Article

A new species of *Mantidactylus* (subgenus *Chonomantis*) from Ranomafana National Park, eastern Madagascar (Amphibia, Anura, Mantellidae)

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Abstract

We describe a new frog species of *Mantidactylus* belonging to the subgenus *Chonomantis* from Ranomafana National Park, in the Southern Central East region of Madagascar, at mid-elevations (about 950 m above sea level). Specimens of *Mantidactylus paidroa* **sp. nov.** were observed during the day in cavities under large rocks next to a stream in rainforest. Their advertisement calls are unique in *Chonomantis* and consist of a long series of note pairs. The new species shows a high divergence to other *Chonomantis* species in DNA sequences of the mitochondrial 16S rRNA gene (5.6–10.8%). *Mantidactylus paidroa* is so far only known from several streams in Ranomafana National Park but may have been overlooked at other rainforest sites in eastern Madagascar. We propose an IUCN threat status of Data Deficient for this new species.

Key words: Amphibia, Anura, Mantellidae, *Mantidactylus paidroa* sp. nov., Madagascar

Introduction

Frog species in the family Mantellidae form a highly diversified group that is endemic to Madagascar and the Comoro island of Mayotte (Blommers-Schlösser & Blanc 1991, Glaw & Vences 2003). Within this family, the genus *Mantidactylus* is one of the most species-rich groups and is further subdivided into various subgenera. One of these, the subgenus *Chonomantis*, has mainly been defined by tadpole morphology since the larvae of all *Chonomantis* species have characteristically derived funnel-shaped mouthparts. Adults of *Chonomantis* are relatively small, mainly ground-dwelling frogs most of which have a characteristically sharp dorsolateral border between the dark brown lateral and lighter brown dorsal colouration (Vences & Glaw 2004). Many species are furthermore characterized by a frenal stripe, that is, a white stripe running under the eye along the upper lip. Ventrally individuals are usually dark coloured, sometimes with a pattern of white spots or a median white line, especially on the throat. Like all *Mantidactylus*, males have femoral glands with a medial depression, and the size and distinctness of these appear to be species-specific. Species of *Chonomantis* are generally diurnal but also show crepuscular and nocturnal activity, and are mostly found in rainforest habitats close to streams. Males are smaller than females and in most species they have a distinctly larger tympanum. At present, the subgenus is composed of eight species: *Mantidactylus aerumnalis, M. albofrenatus, M. brevipalmatus, M. charlotteae, M. delormei, M. melanopleura, M. opiparis* and *M. zipperi* (Vences & Glaw 2004, Glaw & Vences 2006, 2007).

In this paper we describe a new species of *Chonomantis* that we discovered during a recent field survey in Ranomafana National Park, in mid-elevation rainforest, in the Southern Central East of Madagascar.

Materials and methods

The new species was first discovered by its typical advertisement calls during a general amphibian survey along a transect at a site locally named Ankerana, within Ranomafana National Park. Calls were recorded with the internal

microphone of an Edirol R09 digital recorder at a distance of approximately two meters, and photographs were taken at the collecting site. Collected specimens were fixed in 95% ethanol and preserved in 70% ethanol. Tissue samples were taken from each specimen a few months after collection from the femoral muscles and/or the tongue, and preserved in 99% ethanol. Specimens were numbered using field numbers of the Zoological Collection of Miguel Vences (ZCMV) and are stored in the Zoologische Staatssammlung München, Germany (ZSM). Morphometric measurements were taken by the first author using a digital caliper (TCM 234 990) to the nearest 0.1 mm: Snout-vent length (SVL); maximum head width (HW); head length; (HL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); distance between anterior edge of eye and nostril (END); distance between nostril and tip of snout (NSD); distance between both nostrils (NND); forelimb length, from limb insertion to tip of longest finger (FORL); hand length, to the tip of the longest finger (HAL); hindlimb length from the cloaca to the tip of the longest toe (HIL); tibia length (TIL); foot length including tarsus (FOTL); foot length (FOL). Webbing formula is given according to Blommers-Schlösser (1979).

