

A revision of *Mantidactylus microtis* and *M. microtypanum*, and a comparison with other large Madagascan stream frogs (Anura: Mantellidae: Mantellinae)

FRANCO ANDREONE¹ & RONALD A. NUSSBAUM²

¹ Museo Regionale di Scienze Naturali, Sezione di Zoologia, Via G. Giolitti, 36, I-10123, Torino, Italy; e-mail: f.andreone@libero.it

² Division of Reptiles and Amphibians, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, USA; email nuss@umich.edu

Abstract

We revise two stream frogs, *Mantidactylus microtis* and *M. microtypanum*, providing data on its known distribution and life history traits, based upon observations in nature. For *M. microtis* we show for the first time photographs of the live individuals, while for *M. microtypanum* we also describe its putative tadpoles. The transfer of *microtis* from *Boophis* to *Mantidactylus* is formally justified by morphological and ecological traits, e.g., the lack of nuptial pads, the torrenticolous life style and the low number of eggs. *Mantidactylus microtis* shares some characters with *M. microtypanum*: distribution (both live in south-eastern Madagascar), natural history (both are stream frogs), morphology (wide digital expansions, lack of femoral glands, presence of a mostly unforked omosternum, cryptic dorsal colouration, small tympanum, and presence of a derived cloacal structure). *Mantidactylus microtypanum* differs from the species of the subgenus *Mantidactylus* (*M. grandidieri* and *M. guttulatus*), to which it was so far ascribed, for the lack (vs. presence) of femoral glands, and presence of expanded (vs. moderately expanded) fingertips. Whether *M. microtis* and *M. microtypanum* are phylogenetically related, or their overall similarity is due to convergence, is discussed.

Key words: *Mantidactylus*, *Boophis*, Madagascar, Ecology, Generic attribution

Introduction

The ranoid family Mantellidae is endemic to Madagascar and Comoros, and includes a wide range of species and ecological forms currently ascribed to five genera: *Mantidactylus*, *Mantella*, *Boophis*, *Laliostoma*, and *Aglyptodactylus* (Vences *et al.* 2003). The most speciose mantellid genera are *Mantidactylus* and *Boophis*, respectively with around 80 and 40 species (Andreone 2003, Cadle 2003).

Within the genus *Mantidactylus* Blommers-Schlösser & Blanc (1991) recognized 10 species groups, accepted with some modifications as different subgenera by Dubois (1981) and Glaw & Vences (1994). So far, the genus *Mantidactylus* includes a heterogeneous assemblage of species, characterised by egg laying outside water, larval development in water or direct, lack of real amplexus, and habits varying from terrestrial to arboreal. On the other hand, the *Boophis* species appear quite homogeneous in morphology and other characters (e.g., Aprea *et al.* 2004) and differ from *Mantidactylus* in being primarily arboreal, with axillary amplexus, eggs laid in water, and larval development occurring in water.

Many species currently attributed to *Mantidactylus* were included in the past within *Rhacophorus* (e.g., Guibé 1978) and then often transferred to *Boophis*, especially when data on their life history were missing or insufficient. A typical example is *Mantidactylus leucomaculatus*, which was attributed to *Boophis* by Blommers-Schlösser & Blanc (1991) and Glaw & Vences (1992), or *Mantidactylus microtis*, until recently considered a representative of the genus *Boophis* (Glaw & Vences 1994). New collections and observations of its life history now allow us to attribute formally *microtis* to the genus *Mantidactylus* and to provide information on its distribution and ecology. This also gives the opportunity to analyse another little known species, *M. microtypanum* and discuss their similarities in terms of morphology and general ecology. In addition, we introduced a discussion on the phylogenetic relationships of these two species with other large stream *Mantidactylus* species, such as *M. guttulatus* and *M. grandidieri*.

Material and Methods

Newly collected frogs were sought during the night using hand and head-torches, captured by hand, and anaesthetised by immersion in chlorobutanol. Specimens were fixed in buffered 10% formalin or 90% ethanol and finally preserved in 70% ethanol. Tadpoles and eggs were fixed and preserved in 10% formalin. Further preserved specimens were obtained from several museum collections. Institutional abbreviations are as follows: MNHN (Muséum national d'Histoire naturelle, Paris); MRSN (Museo Regionale di Scienze Naturali, Torino); ZSM/FGZC (Zoologische Staatssammlung München, Frank Glaw Zoological Collection), UMMZ (University of Michigan, Museum of Zoology, Ann Arbor). Data reported in the lists are those accompanying the specimens in catalogues and labels.

Measurements of metamorphosed specimens were taken with a caliper to the nearest 0.1 mm as follows: SVL (snout-vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril-distance), IED (inter-eye distance), TD (tympanum diameter), HAL (hand length), FORL (forelimb length), FOL (foot length), FOTL (foot length including tarsus). Sex determination was based upon the analysis of the sexually dimorphic cloaca,

and by direct examination of the gonads via a short lateral, abdominal slit. If this failed, the sex was left as undetermined. Tadpoles were measured for the total length, body length, and height of caudal fins.

Morphological comparisons were done with two other species of large stream *Mantidactylus*. In particular, we compared *M. microtis* and *M. microtympanum* with individuals currently attributed to *M. guttulatus*, from NW Madagascar [reference specimen: MRSN A3645 from Tsaratanana Massif, Andavaka], and with individuals currently attributed to *M. grandidieri*, from NE Madagascar [reference specimens: MRSN A2558 and A5455 from Masoala Peninsula]. A revision of *M. grandidieri* and *M. guttulatus* will be provided in a further paper.

Results

The history of *Mantidactylus microtis*

Guibé (1974) described *Rhacophorus microtis* based upon a series (MNHN 1973-1080/1086) collected on the Anosy Chain, SE Madagascar, by Ch. P. Blanc (Paulian *et al.* 1973). In that paper he gave basic information on its morphology, but nothing about its ecology. Guibé (1978) justified its inclusion in the genus *Rhacophorus* basing mainly upon the presence of an unforked omosternum, which was considered to be one of the main generic diagnostic characters. Additional characters supported this attribution, e.g., flattened body, lack of femoral glands, and enlarged fingertips.

Subsequently, several *Rhacophorus* species were moved by Blommers-Schlösser (1979) to the genera *Mantidactylus*, *Gephyromantis*, *Laurentomantis*, and *Boophis*. Typically, the arboreal species with axillary amplexus, evident nuptial pads, and eggs laid in water were ascribed to the genus *Boophis*, while the remaining ones constituted the bulk of the genus *Mantidactylus*.

