

A review of the genus *Mantella* (Anura, Ranidae, Mantellinae): taxonomy, distribution and conservation of Malagasy poison frogs

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In this paper, 17 species of the genus *Mantella* are recognized and the genus is partitioned into six species groups which can be distinguished by combination of bioacoustic, morphological, osteological and coloration characters. The following species and species groups are recognized: *Mantella betsileo* group (*Mantella betsileo*, *Mantella viridis*, *Mantella expectata*, *Mantella* sp. 1, and one new species described herein); *Mantella laevigata* group (*Mantella laevigata*); *Mantella cowani* group (*Mantella cowani*, *Mantella baroni*, *Mantella* aff. *baroni*, *Mantella haraldmeieri*, *Mantella nigricans*); *Mantella bernhardi* group (*Mantella bernhardi*); *Mantella madagascariensis* group (*Mantella madagascariensis*, *Mantella pulchra*); *Mantella aurantiaca* group (*Mantella aurantiaca*, *Mantella crocea*, *Mantella milotympanum*). This partition is of rather high resolution, and some of the groups may also be regarded as superspecies or species complexes.

A detailed type re-examination showed that *M. madagascariensis* and *M. baroni* represent two different species which are very similar in dorsal coloration, but *M. madagascariensis* can be distinguished by some characters of ventral coloration (horseshoe marking on the throat, reddish color ventrally on femur) and morphology (large inner metatarsal tubercle) from *M. baroni*.

Specimens from Marojezy preserved in the Paris museum are catalogued as *M. cowani nigricans* and must therefore be considered as syntypes of this taxon. The syntype series is heterogeneous, also containing specimens of *M. laevigata*. The name *nigricans* is stabilized by designation of a lectotype corresponding to a *M. cowani* group form from Marojezy. The name *Mantella cowani nigricans* Guibé, 1978 is revalidated and raised to species rank as *Mantella nigricans*.

A big problem in *Mantella* systematics is that, in recent years, hobbyists increasingly tend to publish "phantom" scientific names without type designation which in several cases lead to involuntary but nomenclaturally available new nominal taxa. Two phantom names which must be considered as nomenclaturally available are *Mantella aurantiaca milotympanum* Staniszewski, 1996 and *Mantella aurantiaca rubra* Staniszewski, 1996. We consider the name *rubra* as synonym of *M. aurantiaca*, but preliminarily attribute specific status to *M. milotympanum*.

Lectotypes (in addition to *M. nigricans*) are designated for *M. cowani*, *M. aurantiaca*, *M. betsileo*, *Mantella attemsi* (synonym of *M. betsileo*), *M. aurantiaca rubra* (synonym of *M. aurantiaca*) and *M. milotympanum*.

(from published figure). Clarifications on types and type series are provided for several species.

We provide a key to the species of the genus *Mantella*, and describe and discuss their color variability. In several species, a large intraspecific color variability was recorded (*M. aff. baroni*, *M. nigricans*, *M. croceo*). A detailed review of all published *Mantella* localities and the corresponding voucher specimens results in updated distribution maps. Sympatric and syntopic occurrence was reliably only found in species from different species groups, the species within each group being allopatrically distributed. Future studies on contact and hybrid zones may demonstrate that some of the species recognized herein should possibly better be regarded as subspecies; however, for practical reasons, we here regard all taxa as species.

In an attempt to provide an estimate of the conservation status of each *Mantella* species, we combined data on distribution (maximum locality distance, number of known localities), habitat (primary forest restriction), trade intensity and attractiveness to the pet trade. We group the species in various classes, according to their potential vulnerability, and outline priorities of research needed to get a more reliable data basis for such estimates.

INTRODUCTION

The ranoid subfamily Mantellinae currently contains two genera, both endemic to Madagascar (GLAW & VENCES, 1994): the type genus *Mantella*, and the large and heterogeneous *Mantidactylus* with currently 63 species. *Mantella* are small, largely diurnal and often colorful frogs, which were named Malagasy (or Madagascan) poison frogs due to the presence of alkaloid toxins in their skin (e.g. DALY et al., 1996).

Accounts on the genus were published by GUIBÉ (1964, 1978) and BUSSE (1981). BLOMMERS-SCHLÖSSER & BLANC (1991) largely relied on BUSSE's revision which they complemented by detailed distribution maps. The description of four new species by PENTAK & BÖHME (1988, 1990), BUSSE & BÖHME (1992) and VENCES et al. (1994) demonstrated, however, that those accounts were far from being complete. While GUIBÉ (1978) listed only four species and one subspecies, GLAW & VENCES (1994) already accepted 13 different species.

