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New Dwarf Species of *Mantidactylus* from Northwestern Madagascar (Anura: Mantellidae)

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A new frog species of the genus *Mantidactylus* is described from the lowland areas of northwestern Madagascar known as the Sambirano Region. *Mantidactylus madinika* reaches 11–13 mm snout–vent length in males and 15–16 mm in females and is thereby the smallest species in the family Mantellidae. It is included in the subgenus *Blommersia* based on external morphology but differs from other species of the subgenus by its relative finger length. Several features of the new species (only slightly bifid tongue, absence of vomerine teeth, reduction of maxillary teeth, absence of dark pigment on oocytes) are similar to the states observed in the genus *Mantella*, which is known to be phylogenetically nested within the paraphyletic *Mantidactylus*. Miniaturization in the ancestor of *Mantella* may explain several of the derived character states in this genus.

MINIATURIZATION of body size is a widespread phenomenon in animals (Hanken and Wake, 1993). In frogs, it evolved several times convergently in tropical environments (Clarke, 1996; Estrada and Hedges, 1996). Dwarf species use different resources than their normal-sized relatives (e.g., Simon and Toft, 1991). By avoiding competition, miniaturization may therefore be one mechanism that enhances species diversity in amphibian communities (Clarke, 1996). Among the many new anuran species described from Madagascar in the last decade (Glaw and Vences, 2000), a relatively large number are of small size. The microhylid *Stumpffia pygmaea*, described in 1991, is among the smallest frogs in the world, with an adult snout–vent length (SVL) of 10–12 mm. Its juveniles hold the record (< 3 mm SVL) as smallest metamorphosed frogs worldwide (Glaw and Vences, 1994), although this may be challenged when juveniles of other diminutive frog species become known (Estrada and Hedges, 1996). Several other recently discovered species do not reach 20 mm SVL: *Stumpffia tetradactyla*, *Stumpffia gimmeli*, *Mantidactylus kely*, *Mantidactylus sarotra* (Glaw and Vences, 1994, 2002). All these species are common at relatively well-sampled localities, suggesting that they simply had been overlooked or mistaken for juveniles of other species by previous workers.

Mantidactylus is the most diverse anuran genus from Madagascar, currently containing about 70 nominal species (Vences and Glaw, 2001). It is paraphyletic (Richards et al., 2000), indicating that its partition will be necessary once its intrageneric phylogeny is sufficiently well understood. At present, it is divided into 12 subgenera (Glaw and Vences, 1994). The largest species are assigned to the subgenus *Mantidactylus*: *Mantidactylus guttulatus* can attain 120 mm SVL (Blommers-Schlösser and Blanc, 1991). In contrast, the smallest forms are included in the subgenus *Blommersia*. This subgenus contains *Mantidactylus argenteus*, *M. guibei*, and *Mantidactylus bertini* and the phenetic *Mantidactylus domerguei* species group, with *Mantidactylus blommersae*, *Mantidactylus domerguei*, *Mantidactylus grandisonae*, *M. kely*, *M. sarotra*, and *Mantidactylus wittei*. The smallest species, ranging from 14–21 mm SVL, are *M. kely*, *M. domerguei*, *M. sarotra*, and *M. blommersae*, which all live in mid- to high-altitude areas (700–2000 m above sea level) in central-eastern Madagascar (Glaw and Vences, 1994, 2002).

During recent fieldwork, we discovered a new dwarf species of *Mantidactylus* (*Blommersia*) from the northwestern lowlands of Madagascar. This species, which will be described herein, is characterized by a male SVL of 11–13 mm and is therefore the smallest known representative of the family Mantellidae (sensu Vences and Glaw, 2001), which currently contains 131 nominal species.

MATERIALS AND METHODS

Frogs were collected by opportunistic searching of the ground. The frogs were sacrificed using chlorobutanol, fixed in 5% formalin or 90% ethanol, and preserved in 70% ethanol. Vouchers were deposited in the herpetological collections of the Museo Regionale di Scienze Naturali, Torino (MRSN), the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK), and the Zoologische Staatssammlung München (ZSM).

