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Diversity, external morphology and 'reverse taxonomy' in the specialized tadpoles of Malagasy river bank frogs of the subgenus *Ochthomantis* (genus *Mantidactylus*)

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Abstract

We provide detailed morphological descriptions of the tadpoles of Malagasy river bank frogs of the subgenera *Ochthomantis* and *Maitsomantis* (genus *Mantidactylus*, family Mantellidae), and data on relative abundance and habitat preferences of *Ochthomantis* species from Ranomafana National Park in south-eastern Madagascar. Our study includes the tadpoles of six described and four undescribed candidate species. Eight of these larvae were previously unknown. Tadpoles were identified by DNA barcoding. Due to the very rudimentary taxonomic knowledge on *Ochthomantis*, we followed a 'reverse taxonomy' approach in which adult classification was to a great part determined on the basis of larval differences. By this procedure we even identified one candidate species whose adults remain still unknown. The majority of tadpoles in *Ochthomantis* and *Maitsomantis* have a rather similar body shape and they usually have similar habitat requirements. However, on the basis of the structure of their oral disk we identified three distinct groups: the first includes the *femoralis*-like tadpoles of *Mantidactylus femoralis*, *M. ambreensis*, *M. zolitschka*, *M. argenteus*, and of the candidate species named *M.* sp. 42, *M.* sp. 43 and *M.* sp. 47. They all have a reduced oral disk with poorly keratinized jaw sheaths and labial teeth. The *mocquardi*-like tadpoles of *M. mocquardi* and *M.* sp. 64 are placed in the second group and are characterized by a further reduction of oral disk structures, *i.e.* a complete lack of labial teeth. The third group includes only *M. majori* and is characterized by the transformation of the upper jaw sheath into three thorn-shaped projections. Based on a preliminary molecular phylogenetic analysis the reduction of keratinized oral structures in *M. majori* may have occurred convergently to that in *M. mocquardi*. The ecological data indicate that the tadpoles of the three most abundant species in Ranomafana (*M. femoralis*, *M. majori* and *M.* sp. 47) do not obviously differ in their choice of microhabitat although the differences in their oral structures indicate that they might use different food resources. They all show a preference for the stream areas with slow current and leaf litter substrate.

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Introduction

In the Malagasy family Mantellidae, frogs of the genus *Mantidactylus* form one of the most diverse groups especially in terms of their larval morphology. While the phylogenetic relationships among the various subclades (subgenera and species groups) of *Mantidactylus* are relatively well understood due to the application of molecular phylogenies (*e.g.* Glaw and Vences 2006; Glaw *et al.*, 2006), their species-level systematics are very poorly explored, and numerous candidate species await formal description (*e.g.* Vieites *et al.*, 2009). Within *Mantidactylus*, the subgenus *Ochthomantis*, according to the latest revisions by Glaw and Vences (2004, 2006) currently consists of five valid species: *Mantidactylus ambreensis* Mocquard, 1895; *M. femoralis* (Boulenger, 1882); *M. majori* Boulenger, 1896; *M. mocquardi* Angel, 1929; and *M. zolitschka* Glaw and Vences, 2004. Within this subgenus there is strong evidence for additional cryptic diversity, and numerous new candidate species have already been identified (Glaw and Vences, 2004; Rabibisoa *et al.*, 2008; Vieites *et al.*, 2009). At present, three distinct species in the subgenus are relatively easy to diagnose: *M. ambreensis*, *M. majori* and *M. zolitschka*. In contrast, *M. femoralis* and *M. mocquardi* as currently understood are complexes of multiple species (Glaw and Vences, 2007).

Anuran larvae show many special and characteristic features which are distinctly different from those of the adult frog stage, encompassing ecology, morphology and habits (McDiarmid and Altig, 1999). These features can also be very diverse among tadpoles, and likely are the results of adaptation to their environment. However, tadpole characters also are partly determined by the phylogenetic history of the respective species, and have successfully been used for phylogenetic reconstruction (Haas, 2003).

Descriptions of anuran species, as a rule almost without exception, are based on type material in the metamorphosed, usually adult, stage. In fact, for many species – possibly from the majority of frog species worldwide – the larval stages are not reliably known. Only recently has the identification of different life-history stages of an organism by matching their DNA sequences become possible, a technique usually called DNA barcoding (Hebert *et al.*, 2003). The application of this technique to amphibians is promising (Thomas *et al.*, 2005; Vences *et al.*, 2005) and allows efficient surveys of the species and larval diversity of tropical frog communities (Vences *et al.*, 2008). In some taxonomically poorly studied frog groups the paradoxical result might be that the tadpoles are better known than the adults, both regarding their ecology and their morphology.

In other poorly known organisms such as the meiobenthic fauna, studies often end up with many taxa being only identified via their DNA sequences and not by their morphology, an approach for which Markmann and Tautz (2005) proposed the term ‘reverse taxonomy’. Such a situation applies to the frogs in the subgenus *Ochthomantis*. These frogs are rather inconspicuous regarding adult morphology, and candidate species have largely been identified on the basis of DNA sequences (Vieites *et al.*, 2009). Several of the described *Ochthomantis* species and most candidate species appear to be diagnosable as adults only by the application of detailed morphometric analyses (Rabibisoa *et al.*, 2008). The morphology of tadpoles has not been assessed for most species of *Ochthomantis*, and it is thus far unknown whether tadpole characters might perform better in species discrimination than adult morphology. So far, only tadpoles assigned to *M. femoralis* have been briefly described by Blommers-Schlösser (1979) and a larva of an unidentified species from the Chaines Anosyennes (1060 m a.s.l.), probably referable to the subgenus *Ochthomantis*, was briefly characterized by Blommers-Schlösser and Blanc (1991).

In contrast to the uniform and inconspicuous adult morphology of *Ochthomantis*, their tadpoles have unique specialized mouthparts which make them easy to distinguish from tadpoles of other mantellid genera and subgenera. Their oral disk is characterized by (1) a strong reduction of the number of labial tooth rows and the density of labial teeth, and (2) a reduction of the keratinisation of the jaw sheaths. Such divergent oral disk structures probably are specializations either on particular food items and/or feeding behaviour. In general, such specialized larval adaptations may be one key to understand the high diversity of tropical amphibian communities (Strauß *et al.*, 2010).

In this study, we provide descriptions of the external morphology of the tadpoles of ten species of *Mantidactylus* (*Ochthomantis* and *Maitsomantis*), eight of them for the first time. We here do not include details of buccal anatomy or microstructures such as labial teeth on which we will focus in a future comprehensive survey of tadpole buccal cavities in the Mantellidae. We assign species and candidate species to three separate morphological clysters on the basis of external tadpole morphology, and discuss the evolution of specialization of oral structures in *Ochthomantis* as well as the advantages of DNA barcoding for identifying tadpoles.

Material and methods

Morphological study of tadpoles

Tadpoles were collected using different types of nets having mesh sizes from 2 to 5 mm, depending on the size of the streams, the strength of the current and the type of substrate. They were euthanized by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here called 'DNA voucher'. All detailed morphological tadpole characterizations and drawings are based on this DNA voucher, whereas observation for the variation refer to further DNA voucher specimens from the same locality or from different localities, and sometimes to the non-sequenced specimens of the same series. After tissue collection, all specimens were preserved in 5% formalin or 70% ethanol. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). When referring to voucher specimens the original field numbers (FG/MV, FAZC, FGZC, T, TAD, ZCMV) are usually provided together with the final ZSM catalogue numbers. Tadpoles were identified using a DNA barcoding approach (see below). Tadpoles studied in this paper are listed in Tables 1-2 including data concerning the site and its coordinates, the date of the capture and the collectors.

For detailed morphological examination, especially to determine developmental stages and assess characters of the oral disk, preserved tadpoles were stained slightly with methylene blue. Tadpoles were examined under water and few drops of methylene blue were applied to the oral disk, hind limb, spiracle narial opening and vent tube for having a better view of their structure. Developmental stages are determined following Gosner (1960). Description, measurements and drawings were done on digital pictures of the preserved tadpoles taken with a Stereomicroscope Zeiss Discovery V12 connected to a computer, following the landmarks, terminology and definitions of McDiarmid and Altig (1999). New landmarks are also introduced herein (Fig. 9). Developmental stages are described following Gosner (1960). The formula of labial tooth rows (LTRF) is given according to Altig and McDiarmid (1999). Labial teeth are also referred to as keratodonts following Dubois (1995). When describing interruptions of keratodont rows we considered these as scattered when they have more than a single medial interruption. Drawings of the preserved tadpoles are shown in the Appendix. When categorizing morphometric ratios, we consider them as 'almost equal' if ratios of the measured values are 95-96% or 104-105%, as '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 as 'in the middle' if they are in the range 47-53%.

The following abbreviations are used (see also fig. 9): 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), $A_{1\text{-}3\ den}$ (density of the keratodonts in row $A_{1\text{-}3}$), $A_{1\text{-}3\ len}$ (length of $A_{1\text{-}3}$), $A_{1\text{-}3\ num}$ (number of keratodonts in $A_{1\text{-}3}$), BH (maximal body height), BL (body length), BW (maximal body width), DF (dorsal fin height at midtail), DG (size of the dorsal gap of marginal papillae), DMTH (distance of maximal tail height from the tail-body junction), ED (eye diameter), EH (eye height - measured from the lower curve of the belly), 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), IOD (inter-orbital distance), JW (maximal jaw sheath width), MC (medial convexity of the upper sheath), 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 curve of the belly), NP (naris-pupil distance), OD (oral disk), ODW (maximum oral disk width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), $P_{1\text{-}3\ den}$ (density of the keratodonts in $P_{1\text{-}3}$), $P_{1\text{-}3\ len}$ (length of $P_{1\text{-}3}$), $P_{1\text{-}3\ num}$ (number of keratodonts in $P_{1\text{-}3}$), R/L (right/left), RN (rostro-narial distance), 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), SH (spiracle height - measured from the lower curve of the belly), SL (spiracle length), SMP (submarginal papillae), SS (snout-spiracle distance), SV (spiracle-vent distance), 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 midtail), VG (size of the ventral gap of marginal papillae), VL (vent tube length).

Molecular analyses

DNA barcoding was based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Vences *et al.*, 2005). We amplified a fragment of ca. 550 bp using primers 16Sar-L and 16Sbr-H from Palumbi *et al.* (1991), or a shorter fragment of ca. 400 bp using the newly developed specific mantellid primers 16S-Frog-L1 (CAT AAT CAC TTG TTC TTT AAA) and 16S-Frog-H1 (GAT CCA ACA TCG AGG TCG). PCR was carried out with standard protocols (Vences *et al.*, 2003) and sequences resolved on automated sequencers. Sequences were preliminarily identified using BLAST searches against a near-complete database of sequences of adult Malagasy frog species. Results were subsequently verified by manually aligning and comparing sequences to the closest hits in the data base. Identification was considered to be unequivocal when the tadpole sequence was 99-100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. When no identity with adult specimens was found and divergence was >3% we considered the corresponding tadpoles to belong to additional candidate species, a situation that arose in a single case. DNA sequences were deposited in GenBank (accession numbers of newly determined DNA sequences HQ610836-HQ610924; see also Table 2).

To visualize the molecular relationships among adult and larval *Ochthomantis*, sequences were aligned by eye. We performed a Bayesian phylogenetic analysis using the program Mrbayes 3.1 (Ronquist and Huelsenbeck, 2003). We used MrModeltest version 2.2 (Nylander, 2004) to choose the appropriate model of sequence evolution. Analyses consisted of four Markov chains that ran for 5 millions of generations, sampled every 1000 generations, with a random starting tree and default priors. The burn-in was empirically estimated by plotting – ln L against the generation number, and the trees corresponding to the first 4 million generations discarded. Based on more extensive studies of the phylogeny of mantellids (Glaw and Vences, 2006; Glaw *et al*., 2006) we included in our analysis *Mantidactylus* (*Maitsomantis*) *argenteus* which is closely related to *Ochthomantis*, and used *Mantidactylus* (*Hylobatrachus*) *cowanii* as the outgroup because *Hylobatrachus* has been recovered previously as member of the sister clade of *Ochthomantis*+*Maitsomantis* (Glaw *et al*., 2006).

Habitat preference analysis

In the framework of a study on stream tadpole communities in the Ranomafana National Park (RNP) in the Southern Central East of Madagascar, breeding site choice and tadpole microhabitat preferences were evaluated at 33 stream sections.

To evaluate the correlation of habitat (stream) characteristics with breeding site choice of *Ochthomantis* species (*i.e.* tadpole occurrence), the following habitat variables of the streams and their surrounding forest area were recorded: slope, width, depth, overhanging

Table 1. Localities of the tadpoles included in this study.

Locality	Site	Species	Coordinates	Date	Collectors
Ambohitsara		*M. mocquardi*	21°21.431' S 47°48.941' E 294 m a.s.l.	03.iii.2007	R.D. Randrianiaina, T. Rasolonjatovo- H., S. Ndriantsoa, E. Reeve, A. Strauß, J. Glos, M. Vences
An'Ala	Andohanisity	*M. argenteus* *M. femoralis* *M. mocquardi* *M. zolitschka*	18°55.156' S 48°29.277' E 889 m a.s.l.	08.ii.2006	R.D. Randrianiaina, L. Raharivololoniaina, D.R. Vieites, J. Patton, C. Patton, M. Vences
Isalo National Park	South of Tevan'ny mpiolitsa	*M. femoralis*	22°30.085' S 45°17.177' E 869 m a.s.l.	04.iv.2007	R.D. Randrianiaina, S. Ndriantsoa
Mahasoa		*M. mocquardi*	17°17.861' S 48°42.119' E 1032 m a.s.l.	13.ii.2008	M. Vences, D.R. Vieites, P. Bora, J. Patton, C. Patton
Marojejy National Park	Camp Mantella	*M. femoralis* *M.* sp. 43	14°26.0972' S 49°47.214' E 327 m a.s.l.	19.ii.2005	R.D. Randrianiaina, M. Vences, F. Glaw
Montagne d'Ambre National Park	Voie des milles arbres	*M. ambreensis* *M.* sp. 42	12°31.616' S 49°10.316' E 1050 m a.s.l.	17.ii.2003	R.D. Randrianiaina, F. Glaw

Table 1, continued.

Locality	Site	Species	Coordinates	Date	Collectors
Ranomafana	RNP Sahamalaotra	*M. majori*	21°14.112' S 47°23.767' E 1124 m a.s.l.	25.ii.2006	R.D. Randrianiaina, L. Raharivololoniaina, A.F. Ranjanaharisoa
	RNP Talatakely	*M.* sp. 47	21°15.846' S 47°25.161' E 966 m a.s.l.	24.ii.2006	T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences
	RNP Maharira	*M.* sp. 47	21°19.547' S 47°24.147' E 1200 m a.s.l.	26.i.2004	M. Vences, I. De la Riva
	Vohiparara	*M. femoralis*	21°14.143' S 47°23.152' E 1118 m a.s.l.	20.ii.2006	R.D. Randrianiaina, L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences
	Ranomafana village	*M.* sp. 64	21°15.699' S 47°27.571' E 619 m a.s.l.	21.ii.2006	R.D. Randrianiaina, L. Raharivololoniaina, D.R. Vieites, J. Patton, C. Patton, M. Vences
Vevembe forest		*M. femoralis* *M. majori*	22°47.686' S 47°11.228' E 581 m a.s.l.	10.ii.2004	M. Vences

Table 2. Collection numbers and GenBank accession numbers of the tadpoles studied, as well as of the adult specimens included in the molecular analysis (marked with an asterisk). Collection acronyms are as follows: FG/MV, FGZC, TAD, ZCMV (field numbers), ZSM (Zoologische Staatssammlung München). Missing accession numbers indicate that sequences were too short or of poor quality and were therefore not submitted to GenBank.

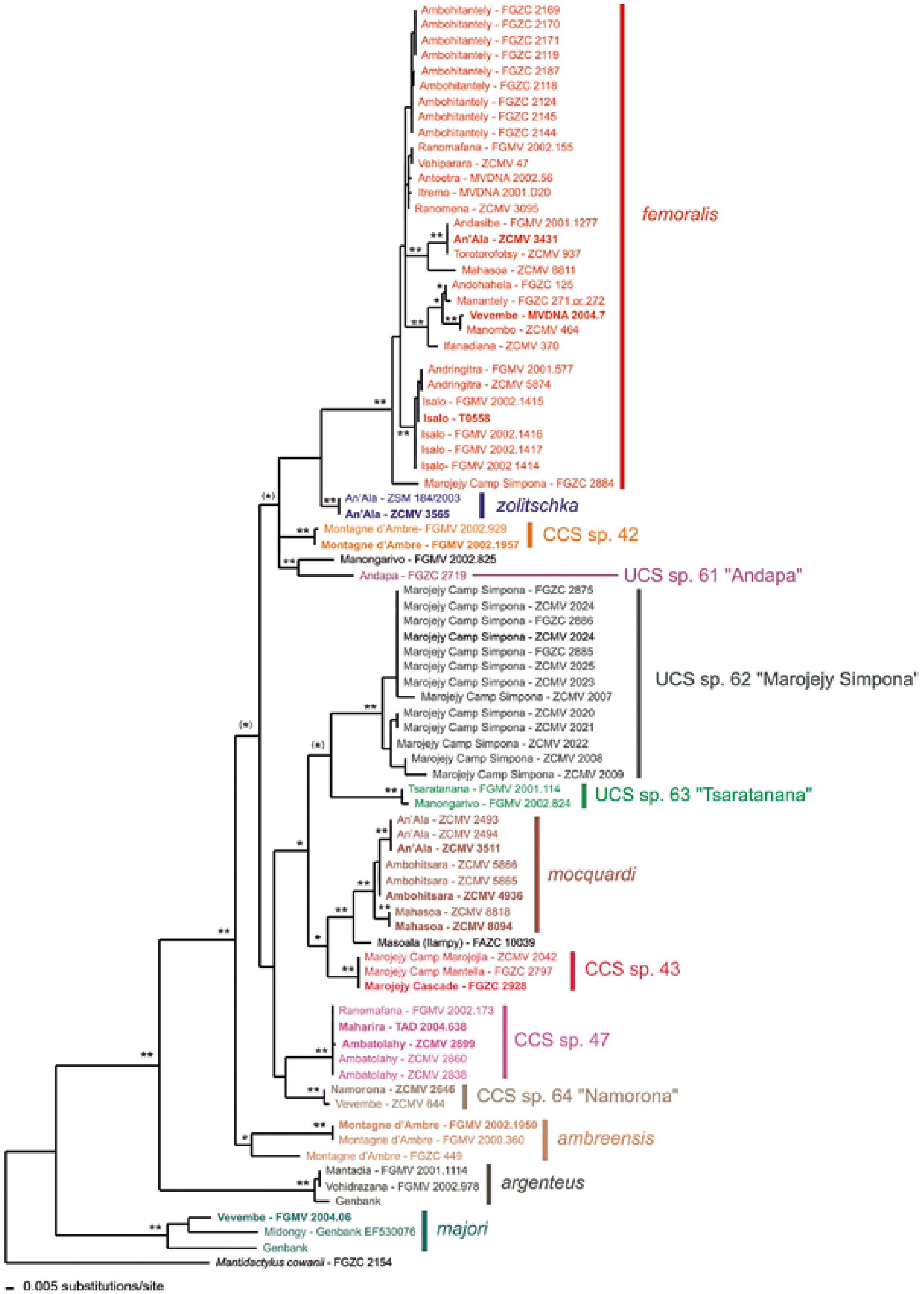
Locality	Species	ZSM- and Field number	Accession number
Ambohitsara	*M. mocquardi*	ZSM 72/2008-ZCMV 4936	GU975710
		ZCMV 5866*	HQ610919
Ambohitantely	*M. femoralis*	FGZC 2124*	HQ610904
		FGZC 2144*	HQ610905
		FGZC 2145*	HQ610906
		FGZC 2169*	HQ610907
		FGZC 2170*	HQ610908
		FGZC 2171*	HQ610909
		FGZC 2187*	HQ610910
		FGZC 2118*	HQ610911
		FGZC 2119*	HQ610912
An'Ala	*M. argenteus*	ZSM 1573/2007-ZCMV 3575	HQ610836
		ZSM 1815/2007-ZCMV 3516	---
		ZSM 1849/2007-ZCMV 3566	---
	M. femoralis	ZSM 1736/2007-ZCMV 3431	HQ610837
		ZSM 1554/2007-ZCMV 3536	HQ610838
		ZSM 1555/2007-ZCMV 3537	HQ610839
		ZSM 1733/2007-ZCMV 3428	HQ610840
		ZSM 1781/2007-ZCMV 3476	HQ610841
		ZSM 1834/2007-ZCMV 3554	HQ610842
		ZSM 1848/2007-ZCMV 3572	HQ610843

Table 2, continued.

Locality	Species	ZSM- and Field number	Accession number
	M. mocquardi	ZSM 1540/2007-ZCMV 3511	HQ610852
		ZSM 1539/2007-ZCMV 3510	HQ610853
		ZSM 1541/2007-ZCMV 3513	HQ610854
		ZSM 1746/2007-ZCMV 3441	HQ610855
		ZSM 1761/2007-ZCMV 3457	HQ610856
		ZSM 1771/2007-ZCMV 3469	HQ610857
		ZSM 1805/2007-ZCMV 3447	HQ610858
		ZSM 1813/2007-ZCMV 3509	HQ610859
		ZSM 1844/2007-ZCMV 3567	HQ610860
		ZSM 1846/2007-ZCMV 3570	HQ610861
		ZCMV 2493*	HQ610920
		ZCMV 2494	HQ610922
	M. zolitschka	ZSM 1843/2007-ZCMV 3565	HQ610863
		ZSM 1741/2007-ZCMV 3436	HQ610864
		ZSM 1759/2007-ZCMV 3455	HQ610865
		ZSM 1768/2007-ZCMV 3464	HQ610866
		ZSM 1841/2007-ZCMV 3563	HQ610867
Andringitra	*M. femoralis*	ZCMV 5874*	HQ610918
Ifanadiana	*M. femoralis*	ZCMV 370*	HQ610914
Isalo National Park	*M. femoralis*	ZSM 1928/2007-T 558	HQ610844
Mahasoa	*M. mocquardi*	ZSM 686/2008-ZCMV 8094	HQ610862
		ZCMV 8818*	HQ610921
Manantantely	*M. femoralis*	FGZC 271*	HQ610913
Manombo	*M. femoralis*	ZCMV 464*	HQ610916
Marojejy National Park	*M. femoralis*	ZSM 1630/2007-FGZC 2955	HQ610845
	M. sp. 43	ZSM 1610/2007-FGZC 2928	HQ610868
		ZCMV 2042*	HQ610903
	M. sp. 62	FGZC 2875*	HQ610898
		FGZC 2885*	HQ610899
		FGZC 2886*	HQ610900
		ZCMV 2020*	HQ610892
		ZCMV 2021*	HQ610893
		ZCMV 2023*	HQ610901
		ZCMV 2025*	HQ610902
		ZCMV 2007*	HQ610894
		ZCMV 2008*	HQ610895
		ZCMV 2009*	HQ610896
		ZCMV 2022*	HQ610897
Montagne d'Ambre National Park	*M. ambreensis*	ZSM 762/2004-FG/MV 2002.1950	HQ610870
	M. sp. 42	ZSM 774/2004-FG/MV 2002.1957	HQ610869
Ranomafana National Park	*M. femoralis*	ZSM 1198/2004-TAD 2004/1385	---
		ZSM 396/2008-ZCMV 2640	HQ610846
		ZSM 1643/2007-ZCMV 3708	HQ610847
		ZSM 1696/2007-ZCMV 3773	---

Table 2, continued.

