

Systematic revision of the enigmatic Malagasy broad-headed frogs (*Laurentomantis* Dubois, 1980), and their phylogenetic position within the endemic mantellid radiation of Madagascar

Miguel Vences¹, Frank Glaw², Franco Andreone³, Riccardo Jesu⁴ & Giovanni Schimmenti¹

¹Muséum national d'Histoire naturelle, Laboratoire des Reptiles et Amphibiens, 25 rue Cuvier, 75005 Paris, France; address for correspondence: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany; email: m.vences@t-online.de; ²Zoologische Staatssammlung, Münchhausenstr. 21, 81247 München, Germany; e-mail: Frank.Glaw@zsm.mwn.de; ³Museo Regionale di Scienze Naturali, Sezione di Zoologia, Via G. Giolitti, 36, 10123, Torino, Italy; email: frandreone@libero.it; ⁴Acquario di Genova, Area Porto Antico, Ponte Spinola, 16128 Genova, Italy.

Keywords: Amphibia; Mantellidae, *Mantidactylus*, subgenus *Laurentomantis*, *Aglyptodactylus*, *Boophis*, *Laliostoma*, *Mantidactylus*, *Mantella*, systematics, phylogeny, radiation, new species, tibial glands, Madagascar.

Abstract

A revision of species included in the subgenus *Laurentomantis* (genus *Mantidactylus*) yielded new information about phylogeny, taxonomy, and biogeography of the endemic mantellid frog radiation in Madagascar. Four *Laurentomantis* species, distinguished by morphology and advertisement calls, are recognized: *Mantidactylus* (*Laurentomantis*) *horridus* (Northern and North-Western biogeographic regions), *M. (L.) ventrimaculatus* (South-East and East); *M. (L.) malagasius* (East); and the new species *M. (L.) striatus* (North-East). *M. striatus* and *M. malagasius* are probably sister species based on bioacoustic and morphological affinities. A tibial gland, so far unknown in anurans, is described in *M. malagasius* and *M. horridus*. A phylogenetic analysis of 54 mainly osteological and morphological characters in 33 endemic Malagasy anurans resulted in a position of *Laurentomantis* close to species of the subgenera *Spinomantis* and *Gephyromantis* (genus *Mantidactylus*), in accordance with its subgeneric status. However, also the well-established genus *Mantella* resulted to be nested within *Mantidactylus*, supporting the need of generic partitioning of the latter.

Contents

Introduction	191
Materials and methods	192
Systematic accounts	193
Key to species of <i>Laurentomantis</i>	204
Phylogenetic analysis	205
Discussion	206
Phylogenetic relationships of <i>Laurentomantis</i>	206
Biogeography	206

Relationships and origin of mantellids	206
Acknowledgements	209
References	209
Appendix: Characters used for analysis	210

Introduction

Recent phylogenetic studies based on mitochondrial DNA sequences suggested that the endemic Malagasy frogs of the genera *Aglyptodactylus*, *Boophis*, *Laliostoma* (previously *Tomopterna*), *Mantidactylus* and *Mantella* form a monophyletic lineage (Richards and Moore, 1998; Bossuyt and Milinkovitch, 2000; Richards et al., 2000; Vences et al., 2000), although they had been previously assigned to three different subfamilies in the family Ranidae (Blommers-Schlösser, 1993). Based on the genetic evidence, Vences and Glaw (2001) proposed including representatives of the five genera in a separate family Mantellidae, with three subfamilies (Mantellinae, Boophinae, Laliostominae).

Molecular studies on *Mantidactylus* included single representatives of eight subgenera (Richards et al. 2000), but morphological phylogenies of this genus based on an adequate number of characters and terminal taxa have so far not been published (see Glaw et al., 1998). While *Mantella*, *Aglyptodactylus* and *Laliostoma* are well defined lineages

with a limited number of species, *Boophis* and *Mantidactylus* are speciose, with about 40 and 75 nominal species, respectively. Especially *Mantidactylus*, currently partitioned into 12 subgenera (Glaw and Vences, 1994), contains very diverse frogs both in size and morphology as well as in habits and reproductive modes. Basic data on ecology and reproductive biology are incomplete or totally lacking for many species of *Mantidactylus* and *Boophis*. To understand how the mantellid radiation could give rise to its present extraordinary diversity in Madagascar, it is crucial to gather information on its less known lineages.

