

## Phylogeny and genus-level classification of mantellid frogs (Amphibia, Anura)

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### Abstract

We propose a novel classification of frogs in the family Mantellidae, based on published phylogenetic information and on a new analysis of molecular data. Our molecular tree for 53 mantellid species is based on 2419 base pairs of the mitochondrial 12S rRNA, 16S rRNA, tRNA<sup>Val</sup> and cytochrome b genes, and of the nuclear rhodopsin gene. Because the genus *Mantidactylus* Boulenger sensu lato is confirmed to be paraphyletic with respect to *Mantella* Boulenger, and is highly diverse in morphology and reproductive biology, we propose to partition *Mantidactylus* into seven genera by elevating four subgenera to genus rank (*Blommersia* Dubois, *Guibemantis* Dubois, *Spinomantis* Dubois, and *Gephyromantis* Methuen) and creating two new genera (*Boehmantis* gen. n. and *Wakea* gen. n.). In addition, we create the new subgenera *Boophis* (*Sahona*) subgen. n., *Gephyromantis* (*Duboimantis*) subgen. n., *G.* (*Vatomantis*) subgen. n., and *Mantidactylus* (*Maitsomantis*) subgen. n. The following species are transferred to *Spinomantis*, based on their phylogenetic relationships: *S. elegans* (Guibé) comb. n. (formerly in *Mantidactylus* subgenus *Guibemantis*); *S. bertini* (Guibé) comb. n. and *S. guibei* (Blommers-Schlösser) comb. n. (both formerly in *Mantidactylus* subgenus *Blommersia*); *S. microtis* (Guibé) comb. n. (formerly in *Boophis* Tschudi). Within *Boophis*, the new *B. mandraka* species group and *B. albipunctatus* species group are established. *Boophis rhodoscelis* (Boulenger) is transferred to the *B. microtympanum* group. The following five species are revalidated: *Mantidactylus bellyi* Mocquard and *M. bourgati* Guibé (not junior synonyms of *M. curtus* (Boulenger)); *M. cowanii* (Boulenger) (not syn. *M. lugubris* (Duméril)); *M. delormei* Angel (not syn. *M. brevipalmatus* Ahl); *Mantella ebenau* (Boettger) (not syn. *M. betsileo* (Grandidier)). The new classification accounts for recent progress in the understanding of the phylogeny and natural history of these frogs, but it is still tentative for a number of species. Future modifications may be necessary, especially as concerns species now included in *Gephyromantis* and *Spinomantis*.

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### Introduction

Mantellidae as defined by Vences and Glaw (2001a) comprised five genera of highly diverse morphology and habits, that are endemic to Madagascar and the

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Comoroan island of Mayotte (Blommers-Schlösser and Blanc 1991; Vences et al. 2003). These were divided in three subfamilies: Boophinae (genus *Boophis*), Laliostominae (genera *Aglyptodactylus* and *Laliostoma*), and Mantellinae (genera *Mantella* and *Mantidactylus*) (Fig. 1).

The classification of these frogs has been controversial. For a long time the treefrogs of the genus *Boophis* were considered to belong to the mainly Asian family Rhacophoridae Hoffman, 1932; the single species of *Laliostoma*, *L. labrosum*, was seen as a representative of the African-Asian ranid genus *Tomopterna* Duméril & Bibron, 1841, and *Mantella* and *Mantidactylus* were often placed as subfamily Mantellinae in the family Ranidae Rafinesque, 1814 or as a separate family Mantellidae (Blommers-Schlösser and Blanc 1991). The affinities of *Aglyptodactylus* were most disputed until Glaw et al. (1998) demonstrated its relations to *Laliostoma labrosum* (as *Tomopterna labrosa*) based on morphological and other non-molecular characters. Eventually, molecular data revealed that all those taxa

belong to one well-supported monophyletic radiation (Bossuyt and Milinkovitch 2000; Vences et al. 2000, 2003), considered as family Mantellidae by Vences and Glaw (2001a). It is likely that this clade is the sister group of the Asian Rhacophoridae (Bossuyt and Milinkovitch 2000), but so far only one study (Roelants et al. 2004) has provided adequate support for this hypothesis.

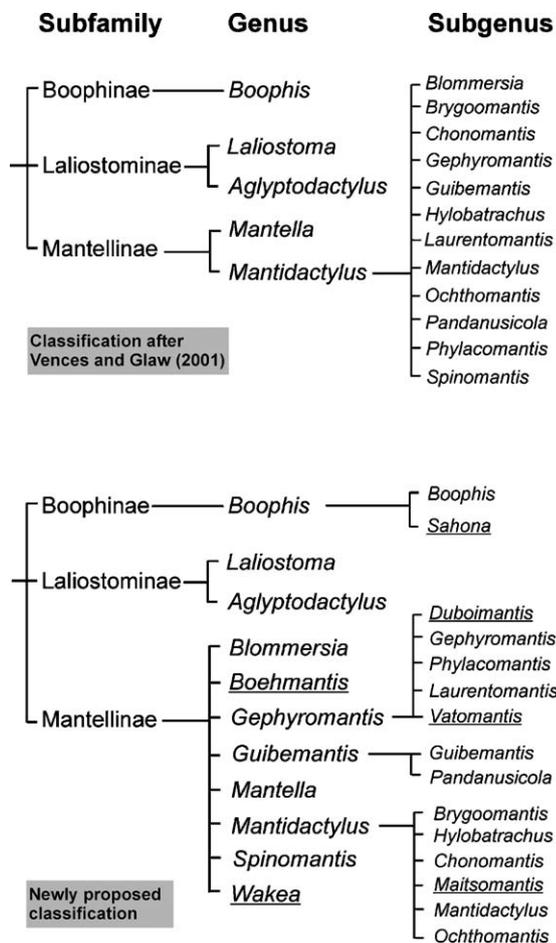
According to current knowledge as summarized here, Mantellidae comprises 164 described and valid species; see Part 1 of the accompanying Organisms Diversity and Evolution Electronic Supplement (<http://www.senckenberg.de/odes/06-11.htm>). While *Laliostoma* and *Aglyptodactylus* include only one and three species, respectively, *Boophis* (54 species), *Mantella* (16 species) and *Mantidactylus* (90 species, including those resurrected below) are very diverse. *Boophis* and *Mantella* are subdivided into various phenetic species groups (Blommers-Schlösser 1979a, b; Blommers-Schlösser and Blanc 1991; Vences et al. 1999; Glaw and Vences 2003), whereas *Mantidactylus* was subdivided in 12 subgenera (Dubois 1992; Glaw and Vences 1994; Fig. 1).

Recent work has led to a spectacular increase of species numbers in Mantellidae. Whereas Blommers-Schlösser and Blanc (1991) recognized 84 species, the number reached 108 in Glaw and Vences (1994), and 141 in Glaw and Vences (2003). Many additional species have been identified but not yet named. This progress in knowledge results from intensive exploration of poorly known regions in Madagascar and from systematic application of bioacoustic and molecular techniques (Köhler et al. 2005).

In light of these discoveries as well as new molecular insight into the phylogenetic relationships within Mantellidae, a new and updated classification of these frogs has been overdue. This especially applies to the genus *Mantidactylus* which so far included frogs extremely diverse in morphology and reproductive modes (Blommers-Schlösser 1979b; Glaw and Vences 1994; Andreone 2003), and was paraphyletic with respect to the well-established genus *Mantella* (Richards et al. 2000; Vences et al. 2003). Based on published and novel phylogenetic data we here propose a partitioning of *Mantidactylus* and provide an updated classification of all currently recognized species of mantellid frogs.

## Material and methods

For the most part, this paper presents a synthesis of previously published data. However, in order to obtain an updated analysis of mantellid relationships we complemented the molecular data set of Vences et al. (2003) with additional DNA sequences. The original



**Fig. 1.** Comparison of classifications to subgenus level for the family Mantellidae. Top: after Vences and Glaw (2001a); bottom: present proposal (new taxa underlined).

dataset was composed of sequences of the mitochondrial 12S rRNA, tRNA<sup>Val</sup> and 16S rRNA genes, and the nuclear rhodopsin gene, from 47 mantellid species. We have added data on additional six crucial species as well as on another gene region: a 551 base-pair fragment of the mitochondrial cytochrome b gene. The newly obtained sequences have been deposited in GenBank under the accession numbers [DQ235414–DQ235445](#), [DQ235447–DQ235451](#), and [DQ235453–DQ235455](#). Complete sequence sets were not available for all species, especially as regards cytochrome b. For the full list of GenBank accession numbers and voucher specimens associated with the present study see Part 2 of the Electronic Supplement.

After exclusion of hypervariable regions and gapped sites of the ribosomal RNA genes the character supermatrix consisted of 2419 base pairs each for 53 mantellid and three outgroup taxa. The phylogeny was reconstructed with a partitioned Bayesian analysis using the program MrBayes (Ronquist and Huelsenbeck 2003). We ran one million generations, sampling one out of every 100 trees and discarding the first 2000 trees as ‘burn in’, based on empirical evaluation. The dataset was divided into seven partitions, one for the 12S and 16S rRNA genes, and one for first, second, and third codon positions of the rhodopsin and cytochrome b genes. Robustness of nodes was tested by a bootstrap analysis of 2000 replicates in PAUP\* (Swofford 2002) under the maximum parsimony optimality criterion, with all characters unweighted, tree bisection-reconnection branch swapping, and random addition sequences with 10 replicates.