Locality	Species	ZSM- and Field number	Accession number
		ZSM 188/2008-ZCMV 3821	---
		ZSM 192/2008-ZCMV 3825	---
		ZSM 257/2008-ZCMV 3675	HQ610848
		ZSM 439/2008-ZCMV 2684	HQ610849
		ZSM 472/2008-ZCMV 3703	HQ610850
		ZCMV 3095*	HQ610915
	M. majori	ZSM 1684/2004-ZCMV 3761	---
		ZSM 42/2007-ZCMV 4155	HQ610871
		ZSM 93/2007-ZCMV 4132	GU975191
		ZSM 335/2007-T 172	GU975194
		ZSM 379/2007-ZCMV 4235	GU975188
		ZSM 495/2007-ZCMV 4699	GU975187
		ZSM 502/2007-ZCMV 4517	GU975185
		ZSM 609/2007-T 410	GU975195
		ZSM 682/2007-ZCMV 5391	GU975189
		ZSM 954/2007-ZCMV 5979	GU975190
		ZSM 1062/2007-T 32	HQ610872
		ZSM 1063/2007-T 168	HQ610873
		ZSM 1078/2007-T 38	GU975192
		ZSM 1285/2007-ZCMV 4417	GU975184
		ZSM 1328/2007-T 156	GU975193
		ZSM 1382/2007-ZCMV 4534	GU975186
		ZSM 1653/2007-ZCMV 3722	HQ610874
		ZSM 1676/2007-ZCMV 3749	HQ610875
		ZSM 1684/2007-ZCMV 3761	HQ610876
		ZSM 1699/2007-ZCMV 3776	---
		ZSM 1700/2007-ZCMV 3777	---
		ZSM 1701/2007-ZCMV 3778	---
		ZSM 171/2008-ZCMV 3806	---
		ZSM 202/2008-ZCMV 3835	---
		ZSM 203/2008-ZCMV 3836	HQ610877
		ZSM 229/2008-ZCMV 3627	HQ610878
		ZSM 256/2008-ZCMV 3672	HQ610879
		ZSM 429/2008-ZCMV 2674	HQ610879
		ZSM 441/2008-ZCMV 2686	HQ610880
		ZSM 447/2008-ZCMV 2694	HQ610881
		ZSM 445/2008-ZCMV 2690	HQ610882
		ZSM 455/2008-ZCMV 2698	HQ610883
		ZSM 473/2008-ZCMV 3704	HQ610884
	M. sp. 47	ZSM 456/2008-ZCMV 2699	HQ610886
		ZSM 1697/2007-ZCMV 3774	---
		ZSM 254/2008-ZCMV 3669	HQ610887
		ZSM 315/2008-ZCMV 3620	HQ610888
		ZSM 478/2008-ZCMV 3724	HQ610889
		ZSM 506/2008-ZCMV 3791	---
		ZCMV 2838*	HQ610923
	M. sp. 64	ZSM 401/2008-ZCMV 2646	HQ610890
		ZCMV 9291 (to be catalogued in ZSM)	HQ610891
Torotorofotsy	*M. femoralis*	ZCMV 937*	HQ610917
Vevembe forest	*M. femoralis*	ZSM 1385/2004-TAD 2004/07	HQ610851
	M. sp. 64	ZCMV 644*	HQ610924
	M. majori	ZSM 1384/2004-TAD 6 Vevembe	HQ610885


Ambohitantely - FGZC 2169
Ambohitantely - FGZC 2170
Ambohitantely - FGZC 2171
Ambohitantely - FGZC 2119
Ambohitantely - FGZC 2187
Ambohitantely - FGZC 2118
Ambohitantely - FGZC 2124
Ambohitantely - FGZC 2145
Ambohitantely - FGZC 2144
Ranomafana - FGMV 2002.155
Vohiparara - ZCMV 47
Antoetra - MVDNA 2002.56
Ibremo - MVDNA 2001.D20
Ranomena - ZCMV 3095
Andasibe - FGMV 2001.1277
An'Ala - ZCMV 3431
Torotorofotsy - ZCMV 937
Mahasoa - ZCMV 8811
Andohahela - FGZC 125
Manantely - FGZC 271 or 272
Vevembe - MVDNA 2004.7
Manombo - ZCMV 464
Ifanadiana - ZCMV 370
Andringitra - FGMV 2001.577
Andringitra - ZCMV 5874
Isalo - FGMV 2002.1415
Isalo - T0558
Isalo - FGMV 2002.1416
Isalo - FGMV 2002.1417
Isalo- FGMV 2002 1414
Marojejy Camp Simpona - FGZC 2884
femoralis
An'Ala - ZSM 184/2003
An'Ala - ZCMV 3565
zolitschka
Montagne d'Ambre- FGMV 2002.929
Montagne d'Ambre - FGMV 2002.1957
CCS sp. 42
Manongarivo - FGMV 2002.825
Andapa - FGZC 2719
UCS sp. 61 "Andapa"
Marojejy Camp Simpona - FGZC 2875
Marojejy Camp Simpona - ZCMV 2024
Marojejy Camp Simpona - FGZC 2886
Marojejy Camp Simpona - ZCMV 2024
Marojejy Camp Simpona - FGZC 2885
Marojejy Camp Simpona - ZCMV 2025
Marojejy Camp Simpona - ZCMV 2023
Marojejy Camp Simpona - ZCMV 2007
Marojejy Camp Simpona - ZCMV 2020
Marojejy Camp Simpona - ZCMV 2021
Marojejy Camp Simpona - ZCMV 2022
Marojejy Camp Simpona - ZCMV 2008
Marojejy Camp Simpona - ZCMV 2009
UCS sp. 62 "Marojejy Simpona'
Tsaratanana - FGMV 2001.114
Manongarivo - FGMV 2002.824
UCS sp. 63 "Tsaratanana"
An'Ala - ZCMV 2493
An'Ala - ZCMV 2494
An'Ala - ZCMV 3511
Ambohitsara - ZCMV 5866
Ambohitsara - ZCMV 5865
Ambohitsara - ZCMV 4936
Mahasoa - ZCMV 8818
Mahasoa - ZCMV 8094
mocquardi
Masoala (Ilampy) - FAZC 10039
Marojejy Camp Marojejia - ZCMV 2042
Marojejy Camp Mantella - FGZC 2797
Marojejy Cascade - FGZC 2928
CCS sp. 43
Ranomafana - FGMV 2002.173
Maharira - TAD 2004.638
Ambatolahy - ZCMV 2699
Ambatolahy - ZCMV 2860
Ambatolahy - ZCMV 2838
CCS sp. 47
Namorona - ZCMV 2646
Vevembe - ZCMV 644
CCS sp. 64 "Namorona"
Montagne d'Ambre - FGMV 2002.1950
Montagne d'Ambre - FGMV 2000.360
Montagne d'Ambre - FGZC 449
ambreensis
Mantadia - FGMV 2001.1114
Vohidrazana - FGMV 2002.978
Genbank
argenteus
Vevembe - FGMV 2004.06
Midongy - Genbank EF530076
Genbank
majori
Mantidactylus cowanii - FGZC 2154
0.005 substitutions/site

vegetation, and canopy cover of the stream; the density of shrubs, small trees, large trees, depth of forest floor leaf litter, slope of the forest floor, and canopy cover of the forest (exact definitions of these variables are in Strauß *et al*., 2010).

For each stream, 30 m long stream sections were as exhaustively as possible sampled for tadpoles, separately for all available microhabitats within the section. These microhabitats were predefined based on the structure of the ground substrate (categories rock, gravel, leaves, sand) and by stream velocity, with the categories 'fast' (obviously running) and 'slow' (almost stagnant) resulting in eight different possible types of microhabitat. To test for microhabitat preferences, the frequency of the microhabitats available was recorded for each stream. For details of sampling methods see Strauß *et al*. (2010).

Tadpole sampling was conducted in the wet season (January and February) 2008 and repeated in a subset of the streams during the dry season (July) 2008. Statistical analyses were exclusively based on data from the rainy season as both the presence and abundance of *Ochthomantis* tadpoles during the dry season were very limited. Analysis were performed in R 2.9.2 (R Development Core Team, 2009) including library car (Fox, 2008).

To identify the habitat variables of the stream and the surrounding forest that correlate with the presence of *Ochthomantis* tadpoles (all species pooled), first a principal component analysis (PCA) was performed. PCA was performed on the correlation matrix in order to standardise for the influence of unequal variance. To evaluate data outliers and linear interdependence of variables, box-plots and pair-plots (Zuur *et al*., 2007) were used. As PCA requires multinormality of data, box-cox-power-transformations (Box and Cox, 1964) were applied when necessary. The significance of the PC loadings was assessed based on the bootstrapped-eigenvector method as suggested by Peres-Neto *et al*. (2003). The number of meaningful PCs was estimated by a scree plot (Zuur *et al*., 2007). A multiple logistic regression (generalized linear model, GLM, with binomial errors) with the first three PCs as independent variables and the presence/absence of *Ochthomantis* tadpoles as binary dependent variable was performed to extract the key habitat variables important for breeding site choice of *Ochthomantis* frogs. Independent terms and interaction terms were deleted sequentially from the full model based on the Akaike Information Criterion (Burnham and Anderson, 1998) until the minimum adequate model was reached. In order to quantify microhabitat preference of *Ochthomantis* tadpoles within streams, Ivlev's electivity index E (Ivlev, 1961) was calculated for each *Ochthomantis* species occurring in RNP. E is defined as $E = (r-p)/(r+p)$ with r being the proportions of the microhabitats used (using tadpole abundance) and p the proportion of microhabitats available. To test whether the E values differ between the single species, a factorial ANOVA was run with E as dependent variable and the factors 'species' and 'microhabitat' as independent variables. This provides information whether E is different for the different microhabitats and whether observed differences vary between species. Only the three abundant species were included in this analysis.

Results

Larval and adult diversity in Ochthomantis

The molecular tree of 81 adults and larvae of the *Mantidactylus* subgenera *Ochthomantis* and *Maitsomantis* (Fig. 1) supports previous conclusions (Glaw and Vences, 2004; Vieites *et al*., 2009) of a high undescribed species diversity of *Ochthomantis*. Adult specimens of all described species in the genus (*M. ambreensis*, *M. femoralis*, *M. majori*, *M. mocquardi*, *M. zolitschka*) were recovered as monophyletic and genetically distinct groups, together with their respectively assigned tadpoles. In addition, several clusters were identified that we here define as candidate species according to the terminology and criteria of Vieites *et al*. (2009). Although the tree provides

◀ *Fig. 1*. Bayesian inference tree calculated on the basis of up to 500 base pairs of the mitochondrial 16S rRNA gene. Asterisks denote Bayesian posterior probability values: (*), >90%; * >95%, ** >99%. Different species and candidate species are indicated by different colours. Sequences from tadpoles are in bold. The tree shows clusters of individuals (adults and tadpoles) assigned to species and candidate species based on their mitochondrial similarity, but was not primarily reconstructed to assess the phylogeny among *Ochthomantis* for which a more extensive multi-gene dataset would be necessary. Note that the tree does not include a few available sequences (*M. majori*, adults from Ranomafana and tadpole ZCMV 3761 from Ranomafana; *M. femoralis*, tadpole ZCMV 2640 from Ranomafana) because these contained too many missing data; species identification on the basis of these short sequences was, however, unambiguous in analyses based on an adjusted alignment of ca. 200 bp. Two adult specimens were not assigned to species or candidate species: FAZC 10039 (possibly *M. mocquardi*), FG/MV 2002.825 (possible additional UCS from Manongarivo).

significant Bayesian posterior probabilities for various relationships among species in the subgenus *Ochthomantis*, we emphasize that its purpose is not to provide a phylogenetic hypothesis but merely to visualize molecular differentiation among clusters of individuals that correspond to species and candidate species.

Because we were able to assign adult specimens (Fig. 2) and larvae (Fig. 3) to most of the molecular clusters, we understand which of these are supported as evolutionary independent units by the congruence of independent data sets, mainly larval morphology and mitochondrial DNA sequences. Consequently, we defined as confirmed candidate species (CCS) those where congruent molecular and morphological results were available. Others were only identified as molecular clusters (with pairwise 16S divergences of >3% to other clusters; Vieites *et al*., 2009) without additional evidence from morphology of tadpoles, or morphology or bioacoustics

Fig. 2. Diversity of adults in the *Mantidactylus* subgenera *Maitsomantis* (*M. argenteus*) and *Ochthomantis*. Morphological identification of several species is unambiguous: *Mantidactylus argenteus* (FG/MV 2002.537 from Ranomafana), *M. majori* (specimen from Ranomafana, not collected), *M. ambreensis* (specimen from Montagne d’Ambre), *M. zolitschka* (paratype ZFMK 60116 from An’Ala). Others were identified by DNA barcoding, *i.e.*, on the basis of the molecular tree in Fig. 1: *M. femoralis* (FG/MV 2002.56 from Antoetra); *M. mocquardi* (ZCMV 5865 from Ambohitsara), *M.* sp. 63 (specimen from Tsaratanana), *M.* sp. 62 (ZSM 309/2005-FGZC 2885 from Marojejy, Camp Simpona), *M.* sp. 61 (ZSM 221/2005-FGZC 2719 from Andapa), *M.* sp. 42 (specimen from Montagne d’Ambre, assignment to this confirmed candidate species is tentative and not based on molecular data), *M.* sp. 43 (ZSM 253/2005-FGZC 2797 from Marojejy Camp Mantella), *M.* sp. 47 (specimen from Ambatolahy).

of adults, and are therefore defined as unconfirmed candidate species (UCS). Both CCS and UCS were named following Vieites *et al.* (2009) who numbered all candidate species in *Mantidactylus* from 1-60. The four additional candidate species identified herein are consecutively numbered 61-64. While the present study was under review, a publication by Padial *et al.* (2010) proposed a new scheme for naming candidate species. We endorse this new proposal and will apply it in further studies, but have here refrained to apply it yet to candidate species in *Ochthomantis* because we felt that consistency with the candidate species names of Vieites *et al.* (2009) is preferable at this point of time.

The following accounts briefly characterize the various species and candidate species by their larval and adult morphology, as far as currently possible. Detailed descriptions of the tadpoles are provided in the appendix, measurements and morphometric ratios of DNA voucher specimens in Tables 3-4, a comparison of the main morphological features of the different species in Table 5, and a summary of collection localities and specimens examined in Tables 1-2. Interestingly, in *Ochthomantis*, larval characters especially of the oral disk proved to be highly derived in all species and provided various clear morphological differences among species, whereas morphological differentiation of adults is more subtle (see also Glaw and Vences, 2004; Rabibisoa *et al*., 2008). In the following, species are therefore roughly listed by their degree of larval specialization. We first provide some detailed morphological data for one of the least specialized species, *Mantidactylus femoralis*, and then highlight distinctive features and specializations of the other species.

Mantidactylus femoralis. – Following Glaw and Vences (2004) we define *M. femoralis* as the most widespread and most common species in the subgenus *Ochthomantis*. Adults of this species are characterized by medium size, a more or less tubercular back, and a distinct and often rather large yellow inguinal patch (Fig. 2). According to the molecular data herein, this species is known from the South East (Andohahela, Manantantely, Vevembe, Manombo) to the North East (Marojejy), including many localities in the intervening areas (in a south-north direction: Andringitra; Isalo; Antoetra; Itremo; Ifanadiana; Ranomafana including Vohiparara, Ranomena and other sites; An'Ala; Andasibe; Torotorofotsy; Ambohitantely; Mahasoa).

The tadpole of *M. femoralis* (based on ZSM 1736/2007-ZCMV 3431, Gosner stage 28 from An'Ala (see appendix and Fig. 10 for preserved tadpole) and on ZSM 188/2008-ZCMV 3821 from Ranomafana (Fig. 3 for tadpole in life) has an elliptical body, a narrowly rounded snout in dorsal view and a constriction behind the point where the maximal body width is attained (between the proximal 2/5 and 3/5 of the body). In lateral view the body is depressed; the maximal body height is attained between the proximal 3/5 and 4/5 of the body; and the snout is narrowly rounded. Eyes are small, not visible in ventral view, positioned high dorsally and directed laterally, and situated between the proximal 3/10 and 4/10 of the body. The distance between the eyes is moderately wide. Nares are small, rounded, marked with a marginal rim, positioned high dorsally and oriented anterolaterally, situated nearer to snout than to eye and below eye level. The distance between nares is moderately wide. A red patch is present on the back of the nares. The spiracle is sinistral, moderately large, directed posteriorly, visible from dorsal and ventral views, and perceptible from lateral view. Its inner wall is free from the body and formed such that the aperture opens posteriorly. The opening is rounded, situated between the proximal 3/5 and 4/5 of the body, located high and at the height of the point where the axis of the tail myotomes contacts the body. The vent tube is dextral, moderately long, attached to the ventral fin and its inner wall is present. The tail is short; the caudal musculature is moderately developed; the tail muscle reaches the tail tip. Fins are very low; the dorsal fin originates on the tail muscle on the proximal 1/5 of the tail and the ventral fin originates at the ventral terminus of the body. The maximal tail height is located at a position after the proximal 2/5 of the tail. The lateral tail vein and the myosepta are slightly visible on the proximal 3/4 of the tail musculature, the point where the axis of the tail myotomes contacts the body is high and the axis of the tail myotomes is parallel with the axis of the trunk. The tip of the tail is narrowly rounded.

The oral disk (Fig. 4) is moderately large, reduced, not emarginated, positioned ventrally, and directed anteroventrally. It is visible in dorsal view and the upper labium is a continuation of the snout. There is a single row of marginal papillae interrupted by a wide gap on the upper labium and the gap on the lower labium is absent. There are 59 marginal papillae and 69 submarginal papillae which are complete on the lower labium and laterally on the upper labium. Very short but moderately wide papillae with rounded tips exist and the longest marginal and submarginal papillae measure 0.08 mm. Papillae are visible in dorsal view. LTRF is

3(2-3)/3(1-2). A_1 is moderately long and the density of its keratodonts is 39/mm. The gap in the first upper interrupted row is wide. Lower keratodont rows form a chevron, P_1 and P_2 are interrupted and P_2 and P_3 are scattered. Keratodonts are very short and distinguishable. Distal keratodonts have the same lengths as those in the centre. There is considerable space between marginal papillae and keratodont rows. Jaw sheaths are moderately wide and poorly keratinized. The upper sheath has a short widely rounded medial convexity. The edge of the medial convexity is black coloured and the remainder is whitish. Serrations are finely pointed. The lower sheath is V-shaped, partially keratinized and totally hidden by the upper one.

In life, the tadpole is generally uniformly dark (Fig. 3). Dorsal sides of the head and trunk are covered by dark patches and gold blotches. Ventrally, oral disk and gular regions are transparent, the branchial region is reddish, and the abdominal surface is transparent. The tail musculature is yellow-reddish and covered by brown reticulations. Fins are transparent and the dorsal fin has brown reticulations. In preservative, the tadpole is uniformly dark brown. Brown pigment is positioned in deep integumental layers and covers the dorsum and flank of the body. Some dark brown patches are scattered on the dorsal skin. Ventrally, the oral disk, gular and branchial regions are patched; the abdominal surface is pale. The intestinal coils are perceptible and regular spiral shaped. The lower part of the flanks has the same colouration as ventrally and the intestinal coils are perceptible laterally. The tail musculature is overlain by dark brown reticulations. Fins are pale; the dorsal fin is covered with sparse brown reticulations.

Six DNA voucher specimens from the same locality, eight DNA voucher specimens from Ranomafana National Park, one DNA voucher specimen from Vevembe forest and one DNA voucher specimen from Isalo National Park attributed to *M. femoralis* show the same oral disk morphology (Fig. 4), but one tadpole from Ranomafana National Park differs by its LTRF of 2(2)/3(1-2). A single tadpole from Marojejy National Park assigned to *M. femoralis* (by molecular data) differs by some variables like its lower numbers of only 43 marginal and 30 submarginal papillae.

Mantidactylus ambreensis. – A species easily recognizable by its adult colouration (Fig. 2), with a rather uniform dark brown dorsum with a continuous white (rarely yellowish) lateral line. This species is known from the North (Montagne d’Ambre) and Sambirano regions (Benavony, western slope of the Tsaratanana massif; Glaw and Vences, 2007). We have also recently collected specimens from the western slopes of the Makira plateau near Mandritsara (unpublished data). The tadpole of this species (based on ZSM 762/2004-FG/MV 2002.1950, Gosner stage 25 from the type locality Montagne d’Ambre National Park; see Figs 4 and 11) is differentiated from *M. femoralis* by its beige-brownish colouration in preservative (no data on

Fig. 3. Colouration in life of tadpoles of four species in the *Mantidactylus* subgenus *Ochthomantis*, all collected in Ranomafana National Park and surroundings. *M. femoralis* (ZCMV 3821 – ZSM 188/2008) – (a) dorsal view, (b) lateral view, (c) ventral view. *M. majori* (T 09/746, to be catalogued in ZSM) – (d): dorsal view, (e) lateral view, (f) ventral view. *M.* sp. 47 (ZCMV 3791 – ZSM 506/2008) – (g) dorsal view, (h) lateral view, (i) ventral view. *M.* sp. 64 (ZCMV 9291, to be catalogued in ZSM) – (j) dorsal view, (k) ventral view.

life colouration is available). The dorsal sides of the head and trunk and the higher part of the flank are beige with light brown reticulations between nares and eyes, on the frontal and along the vertebral area. The tail musculature is beige with brown blotches which fuse in some areas to form a network. Differences are also found regarding the body form in dorsal view, the size of the eyes and nares, the distance between the eyes and between the nares, the direction of the spiracle, the location of the spiracle opening, the length of the vent tube and the tail, the origin of the dorsal fin, the size of the caudal musculature, the visibility of the myosepta and the oral disk, the number of papillae, the state of P_2, the LTRF which is 2(2)/3(1-2), the density of keratodonts in A_1, the size of the gap in A_2, and the shape of the medial convexity. The examination of four additional specimens belonging to the same series (but not identified by DNA barcoding) revealed similar morphological characteristics, mainly in the oral structure, but the LTRF showed some variation: 2(2)/3(1-2) and 3(2-3)/3(1-2).