Morphological measurements were taken with a caliper to the nearest 0.1 mm by the first

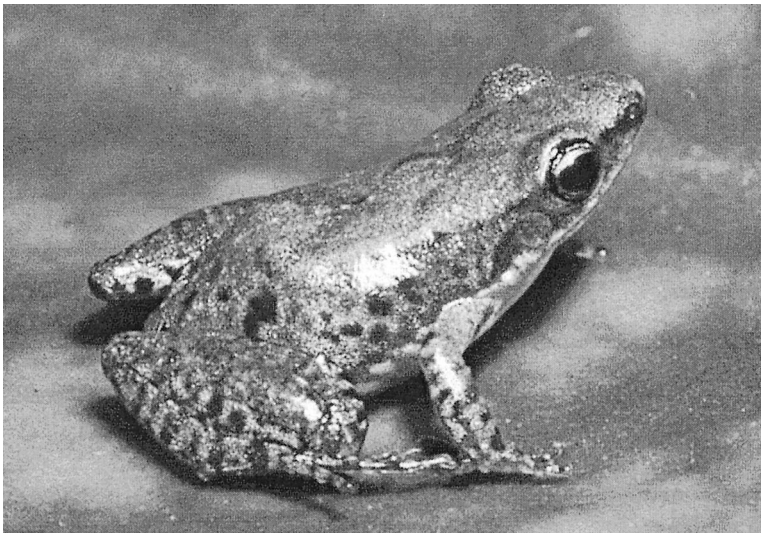

Fig. 1. Male holotype (ZSM 601/2001) of *Mantidactylus madinika*.

author. These measurements were SVL (snout–vent length), HW (maximum head width), HL (head length, from the maxillary commissure to the snout tip), ED (horizontal eye diameter), END (eye–nostril distance, from the anterior corner of the eye to the center of the nostril), NSD (nostril–snout tip distance, from the center of the nostril to the snout tip), NND (distance between centers of nostrils), TD (horizontal tympanum diameter), HAL (hand length, from the carpal-metacarpal articulations to the tip of the longest finger), FORL (forelimb length, from the axil to the tip of the longest finger), HIL (hind-limb length, from the cloaca to the tip of the longest toe), FOL (foot length, from the tarsal-metatarsal articulations to the tip of the longest toe), FOTL (foot length including tarsus, from the tibiotarsal articulation to the tip of the longest toe).

Each measurement is given as a range, with mean ± standard deviation and number of measured units in parentheses.

Mantidactylus madinika sp. nov.
Figures 1–3

Holotype.—ZSM 601/2001, adult male, collected by M. Vences, F. Andreone, F. Mattioli and J. E. Randrianirina on 30 January 2001, in a plantation at the edge of the Sambirano river, approximately 200 m upstream from Antsirasira (on the river side opposite to the larger village of Marovato), Marovato Fivondronana, Antsiranana Faritany (Diégo Suarez Province), northwestern Madagascar (13°56′22″S, 48°33′16″E, less than 100 m above sea level; Figs. 1–2).

Paratypes.—MRSN A2066 and ZSM 600/2001 (Fig. 3), two adult females, same locality and collecting data as holotype; ZFMK 76103 and ZSM 603/2001–607/2001, five adult males and

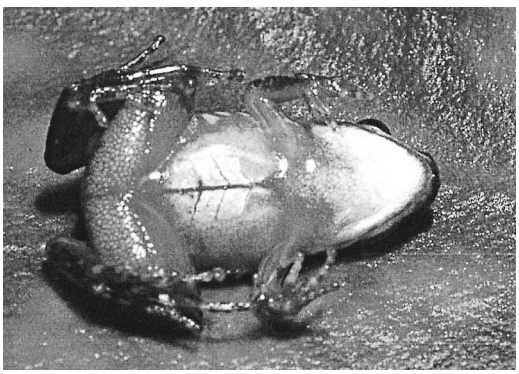

Fig. 2. Ventral view of male holotype (ZSM 601/2001) of *Mantidactylus madinika*.