Call recordings were analyzed using the software Cool Edit Pro 2.0 on a personal computer with Windows XP Professional operating system. Temporal parameters of the calls are reported in milliseconds (ms) as mean ± standard deviation, followed by minimum-maximum values. Environmental or body temperature during call emission were not recorded.

From each tissue sample, DNA was extracted and a fragment of the mitochondrial 16S rRNA gene was amplified and resolved on automated sequencers following standard methods (e.g., Vences *et al.* 2003). Sequences newly obtained for this paper were deposited in Genbank under accession numbers GQ845005–GQ845007. Additional sequences of tadpoles of the new species described herein (from Grosjean *et al.* in press) have the accession numbers GU808450-GU808467. For comparing genetic distances among closely related species, we used DNA sequences of the mitochondrial 16S rRNA gene produced by Vieites *et al.* (2009). These previously obtained sequences had the numbers: *Mantidactylus aerumnalis,* AY848125; *M. albofrenatus,* AY848267; *M. charlotteae,* FJ559236; *M. delormei,* AY848148; *M. melanopleura,* FJ559239, AY848193, and AY848195; *M. opiparis,* FJ559240; *M. zipperi,* FJ559283. For analysis, sequences were aligned using the Clustal algorithm in MEGA (Kumar *et al.* 2004) and the alignment subsequenctly adjusted manually.

Description of a new species

Mantidactylus paidroa sp. nov.
(Fig. 1a–c)

Remarks. This species has been referred to as *Mantidactylus* sp. 59 by Vieites *et al.* (2009) and Grosjean *et al.* (in press).

Holotype. ZSM 1777/2008 (field number ZCMV 7108), adult male (Fig. 1), collected by P. Bora, J. Solo and D. Razafindraibe on 24 January 2008 at a site locally named Ankerana, in Ranomafana National Park, Southern Central East of Madagascar (21°15.582'S, 47°25.320'E), approximately 963 m above sea level.

Paratypes. ZSM 1778/2008 (field number ZCMV 7109, male) and ZSM 1776/2008 (ZCMV 7107, female), same collecting data as holotype.

Diagnosis. Assigned to the genus *Mantidactylus* based on the presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), and of a central depression in femoral glands and presence of a rudimentary femoral gland in the female. Within *Mantidactylus*, assigned to the subgenus *Chonomantis* based on: (a) a specialized funnel-mouth tadpole, (b) a sharp dorsolateral colour border between dorsal and lateral coloration, (c) presence of a frenal stripe, (d) diurnal calling activity close to streams, (e) intersexual difference in tympanum size, (f) relatively small size (male SVL 22 mm).

Mantidactylus paidroa sp. nov is distinguished from all other species in the subgenus *Chonomantis* by presence of serial double notes in advertisement calls (vs. single notes) and a substantial genetic differentiation (see below). In addition, it is distinguished from *Mantidactylus aerumnalis, M. brevipalmatus, M. charlotteae,* and *M. delormei* by a bigger ratio of tympanum/eye diameter in males (1.4–1.5 vs. 0.7–1.3); from *M. aerumnalis, M. charlotteae, M. opiparis, M. melanopleura*, and *M. zipperi* by a lower amount of webbing on fifth toe (2 vs. 0.75–1.5 phalanges free of web); from *M. brevipalmatus* and *M. delormei* by smaller body size (male SVL 22 vs. 28–35

mm) and by shorter hindlimbs (tibiotarsal articulation reaching anterior eye corner vs. reaching beyond snout tip); from *M. opiparis*, *M. melanopleura* and *M. charlotteae* by presence of distinct and rather large femoral glands in males (vs. small glands), from *Mantidactylus aerumnalis* by presence of a frenal stripe between forelimb and eye (vs. absence); from *M. aerumnalis*, *M. opiparis,* and *M. zipperi* by a well-delimited narrow extension of the frenal

FIGURE 1. (a), (b) and (c), Photographs of male holotype of *Mantidactylus paidroa* (ZSM 1777/2008) in life (SVL 22.3 mm), in dorsolateral and ventral views.

stripe (bending upwards) between eye and nostril (vs. absence), and from *M. aerumnalis, M. melanopleura* and *M. opiparis* by having the third toe longer than the fifth (vs. fifth toe longer than third). *Mantidactylus paidroa* is morphologically most similar to *M. albofrenatus* from which it can be mainly distinguished by the throat colouration, which has a continuous median white line (vs. a row of spots in *M. albofrenatus*). Tadpoles of *M. paidroa* differ from those of all other *Chonomantis* by the presence of very few keratodonts on the upper labium of the oral disk (vs. complete absence; see Grosjean *et al.* in press). Table 1 includes a comparison of diagnostic characters in *Chonomantis* species.