Mantidactylus zolitschka. – So far this species, characterized mainly by its rather small adult size and low sexual size dimorphism (Glaw and Vences, 2004) is only known from its type locality, An'Ala. Its tadpole (based on ZSM 1843/2007-ZCMV 3565, Gosner stage 27 from An'Ala; see Figs 4 and 12) is characterized by the faintness of the pigmentation of the keratodonts and the narrow elongated shape of the upper jaw sheath. The external morphology of the tadpoles differs from that of the tadpoles of *M. ambreensis* by body size, external pattern and colouration, LTRF, number of papillae and the configuration of the medial convexity. The tadpoles of *M. zolitschka* are similar to those of *M. femoralis* by the presence of a small constriction at midbody, but they can be differentiated by their colouration in preservative (no data on life colouration is available). *Mantidactylus zolitschka* tadpoles are generally beige-brownish with a light brown network of pigments positioned in deep integumental layers. These pigments cover the major surface of the dorsal sides of the head and trunk and the flank. Dark brown spots form patches which are scattered on the dorsal skin. Dark brown spots coalesce to form networks which are scattered irregularly on the tail musculature. Further differences to *M. femoralis* are the shape of the snout, the size and the direction of the eyes, the presence of reddish patches on the back of the nares, the distance between the nares and their direction, the location of the spiracle opening, the size of the caudal musculature, the origin of the dorsal fin, the visibility of the myosepta and the lateral tail vein, the shape of the tail tip, the direction of the oral disk, the size of the dorsal gap of the marginal papillae, the number of marginal and submarginal papillae, the shape and the size of papillae, the density of keratodonts on A_1, the state of P_2, and the size and shape of the upper jaw sheath. Four DNA voucher specimens from the same locality attributed to *M. zolitschka* show the same oral disk configuration and pigmentation, one tadpole having a different LTRF, 2(2)/3(1-2).

Mantidactylus argenteus. – This species, classified in a separate subgenus *Maitsomantis*, is characterized by a very distinct adult morphology with a small body size, greenish dorsal colour, and very large and semi-transparent tympanum in males. However, its larva (already described previously by Vejarano *et al*., 2006) is in general similar to that of species of *Ochthomantis*: The tadpole (based on ZSM 1573/2007-ZCMV 3575, Gosner stage 27 from An'Ala; see Figs 4 and 13) is characterized by *(1)* its unique colouration: presence of transversal clear bands between nares and eyes, between eyes and spiracle and before the body-tail junction, and a longitudinal clear band on the tail dorsum, *(2)* the protuberated snout, and *(3)* its small eyes and short spiracle. This tadpole is similar to that of *femoralis*-like tadpoles (and differs from the *mocquardi*-like, *M. mocquardi* and *M.* sp. 64, and the *majori* tadpoles) by the presence of labial teeth. The general configuration of the oral disk of *M. argenteus* tadpoles is similar to that of *femoralis*-like tadpoles (*M. femoralis*, *M. ambreensis*, *M. zolitschka*, *M.* sp. 42, *M.* sp. 43 and *M.* sp. 47), except a few characteristics, like the low number of papillae. The LTRF (2(2)/3(1-2) is similar to that of *M. ambreensis* and *M.* sp. 43, but the upper sheath configuration (narrowly pointed) is similar to that of *M. zolitschka*.

Mantidactylus sp. 42. – This candidate species has so far been recorded only from Montagne d'Ambre. Diagnostic features of the adult are not well understood since it cannot be excluded that more than one species of the subgenus *Ochthomantis* occur in Montagne d'Ambre (in addition to *M. ambreensis*). The single tadpole assigned to *M.* sp. 42 (ZSM 774/2004-FG/MV 2002.1957, Gosner stage 28 from Montagne d'Ambre National Park; see Figs 4 and 14) resemble *M. femoralis* tadpoles regarding the LTRF (3(2-3)/3(1-2)) and its general colouration except the low density of the reticulations on the tail musculature and the clear surface on the dorsum in preservative (no data on life colouration is available). Some parameters like the shape of the snout in lateral view, the location of the spiracle opening, the tail length, the origin of the dorsal fin, the direction of the oral disk, the size of the dorsal gap of the papillae, the low number of papillae, the shape and the size of the papillae, the size of A_1 and the density of its papillae, and the size of the gap on the A_2 also appear to differentiate the tadpoles of these two species. *Mantidactylus* sp. 42 tadpoles have high similarities to those of *M. ambreensis* in their external pattern and colouration but they can be differentiated generally by larger body size, the LTRF with three instead of two upper keratodont rows, and the number of papillae. *Mantidactylus* sp. 42 tadpoles can be distinguished from those of *M. zolitschka* by their external colouration and pattern and relevant differences in keratodont density and papillae number, but they have the same LTRF. *Mantidactylus* sp. 42 is also characterized by its keratodont rows which do not form a real chevron pattern as in other *femoralis*-like tadpoles.

Mantidactylus sp. 43. – A species phylogenetically close to *M. mocquardi* but differing in its tadpole morphology. We found adult and larval specimens at lowland sites in the Marojejy massif, and similar to *M. mocquardi*, adults had conspicuous silvery colour with a black pattern on the venter (Fig. 2). The single tadpole assigned to this candidate species (ZSM 1610/ 2007-FGZC 2928, Gosner stage 25 from Marojejy National Park; see Figs 4 and 15) is easily distinguished from *M. femoralis*, *M. ambreensis*, *M. zolitschka* and *M.* sp. 42 tadpoles by its uniformly pale colouration in preservative (no data on life colouration is available). Dorsal surface of body and of tail muscle are flecked. Speckles are positioned in deep integumental layers, darker patches dissipate between eyes and along the vertebral area and brown spots disperse on dorsal and dorsolateral parts of body. The tail musculature has brown mottles which coalesce in some areas to form sparse reticulations. Fins are pale, with speckles especially on the proximal 1/4 of the dorsal fin. This tadpole is characterized by the scattered state of A_1, and its LTRF differs from those of *M. femoralis*, *M. zolitschka* and *M.* sp. 42 (but not from *M. ambreensis*) by having two instead of three upper rows of keratodonts. The presence of keratodonts makes it also easy to differentiate it from *M. mocquardi* (which lacks keratodonts).

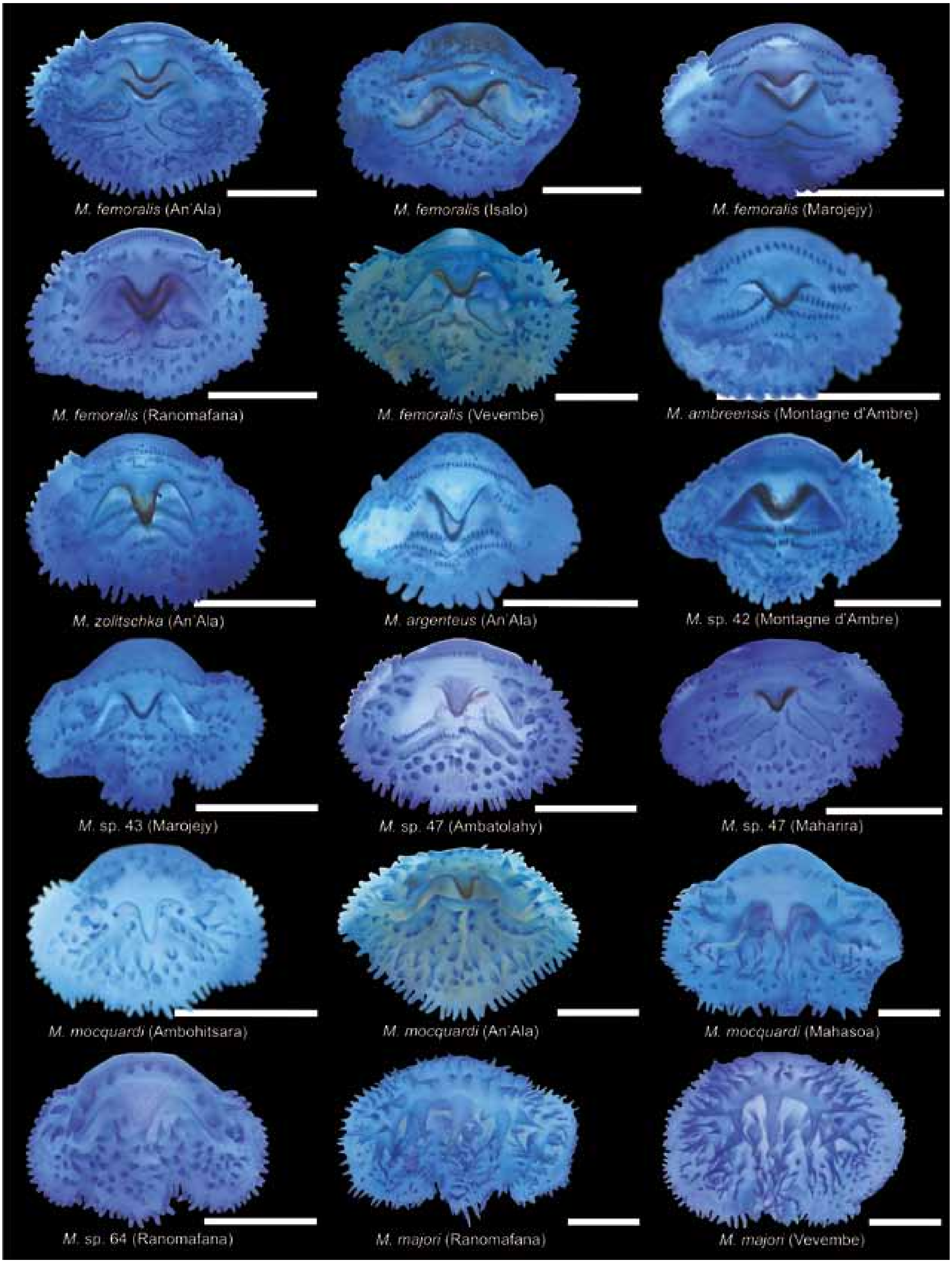
Mantidactylus sp. 47. – This confirmed candidate species is known from various sites in the Ranomafana region. Especially at Ambatolahy it is a very common species in a fast-flowing large stream where adult males and females are regularly found on large boulders next to the water. Females are much larger than males. In the adult stage, the ventral side is not conspicuously silvery, and there is no large and distinct yellow inguinal patch (Fig. 2). The tadpole of *Mantidactylus* sp. 47 (based on ZSM 456/2008-ZCMV 2699, Gosner stage 31 from Ambatolahy next to Ranomafana National Park; see Figs 3, 4 and 16) has a small constriction anterior to the point where the maximal body width is attained. It shares the LTRF with *M. femoralis*, *M. zolitschka* and *M.* sp. 42 tadpoles (with three upper keratodont rows), but differs from *M. ambreensis* and *M.* sp. 43 (with only two upper rows). It can also be differentiated from the tadpoles of *M. femoralis*, *M. ambreensis* and *M.* sp. 42 by its variegated light brown colouration. It is characterized by the presence of slightly visible domino-like structure on the dorsum. In life, the body is covered by brown patches in deep integumental layers that are condensed especially between the eyes and on the vertebral region. Some dark brown and golden patches spread over the skin. Ventrally, gular region beige, branchial region reddish and abdominal surface transparent. Tail musculature beige with dark brown dots forming patches. Fins transparent, dorsal fin with many patches than the ventral fin. In preservative, it is largely brownish. Light brown pigment in deeper integument layers covers the dorsum and flanks of the body. Dark brown patches disperse on the skin. Brown spots coalesce to form networks which spread irregularly on the tail musculature. Fins are pale and the dorsal fin has some brown reticulations. Five additional DNA voucher specimens attributed to this species from the same locality and many additional specimens belonging to these series agree in most cases with the typical oral disk configuration (Fig. 4) and the external pigmentation of this species. The LTRF shows some variation: 2(2)/3(1-2) and 3 (2-3)/3(1-2).

Mantidactylus mocquardi. – We consider as *M. mocquardi* a species characterized, in the adult stage, by a relatively large size, especially of some females, a somewhat tubercular dorsum, small and indistinct yellow inguinal patch, and distinct silvery belly (with or without black pattern; Fig. 2). We confirm the taxonomic rationale of Glaw and Vences (2004) in assigning the nomen *mocquardi* to this species, because in the Northern Central East of Madagascar where the type locality of *M. mocquardi* is located, no other species except the one with silvery bellies was found which would be characterized by a large size of females and thus would morphologically conform with the *M. mocquardi* holotype (which is a large-sized female as well). Based on molecular data, we observed *M. mocquardi* at Ambohitsara, An'Ala, and Mahasoa forest.

The tadpole of *Mantidactylus mocquardi* (based on ZSM 1540/2007-ZCMV 3511, Gosner stage 25 from An'Ala; see Figs 4 and 17) is characterized by its light beige-brownish colouration in preservative, no data of the life colouration is available. Light brown blotches positioned in deep integumental layers form dark patches between nares and eyes and along the vertebral area and flank of the body. Some dark brown patches are scattered irregularly on the skin. The tail musculature is beige with a few patches which are dissipated irregularly. Fins are pale, with brown blotches in the dorsal fin. A reddish patch on the back of the nares is present. This tadpole has a very characteristic oral disk. It has a long narrowly pointed medial convexity, no keratodonts, a few short to moderately long and moderately large papillae, but no dorsal gap of marginal papillae (Fig. 4). In comparison with the *femoralis*-like tadpoles, the main difference is the absence of keratodonts and the state of the papillae. Nine additional DNA voucher specimens from the same locality and one DNA voucher specimen from Ambohitsara-Tsitola assigned to this species show the same characteristic oral disk configuration and the same external pigmentation.

Tadpoles (ZSM 686/2008-ZCMV 8094; Fig. 18) collected at Mahasoa forest differed by several external parameters but are here preliminarily assigned to *M. mocquardi* because genetically, this population is very similar to the other populations examined. The lack of keratodonts allows distinguishing these tadpoles from those of *M.* sp. 43 (the next closest relative of *M. mocquardi*). The tadpole has a rather large size in comparison to all other tadpoles studied, and a pale-brownish colouration in preservative (no data on life colouration is available). Light pale brown pigment covers the dorsum and is condensed especially behind the eyes, on the vertebral region and on the flank of the body. Some dark brown patches are scattered on the skin. The tail musculature has light brown speckles and dark brown spots which form patches. Fins are pale and the dorsal fin has brown spots which group to form patches. On the ventral fin, patches spread around tail tip. It has also the typical *M. mocquardi* oral disk. It furthermore is the only tadpole with a position of the maximal body height in the distal 1/4. Differences to *M. mocquardi* are in the shape of the snout in lateral view, the configuration and the form of the spiracle opening, the length of the tail, the origin of the dorsal fin, the location of the maximal tail height, the position and the direction of the oral disk, the low number of papillae, and the size of the medial convexity. Four additional specimens belonging to the same series (but not identified by DNA barcoding) have the same external morphology as the voucher specimen including oral disk configuration.

Mantidactylus sp. 64. – This candidate species was first discovered by its deviant tadpole morphology, based on specimens from the Ranomafana area. So far, nothing is known about its adult morphology, although one adult has been collected at Vevembe (not available for morphological examination in the framework of this study). Based on mitochondrial DNA sequences this species appears to be closely related to *M.* sp. 47 (Fig. 1). Its tadpole (based on ZSM 401/2008-ZCMV 2646, Gosner stage 39 from Ranomafana National Park (Figs 4, and 19) for the preserved tadpole and on ZCMV 9291 - not yet catalogued in ZSM (Fig. 3) for the living tadpole) is characterized by its reddish-brown colouration in life. The body and the tail are covered by brown blotches which are condensed and give a dark brown colouration to the tadpole. Ventrally, gular region beige, branchial regions reddish, abdominal surface beige. In preservative, it is dark. Brown pigment covers the dorsum and flank of the body, and dark brown patches are scattered on the skin. The tail musculature is pale and covered by dark brown reticulations. Fins are pale and have brown reticulations close to the tail tip. This tadpole is similar to that of *M. mocquardi* (and differs from the *femoralis*-like tadpoles) by the configuration of its oral disk, *i.e.* absence of keratodonts and of a dorsal gap of marginal papillae. However, the pigmented and moderately wide oral disk with rather small and short conical papillae is unique to this species. There are further morphological differences to *M. mocquardi*, like the uniformly dark colouration that the tadpoles of this species have. In lateral view, the snout is narrowly rounded (broadly rounded in *M. mocquardi*). The eyes are situated between the proximal 2/10 and 3/10 of the body (vs. between the proximal 3/10 and 4/10 in *M. mocquardi*). The vent tube is moderately long, the tail is long, tail musculature is moderately developed and the tail tip is narrowly rounded, and the medial convexity is short and widely rounded (vs. short vent tube, short


M. femoralis (An'Ala)
M. femoralis (Isalo)
M. femoralis (Marojejy)
M. femoralis (Ranomafana)
M. femoralis (Vevembe)
M. ambreensis (Montagne d'Ambre)
M. zolitschka (An'Ala)
M. argenteus (An'Ala)
M. sp. 42 (Montagne d'Ambre)
M. sp. 43 (Marojejy)
M. sp. 47 (Ambatolahy)
M. sp. 47 (Maharira)
M. mocquardi (Ambohitsara)
M. mocquardi (An'Ala)
M. mocquardi (Mahasoa)
M. sp. 64 (Ranomafana)
M. majori (Ranomafana)
M. majori (Vevembe)

tail, developed tail musculature and pointed tail tip, and long and narrowly pointed medial convexity in *M. mocquardi*). The dorsal fin originates at the proximal 1/10 of the caudal musculature (vs. on the dorsal body-tail junction in *M. mocquardi*). One further uncatalogued DNA voucher specimen (ZCMV 9291) from Sakaroa in Ranomafana National Park attributed to this species displays the same external pigmentation in preservative. A more detailed examination of its oral disk was not possible because the specimen was not available for further examination.

Mantidactylus majori. – This species is in its adult phase easily recognizable by the rather uniform light brown dorsal colouration bordering at the flanks rather sharply to the white venter, absence of a yellow inguinal patch, a smooth dorsum, and a pointed snout (Fig. 2). The species is common in the Southern Central East and South East; based on molecular identification, we confirm its occurrence in the Ranomafana region, Vevembe, and Midongy du Sud; recently, it has also been found in Sahafina in the Northern Central East (Gehring *et al*., 2010). As reported by Lehtinen (2003), Vences and De la Riva (2005), and Altig (2008), this species deposits eggs on leaves overhanging streams, guarded by the male. We confirm this reproductive mode by molecular identification of clutches, and also confirm that in these clutches, small tadpoles develop which eventually drop into the stream (Fig. 5). The tadpoles of *M. majori* (based on ZSM 1684/2007-ZCMV 3762 Gosner stage 29 and T 09/746 Gosner stage 25 from Ranomafana National Park; see Figs 3, 4, and 20) have the most derived oral disk among *Ochthomantis*, lacking all keratinized components (keratodonts and jaw sheath). The upper jaw sheath is transformed into three very large flexible, slightly curved and thorn-shaped projections and a dozen of large papillae are situated near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath that is totally hidden by the upper jaw sheath (Fig. 4).

In life, colouration of these tadpoles is beige-orange with brown patches. Light brown patches are positioned in deep integumental layers are between the eyes and on the vertebral region. Dark brown and golden patches spread over the skin. Ventrally, gular region beige, branchial region reddish, abdominal surface transparent with golden patches, intestinal coil visible with regular spiral-shaped intestine. Tail musculature is orange-yellowish with light brown dots arranged in patches. Fins are transparent. The dorsal fin has more patches than the ventral fin.

In preservative, colouration is generally yellowish with brown patches between the eyes and the nares that are positioned in deep integumental layers. Light brown patches disperse on the dorsum and the upper part of the flank and dark brown blotches dissipate on the dorsum and the flank. Tail musculature is pale with light brown dots that fuse in some areas and form patches towards the tail tip. Fins are transparent, the dorsal fin and the distal part of the ventral fin have the same colouration as the tail muscle. The external morphology of this tadpole differs from that of the *M. mocquardi* tadpole by the remarkable ovoid body form in dorsal view, the lateral eye direction, the wide distance between the eyes, the moderately sized and the elliptical shape of the opening of the nares, the moderately wide distance between the nares, the configuration of the spiracle opening, the size of the vent tube and the tail, the origin of the dorsal fin, and the shape of the tail tip. Thirty-two additional DNA voucher specimens from the same locality and one voucher specimen from Vevembe forest attributed to this species reveal the same characteristic oral disk configuration, the external pigmentation, and all other morphological characteristics of this species.

Three further candidate species of the subgenus *Ochthomantis* are only known from adults so far and are here considered as UCS: *Mantidactylus* sp. 61 from Andapa is known to us from a single specimen with a distinct frenal stripe, smooth dorsal skin and a rather pointed head. *Mantidactylus* sp. 62 from higher elevations of the Marojejy massif (ca. 1100 m a.s.l., at a site locally known as Camp Simpona) is a rather characteristic species with smooth skin, large-sized females, and a more or less uniform beige venter without white-silvery colour. *Mantidactylus* sp. 63 from the Tsaratanana and Manongarivo massifs in the Sambirano region is a relatively large species with a discontinuous yellowish lateral line bordered dorsally by areas of black skin, and with a venter with yellow colour and a distinct pattern of black spots.

◀ *Fig. 4*. Photographs of the oral disk of the preserved voucher specimens of *Mantidactylus* subgenus *Ochthomantis* and *Maitsomantis* tadpoles described in this paper (stained with methylene blue). The scale bars represent 1 mm.