One of the major problems in *Mantella* systematics has been weak morphological differentiation. Since early workers generally studied only preserved material, they had to rely largely on color pattern for species diagnoses. GUIBÉ (1964, 1978) and especially BUSSE (1981) considered single species (named *M. cowani* or *M. madagascariensis*, respectively) as highly variable in coloration, but they never proved this variability in specimens from a single locality (DALY et al., 1996). Without definite knowledge of intra- and interpopulational color variability, the attribution of type specimens of early names (*M. madagascariensis*, *M. cowani*, *M. baroni*, *M. pulchra*) largely depended on the subjective impression of the corresponding author, causing large confusion in the usage of these names in scientific and non-scientific literature.

In the following we report the main results on taxonomy, distribution and color variability of *Mantella* which were gathered in the framework of a comprehensive study of the genus. Contributions to the morphometry, osteology, tadpole morphology, reproduction, karyology, as well as bioacoustic and allozyme differentiation within *Mantella* are being published elsewhere. The aim of the present paper is mainly to clarify the taxonomy and nomenclature

of *Mantella* species as well as their distribution, in order to give a more stable basis for future investigations of these frogs. We divide the genus into phenetic species groups, and use our new scheme of *Mantella* systematics to discuss biogeographical subjects and to summarize conservation needs.

MATERIAL AND METHODS

SPECIMENS EXAMINED

The present review is mainly based on preserved material of the following collections: The Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo Regionale di Scienze Naturali, Torino (MRSN/MZUT); Naturhistorisches Museum Basel (NMB); Naturhistorisches Museum Wien (NMW); Transvaal Museum, Pretoria (TM); Zoologisch Museum Amsterdam (ZMA); Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Specimens were examined in detail and their color patterns and morphology recorded. Locality and collector are generally literally given according to the corresponding catalogue. Abbreviations used are: CS, cleared and stained specimens; TE, tissue extracted for electrophoresis, specimens only partly preserved (generally liver extracted and two limbs amputated); NIL, specimens not individually labeled. The term "ex" is used in the sense of "formerly" to characterize old collection numbers.

LOCALITIES AND DISTRIBUTION MAPS

The examined material is the basis of the locality maps and the statements on color variability. Localities are numbered, the numbers corresponding to those in the respective distribution maps. A star behind the locality number marks the localities which were confirmed by FG (and partly by MV) in the field. The type locality, in the nomenclatural account on each taxon, is given in quotation marks literally as in the original description; additional discussions, when necessary, are provided in the *Comments* sections.

DESCRIPTION OF COLOR PATTERNS

Variation of color patterns is described in a standardized way and generally refers to live coloration of adult specimens. Terms which we use to refer to certain color elements are defined as follows: (1) dorsolateral color border: a sharp longitudinal border between the color of the flanks (darker) and the dorsum (lighter); (2) frenal stripe: a light longitudinal stripe along the upper lip; (3) rostral stripe: a light (yellowish, greenish or brownish) stripe running from anterior head tip and nostril above the eye to a point behind the eye;

(4) diamond marking: a central (dark) marking on the back of more or less distinct double-rhomboid shape; (5) flank blotches: light markings of varying extension which are located posterodorsally around the forelimb insertion and anterodorsally around the hindlimb insertion; they mostly can be seen as an extension of the dorsal humerus/femur color on the flanks; (6) flashmark: a sharply delimited, bright orange or red marking on the posterodorsal femur, knee hollow and ventral tibia which in some species can cover the ventral tibia nearly entirely; (7) horseshoe marking: a light (generally whitish blue) continuous marking on the throat, running more or less broadly along the lower lip and thus horseshoe-shaped. The terms femur, tibia, and tarsus, as used in the sections on coloration, do not refer to the skeletal elements but to the external coloration of the corresponding hindlimb sections.

MORPHOMETRY AND MORPHOLOGY

Measurements taken were: SVL: snout-vent length; HW: maximum head width; HL: head length, measured from snout tip to forelimb insertion (not to maxilla articulation); Eye: horizontal eye diameter; Tym: horizontal tympanum diameter; Eye-Ns: distance between eye and nostril; Ns-St: distance between nostril and snout tip; ForL: forelimb length; HaL: hand length; HiL: hindlimb length; FoTL: foot length including tarsus; FoL: foot length; ToL1: length of first toe; FW3: width of third finger just before terminal finger disk; DW3: width of terminal disk of third finger; IMTL, IMTH, IMTW: length, height and width of inner metatarsal tubercle. All measurements were made by the senior author with a precision calliper to the nearest 0.1 mm, except FW3, DW3, IMTL, IMTH, IMTW which were measured using a binocular with measuring device to the nearest 0.01 mm or, when no binocular was available, with a calliper to the nearest 0.1 mm. Original measurements in the present paper are only given for type specimens, but the size ranges and morphometric ratios in the species accounts refer to a total of about 400 measured specimens.