Basically the same information was subsequently given by Blommers-Schlösser & Blanc (1991), who assigned *B. microtis* to the *Boophis tephraeomystax* group for a series of features: (1) presence of vomerine teeth, (2) presence of an unpaired median vocal sac, (3) reduced hand webbing, (4) tibia longer than the foot, (5) absence of fringes on the forearm and tibia, (6) absence of outer metatarsal tubercle, and (7) transverse dark bands on the legs. A further ecological character typical of the group, the larval development in still water (typical of the *B. tephraeomystax* group) was not documented. Glaw & Vences (1992) still included *microtis* in the *B. tephraeomystax* group, but already recognized that it would be better included within *Mantidactylus*. Later they highlighted this similarity (Glaw & Vences 1994), but, waiting for further data, they did not transfer *microtis* to *Mantidactylus*. The inclusion of *microtis* within this genus was done by Andreone & Randriamahazo (1997), and successively reaffirmed by Andreone (2003), who recognised its phenetic similarity with another species of this genus, *M. microtympanum*. Then, it was considered a *Mantidactylus* by Andreone & Luiselli (2003), Andreone *et al.* (2005), and in the Global Amphibian Assessment web page (IUCN *et al.* 2004.)

Systematic account

Mantidactylus microtis (Guibé 1974)

(Figs. 1–4)

Material examined.—MNHN 1973–1080, 1081 (holotype and paratype), Chaînes Anosyennes, ruisseau, Camp Sommital (= Camp VII), 23.XI.1971, leg. Ch.P. Blanc; MNHN 1973–1082, same locality and collector, 16.XI.1971; MNHN 1973–1083, 1084 (paratypes), Chaînes Anosyennes, Cuvette, Sommet (proche des Camps VI–VII), leg. Ch. P. Blanc, 16.XI.1971; MNHN 1973–1085 (paratype) Chaînes Anosyennes, Camp IV e IIIbis, leg. Ch. P. Blanc, 2.XII.1971; MNHN 1973–1086 (paratype), Chaînes Anosyennes, Camp V, leg. Ch. P. Blanc, 1.XII.1971; MNHN 1975–2636/2649 and 2651/2655, Andohahelo [= Andohahela], 1800 m, torrent, leg. J. Arnoult, I.1954; UMMZ 198414–198421, Ampamakiesiny Pass, C. J. Raxworthy, 26.XII.1990, UMMZ 198422, same locality and collector, 28.XII.1990, UMMZ 214574–214586, PN d’Andohahela, Parcel 1, 13.5 Km NW of Eminiminy, 1100 m, leg. A. P. Raselimanana & J. B. Ramanamanjato, 13.XI.1995, UMMZ 214587, PN d’Andohahela, Parcel 1, 15 Km NW of Eminiminy, leg. A. P. Raselimanana & J. B. Ramanamanjato, 18.XI.1995; UMMZ 214588, same locality and collectors, 19.XI.1995; UMMZ 214589, PN d’Andohahela, Parcel 1, 15 Km NW of Eminiminy, 1440 m, leg. A. P. Raselimanana & J. B. Ramanamanjato, 24.XI.1995; UMMZ 214590, PN d’Andohahela, Parcel 1, 20 Km SE of Andranondambo, leg. A. P. Raselimanana & J. B. Ramanamanjato, 2.XII.1995; UMMZ 214591–214592, PN d’Andohahela, Parcel 1, 20 Km SE of Andranondambo, 1600–1660 m, leg. A. P. Raselimanana & J. B. Ramanamanjato, 2.XII.1995; UMMZ 217629, Ampamakiesiny Pass, leg. C. J. Raxworthy, 26.XII.1990; ZSM/FGZC 2437, 2439, 2489–2491, 2494, 2495, Andohahela National Park, 1600–1700 m, leg. P. Bora, 28.I.2005; ZSM/FGZC 2532, Andohahela National Park, 1600–1700 m, leg. P. Bora, 30.I.2005.

Original name. *Rhacophorus microtis* Guibé, 1974.

Diagnosis. A medium sized *Mantidactylus*, adults up to 60 mm SVL (Tab. 1). Fingers with large and sub-triangular expansions. Hands not webbed. Toes with sub-triangular dilatations smaller than fingers. Feet totally webbed. Femoral glands absent. Sub-articular tubercles small. Inner and outer metatarsal tubercle absent. Tibio-tarsal articulation of appressed hindlimb reaching tip of snout or beyond. Vomerine teeth present. Head quite flattened, with prominent nostrils. From above the head profile is rounded, larger than longer, reaching the point of maximum width at the level of the eye. Tympanum ovoid, very small and rather indistinct, much narrower than terminal expansions of fingers. Skin from finely granular to granular on back, smoother on belly. Cloaca simple to tubular. In males sometimes the cloaca is overhung by a bilobed epidermic flap. In life, greyish-brown or light brownish on back with darker dots that mimic the colouration of the stone on which it lives. Transverse darker bands are present on upper part of fore- and hindlegs.

The warts of the dorsal skin are evident and rounded, and with a lighter top. Finger and toe expansion are white, with a median longitudinal darker ridge. Eye brownish-yellowish with golden glitterings. Sub-horizontal black pupilla. Outer perimeter of the iris black. Belly dirty whitish shading to yellowish, except area near cloaca, which appears lighter.



FIGURE 1. *Mantidactylus microtis*. Live individual from Andohahela, 20 Km SE of Andranondambo (photo by A. P. Raselimanana).



FIGURE 2. *Mantidactylus microtis*. Live individual from Andohahela, unnamed site (photo by F. Glaw and M. Vences).

Distribution. (1) Chaînes Anosyennes (TT); (2) Andohahela RN 11, Parcel 1 (20 Km SE of Andranondambo); (3) Andohahela RN 11, Parcel 1 (unnamed site); (4) Ampamakiesiny, Pass. Altitude range: 1100–1800 m a.s.l.

Eggs and tadpoles. Just laid eggs were observed on 2–3 December 1995 at Andohahela (20 Km SE of Andranondambo) by A. P. Raselimanana (Nussbaum *et al.* 1999). They were laid in a jelly mass on stones above water level, usually above areas where it hunts or reposes. One individual (undetermined sex) was observed as resting with

the eggs after they were deposited (A. P. Raselimanana, pers. comm.). Eggs are quite large and quite blackish in colour: one dissected female (UMMZ 198418) revealed 42 eggs, with a mean diameter of 3.18 ± 0.25 mm.

TABLE 1. Morphometric data for *Mantidactylus microtis* and *M. microtympenum*. For abbreviations see Material and Methods. Values are provided as mean \pm standard deviation (at 0.1 mm). Minimum and maximum values are given between parentheses.

