5(2–5)/3(1). Single rows of keratondonts per ridge. Moderately long A_1 (54% of ODW). Density of keratodonts varies from 30/mm to 99/mm, A_1 99/mm (total 250). Very narrow gap in the first anterior interrupted row (A_{2gap} 7% of A_2). Row alignment regular. Long discernible keratodonts (0.16 mm). Distal keratodonts of the same length as those in the middle; prominent space between marginal papillae and keratodont rows. Fully keratinised jaw sheath with rounded serrations; moderately wide (JW 42% of ODW), with a very short, wide, and rounded medial convexity (MCL 0.5% of JW). Lower jaw sheath V-shaped and partially hidden by the upper ones.

In life, body generally brown with a reddish tint. Dorsally, body covered with iridophoric pigments. Laterally, jugal area covered with sparse iridophoric pigments; dorsal pattern continued on dorsolateral flank, patched ventrolaterally; abdominal region transparent with sparse iridophoric patches. Tail musculature reddish from melanophoric and iridophoric spots. Fins spotted. Ventrally, oral disc transparent, gular and branchial regions reddish, beating heart visible; venter transparent, regularly spiralled intestinal coils visible (Fig. 2A, B).

In preservative, uniform dark. Brown melanophoric pigments in deeper layers of the skin cover the dorsum and flank, leaving a slightly transparent lateral area. Some dark brown blotches scattered on the dorsal skin, condensed to form dark patches above the brain and the vertebral region. Laterally, jugal area and flank covered by dark brown blotches, leaving out a transparent spiracle on the body wall. Lower part of the flank pigmented. Tail musculature overlain with dark brown reticulations. Fins pale, covered with brown reticulations. Ventrally, oral disc, gular and branchial regions pale; venter transparent and blotched, intestinal coils visible and regularly spiral-shaped.

Remarks: The other seven specimens (ZSM 2236/2007, ZSM 2238/2007, ZSM 2240/2007, ZSM 2242–2245/2007) from the same locality show the same morphology and oral disc configuration as the described specimen, independent of their developmental stages (see Tables 1–3 of the Appendix). These tadpoles, reliably identified by DNA barcoding, were similar to those of other basal, pond-breeding mantellids of the genera *Aglyptodactylus* and *Laliostoma*, suggesting that their morphology probably represents a plesiomorphic condition for Mantellidae.

Discussion

The tadpole of *Tsingymantis antitra* is generally uniform dark with a short tail. To a slight degree, some morphological characters (e.g., low fins, high caudal muscles, and a moderately depressed body) are shared by tadpoles adapted to lotic and benthic habitats (Altig & McDiarmid 1999). However, tadpoles restricted to lotic waters usually exhibit a more explicitly marked morphology as compared to that of *T. antitra*.

The oral disc is characterized by the presence of lateral emarginations, completely keratinised and strong jaw sheaths, and double rows of marginal papillae, but without ventral gap. The emarginated oral disc with double rows of marginal papillae and without a ventral gap is also found in other mantellid genera: *Aglyptodactylus* (Glos & Linsenmair 2004), *Laliostoma* (Schmidt et al. 2009a), *Bo-*