In the text, besides SVL, we use the abbreviations IMT for inner metatarsal tubercle, and TTA for tibiotarsal articulation. The size (SVL) is given as range of adult specimens, followed where possible by the range recorded in the males and females which could be reliably sexed. Since in many cases specimens could not be sexed with a sufficient reliability, known adult size range may be wider than that recorded in males and females separately.

DESCRIPTION OF CALLS

Detailed call descriptions will be published elsewhere; here we tentatively distinguish four different general call types: (1) double click calls are series of notes which each are composed of two emphasized and very short "metallic" clicks; (2) single click calls are series of notes which each are composed of one emphasized and very short "metallic" click; (3) trill calls are (irregularly repeated) notes composed of up to 10 short clicks; (4) chirp calls consist of (irregularly or regularly repeated) notes with a less "metallic" appearance than in click calls as used above (a note is often composed of 2-3 emphasized pulses).

SYNONYMIES

For each *Mantella* species, we present a synonymy and chresonymy (for the definition of the term chresonymy, see SMITH & SMITH, 1973), following the scheme used by DAVID & VOGEL (1996). The overwhelming number of publications in which at least one species of *Mantella* is mentioned makes it impossible to provide a complete chresonymy. Instead, we present a selection of references (partial chresonymy) which either (1) discuss intrageneric taxonomy and systematics, (2) provide original data for at least one species, (3) include pictures of at least one species, or (4) were published before GUIBÉ's (1964) revision of the genus (the latter, however, must be seen with reservation since it is often difficult to understand to which species the author actually referred). Page numbers are only given if necessary to locate a deviating name usage or a figure. Only publications which contain either original data or figures are listed in the chresonymies of the species. Exceptions are the works of GUIBÉ (1964, 1978), BUSSE (1981), BLOMMERS-SCHLÖSSER & BLANC (1991) and GLAW & VENCES (1992a, 1994), which are here considered as monographic accounts on the genus. All names used in these works are listed in the corresponding synonymies. Generally, taxa which were defined in a publication in a way that, according to present definition, they were in fact composed of several species, are listed as "partim-chresonyms" ("part.") in the chresonymies of each of these species (in the case of monographs) or of the species which were shown or explicitly meant (in the case of other papers). Nomenclatural validity of names is discussed according to the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985; cited below as "the Code").

RESULTS

THE GENUS *MANTELLA*

Definition of the genus

Following the data of GUIBÉ (1978), BLOMMERS-SCHLÖSSER & BLANC (1991), BLOMMERS-SCHLÖSSER (1993), DALY et al. (1996), GLAW et al. (1998b), PINTAK et al. (1998), VENCES & KNILL (1998) and VENCES et al. (1998, 1999a), the genus *Mantella* can be defined by the combination of the following characters:

(1) Eight presacral vertebrae; (2) vertebral centrae procoelous; (3) sacral diapophyses not enlarged; (4) atlantal cotyles widely separated; (5) three free distal tarsals; (6) six free distal carpals; (7) terminal phalanges slightly Y-shaped; (8) hyoid with anterolateral and posterolateral processes; (9) anterior processes of hyalia forming complete arch in some specimens of most or all species; (10) palatines present; (11) maxillary and premaxillary teeth absent; (12) vomer present; (13) dentigerous process of vomer (and thus vomerine teeth) absent; (14) squamosal with reduced zygomatic process; (15) frontoparietals anteriorly convex-shaped and separated along their whole length; (16) process of pars fascialis of maxilla reduced; (17) shoulder girdle firmisternal; (18) ossified sternum and omosternum present; (19) sternum