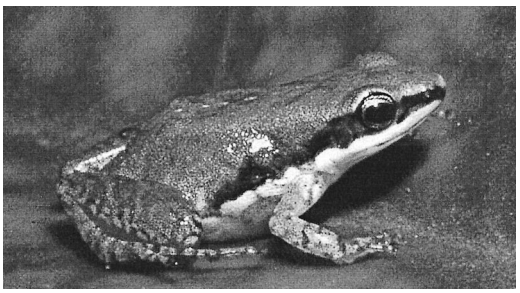

Fig. 3. Female paratype (ZSM 600/2001) of *Mantidactylus madinika*.

one adult female, collected by M. Vences on 12 February 2001 at the type locality.

Diagnosis.—A member of *Mantidactylus* based on absence of nuptial pads and presence of distinct femoral glands in males. Assigned to the *M. domerguei* group in the subgenus *Blommersia* based on (1) small size (SVL < 20 mm), (2) white single subgular vocal sac, (3) patchlike femoral glands in males (absent in females), intermediate between type 1 and 2 (Glaw et al., 2000a), (4) short relative hand length (21–27% of SVL), (5) relatively small tympanum diameter (< 80% of eye diameter) without sexual dimorphism. From the six other known representatives of the *M. domerguei* group (see Glaw and Vences, 1994, 2002), it is distinguished as follows: (1) from *M. wittei* by completely connected lateral metatarsalia (vs separated), presence of a white frenal stripe continued onto the flanks (vs absence), small body size (SVL of males 11–13 mm vs 22–25 mm), short fourth finger (not longer than second finger vs distinctly longer than second finger), absence of webbing between toes (vs presence) and absence of vomerine teeth (vs presence); (2) from *M. grandisonae* by completely connected lateral metatarsalia (vs separated), small body size (SVL of males 11–13 mm vs 18–23 mm); a silvery white throat (vs yellowish), absence of webbing between toes (vs presence), and a short fourth finger (not longer than second finger vs distinctly longer than second finger); (3) from *M. kely* by presence of a white frenal stripe continued onto the flanks (vs absence), smaller body size (SVL of males 11–13 mm vs 14–16 mm), absence of a yellowish middorsal stripe (vs presence), smooth dorsal skin (vs granular), and a short fourth finger (not longer than second finger vs distinctly longer than second finger); (4) from *M. domerguei* by presence of a white frenal stripe continued onto the flanks (vs absence), smaller body size (SVL of males 11–13 mm vs 15–17 mm) , a silvery white throat (vs not white), absence of longitudinal dark markings on the dorsum (vs presence), and a short fourth finger (not longer than second finger vs distinctly longer than second finger); (5) from *M. blommersae* by presence of a white frenal stripe continued onto the flanks (vs absence), absence of webbing between toes (vs presence), smaller body size (SVL of males 11–13 mm vs 18–21 mm), a silvery white throat (vs not white), and a short fourth finger (not longer than second finger vs distinctly longer than second finger); (6) from *M. sarotra* by complete absence of webbing between toes (vs presence of rudiments), smaller body size (SVL of males 11–13 mm vs 15–17 mm), and a short fourth finger (not longer than second finger vs distinctly longer than second finger).

Description of the holotype.—Specimen in good state of preservation. Part of right tibia removed as tissue sample for genetic analysis. SVL 11.9 mm. For measurements, see Table 1. Body slender; head distinctly longer than wide, not wider than body; snout slightly rounded in dorsal and lateral views, nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, straight; loreal region straight; tympanum distinct, rounded, 67% of eye diameter; supratympanic fold indistinct; tongue ovoid, slightly notched posteriorly but not bifid; vomerine teeth absent, maxillary teeth rudimentary; choanae rounded. Arms slender, distinct single subarticular tubercles; inner and outer metacarpal tubercles distinct; fingers without webbing; relative length of fingers 1<4<2<3, fourth finger slightly shorter than second finger; finger disks slightly enlarged; nuptial pads absent. Hind limbs relatively robust; tibiotarsal articulation reaches center of eye when the hind limb is adpressed along the body; lateral metatarsalia connected; inner metatarsal tubercle small, outer metatarsal tubercle indistinct; webbing between toes absent; relative length of toes 1<2<5<3<4. Skin on the dorsal surface smooth, without folds or ridges. No distinct enlarged tubercles in the cloacal region; ventral skin uniformly smooth. Femoral glands distinct in life but not easily recognizable in alcohol.