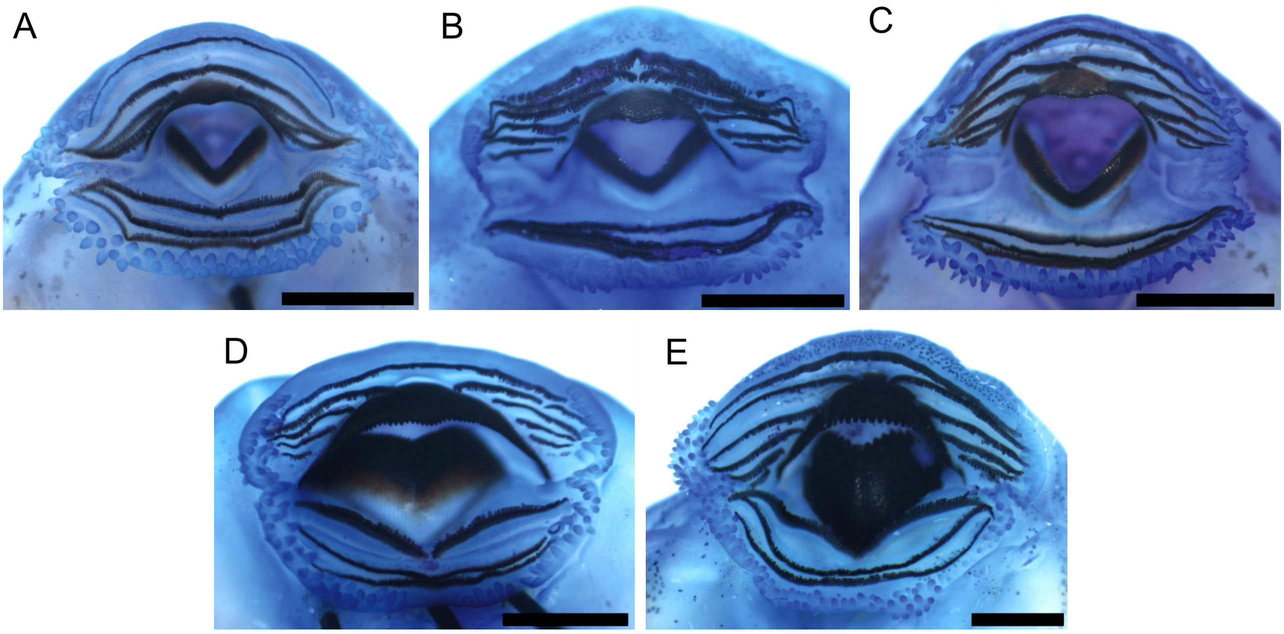

Figure 5. Photographs of the oral disc of the preserved voucher specimens of tadpoles described and used in this paper (stained with methylene blue): (A) *Aglyptodactylus laticeps* (uncataloged); (B) *Aglyptodactylus madagascariensis* (Tad 2004.65 – ZSM 290/2008); (C) *Aglyptodactylus securifer* (Tad 2004.82 – ZSM 305/2008); (D) *Laliostoma labrosum* (Tad 2004.8 – ZSM 573/2008); (E) *Tsingymantis antitra* (FGZC 1121 – ZSM 2237/2007). Scale bars each represent 1 mm.

ophis (Glos & Linsenmair 2005, Raharivololoniaina et al. 2006), *Gephyromantis* (Randrianiaina et al. 2007), *Guibemantis* (Vejarano et al. 2006a), *Mantidactylus* (Schmidt et al. 2009b), *Mantella* (Jovanovic et al. 2009) and *Spinomantis* (Vejarano et al. 2006b).

Glaw et al. (2006) presented a molecular phylogeny that placed *Tsingymantis* sister to the Mantellinae, and the Laliostominae (*Aglyptodactylus* and *Laliostoma*) sister to the *Tsingymantis*/Mantellinae clade, with the Boophinae (genus *Boophis*) in the most basal position. Based on this phylogeny, these authors hypothesized that the ancestor of the mantellid clade might have been adapted to relatively dry conditions with a reproductive mode that is still found in today's *Boophis tephraeomystax* group and Laliostominae. This hypothesis is less strongly supported if the phylogenetic scheme of Kurabayashi et al. (2008) holds true, where the mantellines were sister to a Boophinae/Laliostominae/*Tsingymantis* clade. However, given that a rather generalised tadpole with an emarginated oral disc, a ventral gap, and double rows of marginal papillae, is present in *Tsingymantis*, all laliostomines, many boophines, and in numerous mantellines, it seems likely that this kind of oral morphology is plesiomorphic for the Mantellidae.