shorter than omosternum; (20) omosternum forked at its base; (21) complete ventral circum-marginal groove on terminal finger and toe expansions; (22) SVL of adults 18-31 mm; (23) tibiotarsal articulation reaching between forelimb insertion and nostril; (24) tympanum visible externally, mean tympanum/eye ratio 1/2 to 2/3; (25) lateral metatarsalia connected; (26) no webbing between fingers nor toes; (27) inner and outer metatarsal tubercle present; (28) no dorsal "scutes" on finger and toe tips; (29) karyotype $2n = 26$, with 5 pairs of large and 8 pairs of small chromosomes which are meta- or submetacentric; (30) tongue very slightly notched; (31) microphagous and myrmecophagous feeding; (32) skin alkaloids present; (33) long prey-capture jumps absent; (34) colorful pattern at least ventrally (black/blue, yellow or orange), often also dorsally; (35) activity largely diurnal; (36) calls consisting of short clicks, chirps or trills; (37) no strong mating amplexus; (38) eggs generally laid outside of the water; (39) eggs unpigmented; (40) tadpoles with horny beak and keratodont formula 1:2+2/3 to 1:5+5/3 (formula according to DUBOIS, 1995); (41) no tadpole transport; (42) no external gills in early larval stages; (43) egg clutches consisting of less than 200 eggs; (44) no externally prominent femoral glands as in many *Mantidactylus*, but granular thigh patches present (see also DALY et al., 1996), most distinct in males (exact structure of these patches will be subject to a forthcoming publication).

Character states 9, 11, 14, 30, 31, 32, 33 and 34 are, as far as known, not found in *Mantidactylus*, the second genus of the Mantellinae. They all can be considered as derived in *Mantella* (based on outgroup comparison with other ranid frogs, e.g. the Malagasy rhacophorines of the genus *Boophis*). However, states of characters 11, 13, 14, 16, 30, 32, 33, 34 and 35 are all part of a character complex related to microphagy (character 31), which reduces their value as independent characters for the assessment of phylogenetic relationships (see VENCES et al., 1998). In fact, most of them are also found in the Dendrobatidae which, too, are microphagous but clearly differ from *Mantella* in other characters (different states in characters 5, 6, 7, 18, 20, 28, 29, 30, 40, 41 and 42; for references, see VENCES et al., 1998). Apomorphic states supporting the status of *Mantella* as a monophyletic (holophyletic) group within the Mantellinae are thus the microphagy character complex (see above) and the hyoid structure (character 9).

Etymology of the generic name

The genus *Mantella* was erected by BOULENGER (1882) to accommodate the species *betsileo*, *madagascariensis* and *ebenau*; in an addendum he described the new species *cowanii*. The type species is *Mantella betsileo*, as designated by LIEM (1970). No etymology was given in the original description of the genus. The generic name is most probably a diminutive of *mantis* (Classical Greek *mantis*, prophet) which was used with the meaning "treefrog" in the sense of a weather prophet by HESYCHIUS. This meaning of *mantis* is included in several Greek-German dictionaries (e.g. PAPE, 1888) but was not found in Greek-French or Greek-English dictionaries (see GLAW & VENCES, 1994: 400). The term *mantis* was often used for generic anuran names; BOULENGER himself erected in 1895 the genus *Mantidactylus* for several Madagascan frogs which today are included together with *Mantella* in the Mantellinae.

A second etymology for *Mantella*, however, cannot be totally excluded. One of the early subjects of BOULENGER's studies were dinosaur fossils found in Belgium, which belonged to the genus *Iguanodon*. The first *Iguanodon* fossils had been found by an English doctor,

G. MANTILL, and his wife, and were subsequently described as *Iguanodon mantelli* (see BULTYNCK, 1987). Still less probable is a derivation from the Italian word *mantella* (cloak) which is sometimes used to describe animal (mammal) color patterns.

DEFINITION OF SPECIES GROUPS

Although several authors have stressed similarities between selected *Mantella* species and erected species groups within the genus (GLAW & VENCES, 1994; ZIMMERMANN, 1996a; STANISZEWSKI, 1996), no comprehensive attempt has so far been published to partition the whole genus into such groups, and to explicitly list the characters distinguishing them. We here divide the genus into six phenetic species groups, a subdivision of rather high resolution; in fact, some groups could also be characterized as superspecies or species complexes. The differential characters between species groups are summarized in tab. 1.

Mantella betsileo group (contains: *Mantella betsileo*, *M. sp. 1*, *M. viridis*, *M. expectata*, and one new species described herein). – This group is characterized by the combination of several characters which, however, are each also present in at least one other species group: double click call (also in *M. laevigata*), horseshoe marking (also in several other groups), frenal stripe (also in *M. crocea* and some *M. madagascariensis*), hindlimbs ventrally black without orange and red (also in *M. laevigata* and *M. nigricans*).

Mantella laevigata group (contains: *Mantella laevigata*). – The classification of *Mantella laevigata* in a separate species group is clearly justified by its unique habits (partly arboreal, tree hole breeding, single eggs) and its distinctly enlarged finger tips. It is the only species with a double click call which lacks a horseshoe marking.