Species	<i>Mantidactylus microtis</i>		<i>Mantidactylus microtympenum</i>	
	Males	Females	Males	Females
No. of measured specimens	17	10	28	12
SVL	41.3 \pm 6.0 (34.3–55.8)	44.4 \pm 3.4 (37.2–48.4)	52.9 \pm 5.6 (40.6–64.2)	75.7 \pm 10.7 (61.5–96.2)
HW	15.3 \pm 2.1 (13.2–20.8)	16.4 \pm 1.2 (14.6–17.6)	19.7 \pm 4.2 (13.6–29.7)	29.1 \pm 7.5 (11.9–49.5)
HL	13.8 \pm 2.0 (11.8–19.7)	14.9 \pm 1.3 (12.8–16.7)	17.3 \pm 3.2 (12.0–28.8)	25.4 \pm 5.0 (17.8–36.5)
ED	6.0 \pm 0.7 (5.23–7.70)	6.3 \pm 0.6 (5.63–7.76)	8.1 \pm 0.9 (6.13–10.15)	10.6 \pm 1.3 (8.70–13.69)
END	3.6 \pm 0.5 (2.8–5.0)	4.09 \pm 0.5 (3.2–4.8)	4.6 \pm 0.7 (3.1–6.5)	6.4 \pm 0.9 (5.3–8.3)
NSD	2.7 \pm 0.6 (2.0–4.5)	2.9 \pm 0.5 (2.2–4.0)	4.2 \pm 0.7 (3.1–5.9)	6.1 \pm 1.1 (3.7–8.3)
NND	4.5 \pm 0.8 (2.7–5.6)	5.1 \pm 0.7 (3.9–6.5)	5.7 \pm 0.9 (3.1–7.9)	6.9 \pm 1.2 (5.0–9.3)
IED	5.8 \pm 0.8 (4.5–7.6)	6.1 \pm 0.5 (5.6–7.1)	6.2 \pm 0.8 (4.2–8.4)	8.39 \pm 1.3 (6.2–10.5)
TD	1.6 \pm 0.2 (1.2–2.0)	2.0 \pm 0.4 (1.4–2.7)	2.3 \pm 1.1 (1.3–7.8)	3.0 \pm 0.9 (2.0–4.9)
HAL	13.6 \pm 1.4 (11.5–16.4)	15.0 \pm 3.4 (12.1–24.1)	15.9 \pm 2.1 (11.4–21.2)	21.4 \pm 3.0 (17.2–27.6)
FORL	19.6 \pm 2.0 (15.8–24.3)	21.7 \pm 1.9 (19.0–24.3)	23.5 \pm 3.1 (15.6–29.2)	33.4 \pm 4.0 (28.6–40.6)
FOL	20.0 \pm 3.9 (16.7–29.4)	21.4 \pm 4.0 (18.1–31.2)	27.0 \pm 3.2 (20.4–33.8)	36.2 \pm 5.4 (23.7–45.8)
FOTL	28.1 \pm 4.6 (17.3–38.5)	30.7 \pm 1.2 (28.8–32.4)	35.4 \pm 5.0 (21.8–44.7)	49.4 \pm 4.5 (43.3–56.5)

Habits. According to the original notes by Ch. P. Blanc, the holotype MNHN 1080 and one paratype MNHN 1081 were found within vegetation next to a stream, while another paratype MNHN 1082 was found within moss percolated by water. A. P. Raselimanana (pers. comm.) observed the species at Andohahela, between 990 and 1500 m of elevation (apparently most abundant at about 1100 m). Individuals were observed within and along

some streams with large boulders. They preferred boulders along small waterfalls 0.50 to 3.0 m in height. Frogs usually adhered to stones, by flattening their body and with spread legs. These habits were confirmed by, P. Bora, F. Glaw and M. Vences, who found the species at Andohahela, at about 1600–1700 m of altitude. So far, no acoustic behaviour is known.

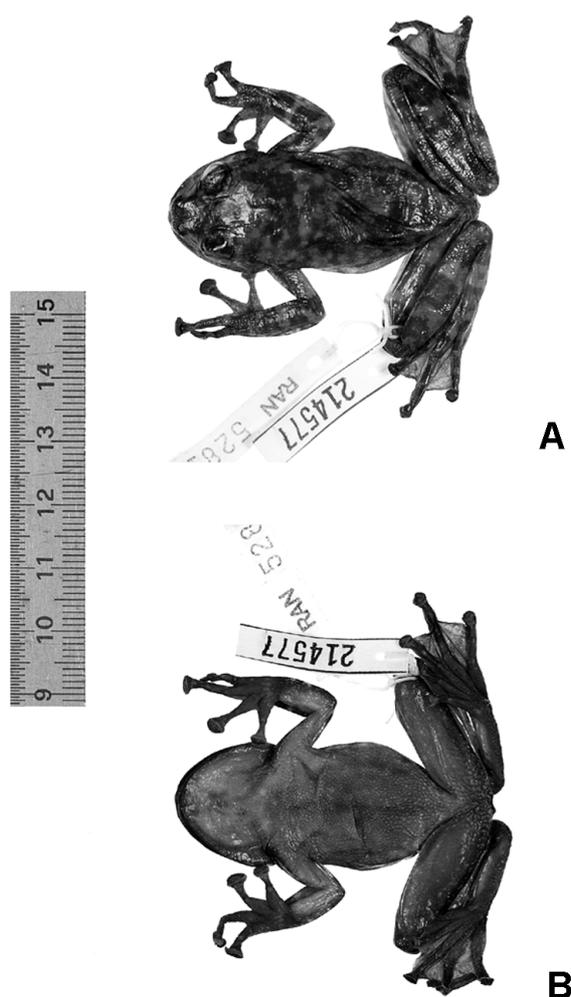


FIGURE 3. *Mantidactylus microtis*. Preserved specimen from Parc National dAndohahela, Parcel 1, 13.5 Km NW of Eminiminy, 1100 m (UMMZ 214577): A, dorsal side; B, ventral side.

Sexual dimorphism. Adult males smaller than females. The body size in males ranged 34.30–55.80 mm (mean \pm SD = 41.30 \pm 6.03 mm, n = 17), and 37.20–48.40 mm in females (44.40 \pm 5.25 mm, n = 10). There is no evident sexual difference in overall coloration. The only apparent dimorphic feature between some males and females is the morphology of the cloacal opening. In likely immature or reproductively inactive individuals, the cloaca is a simple terminal slit, as in most other *Mantidactylus* species. In

adult females (most likely in reproductive season), the cloaca is tubular and curved downwards. In adult males the cloaca is similarly directed downwards, while the opening is overhung by a skin flap, sometimes bilobed. Considering the habitat where the species lives (fast streams), we suspect that the cloacal morphology is functional in regards to the egg laying in running waters. During egg deposition the male and female cloacae are likely juxtaposed, thus forming a nearly closed structure which allows for more efficient fertilization. A somehow similar structure was observed for *Boophis albilabris* and *B. occidentalis*, two species that like *M. microtis* frequent fast running streams (Cadle 1995, Andreone *et al.* 2002). Although Guibé (1974) and Blommers-Schlösser & Blanc (1991) indicated the presence of a vocal sac we were unable to detect it in the analysed *M. microtis* specimens. We suspect that their note was based upon the analysis of a series housed in Paris (MNHN 1975-2636/2649 and 2651/2655). These animals, coming from “Andohahelo” (a misspelling for Andohahela), and collected by J. Arnould (in January 1954), are badly conserved and were likely not well fixed. For this the skin of these specimens is loose, and especially the throat is so relaxed that may have given the aspect of a vocal sac. In specimens more recently collected (e.g., those from UMMZ and ZMS series) there is no evidence of this structure.

