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

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## 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.

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## 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 accomodate their taxon *malagasius* (as *M. malagasia*), 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 *Laurentomantis*, 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), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), IMTL, IMTH (length and height of inner metatarsal tubercle), TI.1 (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); PBZT (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 (Zoölogisch 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 significance 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 ± 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'Ambararato), 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.

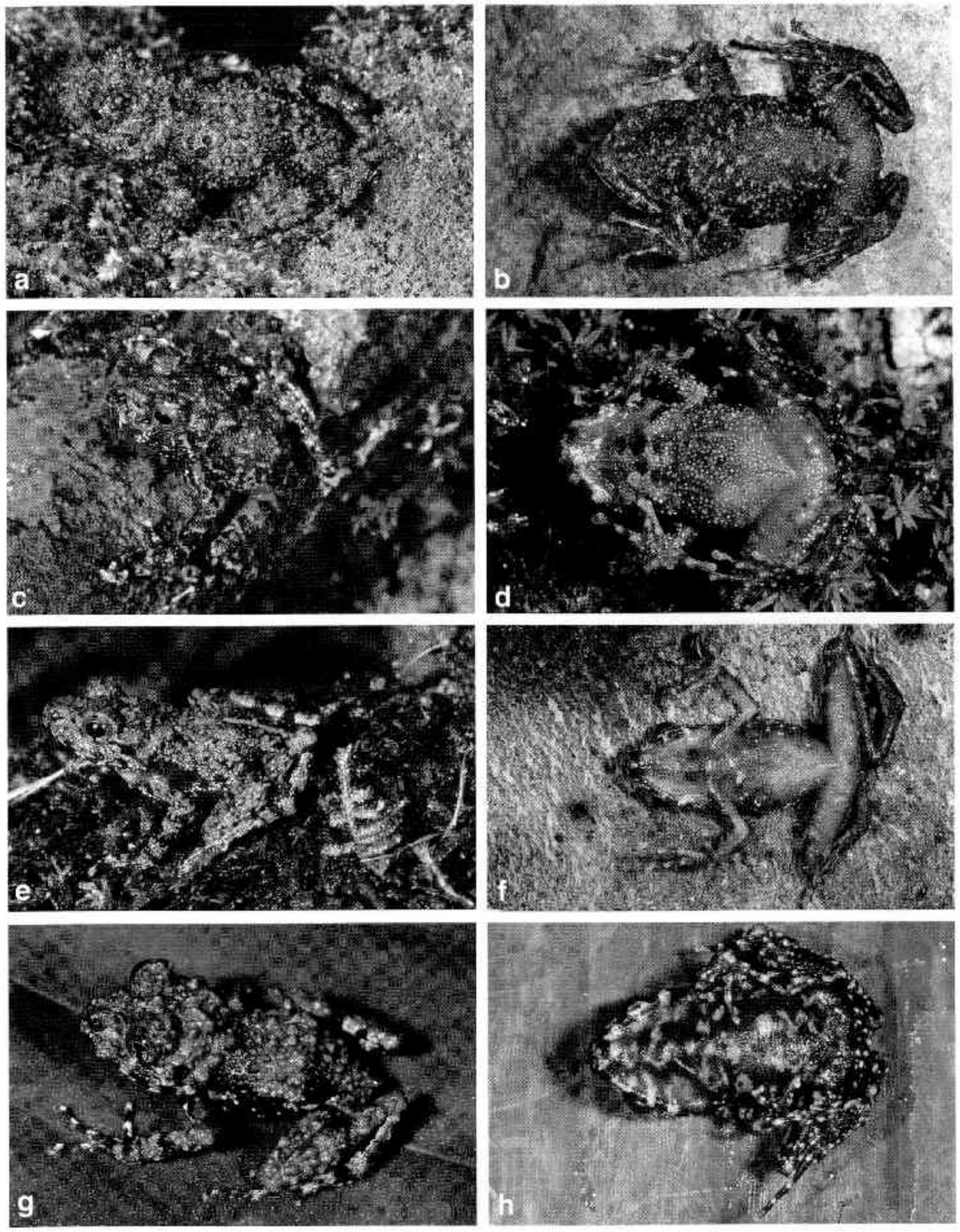
Included species. – *Mantidactylus horridus*, *M. malagasius*, *M. striatus* sp. n., *M. ventrimaculatus*.