Mantella cowanii group (contains: *Mantella baroni*, *M. aff. baroni*, *M. cowanii*, *M. nigricans*, *M. haraldmeieri*). – A group characterized by light (mostly yellow or red) flank blotches of variable extension (also found in the *M. madagascariensis* group and in *M. bernhardi*) and single click calls (exclusive to this group).

Mantella bernhardi group (contains: *Mantella bernhardi*). – Classification of *M. bernhardi* in a separate species group is mainly based on its relevant allozyme differentiation (VENCES et al., 1999b) and its trill calls.

Mantella madagascariensis group (contains: *Mantella madagascariensis*, *M. pulchra*). – The species included in this group are mainly characterized by a very large IMT (see diagnosis of *M. pulchra* in GUBÉ, 1964, 1978). Light flank blotches of varying extension, horseshoe markings and flashmarks are present. Calls, as far as known, are chirp calls.

Mantella aurantiaca group (contains: *Mantella aurantiaca*, *M. crocea*, *M. milotympanum*). – Species of this group are characterized by a rather stout body shape, distinct flashmarks and a chirp call. In contrast to species of the *M. madagascariensis* group, there are no flank blotches and the IMT is smaller. Two species (*M. aurantiaca*, *M. milotympanum*) are characterized by a largely uniform yellow to red dorsal and ventral coloration. *M. crocea* is included in this group since specimens with color pattern intermediate between *M. crocea* and *M. milotympanum* are known (GLAW & VENCES, 1998), and juvenile coloration of *M. crocea* and *M. aurantiaca* is very similar (personal observation). The close relationships between the

Table 1. — Differential characters between *Mantella* species groups. Not all characters have been ascertained in all species of the groups. See Definition of species groups section for more information. Sternum shape is given according to VENCES et al. (1999a). IMT, inner metatarsal tubercle.

Character	<i>Mantella betsileo</i> group	<i>Mantella laevigata</i> group	<i>Mantella cowani</i> group	<i>Mantella bernhardi</i> group	<i>Mantella madagascariensis</i> group	<i>Mantella aurantiaca</i> group
Call	mostly double click, series	double click, series	single click, series	trill, mostly no series	chirp, series	chirp, mostly no series ¹
Sternum	forked	forked	unforked	unforked	forked	forked
Horseshoe marking	present	absent	absent	present	present	present/absent
Frenal stripe	present	absent	absent	absent	absent (present) ²	present/absent
Flank blotches	absent	absent	large/small	small	large	absent
Orange/red ventral color on hindlimbs	absent	absent	present (absent) ³	present	present	present
Habitat	terrestrial	partly arboreal	terrestrial	terrestrial	terrestrial	terrestrial
Eggs laid as	clumps	single eggs	clumps	clumps	clumps	clumps
Egg feeding of tadpoles	absent	present	absent	absent	absent	absent
IMT	small	small	small	small	large	small

¹ Only ascertained in *M. aurantiaca*; *M. crocea* calls are also chirp calls (personal observation), but notes may be arranged more often in series than in *M. aurantiaca*.

² A frenal stripe may be present in certain specimens of the "variable" morph of *M. madagascariensis*.

³ Orange/red ventral color on hindlimbs is present in all species of the *M. cowani* group except *M. nigricans*.

species of the *M. aurantiaca* group were supported by chromosome morphology (PINTAK et al., 1998) and by studies on allozyme variation (VENCES et al., 1999b). ZIMMERMANN (1996) also mentioned a *M. aurantiaca* group which included *M. aurantiaca* and *M. crocea*.

SPECIES ACCOUNTS

In the following, we list *Mantella* species separately for each species group; within the groups, species are arranged alphabetically. Photographs of living specimens of all species are shown in fig. 1-3, dorsal and ventral views of holotypes and lectotypes (all photographed 1992-1999) in fig. 4-5, and variation of ventral pattern in fig. 6-8. Distribution maps are shown in fig. 9.

Mantella betsileo group

Mantella betsileo (Grandidier, 1872)

Dendrobates betsileo Grandidier, 1872. — Name-bearing type: lectotype, by present designation, MNHN 1895.278, sex unknown due to bad state of preservation, SVL 19.0 mm. — *Type locality*: "Pays des Betsileos" according to original description and MNHN catalogue. — *Other types*: paralectotype, following present lectotype designation, MNHN 1895.279. — *Etymology*: named after the type locality, the region Betsileo.