When comparing the oral structures of *Tsingymantis* with those of other generalized tadpoles, it is conspicuous that it has strongly enlarged and keratinised jaw sheaths with strong serrations in the upper and lower jaw. Such massive jaw sheaths, often associated with reduced labial teeth, are typical for oophagous tadpoles (e.g., Wells 2007). For instance, among mantellids, the oophagous tadpole of *Mantella laevigata* has much stronger jaw sheaths and fewer labial tooth rows than other *Mantella* tadpoles (Jovanovic et al. 2009). In *Tsingymantis,* no direct behavioural evidence for oophagy or predatory feeding exists, and a reduction of labial teeth is not obvious. Nevertheless, the combination of oral morphology and larval habitats, which are characterized by potentially limited food resources, could be an indication for oophagy or predatory feeding in tadpoles of *Tsingymantis*. This hypothesis requires further testing and emphasizes that research on the life history of this frog would potentially be rewarding.

The specialization of *Tsingymantis* to breeding in small rock pools is at first surprising. Although Ankarana receives strong rains in the wet season, Tsingy environments in general are relatively dry. Furthermore, Madagascar's climate is largely characterized by a high degree of variability and unpredictability as compared to other tropical environment (Dewar & Richard 2007). This would suggest that especially small waterbodies that are fed mainly by these rains would not make a stable and reliable resource for reproduction in such a habitat. However, the relatively large size of adult *Tsingymantis* (SVL up to 65 mm; Raselimanana et al. 2007) suggests that these animals live for several years, which might provide an adequate buffer for years with drier conditions in which no reproduction is possible. Taking the age of the most basal mantellid splits according to Kurabayashi et al. (2008) as a benchmark, *Tsingymantis* is an isolated phylogenetic lineage of probably around 40 million years of evolutionary history. Its specialization and small geographic range suggests that it has survived for much of this period in the Tsingy environment of the Ankarana massif, and that breeding in rock pools is an adequate and in the long term successful strategy in the karstic limestone areas of northern Madagascar.

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References

Altig, R. & R. W. McDiarmid (1999): Body plan. Development and morphology. – pp. 24–51 in McDiarmid, R. W. & R. Altig (eds.): Tadpoles. The biology of anuran larvae. – The University of Chicago Press Chicago & London.

Bora, P., J. C. Randrianantoandro, R. Randrianavelona, E. F. Hantalalaina, R. R. Andriantsimanarilafy, D. Rakotondravony, O. R. Ramilijaona, M. Vences, R. K. B. Jenkins, F. Glaw & J. Köhler (2010): Amphibians and reptiles of the Tsingy de Bemaraha Plateau, western Madagascar: checklist, biogeography and conservation. – Herpetological Conservation and Biology, **5**: 111–125.

Dewar, R. E. & A. F. Richard (2007): Evolution in the hypervariable environment of Madagascar. – Proceedings of the National Academy of Sciences of the U.S.A., **104**: 13723–13727.

Du Puy, D. J. & J. Moat (2003): Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. – pp. 51–74 in Goodman, S. M. & J. P. Benstead (eds.): The Natural History of Madagascar. – The University of Chicago Press, Chicago and London.

Glaw, F., S. Hoegg & M. Vences (2006): Discovery of a new basal relict lineage of Madagascan frogs and its implications for mantellid evolution. – Zootaxa, **1334**: 27–43.

Glaw, F. & M. Vences (2006): Phylogeny and genus-level classification of mantellid frogs. – Organisms Diversity and Evolution, **6**: 236–253.

Glaw, F. & M. Vences (2007): A field guide to the amphibians and reptiles of Madagascar. Third Edition. – Köln, Vences & Glaw, 496 pp.

Glos, J. & K. E. Linsenmair (2004): Descriptions of the tadpoles of *Aglyptodactylus laticeps* and *Aglyptodactylus securifer* from western Madagascar, with notes on life history and ecology. – Journal of Herpetology, **38**: 131–136.

Glos, J. & K. E. Linsenmair (2005): Description of the tadpoles of *Boophis doulioti* and *B. xerophilus* from western Madagascar with notes on larval life history and breeding ecology. – Amphibia-Reptilia, **26**: 459–466.

Gosner, K. L. (1960): A simplified table for stageing anuran embryos and larvae with notes on identification. – Herpetologica, **16**: 183–190.

HAAS, A. (2003): Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). – Cladistics, **19**: 23–90.

JOVANOVIC, O., J. GLOS, F. GLAW, R.-D. RANDRIANIAINA & M. VENCES (2009): Comparative larval morphology in Madagascan frogs of the genus *Mantella* (Amphibia: Mantellidae). – Zootaxa, **2124**: 21–37.