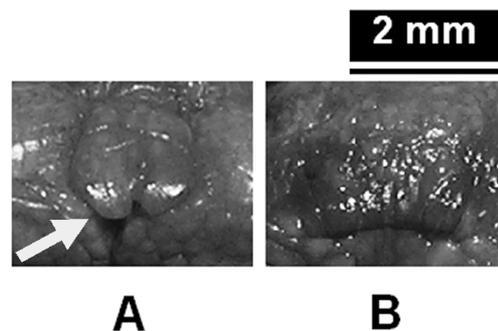


FIGURE 4. Details of the cloaca in a *Mantidactylus microtis*: A, male (UMMZ 214578); B, female (UMMZ 214577). The arrow indicates the bilobed flap typical of most males.

Similar species. *Mantidactylus microtis* differs from *M. microtypanum* (which has a somehow similar colouration) in having a smaller size and more slender habitus, and for the skin texture, which is more granular, and the belly colour, which is more uniformly whitish or greyish, while in *M. microtypanum* there are several spots on the throat. The head of *M. microtis* is more flattened and more roundish seen from above than in *M. microtypanum*, in which the snout is pointed. Furthermore, the nostrils are more relevant when seen from the profile. *Mantidactylus microtis* is also similar in overall habits and morphology to *M. lugubris*, which is smaller at adult size (around 30–45 mm), has a blackish or black and greenish banded colouration (mostly greyish with darker spots and dots in *M. microtis*), relevant femoral glands (absent in *M. microtis*), and a pointed snout.

Furthermore, *Mantidactylus lugubris* emits trilling vocalisations, while *M. microtis* is not yet known to vocalise.

***Mantidactylus microtympanum* Angel, 1935**

(Figs. 5–11)

Materials examined. MNHN 19735-170/171, Isaka-Ivondro, syntypes, R. Catala I.1935; MNHN 1972-601, 602, Mananjara-Bekaza, leg. Ch. P. Blanc, 10.VII.1971; MNHN 1972-1256 Ambana-Soavala (Chaînes Anosyennes), leg. Ch. P. Blanc, 3.XII.1971; MNHN 1972-1257/1316 Camp IV (Chaînes Anosyennes), leg. Ch. P. Blanc, XI.1971; MNHN 1972-1317/1318, Bekazaha (Chaînes Anosyennes), leg. Ch. P. Blanc, XII.1971; MNHN 1994-689, eggs, Chaînes Anosyennes; MNHN 1994.690 (tadpole), Chaînes Anosyennes, MRSN A649.1–5; forest between Isaka-Ivondro and Eminiminy, leg. R. Nincheri, 25–31.VIII.1993; MRSN A724.1–2, forest between Isaka-Ivondro and Eminiminy, leg. F. Andreone, 18.IV.1994; MRSN A774, same locality and collector, 17.IV–4.V.1994; MRSN A1653.1–3, same locality and collector, 8.V.1994; MRSN A117.1–3; same locality and collector, 8.XI.1994; MRSN A753, same locality and collector, 9.V.1994 (eggs laid at the Parc Botanique et Zoologique de Tsimbazaza); MRSN A5262, Mandena, “domaine de la cascade”, Fort Dauphin, leg. F. Andreone & G. Aprea, 25.XII.1997; UMMZ 197934, Andohavola 12 km N of Tolagnaro, leg. C. J. Raxworthy, 18.IX. 1990; UMMZ 197935, Manantantely Forest, leg. R. A. Nussbaum, C. J. Raxworthy, A.P. Raselimanana & J. B. Ramanamanjato, 1.XI.1990; UMMZ 197939, same locality and collectors, 9.XI.1990; UMMZ 197943, same locality and collectors, 10.XI.1990; UMMZ 197941–197942, same locality and collectors, 11.XI.1990; UMMZ 197944, same locality and collectors, 12.XI.1990; UMMZ 197953–197954, UMMZ 214118, same locality and collectors, 30.X.1990 (skeleton) Nahampoana Forest, same collectors, 21.XI.1990; UMMZ 197955–197957, Ampamakiesiny Pass, leg. C. J. Raxworthy & A.P. Raselimanana & J. B. Ramanamanjato, 18.XII.1990; UMMZ 197958, same locality and collectors, 20.XII.1990; UMMZ 197959, same locality and collectors, 21.XII.1990; UMMZ 198933, same locality and collectors, 22.XII.1990, (tadpole and eggs); UMMZ 197966–197970, Manongotry, leg. C. J. Raxworthy & A. P. Raselimanana & J. B. Ramanamanjato, 3.I.1991; UMMZ 197971, same locality and collectors, 4.I.1991; UMMZ 213221–213223 Anosy Mountains of Andohahela, 4 Km N of Ankaramena, Antsoroko River, 50–200 m, leg. R. A. Nussbaum, 30.V.1993, UMMZ 214593, leg. A. P. Raselimanana & J. B. Ramanamanjato, 20.X.1995, Andohahela RNI 11, Parcel 1, 8 km NW of Eminiminy, 400 m; UMMZ 214594, same locality and collectors, 420 m, 22.X.1995; UMMZ 214595–214596, Andohahela RN 11, Parcel 1, NW of Eminiminy at Andranomintilina Cascade, leg. A. P. Raselimanana & J. B. Ramanamanjato, 28.X.1995; UMMZ 214597–214599, Andohahela RN 11, Parcel 1, NW of Eminiminy at Andranomintilina Cascade, leg. A. P. Raselimanana & J. B. Ramanamanjato, 28.X.1995; UMMZ 214600, Andohahela RN 11, Parcel 1, 13.5

Km NW of Eminiminy, 1120 m, leg. A.P. Raselimanana & J. B. Ramanamanjato, 13.XI.1995; UMMZ 217631, Marosohy Forest, Andranoroa Rivers waterfall, 725 m, leg. C. J. Raxworthy, 23.XI.1989; UMMZ 217632, Marosohy Forest, Andranoroa River, 290 m, leg. R. A. Nussbaum, 26.XI.1989; UMMZ 217633, Marosohy Forest, Andranoroa River, 725 m, leg. R. A. Nussbaum & C. J. Raxworthy, 28.XI.1989.