Mantella betsileo: BOULENGER, 1882, 1888; VAILLANT, 1885; WERNER, 1901; MOCQUARD, 1909; METHUEN & HEWITT, 1913; MILLOT & GUIBÉ, 1951; GUIBÉ, 1964, 1978; LIEM, 1970; BACHMANN & BLOMMERS-SCHLÖSSER, 1975; BLOMMERS-SCHLÖSSER, 1978, 1979a; MEIER, 1980 (part., p. 353, third figure from above), 1986 (Abb. 3); BUSSE, 1981 (part., see *M. haraldmeieri*); PINTAK, 1990; BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (plate 19,101); ANDREONE, 1992 (pl. III fig. 3-4); GLAW & VENCES, 1992a (part., see localities), 1992b (fig. p. 29), 1994 (part., see localities); ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5.17); GARRAFFO et al., 1993; HERRMANN, 1993 (fig.); KÜCHLING, 1993; BARTLETT, 1995 (fig. p. 26); HENKEL & SCHMIDT, 1995 (fig. p. 50); CARISSIMI-PRIORI, 1995 (fig. p. 42); VENCES et al., 1996, 1998; DALY et al., 1996; STANISZEWSKI, 1997a (fig.), 1997b (fig.); LARSEN, 1997; PINTAK et al., 1998; VENCES & KNIEL, 1998.

Dendrobates ebenau Boettger, 1880. — Name-bearing type: lectotype, by designation of MERTENS (1967: 44), SMF 7323 (ex 1141, 1a), adult female. — *Type locality*: "insula Nossi Bé", according to original description. — *Other types*: possibly one paralectotype, FMNH 18236 or 183237 (see MARX, 1958, and comment below). — *Etymology*: named after C. EBENAU who provided the type material.

Dendrobates ebenau: MOCQUARD, 1909 (syn. *betsileo*); MERTENS, 1922 (syn. *betsileo*); MERTENS, 1967 (syn. *betsileo*).

Dendrobates ebenau: GUIBÉ, 1964, 1978 (syn. *betsileo*); BUSSE, 1981 (syn. *betsileo*); BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *betsileo*); GLAW & VENCES, 1994 (syn. *betsileo*; p. 411).

Mantella ebenau: BOULENGER, 1882; WERNER, 1901; METHUEN & HEWITT, 1913 (syn. *betsileo*).

Mantella attemsi Werner, 1901. — Name-bearing type: lectotype, by present designation, NMW 20837, female, SVL 25.6 mm. — *Type locality*: uncertain, but (in original description) was speculated to be probably "Madagascar oder Nossi-Bé". — *Other types*: paralectotype, following present lectotype designation, ZMB 16588. — *Etymology*: named after C. ATTEM who provided the type specimens from Zanzibar.

Mantella attemsi: MOCQUARD, 1909.

Mantella attemsi: GUIBÉ, 1964, 1978 (syn. *betsileo*); BUSSE, 1981 (syn. *betsileo*); BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *betsileo*); GLAW & VENCES, 1994 (syn. *betsileo*; p. 412); HÄUPL et al., 1994 (syn. *betsileo*).

Identity. — DALY et al. (1996) were concerned about the fact that the type locality of *M. betsileo* (see below) is outside the known range of the species. They questioned whether the name is currently correctly applied. A re-examination of the types (see below) leads us to

conclude that they (1) cannot be conspecific with any species having red or orange ventral color on the hindlimbs, (2) are morphologically different from *M. laevigata* and *M. nigricans*, and (3) are smaller than *M. viridis*, *M. sp. 1* and *M. expectata*. It seems therefore likely that the name is currently (e.g. GLAW & VENCES, 1994) correctly applied.

