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. crocea*). 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 PINTAK & 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); Zoölogisch 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 litterally 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 litterally 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 (1992*a*, 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. (1998*b*), Pintak et al. (1998), Vences & Kniel (1998) and Vences et al. (1998, 1999*a*), 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