KÖHLER, J., M. VENCES, N. D'CRUZE & F. GLAW (2010): Giant dwarfs: discovery of a radiation of large-bodied 'stump-toed frogs' from karstic cave environments of northern Madagascar. – Journal of Zoology, **282**: 21–38.

KURABAYASHI, A., M. SUMIDA, H. YONEKAWA, F. GLAW, M. VENCES & M. HASEGAWA (2008): Phylogeny, recombination, and mechanisms of stepwise mitochondrial genome reorganization in mantellid frogs from Madagascar. – Molecular Biology and Evolution, **25**: 874–891.

PALUMBI, S. R., A. MARTIN, S. ROMANO, W. O. MCMILLAN, L. STICE & G. GRABOWSKI (1991): The Simple Fool's Guide to PCR, Version 2.0. – Privately published document compiled by S. Palumbi, Department of Zoology, University of Hawaii, Honolulu.

RAHARIVOLOLONIAINA, L., S. GROSJEAN, N. RASOAMAMPIONONA RAMINOSOA, F. GLAW & M. VENCES (2006): Molecular identification, description and phylogenetic implications of the tadpoles of 11 species of Malagasy treefrogs, genus *Boophis*. – Journal of Natural History, **40**: 1449–1480.

RANDRIANIAINA, R.-D., F. GLAW, M. THOMAS, J. GLOS, N. RAMINOSOA & M. VENCES (2007): Descriptions of the tadpoles of two species of *Gephyromantis*, with a discussion of the phylogenetic origin of direct development in mantellid frogs. – Zootaxa, **1401:** 53–61.

RANDRIANIAINA, R.-D., A. STRAUSS, J. GLOS, F. GLAW & M. VENCES (2011): Diversity, external morphology and 'reverse taxonomy' in the specialized tadpoles of Malagasy river bank frogs of the subgenus *Ochthomantis* (genus *Mantidactylus*). – Contributions to Zoology, **80**: 17–65.

RASELIMANANA, A. P., F. GLAW & M. VENCES (2007): Lack of secondary sexual characters in a male of *Tsingymantis antitra* confirms its position as most basal manteline frog lineage. – Zootaxa, **1557**: 67–68.

SCHMIDT, H., F. GLAW, M. TESCHKE & M. VENCES (2009a): The tadpole of the Madagascar bullfrog, *Laliostoma labrosum*. – Zootaxa, **2005**: 67–68.

SCHMIDT, H., A. STRAUSS, F. GLAW, M. TESCHKE & M. VENCES (2009b): Description of tadpoles of five frog species in the subgenus *Brygoomantis* from Madagascar (Mantellidae: *Mantidactylus*). – Zootaxa, **1988**: 48–60.

THOMAS, M., R. RAHARIVOLOLONIAINA, F. GLAW, M. VENCES & D. R. VIEITES (2005): Montane tadpoles in Madagascar, molecular identification and description of the larval stages of *Mantidactylus elegans, M. madecassus* and *Boophis laurenti* from the Andringitra Massif. – Copeia, **2005**: 174–183.

VEJARANO, S., M. THOMAS & M. VENCES (2006a): Comparative larval morphology in Madagascan frogs of the genus *Guibemantis* (Anura: Mantellidae). – Zootaxa, **1329**: 39–57.

VEJARANO, S., M. THOMAS & M. VENCES (2006b): Comparative tadpole morphology in three species of frogs of the genus *Spinomantis* (Amphibia: Mantellidae). – Contributions to Zoology, **75**: 99–108.

VIEITES, D. R., K. C. WOLLENBERG, F. ANDREONE, J. KÖHLER, F. GLAW & M. VENCES (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. – Proceedings of the National Academy of Sciences of the U.S.A., **106**: 8267–8272.

WELLS, K. D. (2007): The ecology and behavior of amphibians. – The University of Chicago Press.

Appendix

Table 1. Measurements (all in mm) of tadpoles described in this paper. For abbreviations, see Material and methods.