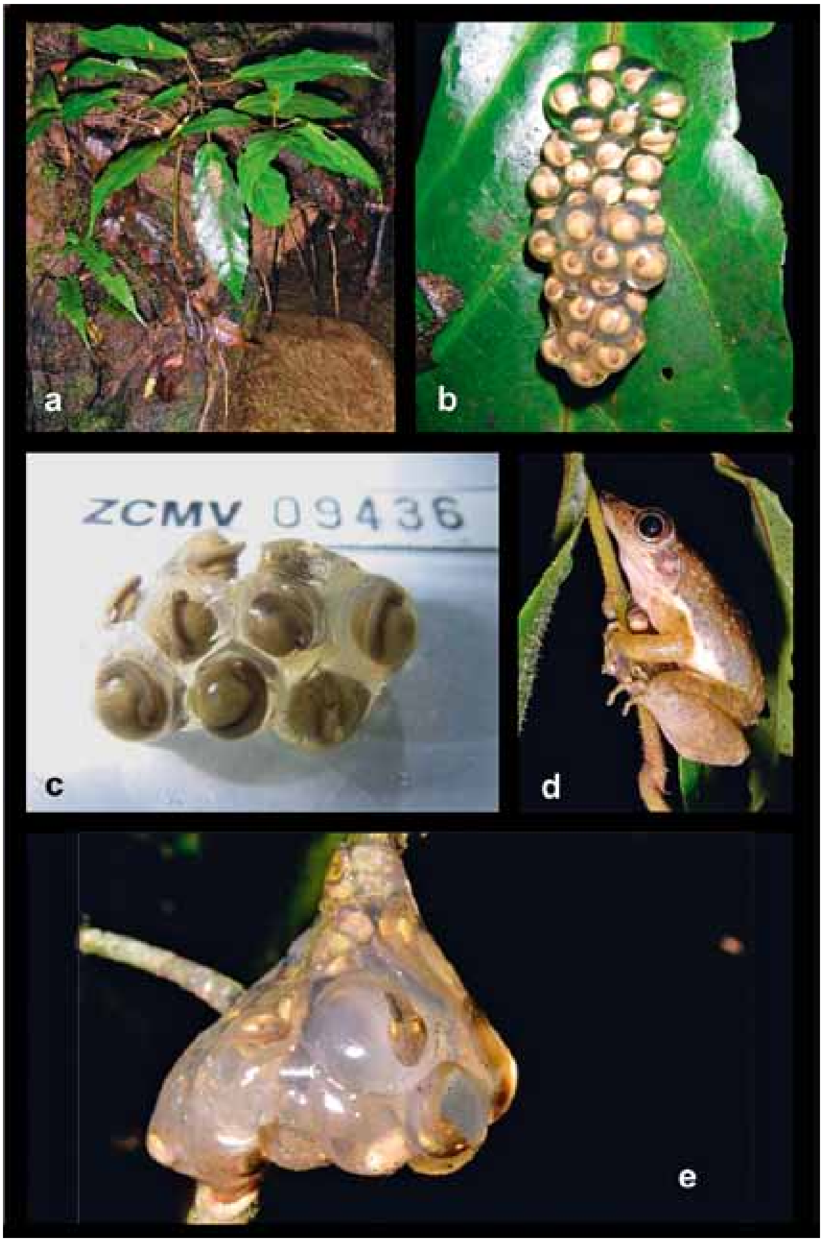


Fig. 5. Clutches and egg guarding behaviour of *Mantidactylus majori*. (a) and (b) show a clutch (ZCMV 9436) attached to a leaf, 40 cm above water body (Ranomafana, Ambatovory Barrage), (c) shows a part of the same clutch, (d) shows an adult *M. majori* guarding a clutch attached to vegetation about 80 cm above water body (Ranomafana, Ambatolahy), (e) shows a clutch of *M. majori* (ZCMV 9537, no ZSM) with well developed tadpoles attached to a branch about 1 m above water body (Ranomafana, Sahamalaotra bridge).

Ecological analysis

In Ranomafana National Park, during the rainy season, tadpoles of 44 species were found in streams including four species of the subgenus *Ochthomantis*: *Mantidactylus femoralis*, *M. majori*, *M.* sp. 47 and *M.* sp. 64. *Ochthomantis* tadpoles were found in 20 out of 33 streams, and often tadpoles of different species occurred together in the same streams. They were never the most abundant species but three of the species represented in some streams a considerable proportion of the overall number of tadpole specimens collected. *Mantidactylus femoralis* occurred in seven streams with a mean of five specimens per 30 m sample transect (range: 1 to 13 specimens), *M. majori* occurred in eleven streams with a mean of 16 specimens (1 to 68), and *M.* sp. 47 occurred in 16 streams with a mean of 6 specimens (1 to 25), *M.* sp. 64 was only found with a single specimen at one stream. For *M. majori*, several observations on clutches and embryonal development were made (Fig. 5). One clutch with about 40 embryos was found attached to a leaf 40 cm above a stream. Further two clutches with already well developed tadpoles were found attached to a branch of a shrub and attached to a *Pandanus* leaf, respectively, both about 1.2 m above another stream. Tadpoles were hatching from the jelly immediately after induced vibrations. An adult *M. majori* male was observed guarding an egg clutch that was attached to a leaf 80 cm above a stream.

During the dry season, congruent with the generally low number of tadpole specimens of mantellid species in this area and season, *Ochthomantis* tadpoles were present but in only very low numbers. Out of 13 sampled streams, *Mantidactylus femoralis* occurred in one stream with two specimens, *M. majori* occurred in three streams with a mean of nine specimens per 30 m transect (range: 2 to 20 specimens), and *M.* sp. 47 occurred in five streams with a mean of four specimens (1 to 9). No tadpoles of *M.* sp. 64 were found in the dry season; however, none of the streams where they have been observed before were sampled. In four streams, tadpoles of two *Ochthomantis* species (*M. femoralis* and *M.* sp. 47) were observed in the dry but not in the rainy season.

In our statistical analyses of habitat choice (Fig. 6-8) we first compared breeding site choice of *Ochthomantis* species on the spatial level of Ranomafana NP, *i.e.* the distribution of tadpoles between 33 different streams, applying data ordination (principal component analysis; PCA) and subsequently including the PC factors as independent variables in a generalized linear model (GLM). PCA on the original habitat (stream) variables and the surrounding forest resulted in three PCs, explaining together 67.6% of the variation in the data. Based on the loadings of the PCs and the results of the bootstrapped-eigenvector method (Peres-Neto *et al.*, 2003) we identified the following habitat variables being well represented ('+' positive correlation, '–' negative correlation): PC1 (33.9%) slope (+), canopy cover of forest (+) and stream (+), overhanging vegetation (+), width (–) and depth (–) of the stream. The variables that contributed the most to PC2 (18.0%) were slope of the stream (+), the number of shrubs in the forest (+), number of trees (–) and leaf litter depth (–) in the forest. The number of small trees and shrubs in the forest (+) and overhanging vegetation (+) contributed to PC3 (15.7%). However, according to bootstrapped-eigenvector method both PC2 and PC3 do not well represent the above mentioned habitat variables.

The presence or absence of *Ochthomantis* tadpoles was negatively correlated with PC1 (Fig. 6; GLM with binomial error distribution; residual deviance = 26.6 on 31df, p = 0.009), all other PCs as well as interactions could be removed from the model. Therefore, *Ochthomantis* species prefer larger streams with an open canopy directly at the stream and also a relatively open canopy in the surrounding forest, and with a gentle slope (*i.e.*, slow running streams; see also Fig. 8).

Second, we compared microhabitat choice of *Ochthomantis* species on the spatial level of each stream, *i.e.* the distribution of tadpoles within each stream. The tadpoles were not found in all microhabitats that were available in the streams. Most of the specimens were found in those areas of a stream with leaves or sand as substrate combined with slow moving to almost stagnant water (Fig. 7A). In detail, *Ochthomantis* tadpoles avoided most microhabitats including all microhabitats in fast moving water (E<0; factorial ANOVA, $F_{7,233}$ = 26.93, fast rock (E = −1±0.14; mean ± SE), fast gravel (E = −0.95±0.096), fast sand (E = −0.87±0.13), fast leaves (E = −0.77±0.13), slow rock (E = −0.79±0.14) and slow gravel (E = −1± 0.15, p always <0.001) (Fig. 7B). We also detected a non-significant trend of avoidance for the microhabitat slow sand (E = −0.17±0.09, p = 0.063). Slow leaves was the only microhabitat significantly preferred by *Ochthomantis* tadpoles (E>0; factorial ANOVA, E = 0.33±0.09, p<0.001). It needs to be noted, however, that the general strong avoidance values can partly be caused by a high number of non-occurrence events in the specific microhabitats in some streams. As all microhabitat-species interactions could be removed from the model, our data do not show significant differences in the choice of microhabitat for the three most abundant *Ochthomantis* species. Due to their low abundance, no index of preference was calculated for *M.* sp. 64 tadpoles. However, the few specimens were exclusively found in slow leaves microhabitat.

Discussion

Specialization of the oral disk in Ochthomantis *tadpoles*

Ochthomantis tadpoles have morphological characters showing a high degree of specialization, which are *(1)* reduction and *(2)* change in the components of the oral disk. Because of the character reduction seen in some species, the states of many characters cannot be assessed which makes some inter-species comparisons difficult. The general external morphology of these

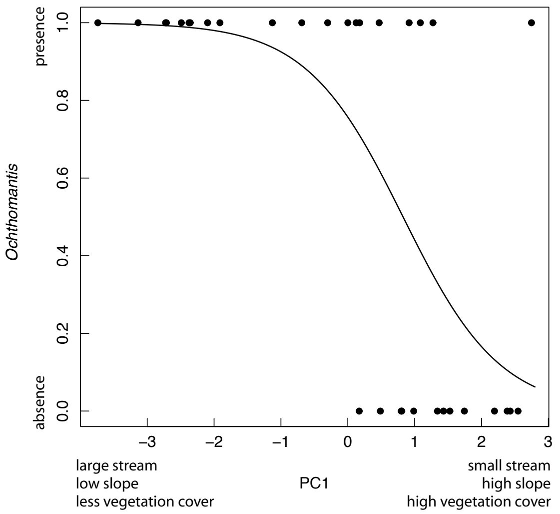


Fig. 6. Presence and absence of *Mantidactylus* subgenus *Ochthomantis* tadpoles in streams of RNP along the PC1 gradient. PC1 explains 34% of the variation in the original data. Each point represents a stream, the regression line of the logistic regression is plotted.

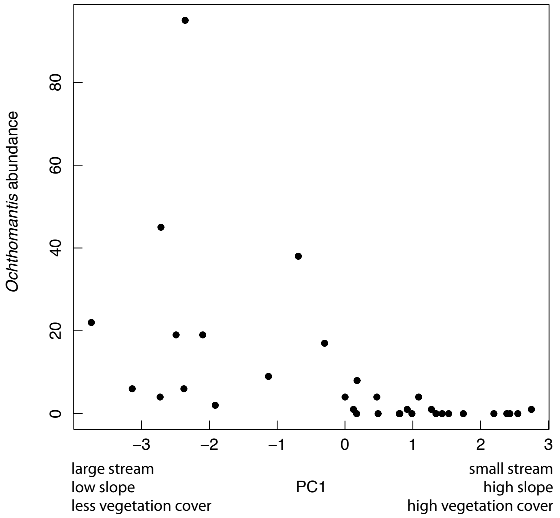


Fig. 8. Abundance of *Mantidactylus* subgenus *Ochthomantis* tadpoles in streams of RNP along the PC1 gradient. PC1 explains 34% of the variation in the original data. Each point represents a stream.

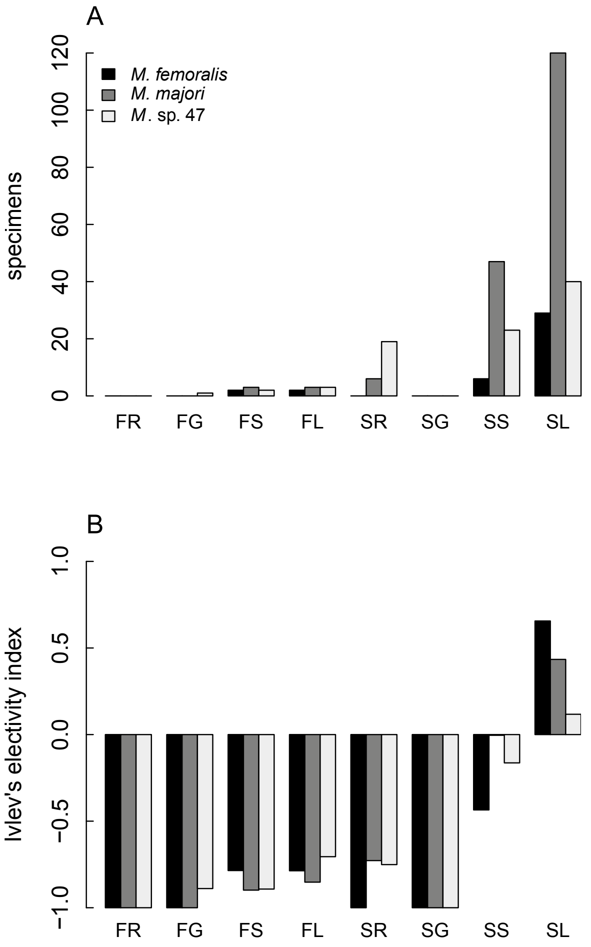


Fig. 7. Habitat use and habitat preferences of the three abundant species of *Mantidactylus* subgenus *Ochthomantis* sampled in January and February 2008 in Ranomafana National Park. Plotted is (a) the distribution of specimens and (b) Ivlev's electivity index (Ivlev, 1961) across eight microhabitats (FR = fast rocks, FG = fast gravel, FS = fast sand, FL = fast leaves, SR = slow rocks, SG = slow gravel, SS = slow sand, SL = slow leaves). Negative values show avoidance, positive values preferences for the respective microhabitat. $N_{M. femoralis} = 7$, $N_{M. majori} = 11$, and $N_{M. sp. 47} = 16$ (N is the number of streams where the species was found). The general low values in (b) are caused by a high number of non-occurrence events in the specific microhabitats in some streams.

tadpoles shows no large differentiation. They are in general tadpoles with a rather low dorsal fin and were all collected in flowing waters. Only few external characters other than the mouthparts show differences among species, such as the position of the spiracle and the colour.

Summarizing the most relevant variation, it is possible to distinguish three main morphological clusters of *Ochthomantis* tadpoles that probably represent different evolutionary steps of reduction and change in the oral disk:

(1) Mantidactylus femoralis, *M. ambreensis*, *M. zolitschka*, *M.* sp. 42, *M.* sp. 43 and *M.* sp. 47 possess reduced jaw sheaths and keratodonts. Summarizing

morphological characters, these tadpoles are characterized by a small to moderately wide oral disk (ODW 32 to 47% of BW), moderately wide and poorly keratinized jaw sheaths (JW 35 to 54% of ODW), an upper jaw sheath having a short to long, narrowly to widely, pointed or rounded medial convexity (MCL 17 to 31% of JW) and many finely pointed serrations, a lower jaw sheath totally hidden by the upper ones, very few (MP 31 to 71, SMP 18 to 59) short (MP 0.08 to 0.12 mm, SMP 0.08 to 0.20 mm) and moderately large conical papillae with rounded tips, a moderately wide dorsal gap of papillae (DG 45 to 66% of ODW), an absence of ventral gap of papillae, a LTRF of 2(2)/3(1-2) or 3(2-3)/3(1-2), small keratodonts (0.04 to 0.09 mm), lower keratodont rows forming a chevron and P_2 and P_3 are usually scattered, a wide A_2 gap (61 to 82% of A_2). All of these tadpoles show what we interpret as the first step of reduction of keratinized structures, namely *(1)* the jaw sheath is not fully keratinized (*i.e.*, only at the edge) and has a medial convexity, and *(2)* there are only few upper keratodont rows (usually three, further reduced to only two in *M. ambreensis* and *M.* sp. 43), there are only relatively low numbers of keratodonts per row, the second lower tooth row is interrupted (uninterrupted in generalized mantellid tadpoles), and all lower rows are scattered and form a chevron. In addition, *M. zolitschka* shows a reduction of the keratinisation of the keratodonts which become difficult to recognize without using a staining agent such as methylene blue. Also *M.* sp. 43 has reduced the keratodonts on A_1.

(2) The second group contains *M. mocquardi* and *M.* sp. 64. These tadpoles are characterized by a small to moderately wide oral disk (ODW 34 to 47% of BW), moderately wide and poorly keratinized jaw sheaths (JW 32 to 55% of ODW), an upper jaw sheath having a long to very long narrowly pointed medial convexity (MCL 21 to 57% of JW) and many finely pointed serrations, a lower jaw sheath totally hidden by the upper ones, few (MP 64 to 89, SMP 77 to 104) and very short to long (MP 0.09 to 0.25 mm, SMP 0.12 to 0.35 mm) and large conical to elongated papillae with rounded (MP) and pointed (SMP) tips, an absence of dorsal and ventral gaps of papillae, and an absence of keratodonts (LTRF 0/0). In terms of reduction of keratinized structures, the jaw sheaths in these species have the same state as found in the first morphological group but the keratodonts are completely reduced and many submarginal papillae are present in the area occupied by keratodont rows in the other species. The row of marginal papillae is complete (*i.e.*, there is no dorsal gap). These tadpoles have long and moderately large elongated papillae, mainly in *M. mocquardi* from Mahasoa whose submarginal papillae show similarities to those of *M. majori*.

(3) The third group only contains the highly modified tadpoles of *M. majori* which are characterized by a small oral disk (ODW 38 to 40% of BW), an upper jaw sheath transformed into three thorn-shaped papillae (projections), a lower jaw sheath totally hidden by the upper ones, moderately many (MP 72 to 105, SMP 135 to 201) long to very long (MP 0.22 to 0.25 mm, SMP 0.41 to 0.52 mm) and very large elongated papillae with pointed tips, an absence of dorsal and ventral gaps of papillae, an absence of keratodonts (LTRF 0/0). The modification of the area of the jaw sheaths in this species is extreme and besides the three very large flexible slightly curved thorn-shaped papilla-like structures there are some large elongated papillae projecting from near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath.

The phylogenetic tree shown here (Fig. 1) needs to be considered as tentative because it is based on a rather short fragment of only one mitochondrial gene. We therefore refrain from a detailed discussion here but just mention some aspects that seem to be well supported (Bayesian posterior probabilities of >0.95). However, the phylogenetic relationships proposed in this tree are in need of further confirmation by a forthcoming multi-gene analysis. First, it seems clear that *M. majori* is the most divergent *Ochthomantis* and may even be more distant to other *Ochthomantis* than is *Mantidactylus* (*Maitsomantis*) *argenteus*. This could indicate that the reduction of keratinized oral structures in *M. majori* occurred convergently to what is observed in the *M. mocquardi*-like species. Second, it seems clear that *Ochthomantis* cannot be simply divided into two clades, one with a *M. femoralis*-like tadpole morphology and one with a (more specialized) *M. mocquardi*-like morphology. This situation is exemplified by the clade containing *M. mocquardi* and *M.* sp. 43 on one hand, and the clade containing *M.* sp. 47 and *M.* sp. 64 (which however is not strongly supported) on the other hand: In fact, *M. mocquardi* and *M.* sp. 64 show a full loss of keratodonts which is not shown by their respective sister taxa (*M.* sp. 43 and *M.* sp. 47), indicating that this loss may have occurred convergently in the two lineages. The tendency of keratodont loss on A_1 of *M.* sp. 43 nevertheless indicates an early tendency of loss of keratodonts in this lineage.

Comparisons with other mantellid tadpoles

A convergence in the reduction of the oral disk in mantellid tadpoles is found between the subgenus *Ochthomantis* and the genus *Boophis* (*B. majori*; Schmidt *et al.*, 2008, and pers. obs.). *Boophis majori* tadpoles have a small oral disk, a poorly keratinized jaw sheath with a very long narrowly pointed medial convexity and finely pointed serrations, a wide dorsal gap of marginal papillae an absent ventral gap of papillae. The difference is that *B. majori* tadpoles do not possess any conspicuous modifications of the keratodonts. They have one interrupted lower row as it is typical for many *Boophis* tadpoles, and their LTRF are 4(1-4)/3(1) (Schmidt *et al.*, 2008, pers. obs.) or 5(2-5)/3(1) (pers. obs.). The tadpoles of *B. picturatus* (Altig and McDiarmid, 2006; pers. obs. of many DNA voucher specimens from Ranomafana National Park) show the most extreme evolutionary specialization in having an extraordinary reduction of various oral disk characters.

Mantidactylus argenteus is classified in the subgenus *Maitsomantis* because of its largely arboreal habits in the adult stage which is unique in *Mantidactylus* (Glaw and Vences, 2006). Its tadpoles are easy to recognize because of the bands on the body, but the oral disk is *femoralis*-like with a LTRF of 2(2)/3(1-2) (see Fig. 4). This would imply that the ancestor of *Maitsomantis* and *Ochthomantis* probably had *femoralis*-like tadpole features. There is a further tendency of specialization in the mouthparts of the *mocquardi*-like lineage. According to the molecular tree presented here, the subgenus *Ochthomantis* would be paraphyletic, with *M. majori* being sister to a clade of all other *Ochthomantis*, plus *M. (Maitsomantis) argenteus*. However, because this tree is based on only few sequences, we consider this grouping as in need of confirmation. So far, no comprehensive phylogenetic analysis of morphological character states of mantellid tadpoles have been published, but an own study in progress indicates that various of the states of *Ochthomantis* and *Maitsomantis* (*e.g.* the reduction of keratodont rows) are derived, indicating that tadpole characters may provide support for their phylogenetic relationships. A further derived character state shared by *M. majori* and *M. argenteus* is the male egg-guarding of eggs deposited on leaves overhanging running water (Vences and De la Riva, 2005; Glaw and Vences, 2007; Altig, 2008). Vejarano *et al.* (2006) reported the presence of three interrupted lower rows (2(2)/3(1-3)) in *M. argenteus* tadpoles, but based on our data presented herein, we assume that it normally has only two interrupted lower rows, *i.e.* an LTRF of 2(2)/3(1-2) (as indicated by the intact state of P_3 of the specimens examined herein; Fig. 4). The data of Vejarano *et al.* (2006) might be due to the fact that the lower rows, mainly the third, are scattered in *M. argenteus*, similar to the situation in all *femoralis*-like tadpoles. Taking into account that *M. argenteus* tadpoles still have an uninterrupted third lower row agrees with the state in the first group of *Ochthomantis* tadpoles.

Previous descriptions of tadpoles of *Ochthomantis* have not been based on DNA barcoding, and given the high similarity among adults, species identification in these previous works is doubtful. Blommers-Schlösser (1979 in her Figs 9-10) provides a brief description of a tadpole assigned to be *M. femoralis* which shows scattered keratodonts on P_2. The tadpole has poorly keratinized jaw sheaths which are typical in *Ochthomantis*, but the combination of having both complete marginal papillae rows and keratodonts does not fit any *femoralis*-like tadpoles, since according to our observations only the tadpoles which have no keradotonts present no dorsal gap of marginal papillae (*mocquardi*-like tadpoles). Also, the LTRF 0/2+2 does not correspond with any *femoralis*-like nor *mocquardi*-like tadpoles. Maybe this is due to the captive rearing of the tadpoles by Blommers-Schlösser (1979), or an artefact in the observation, or these tadpoles belong to yet another *Ochthomantis* candidate species that is not present in our samples.

Altig and McDiarmid (2006) described a tadpole from Ranomafana with strongly reduced keratinized structures in the oral disk and assigned it tentatively to *Mantidactylus guttulatus*, the largest mantellid frog whose life history is so far largely unknown. However, a comparison of the description and drawing with our study leaves little doubts that the authors in fact described the tadpole of *M. majori*. Altig and McDiamid (2006) had based their tentative identification on the morphology of juveniles which however can be very similar among *M. majori* and *M. guttulatus*.

Habitat selection and ecology of Ochthomantis *tadpoles*

Ochthomantis tadpoles are almost omnipresent in stream communities in the mid-elevational rainforests of Madagascar. Some *Ochthomantis* species can be found in many streams with considerable abundances, however, by far they do not represent the most common species (own unpublished data). *Ochthomantis* tadpoles occur throughout the year but with a strongly reduced abundance in the dry season. As all streams sampled were permanently water-bearing the reduced abundance may be caused by the low temperature, which is a main factor for frog reproduction in RNP (Andreone, 1996). The presence of *Ochthomantis* species in four streams in the dry season where this species was not found in the preceding rainy season indicates that reproduction occurs throughout the year.