FIGURE 5. *Mantidactylus microtympanum*. Live individual from Parc National d'Andohahela, between Isaka-Ivondro and Eminiminy (photo by F. Andreone).



FIGURE 6. *Mantidactylus microtympanum*: Live juvenile from Parc National d'Andohahela, between Isaka-Ivondro and Eminiminy (TL = 50 mm) (photo by F. Andreone).

Diagnosis. A large brook *Mantidactylus*, reaching around 100 mm SVL (Tab. 1 and Andreone 1998). Fingers with wide sub-triangular expansions. Toes with dilatations smaller than fingers. Finger and toe expansion white. No webbing between fingers, feet completely webbed. Femoral glands absent. Sub-articular tubercles small, inner metatarsal tubercle present and longish. Outer metatarsal tubercle absent. Vomerine teeth present. Tympanum rather indistinct, about 1/4 of eye diameter. Tibiotarsal articulation of

appressed hindlimb may reach as far forwards as nostrils. Skin finely granular on dorsum, smoother on belly. Nostrils nearer to tip of snout than to eye. Cloaca simple to tubular. Dorsal surface marbled grayish and brownish, with greenish shades. Ventral surface white with dark spots, spotting denser on throat. Eyes large and prominent, with golden iris, and a sub-horizontal pupilla. Upper lip and surrounding parts of eye with whitish spots. This colouration extends to lower flanks. Iris brownish-copper with fine blackish spots. The finger and toe tip expansions are whitish. Juveniles similar to adults in colouration, but more contrasted.

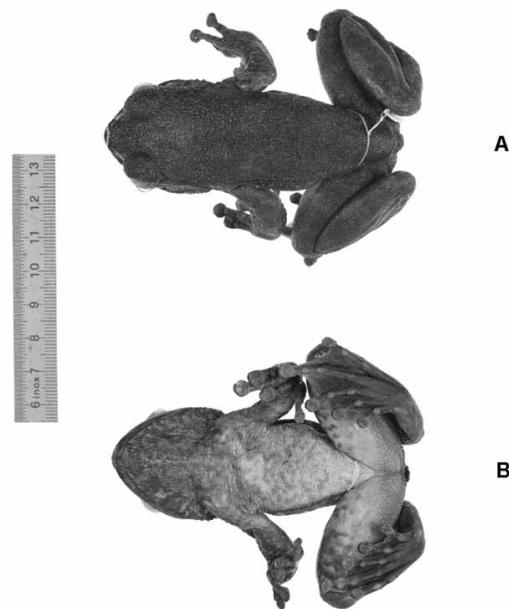


FIGURE 7. *Mantidactylus microtypanum*. Preserved specimens from Parc National d'Andohahela, between Isaka-Ivondro and Eminiminy, 400 m. (MRSN A649): (A) dorsal side, (B) ventral side.

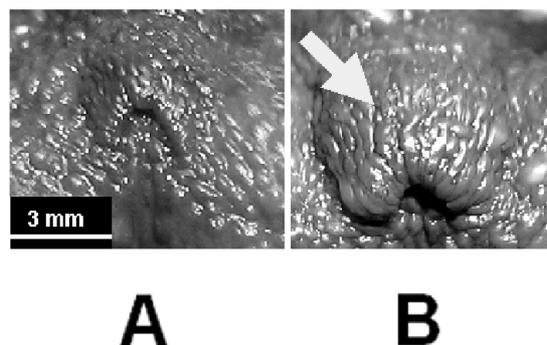


FIGURE 8. Details of the cloaca in a *Mantidactylus microtypanum*: A, male (MNHN 1972-1312); B, female (MNHN 1972-1274). The arrow indicates the tubular cloaca visible in most adult females.

Distribution. (1) Isaka-Ivondro (TT); (2) Ambana-Soavala; Ampamakiesiny Pass; (3) Andohahela RN 11, Parcel 1, 13.5 Km NW of Eminiminy; (4) Andohahela RN 11, Parcel 1, NW of Eminiminy at Andranomintilina Cascade; (5) Andohahela RNI 11, Parcel 1, 8 km NW of Eminiminy; (6) Andohahela, RN 11, Parcel 1, between Isaka-Ivondro and Eminiminy; (7) Anosy Mountains of Andohahela, 4 Km N of Ankaramena; Antsoroko River; (8) Bekazaha; (9) Mandena, “domaine de la cascade”, next to Fort Dauphin; (10) Chaînes Anosyennes; (11) Manantantely; (12) Manongotry; (13) Marosohy; (14) Nahampoana. Altitude range: 50–1120 m a.s.l.

Eggs and tadpoles. Eggs collected at Isaka-Ivondro within a small pool in a depression on a stone (MRSN A752 and A757) are attributed to *M. microtypanum* based on close similarity in morphology, colouration, and size to those laid in captivity (MRSN A753), and others taken in nature currently held at Paris (MNHN 1994-689/690). They are small (mean diameter of about 2 mm, with the jelly capsule about 6.5 mm), and whitish (Andreone & Randriamahazo 1997). The dissection of one female (MNHN 1972-1316) revealed 373 eggs, and another female (UMMZ 197941) 320 eggs: a subsample of them ($n = 47$) yielded a mean diameter of 2.1 ± 0.3 mm. Tadpoles tentatively attributed to *M. microtypanum* are housed in Paris (MNHN 1994-689/690) and Ann Arbor (UMMZ 128933). We also found much similar tadpoles at Andohahela (MRSN A 752), in the same small depression full of water where we collected eggs (MRSN A757). We are confident that the tadpoles belong to *M. microtypanum*, since no other *Mantidactylus* was seen to live within the stream (excepting *M. lugubris*, that has a very specialised tadpole: see Glaw & Vences 1994). The putative tadpoles attributed to *M. microtypanum* are of the benthic type (McDiarmid & Altig 1999), and have a typical ranoid form. The body is elliptical in lateral and ovoid in dorsal view. The snout is dorsally rounded, while in lateral view it slopes gently to the oral region and then turns strongly. The external nares are located dorsolaterally, almost half way from eyes to snout tip. The eyes are small and directed dorsally. The tail fins are low and of about equal height; while the dorsal fin are lower than the ventral at the plane of the vent tube. The origin of dorsal fin is a little before the tail-body junction and origin of ventral fin at the posterior ventral terminus of the body. The maximum tail height is reached at the middle of the tail. The tail tip is slightly pointed with the tail muscle almost reaching the tip of the fins. The spiracle is sinistral, with a midlateral opening directed posteriorly. The vent tube is parallel to the ventral margin of the fin, tubular in shape, and displaced dextrally with a medial aperture. The oral disc is anteroventral, sub-elliptical, with a uniserial row of marginal papillae in the lower labium and on the lateral side of the upper labium. The labial tooth row formula is 4(2–4)/3. Basing upon the sample MRSN A761, represented by 12 tadpoles at Gosners (1960) stage 25, the overall measurement are as follows: total length 23.9 ± 2.8 mm (range 20.0–28.3 mm), body length 9.8 ± 1.3 mm (range 7.5–11.9 mm), tail height 4.4 ± 0.6 mm (range 3.4–5.2). In life, the tadpoles are uniformly brownish and speckled with some sparse melanophores, more dense in the dorsal and lateral posterior part of the body. The tail fins

are transparent, scattered with dark spots, especially on the dorsal fin. After about ten years of preservative the tadpoles are brownish on the body, while the muscular part of the tail is whitish.