Species	*Aglyptodactylus laticeps*	*Aglyptodactylus madagascariensis*	*Aglyptodactylus securifer*	*Laliostoma labrosum*	*Tsingymantis antitra*							
Site	Kirindy CFPF	Mt d'Ambre N. P.	Ankarana N. P.	Ejeda-Ampanihy	Ankarana N. P.							
Field number		Tad 2004.65	Tad 2004.82	Tad 2004.8	FGZC 1120	FGZC 1121	FGZC 1122	FGZC 1123	FGZC 1142	FGZC 1143	FGZC 1145	FGZC 1146
ZSM	Un-cataloged	290/2008	305/2008	573/2008	2236/2007	2237/2007	2238/2007	2240/2007	2242/2007	2243/2007	2244/2007	2245/2007
GOS	33	35	40	39	39	38	39	39	38	36	40	29
BL	9.2	9.4	8.6	15.6	15.6	15.8	15.4	15.1	15.4	15.3	12.7	10.9
BW	6.1	5.6	5.3	9.8	9.0	9.3	9.2	9.4	9.6	8.7	7.6	5.8
SBW	5.7	4.2	4.1	7.5	7.0	10.1	6.9	10.0	10.7	7.4	6.2	6.9
BH	4.4	4.2	4.0	7.5	6.4	6.9	6.5	7.3	7.0	6.5	4.9	4.1
SBH	6.5	7.2	6.3	11.5	9.6	10.8	10.4	10.3	11.0	10.6	8.9	6.8
ED	0.9	1.1	1.2	2.1	1.6	1.7	1.8	1.8	1.9	1.8	1.7	1.0
SE	2.6	3.0	2.8	4.6	4.8	5.1	4.4	4.5	4.6	4.6	3.6	3.1
EH	3.5	3.1	3.0	5.3	4.8	5.4	5.0	5.7	5.7	4.9	3.5	3.2
IOD	2.7	2.8	3.0	5.7	4.8	4.6	4.9	4.6	5.0	5.0	4.2	2.7
ND	0.2	0.3	0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.3
NH	3.0	2.6	2.4	4.9	3.9	4.9	4.3	4.9	5.2	4.3	3.1	2.7
IND	1.7	2.0	1.9	2.4	2.4	2.4	2.3	2.2	2.4	2.4	2.1	1.9
RN	1.1	1.3	1.1	1.9	2.1	2.3	1.8	1.8	1.9	2.0	1.3	1.4
NP	1.5	1.7	1.7	2.7	2.7	2.7	2.7	2.7	2.7	2.7	2.3	1.8
SP	1.4	1.9	1.4	2.3	2.5	2.3	2.0	2.8	2.4	2.2	2.1	1.6
SS	6.0	6.2	6.1	10.0	9.5	9.8	8.7	9.3	9.0	9.1	8.9	6.1
SV	3.2	3.2	2.5	5.6	6.1	6.0	7.7	5.8	4.4	6.2	3.8	4.8
SH	1.9	1.7	1.5	2.4	1.9	2.6	2.8	3.4	3.5	2.3	1.9	1.7
VL	1.8	0.8	0.9	2.6	1.2	2.5	1.9	1.7	1.8	2.2	1.5	1.9
TAL	17.7	15.1	15.2	29.9	27.5	24.8	26.5	25.4	25.1	28.0	21.4	18.0
TMW	1.9	2.2	1.9	4.0	3.2	3.6	3.9	3.7	3.7	3.8	2.7	2.3
TMH	2.2	2.4	2.0	4.5	3.4	3.4	3.4	3.6	3.7	3.3	2.8	2.3
TH	4.2	4.1	3.3	6.8	4.6	5.2	4.6	5.0	5.5	4.9	4.3	3.0
TMHM	1.5	2.1	1.7	2.9	1.9	2.2	2.1	2.2	2.3	2.4	1.7	1.5
THM	4.4	4.5	3.5	7.3	5.2	5.9	5.1	4.7	4.8	5.3	3.0	2.9
MTH	4.4	4.6	3.6	7.9	5.3	5.9	5.5	5.5	4.8	5.3	3.8	3.2
DMTH	8.3	6.5	6.5	11.4	11.3	11.5	8.5	9.3	10.7	11.0	8.0	7.1
DF	1.6	1.4	1.1	2.6	1.8	2.2	1.6	1.5	1.4	1.5	0.7	0.8
VF	1.3	1.1	0.7	1.9	1.5	1.5	1.4	1.1	1.1	1.3	0.6	0.5
HAB	3.0	2.6	2.9	5.0	4.0	4.8	4.5	5.1	5.0	4.5	3.3	2.6
TL	26.9	24.4	23.9	39.7	43.1	40.6	41.9	40.4	40.5	43.3	34.1	28.9