*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. Piso, 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).






Diagnosis. – Distinguished from other known *Laurentomantis* by larger body size (male SVL 26-28 mm vs. 20-25 mm; female SVL 35 mm vs. 23-29 mm), long note duration (1271-2521 ms vs. 407-1468 ms) and low pulse repetition rate in advertisement calls (13/s vs. 18-40/s). Further distinguished from *M. ventrimaculatus* by absence of prominent dorsal ridges, from *M. ventrimaculatus* and *M. striatus* by a granular belly, and from *M. malagasius* by absence of red color on limbs.

Morphology. – For measurements see Tables I and II. The skin of the dorsum is coarsely granular; granules are only sometimes indistinctly arranged as continuous ridges on the anterior back (e.g. UADBA 10001). The vocal sac, as far as recognizable in preserved specimens, is single subgular. Throat and limbs are ventrally smooth, the belly is granular. A tibial gland is present in all male specimens from Tsaratanana (although less prominent than in *M. malagasius*), but absent in the single female from Montagne d'Ambre. Femoral glands in MSNG 49125C (size 3.6 x 1.9 mm; Fig. 2) in internal view consist of five granules on one limb and six granules on the other limb (granule diameter 0.8-1.3 mm). The tibial gland in this specimen, in internal view, has a structure similar to that found in femoral glands of type 2 *sensu* Glaw et al. (2000). It consists of a densely packed field of ca. 60 granules (granule diameter 0.2-0.4 mm). Externally, about 60 distinct pores are visible on the gland surface (absent from the surrounding skin), indicating that each granule may have one separate secretion pore (Fig. 3). Size of the tibial gland is 8.0 x 2.2 mm.

No significant sexual dimorphism in relative tympanum size and relative size of inner metatarsal tubercle was detected in the single female available. Mean male size was 76% of female size.

Coloration. – In preservative, dorsally greyish brown with a very faint and poorly delimited dark pattern which forms 2-3 indistinct broad transversal bands. Limbs with dark crossbands of variable width: 2-4 on femur, 2-3 on tibia, 7-8 on tarsus and foot, 1-2 on humerus, 4-5 on radius and hand. Ventral side uniformly diffuse greyish-brown with small light grey (throat and belly) or cream (limbs) markings. In life similar. The light ventral markings were rather indistinct. The iris was yellowish brown, with a narrow, more intense orange circle around the pupil.

Distribution. Known from (1) the type locality Nosy Be, (2) Montagne d'Ambre, and (3) Tsaratanana (altitude 1300 m) (Fig. 5). At Montagne d'Ambre, the species has also been recorded at an altitude of 1200 m by Raxworthy and Nussbaum (1994). The highest elevation of the island of Nosy Be is 430 m in the Lokobe reserve. Altitudinal range is therefore 430 m (probably also lower altitudes at Nosy Be) to 1300 m. Blommers-Schlösser and Blanc (1991) listed three further localities: Marojejy, Fenerive and Tampolo. While the latter two localities both refer to the specimen MNHN 1953.130 which is here assigned to *M. malagasius* (see section on distribution of that species), we did not find any voucher for the locality Marojejy in the MNHN and ZMA collections on which the distributional data of Blommers-Schlösser and Blanc (1991) were largely based; the Marojejy locality – which possibly refers to *M. striatus* – is therefore considered in need of confirmation. The specimen shown as *M. horridus* in Hofrichter (1998) is actually a *M. ventrimaculatus* (NMBE 268/96, see below).