FIGURE 9. Eggs of *Mantidactylus microtypanum* photographed in the field between Isaka-Ivondro and Eminiminy, Andohahela (MRSN A752).



FIGURE 10. Eggs of *Mantidactylus microtypanum* laid in captivity by individuals collected between Isaka-Ivondro and Eminiminy, Andohahela (MRSN A753).

Habits. This large and crepuscular-nocturnal frog usually stations upon large stones and boulders along streams, and is usually not found more than a few meters away from the water. When disturbed it jumps in the water, splashing upon the water surface until it reached other emergent objects. Smaller individuals are able to skitter more rapidly on the water surface, like *M. lugubris*. In no case we observed this species diving in the water, differently from *M. grandidieri* and *M. guttulatus*. Acoustic behaviour is unknown for this

species. *Mantidactylus microtypanum* was observed preying upon *Boophis luteus* (Andreone & Randriamahazo 1997). In captivity at the Parc Botanique et Zoologique de Tsimbazaza (Antananarivo), some individuals were fed with live *Ptychadena mascariensis* and *Mantidactylus alutus*. This batrachophagy was confirmed by the analysis of a preserved female (MNHN 1972–1316), 86 mm long, which had in its stomach in addition to remains of a coleopteran and a freshwater crustacean a still intact (but with skin mostly digested) microhylid frog (likely a *Plethodontohyla bipunctata*), 27 mm long. During a study on the population density of the species (Andreone 1998), no evident interaction or territorial behaviours were observed. The individuals seem to be mostly sedentary, using a cavity under a rock in the stream as refuge. The secondary sex-ratio did not differ significantly from the expected 1 : 1 ratio. A population of 79 individuals was estimated over a surface of about 800 m². The mean longevity was of 4.1 ± 1.1 years in males, and 4.9 ± 0.9 years in females, with a maximum life span of 7 years (Guarino *et al.* 1998).

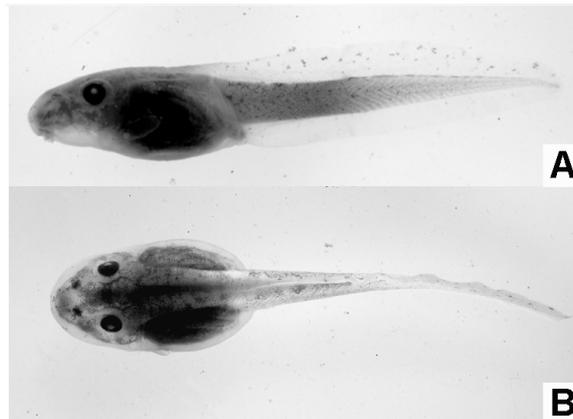


FIGURE 11. Putative tadpole of *Mantidactylus microtypanum*. (MRSN A761), collected between Isaka-Ivondro and Eminiminy, Andohahela: A, lateral side; B, dorsal side (TL = 28 mm).

Sexual dimorphism. Males are usually smaller than females. The range of SVLs in males is 40.60–64.22 mm (mean \pm SD = 52.9 ± 5.6 mm), and 61.57–96.20 mm in females (75.8 ± 10.8 mm). These values (obtained from the measured preserved specimens) are comparable to those previously provided for live specimens by Andreone (1998) and Andreone & Guarino (1998), although in the latter cases the sex was quite uncertain due to its determination in the field. Furthermore, the size ranges in the females is quite wide, being the smallest females about 65% of the largest one. This is due to the fact that it was not always possible to establish with certainty the status of gonadal maturation, and for this reason it is likely that some of the measured females fell within the juvenile category. In terms of other characters allowing to distinguish the sexes, it is remarkable that in this species too the cloaca is dimorphic. Differently from *M. microtis* (in which the males have

a more derived cloaca), in *M. microtypanum* females have a tubular cloaca directed downwards, whereas males usually have a simple terminal cloaca with a \wedge slit.

Similar species. *M. microtypanum* is similar to *M. microtis* in general morphology and frequented habitats (see above). For size and general habitat requirements it is externally similar to *M. grandidieri* and *M. guttulatus*. It differs from the latter two species in lacking femoral glands and having larger digital expansions and no marblings on the lower surface of the thighs. Juveniles are similar in colouration, general morphology, and behaviour to *M. microtis* and *M. lugubris*. While *M. lugubris* usually prefers vertical walls to adhere and for laying eggs, *M. microtypanum* rests and lays eggs on horizontal surfaces.

Discussion

Justification of the attribution of microtis to the genus Mantidactylus

The analysis of the *Rhacophorus microtis* types and further specimens held at Paris, Ann Arbor and Munich, corroborated by recent observations in nature (A. P. Raselimanana in 1995; P. Bora, F. Glaw and M. Vences in 2005), supports the species inclusion within the genus *Mantidactylus* (Andreone 2003), mainly for the following reasons: (1) it lacks nuptial pads, which are structures typical of amphibians with axillary amplexus, present within the mantellid radiation in *Boophis*, *Aglyptodactylus*, and *Laliostoma*, while they are absent in *Mantidactylus* and *Mantella* (Andreone 2003); (2) the low number of eggs indicates that *microtis* is a K-oriented species, as most of the *Mantidactylus* are (Vences *et al.* 1999), in opposition to *Boophis* that lay a very high number of eggs; (3) so far, no species of *Boophis* has a true torrenticolous life style, although large individuals of the *Boophis madagascariensis* and *B. albilabris* groups may lead a rather terrestrial life and may be sometimes found on rocks along streams.

All these morphological and behavioural characters indicate that *B. microtis* is a mantelline mantellid belonging to the genus *Mantidactylus* (in the present conception), and that the inclusion in the genus *Boophis* (*B. tephraeomystax* group) by Blommers-Schlösser & Blanc (1991) and Glaw & Vences (1992, 1994) was clearly erroneous. This is also confirmed by still unpublished molecular data (Glaw & Vences, in press). The assignment to *Boophis* by these authors was clearly due to some weird aspects of morphology shared with *Boophis* (e.g., absence of femoral glands, morphology of the omosternum, wide expansions of digital tips), and a general absence of life history information. Furthermore, the development of *M. microtis* tadpoles in still water (as it is the standard for the species belonging to the *B. tephraeomystax* group) is unlikely, and it is evident that tadpoles will be found in running water or in small pools as for *M. microtypanum*.