TABLE 1. Morphometric ratios and distinctive morphological and bioacoustic characters in *Mantidactylus paidroa* sp. nov. compared with other species of *Chonomantis,* based on data published by Vences & Glaw (2004). Abbreviations used: SVL, snout-vent length; TD, tympanum diameter; ED, eye diameter; FOL, foot length; HAL, hand length; RHL, relative hindlimb length; TT, tibiotarsal articulation. Measurement values are mean ± standard deviation, followed by minimum–maximum values in parentheses. Data for *M. delormei* are based on the female holotype and photos of additional specimens in Glaw & Vences (2007) for colour in life.

	M. paidroa sp. nov.	*M. aerumnalis*	*M. albofrenatus*	*M. brevipalmatus*	*M. charlotteae*	*M. delormei*	*M. melanopleura*	*M. opiparis*	*M. zipperi*
SVL males (mm)	22.0–22.3	22.8–26.6	19.3–23.0	27.6–35.3	22.4–26.2	--	29.9–39.5	23.8–26.1	21.5–23.4
SVL females (mm)	27.0	28.3–31.0	25.3–27.1	34.8–44.9	26.3–32.2	38.9	32.3–40.5	27.0–33.2	29.5
TD/ED ratio males	1.45 (1.4–1.5)	0.77 ± 0.08 (0.67–0.87)	1.27 ± 0.10 (1.10–1.38)	1.17 ± 0.08 (1.05–1.31)	0.92 ± 0.13 (0.70–1.13)	--	1.24 ± 0.16 (0.93–1.47)	1.34 ± 0.14 (1.20–1.50)	1.24 ± 0.16 (1.03–1.44)
TD/ED ratio females	1.04	0.68 ± 0.05 (0.61–0.74)	0.73–0.74	0.82 ± 0.07 (0.70–091)	0.75 ± 0.08 (0.62–0.84)	0.66	0.80 ± 0.03 (0.76–0.85)	0.81 ± 0.09 (0.62–0.91)	0.79
FOL/SVL ratio	0.48 (0.46–0.49)	0.56 ± 0.03 (0.51–0.60)	0.51 ± 0.05 (0.46–0.63)	0.66 ± 0.04 (0.60–0.71)	0.49 ± 0.03 (0.45–0.56)	0.64	0.54 ± 0.06 (0.51–0.80)	0.54 ± 0.04 (0.49–0.62)	0.52 ± 0.03 (0.47–0.55)
HAL/SVL ratio	0.28 (0.26–0.29)	0.29 ± 0.01 (0.27–0.32)	0.29 ± 0.02 (0.27–0.31)	0.30 ± 0.02 (0.27–0.32)	0.29 ± 0.01 (0.27–0.33)	0.30	0.27 ± 0.01 (0.25–0.31)	0.29 ± 0.02 (0.25–0.32)	0.30 ± 0.02 (0.27–0.33)
RHL of most specimens	TT reaches at most nostril	TT reaches snout tip or beyond	TT reaches at most nostril	TT reaches beyond snout tip	TT reaches at most nostril	--	TT reaches beyond snout tip	TT reaches snout tip or beyond	TT does not reach snout tip
Webbing of toe 5	2	0.75–1	1.5–2	2	1.25	--	1	1	1.5
Femoral glands in males	large, prominent	large, prominent	large, prominent	large, very prominent	small to large, not very prominent	--	small, indistinct	small, indistinct	large, not very prominent
Frenal stripe between forelimb and eye	present	absent	present	present	present	present	present	present	present
Frenal stripe between eye and nostril	present, reaches close to nostril	absent	present, reaches nostril or close to it	present, reaches close to nostril	usually stops anterior to the eye	slightly fading anterior to eye	present, reaches nostril or close to it	fades anterior to eye	fades anterior to eye
Throat coloration	black or dark brown, with a median line and spots	black with a distinct white stripe which is continued onto the venter	grey with large white spots forming a median row	light with indistinct, weak darker marbling	black, with small white spots which form a median row, sometimes fusing to a median stripe	light	black or dark brown, with a median line or row of spots	black or dark brown, with a median line or row of spots	light grey–yellowish, with a rather broad light median stripe which begins as distinct white spot close to the lip