Ochthomantis tadpoles avoid small, fast running streams surrounded by dense vegetation for reproduction. This may partly conflict with the fact that adults of at least *M. majori* attach eggs on vegetation above the water. However, these structures are obviously not a limiting resource even in the larger streams. A dense vegetation above the stream, here measured as overhanging vegetation and canopy cover, may cause decreasing light, lower dissolved oxygen, reduced temperature and reduced availability of food for tadpoles in ponds (Werner and Glennemeier, 1999) and influence periphyton growth and thus food availability in streams (Altig *et al*., 2007; Mallory and Richardson, 2005). However, given that *Ochthomantis* tadpoles most probably live and feed among dead leaves on the ground of the streams, it is unlikely that periphyton growth would have strong influences on the amount of food available to them. Since the adults of *Ochthomantis* typically are found along or at few meters distance from the streams, dense vegetation along the streams might influence adults rather than tadpoles. Testing this hypothesis would require an analysis of the habitat preferences of adult *Ochthomantis* which so far has not been carried out.

Within a stream, *Ochthomantis* tadpoles of the three most abundant species do not obviously differ in their choice of microhabitat based on the rather rough microhabitat categories distinguished in our sampling scheme. They prefer those areas of a stream with a slow current and an abundance of leaf litter. The same microhabitat preference was observed for tadpoles in the *Mantidactylus* subgenus *Chonomantis* (Grosjean *et al*., 2011). In general, microhabitat choice of tadpoles can be related to oral disk characteristics and therefore feeding mode (Altig and Johnston, 1989). The fact that these morphologically very different tadpoles (*i.e*., *Chonomantis* have funnel-shaped oral disks) show a similar habitat choice indicates that this might be a general pattern for most mantellid stream tadpole species that have no obvious adaptations to strong water currents (like *e.g.* some *Boophis*, Glos *et al*., 2007). As all other substrates in the slow running areas of the streams have been avoided, the strength of the water current may be only one important factor for microhabitat choice. It is therefore the combination of low water current and the high availability of nutrients within the leaf litter that is of importance for the preference for this microhabitat.

However, because *Ochthomantis* tadpoles occurring in Ranomafana show distinct tadpole morphologies and that some of them have unique oral disks (especially those of *M. majori*) it is unlikely that all of them use precisely the same food resources, despite a general agreement in rough microhabitat categories. Certainly, the species with the most derived oral disks (the second and third guild as defined above), without keratodonts and partly with modified jaw sheaths, are not able any more to graze and scrape as generalized tadpoles do, but it is uncertain whether tadpoles of the first group might show such a behaviour or feed differently.

Although larvae of *Ochthomantis* and *Chonomantis* also share a similar choice of rough microhabitat categories (Grosjean *et al*., 2011) it is almost certain that these taxa will not use the same nutrient resources. Their very different and specialized oral disk structures strongly suggest different feeding behaviour, *e.g. Chonomantis* tadpoles may feed at least partly from the water surface as is known from other funnel-mouthed tadpoles (Grosjean *et al*., 2011), so that competition for food is not necessarily to be expected. In general, the high amount of morphological larval variation among *Ochthomantis* tadpoles stands in stark contrast to the situation in *Chonomantis* which show a very limited morphological differentiation although up to five *Chonomantis* species have been detected syntopically (Grosjean *et al*., 2011).

Tadpoles of the different species of *Ochthomantis* (and *Chonomantis*) often occurred together in the same stream, which demonstrates that they are not excluding each other and indicates that direct competition might be of minor importance. We assume that rather habitat characteristics and drift events determine the presence, abundance or absence of a species in a stream. Further insights into resource partitioning among these tadpoles will require detailed behavioural and ecological studies focusing on intestine contents, feeding behaviour and feeding microhabitat, and activity periods.

Applying the definitions of ecomorphological tadpole guilds proposed by Altig and Johnston (1989) is generally difficult in Malagasy tadpoles because of the lack or different expression of some of the characters that these authors have used (Randrianiaina *et al*., 2009). Therefore, none of the guilds defined by these authors, nor the ones defined by Raharivololoniana *et al*. (2006) for *Boophis* tadpoles, are fully applicable to tadpoles of *Ochthomantis*. Based on our assumption that the different morphologies of the oral disk might correspond to the use of different nutrient resources, the three morphological clusters of *Ochthomantis* tadpoles defined above might in the future be considered as three ecomorphological guilds. However, such definitions will make more sense if proposed in the context of a future more comprehensive analysis of the morphology of mantellid tadpoles.

'Reverse taxonomy', *i.e.* the initial survey of the diversity of a group of organisms via DNA barcoding only, has been introduced for cases where taxon diversity cannot be handled with traditional approaches (Markmann and Tautz, 2005). Although such cases will usually refer to groups of insufficiently assessed taxa such as meiobenthos or nematodes (Blaxter, 2004; Markmann and Tautz, 2005), our example shows that it may also be fruitful in generally better studied groups such as vertebrates.

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Appendix

Morphological descriptions of tadpoles

Mantidactylus femoralis (Boulenger, 1882)

The following description refers to one tadpole in developmental stage 28 (field number ZCMV 3431-ZSM 1736/2007, BL 11.4 mm, TL 34 mm) from the stream Andohan'i Sity (transect 1) in An'Ala forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of a *Mantidactylus femoralis* adult specimen (accession AY324812) from Andasibe.

In dorsal view, body elliptical (BW 57% of BL), maximal body width between the proximal 2/3 and 3/5 of the body (SBW 47% of BL), with a constriction behind the point of the maximal body width, narrowly rounded snout. In lateral view, body depressed (BW 141% of BH), maximal body height between the

Table 3. Morphometric measurements (all in mm) of all the DNA voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. For abbreviations, see Material and methods.

Species	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. ambreensis*	*M. zolitschka*	*M. argenteus*
Site	An'Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An'Ala	An'Ala
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575
ZSM	1736/2007	1928/2007	1630/2007	396/2008	1385/2004	762/2004	1843/2007	1573/2007
Gos	28	26	25	28	37	25	27	27
BL	11.4	12.2	6.4	10.2	12.7	5.7	9.2	12.2
BW	6.5	7.6	3.4	5.8	7.7	3.1	5.1	5.7
SBW	5.4	7.1	3.2	5.0	9.3	2.5	3.7	6.1
BH	4.6	5.0	2.6	3.5	5.4	2.5	3.4	5.2
SBH	8.0	7.3	4.4	7.9	9.3	3.4	6.5	6.8
ED	1.1	1.2	0.7	1.1	1.5	0.6	1.0	1.1
SE	3.7	3.5	2.2	3.2	3.2	2.1	2.8	2.6
EH	3.4	3.7	1.9	2.2	3.3	1.7	2.3	3.0
IOD	3.4	3.6	2.2	3.6	3.8	2.1	2.9	3.6
ND	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
NH	2.8	3.2	1.8	1.7	2.5	1.4	2.0	2.5
IND	2.0	2.0	1.2	2.1	2.3	1.4	1.8	1.9
RN	1.7	1.3	1.0	1.2	1.2	0.9	1.1	1.0
NP	2.0	2.2	1.2	2.1	2.1	1.3	1.7	1.5
SL	1.8	2.1	1.1	3.1	2.3	0.8	1.6	1.1
SS	7.4	7.5	4.2	7.9	7.8	4.1	5.7	6.6
SV	4.0	3.6	2.2	2.3	4.9	1.7	3.5	5.5
SH	3.2	3.0	1.4	1.4	2.8	1.4	1.4	2.5
VL	1.5	1.1	0.5	1.1	1.7	0.5	1.0	1.8
TAL	22.6	19.7	12.8	17.9	25.5	12.8	15.4	21.8
TMW	3.4	2.7	1.9	2.5	3.6	1.7	2.3	3.4
TMH	3.2	3.1	1.8	2.9	3.4	1.8	2.2	3.5
TH	4.0	4.1	2.4	3.3	4.8	2.1	3.2	4.3
TMHM	2.6	2.1	1.5	2.4	2.6	1.3	1.2	2.8
THM	4.4	3.9	2.8	4.2	5.4	2.1	3.4	5.0
MTH	5.1	4.3	2.9	4.3	5.5	2.3	3.6	5.5
DMTH	9.0	6.0	5.1	10.1	11.3	5.8	6.6	8.0
DF	1.0	1.0	0.7	1.1	1.4	0.4	1.0	1.2
VF	1.0	0.9	0.6	0.7	1.1	0.3	0.8	1.1
HAB	3.4	3.8	1.5	2.2	3.6	1.6	2.4	3.3
TL	34.0	31.9	19.2	28.1	38.2	18.4	24.6	34.0

proximal 3/5 and 4/5 of the body (SBH 70% of BL), pointed snout. Moderately large eyes (ED 10% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 32% of BL), moderately wide distance between eyes (IOD 52% of BW). Small elliptical nares (ND 1.1% of BL), marked with a marginal rim, positioned high (NH 60% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 83% of NP) and below eye level (NH 83% of EH), moderately wide distance between nares (IND 58% of IOD), red coloured region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral views, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 65% of BL), located high on the body (SH 69% of BH) and almost at the height of the point where the axis of the tail myotomes contacts the body (SH 96% of HAB). Moderately long dextral vent tube (VL 13% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 198% of

Table 3. continued.

M. sp. 42	*M.* sp. 43	*M.* sp. 47	*M.* sp. 47	*M. mocquardi*	*M. mocquardi*	*M. mocquardi*	*M.* sp. 64	*M. majori*	*M. majori*
Ambre	Marojejy	Ambatolahy	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Ranomafana	Vevembe
FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	Tad 6 Vevembe	ZCMV 3761
774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
28	25	31	25	26	25	27	39	29	27
11.1	7.0	12.1	8.2	11.4	7.0	13.8	10.8	13.1	13.5
6.2	4.2	6.2	4.5	6.9	4.0	8.6	6.4	8.4	9.1
7.9	3.8	8.4	3.4	5.4	3.8	6.6	5.2	6.5	6.5
5.1	3.0	4.8	3.2	4.6	2.8	6.4	4.7	5.7	6.5
7.6	5.0	8.3	5.5	8.3	4.6	11.2	7.5	8.9	10.3
1.2	0.9	1.5	1.0	1.3	0.8	1.8	1.4	2.0	1.9
3.1	2.8	3.1	2.5	4.0	2.6	4.4	2.9	4.9	5.3
3.4	2.3	3.5	2.2	3.4	2.1	4.3	3.7	4.5	4.8
3.5	2.5	3.7	3.1	3.7	2.6	4.7	4.1	5.5	5.3
0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.3	0.4
2.4	1.9	2.5	1.5	2.7	1.6	3.4	2.9	3.6	3.9
2.0	1.4	2.2	1.9	2.5	1.7	3.3	2.0	3.0	3.1
1.1	1.2	1.0	0.8	1.6	0.9	1.7	0.9	1.8	2.0
2.0	1.6	2.1	1.8	2.4	1.6	2.8	2.1	3.1	3.3
1.7	1.1	1.7	1.2	1.8	0.7	1.4	2.0	2.1	2.4
6.9	5.2	6.7	5.2	7.7	5.1	9.8	7.0	9.9	11.2
4.0	1.8	5.4	3.0	3.7	1.9	4.0	3.8	3.2	2.4
2.8	1.5	2.4	1.6	1.9	1.3	3.0	2.5	2.2	2.9
1.4	0.5	1.4	0.4	1.0	0.6	1.7	1.1	1.5	1.0
23.7	14.0	20.1	14.5	21.1	13.2	28.8	21.1	23.8	23.7
3.9	2.1	3.9	2.1	3.5	1.9	4.9	3.2	2.2	4.2
3.6	1.9	3.5	2.2	3.4	1.6	4.9	3.0	4.0	4.2
4.9	2.8	4.3	2.6	4.2	2.5	6.2	4.2	5.1	5.8
3.1	1.6	3.0	1.7	2.8	1.3	3.7	2.6	3.0	3.9
5.3	3.2	4.4	2.6	4.7	2.8	6.9	4.8	5.4	7.5
5.4	3.3	4.8	3.0	4.7	2.9	6.9	4.9	5.8	7.6
9.5	4.4	8.1	3.9	8.7	4.8	14.3	8.9	9.8	11.3
1.2	0.9	0.8	0.5	1.2	1.0	1.9	1.2	1.6	2.4
1.4	0.6	0.7	0.4	0.7	0.5	1.3	1.1	0.8	1.2
3.1	1.8	3.2	2.0	2.8	1.7	4.0	3.3	3.5	4.3
34.8	21.0	32.1	22.7	32.5	20.2	42.6	31.9	36.9	37.3

Table 4. Relative values (%) of the morphometric parameters of the DNA voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. For abbreviations, see Material and methods.

Species	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. ambreensis*	*M. zolitschka*	*M. argenteus*
Site	An'Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An'Ala	An'Ala
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575
ZSM	1736/2007	1928/2007	1630/2007	396/2008	1385/2004	762/2004	1843/2007	1573/2007
Gos	28	26	25	28	37	25	27	27
BW/BL	57	62	53	57	61	55	55	47
SBW/BL	47	58	49	49	73	43	40	50
BW/BH	141	152	133	164	142	127	148	111
SBH/BL	70	60	69	77	73	60	71	56
ED/BL	10	10	11	11	12	11	11	9
SE/BL	32	28	34	32	25	37	30	21
EH/BH	73	73	73	61	62	68	68	58
IOD/BW	52	47	66	61	50	66	56	63
ND/BL	1.1	1.1	1.7	1.1	0.9	2.3	1.3	0.8
NH/BH	60	63	69	49	46	58	58	48
RN/NP	83	61	82	57	57	67	61	68
NH/EH	83	86	95	81	75	85	86	84
IND/IOD	58	56	55	59	60	65	64	54
SL/BL	16	17	17	30	18	14	17	9
SS/BL	65	62	66	77	61	72	62	55
SH/BH	69	60	56	40	52	55	40	49
SH/HAB	96	80	93	66	79	85	58	77
VL/BL	13	9	8	11	13	9	11	14
TAL/BL	198	161	200	175	200	225	167	180
TMW/BW	52	35	56	44	46	55	45	60
TMH/BH	68	63	71	82	62	74	64	67
TMH/MTH	62	73	62	67	61	79	61	63
TH/BH	85	82	95	95	90	85	92	84
TMHM/THM	58	53	53	56	48	62	34	55
TMHM/MTH	50	48	50	55	47	55	33	51
THM/BH	95	78	109	120	99	83	100	97
THM/MTH	87	91	95	98	97	88	96	92
MTH/BH	109	86	115	123	102	94	105	106
DMTH/TAL	40	31	40	57	44	45	43	37
DF/TMHM	40	47	48	46	56	33	82	43
VF/TMHM	37	42	41	31	43	27	68	41
DF/VF	107	111	115	151	131	124	122	104
HAB/BH	72	75	60	61	66	65	70	64

BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail almost equal to body height and lower than maximal tail height (THM 95% of BH and 87% of MTH), tail height at the beginning of the tail lower than body height (TH 85% of BH). Moderately developed caudal musculature (TMW 51% of BW, TMH 68% of BH, TMH of 80% of TH and 62% of MTH, TMHM 58% of THM and 50% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 40% of TMHM, VF 37% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 107% of VF). Dorsal fin originates on tail muscle on the proximal 1/5 of the tail, increases abruptly to attain its maximal height before midtail and then progresses horizontally until the 9/10 of the tail and finally decreases gradually towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases to tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH

Table 4. continued.

M. sp. 42	*M.* sp. 43	*M.* sp. 47	*M.* sp. 47	*M. mocquardi*	*M. mocquardi*	*M. mocquardi*	*M.* sp. 64	*M. majori*	*M. majori*
Ambre	Marojejy	Ambatolahy	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Ranomafana	Vevembe
FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	TAD 6 Vevembe	ZCMV 3761
774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
28	25	31	25	26	25	27	39	29	27
56	60	52	55	60	58	63	59	64	67
71	54	69	42	47	54	48	48	49	48
123	142	130	143	148	143	136	136	147	141
68	71	69	67	73	66	81	69	68	77
11	13	13	12	12	11	13	13	15	14
28	39	26	31	35	36	32	27	38	39
67	78	73	69	73	73	67	79	78	75
55	59	59	69	53	65	54	64	66	58
1.1	2.0	1.1	1.1	1.4	2.0	1.6	1.3	2.5	3.3
47	65	53	49	59	58	53	62	64	60
57	76	48	43	67	57	59	43	59	59
70	84	72	71	81	79	79	79	81	81
57	58	58	60	68	64	70	48	53	58
15	15	14	14	16	11	10	19	16	18
62	75	56	63	67	73	71	64	76	83
55	52	51	50	42	45	48	54	38	45
89	85	76	81	70	76	76	76	61	67
13	7	11	5	9	8	12	10	11	7
214	201	166	176	185	189	209	196	181	176
62	49	63	47	51	46	56	50	26	46
72	64	73	71	74	56	78	64	70	66
67	58	73	75	73	54	71	62	69	56
96	94	90	83	91	87	97	89	89	90
58	51	67	65	60	46	54	55	56	53
57	50	62	56	59	44	54	53	52	52
105	107	90	82	91	99	97	89	94	116
98	96	93	87	99	96	100	97	93	98
107	111	100	95	102	103	109	103	101	118
40	31	40	27	42	36	50	42	41	47
40	57	28	32	41	75	52	44	53	60
45	39	24	24	25	42	34	42	27	29
87	148	117	133	162	178	154	106	195	205
62	60	67	62	60	60	63	70	62	67

40% of TAL), lateral tail vein and myosepta slightly visible on the proximal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 72% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Small reduced oral disk (ODW 24% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 48% of ODW), gap on the lower labium absent; total number of marginal papillae 59. Sixty-nine submarginal papillae on the lower labium and laterally on upper labium. Short and moderately wide conical papillae with rounded tips, longest marginal papillae measured 0.15 mm and 0.16 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single

Table 5. Comparison of the oral disk characteristics of the voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. JW, Thorn-pap, MCL, DG, $A_{1\text{-}2\ \mathrm{len}}$, $P_{1\text{-}3\ \mathrm{len}}$, $A_{2\ \mathrm{gap}}$, $A_{2\ \mathrm{row+gap}}$, Kerat len, MP len and SMP len are in mm. ODW/BW, DG/ODW, JW/ODW, MCL/JW, A_1/ODW and A_2Gap/A_2 are in %. $A_{1\text{-}2\ \mathrm{den}}$, $P_{1\text{-}3\ \mathrm{den}}$, is density (number/mm). UR, LR, A_1 num, MP, SMP and Tot pap are total numbers. A: ventrally; B: anteroventrally; C: soft partially keratinised with smooth surface; D: thorn-shaped papillae, not keratinized; E: lower sheath totally hidden; F: short widely pointed; G: short

Species	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. ambreensis*	*M. zolitschka*	*M. argenteus*
Site	An’Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An’Ala	An’Ala
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575
ZSM	1736/2007	1928/2007	1630/2007	396/2008	1385/2004	762/2004	1843/2007	1573/2007
Gos	28	26	25	28	37	25	27	27
ODW	2.8	2.5	1.6	2.2	3.0	1.1	2.0	1.8
LTRF	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	2(2)/3(1-2)	3(2-3)/3(1-2)	2(2)/3(1-2)
UR	3	3	3	3	3	2	3	2
LR	3	3	3	3	3	3	3	3
JW	1.3	1.1	0.6	1.2	1.1	0.6	1.0	0.8
Thorn-pap	not app	not app	not app	not app	not app	not app	not app	not app
MCL	0.24	0.23	0.14	0.25	0.30	0.10	0.29	0.25
DG	1.32	1.41	0.86	1.37	1.24	0.73	1.12	1.09
VG	abs	abs	abs	abs	abs	abs	abs	abs
$A_{1\ \mathrm{len}}$	1.23	1.49	1.02	1.34	0.97	0.72	0.93	1.15
$A_{2\ \mathrm{len}}$ (R/L)	0.20/0.22	0.23/0.18	0.24/0.29	0.29/0.26	0.16/0.22	0.12/0.13	0.20/0.19	0.14/0.20
$A_{2\ \mathrm{gap}}$	0.83	1.06	0.44	0.85	0.98	0.49	0.72	0.58
$A_{2\ \mathrm{row+gap}}$	1.25	1.47	0.97	1.40	1.36	0.84	1.11	0.92
$A_{3\ \mathrm{len}}$ (R/L)	0.11/0.14	0.07/0.11	0.12/0.14	0.20/0.19	0.16/0.19	abs	0.14/0.08	abs
$P_{1\ \mathrm{len}}$ (R/L)	0.59/0.61	0.56/0.57	0.43/0.45	0.55/0.50	0.72/0.62	0.30/0.27	0.60/0.45	0.28/0.27
$P_{2\ \mathrm{len}}$ (R/L)	0.57/0.65	0.62/0.48	0.47/0.44	0.62/0.50	0.57/0.50	0.26/0.26	0.66/0.34	0.4570.43
$P_{3\ \mathrm{len}}$	0.57	1.12	0.57	0.41	0.38	0.31	0.25	0.19
Kerat len	0.06	0.06	0.06	0.07	0.08	0.04	0.05	0.06
MP len	0.17	0.10	0.09	0.09	0.12	0.08	0.10	0.15
SMP len	0.16	0.13	0.08	0.11	0.20	0.08	0.15	0.07
ODW/BW	42	32	46	38	39	35	40	31
DG/ODW	48	58	55	63	41	66	56	62
JW/ODW	49	46	37	53	35	53	47	43
MCL/JW	18	21	24	22	28	17	31	33
A_1/ODW	45	61	65	62	32	65	46	65
A_2Gap/A_2	66	72	45	61	72	58	65	63
$A_{1\ \mathrm{num}}$	48	50	55	43	39	21	25	41
$A_{2\ \mathrm{num}}$ (R/L)	10/10	10/7	12/13	10/10	8/11	6/6	7/8	5/6
$A_{3\ \mathrm{num}}$ (R/L)	7/6	3/5	5/7	10/11	5/9	abs	7/3	abs
$p_{1\ \mathrm{num}}$ (R/L)	28/29	20/20	24/24	30726	42/38	12/13	22/25	8/9
$P_{2\ \mathrm{num}}$ (R/L)	21/24	21/15	21/22	30/28	22/25	13/14	20/20	16/15
$P_{3\ \mathrm{num}}$	20	15	27	17	15	10	11	5
MP	59	50	43	59	71	30	69	31
SMP	69	69	30	65	60	18	46	18
Total pap	128	119	73	124	131	48	115	49
$A_{1\ \mathrm{den}}$	39	34	53	32	40	29	27	36
$A_{2\ \mathrm{den}}$	48	33	47	54	53	abs	38	32
$A_{3\ \mathrm{den}}$	50	44	46	44	38	abs	46	abs
$p_{1\ \mathrm{den}}$	48	35	55	53	60	44	45	31
$P_{2\ \mathrm{den}}$	37	32	47	52	45	52	40	35
$P_{3\ \mathrm{den}}$	35	39	47	41	39	32	44	26
OD orient	B	A	A	A	A	B	B	B
Up sheaths	C	C	C	C	C	C	C	C
Low sheath	E	E	E	E	E	E	E	E
MC	G	I	G	I	I	F	K	K
Up labium	M	M	M	M	M	M	M	M
Papillae	O	O	O	O	O	O	O	O
Lower row	R	R	R	R	R	R	R	R

widely rounded; H: moderately long widely pointed; I: moderately long widely rounded; J: moderately long narrowly pointed; K: long narrowly pointed; L: very long narrowly pointed; M: upper labium is a continuation of the snout; N: anterior margin is separated by a shallow crevice; O: moderately long with rounded tip; P: long, MP rounded tip, SMP pointed tip; Q: long, with pointed tip (MP and SMP); R: scattered and forming chevron; S: lower row absent; not app: not applicable; abs: absent. For further abbreviations, see Material and methods.