Coloration of the holotype (Figs. 1–2).—In life, the dorsum was light brown, with a distinct border toward the grayish brown flanks. A grayish X-shaped marking was present on the anterior portion of the dorsum, and an inversed V-shaped marking on the posterior portion of the dorsum. The head was brown laterally with an indistinct whitish frenal stripe running toward the insertion of the forelimb. On the flanks, the color became lighter toward the inguinal region, and several well-delimited black spots were present. A pair of larger blackish spots was also present on the posterior portion of the dorsum close to the inguinal region. The limbs were light brown dorsally, with dark marbling and indistinct dark crossbands. The iris was light brown in its upper half and dark brown in its lower half. The ventral skin was translucent, but the belly appeared silvery because of subcutaneous pigment. The throat was silvery white.

After about five months in preservative, the

TABLE 1. MORPHOMETRIC MEASUREMENTS (ALL IN MILLIMETERS) OF HOLOTYPE AND PARATYPES OF *Mantidactylus madinika*. For abbreviations of measured variables, see Materials and Methods. Further abbreviations used: M (male); F (female); HT (holotype); PT (paratype); RHL (relative hind-limb length: point reached by tibiotarsal articulation when the hind limb is adpressed along the body).

Specimen	Status	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	RHL
ZSM 601/2001	HT	M	11.9	3.6	4.5	1.0	1.5	1.4	1.0	1.5	3.0	6.8	18.6	9.0	6.1	eye center
ZFMK 76103	PT	M	11.7	3.9	4.8	1.0	1.6	1.3	1.0	1.7	3.0	7.0	18.9	9.1	5.9	eye center
ZSM 603/2001	PT	M	11.3	3.8	4.5	1.0	1.7	1.2	1.0	1.4	3.1	6.5	18.7	9.2	6.9	eye center
ZSM 604/2001	PT	M	11.8	3.6	4.4	1.1	1.5	1.3	1.0	1.4	3.2	7.1	18.3	9.0	5.5	anterior eye corner
ZSM 605/2001	PT	M	12.5	4.0	4.6	1.0	1.6	1.4	1.1	1.6	3.0	7.6	18.7	8.6	6.0	eye center
ZSM 606/2001	PT	M	12.3	3.8	4.7	0.8	1.7	1.4	0.9	1.6	3.0	6.8	18.5	9.3	5.6	eye entre
ZSM 600/2001	PT	F	15.6	4.3	5.1	1.1	1.7	1.3	0.9	1.8	3.5	7.4	19.8	10.3	6.4	tympanum
ZSM 607/2001	PT	F	14.7	4.2	5.0	1.0	2.0	1.4	1.0	1.7	3.1	8.4	21.0	9.8	6.3	tympanum
MRSN A2066	PT	F	14.8	4.4	5.1	1.1	1.6	1.2	1.0	1.8	3.5	8.2	21.8	10.8	7.1	tympanum

dorsum was grayish brown with indistinct darker markings, especially on the flanks. Dark crossbands were present on thigh, shank, foot, upper arm, and hand. The ventral surface was uniformly yellowish white; a line of white markings ran along the flanks, separating dorsal from ventral coloration and was continued into a white frenal stripe.

Variation.—The female paratypes are larger than the available males. Female SVL is 14.7–15.6 mm (mean 15.0 mm), male SVL is 11.3–12.5 mm (mean 11.9 mm). The male paratypes are similar to the holotype in morphology and coloration. In life, the frenal stripe is sometimes prolonged along the entire flank. In females, the frenal stripe is much more distinct, the dorsum is sometimes reddish brown, and no white color is present on the throat. The yellow oocytes are visible through the skin of the belly.