TABLE 1 (continued)

	M. paidroa sp. nov.	M. aerumnalis	M. albofrenatus	M. brevipalmatus	M. charlotteae	M. delormei	M. melanopleura	M. opiparis	M. zipperi
Duration of single notes in advertisement calls (ms)	8–14	unknown	56–80	9–21	91–304	unknown	19–54	69–126	21–31
Duration of double notes in advertisement calls (ms)	12–16	unknown	absent	absent	absent	unknown	absent	absent	absent
Relative toe length	5<3	5=3	5<3	5>3	5<3	5>3	5>3	5>3	5<3

Etymology. The specific name—paidroa—refers to the typical advertisement call of the species, and derives from Malagasy words paika (meaning notes) and roa (double or two) (according to Malagasy grammar, the ending —ka is replaced by —d in the composite word). The name is used as an invariable noun in apposition.

Description of the holotype. SVL 22.3 mm. Body relatively slender; head longer than wide, of same width as body; snout rounded in dorsal view, slightly pointed in lateral view; nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye; canthus rostralis rather indistinct, straight; loreal region concave; tympanum distinct, oval, wider horizontally than vertically, its horizontal diameter 143% of eye diameter; supratympanic fold indistinct; tongue absent, taken for tissue sampling; vomerine teeth distinct, one rounded aggregation on each side of buccal roof, positioned posteromedian to choana; choanae small, rounded. Arms slender, subarticular tubercles distinct, single; inner metacarpal tubercle distinct and ovoid, outer metacarpal tubercle dinstinct but smaller and rounded; fingers without webbing; comparative finger length 1<2<4<3, second finger distinctly shorter than fourth finger; finger disks slightly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches the anterior eye corner; lateral metatarsalia not connected; comparative toe length 1<2<5<3<4; third toe slightly longer than fifth toe; inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable; webbing between toes weakly expressed, formula 1 (1), 2i (>>1), 2e (1), 3i (2.25), 3e (2), 4i (3.5), 4e (3.25), 5 (2). Exact extension of web on 2i cannot be determined more in detail because only one subarticular tubercle is recognizable. Dorsal skin smooth; dorsum with distinct dorsolateral folds; ventral skin smooth, slightly granular in the cloacal region; no distinct tubercles in the cloacal region. Femoral glands large and distinct (length 5.0, width 3.5 mm, distance between internal borders of glands on opposite thighs 0.7 mm (almost in contact in the cloacal region), of type 3 with central depression as defined by Glaw *et al.* (2000).

Colour of the holotype. Colour in life (Fig. 1a–c) is dorsally light brown with irregular black blotches, with a conspicuous dorsolateral bold black border that separates the dorsum from the dark brown flanks, which have a few irregular bronze and white spots. From the insertion of forelimbs there is a white frenal stripe running under the tympanum and the eye, bending upward anterior to the eye and reaching the nostril. In the area between upper lip and nostril there are small bronze to light brown flecks. The iris is light brown in its upper and lower parts, with reddish brown colour in its anterior and posterior parts. The hindlimbs are light brown with dark brown transversal stripes. The ventral side is dark brown on the throat and greyish on the venter, with rounded white spots and a discontinuous median narrow white stripe running from the snout tip to the venter. The limbs are ventrally blackish with dark grey blotches. After two years in preservative, the colour tones are much less contrasted and especially the white and bronze elements have partly faded to dirty grey.

Variation. The male paratype is morphologically similar to the holotype. The female paratype, in contrast, in preservative has a much lighter dorsal and ventral colouration with only indistinct white ventral spots and an indistinct white midventral line. The female has rudimentary femoral glands.