Table 2. Relative values (%) of the morphometric variables of the DNA voucher specimens described in this paper. For abbreviations, see Material and methods.

Species	*Aglypto-dactylus laticeps*	*Aglypto-dactylus madagas-cariensis*	*Aglypto-dactylus securifer*	*Laliostoma labrosum*	*Tsingymantis antitra*							
Site	Kirindy CFPF	Mt d'Ambre N. P.	Ankarana N. P.	Ejeda-Ampanihy	Ankarana N. P.							
Field number		Tad 2004.65	Tad 2004.82	Tad 2004.8	FGZC 1120	FGZC 1121	FGZC 1122	FGZC 1123	FGZC 1142	FGZC 1143	FGZC 1145	FGZC 1146
ZSM	Un-cataloged	290/2008	305/2008	573/2008	2236/2007	2237/2007	2238/2007	2240/2007	2242/2007	2243/2007	2244/2007	2245/2007
GOS	33	35	40	39	39	38	39	39	38	36	40	29
BW/BL	66	60	61	62	57	59	60	62	62	57	60	53
SBW/BL	62	45	48	48	45	64	45	67	70	48	48	63
BW/BH	136	133	131	130	139	136	142	129	137	133	155	140
SBH/BL	71	77	73	73	61	68	68	68	72	69	70	63
ED/BL	10	12	14	14	10	11	12	12	12	12	13	9
SE/BL	28	32	33	29	31	32	29	30	30	30	28	29
EH/BH	78	74	74	71	74	78	77	78	82	75	72	77
IOD/BW	45	50	57	58	53	49	53	49	53	58	56	47
ND/BL	2	3	3	2	3	3	3	3	2	3	3	3
NH/BH	68	61	60	64	61	72	66	67	74	65	63	66
RN/NP	73	74	68	71	79	85	66	68	69	75	55	76
NH/EH	88	83	81	91	83	92	85	86	91	87	88	86
IND/IOD	61	73	63	43	47	54	46	48	47	47	50	68
SP/BL	16	20	16	15	16	14	13	18	15	14	16	14
SS/BL	65	66	70	64	61	62	57	62	59	59	70	56
SH/BH	43	40	36	31	29	38	42	47	51	35	39	41
SH/HAB	62	66	51	48	46	54	62	66	71	51	57	64
VL/BL	20	8	10	17	8	16	12	12	12	14	12	18
TAL/BL	192	161	176	191	176	157	172	168	163	182	168	166
TMW/BW	32	39	36	41	35	38	42	40	39	44	35	40
TMH/BH	50	56	50	59	54	50	52	50	52	51	56	56
TMH/TH	53	58	60	66	75	66	73	72	66	68	65	77
TMH/MTH	50	51	55	56	65	58	61	65	76	63	73	72
TH/BH	94	98	83	90	71	76	71	69	79	75	87	73
TMHM/THM	33	47	49	39	37	38	41	46	49	45	56	54
TMHM/MTH	33	46	47	36	36	38	39	39	49	45	45	48
THM/BH	99	108	86	97	81	85	79	64	68	80	62	70
THM/MTH	100	98	96	93	98	99	94	85	99	99	80	89
MTH/BH	99	110	90	105	82	86	85	76	69	82	77	78
DMTH/TAL	47	43	42	38	41	46	32	37	43	39	37	39
DF/TMHM	112	64	64	93	91	98	75	69	61	64	41	53
VF/TMHM	92	50	39	66	78	68	67	52	48	56	37	33
DF/VF	122	129	165	140	116	145	113	132	127	115	111	159
HAB/BH	68	61	71	66	63	70	69	71	71	68	68	64