Despite of the important recent progress in knowledge on the batrachofauna of Madagascar (Glaw and Vences, 2000), a number of groups remain largely unknown. Such is the case for the frog species classified in *Laurentomantis*, which at present (Glaw and Vences, 1994) is considered as subgenus of *Mantidactylus*: *Mantidactylus* (*Laurentomantis*) *horridus* (Boettger, 1880), *M. (L.) malagasius* (Methuen and Hewitt, 1913) and *M. (L.) ventrimaculatus* (Angel, 1935). The monograph of Blommers-Schlösser and Blanc (1991) contained no information on habitat, biology or life coloration of any *Laurentomantis* species. Blommers-Schlösser and Blanc (1993) showed, for the first time, a photograph of a living *M. malagasius*. Glaw and Vences (1994) provided photographs, call descriptions and natural history notes for two different morphs referred to this species from the Central East and Marojejy in the North-East, and reported the discovery of an adult *M. horridus* at Montagne d'Ambre in northern Madagascar.

The nomenclatural and taxonomic history of *Laurentomantis* is extensive and still confusing. While Boettger (1880) described the taxon *horridus* as *Hemimantis horrida*, Boulenger (1882) treated this species as *Arthroleptis horridus*. Methuen and Hewitt (1913) erected the genus *Microphryne* to accommodate their taxon *malagasius* (as *M. malagasita*), and assumed that *horrida* belonged to this genus as well. As the name *Microphryne* was preoccupied, Methuen (1920) created the replacement name *Trachymantis*. However, as demonstrated by Dubois (1980), *Trachymantis* was also preoccupied (by *Trachymantis* Giglio-Tos, 1917). Dubois (1980) thus created the replacement name *Laurento-*

mantis, which was considered to merit genus rank by Blommers-Schlösser and Blanc (1991) and Dubois (1992). Glaw and Vences (1994), however, concluded that no phylogenetic data exist to consider *Laurentomantis* as a separate genus in addition to the speciose *Mantidactylus*, and consequently considered *Laurentomantis* as a subgenus of *Mantidactylus*.

During the last years, numerous additional specimens of *Laurentomantis* were collected during surveys in several regions of Madagascar. In the present paper we review the *Laurentomantis* material available to us (more than 45 specimens), provide detailed morphological and bioacoustic data, and describe one new species. We furthermore undertake a phylogenetic analysis of 33 species, representing all mantellid genera, to assess the position of *Laurentomantis* relative to them, and to draw hypotheses on the origin and evolution of this radiation.

Materials and methods

Vocalizations were recorded using portable tape recorders with external microphones and were analyzed either with the MEDAV sound analyzing system Spektro 3.2 (*M. malagasius*, *M. striatus*, *M. ventrimaculatus*) or on a PC using the software CoolEdit (Syntrillium Software Corp.) (*M. horridus*).

The following morphological measurements were taken with a calliper to the nearest 0.1 millimeter: SVL (snout-vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), HAL (hand length), FORL (forelimb length), IHL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), IMTL, IMTH (length and height of inner metatarsal tubercle), TL1 (length of first toe).

Institutional abbreviations are as follows: BMNH (The Natural History Museum, London); FAZC (Franco Andreone Zoological collection; preliminary numeration of specimens which will be deposited in MRSN); FMNH (Field Museum, Chicago); MNHN (Muséum National d'Histoire Naturelle, Paris); MRSN (Museo Regionale di Scienze Naturali, Torino); MSNG (Museo di Storia Naturale di Genova); NMBE (Naturhistorisches Museum Bern); PBZI (Parc Botanique et Zoologique de Tsimbazaza, Antananarivo); TM (Transvaal Museum, Pretoria); UADBA (Université d'Antananarivo, Département de Biologie Animale); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZMA (Zoologisch Museum, Amsterdam); ZSM (Zoologische Staatssammlung München).

Statistical analyses were carried out using SPSS for Windows, version 9. We performed Mann-Whitney U-tests to assess sig-

nificance of intersexual and interspecific differences in size and morphometric ratios (relative tympanum length and head width, ratios TD/SVL and HW/SVL; relative size of inner metatarsal tubercle, IMTL/SVL and IMTH/SVL). Temporal and metric measurements are given as range, with mean \pm standard deviation in parentheses. Terminology for the description of femoral and tibial glands follows Glaw et al. (2000). Number of crossbands on hand and foot are given to the tip of the longest finger or toe, respectively. The term "tibial gland" is here coined for the prominent gland structures on the dorsal surface of the tibiae of *Mantidactylus horridus* and *M. malagasius* (see descriptions in the corresponding sections). The terms femur, tibia, humerus and radius, in the descriptive species accounts, are used to refer to the corresponding external limb segments, and not to the bones.