Measurements. All given in mm. The first value refers to the holotype, the second and third values (in parentheses, male and female) to the paratypes. SVL 22.3 (22.0; 27.0), HW 7.3 (7.4; 8.0), HL 9.5 (9.0; 10.0), TD 3.3 (3.3; 2.4), ED 2.3 (2.2; 2.3), END 2.4 (2.2; 2.4), NSD 1.7 (1.7; 1.8), NND 3.0 (3.3; 3.3), FORL 14.3 (13.3; 16.0), HAL 6.2 (6.3; 7.0), HIL 35.0 (36.0; 41.5), FOTL 15.5 (16.0; 18.3), FOL 10.7 (10.8; 12.5), TIL 11.1 (11.1; 13.0).
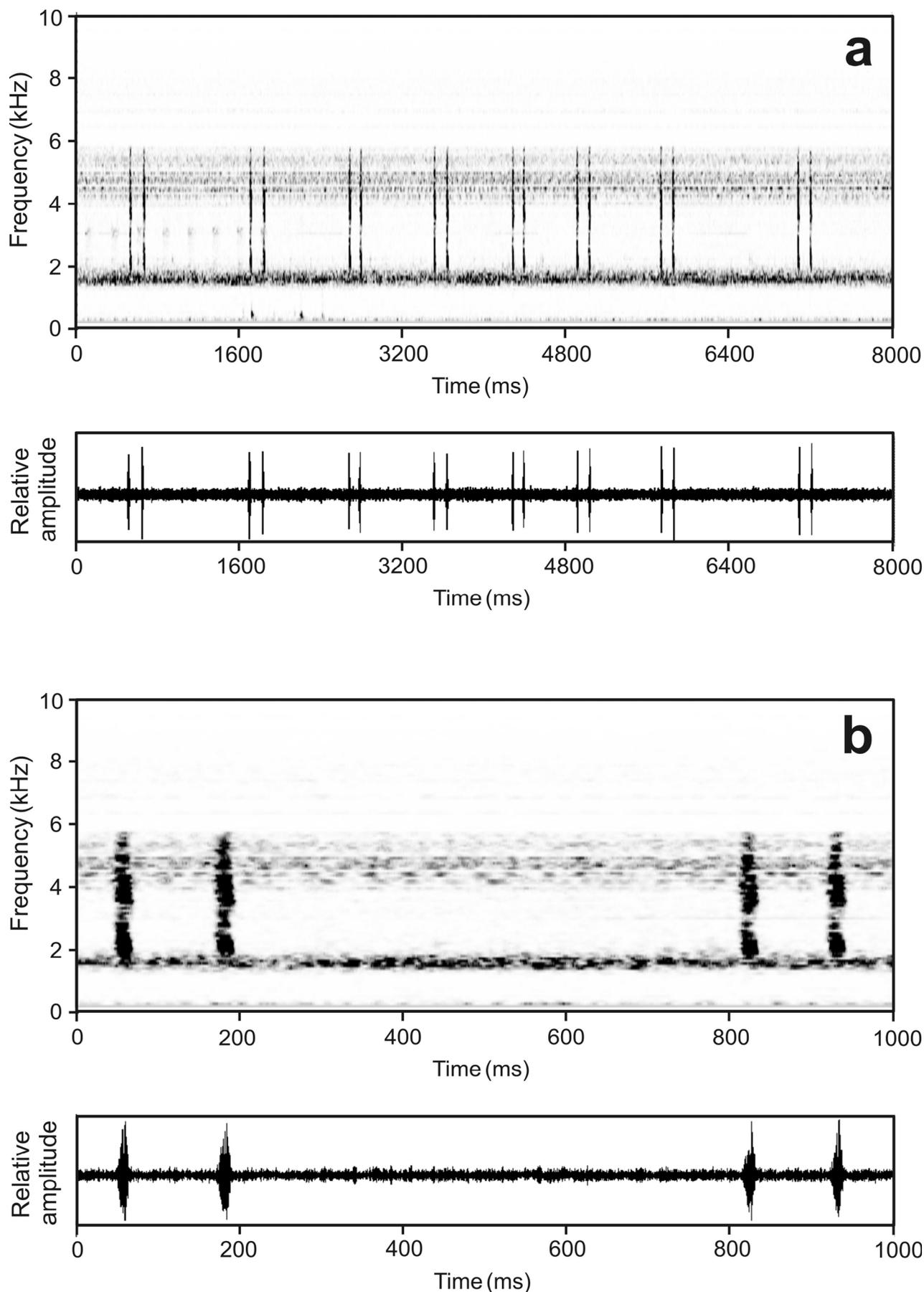
FIGURE 2. Sonagrams and oscillograms of parts of a series of double notes, recorded from the holotype of *Mantidactylus paidroa* on 24 January 2008; (a) fragment of the call with 8 double notes; (b) enlarged view of two double notes.