Natural history. – On the Tsaratanana Massif, *M. horridus* was collected within the primary rainforest of Manarikoba, which was described by Perrier de la Bathie (1927) and characterised by trees heavily covered with mosses and herbaceous under-

←
*Fig. 1.* Dorsolateral and ventral views of species in the subgenus *Laurentomantis* in life. a-b, *Mantidactylus* (*Laurentomantis*) *horridus*, female ZFMK 57433 from Montagne d'Ambre; c-d, *Mantidactylus* (*Laurentomantis*) *malagasius*, male from Andasibe; e-f, *Mantidactylus* (*Laurentomantis*) *striatus*, male from Marojejy; g-h, *Mantidactylus* (*Laurentomantis*) *ventrimaculatus*, male from Vohiparara.

*Table 1.* Measurements (in mm) of *Laurentomantis* specimens. See Materials and Methods section for abbreviations of characters. M, male; F, female; SA, subadult; HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype; RHL (relative hindlimb length) gives the position reached by the tibiotarsal articulation when the hindlimbs are adpressed along the body: (0) eye centre, (1) anterior eye corner, (2) between eye and nostril, (3) nostril, (4) snout tip, (5) beyond snout tip.

| ZFMK | Sex | Locality | SVL | HW | HL | TD | ED | END | NSD | NND | FORL | HAL | HIL | FOTL | FOL | RHL | TL1 | IMTL | IMTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *M. horridus* | | | | | | | | | | | | | | | | | | | |
| SME 7177 (HT) | SA | Nosy Be | 16.4 | 6.8 | 7.4 | 1.2 | 2.5 | 2.0 | 1.5 | 1.9 | 11.6 | 4.8 | 26.3 | 11.5 | 7.3 | 1 | – | – | – |
| MSNG 49125A | M | Tsaratanana | 27.1 | 10.6 | 11.0 | 1.5 | 3.9 | 3.0 | 2.2 | 2.8 | 20.5 | 10.0 | 42.6 | 19.8 | 12.5 | 1 | 2.5 | 1.9 | 0.9 |
| MSNG 49125B | M | Tsaratanana | 27.3 | 10.7 | 10.5 | 1.6 | 3.6 | 3.2 | 2.2 | 3.0 | 19.5 | 9.1 | 41.4 | 18.1 | 11.7 | 1 | 2.7 | 1.4 | 0.7 |
| MSNG 49125C | M | Tsaratanana | 26.0 | 10.3 | 10.6 | 1.3 | 3.7 | 2.9 | 2.1 | – | 18.9 | 8.9 | 40.8 | 17.7 | 11.3 | 1 | – | – | – |
| UADBA 10001 | M | Tsaratanana | 28.1 | 10.4 | 10.7 | 1.5 | 4.0 | 3.0 | 2.2 | 2.7 | 20.4 | 9.3 | 43.0 | 19.7 | 12.3 | 2 | 2.6 | 1.5 | 0.9 |
| UADBA 10002 | M | Tsaratanana | 26.5 | 10.6 | 11.1 | 1.5 | 3.8 | 2.8 | 1.8 | 2.9 | 20.1 | 9.4 | 41.8 | 18.9 | 12.2 | 2 | 2.6 | 1.6 | 0.8 |
| ZFMK 57433 | F | Montagne d'Ambre | 35.4 | 13.9 | 13.8 | 1.9 | 3.9 | 3.7 | 2.2 | 3.4 | 23.7 | 10.8 | 52.6 | 24.1 | 15.5 | 0 | 2.7 | 1.3 | 0.7 |