Table 3. Comparison of the oral disc characteristics of the voucher specimens described in this paper (JW, Thorn-pap, MC, DG, A_1, A_2, $A_{2\ gap}$, $A_{2\ row+gap}$, Kerat length, MP lenght and SMP length are in mm; ODW/BW, DG/ODW, JW/ODW, MC/JW, A1/ODW and

Species	*Aglyptodactylus laticeps*	*Aglyptodactylus madagascariensis*	*Aglyptodactylus securifer*	*Laliostoma labrosum*
Site	Kirindy CFPF	Mt d'Ambre N. P.	Ankarana N. P.	Ejeda-Ampanihy
Field number		Tad 2004.65	Tad 2004.82	Tad 2004.8
ZSM	Uncataloged	290/2008	305/2008	573/2008
GOS	33	35	40	39
ODW	2.9	3.0	3.2	3.4
LTRF	5(2–5)/3(1)	1:6+7/1+1:2	1:6+7/1+1:2	5(2–5)/3(1)
UR	5	7	7	5
LR	3	3	3	3
JW	1.13	1.38	2.27	2.04
MCL	0.03	0.03	0.03	0.04
DG	1.85	2.05	2.27	2.25
VG	abs	abs	abs	0.49
A_1	2.47	2.09	1.92	2.52
A_2	1.22/1.18	1.00/1.02	1.12/1.07	1.10/1.11
$A_{2\ gap}$	0.05	0.05	0.04	0.47
$A_{2\ row+gap}$	2.45	2.07	1.23	2.68
$A_{2\ row-gap}$	2.40	2.05	1.19	2.21
A_3	0.99/1.04	0.86/0.78	0.98/1.00	0.75/0.79
A_4	0.83/0.85	0.61/0.65	0.78/0.80	0.49/0.51
A_5	0.57/0.64	0.49/0.51	0.63/0.70	0.25/0.37
A_6	0.20/0.23	0.42/0.44	0.49/0.47	abs
A_7	abs	0/0.27	0/0.16	abs
P_1	1.06/1.12	1.01/1.15	1.21/1.18	1.16/1.17
P_2	2.63	2.06	2.33	2.26
P_3	2.49	1.79	2.39	2.02
Kerat length	0.08	0.10	0.09	0.15
MP lenght	0.13	0.19	0.13	0.16
SMP length	0.12	abs	abs	abs
ODW/BW	48	55	60	35
DG/ODW	64	67	72	66
VG/ODW	abs	abs	abs	14
JW/ODW	39	45	72	60
MCL/JW	2.7	2.2	1.3	2.0
A_1/ODW	86	69	61	74
A_2Gap/A_2Row	2.0	2.4	3.3	17.5
A_1	186	87/88	216	177
A_2	90/97	84/85	121/108	78/74
A_3	74/75	67/63	105/99	58/60
A_4	66/67	51/64	85/67	36/38
A_5	42/49	48/49	61/63	19/25
A_6	15/14	45/38	41/37	abs
A_7	abs	0/17	0/9	abs
P_1	70/72	140	182	88/78
P_2	202	165	221	164
P_3	258	163	258	147
MP	79	76	122	35/37
SMP	8	abs	abs	15/13
Total papillae	87	76	123	100
A_1 density	75	84	113	70
A_2 density	78	88	108	99
A_3 density	73	79	103	77
A_4 density	79	91	96	74
A_5 density	67	137	93	71
A_6 density	67	97	81	abs
A_7 density	abs	63	56	abs
P_1 density	65	65	78	71
P_2 density	77	80	95	73
P_3 density	104	91	108	73

A_2Gap/A_2Row are in %; A_1 is density = number/mm; UR, LR, A1 num, MP, SMP and Total papillae are total numbers). For abbreviations, see Material and methods.