Natural History. Calls of *Mantidactylus paidroa* were heard only at the type locality, Ankerana, in Ranomafana National Park, which is also the only locality where adults were collected. Other syntopic anurans at this site included two *Chonomantis* species (*Mantidactylus opiparis*, *M. melanopleura*) as well as *Mantidactylus biporus*, *Gephyromantis asper*, *G. tschenki*, and *Stumpffia* sp.

The type locality is characterized by the presence of various rocks of different size along a small, slow-running stream in rainforest. Specimens were found in humid sites under big rocks. Calls were emitted by the holotype during the day, on 24 January 2008 between 13:30–15:30. The two paratypes were collected close to the holotype. The female was found next to a rock under which the second male was calling, at about 5 m distance from the collecting site of the holotype.

The tadpole of *M. paidroa* is described in detail in Grosjean *et al.* (in press). It is of the funnel-mouthed type typical for *Chonomantis,* but as a character state unique in the subgenus, it has rudimentary labial teeth (keratodonts).

Advertisement calls. The call of *Mantidactylus paidroa* consists of a series of pulsatile note pairs (Fig. 2). One completely recorded series had a duration of 47 seconds. At the beginning of the series, five single notes were emitted, followed by 33 note pairs, with a single note emitted in one case in-between two note pairs. Call frequency ranged from 1500–5900 Hz. Temporal call parameters are as follows: note length of single notes 8–14 ms (10.6±10.6 ms; n= 5); note length of first note in note pairs 12–14 ms (12.6±0.8 ms; n=11); note length of second note in note pairs 12–16 ms (13.4±1.1 ms; n=11); interval between single notes 908–1915 ms (1218.5±468.2 ms; n=4); interval between notes in note pairs 100–135 ms (116±8.6 ms; n=11); interval between note pairs 479–1471 ms (980.7±368.7 ms; n=11). For comparison of some call characters with other species in the subgenus see Table 1.

Genetic divergence. In the alignment of 458 nucleotides of the 16S rRNA gene (after deleting portions at the beginning and the end of the DNA fragment that were missing in some taxa), the male paratype of *Mantidactylus paidroa* differed by a single substitution from the holotype and female paratype, which had identical sequences. The new species was strongly differentiated from all other species of *Chonomantis* (sequences as reported by Vieites *et al.* 2009). We found 24–46 substitutions in pairwise comparisons to all other species, corresponding to 5.6–10.8% uncorrected pairwise sequence divergence (p-distances). The lowest distances (24–25 substitutions; 5.6–5.8% divergence) were found to *Mantidactylus brevipalmatus.* For a preliminary phylogenetic analysis of the 16S sequences that however could not satisfyingly resolve relationships among species of *Chonomantis*, see supplementary information of Vieites *et al.* (2009) where the species is included as *Mantidactylus* sp. 59.

Discussion

In general, diversity of Malagasy frogs is concentrated along the eastern rainforest band of the island. The highest species richness is in the latitudinal center of this band (Lees *et al.* 1999). However, localities in the Southern Central East and to a lesser degree in the South East, also have a high species diversity, with 116 species of amphibians currently known from Ranomafana National Park and its surroundings (Vieites *et al.* 2009), at least 57 species known from Andringitra National Park (Raxworthy & Nussbaum 1996), 30 species from Befotaka-Midongy National Park (Bora *et al.* 2007) and 45 species from Andohahela National Park (Nussbaum *et al.* 1999). The new species described here highlights the existence of undescribed diversity and possible local endemics in this part of Madagascar's rainforests.