In addition, we obtained information from a large dataset of 16S rDNA sequences from the vast majority of mantellid species (including many undescribed taxa), assembled in the framework of a DNA barcoding study of the Malagasy amphibian fauna (Vences et al. 2005b). Phylogenetic analysis of these sequences (GenBank accession numbers [AY847959–AY848683](#)) has provided confirmation for the subgeneric placement of many taxa (results not shown).

Further insights came from the morphological phylogeny of Vences et al. (2002c), and from an unpublished DNA sequence set of the nuclear Rag-2 gene in 43 mantellids that is currently being analysed by S. Hoegg, University of Konstanz (Germany), to be published elsewhere.

Morphological and osteological data in the following are described using the terminology of Blommers-Schlösser and Blanc (1991) and Vences et al. (2002c). Femoral glands are described according to Glaw et al. (2000b). The data presented summarize current knowledge, but the states of many characters are unknown for numerous species; therefore diagnoses of various subgenera and genera are liable to change upon future studies.

## Results and discussion

The tree resulting from Bayesian analysis of five genes in 53 mantellid species is shown in Fig. 2. Its general topology agrees with that presented in Vences et al. (2003), suggesting that the addition of another gene (cytochrome b) stabilized the reconstruction. The three subfamilies in Mantellidae resulted as monophyletic groups.

Based on these results, and on additional analyses in Vences et al. (2002a, 2002c) and Vences and Glaw (2001b, 2005), we propose a number of changes to mantellid classification as summarized below (see also Fig. 1). A complete classification of all species in the Mantellidae is given in Part 1 of the Electronic Supplement. No changes are proposed concerning the subfamily Laliostominae. For Boophinae we propose a subdivision of the genus *Boophis* into two subgenera, establishment of two new phenetic species groups, and changes in group placement of a few species. The most extensive modifications affect the largest subfamily, Mantellinae. Paraphyly of *Mantidactylus* sensu lato relative to *Mantella*, and the enormous diversity within the former in terms of morphology and reproductive habits warrant its division into several genera, as well as the creation of new subgenera.

### Subfamily diagnoses

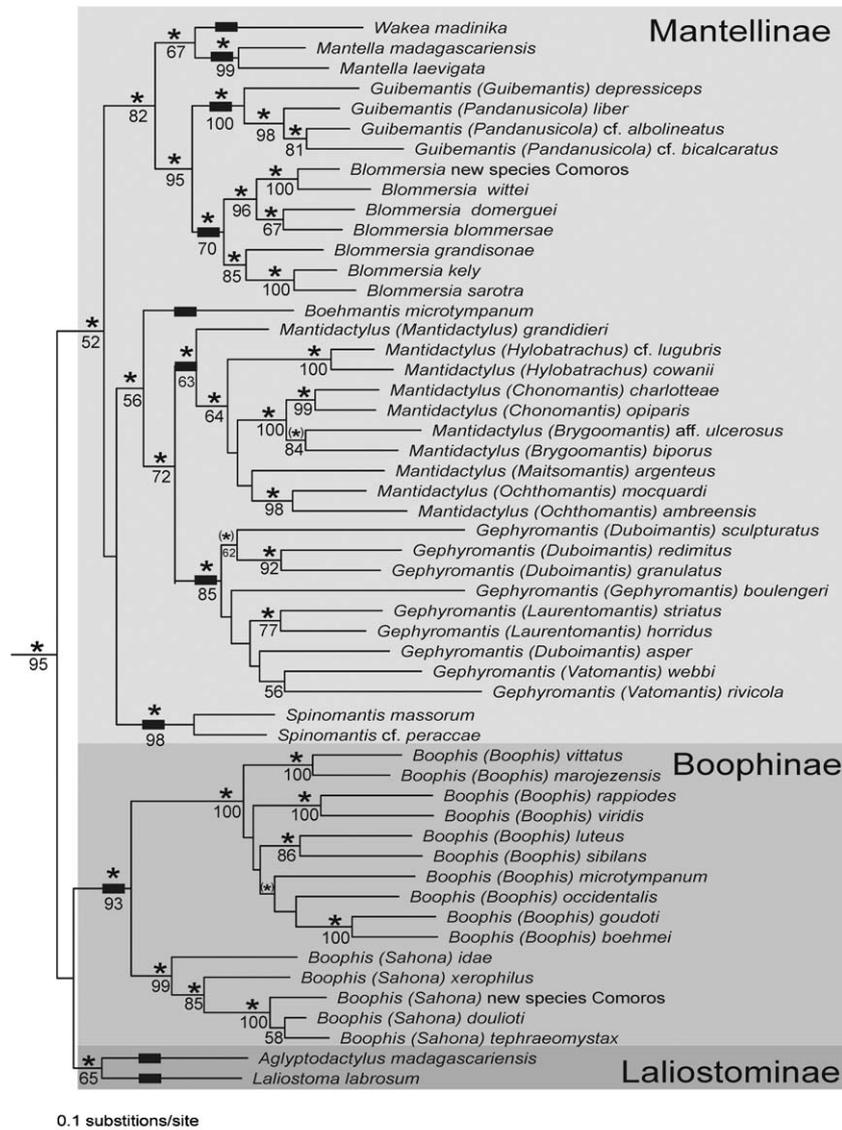
Vences and Glaw (2001a) defined Boophinae, Laliostominae and Mantellinae using a number of morphological and osteological characters. We here provide more extensive diagnoses for these subfamilies.

According to the rules concerning the formation of scientific names set out by the International Code of Zoological Nomenclature (ICZN 1999), the correct derivation of the subfamilial name based on the genus name *Laliostoma* would have been Laliostomatinae. The etymology of the genus name *Boophis* is unclear; therefore grammatically correct derivation of the corresponding subfamilial name is ambiguous. Boophinae is correct if *Boophis* is an arbitrary combination of letters, whereas Boophiinae would have been correct if *Boophis* is derived from the Ancient Greek “ophis” (= snake, reptile). In any case, under Code Article 29.4 the original spellings of both subfamily names, Laliostominae and Boophinae, “must be maintained” (ICZN 1999).

### Subfamily Boophinae Vences & Glaw, 2001

Type genus: *Boophis* Tschudi, 1838. Distribution: Madagascar and Mayotte (Comoro Islands).

Arboreal (some species partly terrestrial), firmisternal frogs with a bony sternal style and an intercalary element between ultimate and penultimate phalanges of



**Fig. 2.** Consensus tree from Bayesian analysis, showing preliminary relationships among mantellids based on 12S and 16S rRNA, tRNA<sup>Val</sup>, rhodopsin, and cytochrome b gene sequences. Species names given according to present new classification. Black bars mark nodes supporting monophyly of genera as defined herein. Asterisks mark nodes of Bayesian posterior probabilities of 0.99–1.00, asterisks in parenthesis mark values of 0.95–0.98. Numbers are support values in percent from a bootstrap analysis under the maximum parsimony optimality criterion (2000 replicates). Tree rooted using *Rana temporaria*, *R. temporalis* (family Ranidae), and *Polypedates cruciger* (Rhacophoridae) as outgroups.

fingers and toes. Terminal phalanges distinctly bilobed or slightly Y-shaped. Two free tarsal elements (plus a small third one in some *Boophis* (*Sahona*)). Maxillary teeth present. Atlantal cotyles widely separated. Vertebral column procoelous. Omosternum unforked at its base (exceptionally slightly forked in representatives of *Boophis* (*Sahona*)). Anterolateral process of hyoid plate present in some *Boophis* (*Sahona*), absent in *Boophis* s. str. Finger and toe pads with a complete circummarginal groove. First finger shorter than or subequal to second finger. Webbing between fingers present or absent. Males with nuptial pads but without femoral glands. General-

ized reproductive behaviour with axillary amplexus; eggs (no foam nests) are laid into open water (not in leaf axils or treeholes). Exotrophic tadpoles of Orton type IV. Males distinctly smaller than females (of similar size only in *Boophis albilabris*, and *B. occidentalis*, see Cadle 1995 and Andreone et al. 2002). Karyotype:  $2n = 26$ ; meta- and submetacentric chromosomes only (Blommers-Schlösser 1978; Aprea et al. 2004).

#### Subfamily Laliostominae Vences & Glaw, 2001

Type genus: *Laliostoma* Glaw, Vences & Böhme, 1998. Distribution: Madagascar.

Terrestrial firmisternal frogs with a bony sternal style and with (*Aglyptodactylus*) or without (*Laliostoma*) intercalary element between ultimate and penultimate phalanges of fingers and toes. Terminal phalanges knob-shaped. Two free tarsal elements. Maxillary teeth present. Atlantal cotyles narrowly separated. Vertebral column diplasiocoelous. Omosternum slightly forked at its base. Anterolateral process of hyoid plate present. Finger and toe pads without a circummarginal groove. First finger distinctly longer than second. No webbing between fingers. Males with blackish nuptial pads (when breeding) but without femoral glands. Generalized reproductive behaviour with axillary amplexus; eggs are laid into stagnant open water, generally as a monolayer on the water surface (Glos 2003). Exotrophic tadpoles of Orton type IV. Breeding males of two species (*Aglyptodactylus madagascariensis*, *A. securifer*) are known to turn yellow. Males distinctly smaller than females. Karyotype:  $2n = 26$ ; biarmed chromosomes (Blommers-Schlösser 1978).