All these observations show that some morphological characters are clearly not always diagnostic of the genus attribution when distinguishing *Mantidactylus* and *Boophis*. The

outer metatarsal tubercle is present in some but not in all *Mantidactylus* species. In both *M. microtis* and *M. microtypanum* it is absent, although in the latter a sort of wart is sometimes visible. In *M. microtis*, moreover, the inner metatarsal tubercle too is absent. The omosternum shape is another apparently diagnostic character that instead is variable within the genus *Mantidactylus* as currently understood, and likely subject to ontogenetic variation and evolution. Glaw & Vences (1994) already observed that the omosternum was variable in different sized individuals of *M. microtypanum*. This is also confirmed by our observations. Indeed in *M. microtis* it is largely unforked and unnotched, thus confirming the original observations by Guibé (1974). In three large *M. microtypanum* (MNHN 1972-1272, 1972-1276, and MRSN A649.1), with a SVL respectively of 54.5, 47.2, and 78.6 mm, the omosternum is clearly forked. In the small and subadult individuals (MNHN-1972-1283, 1972-1292, and MRSN 1653.1; SVL respectively of 34.6, 30.9, and 32.5 mm) the omosternum appears less mineralised and unforked. In both species the proximal portion (style, including the procoracoid elements) is mineralized, whereas the distal portion is non-mineralized, translucent, and fan-shaped with a median indentation.

Considerations about the attribution of microtypanum to the subgenus Mantidactylus

Dubois (1981) and Glaw & Vences (1994) ascribed *M. microtypanum* to the subgenus *Mantidactylus*, together with *M. grandidieri* and *M. guttulatus*. This was justified by the large size shared by these species. However, as is evident in Tab. 2 this is the only shared character. Indeed, *M. grandidieri* and *M. guttulatus* have very well developed femoral glands, which are absent in *M. microtypanum*. Also, *M. grandidieri* and *M. guttulatus* do not have large and sub-triangular finger and toe expansions, and in general they live along the streams and forest torrents, but are not able to adhere to humid walls as *M. microtypanum* does.

For these reasons Andreone (2003) suggested that the subgenus *Mantidactylus* should be restricted to *M. guttulatus* and *M. grandidieri* only, while a new group (or subgenus) should be created to accommodate *M. microtypanum* and *M. microtis*. Indeed the latter two species apparently share several aspects of geography and life history. Their distribution is restricted to fast flowing streams in the rainforests of SE Madagascar. They are typical “jump and skitter” stream frogs with expanded finger and toe-tips, and they adhere to emerging objects. Furthermore, they also have a small tympanum, as indicated by their Latin specific names (*microtis* and *microtypanum*). At present, we are not aware of vocalisations emitted by *M. microtis* and *M. microtypanum*, while they are known for specimens attributed to *M. guttulatus*, and coming from NW Madagascar (Vences *et al.* 2004).

A further peculiar character in both species is the cloacal morphology. In mature females of both *M. microtis* and *M. microtypanum* the funnel cloaca is directed downward, although in males the situation is different. In males of *M. microtis* the cloaca is similar to that of females, although in some cases the overhanging part holds a skinny

flap. On the other hand, in males of *M. microtypanum*, the cloaca consists of a simple slit. We interpret both these structures as adaptations to laying eggs in running water, although we do not know whether they are homologue. The strong current of the rainforest streams where both species live makes it necessary to prevent the mobility of the eggs. Andreone & Randriamahazo (1997) observed eggs of *M. microtypanum* laid on stones subject to strong currents, glued in a horizontal position. For *M. microtis*, unpublished observations by A. P. Raselimanana (pers. comm.) indicate that the eggs are attached to vertical and humid stones, usually in the splash area next to waterfalls. Most likely pairs of *M. microtypanum*, and *M. microtis* as well, utilise their funnel cloacae to deposit eggs just on stone surfaces, especially in the case of fast running water.

TABLE 2. Characters of morphology, distribution, colouration and natural history in *Mantidactylus microtis*, *M. microtypanum*, and in the two large species included within the subgenus *Mantidactylus*.

SPECIES	<i>Mantidactylus microtis</i>	<i>Mantidactylus microtypanum</i>	<i>Mantidactylus grandidieri</i>	<i>Mantidactylus guttulatus</i>
Distribution	SE	SE	NE*	NW*
Maximum snout-vent length	50–60 mm	100 mm	100–110 mm	100–110 mm
Dorsal colouration	Greyish, with darker dots	Greyish, with darker dots	Greyish, with yellowish shadings	Greyish-blackish
Ventral colouration	Whitish	Whitish with dark spots on the throat	Whitish-yellowish, with dark spots	Whitish, with dark spots on the throat
Digital expansions	Sub-triangular, widely enlarged	Sub-triangular, widely enlarged	Ovoidal, narrow	Ovoidal, slightly enlarged
Femoral glands	No	No	Yes	Yes
Cloacal morphology	Tubular, sometimes with flap (males)	Tubular (females)	Simple	Simple
Omosternum shape	Unforked	Unforked / Forked	Forked	Forked
Habits and life history	Torrenticolous, glittering, hanging on emerging rocks	Torrenticolous, partly glittering, hanging on emerging rocks	Semi-aquatic, stationing on banks and horizontal surfaces	Semi-aquatic, stationing on banks and horizontal surfaces
Reproduction and development	Eggs laid on humid stones	Eggs laid on humid stones, and aquatic tadpoles	Unknown	Unknown
Vocalisations	Unknown	Unknown	Unknown	Yes

* Characters and maximum size based upon individuals from NE Madagascar (Masoala Peninsula) for *M. grandidieri*, and upon individuals from NW Madagascar (Tsaratanana Massif) for *M. guttulatus*.

Whether the ecological and morphological similarities of *M. microtis* and *M. microtympenum* are evidence of phylogenetic affinity (as hypothesised by Andreone 2003) or are the result of homoplasy, will be the subject of further investigations. All these aspects also indicate that the genus *Mantidactylus* as currently defined (Glaw & Vences 1994) is an heterogeneous (likely poliphyletic) assemblage, and that most groups or subgenera will deserve a full generic status. It is clear that such a splitting of *Mantidactylus* in several genera should be accompanied by an overall molecular approach.