In the male ZSM 605/2001, the femoral gland in internal view (after dissection and reflection of skin; Glaw et al., 2000a) is an ill-defined, ovoid patch of 3.9 × 1.6 mm, consisting of ca. 100 small granules of variable size. The unusual relative finger length of the holotype (fourth finger shorter than second) is not homogeneous in the available sample, but in all specimens, these two fingers are at least of the same length. The state typical for most other *Mantidactylus* species (also observed in all specimens of *M. sarotra* examined), in which the fourth finger is distinctly longer than the second finger, is not seen in any *M. madinika.*

Etymology.—The name is derived from *madinika*, meaning small in Malagasy language and referring to the diminutive body size of the species. The name is treated as a noun in apposition to the generic name.

Natural history.—All specimens of *M. madinika* were captured in the vicinity of a small pond in a plantation of large trees and scattered cacao plants. The site was only about 100 m from the Sambirano River, but no brook suited for anuran reproduction was nearby. No plants used by phytotelmic breeders were seen (*Pandanus*, *Ravenala*). It can therefore be concluded that *M. madinika* probably reproduces in the pond which was also used by *Mantidactylus wittei*, *Mantella betsileo*, *Dyscophus* cf. *insularis*, and *Boophis tephraeomystax*. Furthermore, numerous *Stumpffia* cf. *gimmeli* were found in the leaf litter. Although *M. wittei* were mostly found in the immediate pond surroundings, specimens of *M. madinika* were most frequent in the leaf litter of a flat area prone to flooding. They were col-

lected both during day and night. At night, one male was seen to emit feeble chirps by slight inflation of its single subgular vocal sac. The female MRSN A2066 contained 28 yellowish oocytes of 0.9 mm in diameter as ascertained by dissection.

Discussion

Mantidactylus madinika shares the following set of characters with the recently described *M. sarotra*: white vocal sac, contrasted white lateral stripe, frenal stripe, general body shape. However, *M. sarotra* occurs in midaltitude rain forests of central eastern Madagascar (Mandraka, Andasibe, Antorotorofotsy, Moramanga, Ranomafana), which have a low faunal similarity to the Sambirano region. *Mantidactylus sarotra* deposits its clutches into leaf litter and tadpoles are probably washed into ponds by floods after heavy rain (Glaw and Vences, 2002). A similar reproductive mode may be found in *M. madinika* and would constitute another similarity between both species. However, femoral gland morphology in *M. madinika* differs from the state observed in the subgenus *Blommersia*; as far as known, species of *Blommersia* have well-defined gland patches composed of a limited number of granules (44 in *M. wittei* and 10 in *M. sarotra*; Glaw et al., 2000a; Glaw and Vences, 2002). The high number of granules in *M. madinika* (about 100) is similar to species of the subgenus *Guibemantis* (e.g., *M. depressiceps*). This mosaic of character states indicates that the subgenera *Blommersia* and/or *Guibemantis* may not be monophyletic.

According to the molecular data of Richards et al. (2000), *Mantidactylus* is paraphyletic with respect to the Malagasy poison frogs (*Mantella*). This genus is nested within *Mantidactylus*. *Mantella* is a well-defined monophyletic group characterized by a character complex related to microphagous specialization (Vences et al., 1998). For example, the tongues of these frogs are only slightly notched instead of distinctly bifid, and their maxillary teeth are reduced. *Mantidactylus madinika* is the only known representative of its genus that shares these states with *Mantella*. Furthermore, the assumed mode of reproduction in *M. madinika* (deposition of egg into the leaf litter) and the lack of dark pigment in its eggs also is similar to *Mantella* species (Glaw et al., 2000b). These characters may indicate phylogenetic relatedness of *Mantidactylus madinika* to the genus *Mantella*. In this case, the evolution of microphagous specialization in *Mantella* could have been linked to a hypothetical miniaturization in body size of their ancestor.

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