#### Subfamily Mantellinae Laurent, 1946

Type genus: *Mantella* Boulenger, 1882. Distribution: Madagascar and Mayotte (Comoro Islands).

Arboreal, scansorial, terrestrial or semi-aquatic firmisternal frogs with a bony sternal style and an intercalary element between ultimate and penultimate phalanges of fingers and toes. Terminal phalanges at least slightly bilobed, sometimes distinctly Y-shaped. Almost all species with three free tarsal elements, although third element can be very small in many species and absent in rare cases. Maxillary teeth present or absent. Atlantal cotyles widely separated except in *Mantidactylus* (*Mantidactylus*) (unknown for *Wakea*, *M. (Brygoomantis)*, *M. (Ochthomantis)*). Vertebral column procoelous or diplasiocoelous. Forking of omosternum variable, ranging from unforked (in *Gephyromantis* (*Laurentomantis*) and *G. (Vatomantis)*) to broadly forked. Anterolateral process of hyoid plate present (exceptionally as rudiment only). Finger and toe pads with a complete circummarginal groove. First finger shorter than or subequal to second finger. Generally no webbing between fingers (rudiments can be present in *Guibemantis* s. str., *G. (Pandanusicola)*, and *Spinomantis*). Males without nuptial pads, mostly with femoral glands. Derived reproductive biology (absence

of strong mating amplexus, egg deposition outside of water; Fig. 3). Males distinctly smaller than females in some clades, of similar size as females in others. Karyotype: chromosomes meta- and submetacentric only (*Mantella*, *Guibemantis*, *Blommersia*, *Spinomantis*, and *M. (Mantidactylus)*), or meta-, submeta-, and acrocentric (*Gephyromantis* (*Duboimantis*), *M. (Brygoomantis)*, *M. (Chonomantis)*, *M. (Hylobatrachus)*, *M. (Ochthomantis)*). Karyotype:  $2n = 26$ , except  $2n = 24$  in *Spinomantis aglavei* and species of *M. (Brygoomantis)* (Blommers-Schlösser 1978).

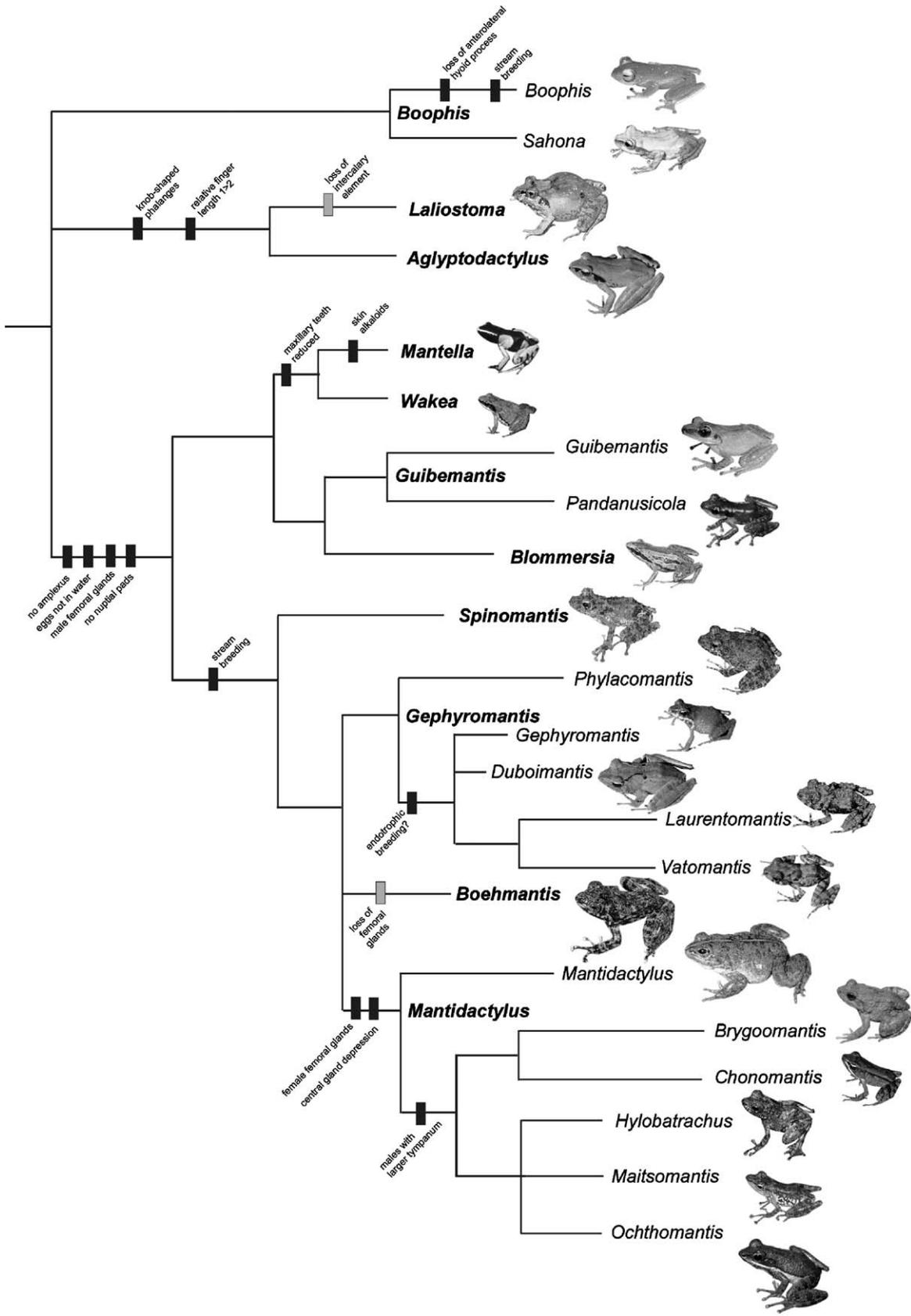
#### Classificatory changes in the Boophinae

(1) Based on analyses of 16S rDNA sequences in which it clearly formed a clade with *Boophis microtympanum* and *B. williamsi*, we transfer *Boophis rhodoscelis* to the *B. microtympanum* group (Vences et al. 2005a). Previously, group assignment in this case was seen as difficult and changed several times. Blommers-Schlösser (1979b) used a *B. rhodoscelis* group that otherwise included *B. difficilis* (now *B. pyrrhus*), *B. miniatus* and *B. majori*. Blommers-Schlösser and Blanc (1991) assigned *B. rhodoscelis* to the *B. goudoti* group. This arrangement was followed by Glaw and Vences (1994) and Glaw et al. (2001). The present inclusion in the *B. microtympanum* group is supported by non-molecular data as well: brownish specimens of *B. microtympanum* can be extremely similar to *B. rhodoscelis* (Glaw and Vences 1994, p. 111). The members of both species occur at rather high altitudes (above 1000 m), exhibit reddish colour on the ventral sides of the hindlimbs, and a relatively low sound frequency in advertisement calls.

(2) 16S and cytochrome b data show non-monophyly of the *B. rappiodes* group (Vences et al. 2002a and unpublished data); consequently, we erect the new *Boophis mandraka* group to accommodate *B. mandraka*, *B. liami*, *B. sambirano*, and *B. solomaso*, resulting in two monophyletic species groups (see also Vences and Glaw 2005b).

*Group diagnosis:* Small-sized (male snout-vent length 17–26 mm), yellowish treefrogs, probably all with greenish bones. In contrast to the other species groups, except for the *B. rappiodes* group, ventral surface in life is transparent, similar to the Neotropical family Centro-

**Fig. 3.** Schematic representation of phylogenetic relationships among genus-group taxa in Mantellidae, with photographs of typical representatives of each terminal taxon. Genus names shown in boldface. Branch lengths adjusted for layout purposes, thus not phylogenetically informative. Photographs not to scale, but larger species represented slightly larger than small species. Vertical bars indicate sets of selected morphological and biological synapomorphies of major clades; black bars denote derived characters, grey bars reversals. Placement of endotrophic-breeding synapomorphy in a clade within *Gephyromantis* is hypothetical: endotrophic development is not clear for all clade members. Another derived character, stream breeding, has also evolved in some *Mantella* and one *Blommersia* species, and reversed in some *Brygoomantis*. Femoral gland structure and presence in females may have reversed in *Maitsomantis*, but details require further study.



lenidae. Tibiotarsal articulation reaches beyond snout tip in most males. Besides the genetic differences, species of the *B. mandraka* group differ from those of the *B. rappiodes* group as restricted here in at least one derived morphological character (nostril nearer to eye than to snout tip vs. vice versa) and one chromatic character (dorsal surface without distinct red dots or spots vs. dorsal surface mostly with distinct red dots or spots); see Vallan et al. (2003).

(3) The new *Boophis albipunctatus* group is erected for several smaller species of the former *Boophis luteus* group (*B. albipunctatus*, *B. ankaratra*, *B. sibilans*, *B. schuboeae*) which is a monophyletic clade according to 16S data (not shown).