Acknowledgements

This work was done with the help of several persons and institutions. G. Schneider assisted during F.A.'s visit to Ann Arbor, and facilitated with loans. M. Vences and F. Glaw provided references and museum specimens. Ch. P. Blanc, P. Bora, F. Glaw, A. P. Raselimanana, and M. Vences provided novel information on the life history of *M. microtis*. W. Böhme, A. Dubois, F. Glaw, A. Ohler, and G. Schneider allowed the study of specimens housed in their institutions. J. E. Randrianirina, H. Randriamahazo, F. Mattioli, D. Vallan, and G. Aprea were of help in the field. M. Brocchieri assisted with the measurements of preserved specimens. The work of F. Andreone and R. A. Nussbaum in Madagascar was possible due to the agreement of MEF and ANGAP, which delivered the requested authorisations. F. Andreone benefited on a Vicepresident studentship, and financial funding from the Nando Peretti Foundation, Wildlife Conservation Society, Conservation International, Istituto Oikos, the Gondwana Conservation and Research, and Madagascar Fauna Group. Thanks to D. Vallan and M. Vences for comments on an earlier draft of this paper.

References

- Andreone, F. (1998) Capture-recapture study of *Mantidactylus microtympenum* (Ranidae: Mantellinae), Anuran from the rainforests of southern Madagascar. *Amphibia-Reptilia*, 19, 451–455.
- Andreone, F. (2003) Mantellidae: *Mantidactylus*. In: Goodman, S. M. & Benstead, J. P. (Eds), *The Natural History of Madagascar*. University Press, Chicago, 910–913.
- Andreone, F., Cadle, J.E., Cox, N., Glaw, F., Nussbaum, R.A., Raxworthy, C.J., Stuart, S.N., Vallan, D. & Vences, M. (2005) Species review of amphibian extinction risks in Madagascar: conclusions from the Global Amphibian Assessment. *Conservation Biology*, 19 (6), 1790–1802.
- Andreone, F. & Luiselli, L.M. (2003) Conservation priorities and potential threats influencing the hyper-diverse amphibians of Madagascar. *Italian Journal of Zoology*, 70, 53–63.
- Andreone, F. & Randriamahazo, H. (1997) Ecological and taxonomic observations on the amphibians and reptiles of the Andohahela low altitude rainforest, S. Madagascar. *Revue Française d'Aquariologie*, 3/4, 95–128.
- Andreone, F., Vences, M., Guarino, F.M., Glaw, F. & Randrianirina, J.E. (2002) Natural history and larval morphology of *Boophis occidentalis* (Anura: Mantellidae: Boophinae) provide new

- insights into the phylogeny and adaptive radiation of endemic Malagasy frogs). *Journal of Zoology, London*, 257, 425–438.
- Aprèa, G., Andreone, F., Capriglione, T., Odierna G., & Vences, M. (2004) Evidence for a remarkable stasis of chromosome evolution in Malagasy treefrogs (Boophis: Mantellidae). *Italian Journal of Zoology, Supplement*, 2, 237–243.
- Blommers-Schlösser, R.M.A. (1979) Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae). *Beaufortia*, 352 (2), 1–77.
- Blommers-Schlösser, R.M.A. & Blanc, Ch.P. (1991) *Amphibiens (première partie)*. Faune de Madagascar 75 (1). Muséum National d'Histoire Naturelle, Paris, 379 pp.
- Cadle, J. E. (1995) A new species of *Boophis* (Anura: Rhacophoridae) with unusual skin glands from Madagascar, and a discussion of variation and sexual dimorphism in *Boophis albilabris* (Boulenger). *Zoological Journal of the Linnean Society*, 115, 313–345.
- Cadle, J. E. (2003) Mantellidae: *Boophis*. In: Goodman, S. M. & Benstead, J. P. (Eds), *The Natural History of Madagascar*. University Press, Chicago, 916–919.
- Dubois, A. (1981) Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du Monde, avec identification de leurs espèces-types: conséquences nomenclaturales. *Monitore Zoologico Italiano*, 15, 225–284.
- Glaw, F. & Vences, M. (1992) *A Fieldguide to the Amphibians and Reptiles of Madagascar*. Vences & Glaw Verlag, Cologne, 331 pp.
- Glaw, F. & Vences, M. (1994) *A Fieldguide to the Amphibians and Reptiles of Madagascar, second edition*. Glaw Verlag, Cologne, 480 pp.
- Glaw, F. & Vences, M. (in press). Phylogeny and genus-level classification of mantellid frogs. *Organisms Diversity & Evolution*.
- Gosner, K. L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.
- Guarino, F. M., Andreone, F. & Angelini, F. (1998) Growth and longevity by skeletochronological analysis in *Mantidactylus microtypanum*, a rain-forest anuran of southern Madagascar. *Copeia*, 1998 (1), 194–198.
- Guibé, J. (1974) Batraciens nouveaux de Madagascar. *Bulletin du Muséum national d'Histoire naturelle*, série 3, 145, 1009–1017.
- Guibé, J. (1978) Les Batraciens de Madagascar. *Bonner Zoologische Monographien* 11. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 140 pp.
- IUCN, Conservation International & NatureServe. 2004. Global Amphibian Assessment. <www.globalamphibians.org>. Downloaded on 18 July 2005.
- McDiarmid, R.W. & Altig, R. (1999) Materials and Techniques. In: Mc Diarmid R.W. & Altig, R. (Eds.), *Tadpoles: the Biology of Anuran Larvae*. Chicago, Chicago University Press, pp, 7–23.
- Nussbaum, R.A., Raxworthy, C.J., Raselimanana, A.P. & Ramanamanjato, J.B. (1999) Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In: Goodman, S. M. (Ed.), *A floral and faunal inventory of Réserve Naturelle Intégrale d'Andohahela, Madagascar: with reference to elevational variation*. *Fieldiana Zoology*, n.s. 94, 155–173
- Paulian, R., Blanc, Ch.P., Guillaumet, J.L., Betsch, J.M., Griveaud, P. & Péyrieras, A. (1973) Etude des écosystème montagnards dans la région malgache. II. Les chaînes Anosyennes. Géomorphologie, climatologie et groupements végétaux. (Campagne RCP 225, 1971–1972). *Bulletin du Muséum national d'Histoire naturelle*, série 3, 118, 1–40.
- Vences, M., Andreone, F. & Glaw, F. (2004) Voice of a giant. Bioacoustic data for *Mantidactylus guttulatus* (Amphibia: Mantellidae). *Amphibia-Reptilia*, 25, 112–115.
- Vences, M., Glaw, F. & Zapp C. (1999) Bemerkungen zu Eizahlen und Eigrößen bei madagassischen Fröschen der Gattungen *Tomopterna*, *Aglyptodactylus*, *Boophis* und *Mantidactylus* (Amphibia: Ranidae). *Salamandra*, 35 (2), 77–82.

Vences, M., Vieites, D.R. Glaw, F. Brinkmann, H. Kosuch, J., Veith, M. & Meyer, A. (2003) Multiple overseas dispersal in amphibians. *Proceedings of the Royal Society B*, 270, 2435–2442.