Comments. – (1) The taxon *betsileo* was originally based on the syntypes MNHN 1895.278-279. The lectotype MNHN 1895.278 (SVL 19.0 mm; sex unknown) is larger and in slightly better state of preservation. The paralectotype MNHN 1895.279 is probably a subadult specimen (SVL 15.7 mm). In both types, coloration has become a contrastless, nearly uniform brown. The dorsolateral coloration border mentioned in the original description cannot be unequivocally recognized. Since the hindlimbs were folded in both specimens, the pattern is less faded on the posteriorly directed (ventral) part of the tibia which was not exposed to light. Here, a distinct light crossband can be recognized, as is typical for species of the *M. betsileo* group (and for *M. laevigata* and *M. nigricans*). Based on this character it can be excluded that the types are conspecific with *Mantella* species having red or orange color ventrally on the hindlimbs. – (2) The type locality of *M. betsileo* is a large region in central Madagascar. Up to now, no *Mantella betsileo* specimens are known to have been collected in the eastern forests south of Nosy Boraha. As discussed by DALY et al. (1996), the travel routes of GRANDIDIER are rather well documented. Maybe, the types were not collected in the eastern Betsileo forests but in western Betsileo, where the occurrence of *M. betsileo* seems more probable due to the existence of several localities in western Madagascar. It also cannot be excluded that the type locality is wrong. – (3) According to the original description (BOETTGER, 1880: 281), *Dendrobates ebenau* was based on two syntypes, a male and a female. However, in his 1892 catalogue, BOETTGER (1892: 21) mentioned “numerous specimens” (“Zahlr. Ste”) of this species from Nossibé, kept in the Frankfurt Museum under number SMF 1141.1a; presumably these specimens included the two original syntypes and several other non-type specimens. MERTENS (1922: 166) stated that the “Typus” of this species was bearing the number SMF 1141.1a, but since this number was used by BOETTGER (1892) as a collective number for a series, this mention cannot be considered as a lectotype designation under article 47 (b) of the Code. Designation of an individual specimen, SMF 7323, as lectotype of this species, was made by MERTENS (1967: 44). Thus, only one paralectotype exists. It might be one of the two FMNH “paratypes” listed by MARX (1958), which were presumably part of the series mentioned by BOETTGER (1892). Further clarification of the status of these two specimens is necessary. – (4) The description of *Mantella attemsi* was based on two specimens (WERNER, 1901), corresponding to the specimens NMW 20837 and ZMB 16588. Both are today in a rather bad state of preservation. Color patterns are largely faded, only the dorsolateral color border is still recognizable. In the lectotype NMW 20837, a few ventral color patterns (light vermiculated markings on the posterior venter) are still faintly recognizable. The paralectotype ZMB 16588 is most probably a male.

Material examined. – Difficulty of identification of specimens as *M. betsileo* is enhanced by the existence of a very similar, undescribed species (*M. sp. 1*, see below). Since this species is generally larger than *M. betsileo*, size was one of the major diagnostic characters for preserved specimens with faded coloration. However, we cannot totally exclude that some specimens may be wrongly identified and in fact be subadults of *M. sp. 1*. In parentheses, we give SVL for most specimens.

The following specimens can clearly be assigned to *M. betsileo*: BMNH 84.11.3.4 (Nosy Be; purch. from “Linnæa”); BMNH 86.2.25.25-28 (Nosy Be; “Senckenberg Museum”; NIL; SVL 23.7 mm,

20.7 mm, 22.2 mm, 23.3 mm); BMNH 1909.10.19.21 (Nosy Be; P. KRIEGER); BMNH 1926.10.27.4-7 (Antongil forest, Maroantsetra; purch. ROSENBERG; NIL; largest female 25.3 mm); BMNH 1952.1.1.55-56 (Rantabe, Antongil bay, Maroantsetra; coll. C. S. WEBB; female 55: 25.7 mm); ZFMK 17604-9 (Maroantsetra; leg. H. MEIER I.1976); ZFMK 27680 (Maroantsetra; leg. H. MEIER X.1979); ZFMK 28867-8 (Nosy Be; through Linnaea 1886; originally Museum Göttingen); ZFMK 46004 (Nosy Boraha [Ile Ste. Marie]; leg. F. W. HENKEL II.1987; CS); ZFMK 46781-3 (Nosy Be; Loucoubé; leg. R. SEIPP IV.1987); ZFMK 47007 (Nosy Be; Loucoubé; leg. F. W. HENKEL & J. SAMLET II.1987); ZFMK 47218 (Sahafary; leg. F. GLAW XI.1987); ZFMK 47289 (Nosy Boraha [Ile Ste. Marie]; leg. H. MEIER XI.1987); ZFMK 48257-8 (Nosy Be; Loucoubé; leg. W. SCHMIDT 1987); ZFMK 52744 (Nosy Boraha [Ile Ste. Marie]; leg. F. GLAW & M. VENCES III.1991); ZFMK 52745 (Nosy Be; leg. F. GLAW & M. VENCES III.1991); ZFMK 51818 (Nosy Boraha [Ile Ste. Marie]; leg. F. W. HENKEL et al. 1988-89); ZFMK 53708-10 (Nosy Be; leg. F. GLAW & J. MÜLLER II.1992; juveniles); ZFMK 59978-9 (Kirindy; leg. F. GLAW I.1995); ZFMK 62685-7 (locality unknown; CS); ZFMK 62689-96 (locality unknown; TE); ZFMK 62688 (Nosy Be; leg. K. SCHMIDT; TE); MRSN A0064.1-4 (Maroantsetra; leg. F. ANDRIEUX 23.IV.1990); MRSN A0068.1-2 (Kirindy; leg. R. NINCHERI 22.XII.1992).