*Group diagnosis*: Small to medium-sized (male snout-vent length 24–33 mm), green treefrogs without translucent belly. As far as known the vocal sac is single, subgular (not paired as in at least several species of the *B. luteus* group). Small white spots on the dorsum are very characteristic for some species (*B. albipunctatus*, *B. sibilans*) and can be present in the others as well. The tadpoles are known to be adapted to fast-flowing water, having a large number of labial tooth rows and papillae, at least in *B. ankaratra*, *B. schuboeae*, and *B. sibilans*, according to Glaw and Vences (1994) and Raharivoloniaina et al. (unpublished).

(4) The *Boophis tephraeomystax* group is transferred to:

#### Subgenus *Sahona* subgen. n.

*Type species*: *Polypedates tephraeomystax* Duméril, 1853.

*Etymology*: The subgenus name is derived from the Malagasy word “sahona” (= frog); its gender is defined as feminine.

*Diagnosis*: Mantellid treefrogs endemic to Madagascar and the Comoro island of Mayotte. See subfamilial diagnosis of Boophinae above for general osteological and morphological features. Terminal phalanges distinctly bilobed or slightly Y-shaped. Two or three free tarsal elements. Maxillary teeth present. Omosternum unforked or slightly forked. Anterolateral process of hyoid plate present or absent. Webbing between fingers absent or rudimentary. In contrast to the remaining *Boophis*, species of *B. (Sahona)* breed in stagnant, often temporary water, are often found outside of rainforest, and also occur in rather arid areas. Known egg numbers per female are rather high, egg diameters rather small. At least some species lay their eggs as a monolayer on the water surface (Glos 2003). Breeding males of some species are known to turn yellow.

*Justification*: Morphological, ecological and molecular data congruently define one clade within the genus *Boophis* as monophyletic group. This group comprises the vast majority of *Boophis* species, i.e. all except those in the *B. tephraeomystax* group. Species in the latter are

characterized by a number of plesiomorphic osteological features (Vences et al. 2002c), and by breeding in ponds, which might be ancestral behaviour in mantellids (Vences et al. 2002a). Not all species in the group have been included in molecular studies; separate analyses based on the 16S and cytochrome b genes (Vences et al. 2002a, Chiari et al. unpublished) failed to define this group as monophyletic. However, the present combined analysis of five genes provides strong support for a clade of all five species included in the analysis. We consider this as sufficient justification to infer monophyly, and thus for erection of a new subgenus.

#### New classification of genera in Mantellinae, and descriptions of new taxa

Besides *Mantella* Boulenger and *Mantidactylus* Boulenger, we propose to recognize the following former subgenera at genus rank: (1) *Guibemantis* Dubois, including subgenera *G. (Guibemantis)* and *G. (Pandanusicola)* Glaw & Vences; (2) *Blommersia* Dubois; (3) *Spinomantis* Dubois; and (4) *Gephyromantis* Methuen, including *G. (Gephyromantis)*, *G. (Laurentomantis)* Dubois, and *G. (Phylacomantis)* Glaw & Vences. In addition, we create two new genera to accommodate *Mantidactylus madinika* (sister taxon to *Mantella*) and *M. microtympnum*, respectively. Considering novel phylogenetic arrangements presented herein (Figs. 2 and 3) and in Vences and Glaw (2001a), we furthermore (1) transfer all species previously in the subgenus *Phylacomantis* (except for the taxa *corvus* and *pseudoasper*) and several species previously in the subgenus *Gephyromantis* to a new subgenus; (2) create a new subgenus for *G. rivicola*, *G. silvanus* and *G. webbi* (previously in *Mantidactylus (Gephyromantis)*); (3) create a new subgenus in *Mantidactylus* for *M. argenteus* (previously in *M. (Blommersia)*); (4) transfer *Mantidactylus bertini* and *M. guibei* (previously in *M. (Blommersia)*), *M. elegans* (previously in *M. (Guibemantis)*), and *Boophis microtis* to the genus *Spinomantis*; and (5) resurrect *Mantidactylus bellyi*, *M. bourgati*, *M. cowanii*, *M. delormei*, and *Mantella ebenau* from previous junior synonymy.

This new classification of the subfamily Mantellinae significantly differs from previous arrangements. We therefore provide new or revised diagnoses for all genus-level taxa in this subfamily (in alphabetical order), mainly based on non-osteological characters.

#### Genus *Blommersia* Dubois, 1992

*Diagnosis* (see also Glaw and Vences 2002): Small frogs (adult snout-vent length 15–26 mm) with cryptic colouration. At least traces of webbing between toes. Lateral metatarsalia connected or separated. Inner and outer metatarsal tubercles present. Finger tips slightly to moderately enlarged. Tibiotarsal articulation does not

reach beyond nostril. Distinct femoral glands of type 1 in male, glands absent in female. Tibial glands absent. Male with single, moderately distensible, subgular vocal sac. Maxillary teeth present, vomerine teeth present or absent. Tongue weakly bifid. Vertebral column diplasiocoelous. Tympanum of same size in male and female. Habits terrestrial or semi-arboreal. Activity diurnal and nocturnal. Eggs pigmented, deposited on leaves above water or hidden in cavities on the ground. Larval development in stagnant or slowly running water bodies. Free swimming and exotrophic tadpoles, with generalized mouthparts. No observations on parental care.

*Justification:* The elevation of *Blommersia* to genus rank is necessary to resolve the paraphyly of *Mantidactylus* sensu lato with respect to *Mantella*. Monophyly of *Blommersia* is clear from molecular characters (Fig. 2).

*Distribution:* Madagascar and Mayotte Island (Comoros).

#### Genus *Boehmantis* gen. n.

*Type species:* *Mantidactylus microtyimpanum* Angel, 1935.

*Etymology:* We are pleased to dedicate this genus to Wolfgang Böhme, Bonn, in recognition of his important contributions to herpetology. For the genus name, the terminal me in “Böhme” has been omitted for easier pronunciation; for derivation of the Ancient Greek “mantis” (= treefrog) see Vences et al. (1999). Gender of genus name: masculine.

*Diagnosis:* Large-sized frogs (adult snout-vent length 60–80 mm). Extended webbing between toes. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercles absent. Finger tips strongly enlarged. Tibiotarsal articulation does not reach beyond nostril. Femoral glands not recognizable externally in either sex. Tibial glands absent. Male probably with single, only slightly distensible, subgular vocal sac (the species has never been heard or seen calling). Maxillary and vomerine teeth present. Tongue bifid. State of vertebral column unknown. Tympanum very small, of same size in male and female. Habits terrestrial on boulders in torrents. Activity nocturnal. Eggs pigmented (Andreone and Randriamahazo 1997). No observations on parental care. Exotrophic tadpoles with morphology as typical for lentic-water dwellers, occurring in rock pools (Andreone and Nussbaum 2006).

*Justification:* Most remarkable is the apparent lack of femoral glands in males and females, suggested by their absence in all known specimens, e.g. the large number of mature males and females studied by Andreone and Nussbaum (2006). This renders *Boehmantis* the only known deep clade of mantellines in which femoral glands are completely absent. Further unusual features are the small tympanum and the fact that none of these frogs has ever been heard calling. Previously, *Boehman-*

*tis microtyimpanum* was considered as closely related to *Mantidactylus grandidieri* and *M. guttulatus*, and thus included in *M. (Mantidactylus)*. However, the latter two species have very distinct femoral glands in males and rudimentary glands in females (see also Andreone and Nussbaum 2006). Molecular data (Fig. 2) place *B. microtyimpanum* as sister to the clade containing *Mantidactylus* and *Gephyromantis* as defined in the present work.

*Distribution:* South-eastern Madagascar.

#### Genus *Gephyromantis* Methuen, 1920

*Diagnosis:* Small to medium-sized frogs (adult snout-vent length 20–50 mm). Webbing between toes present or absent. Lateral metatarsalia connected or separated. Inner metatarsal tubercle present, outer tubercles present or absent. Finger tips moderately enlarged. Hindlimb length variable. Femoral glands mostly of type 2 in male, absent in female. Tibial glands present in several species of subgenus *Laurentomantis*, absent in other subgenera. Male mostly with paired or bilobate (more rarely single), subgular vocal sacs. Maxillary teeth present, vomerine teeth mostly present. Tongue bifid. Tympanum of male often only slightly (though statistically significantly) larger than in female. Habits terrestrial or arboreal, along streams or independent from water bodies. Activity nocturnal and diurnal. Reproduction largely unknown. Known clutches with few and relatively large eggs, deposited outside of water (known only for *G. webbi*, *G. eiselti*, and *G. asper*). Many species probably endotrophic, with direct development (known only for *G. eiselti*) or with non-feeding larval stages that might be hidden in nests (free swimming and exotrophic tadpoles known only in subgenus *Phylacomantis*). Parental care known only from one species of *G. (Vatomantis)*.

*Justification:* Generic separation of *Gephyromantis* from *Mantidactylus* is justified by significant genetic differentiation (see Fig. 2), as well as by major differences in habits (in and along running water in *Mantidactylus* vs. mostly water-independent in *Gephyromantis*) and reproduction (free swimming, exotrophic tadpoles in *Mantidactylus* vs. many presumably endotrophic species in *Gephyromantis*). Moreover, the elevation of *Gephyromantis* emphasizes a synapomorphy of *Mantidactylus* s. str. that is unique within Mantellidae: the presence of small but distinct femoral glands in females (absent in all other mantellid females). The genus *Gephyromantis* itself is characterized by the presence, in most species, of derived vocal sacs which (in contrast to all other mantellids) are bilobate or paired subgular when inflated, and can be identified by dark skin folds along the lower jaw (white in *G. webbi*).