M. sp. 42	*M.* sp. 43	*M.* sp. 47	*M.* sp. 47	*M. mocquardi*	*M. mocquardi*	*M. mocquardi*	*M.* sp. 64	*M. majori*	*M. majori*
Ambre	Marojejy	Ambatolahy	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Ranomafana	Vevembe
FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	Tad 6 Vevembe	ZCMV 3761
774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
28	25	31	25	26	25	27	39	29	27
2.3	2.0	2.3	2.1	3.0	1.7	4.0	2.2	3.4	3.4
3(2-3)/3(1-2)	2(2)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	not app	not app	not app	not app	not app	not app
3	2	3	3	not app	not app	not app	not app	not app	not app
3	3	3	3	not app	not app	not app	not app	not app	not app
1.2	0.8	1.2	0.9	1.3	0.5	1.9	1.2	1.8	1.7
not app	not app	not app	not app	not app	not app	not app	not app	0. 6/0.8/0.7	0.5/0.7/0.5
0.21	0.20	0.23	0.19	0.28	0.24	0.57	0.26	not app	not app
1.06	1.03	1.00	0.92	abs	abs	abs	abs	abs	abs
abs	abs	abs	abs	abs	abs	abs	abs	abs	abs
0.74	0.98	0.95	0.76	abs	abs	abs	abs	abs	abs
0.07/0.12	0.15/0.17	0.16/0.11	0.11/0.16	abs	abs	abs	abs	abs	abs
0.86	0.73	0.84	0.60	abs	abs	abs	abs	abs	abs
1.05	1.10	1.11	0.87	abs	abs	abs	abs	abs	abs
0.07/0.06	abs	0.50/0.50	0.13/0.15	abs	abs	abs	abs	abs	abs
0.52/0.56	0.34/0.40	0.50/0.43	0.41/0.47	abs	abs	abs	abs	abs	abs
0.45/0.42	0.21/0.25	0.45/0.34	0.47/0.50	abs	abs	abs	abs	abs	abs
0.87	0.09	0.25	0.49	abs	abs	abs	abs	abs	abs
0.09	0.07	0.05	0.04	not app	not app	not app	not app	not app	not app
0.13	0.10	0.14	0.09	0.19	0.09	0.25	0.11	0.25	0.22
0.14	0.08	0.11	0.10	0.25	0.12	0.35	0.15	0.41	0.52
36	46	36	47	43	42	47	34	40	38
47	53	44	43	abs	abs	abs	abs	abs	abs
52	41	51	39	43	32	48	56	54	51
18	25	20	23	22	44	30	21	not app	not app
33	51	42	36	not app	not app	not app	not app	not app	not app
82	66	76	69	not app	not app	not app	not app	not app	not app
12	13	14	23	abs	abs	abs	abs	abs	abs
4/6	8/10	5/5	5/6	abs	abs	abs	abs	abs	abs
4/3	abs	2/2	12	abs	abs	abs	abs	abs	abs
24/21	14/16	19/17	17/18	abs	abs	abs	abs	abs	abs
19/19	10/12	18/13	21/21	abs	abs	abs	abs	abs	abs
13	5	9	24	abs	abs	abs	abs	abs	abs
53	78	72	64	74	64	89	81	72	105
42	50	66	58	104	77	88	87	135	201
95	128	138	122	178	141	177	168	207	306
16	13	15	30	not app	not app	not app	not app	not app	not app
53	56	35	39	abs	abs	abs	abs	abs	abs
54	abs	40	43	abs	abs	abs	abs	abs	abs
38	41	39	40	abs	abs	abs	abs	abs	abs
44	63	39	43	abs	abs	abs	abs	abs	abs
30	56	36	49	abs	abs	abs	abs	abs	abs
B	B	B	A	B	B	A	B	A	A
C	C	C	C	C	C	C	C	D	D
E	E	E	E	E	E	E	E	E	E
G	H	H	H	J	L	L	G	not app	not app
M	M	M	M	M	M	M	M	N	N
O	O	O	O	P	P	P	P	Q	Q
R	R	R	R	S	S	S	S	S	S

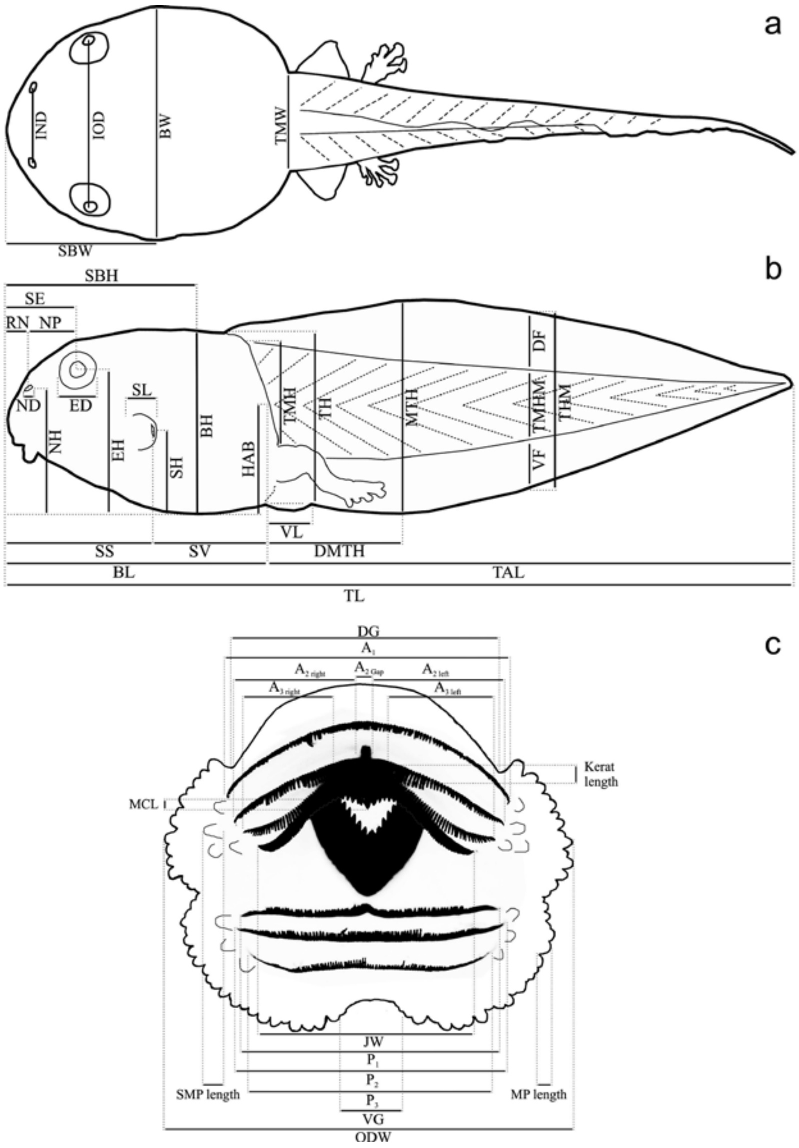

Fig. 9. Drawings representing the landmarks of the measurements: (a) dorsal view, (b) lateral view, (c) oral disk.

row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 45% of ODW). Density of keratodonts varies from 35/mm to 50/mm, $A_{1\ den}$ 39/mm (total 48). Wide gap in the first anterior interrupted row (A_{2gap} 66% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.06 mm). Distal keratodonts have the same lengths as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black coloured and the rest whitish; finely pointed serrations; moderately wide jaw sheath (JW 48% of ODW) with a short widely rounded medial convexity (MCL 18% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Uniformly dark brown. Brown melanic pigment positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body. Some dark brown patches scattered on the dorsal skin. Laterally, jugal area (under eyes and nares) and flank covered by dark brown reticulations. The spiracle is reticulated at the base and transparent at the end, and detectable, and is situated the visible intestinal coils. Lower part of the flank not pigmented.

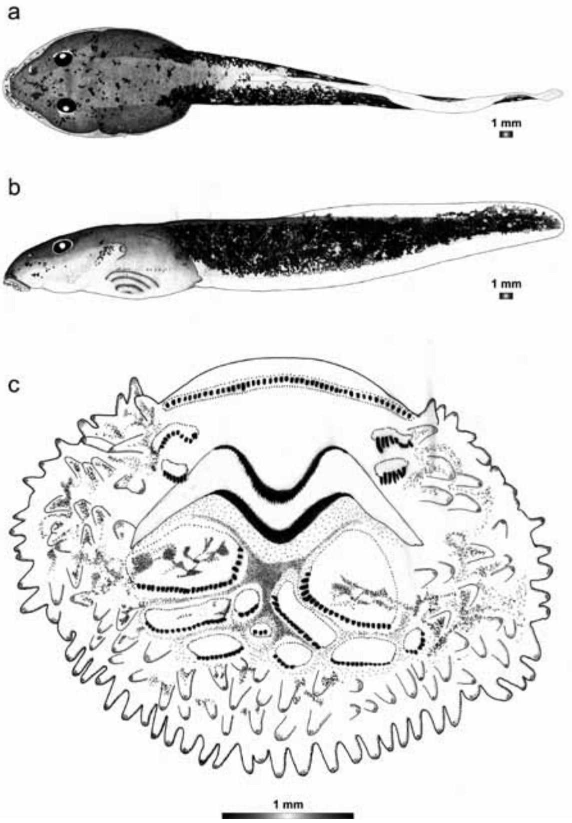

Fig. 10. Drawings of the preserved DNA voucher tadpole of *Mantidactylus femoralis* (ZCMV 3431-ZSM 1736/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

Tail musculature overlain by dark brown reticulations. Fins pale, dorsal fin with sparse brown reticulations. Ventrally, oral disk, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.

Variation. Six voucher specimen (ZSM 1554/2007-ZCMV 3536, ZSM 1555/2007-ZCMV 3537, ZSM 1733/2007-ZCMV 3428, ZSM 1781/2007-ZCMV 3476, ZSM 1834/2007-ZCMV 3554, ZSM 1848/2007-ZCMV 3572) from the same locality show a similar oral disk configuration.

Mantidactylus ambreensis Mocquard, 1895

The following description refers to one tadpole in developmental stage 25 (field number FG/MV 2002.1950-ZSM 762/2004, BL 5.7 mm, TL 18.4 mm) from a stream crossing the track 'Voie des milles arbres' at the Montagne d'Ambre National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus ambreensis* (accession AY324822) from the same locality.

In dorsal view, body ovoid (BW 55% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 43% of BL), narrowly rounded snout. In lateral view, body depressed (BW 127% of BH), maximal body height attained at the 3/5 of the body (SBH 60% of BL), narrowly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 68% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 37% of BL), wide distance between eyes (IOD 66% of BW). Moderately large rounded nares (ND 2.3% of BL), marked with a marginal rim, positioned moderately high (NH 58% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 67% of NP) and below eye level (NH 85% of EH), wide distance between nares (IND 65% of IOD), no dark spot on the back of the nares, ornamentation absent. Short sinistral spiracle (SL 14% of BL), directed posteriodorsally, visible from dorsal and ventral views, perceptible from lateral view; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 72% of BL), located moderately high on the body (SH 55% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 85% of HAB). Short dextral vent tube (VL 9% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 225% of BL), maximal tail height lower than body height (MTH 94% of BH), tail height at midtail lower than body height and maximal tail height (THM 83% of BH and 87% of MTH), tail height at the beginning of the tail lower than body height (TH 85% of BH). Developed caudal musculature (TMW 55% of BW, TMH 74% of BH, TMH of 80% of TH and 79% of MTH, TMHM 62% of THM and 55% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 33% of TMHM, VF 26% of MTHM), higher than ventral fin at mid-tail (DF 124% of VF). Dorsal fin originates between the dorsal body-tail junction and the proximal 1/4 of tail, ascends to attain its maximal height before midtail and then continues straight until the proximal 3/4 of the tail, and then decreases towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains straight until the proximal 3/4 of the tail, and then decreases towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 45% of TAL), lateral tail vein not visible, myosepta perceptible on the proximal ½ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 65% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Small reduced oral disk (ODW 35% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a wide gap on the upper labium (DG 66% of ODW), gap on the lower labium absent; total number of marginal papillae is 30. Eighteen submarginal papillae, continuous on the lower labium and laterally on upper labium. Very short and small rounded papillae with rounded tips, longest marginal and submarginal papillae measured 0.08 mm, papillae not visible from dorsal view. LTRF 2(2)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Long A_1 row ($A_{1\,len}$ 65% of ODW). Density of keratodonts varies from 29/mm to 52/mm, $A_{1\,den}$ 29/mm (total 21). Moderately wide gap in the first anterior interrupted row (A_{2gap} 58% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Very short distinguishable keratodonts (0.04 mm). Distal keratodont have same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black coloured and the rest whitish coloured; finely pointed serrations; moderately wide jaw sheath (JW 53% of ODW) with a short widely pointed medial convexity (MCL 17% of JW). Lower jaw sheath V-shaped, partially keratinized and completely hidden by the upper jaw sheath.

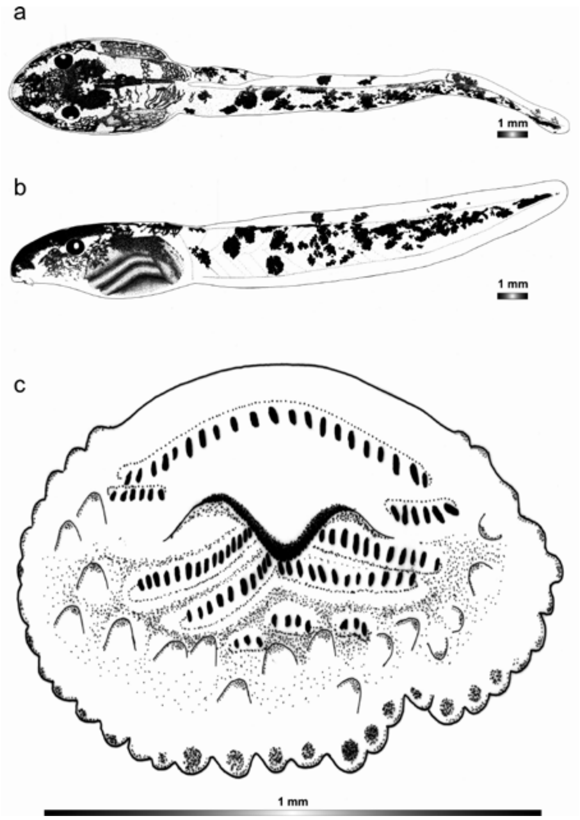

Fig. 11. Drawings of the preserved DNA voucher tadpole of *Mantidactylus ambreensis* (FG/MV 2002.1950-ZSM 762/2004): (a) dorsal view, (b) lateral view, (c) oral disk.

Colouration in preservative. Generally beige-brownish. Dorsal sides of the head and trunk and higher part of the flank beige with light brown reticulations between nares and eyes, on the frontal, between the eyes, along the vertebral area and on the dorsolateral abdominal wall. Region between the vertebral area and the dorsolateral abdominal wall not pigmented except the area close to the body-tail junction. Laterally, jugal area and flank covered by sparse dark brown melanic reticulations leaving out a merged transparent spiracle above the well visible intestinal coils. Lower part of the flank not pigmented. Tail musculature beige with brown blotches of melanophores which fuse in some areas to form networks up to the tail tip. Fins translucent, dorsal fin with few patches. Ventrally, oral disk, gular and branchial regions pale; venter transparent, intestinal coils visible and regularly spiral shaped.

Variation. Four non-voucher specimens belonging to the same series show the same external morphology as the voucher specimen, in particular in the oral. However, LTRF varies between 2(2)/3(1-2) and 3 (2-3)/3(1-2).

Mantidactylus zolitschka Glaw and Vences, 2004

The following description refers to one tadpole in developmental stage 27 (field number ZCMV 3565-ZSM 1843/2007, BL 9.2 mm, TL 24.6 mm) from the stream Andohan'i Sity (transect 2) in An'Ala forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus zolitschka* (accession no AY324811) from the same locality.

In dorsal view, body elliptical (BW 55% of BL), maximal body width attained at the 2/5 of the body

(SBW 40% of BL), small constriction at midbody, narrowly rounded snout. In lateral view, body depressed (BW 148% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), broadly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 68% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 30% of BL), moderately wide distance between eyes (IOD 56% of BW). Small rounded nares (ND 1.3% of BL), marked with a marginal rim, positioned moderately high (NH 58% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 61% of NP) and below eye level (NH 86% of EH), wide distance between nares (IND 64% of IOD), reddish region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 17% of BL), directed posterodorsally, visible from dorsal view and perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 62% of BL), located moderately high on the body (SH 40% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 58% of HAB). Moderately long dextral vent tube (VL 11% of BL), associated with ventral fin, inner wall present. No gland. Short tail (TAL 167% of BL), maximal tail height almost equal to body height (MTH 105% of BH), tail height at midtail equal to body height and almost equal to maximal tail height (THM 100% of BH and 95% of MTH), tail height at the beginning of the tail lower than body height (TH 92% of BH). Moderately developed caudal musculature (TMW 45% of BW, TMH 64% of BH, TMH of 69% of TH and 61% of MTH, TMHM 34% of THM and 33% of MTH). Tail muscle reaches tail tip. Low fins (DF 82% of TMHM, VF 68% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 122% of VF). Dorsal fin originates on the dorsal body-tail junction, keeps straight and almost parallel with tail muscle until proximal 1/4 of the tail, rises regularly to attain its maximal height and then declines progressively toward the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle until close to the tail tip where it declines toward the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 43% of TAL), lateral tail vein not visible, myosepta visible on the distal 1/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 70% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.

Small reduced oral disk (ODW 39% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 56% of ODW), gap on the lower labium absent; total number of marginal papillae 69. Fourty-six submarginal papillae, complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.10 mm and 0.15 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 46% of ODW). Density of keratodonts varies from 27/mm to 45/mm, $A_{1\ den}$ 27/mm (total 25). Wide gap in the first anterior interrupted row (A_{2gap} 65% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Short indiscernible keratodonts (0.05 mm), poorly keratinized. Distal keratodont same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 47% of ODW) with a long narrowly pointed medial convexity (MCL 31% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Generally beige-brownish. Light brown network of melanophores positioned in deep integumental layers and covered major surface of the dorsal sides of the head and trunk and the flank, leaving a slightly transparent lateral area under the skin. Dark brown spots grouped to form patches which scatter on the dorsum skin. Region between the vertebral area and the dorsolateral abdominal wall provided by many brown distinct irregular blotches making the vertebral area detectable. Laterally, jugal area and flank covered by dark brown distinct irregular blotches which group to form slightly dense reticulations leaving a perceptible transparent spiracle above the recognizable intestinal coils. Lower part of the flank not pigmented. Dark roughly distinct irregular brown blotches form irregularly scattered networks on the tail musculature which expand on dorsal fin. Ven-

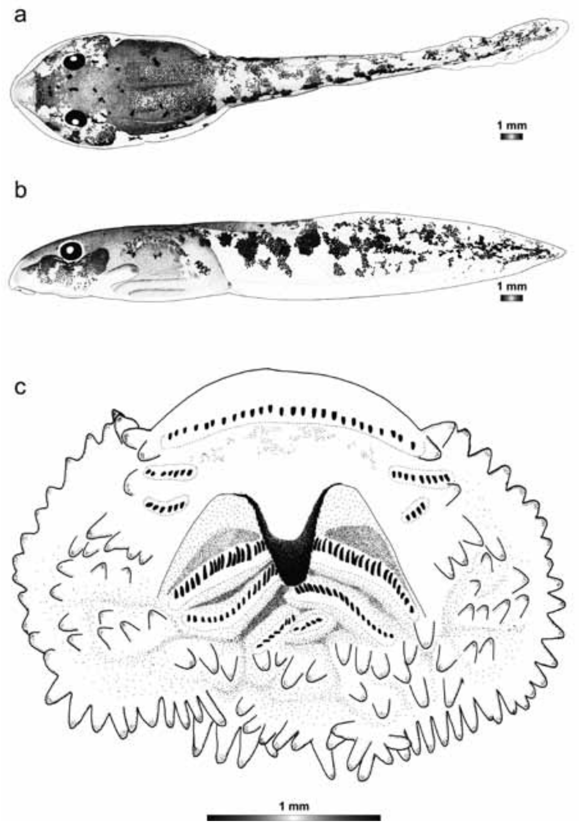

Fig. 12. Drawings of the preserved DNA voucher tadpole of *Mantidactylus zolitschka* (ZCMV 3565-ZSM 1843/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

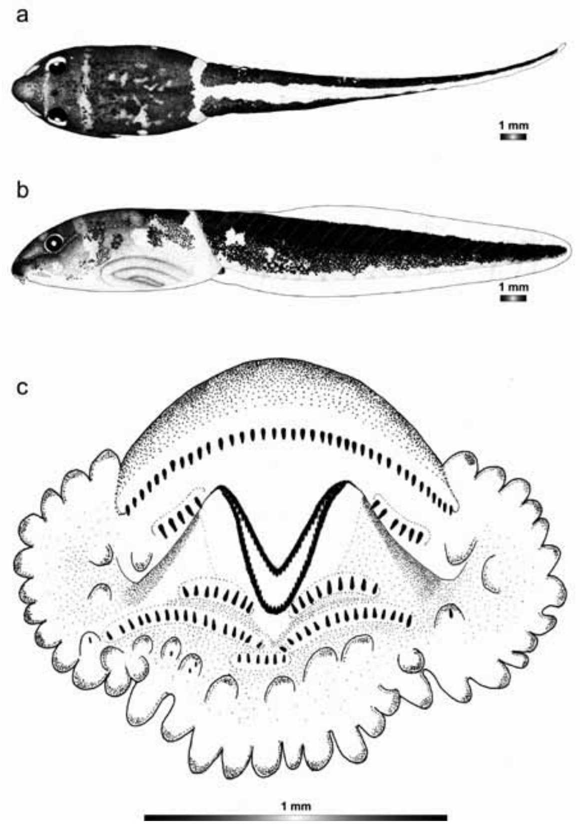

Fig. 13. Drawings of the preserved DNA voucher tadpole of *Mantidactylus argenteus* (ZCMV 3575-ZSM 1573/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

tral fin pale with few spots closed to tail tip. Ventrally, oral disk, gular and branchial regions beige, abdominal surface transparent, intestinal coils well visible and regularly spiral shaped.

Variation. Four voucher specimens attributed to *M. zolitschka* (ZSM 1741/2007-ZCMV 3436, ZSM 1759/2007-ZCMV 3455, ZSM 1768/2007-ZCMV 3464, ZSM 1841/2007-ZCMV 3563) from the same locality show the typical oral disk configuration and the pigmentation of this species and one tadpole has a LTRF of 2(2)/3(1-2).