The following specimens are assigned to *M. betsileo* based on size, general appearance and morphometric characters such as relative hindlimb length: BMNH 94.2.27.21 (Madagascar, coll. LAST, purch. GERARD; pattern totally faded); BMNH 1930.7.1.54-57 (valley 3/4 miles W of Ampoza, 15 miles E of Ankazoabo, SW Madagascar; pres. WHITE; rather small specimens; NIL); MNHN 1884.603-4 (Nosy Be; SVL 25 mm [603], 21 mm [604]); MNHN 1885.34-7 (locality unknown; SVL 21 mm [34], 18 mm [35], 20 mm [36], 18 mm [37]); MNHN 1885.48 (Nosy Be); MNHN 1895.278-9 (lectotype and paralectotype; Pays des Betsileos; MNHN 1896.435-6 (Madagascar, “acquis de l’Institut Linnaea”; color totally faded; SVL 24 mm [435, female?], 23 mm [436]); MNHN 1900.15 (Pays Mahafaly, au Sud; with remark: “male – Joly”; SVL 20 mm); MNHN 1929.225 (source de Namoroko [Ambongo]; juv., SVL 16 mm); MNHN 1953.129, MNHN 1991.1795 [originally 129a] (forêt d’Manjaha; TTA reaches eye center [1795], SVL 25 mm [129], 24 mm [1795], few ventral markings, absent on breast [1795]); MNHN 1953.131, MNHN 1991.1796 [originally 131a] (Bas Manongarivo; SVL 17 mm [131], 16 mm [1796]); MNHN 1953.130, MNHN 1953.133 (locality unknown; SVL 23 mm [130, 133]); MNHN 1953.134 (Nosy-Bé – Lokobe, Manjoky; juv., SVL 13 mm); MNHN 1962.895 (Namoroka, grotte de Bemahara; R. PAULIAN IX.52; TTA reaches eye center, SVL 22 mm); MNHN 1962.896-7 (Anove, forêt littorale; A. DOMERGUE I.1961; TTA reaches eye center [896, 897], SVL 21 mm [896], 22 mm [897]); MNHN 1976.200-2 (Nosy Komba; SVL 21.1 mm [200], 19.7 mm [201], 19.3 mm [203]); TM 9858-67 (Eastern Region, Madagascar; coll. HERSCHILL-CHAUVIN).

The following MNHN specimens with unknown locality are here assigned to *M. betsileo* only based on their size which is given in parentheses: MNHN 1976.181-2 (SVL 22.3 mm [181], 22.0 mm [182]); MNHN 1976.187 (SVL 22.2 mm); MNHN 1976.206 (SVL 19.5 mm); MNHN 1976.222-3 (SVL 20.9 mm [222], 17.6 mm [223]); MNHN 1976.225 (SVL 22.1 mm); MNHN 1976.227 (SVL 22.1 mm); MNHN 1976.230 (SVL 22.8 mm).

The status of two specimens is not sufficiently clarified. They have enlarged disks on fingers and toes and thus resemble *M. laevigata*: MNHN 1953.132, MNHN 1991.1797 [originally 132a] (Tsaratanana; TTA reaches between tympanum and eye [132], SVL 25 mm [132], 20.5 mm [1797]).

Distribution. – Except the type locality “Pays des Betsileos”, all known localities are located in lowlands (altitude between 0 and ca. 500 m), generally near the coast. Also, all east coast localities are in an area north of Betsileo (see DALY et al., 1996: 19). Confirmation of the type locality would therefore be important.

The species is common along the east coast in the Maroantsetra region and on Nosy Boraha, and in the Sambirano region; it also occurs along the west coast. Localities are as follows: [1*] Nosy Boraha (<10 m altitude); [2*] Voloïna (GLAW & VENCES, observations in 1991); [3] Maroantsetra; [4] Rantabe; [5*] Sahafary; [6] Anove; [7] Antanambaobe, and Ambavala near Sandrakatsy in the Mananara reserve (DALY et al., 1996: 100-200 m altitude); [8] Farakaraina near Maroantsetra (DALY et al., 1996: 30 m altitude); [9*] Nosy Be; [10*]