Five subgenera are recognized:

### Subgenus *Duboimantis* subgen. n.

*Type species:* *Limnodytes granulatus* Boettger, 1881.

*Etymology:* We dedicate this subgenus to Alain Dubois, Paris, in recognition of his contributions to the classification of ranoid frogs. Considering the literal meaning of the French “du bois” (= from the forest), the subgeneric name is all the more appropriate for these forest-dwelling frogs. In forming the name, the terminal s in “Dubois” has been omitted for easier spelling; for the “mantis” component see *Boehmantis* above. Gender of subgenus name: masculine.

*Diagnosis:* Medium-sized frogs (adult snout-vent length 27–50 mm). Webbing between toes present. Lateral metatarsalia largely connected or separated. Inner metatarsal tubercle present, outer tubercles present or absent. Finger tips moderately enlarged. Tibiotarsal articulation variable. Femoral glands of type 2 in male, absent in female. Tibial glands absent. Male with single or paired, subgular vocal sacs. Maxillary and vomerine teeth present. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of similar sizes in male and female. Habits terrestrial or arboreal, along streams or independent from water bodies. Activity nocturnal and diurnal. Clutches and tadpoles unknown, at least some species probably without free swimming tadpoles or with direct development.

*Justification:* The phylogenetic relations of species in the former subgenera *M.* (*Phylacomantis*) and *M.* (*Gephyromantis*) are not well established. Sequences from the 16S rRNA (Vences and Glaw 2001a) and cytochrome b (Chiari et al. unpublished) genes as well as karyotype data (Andreone et al. 2003) indicate that *Gephyromantis corvus* + *G. pseudoasper* and *G. asper* (probably + the similar *G. spinifer*) each form a separate clade, whereas the remaining, larger species with separated metatarsalia seem to be closely related to each other. Monophyly and close relationships seem beyond doubt for a group consisting of the following species: *G. granulatus*, *G. cornutus*, *G. leucomaculatus*, *G. redimitus*, *G. tschenki* and *G. zavona* (Vences and Glaw 2001b). Moreover, the inner metatarsal tubercle in most *Duboimantis* species (at least in *G. asper*, *G. spinifer*, *G. ambohitra*, *G. luteus*, *G. plicifer*, *G. redimitus*, *G. cornutus*, *G. granulatus*, and *G. leucomaculatus*) is significantly larger in males than in females. Consequently, erecting the subgenus *Duboimantis* is clearly justified, but it remains to be seen whether some of the included species, especially *G. asper*, *G. spinifer* and *G. ambohitra*, represent separate groups instead.

*Distribution:* Widespread in the rainforest belt of eastern Madagascar, with many species distributed or endemic to the north.

### Subgenus *Gephyromantis* Methuen, 1920

*Diagnosis:* Small frogs (adult snout-vent length 20–33 mm). Webbing between toes absent. Lateral metatarsalia connected. Inner and outer metatarsal tubercle present. Finger tips moderately enlarged. Point reached by tibiotarsal articulation ranges from nostril to beyond tip of snout. Femoral glands of type 2 (sometimes difficult to recognize) in male, absent in female. Tibial glands absent. Male mostly with dark folds in the jaw angles; inflated vocal sacs mostly paired subgular or bilobate, single in *G. eiselti* and *G. thelenae*. Maxillary teeth present, vomerine teeth mostly present. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of same size in male and female. Habits terrestrial or semi-arboreal, independent from water bodies. Activity mainly diurnal. Clutches deposited outside of water. Presumably all species with direct development (known only for *G. eiselti*).

The species included in this subgenus are rather homogeneous in morphology and habits, thus most likely represent a monophyletic clade, perhaps with the exception of the northernmost *M. klemmeri* which is genetically divergent (not shown) and only tentatively placed in this subgenus.

*Distribution:* Eastern Madagascar.

### Subgenus *Laurentomantis* Dubois, 1980

*Diagnosis* (see also Vences et al. 2002c): Small frogs (adult snout-vent length 20–35 mm) with granular dorsal skin. Webbing between toes absent. Lateral metatarsalia connected. Inner and outer metatarsal tubercle present. Finger tips moderately enlarged. Point reached by tibiotarsal articulation ranges from eye to beyond tip of snout. Femoral glands similar to type 2 in male, absent in female. Tibial glands present or absent. Male with single, subgular vocal sac. Maxillary teeth present, vomerine teeth mostly present, but sometimes poorly recognizable. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of same size in male and female. Habits terrestrial or semi-arboreal, calling activity along or independent from water bodies. Activity mainly nocturnal. Reproduction completely unknown.

The species included in this subgenus are similar to each other in morphology, habits and call structure, and several of them are consistently grouped by molecular data (e.g., Fig. 2); the subgenus thus most likely represents a monophyletic clade.

*Distribution:* Eastern Madagascar.

### Subgenus *Phylacomantis* Glaw & Vences, 1994

*Diagnosis:* Medium-sized frogs (adult snout-vent length 31–38 mm). Webbing between toes present. Lateral metatarsalia partly connected. Inner and outer metatarsal tubercle present. Finger tips moderately enlarged. Point reached by tibiotarsal articulation

ranges from eye to nostril. Femoral glands of type 2 in male, absent in female. Tibial glands absent. Male with paired, subgular vocal sacs. Maxillary and vomerine teeth present. Tongue bifid. State of vertebral column unknown. Tympanum and inner metatarsal tubercle of male slightly larger than those of female in *G. pseudoasper*. Habits terrestrial and arboreal, along small forest streams. Activity diurnal and nocturnal. Egg clutches probably terrestrial. Free swimming and exotrophic tadpoles with reduced number of labial tooth rows which can produce clicking vocalizations. The similarities between the two species, especially regarding the unusual tadpoles, clearly indicate the monophyly of *Phylacomantis*.

**Distribution.** Locally in northern, western and south-western Madagascar.

### Subgenus *Vatomantis* subgen. n.

**Type species:** *Rhacophorus webbi* Grandison, 1953.

**Etymology:** Derived from the Malagasy word “vato” (= stone) and the Ancient Greek “mantis” (= treefrog), to reflect that these frogs are usually found on large mossy rocks and boulders along small rainforest streams. Gender of subgenus name: masculine.

**Diagnosis:** Small-sized (adult snout-vent length 22–33 mm) olive-greenish frogs without a light frenal stripe and a distinct black spot in the temporal region. Webbing between toes rudimentary. Lateral metatarsalia connected. Inner metatarsal tubercle present, outer tubercle not recognizable. Finger tips distinctly enlarged. Point reached by tibiotarsal articulation ranges from eye to beyond snout tip. Femoral glands mostly of type 2 in male, absent in female. Tibial glands absent. Male with paired, subgular vocal sacs (no sac recognizable in holotype of *G. silvanus*, but distinct dark folds along lower jaw in new material, ZSM 177/2002 and 178/2002). Maxillary teeth present, vomerine teeth present or rudimentary. Tongue bifid. Vertebral column diplasiocoelous. Tympanum and inner metatarsal tubercle not larger in male than in female. Habits terrestrial on mossy rocks along small streams. Activity diurnal and nocturnal. Clutches of *G. webbi* on boulders above small streams, guarded at night by the male (Andreone 1993, authors' pers. obs.). Tadpoles unknown.

**Justification:** Previously, the three included species were placed in the *Mantidactylus boulengeri* species group (Vences et al. 1997), which becomes *Gephyromantis* s. str. in the present classification. However, *G. webbi* differs from species of the *boulengeri* group by having white (not black), paired, subgular vocal sacs, and the assignment of *G. rivicola* and *G. silvanus* was tentative in the original publication. Sequences from the 16S rRNA (unpublished) and cytochrome b (Chiari et al. unpublished) genes indicate that the *boulengeri*

group is a monophyletic clade if the three *Vatomantis* species and perhaps *G. klemmeri* are excluded.

Species in *G. (Vatomantis)* differ from those in *Gephyromantis* s. str. by (1) an olive-green (vs. brown) dorsal colouration, (2) absence of a light stripe along the upper lip (vs. usual presence), (3) absence of a dark spot in the tympanic region (vs. usual presence), (4) habits and calling activity along forest brooks (vs. habits and calling activity independent from water bodies), and (5) by endemism to northeastern Madagascar (vs. centre of diversity and endemism in southeastern Madagascar).

*Vatomantis* probably is the sister clade of the subgenus *Laurentomantis* (for the problematic position of *G. asper* in Fig. 2 see discussion of *Gephyromantis (Duboimantis)* above). *Vatomantis* and *Laurentomantis* share several characters, especially an entirely or largely unforked omosternum (known from *G. (V.) rivicola*, *G. (V.) webbi*, *G. (L.) striatus* and *G. (L.) horridus*; see Vences et al. 2002c), a character rarely found in other mantellines. Although the general appearance and habits of the larger, rough-skinned and broad-headed *Laurentomantis* species (*G. horridus*, *G. ventrimaculatus*) are very different from those of *Vatomantis* species, the smaller species in both subgenera (e.g. *G. (L.) malagasius* and *G. (V.) rivicola*) show less obvious differences in general appearance. Species of *Vatomantis* differ from those of *Laurentomantis* by the complete absence of an outer metatarsal tubercle (vs. small tubercle present), less granular skin, paired (vs. single), subgular vocal sacs, and by occurrence along streams (vs. mostly independent from water, but *G. striatus* also along streams).