Mantidactylus argenteus Methuen, 1920

The following description refers to one tadpole in developmental stage 27 (field number ZCMV 3575-ZSM 1573/2007, BL 12.2 mm, TL 34 mm) from the stream Andohan'i Sity (transect 3) in An'Ala forest.

In dorsal view, body elliptical (BW 47% of BL), maximal body width at mid-body (SBW 50% of BL), narrowly rounded snout with protuberation. In lateral view, body depressed (BW 111% of BH), maximal body height between the proximal 2/5 and 3/5 of the body (SBH 56% of BL), narrowly rounded snout. Small eyes (ED 9% of BL), not visible from ventral view, positioned moderately high (EH 58% of BH) dorsally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 21% of BL), wide distance between eyes (IOD 63% of BW). Very small elliptical nares (ND 0.8% of BL), marked with a marginal rim, positioned moderately high (NH 48% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 68% of NP) and below eye level (NH 84% of EH), moderately wide distance between nares (IND 54% of IOD), red coloured region on the back of the nares present, ornamentation absent. Very short sinistral spiracle (SL 9% of BL), directed posteriorly, visible from dorsal and ventral views, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, eliptical opening, situated between the proximal 2/5 and 3/5 of the body (SS 55% of BL), located moderately high on the body (SH 49% of BH) and below the point where the axis of the tail myotomes contacts the body (SH 77% of HAB). Moderately long dextral vent tube (VL 14% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 180% of BL), maximal tail height higher than body height (MTH 106% of BH), tail height at midtail almost equal to body height and lower than maximal tail height (THM 97% of BH and 82% of MTH), tail height at the beginning of the tail lower than body height (TH 84% of BH). Moderately developed caudal musculature (TMW 60% of BW, TMH 67% of BH, TMH of 80% of TH and 63% of MTH, TMHM 55% of THM and 51% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 43% of TMHM, VF 41% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 104% of VF). Dorsal fin originates on tail muscle on the proximal 1/10 of the tail, remains almost parallel with the tail muscle up to the ¼ of the tail, where it increases abruptly to attain its maximal height and then progresses horizontally until the 3/4 of the tail, finally decreases gradually towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases to tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 37% of TAL), lateral tail vein invisible and myosepta slightly all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 64% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded. Small reduced oral disk (ODW 31% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a wide gap on the upper labium (DG 62% of ODW), gap on the lower labium absent; total number of marginal papillae 31. Eighteen submarginal papillae on the lower labium and laterally on upper labium. Short and moderately wide conical papillae with rounded tips, longest marginal papillae measured 0.15 mm and 0.07 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 2(2)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Long A_1 row ($A_{1\ len}$ 65% of ODW). Density of keratodonts varies from 26/mm to 36/mm, $A_{1\ den}$ 36/mm (total 41). Wide gap in the first anterior interrupted row (A_{2gap} 63% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.06 mm). Distal keratodonts have the same lengths as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black coloured and the rest whitish; finely pointed serrations; moderately wide jaw sheath (JW 43% of ODW) with a long narrowly pointed medial convexity (MCL 33% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Generally brown, dorsally marked by transversal clear bands between nares and eyes, between eyes and spiracle and before the body-tail junction, and a longitudinal clear band on the dorsum of the tail. Brown melanic pigment positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body. Some dark brown patches scattered on the dorsal skin. Laterally, jugal area (under eyes and nares) and flank covered by dark brown reticulations. The spiracle is reticulated at the base and transparent at the end, and detectable, and is situated the visible intestinal coils. Lower part of the flank not pigmented. Tail musculature overlain by dark brown reticulations. Fins pale, dorsal and ventral fins free from pigments. Ventrally, oral disk, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.

Variation. Two voucher specimen (ZSM 1815/2007-ZCMV 3516, ZSM 1849/2007-ZCMV 3566) from the same locality show similar oral disk configuration and colouration pattern.

Mantidactylus sp. 42
(CCS from Montagne d'Ambre)

The following description refers to one tadpole in developmental stage 28 (field number FG/MV 2002. 1957-ZSM 774/2004, BL 11.1 mm, TL 34.8 mm) from a stream crossing the track 'Voie des milles arbres' at the Montagne d'Ambre National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 42 (accession FJ559267) from the same locality.

In dorsal view, body elliptical (BW 56% of BL), maximal body width between the proximal 3/5 and 4/5 of the body (SBW 71% of BL), narrowly rounded snout. In lateral view, body depressed (BW 123% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 68% of BL), broadly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 67% of BH) dorsally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 28% of BL), moderately wide distance between eyes (IOD 55% of BW). Small elliptical nares (ND 1.1% of BL), marked with a marginal rim, positioned moderately high (NH 47% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 57% of NP) and below eye level (NH 70% of EH), moderately wide distance between nares (IND 57% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 15% of BL), directed posteriorly, visible from dorsal and ventral views, perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 62% of BL), located moderately high on the body (SH 55% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 90% of HAB). Moderately long dextral vent tube (VL 13% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 214% of BL), maximal tail height lower than body height (MTH 72% of BH), tail height at midtail higher than body height and lower than maximal tail height (THM 104% of BH and 98% of MTH), tail height at the beginning of the tail almost equal to body height (TH 96% of BH). Moderately developed caudal musculature (TMW 62% of BW, TMH 72% of BH, TMH of 75% of TH and 67% of MTH, TMHM 58% of THM, and 57% of MTH). Tail muscle reaches tail tip. Very low fins (DF 40% of TMHM, VF 45% of MTHM), dorsal fin lower than ventral fin at mid-tail (DF 87% of VF). Dorsal fin originates at the dorsal body-tail junction, rises gradually to attain the maximal height before the midtail and then descents slightly towards the tail tip. Ventral fin originates at the ventral terminus of the body, expands until midtail, and then decreases towards the tail tip. Maximal tail height located at the 2/5 of the tail (DMTH 40% of TAL), lateral tail vein visible only on the proximal 1/3 of the tail, myosepta visible on the proximal 3/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Small reduced oral disk (ODW 36% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 47% of ODW), gap on the lower labium absent; total number of marginal papillae 53. Fourty-two submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.13 mm, and 0.14 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 33% of ODW). Density of keratodonts varies from 16/mm to 54/mm, $A_{1\ den}$ 16/mm (total 12). Very wide gap in the first anterior interrupted row (A_{2gap} 81% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.09 mm). Distal keratodonts have the same lengths as those in the middle; important space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black coloured and the remainder

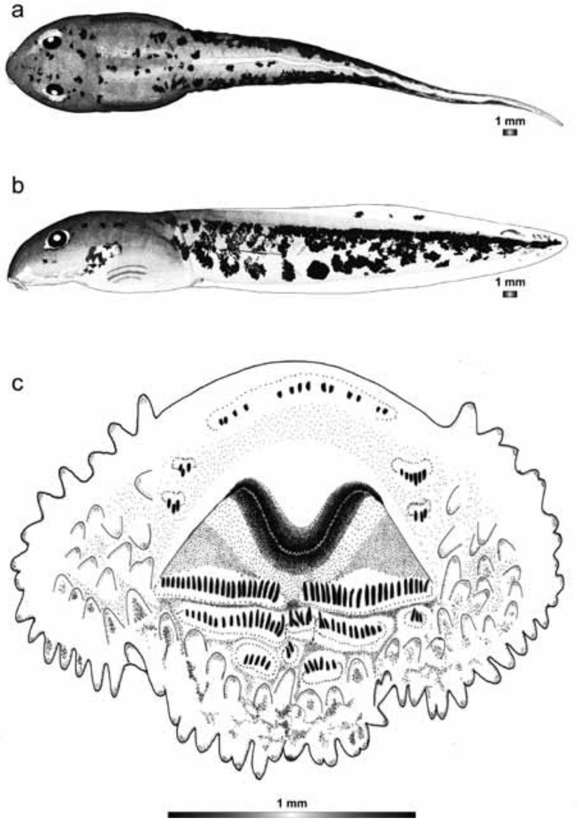

Fig. 14. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 42 (FG/MV 2002.1957-ZSM 774/2004): (a) dorsal view, (b) lateral view, (c) oral disk.

whitish; finely pointed serrations; moderately wide jaw sheath (JW 51% of ODW) with a short widely rounded medial convexity (MCL 18% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Generally brownish. Brown pigments in deep integumental layers covering the dorsum and flank of the body, leaving out a narrow slightly transparent area laterally. Dark brown patches of melanophores scattered on the skin. Rather unpigmented surface on the dorsum between the body wall and the vertebral area perceivable. Irregularly shaped clear dots form a line which runs on the dorsolateral part of the abdominal region, from the body-tail junction to just behind the eyes. There it splits, the first ramification passes below the eyes and runs through the jugal area, then diverts laterally on the sagittal plan of the nares. The second ramification runs above the eyes and approaches the first line of spots on the sagittal plan of the nares and finally merges with it on the snout. Laterally, jugal area and flank covered by dark brown dense reticulation leaving a perceivable opaque reticulated spiracle. Lower part of the flank clear, intestinal coils recognizable. A line formed by irregularly shaped clear dots is visible laterally before the body-tail junction, runs on the dorsolateral part of the abdominal region and splits just behind the eyes. The first ramification passes below the eyes and ends below the nares. The second ramification passes above the eyes and the nares and terminates on the mid-height of the snout. Tail musculature pinkish with brown mottles which coalesce to form rather dense reticulations especially on the dorsolateral part. Fins speckled, dorsal fin patched, some blotches on the ventral fin close to tail tip. Ventrally, oral disk, gular and branchial regions reticulated; venter pale, intestinal coils perceptible and regularly spiral shaped.

Mantidactylus sp. 43
(CCS from Marojejy)

The following description refers to one tadpole in developmental stage 25 (field number FGZC 2928-ZSM 1610/2007, BL 7 mm, TL 21 mm) from a stream crossing the way to the Cascade in Camp Mantella at the Marojejy National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 43 (accession FJ559268) from the same localityIn dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 54% of BL), narrowly rounded snout. In lateral view, body depressed (BW 142% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 39% of BL), moderately wide distance between eyes (IOD 59% of BW). Small rounded nares (ND 2% of BL), marked with a marginal rim, positioned high (NH 65% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 76% of NP) and below eye level (NH 84% of EH), moderately wide distance between nares (IND 58% of IOD), dark spot on the back of the nares absent, ornamentation absent. Short sinistral spiracle (SL 15% of BL), directed posteriorly, visible from dorsal and ventral views and perceptible from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 75% of BL), located moderately high on the body (SH 52% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 85% of HAB). Short dextral vent tube (VL 7% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 200% of BL), maximal tail height higher than body height (MTH 107% of BH), tail height at midtail higher than body height but lower than maximal tail height (THM 107% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 94% of BH). Moderately developed caudal musculature (TMW 49% of BW, TMH 64% of BH, TMH of 68% of TH and 58% of MTH, TMHM 51% of THM and 50% of MTH). Tail muscle reaches tail tip. Very low fins (DF 57% of TMHM, VF 39% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 148% of VF). Dorsal fin originates at dorsal body-tail junction, increases to attain the maximal height before the midtail and then descents slightly towards the tail tip. Ventral fin originates at the ventral terminus of the body, continues straight until the 3/4 of the tail, and then declines towards the tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 31% of TAL), lateral tail vein visible only on the proximal 1/4 of the tail, myosepta visible all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

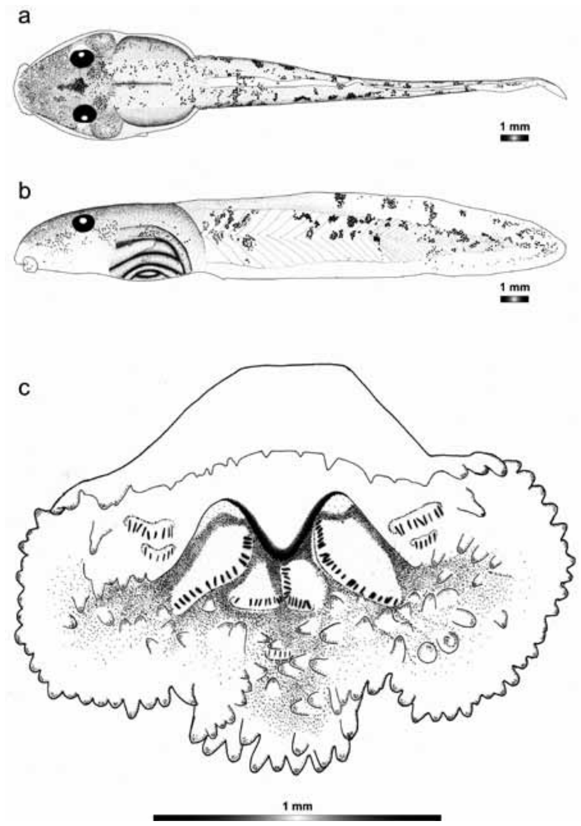

Fig. 15. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 43 (FGZC 2928-ZSM 1610/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

Moderately wide reduced oral disk (ODW 46% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 54% of ODW), gap on the lower labium absent; total number of marginal papillae 78. Fifty submarginal papillae, complete on the lower labium and laterally on upper labium. Very short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.10 mm and 0.08 mm for submarginal papillae, papillae visible from dorsal view. LTRF 2(2) /3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 51% of ODW). Density of keratodonts varies from 13/mm to 63/mm, $A_{1\ den}$ 13/mm (total 13). The first upper row seems to have lost many of its keratodonts. Wide gap in the first anterior interrupted row (A_{2gap} 66% of A_2). Rows alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted. Short discernible keratodonts (0.07 mm). Distal keratodont have same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 41% of ODW) with a moderately long widely pointed medial convexity (MCL 26% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper ones.

Colouration in preservative. Uniformly pale. Body and tail muscle dorsally flecked. Speckles in deeper dermal layers, separately from externalmost (possibly epidermal) skin layer. Darker patches dissipate between the eyes and along the vertebral area; brown irregularly shaped spots dispersed on the dorsal skin. Intestinal coils noticeable on the lateral part of the abdomen. Laterally, jugal area and flank covered by dark sparse brown melanophoric spots, leaving out an opaque, slightly blotched area around spiracle, above the detectable intestinal coils. Lower part of the flank unpigmented. Tail musculature beige with brown distinct mottles which group in some areas to form sporadic patches that extend onto the dorsal fin and their density diminishes towards tail tip. Fins translucent, speckled, especially on the proximal 1/4 of the dorsal fin; brown fused mottles abundant on dorsal fin and scattered mottles on the ventral fin. Ventrally, oral disk, gular and branchial regions beige, sporadically spotted; venter transparent, intestinal coils conspicuous and regularly spiral shaped.

Mantidactylus sp. 47
(CCS from Ambatolahy and other sites around Ranomafana)

The following description refers to one tadpole in developmental stage 31 (field number ZCMV2699-ZSM 456/2008, BL 12.1 mm, TL 32.1 mm) from Imaloka river at the Ranomafana National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 47 (accession FJ559272) from the same locality.

In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 69% of BL), constriction before the point where the maximal body width is attained, narrowly rounded snout. In lateral view, body depressed (BW 130% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 69% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 2/10 and 3/10 of the body (SE 26% of BL), moderately wide distance between eyes (IOD 59% of BW). Small rounded nares (ND 1.1% of BL), marked with a marginal rim, positioned moderately high (NH 53% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 48% of NP) and below eye level (NH 72% of EH), moderately wide distance between nares (IND 58% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 14% of BL), directed posterodorsally, not visible from either dorsal or ventral view, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening situated between the proximal 2/5 and 3/5 of the body and almost at midbody (SS 55% of BL), located moderately high on the body (SH 51% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long dextral vent tube (VL 11% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 166% of BL), maximal tail height equal to body height (MTH 100% of BH), tail height at midtail lower than body height and maximal tail height (THM 90% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 90% of BH). Developed caudal musculature (TMW 63% of BW, TMH 73% of BH, TMH of 81% of TH and 73% of MTH, TMHM 67% of THM and 62% of MTH). Tail muscle reaches tail tip. Very low fins (DF 28% of TMHM, VF 24% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 117% of VF). Dorsal fin originates on the proximal 1/5 of the tail, rises gradually and then progresses horizontally to the tail tip, then decreases. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases. Maximal tail height located at the 2/5 of the tail (DMTH 40% of TAL), lateral tail vein visible only on the proximal 1/4 of the tail, myosepta slightly visible all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 67% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Small reduced oral disk (ODW 36% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 44% of ODW), gap on the lower labium absent; total number of marginal papillae 72. Sixty-six submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.14 mm and 0.11 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 42% of ODW). Density of keratodonts varies from 15/mm to 40/mm, $A_{1\ den}$ 15/mm (total 14). Wide gap in the first anterior interrupted row (A_{2gap} 76% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Short discernible keratodonts (0.05 mm). Distal keratodont same length as those in the middle; important space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 51% of ODW) with a moderately long widely pointed medial convexity (MCL 20% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in life. Typically light brownish with irregular variegated pattern. Dorsal skin irregularly covered by brown melanophores and some gold iridophoric spots or patches. Dorsolaterally and laterally with the same pattern as dorsally. Rather non-pigmented spiracle perceptible. Tail musculature yellowish with roughly distinct, irregular brown blotches that group to form irregular patches. Their density diminishes towards the tail tip. Sporadic golden iridopohoric spots perceptible. Fins translucent, dorsal fin with many dark patches, ventral fin unpigmented. Ventrally, oral disk and gular region not pigmented and bordered by a reticulated body wall; branchial area reddish, gills and beating heart visible; venter transparent, intestinal coils visible and regularly spiral shaped.

Colouration in preservative. Largely brownish. Brown flecks in deep integumental layers cover the dorsum and condense mainly on the vertebral area and the very dark abdominal part. Light brown flecks dispersed on the skin. Roughly distinct irregular brown blotches grouped to form irregularly scattered networks, largely between the eyes and between the vertebral area and the abdominal region. Noticeable transversal lines occur between the vertebral area and the abdominal region showing noticeable abdominal-like structure. Laterally, jugal area and flank covered by irregular brown blotches which fuse to form networks mainly below the nares and between the eyes, and on the abdominal surface leaving a spotted spiracle diverged above the discernible intestinal coils. Lower part of the flanks not pigmented. Tail musculature beige with roughly distinct irregular brown blotches that group to form irregular patches. Their density diminishes towards the tail tip. Fins translucent, dorsal fin with many patches, ventral fin unpigmented. Ventrally, oral disk and gular region beige and bordered by a reticulated body wall; venter pale, intestinal coils visible and regularly spiral shaped.

Variation. Five voucher specimens (ZSM 1697/2007-ZCMV 3774, ZSM 254/2008-ZCMV 3669, ZSM 315/2008-ZCMV 3620, ZSM 478/2008-ZCMV 3724, ZSM 506/2008-ZCMV 3791) attributed to this species from the same locality and many non-voucher specimens belonging to these series indicate the identical oral disk configuration and the external pigmentation of this species. Only the LTRF is variable: 2(2)/3(1-2) and 3(2-3)/3(2-3).

Mantidactylus mocquardi Angel, 1929

The following description refers to one tadpole in developmental stage 26 (field number ZCMV 3511-ZSM 1540/2007, BL 11.4 mm, TL 32.5 mm) from the stream Andohan'i Sity (transect 2) in An'Ala forest. The 16S rDNA sequence of this specimen was 99.3% identical to a reference sequence of an adult specimen of *M. mocquardi* (accession FJ559269; ZCMV 5865; referred to as *Mantidactylus* sp. 44 by Vieites *et al*., 2009) from Ambohitsara-Tsitolaka.

In dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 47% of BL), narrowly rounded snout. In lateral view, body depressed (BW 148% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 73% BL),

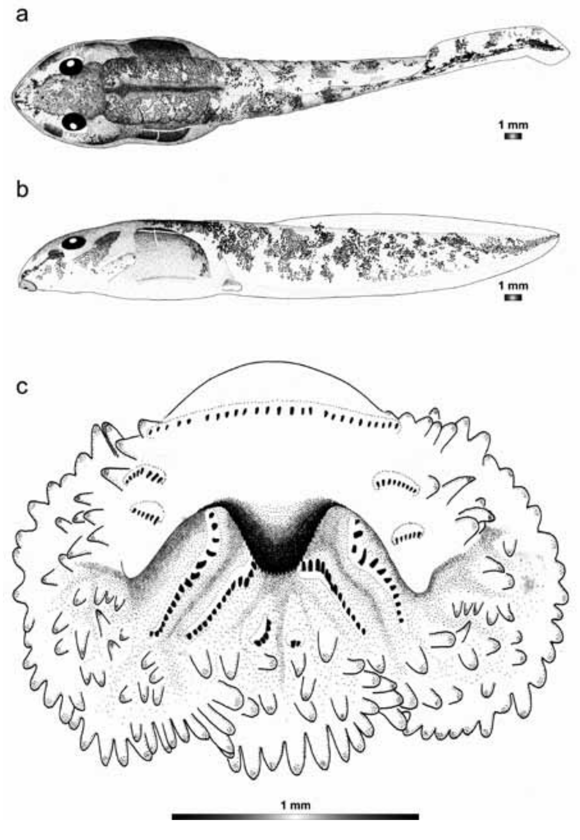

Fig. 16. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 47 (ZCMV 2699-ZSM 456/2008): (a) dorsal view, (b) lateral view, (c) oral disk.

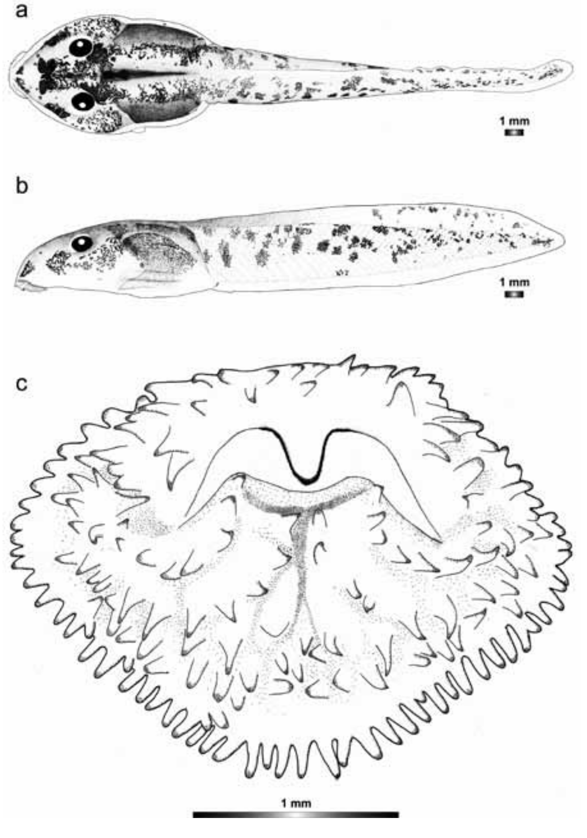

Fig. 17. Drawings of the preserved DNA voucher tadpole of *Mantidactylus mocquardi* (ZCMV 3511-ZSM 1540/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

broadly rounded snout. Moderately large eyes (ED 12% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 35% of BL), moderately wide distance between eyes (IOD 53% of BW). Small rounded nares (ND 1.4% of BL), marked with a marginal rim, positioned dorsally moderately high (NH 59% of BH) and oriented anterodorsolaterally, situated nearer to snout than to eye (RN 67% of NP) and below eye level (NH 81% of EH), wide distance between nares (IND 68% of IOD), reddish region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal, ventral and lateral views; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 68% of BL), located moderately high on the body (SH 42% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 70% of HAB). Short dextral vent tube (VL 9% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 185% of BL), maximal tail height equal to body height (MTH 102% of BH), tail height at midtail lower than body height, but equal to maximal tail height (THM 91% of BH and 99% of MTH), tail height at the beginning of the tail lower than body height (TH 91% of BH). Developed caudal musculature (TMW 51% of BW, TMH 74% of BH, TMH of 81% of TH and 73% of MTH, TMHM 60% of THM and 60% of MTH). Tail muscle reaches tail tip. Very low fins (DF 41% of TMHM, VF 25% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 161% of VF). Dorsal fin originates on the proximal 1/3 of the tail, rises suddenly up to its maximal height, then progresses parallel with caudal musculature, then decreases towards the tail tip at the proximal 1/4 of the tail. Ventral fin originates at the ventral terminus of the body, remains almost parallel with tail muscle up to almost tail tip, then decreases. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 42% of TAL), lateral tail vein not visible, myosepta visible on the distal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.