| *M. ventrimaculatus* | | | | | | | | | | | | | | | | | | | |
| MNHN 1935.172 (PLT) | SA (F?) | Isaka-Ivondro | 22.0 | 9.0 | 9.3 | 1.4 | 3.2 | 2.5 | 1.7 | – | 17.2 | 7.5 | 38.7 | 16.8 | 10.7 | 3 | – | – | – |
| MNHN 1935.173 (LT) | F | Isaka-Ivondro | 29.1 | 12.5 | 11.8 | 1.6 | 3.6 | 3.2 | 2.5 | – | 22.0 | 9.7 | 47.0 | 22.5 | 13.8 | 2 | – | – | – |
| NMBE 268/96 | M | Andasibe | 25.0 | 10.3 | 10.1 | 1.7 | 3.6 | 2.6 | 1.6 | 2.1 | 18.2 | 8.1 | 40.8 | 18.6 | 11.3 | 3 | 2.5 | 1.8 | 0.9 |
| ZFMK 62273 | SA (F?) | Vohiparara | 22.7 | 9.2 | 9.7 | 1.7 | 3.2 | 2.8 | 1.6 | 2.4 | 18.2 | 8.4 | 40.3 | 17.6 | 11.4 | 5 | 2.3 | 1.4 | 0.9 |
| ZFMK 62281 | M | Vohiparara | 23.0 | 9.6 | 9.4 | 1.7 | 3.3 | 3.0 | 1.7 | 2.5 | 18.4 | 8.6 | 40.6 | 18.2 | 12.0 | 4 | 2.2 | 1.4 | 0.7 |
| *M. malagasius* | | | | | | | | | | | | | | | | | | | |
| TM 10076 (HT) | M | Folohy | 20.2 | 8.3 | 8.6 | 1.3 | 2.8 | 2.5 | 1.4 | – | 13.9 | 6.5 | 37.6 | 16.3 | 10.5 | 5 | – | – | – |
| BMNH 1988.590 | M | Ambatovaky | 22.2 | 8.7 | 8.7 | 1.8 | 2.9 | 2.6 | 1.6 | 1.8 | 16.6 | 8.0 | 38.1 | 17.4 | 11.1 | 3 | 2.4 | 1.3 | 0.8 |
| ZMA 8366 | M | Ambatovaky | 21.6 | 8.4 | 8.6 | 1.2 | 2.5 | 2.3 | 1.4 | 1.6 | 16.9 | 7.7 | 38.3 | 17.5 | 10.8 | 3 | 2.4 | 1.2 | 0.8 |
| FAZC 7236 | F | Masoala, Andranobe | 25.6 | 9.9 | 9.9 | 1.2 | 3.0 | 3.0 | 2.1 | 2.3 | 17.5 | 8.2 | 40.1 | 18.2 | 11.7 | 2 | 2.6 | 1.0 | 0.4 |
| FAZC 7254 | F | Masoala, Andranobe | 24.2 | 9.2 | 9.8 | 1.2 | 2.7 | 3.1 | 1.6 | 2.3 | 16.6 | 8.0 | 38.5 | 17.6 | 11.4 | 3 | 2.7 | 1.1 | 0.5 |
| FAZC 7700 | M | Masoala, Camp 2 | 22.5 | 9.0 | 9.0 | 1.5 | 3.0 | 2.4 | 1.7 | 2.1 | 16.2 | 7.9 | 36.3 | 16.5 | 11.1 | 2 | 2.4 | 1.0 | 0.8 |
| FAZC 7730 | F | Masoala, Camp 2 | 24.9 | 9.4 | 9.4 | 1.6 | 3.0 | 2.7 | 2.0 | 2.2 | 16.7 | 7.7 | 38.3 | 16.6 | 11.1 | 1 | 2.1 | 1.0 | 0.4 |
| MNHN 1976.250 | M | – | 25.8 | 9.4 | 9.6 | 1.4 | 3.7 | 2.6 | 1.6 | 2.3 | 16.2 | 8.2 | 39.7 | 16.9 | 10.4 | 2 | 2.2 | 1.0 | 0.7 |
| NMBE 233/96 | M | Ambohitantely | 22.2 | 8.6 | 9.2 | 1.6 | 3.2 | 2.4 | 2.2 | 2.2 | 16.3 | 7.6 | 35.9 | 16.3 | 10.6 | 2 | 1.7 | 0.9 | 0.7 |
| ZFMK 57434 | M | Andasibe | 24.0 | 9.4 | 9.0 | 1.4 | 3.3 | 2.4 | 1.7 | 2.2 | 17.6 | 8.4 | 42.0 | 19.0 | 12.2 | 4 | 2.2 | 1.4 | 0.7 |
| ZFMK 57435 | F | Ankeniheny | 25.7 | 9.3 | 9.8 | 1.6 | 3.4 | 2.7 | 1.8 | 2.1 | 19.0 | 9.2 | 42.5 | 19.4 | 12.4 | 2 | 1.8 | 1.1 | 0.8 |