**Distribution:** Known only from low-altitude rainforest in northeastern Madagascar.

### Genus *Guibemantis* Dubois, 1992

**Diagnosis:** Small to medium-sized frogs (adult snout-vent length 22–59 mm). Moderate or extended webbing between toes. Lateral metatarsalia separated or connected. Inner and outer metatarsal tubercles present. Finger tips distinctly enlarged. Tibiotarsal articulation does not reach beyond snout tip. Femoral glands of type 1 or 2 in male, absent in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary and vomerine teeth present (record of absent maxillary teeth in *G. depressiceps* by Vences et al. 2002c is due to a type-setting error). Tongue bifid. Vertebral column procoelous in subgenus *Pandanusicola*, uncertain in subgenus *Guibemantis*. Tympanum of same size in male and female. Habits arboreal or phytotelmic. Activity diurnal or nocturnal. Eggs deposited above water bodies or phytotelms. Free swimming and feeding tadpoles with generalized mouthparts. Parental care in at least two species of subgenus *Pandanusicola* (Lehtinen 2003), unknown in *Guibemantis* s. str.

**Justification:** The elevation of *Guibemantis* to genus level is justified by distinct morphological and molecular differentiation from *Blommersia*. We consider the alternative possibility to resolve the paraphyly of *Mantidactylus* sensu lato, to elevate only *Blommersia* to genus level and keep *Guibemantis* and *Pandanusicola* as subgenera, as less appropriate.

Two subgenera are recognized:

#### Subgenus *Guibemantis* Dubois, 1992

**Diagnosis** (see also Glaw et al. 2000b; Vences and Glaw 2005a) Medium-sized (adult snout-vent length 33–59 mm), brownish frogs. Extended webbing between toes. Lateral metatarsalia separated. Inner and outer metatarsal tubercles present. Tibiotarsal articulation does not reach beyond nostril. Femoral glands of male of type 1, but not well delimited and often poorly recognizable externally, absent in female. Male with single, largely distensible, white, subgular vocal sac. Habits arboreal. Calling activity nocturnal. Eggs white (*G. depressiceps*, *G. kathrinae*) or pigmented (*G. tornieri*, *G. timidus*), deposited on leaves or boulders above stagnant or slowly running water bodies where the larvae develop. Free swimming and feeding tadpoles with generalized mouthparts.

**Note:** *Guibemantis liber* was included in *M.* (*Guibemantis*) by Glaw and Vences (1994), but molecular data (Lehtinen and Nussbaum 2003) suggest relations to the leaf-axil breeding species of *G.* (*Pandanusicola*), despite its larger relative hand length, same snout-vent length in both sexes, non-breeding in *Pandanus*, loud and exposed nocturnal calling, and femoral gland structure (Glaw and Vences 1994, Glaw et al. 2000b). Lehtinen et al. (2004) suggested that *M. liber* be transferred to subgenus *Pandanusicola*, and we implement that here (though with different generic placement).

**Distribution:** Eastern Madagascar.

#### Subgenus *Pandanusicola* Glaw & Vences, 1994

**Diagnosis:** Small to medium-sized frogs (adult snout-vent length 22–38 mm). Moderate webbing between toes. Lateral metatarsalia connected. Inner and outer metatarsal tubercles present. Tibiotarsal articulation does not reach beyond snout tip. Femoral glands of male of type 2 (type 1 in *G. liber*), absent in female. Male with single, subgular vocal sac. Habits arboreal in phytotelms (mainly *Pandanus*), activity apparently mainly diurnal. Eggs pigmented, deposited on *Pandanus* leaves. Tadpoles develop in these phytotelms; they are able to leave the water and probably have the ability to move between leaf axils. Biology is different in *G. liber*: this largely nocturnal species is not strongly adapted to *Pandanus*; its eggs are deposited above stagnant or slowly running water bodies where the larvae develop. Free swimming exotrophic tadpoles with generalized mouthparts.

**Distribution:** Eastern Madagascar.

#### Genus *Mantella* Boulenger, 1882

**Diagnosis** (see Vences et al. 1999 for further characters): Small frogs (adult snout-vent length 18–31 mm), generally with vivid colouration and skin alkaloids. Webbing between toes absent. Lateral metatarsalia connected. Inner and outer metatarsal tubercles present. Finger tips slightly enlarged (distinctly enlarged in *M. laevigata*). Point reached by tibiotarsal articulation ranges from forelimb insertion to nostrils. Femoral glands of male of type 1 (if recognizable), absent in female. Tibial glands absent. Male with single, moderately distensible, subgular vocal sac. Maxillary and vomerine teeth absent. Tongue not bifid, only slightly notched. Vertebral column procoelous. Tympanum distinct, of same size in male and female. Habits mainly terrestrial. Calling activity mainly diurnal. The white (unpigmented) eggs are hidden in cavities on the ground. Larval development in stagnant or slowly running water bodies (in *M. laevigata* in water-filled treeholes). Free swimming exotrophic tadpoles with generalized mouthparts. Parental care with egg-feeding in *Mantella laevigata* (Glaw et al. 2000a; Heying 2001).

**Distribution:** Madagascar.

#### Genus *Mantidactylus* Boulenger, 1895

**Diagnosis:** Small to large-sized frogs (adult snout-vent length 17–120 mm). Webbing between toes generally extended (rarely rudimentary). Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle present or absent. Finger tips slightly to moderately enlarged. Point reached by tibiotarsal articulation ranges from eye to beyond snout tip. Femoral glands of type 3 or 4 in male, small in female. Tibial glands absent. Male with single, slightly distensible subgular vocal sac. Maxillary teeth present, vomerine teeth present or absent. Tongue bifid. Vertebral column diplasiocoelous or procoelous. Tympanum of male mostly larger than in female (of same size in *Mantidactylus* s. str.). Habits mainly terrestrial, rarely arboreal (subgenus *Maitsomantis*), along small streams or stagnant water bodies. Activity diurnal and nocturnal. Egg clutches poorly known, terrestrial (*Brygoomantis*) or arboreal (*Maitsomantis*). Free swimming and feeding tadpoles with generalized or specialized mouthparts. Parental care in *M.* (*Maitsomantis*) and *M.* (*Ochthomantis*), unknown from other subgenera.

*Mantidactylus* is a clade based on molecular data (Fig. 2) and characterized by synapomorphic femoral glands that involves (1) the presence of an obvious central depression, and (2) the occurrence of small femoral glands in females. Both these synapomorphies were apparently secondarily lost in the subgenus *Maitsomantis*. Within the genus *Mantidactylus* two groups can be distinguished: The nominotypical subgenus *Mantidactylus* exhibits two (plesiomorphic)

character states: the absence of (1) distinct sexual dimorphism in tympanum size, and of (2) modifications to the skin between the femoral glands. *Mantidactylus* s. str. is sister to all other subgenera combined (*Brygomantis* + *Hylobatrachus* + *Chonomantis* + *Ochthomantis* + *Maitsomantis*). The latter, monophyletic clade is confirmed by molecular data (Fig. 2) and characterized by two morphological synapomorphies: (1) very distinct sexual dimorphism in tympanum size, and (2) an area of modified skin between the femoral glands that was termed “structure B” by Glaw et al. (2000b). The only exception concerning the second character, the single species of *Maitsomantis*, is considered to represent a secondary loss of the modified-skin feature.

Six subgenera are recognized:

#### **Subgenus *Brygomantis* Dubois, 1992**

*Diagnosis:* Small to medium-sized frogs (adult snout-vent length 17–68 mm). Generally extended webbing between toes (rudimentary in *M. tricinctus*). Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle present or absent. Finger tips slightly enlarged. Point reached by tibiotarsal articulation ranges from eye to snout tip. Femoral glands of type 3 in male, small in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary teeth present, vomerine teeth present or absent. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of male distinctly larger than in female. Habits semiaquatic and terrestrial, along running or stagnant water bodies. Activity diurnal and nocturnal. Egg clutches terrestrial. Free swimming exotrophic tadpoles with generalized mouthparts.

Although the species presently included in *Brygomantis* might represent a monophyletic lineage, convincing morphological synapomorphies are unknown. The karyotype ( $2n = 24$ ) of at least some species represents a derived condition.

*Distribution:* Widespread in eastern and central, locally distributed in western Madagascar.

#### **Subgenus *Chonomantis* Glaw & Vences, 1994**

*Diagnosis* (see also Vences and Glaw 2004): Small to medium-sized frogs (adult snout-vent length 19–45 mm). Moderately or well developed webbing between toes. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle reduced or absent. Finger tips moderately enlarged. Point reached by tibiotarsal articulation ranges from eye to beyond snout tip. Femoral glands of type 3 in male, small in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary teeth present, vomerine teeth generally present. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of male distinctly larger than in female. Habits terrestrial along small streams. Activity mainly diurnal. Egg clutches deposited outside

of water. Free swimming and water surface-feeding tadpoles with highly specialized, funnel-shaped mouthparts without labial tooth rows. The shared derived larval morphology clearly indicates the monophyly of *Chonomantis*.

*Distribution:* Eastern, central, and locally in western Madagascar.