Field identification of species in the subgenus *Chonomantis* is mostly based on subtle morphological characters. Nonetheless, some qualitative characters or combination of them, as general body shape, presence of a sharp dorsolateral colour border, presence and shape of femoral glands, and frenal stripe, are especially useful to distinguish species belonging to this subgenus. At first glance a confusion is however possible with some species of *Blommersia, Gephyromantis,* and especially *Mantella* which can present a superficially similar colour pattern (Glaw & Vences 2007). At the present state of knowledge, however, an upward curved frenal stripe as found in several *Chonomantis*, including *Mantidactylus paidroa*, is a unique and diagnostic character state for this subgenus.

Ankerana in Ranomafana National Park is to our knowledge the only site where adults of this new species have been collected. In fact, a recent tadpole survey in over 30 streams in this reserve (see Grosjean *et al.* in press) has led to the discovery of *M. paidroa* tadpoles in several additional streams (at sites locally named Ambatolahy, Ambodiamontana, Bibiango, Fomponina and Vatoharanana; see Fig. 3). This indicates that *M. paidroa* is a secretive species of which adults are difficult to observe. It therefore cannot be excluded that this species also occurs

outside Ranomafana National Park and that it has a much wider distribution. Given the general need for a taxonomic revision of species superficially similar to *M. charlotteae, M. albofrenatus,* and *M. paidroa,* which include multiple undescribed candidate species (see Vieites *et al.* 2009) we consider the IUCN conservation status of *Mantidactylus paidroa* as Data Deficient.
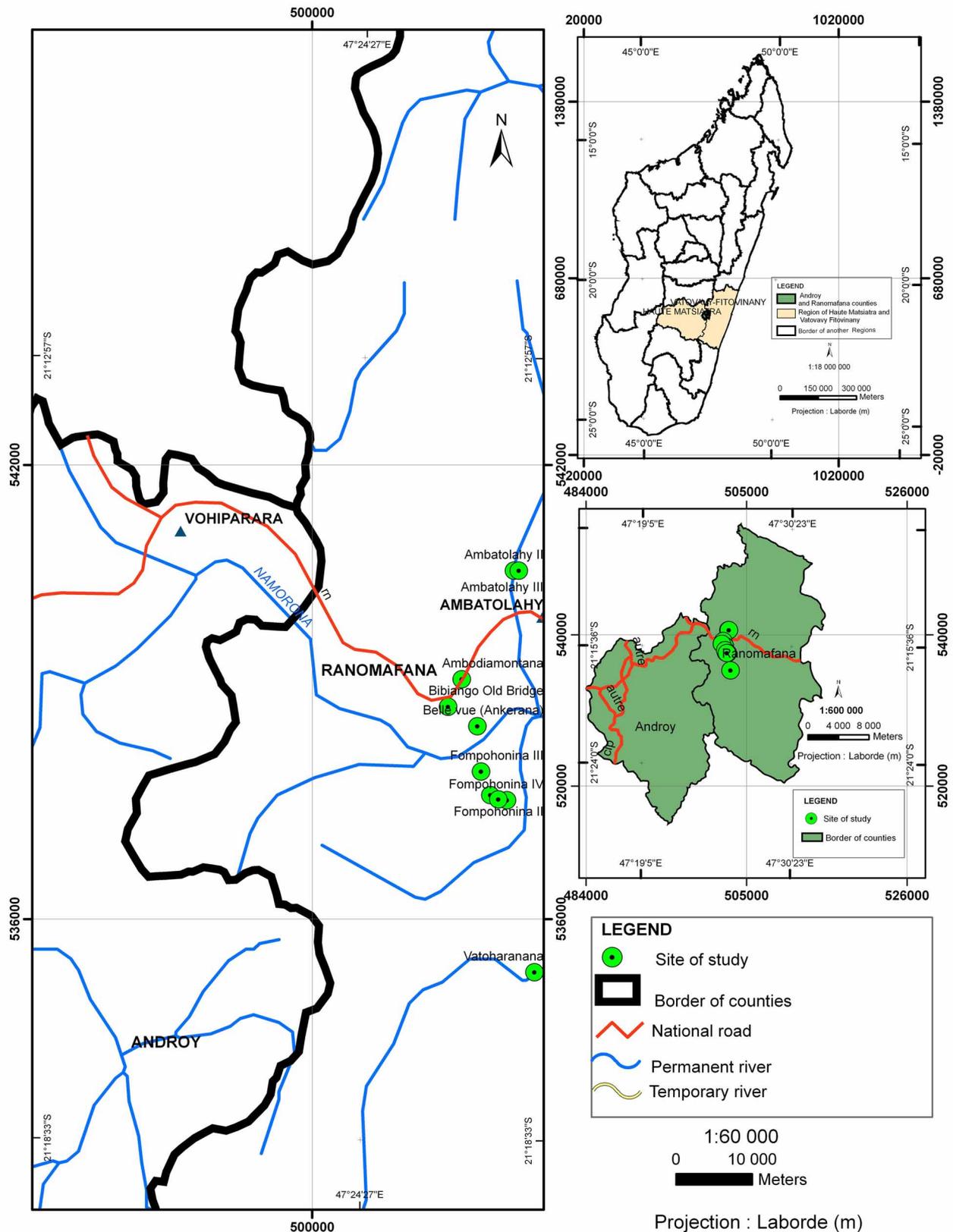