Moderately wide reduced oral disk (ODW 43% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 74. One hundred and four submarginal papillae complete on the lower labium and laterally on upper labium. Moderately long and large elongated papillae with rounded tips on the marginal papillae and pointed tips on the submarginal papillae. Longest marginal papillae measured 0.19 mm and 0.25 mm for submarginal papillae, papillae visible from dorsal view. Keratodonts absent. Partially keratinized jaw sheath, only the edge of the medial convexity is weakly brown coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 43% of ODW) with a moderately long narrowly pointed medial convexity (MCL 22% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Broadly light beige-brownish. Brown blotches in deep integumental layers form dark patches principally along the vertebral area and the abdominal region, leaving out laterally a slightly translucent area. Some dark brown patches scattered irregularly on the skin between nares and eyes, between the eyes, on the jugal area, and on the area between the vertebral and the abdominal area. Light brown flecks spread over the dorsum. Reddish region on the back of the nares present. Laterally, jugal area and flank covered by distinct irregular brown blotches that dissipate on the abdominal region and condense to form sparse networks on the jugal region, mainly on the lateral area between nares and eyes and between the eye and the spiracle, and leaving a visible transparent spiracle diverged above the recognizable intestinal coils. Lower part of the flank spotted. Tail musculature beige with distinct irregular brown blotches which group to form irregularly scattered patches. Their density diminishes towards the tail tip. Fins pale, with brown sporadic patches on the dorsal fin, ventral fin not pigment. Ventrally, oral disk, gular and branchial regions beige; venter transparent, intestinal coils well visible and regularly spiral shaped.

Variation. Nine other voucher specimens (ZSM 1539/2007-ZCMV 3510, ZSM 1541/2007-ZCMV 3513, ZSM 1746/2007-ZCMV 3441, ZSM 1761/2007-ZCMV 3457, ZSM 1771/2007-ZCMV 3469, ZSM 1805/2007-ZCMV 3447, ZSM 1813/2007-ZCMV 3509, ZSM 1844/2007-ZCMV 3567, ZSM 1846/2007-ZCMV 3570) and one voucher specimen from Ambohitsara-Tsitola (ZSM 72/2008-ZCMV 4936) assigned to this species from the same locality reveal the identical oral disk configuration and external pigmentation of this species.

Mantidactylus mocquardi (Mahasoa)

A further description of a tadpole assigned to *M. mocquardi* but with some morphological differences refers to one tadpole in developmental stage 27 (field number ZCMV 8094-ZSM 686/2008, BL 13.8 mm, TL 42.6 mm) from Mahasoa forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus mocquardi* (ZCMV 8818) from the same locality, and 99% identical to an adult of *M. mocquardi* from Ambohitsara (accession number FJ559269).

In dorsal view, body elliptical (BW 63% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), narrowly rounded snout. In lateral view, body depressed (BW 136% of BH), maximal body height attained at the distal 1/5 of the body (SBH 81% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 67% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 32% of BL), moderately wide distance between eyes (IOD 54% of BW). Small rounded nares (ND 1.6% of BL), marked with a marginal rim, positioned moderately high (NH 53% of BH) dorsally and oriented anterodorsolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 79% of EH), wide distance between nares (IND 70% of IOD), dark spot on the back of the nares absent, ornamentation absent. Short sinistral spiracle (SL 10% of BL), directed posteriorly, visible from dorsal and ventral views, recognizable from lateral view; inner wall free from body, its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 71% of BL), located moderately high on the body (SH 48% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long dextral vent tube (VL 12% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 209% of BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail equal to body height and to maximal tail height (THM 97% of BH and 100% of MTH), tail height at the beginning of the tail equal to body height (TH 97% of BH). Developed caudal musculature (TMW 56% of BW, TMH 78% of BH, TMH of 80% of TH and 71% of MTH, TMHM 54% of THM and 54% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 34% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 154% of VF). Dorsal fin originates at the proximal 1/5 of the tail, rises progressively up to its maximal height and then declines towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains almost parallel with tail muscle almost up to the tail tip, then decreases. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein not visible, myosepta visible on the proximal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 63% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.

Moderately wide reduced oral disk (ODW 47% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of

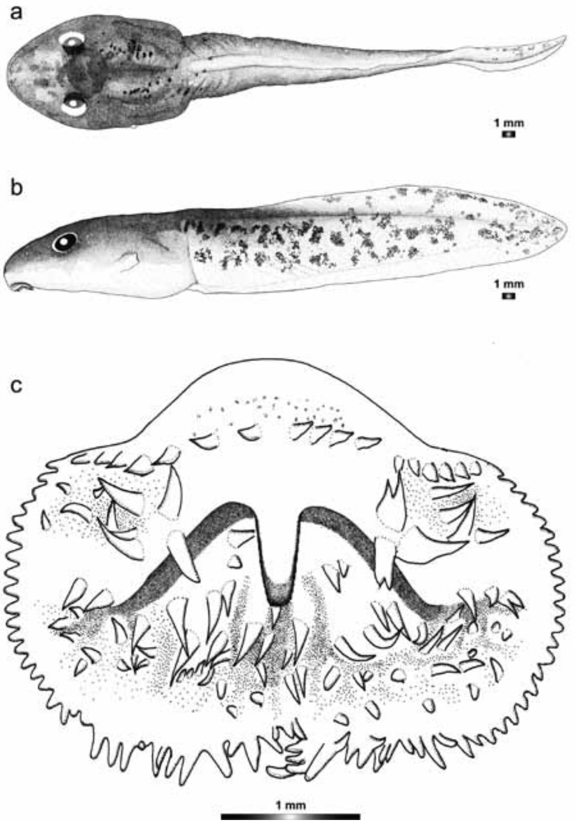

Fig. 18. Drawings of the preserved DNA voucher tadpole of *Mantidactylus mocquardi* from Mahasoa (ZCMV 8094-ZSM 686/2008): (a) dorsal view, (b) lateral view, (c) oral disk.

snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 89. Eighty-eight submarginal papillae complete on the lower labium and laterally on upper labium. Long and large elongated papillae with rounded tips on the marginal and pointed tips on the submarginal papillae, longest marginal papillae measured 0.25 mm and 0.35 mm for submarginal papillae, papillae not visible from dorsal view. Two submarginal papillae on the upper labium beside (left and right) the medial convexity project in the same direction as the medial convexity. Keratodonts absent. Partially keratinized jaw sheath, only the edge of the medial convexity is weakly brown coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 48% of ODW) with a very long narrowly pointed medial convexity (MCL 57% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in preservative. Predominantly pale-brownish. Light pale brown melanophoric pigment covered the dorsum and condensed to form dark patches especially between the eyes, on the vertebral and the abdominal area. Some dark brown patches scattered on the skin. Irregularly shaped clear dots form a line which runs on the dorsolateral part of the abdominal regions, from the body-tail junction to just behind the eyes where it splits, the first ramification passes bellow the eyes and runs through the jugal area, before it diverts laterally on the sagittal plan of the nares. The second ramifications pass above the eyes and approach each other on the sagittal plan of the nares and finish to merge in the snout. Laterally, jugal area and flank covered by speckles leaving an conspicuous flecked spiracle on the pale body wall. Lower part of the flanks unpigmented, intestinal coils laterally not visible. The line formed by irregularly shaped clear dots is visible laterally before the body-tail junction. It runs on the dorsolateral part of the abdominal region and splits just behind the eyes. The first ramification passes below the eyes and ends below the nares. The second ramification passes above the eyes and the nares and terminates on the mid-height of the snout. Tail musculature with irregular brown blotches which group to form irregularly scattered patches. Their density diminishes towards the tail tip. Fins pale, dorsal fin with brown spots which group to form patches, sporadic patches spread around tail tip on ventral fin. Ventrally, oral disk, gular and branchial regions beige with brown spots; venter pale, intestinal coils merge under the abdominals-like structure and regularly spiral shaped.

Variation. Four additional specimens belonging to the same series (but not identified by DNA barcoding) and having the same external morphology as the voucher specimen reveal the identical oral disk configuration and morphological parameters.

Mantidactylus sp. 64
(CCS from Namorona and other sites around Ranomafana)

The following description refers to one tadpole in developmental stage 39 (field number ZCMV 2646-ZSM 401/2008, BL 10. 8 mm, TL 31.9 mm) from the Namorona river in front of Hotel Manja in Ranomafana village. The 16S rDNA sequence of this specimen was 96% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 47 (accession GU975698) from Ambatolahy in the Ranomafana National Park. Since we found morphologically different tadpoles that 100% genetically matched adults of *M.* sp. 47, we conclude that adults of *M.* sp. 64 are so far unknown and the CCS status for this species is based on the distinct morphology of tadpoles that are genetically divergent and occur in sympatry with *M.* sp. 47.

In dorsal view, body elliptical (BW 59% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), narrowly rounded snout. In lateral view, body depressed (BW 136% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 69% of BL), narrowly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 79% of BH) dorsally and directed dorsolaterally, situated between the proximal 2/10 and 3/10 of the body (SE 27% of BL), moderately wide distance between eyes (IOD 64% of BW). Small rounded nares (ND 1.3% of BL), marked with a marginal rim, positioned high (NH 62% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 79% of EH), wide distance between nares (IND 70% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 10% of BL), directed posteriorly, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 71% of BL), located moderately high on the body (SH 54% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB).

Moderately long dextral vent tube (VL 12% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 209% of BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail equal to body height and maximal tail height (THM 97% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 97% of BH). Moderately developed caudal musculature (TMW 56% of BW, TMH 78% of BH, TMH of 72% of TH and 71% of MTH, TMHM 54% of THM and 54% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 34% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 117% of VF). Dorsal fin originates at the proximal 1/10 of the tail, rises gradually to attend its maximal height before mid tail and then progresses horizontally up to the distal 1/5 of the tail, where it decreases. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost up to the tail tip, where it decreases. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 42% of TAL), lateral tail vein not visible, myosepta slightly visible on the proximal 1/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 70% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Moderately wide reduced oral disk (ODW 47% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 81. Eighty-seven submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.11 mm and 0.15 mm for submarginal papillae, papillae not visible from dorsal view. Keratodonts absent. Partially keratinized jaw sheath, edge of the medial convexity weakly brown coloured and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 55% of ODW) with a moderately long widely rounded medial convexity (MCL 21% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Colouration in life. Typically reddish-brown. Body and tail covered by brown blotches which condense and give a dark brown colouration to the tadpole. Golden irridophoric pigments spread over the skin. Dorsolaterally and laterally identical to the dorsal pattern. Rather non-pigmented spiracle perceptible. Tail musculature yellowish with roughly distinct, irregular brown blotches condensed to form networks. Their density extends towards the tail tip. Fins translucent, dorsal fin provided by some dark patches and ventral fin unpigmented. Ventrally, oral disk and gular and branchial reticulated, gills and beating heart perceptible; venter transparent, intestinal coils visible and regularly spiral shaped.

Colouration in preservative. Largely dark. Brown melanophoric pigment covering the skin gave almost uniform dorsal colouration; merged light patches occurred between the eyes, on the vertebral area and on the abdominal region. Sparse dark mottles dispersed mainly on the back of the nares between the eyes and on the dorsum, condensed on the dorsolateral part of the abdomen closed to the body-tail junction to form networks. Perceivable transversal lines occur between the vertebral area and the abdominal region showing noticeable abdominals-like structure. Irregularly

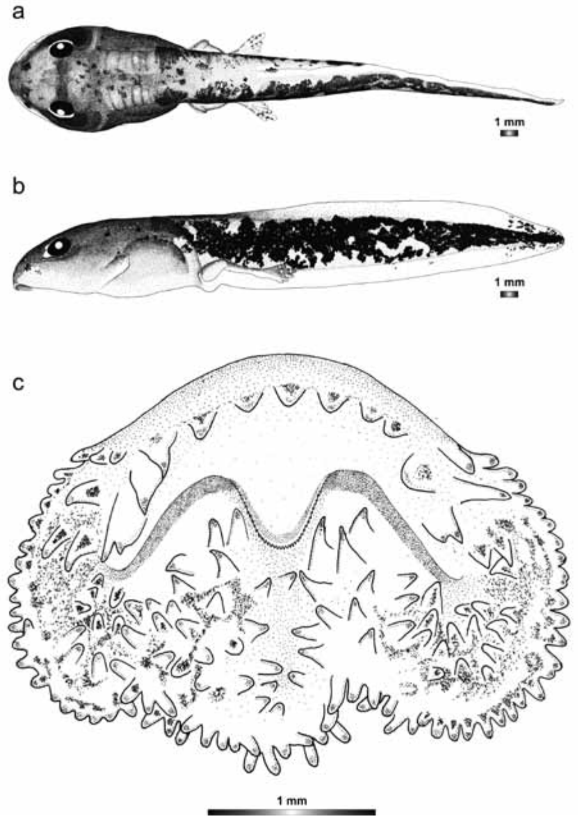

Fig. 19. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 64 (ZCMV 2646-ZSM 401/2008): (a) dorsal view, (b) lateral view, (c) oral disk.

shaped roughly clear dots form a line that runs on the dorsolateral part of the abdominal region, from the body-tail junction to just behind the eyes where it splits, the first ramification passes bellow the eyes and goes through the jugal area, until diverting laterally close to the sagittal plan of the nares. The second ramification passes above the eyes and fades off on the anterior limit of the eyes. Laterally, jugal area and flank covered by dense dark brown melanophoric reticulations leaving a noticeable reticulated spiracle diverged above intestinal coils. Lower part of the flanks unpigmented. The line formed by the irregularly shaped clear dots is conspicuous laterally, before the body-tail junction, runs on the dorsolateral part of the abdominal region and splits just behind the eye, the first ramification passes below the eyes and ends below the nares. The second ramification passes above the eye and fades at the anterior limit of the eye. Tail musculature pale and covered by dark brown reticulations. Their density increases towards the tail tip. Fins pale, with brown reticulations close to the tail tip. First part of dorsal fin mottled. Ventrally, oral disk reticulated, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.

Variation. The picture of one uncatalogued voucher specimen (ZCMV 9291) from Sakaroa in Ranomafana National Park, designated to this species, displays the same external pigmentation. The examination of its oral disk is not possible due to the unavailability of this specimen.

Mantidactylus majori Boulenger, 1896

The following description refers to one tadpole in developmental stage 29 (field number ZCMV 3761-ZSM 1684/2004, BL 11.4 mm, TL 36.9 mm) from the Sahamalaotra stream in the Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus majori* (accession AY848187) from the same locality.

In dorsal view, body elliptical (BW 64% of BL), maximal body width attained almost at midbody (SBW 49% of BL), narrowly rounded snout. In lateral view, body depressed (BW 147% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 68% of BL), broadly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 38% of BL), wide distance between eyes (IOD 66% of BW). Moderately large elliptical nares (ND 2.5% of BL), marked with a marginal rim, positioned high (NH 64% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 81% of EH), moderately wide distance between nares (IND 54% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral view, conspicuous from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 76% of BL), located low on the body (SH 38% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 61% of HAB). Moderately long medial vent tube with lateral displacement (VL 11% of BL), attached to ventral fin. No gland. Short tail (TAL 181% of BL), maximal tail height equal to body height (MTH 101% of BH), tail height at midtail lower than body height and maximal tail height (THM 94% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 88% of BH). Moderately developed caudal musculature (TMW 26% of BW, TMH 70% of BH, TMH of 79% of TH and 69% of MTH, TMHM 56% of THM and 52% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 27% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 195% of VF). Dorsal fin originates at the dorsal body-tail junction, progresses horizontally until the 1/4 of the tail, then ascends abruptly to attain the maximal height before the midtail, progresses more or less horizontally until the 3/4 of the tail, then decreases abruptly towards the tail tip. Ventral fin originates at the ventral terminus of the body, continues parallel with the caudal musculature until midtail, and then decreases continuously towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 41% of TAL), lateral tail vein not visible, myosepta slightly visible on the proximal 3/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Moderately wide highly modified oral disk (ODW 40% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated with the snout by a shallow crevice. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 72. One hundred and thirty-five submarginal papillae complete on the lower labium and upper labium. Very long and very large elongated papillae with pointed tips, longest marginal papillae measured 0.25 mm and 0.41 mm for submarginal papillae, papillae not visible from dorsal view. Keratodonts absent. Moderately wide jaw sheath (JW 54% of ODW), upper jaw sheath transformed into three immense flexible slightly curved thorn-shaped papillae (right 0.56 mm, middle 0.81 mm, left 0.66 mm). A similar papilla is situated laterally to the bases of the two outer papillae. 12 large papillae project from near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath, which is totally hidden by the upper ones.

Colouration in life. Broadly yellowish-orange with brown patches. Brown melanophoric patches in deep integumental layers extended especially between the eyes and on the vertebral region. Dark brown to black melanophoric patches spread sporadically over the skin, golden iridophoric mottles group to form irregular patches mainly on the dorsum. Laterally, body wall overlain by dark patches of melanophores on the jugal region, below the eye and between the eye and the spiracle. Partly reticulated transparent spiracle diverged on the dark abdominal wall. Blotches of iridophores scattered irregularly. Tail musculature orange-yellowish with brown dots forming irregularly scattered patches. Fins translucent, dorsal fin with scattered patches, ventral fin almost unpigmented. Lateral tail vein reddish. Ventrally, oral disk and gular region yellowish; branchial regions reddish, gills and beating heart clearly visible; abdominal surface transparent with golden iridophoric patches, intestinal coils visible and regularly spiral shaped.

Colouration in preservative. Generally beige. Brown patches in deep integumental layers extend between eyes and nares, between the eyes, on the vertebral and abdominal areas, leaving out laterally a slightly transparent area. Light brown flecks cover the dorsal surface and dark brown blotches dissipate irregularly on the dorsal skin. Laterally, jugal area and flank covered by irregular brown blotches that are sparsely spread and that condense to form sparse networks mainly on the lateral area between nares and eyes, and between the eye and the spiracle, leaving out a visible opaque spiracle diverged above the visible intestinal coils. Lower part of the flank not pigmented. Tail musculature orange-yellowish with brown dots consolidated to form irregularly scattered patches. Fins translucent, dorsal fin with scattered patches, ventral fin almost unpigmented. Ventrally, oral disk, gular and branchial regions beige; venter transparent, intestinal coils visible and regularly spiral shaped.

Variation. 32 other voucher specimens (ZSM 42/2007-ZCMV 4155, ZSM 93/2007-ZCMV 4132, ZSM 335/2007-T 172, ZSM 379/2007-ZCMV 4235, ZSM 495/2007-ZCMV 4699, ZSM 502/2007-ZCMV 4517, ZSM 609/2007-T 410, ZSM 682/2007-ZCMV 5391, ZSM 954/2007-ZCMV 5979, ZSM 1062/2007-T 32, ZSM 1063/2007-T 168, ZSM 1078/2007-T 38, ZSM 1285/2007-ZCMV 4417, ZSM 1328/2007-T 156, ZSM 1382/2007-ZCMV 4534, ZSM 1653/2007-ZCMV 3722, ZSM 1676/2007-ZCMV 3749, ZSM 1684/2007-ZCMV 3761, ZSM 1699/2007-ZCMV 3776, ZSM 1700/2007-ZCMV 3777, ZSM 1701/2007-ZCMV 3778, ZSM 171/2008-ZCMV 3806, ZSM 202/2008-ZCMV 3835, ZSM 203/2008-ZCMV 3836, ZSM 229/2008-ZCMV 3627, ZSM 256/2008-ZCMV 3672, ZSM 429/ 2008-ZCMV 2674, ZSM 441/2008-ZCMV 2686, ZSM 447/2008-ZCMV 2694, ZSM

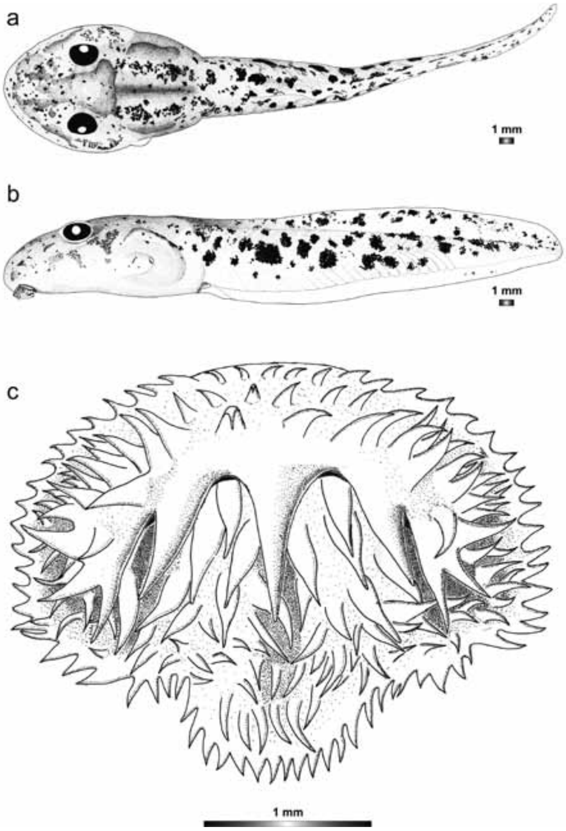

Fig. 20. Drawings of the preserved DNA voucher tadpole of *Mantidactylus majori* (ZCMV 3762-ZSM 1684/2007): (a) dorsal view, (b) lateral view, (c) oral disk.

445/2008-ZCMV 2690, ZSM 455/2008-ZCMV 2698, ZSM 473/2008-ZCMV 3704) from the same locality and one voucher specimen from Vevembe forest (ZSM 1384/2004-TAD 6 Vevembe) attributed to this species reveal the identical oral disk configuration, external pigmentation and other morphological parameters.

Supplementary online material: Morphological descriptions of additional tadpole specimens.