#### **Subgenus *Hylobatrachus* Laurent, 1943**

*Diagnosis:* Medium-sized frogs (adult snout-vent length 30–45 mm). Extended webbing between toes. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle absent. Finger tips distinctly enlarged. Point reached by tibiotarsal articulation ranges from eye to nostril. Femoral glands of type 3 in male, small in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary and vomerine teeth present. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of male distinctly larger than in female. Habits semiaquatic and terrestrial, along streams. Activity diurnal and nocturnal. Egg clutches unknown. Free swimming exotrophic tadpoles with highly derived mouthparts (probably representing a filter-apparatus) without horny beak and labial tooth rows.

The morphological similarities between the two recognized species and several undescribed species may indicate the monophyly of this subgenus. However, further study is necessary to clarify whether *M. majori* belongs to *M. (Hylobatrachus)* rather than to *M. (Ochthomantis)*.

*Distribution:* Eastern Madagascar.

#### **Subgenus *Maitsomantis* subgen. n**

*Type species:* *Mantidactylus argenteus* Methuen, 1920.

*Etymology:* Derived from the Malagasy word “maitso” (= green) and the Ancient Greek “mantis” (= treefrog); refers to the greenish colour of these frogs. Gender of subgenus name: masculine.

*Diagnosis:* Medium-sized (adult snout-vent length 27–34 mm), elongated, greenish frogs. Webbing between toes moderately developed. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle rudimentary. Finger tips distinctly enlarged. Tibiotarsal articulation does not reach beyond nostril. Femoral glands apparently of type 2 in male (more study needed), not recognizable in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary and vomerine teeth present. Tongue bifid. State of vertebral column unknown. Tympanum much larger in male than in female. Habits arboreal along forest streams. Activity mainly diurnal. Egg clutches on leaves above streams, guarded at night by the male. Free swimming and feeding tadpoles with a reduced number of labial teeth and with unpigmented jaw sheaths,

reminiscent of larvae in the subgenus *Ochthomantis* (Vejarano et al. in press).

**Justification:** Previously, this species was included in the subgenus *M.* (*Blommersia*) (now *Blommersia* s. str.). However, molecular data (Fig. 2) unanimously suggest placement within the stream-associated clade here treated as *Mantidactylus* sensu stricto. Males of *M. argenteus* are known to guard their clutches on leaves above streams, a behaviour also observed in *Mantidactylus* (*Ochthomantis*) *majori* (Vences and De la Riva 2005), lending further support to relations between these subgenera. Moreover, most species in *Mantidactylus* s. str. show sexual dimorphism in tympanum size, a condition extremely expressed in *M. argenteus*, but absent in *Blommersia*. *Mantidactylus argenteus* is exceptional in the genus as defined herein in exhibiting no recognizable rudiments of femoral glands in females and no obvious central depression in the femoral glands of the males.

**Distribution:** Rainforest belt of central eastern Madagascar (as yet unrecorded from the northeast and southeast).

#### Subgenus *Mantidactylus* Boulenger, 1895

**Diagnosis:** Large-sized frogs (adult snout-vent length 75–120 mm). Extended webbing between toes. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle very small or absent. Finger tips only slightly enlarged. Tibiotarsal articulation does not reach beyond nostril. Femoral glands of type 4 in male, smaller in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary and vomerine teeth present (record of absent maxillary teeth in *M. grandidieri* by Vences et al. 2002c is due to a typesetting error). Tongue bifid. Vertebral column procoelous. Tympanum of same size in male and female. Habits semiaquatic and terrestrial, along forest streams. Activity nocturnal. Reproduction unknown. The morphological similarities between the two species (size, femoral gland morphology, lack of sexual dimorphism in tympanum size) clearly indicate the monophyly of this subgenus.

**Distribution:** Eastern and northern Madagascar.

#### Subgenus *Ochthomantis* Glaw & Vences, 1994

**Diagnosis** (see also Glaw and Vences 2004): Medium to large-sized frogs (adult snout-vent length 29–63 mm). Well developed webbing between toes. Lateral metatarsalia separated. Inner metatarsal tubercle present, outer tubercle present or absent. Finger tips moderately enlarged. Point reached by tibiotarsal articulation ranges from eye to beyond snout tip. Femoral glands of type 3 in male, small in female. Tibial glands absent. Male with single, subgular vocal sac. Maxillary and vomerine teeth present. Tongue bifid. Vertebral column diplasiocoelous. Tympanum of male larger than in female. Habits semiaquatic and terrestrial, along forest

streams. Activity mainly nocturnal. Egg clutches outside of water. Free swimming and feeding tadpoles with highly specialized mouthparts with reduced horny beak and labial tooth rows. Parental care of eggs deposited on leaves above streams in *M. majori* (Lehtinen 2003; Vences and De la Riva 2005).

**Distribution:** Eastern Madagascar, locally also in the west.

#### Genus *Spinomantis* Dubois, 1992

**Diagnosis:** Small to medium-sized frogs (adult snout-vent length 22–60 mm). Rudimentary to moderate webbing between toes. Lateral metatarsalia connected or separated. Inner metatarsal tubercle present, outer tubercles generally present (absent in *S. elegans*). Finger tips distinctly enlarged. Tibiotarsal articulation does not reach beyond snout tip. Femoral glands of type 2 in male, absent in female. Tibial glands absent. Males of the arboreal species with single, subgular vocal sacs; paired or at least slightly bilobed vocal sacs in *S. bertini* and *S. guibei* (authors' pers. obs., 2005). Maxillary teeth present, vomerine teeth generally present (absent in *S. bertini*). Tongue bifid. Vertebral column diplasiocoelous. Tympanum of same size in male and female. Habits arboreal or terrestrial along or in small streams. Activity generally nocturnal (at least partly diurnal in *S. bertini* and *S. guibei*). Eggs yellowish in the arboreal species, deposited on leaves above streams; unknown in the terrestrial stream species. Known tadpoles develop in streams; tadpoles of *S. elegans* free swimming and feeding with generalized mouthparts (Thomas et al. 2005), those of *S. aglavei* with a specific tooth formula.

**Justification:** The elevation of the former subgenus *M.* (*Spinomantis*) to genus level is justified by its isolated position within the mantelline radiation (see Fig. 2), and by the derived karyotype in the type species *S. aglavei* ( $2n = 24$  vs.  $2n = 26$  in most other mantellid lineages except *M.* (*Brygoomantis*)). According to their morphology and habits, *Spinomantis* species can be tentatively classified into two groups. *Spinomantis aglavei*, *S. fimbriatus*, *S. phantasticus*, *S. massorum* and *S. peraccae* are arboreal and nocturnal species with large femoral glands in the male, and occur in most of the rainforest belt of eastern and northern Madagascar. The remaining species (*S. bertini*, *S. brunae*, *S. elegans*, *S. guibei* and *S. microtis*) are poorly known and morphologically heterogeneous. They live along small streams and are restricted to southeastern Madagascar, often occurring at higher altitudes.

**Note:** Previously, *Spinomantis bertini* and *S. guibei* were included in the *Mantidactylus argenteus* group (Blommers-Schlösser and Blanc 1991) which was later included in the subgenus *M.* (*Blommersia*) (Dubois 1992). *Mantidactylus elegans* was placed in *M.* (*Guibemantis*) (Dubois 1992). *Boophis microtis* was tentatively

kept in *Boophis* (e.g. Glaw and Vences 1994), due to the absence of clear evidence for a better placement, despite its large differences in general appearance from other representatives of that genus. Andreone and Nussbaum (2006) have provided data on the morphology and natural history of this species, confirming its lack of femoral glands but also of nuptial pads in the male. Based on their thorough observations these authors proceeded to formally exclude the species from the genus *Boophis*. However, with no molecular data at their disposal, Andreone and Nussbaum merely transferred *B. microtis* to *Mantidactylus* sensu lato without assigning it to any subgroup. According to unpublished nuclear and mitochondrial gene sequences obtained by S. Hoegg (pers. comm.), *S. bertini*, *S. guibei* and *S. microtis* clearly join a single clade with the other species of *Spinomantis*. However, more work is needed to assess their morphology, variation and taxonomy. According to our data, *S. bertini* comprises several genetically deeply divergent lineages that almost certainly represent different species. The inclusive definition of *Spinomantis* as proposed here appears to be well-supported by molecular data, but may be seen as an hypothesis still requiring confirmation from a morphological and osteological perspective.

*Distribution.* Eastern Madagascar.

### Genus *Wakea* gen. n.

*Type species:* *Mantidactylus madinika* Vences, Andreone, Glaw & Mattioli, 2002.

*Etymology:* We are pleased to dedicate this genus to David and Marvalee Wake, Berkeley, in recognition of their outstanding contributions to the understanding of amphibian biology. We especially wish to emphasize David Wake's studies on miniaturization in amphibians, which might be relevant also in future research on the evolution of the miniaturized *Wakea madinika*, and the origin of microphagy and other specializations in its sister group, *Mantella* (see Vences et al. 1998). Gender of genus name: feminine.

*Diagnosis* (see Vences et al. 2002b): Miniaturized frogs with cryptic colouration. At 11–16 mm snout-vent length the smallest known mantellids. Webbing between toes absent. Lateral metatarsalia connected. Inner metatarsal tubercles small, outer tubercle indistinct. Finger tips slightly enlarged. Point reached by tibiotarsal articulation ranges from tympanum to eye. Femoral glands of male intermediate between types 1 and 2, distinct in life but difficult to recognize in alcohol, glands absent in female. Tibial glands absent. Male with single, whitish, subgular vocal sac. Maxillary teeth rudimentary, vomerine teeth absent. Tongue not bifid, only slightly notched. State of vertebral column and other osteological characters unknown. Tympanum distinct, of same size in male and female. Habits terrestrial. Activity diurnal and nocturnal.