Tsingymantis antitra							
Ankarana N. P.							
FGZC 1120	FGZC 1121	FGZC 1122	FGZC 1123	FGZC 1142	FGZC 1143	FGZC 1145	FGZC 1146
2236/2007	2237/2007	2238/2007	2240/2007	2242/2007	2243/2007	2244/2007	2245/2007
39	38	39	39	38	36	40	29
4.6	4.7	4.4	4.5	4.8	4.5	3.8	3.3
6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)	6(2–6)/3(1)
6	6	6	6	6	6	6	6
3	3	3	3	3	3	3	3
2.03	2.00	1.89	2.00	2.25	1.97	1.64	1.42
0.01	0.01	0.01	0.01	0.08	0.02	0.01	0.01
2.94	3.39	3.03	3.46	3.56	3.12	2.56	2.2
Abs	abs	abs	abs	abs	abs	abs	abs
2.91	2.52	3.72	3.86	4.11	3.59	2.99	2.52
2.07/2 :04	1.99/1.86	2.05/1.87	2.11/1.99	1.92/1.93	1.77/1.84	1.41/1.50	1.35/1.47
0 :07	0.29	0.21	0.06	0.37	0.25	0.14	0.14
4 .18	4.24	4.13	4.16	4.22	3.86	3.05	2.96
4 .11	3.95	3.92	4.10	3.85	3.61	2.91	2.82
1.67/1.65	1.55/1.59	1.60/1.58	1.66/1.66	1.69/1.54	1.51/1.54	1.07/1.15	1.05/0.94
1.38/1.33	1.25/1.18	1.21/1.04	1.29/1.30	1.32/1.31	1.19/1.19	0.81/0.95	0.82/0.77
1.03/0.96	0.81/0.79	0.83/0.67	0.84/0.78	0.94/1.04	0.76/0.81	0.46/0.50	0.66/0.56
0.58/0.51	0.35/0.28	0.48/0.38	0.32/0.29	0.49/0.65	0.36/0.44	0.10/0.21	0.32/0.33
Abs	abs	abs	abs	abs	abs	abs	abs
1.62/1.77	1.82/1.75	1.60/1.61	1.62/1.67	1.95/1.85	1.75/1.68	1.24/1.19	1.09/1.11
3.55	6.28	3.46	3.43	3.88	3.58	2.56	2.37
3.40	3.54	2.69	2.91	3.86	2.36	2.60	2.22
0.16	0.16	0.15	0.16	0.16	0.15	0.10	0.12
0.16	0.17	0.16	0.16	0.19	0.16	0.15	0.17
0.13	0.14	0.13	0.10	0.11	0.12	0.11	0.17
52	50	47	48	50	51	50	57
64	72	69	77	75	70	68	67
Abs	abs	abs	abs	abs	abs	abs	abs
44	42	43	44	47	44	44	43
0.5	0.5	0.5	0.5	3.6	1.0	0.6	0.7
63	54	85	86	86	80	80	76
1.7	6.8	5.1	1.4	8.8	6.5	4.6	4.7
234	250	242	238	272	197	186	171
113/103	93/88	108/90	106/110	103/106	85/84	102/80	79/82
87/84	81/81	78/81	82/88	86/82	78/70	66/63	64/60
66/66	65/59	68/67	69/68	75/70	59/55	44/56	45/47
48/52	41/41	44/45	43/48	49/50	40/40	26/38	34/33
25/24	14/12	27/21	19/18	22/32	18/21	3/7	17/18
ABS	abs	abs	abs	abs	abs	abs	abs
80/86	82/86	77/79	83/87	91/85	73/74	65/75	65/68
196	186	164	193	194	176	171	145
219	112	153	189	224	126	185	165
179	118	166	175	157	130	147	123
15/17	16/15	17/20	13/12	12/11	10/11	15/14	12/12
211	180	203	200	180	151	176	147
80	99	65	62	66	55	62	68
53	46	51	31	54	47	63	57
52	52	50	51	52	49	58	62
49	51	60	53	55	48	57	58
50	51	59	56	50	51	67	55
55	41	56	61	52	49	32	54
abs	abs	abs	abs	abs	abs	abs	abs
49	47	49	52	46	43	58	60
55	30	47	56	50	49	67	61
64	32	57	65	58	53	71	74