FIGURE 3. Map of known distribution records of *Mantidactylus paidroa* in Ranomafana National Park.

Acknowledgements

References

Blommers-Schlösser, R.M.A. (1979) Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae). *Beaufortia*, 29, 1–77.

Blommers-Schlösser R.M.A. & Blanc C.P. (1991) Amphibiens (première partie). *Faune de Madagascar*, 75 (part 1), 1–379.

Bora, P., Randriambahiniarime, M.O., Rabemananjara, F.C., Ramilijaona, O.R., Glaw, F. & Vences, M. (2007) A rapid assessment survey of the herpetofauna at Befotaka-Midongy National Park, south-eastern Madagascar. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 83, 170–178.

Glaw, F. & Vences, M. (2003) Introduction to amphibians. *In:* Goodman, S. M. & Benstead, J. P. (Eds): *The Natural History of Madagascar. University of Chicago Press*, Chicago, pp. 883–898.

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

Glaw, F. & Vences, M. (2007) A *Field Guide to the Amphibians and Reptiles of Madagascar*. 3rd edition. Cologne, Vences & Glaw Verlag.

Glaw, F., Vences, M. & Gossmann, V. (2000) A new species of *Mantidactylus* from Madagascar, with a comparative survey of internal femoral gland structure in the genus (Amphibia: Ranidae: Mantellinae). *Journal of Natural History,* 34, 1135–1154.

Grosjean, S., Strauß, A., Glos, J., Randrianiaina, R.D., Ohler, A. & Vences, M. (in press) Morphological and ecological uniformity in the funnel-mouthed tadpoles of Malagasy litter frogs, subgenus *Chonomantis. Zoological Journal of the Linnean Society.*

Kumar, S., Tamura, K. & Nei, M. (2004) MEGA3: integrated software for molecular evolutionary genetic analysis and sequence alignment. *Briefings in Bioinformatics,* 5, 150–163.

Lees, D.C., Kremen, C. & Andriamampianina, L. (1999) A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biological Journal of the Linnean Society*, 67, 529–584.

Nussbaum, R.A., Raxworthy, C.J., Raselimanana, A.P. & Ramanamanjato, J.B. (1999) Amphibians and reptiles of the Réserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zoology (new series)*, 94, 155–173.

Raxworthy, C.J. & Nussbaum R.A. (1996) Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: A study of elevational distribution and local endemicity. *Fieldiana Zoology (new series),* 85, 158–170.

Vences, M. & Glaw, F. (2004) Revision of the subgenus *Chonomantis* (Anura: Mantellidae: *Mantidactylus*) from Madagascar, with description of two new species. *Journal of Natural History*, 38, 77–118.

Vences, M., Kosuch, J., Glaw, F., Böhme, W. & Veith, M. (2003) Molecular phylogeny of hyperoliid treefrogs: biogeographic origin of Malagasy and Seychellean taxa and re-analysis of familial paraphyly. *Journal of Zoological Systematics and Evolutionary Research,* 41, 205–215.

Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the U.S.A.,* 106, 8267–8272.