Eggs white (only verified through dissection). Larval development probably in stagnant water bodies. Tadpoles unknown, but expected to be free swimming and feeding.

*Justification:* Although this clade contains a single, recently discovered species only, its elevation to genus rank is warranted by molecular as well as morphological data. *Wakea madinika* is the sister taxon to the genus *Mantella* based on 12S and 16S rRNA as well as cytochrome b and Rag-2 genes in separate analyses (not shown). Synapomorphies of *Wakea* and *Mantella* are (1) the reduction or absence of maxillary teeth, (2) the only very slight notching of the tongue, and (3) unpigmented eggs (only verified through dissection in *Wakea*). The alternative option for classification, inclusion of *M. madinika* in the genus *Mantella*, is less appropriate because the former significantly differs genetically from all *Mantella* and does not share its main apomorphies (absence of conspicuous aposematic colouration on both dorsal and ventral sides, and probably absence of skin alkaloids in *Wakea*). *Wakea* differs from the similar species of the genus *Blommersia* by a different morphology of the femoral glands, less distinctly notched tongue, and a large genetic divergence.

*Distribution:* Known from a single low-altitude locality in northwestern Madagascar.

### Species revalidations

#### *Mantidactylus bellyi* Mocquard, 1895, bona species

*Justification and diagnosis:* This species, described from Montagne d'Ambre in extreme northern Madagascar, was previously considered as a synonym of *M. curtus* (e.g. Blommers-Schlösser and Blanc 1991). Sequence data (GenBank accession number AY848226) indicate that *curtus*-like specimens from Montagne d'Ambre are far from *M. curtus* phylogenetically, but constitute the sister group of *M. ulcerosus* instead. The single-note call of *M. bellyi* differs from the call of *M. ulcerosus*, indicating taxonomic distinctness, and in a fragment of the 16S rRNA gene sequence divergence from *M. ulcerosus* collected at the type locality (Nosy Be) is 3.6%. We therefore consider *M. bellyi* as a valid species.

*Distribution:* Reliably identified only from the type locality, Montagne d'Ambre, northern Madagascar. Genetically similar specimens occur at Ankarana, also in northern Madagascar.

#### *Mantidactylus bourgati* Guibé, 1974, bona species

*Justification and diagnosis:* Originally described from the Andringitra Massif in southeastern Madagascar, this was considered as another junior synonym of *Mantidactylus curtus* (e.g. Blommers-Schlösser and Blanc 1991). However, genetic data indicate that specimens from various sites at Andringitra share very similar

mitochondrial haplotypes, but are distinct from those found at Antoetra, Ibity and Itremo, sites within the imprecisely defined type locality “Eastern Betsileo” of *M. curtus* (e.g. sequences AY848228 and AY848288; uncorrected pairwise divergence approx. 8% in a fragment of the 16S rRNA gene). Because a preliminary examination suggests morphological differences as well, we consider it highly unlikely that all these populations are conspecific, and therefore propose to revalidate *M. bourgati*.

**Distribution:** Reliably identified only from the Andringitra Massif, at altitudes between 1400 and 2000 m.

#### ***Mantidactylus cowanii* (Boulenger, 1882), bona species**

**Justification and diagnosis:** Originally described as *Rana cowanii* Boulenger, 1882, and previously considered as a synonym of *M. lugubris* (e.g. Blommers-Schlösser and Blanc 1991) with which it occurs syntopically (e.g. at Mantadia National Park). Distinguished from *M. lugubris* by blackish vs. green-brown colour and a substantial genetic difference (sequences AY341710 vs. AY341711; 7% divergence in a fragment of the 16S rRNA gene).

**Distribution:** Known from several localities in central eastern Madagascar (at least from Andasibe, Ambohitantely and Antoetra). Usually this species occurs more strictly at sites with larger waterfalls than *M. lugubris*.

#### ***Mantidactylus delormei* Angel, 1938, bona species**

**Justification and diagnosis:** Previously considered as a synonym of *M. brevipalmatus* (e.g. by Glaw and Vences 1994). For differentiation from all known species in *M.* (*Chonomantis*), except for *M. brevipalmatus*, see Vences and Glaw (2004). Differs from *M. brevipalmatus* by a more distinct dorsolateral colour border, a dark median area on the dorsum, and a more yellowish venter (Vences and Glaw 2004, p. 85), as well as by 2.3% pairwise distance in a fragment of the 16S rRNA gene (e.g. sequence AY848148 vs. AY848131). This species is an allopatrically distributed sibling of *M. brevipalmatus* in southeastern Madagascar. It seems to be more specialized to forest habitat, as we never found it along high-altitude streams at Andringitra (within its general range), whereas *M. brevipalmatus* is common in such montane habitats in the Ankaratra Massif.

**Distribution:** Reliably identified from its type locality, the Andringitra Massif, and from Maharira forest in Ranomafana National Park. Both localities are in southeastern Madagascar.

#### ***Mantella ebenau* (Boettger, 1880), bona species**

**Justification and diagnosis:** According to Vences et al. (1999), the name *Mantella betsileo* (Grandidier, 1872) applies to populations from the northern east coast and the Sambirano region in northwestern Madagascar, whereas genetically divergent (Schaefer et al. 2002) populations from western and southwestern Madagascar

were listed as an unnamed “*Mantella* sp. 1” (Vences et al. 1999). The situation remained paradoxical, however, because *M. betsileo* had been named after its presumed type locality, the Betsileo region in southeastern Madagascar, where occurrence of neither this nor any related species has ever been confirmed. Recent collections made by F. Andreone and colleagues have demonstrated the presence of populations of *M. betsileo* at localities near Isalo and near Antsirabe on the central plateau. We assume that the collecting locality of the types of *M. betsileo* was located along the travel route of A. Grandidier towards the Betsileo region, rather than in the rainforests of the region itself; the Isalo and especially the Antsirabe localities are not too far away from that route. Based on this assumption, the name *Mantella betsileo* is to be applied as the valid name for “*Mantella* sp. 1”. Consequently, the populations from northeastern and northwestern Madagascar, so far considered to be *M. betsileo*, are in need of a new name. The oldest available name for these populations is *Dendrobates ebenau* Boettger, 1880 (type locality: Nosy Be). We therefore resurrect this name, as *Mantella ebenau* (Boettger), for those populations. *Mantella attemsi*, hitherto considered as a junior synonym of *M. betsileo*, is tentatively regarded as a synonym of *Mantella ebenau*, because there is some probability that the types originated from Nosy Be (the poor condition of the type specimens does not allow definitive attribution; see Vences et al. 1999).

### **Mantellid diversity and classification**

Our new classificatory proposal raises the number of genera in the Mantellidae from five to eleven, and also implies a significant increase in the number of subgenera and species groups. It reflects recent advances in phylogenetic knowledge and represents an improvement on mantellid classification, because the genera now recognized are likely to represent monophyletic units. This contrasts with the previous situation in which *Mantella* was nested within a paraphyletic *Mantidactylus*. In addition, by transferring a number of species to new genera and subgenera, other subgenera have become clearly monophyletic units as well. This is the case for the former subgenera *Blommersia*, *Guibemantis*, *Mantidactylus*, and *Pandanusicola*. On the other hand, assignment of some species to genera and subgenera still remains tentative, and we expect further changes once sufficient molecular data become available for all species in *Mantidactylus* and *Gephyromantis* as defined here.

Isaac et al. (2004), based on examples from birds and primates, recently argued that “taxonomic inflation” due to continued elevations of subspecies and variants to species rank may be the reason for increasing species numbers in some groups of organisms. In this vein, potential critics of our new mantellid classification might also see it as a result of exaggerated splitting,

citing “inflation” in the number of recognized genera and subgenera. However, it needs to be considered that the number of species recognized from Madagascar has experienced a spectacular increase during the past years as well. Köhler et al. (2005) have shown that these new species are genetically as divergent from those known before as are other taxa described during the past century, demonstrating that the new ones are true, first-hand discoveries as with most other new amphibian species detected worldwide. Several of the new species, such as *Mantella bernhardi*, and especially *Wakea madinika*, represented completely new, divergent clades that unquestionably warrant the erection of new species groups, subgenera or genera.

We are convinced that the classification proposed here represents the phylogenetic relationships of these frogs much more closely than previous schemes. It also accounts better for the large diversity of reproductive modes in *Mantidactylus* sensu lato (see Dubois 2005). Nevertheless it is beyond doubt that further modifications will be necessary. Not only will the recognized species diversity of several mantellid genera, especially *Aglyptodactylus*, *Gephyromantis* and *Mantidactylus*, continue to increase by high percentages; we can also anticipate that additional highly divergent lineages will be discovered, like an undescribed new species and genus of mantellid frogs from the “Tsingy” limestone formation of Ankarana in northwestern Madagascar (Glaw et al. 2006). However, several more years of study will be necessary to fully understand the relationships among major mantellid clades. Apart from the need for more extensive taxon coverage of mitochondrial genes, it will be important to obtain more nuclear DNA sequences to solve basal relationships and, especially, detailed information on the osteology and reproductive biology of several key taxa.

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