Coordinates and altitude of collecting localities are listed in Vences and Glaw (submitted). Full names and geographic references of the campsites visited by F. Andreone and quoted in the text are as follows: (1) Masoala Campsite 2 = Forêt de Beanjada, 15°16.8'S, 49°59.8'E, 620 m, Masoala Peninsula, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province); (2) Masoala Campsite 3 = Forêt d'Andasin'i Governera, 15°18.3'S, 50°01.2'E, 700 m, Masoala Peninsula, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province); (3) Ilampy = Masoala Peninsula, Campsite 4 (Antsarahan'Ambarato), 15°23.52'S, 50°02.82'E, 510 m, Antalaha Fivondronana, Antsiranana Faritany (Diégo Suarez Province); (4) Tsararano Campsite 1 = Tsararano Forest, Campsite 1 (Antsarahan'ny Tsararano), Andapa Fivondronana, Antsiranana Faritany (Diégo Suarez Province), 14°54.4'S, 49°41.2'E, 700 m.

Osteological data refer to the cleared and stained specimens listed in Table III. Terminology and character definitions largely follow the accounts of Clarke (1981), Drewes (1984), Blommers-Schlösser (1993), Glaw and Vences (1994), and Glaw et al. (1998). Characters were analyzed with PAUP*, version 4 beta (Swofford 1998). We performed Maximum parsimony (MP) analyses (heuristic searches with TBR branch swapping), coding all characters as unordered. Multistate characters were coded as polymorphisms. Species of *Heterixalus* (Hyperoliidae) were used as outgroup (see Blommers-Schlösser, 1993; Glaw et al., 1998).

Systematic accounts

Laurentomantis Dubois, 1980

Status. – A subgenus of *Mantidactylus* Boulenger, 1895 following Glaw and Vences (1994).

Diagnosis. – Small to medium sized (SVL 20–35 mm) scansorial anurans with a moderately to coarsely granular dorsum and completely connected lateral metatarsalia. Webbing absent from hand and feet. Third toe distinctly longer than fifth toe. A

single inner and two outer metacarpal tubercles; a distinct inner and a small outer metatarsal tubercle; single subarticular tubercles. Intercalary element present between ultimate and penultimate phalanges of all fingers and toes. Ultimate phalanges Y-shaped. Omosternum ossified and unforked. Vertebral column diplasiocoelous. Maxillary teeth present, vomerine teeth present (vomerine odontophore present), but generally concealed under mucous skin of buccal roof. A complete circummarginal groove ventrally on finger and toe pads. Males with a slightly distensible single subgular vocal sac and distinct femoral glands, of type 2 according to Glaw et al. (2000) as assessed by detailed macroscopic examinations, composed of up to nine single large granules; some species with tibial glands; no nuptial pads.

Included species. – *Mantidactylus horridus*, *M. malagasius*, *M. striatus* sp. n., *M. ventrimaculatus*.

Mantidactylus (Laurentomantis) horridus (Boettger, 1880)

Fig. 1a–b

Material. – SMF 7177 (holotype, Nosy Be, collected by C. Ebenau); MSNG 49125A–C and UADBA 10001–10002 (Manarikoba Forest, Tsaratanana Massif, 14°02'24"S, 48°47'02"E; R. Jesu, G. Schimmenti and J. C. Pizo, 15–22 February 1997); ZFMK 57433 (Montagne d'Ambre, F. Glaw, N. Rabibisoa and O. Ramilison, 14–17 March 1994).

Original name. – *Hemimantis horrida* Boettger, 1880

Identity. – The holotype is a subadult specimen of 16.4 mm SVL; it agrees with the other specimens assigned here to the taxon in general morphology and coloration (coarsely granular without distinct ridge elements on the dorsum, with two indistinct broad dark transversal bands), by having short hindlimbs (tibiotarsal articulation reaching anterior eye corner), lacking an unpigmented area on the posterodorsal part of the femur (on which the original pigmentation is still rather well preserved). The area immediately above the cloaca has a very short light marking which may be homologous to the vertebral stripe on the posterior dorsum typical for the new species *M. striatus* (see below).