*Table 1.* Continued.

| ZFMK | Sex | Locality | SVL | HW | HL | TD | ED | END | NSD | NND | FORL | HAL | HIL | FOTL | FOL | RHL | TL1 | IMTL | IMTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ZFMK 59876 | M | Andasibe | 22.0 | 8.2 | 8.2 | 1.2 | 3.0 | 2.3 | 1.5 | 2.1 | 16.7 | 8.2 | 40.5 | 18.3 | 11.8 | 5 | 2.1 | 1.1 | 0.6 |
| ZFMK 60039 | M | Andasibe | 23.0 | 8.7 | 9.0 | 1.3 | 2.7 | 2.7 | 1.5 | 2.1 | 17.0 | 8.2 | 39.7 | 17.2 | 11.4 | 3 | 1.8 | 1.2 | 0.7 |
| ZSM 324/2000 | F | Vohidrazana | 23.2 | 8.6 | 9.0 | 1.7 | 2.8 | 2.4 | 1.7 | 1.8 | 17.6 | 8.1 | 41.0 | 18.2 | 11.2 | 3 | 1.2 | 0.4 | 2.1 |
| *M. striatus* | | | | | | | | | | | | | | | | | | | |
| ZSM 938/2000 (HT) | M | Marojejy | 23.8 | 8.3 | 9.2 | 1.4 | 3.3 | 2.5 | 1.0 | 2.2 | 17.6 | 8.7 | 39.7 | 18.0 | 11.5 | 2 | 2.6 | 1.1 | 0.7 |
| FAZC 7645 (PT) | F | Masoala, Camp 2 | 25.3 | 8.0 | 9.1 | 1.5 | 2.3 | 2.5 | 1.8 | 2.0 | 19.5 | 8.2 | 42.7 | 19.5 | 11.8 | 4 | 2.9 | 0.9 | 0.4 |
| FAZC 7711 (PT) | F | Masoala, Camp 3 | 25.6 | 9.1 | 9.4 | 1.2 | 3.0 | 2.9 | 1.8 | 2.0 | 17.4 | 7.5 | 40.2 | 17.5 | 11.4 | 1 | 2.4 | 1.1 | 0.5 |
| FAZC 7796 (PT) | F | Masoala, Camp 3 | 23.9 | 8.6 | 9.1 | 1.3 | 2.8 | 2.5 | 1.7 | 1.8 | 16.2 | 8.0 | 39.0 | 17.1 | 11.0 | 2 | 2.3 | 1.1 | 0.4 |
| FAZC 7840 (PT) | M | Masoala, Camp 3 | 22.7 | 8.7 | 8.7 | 1.4 | 2.9 | 2.5 | 1.3 | 2.0 | 15.6 | 7.5 | 36.4 | 16.4 | 10.8 | 1 | 2.2 | 1.3 | 0.6 |
| FAZC 7858 (PT) | M | Masoala, Camp 3 | 22.7 | 8.3 | 8.8 | 1.2 | 2.9 | 2.4 | 1.5 | 1.9 | 17.1 | 7.0 | 36.6 | 16.2 | 10.7 | 2 | 2.7 | 0.9 | 0.4 |
| FAZC 7859 (PT) | F | Masoala, Camp 3 | 24.3 | 8.3 | 9.6 | 1.3 | 2.8 | 2.5 | 1.8 | 2.2 | 16.8 | 7.8 | 41.4 | 17.0 | 11.0 | 2 | 2.5 | 1.0 | 0.4 |
| FAZC 7905 (PT) | M | Masoala, Camp 3 | 22.2 | 8.3 | 8.6 | 1.3 | 2.8 | 2.6 | 1.6 | 1.9 | 15.7 | 7.5 | 35.6 | 16.3 | 11.2 | 2 | 2.4 | 0.8 | 0.4 |
| FAZC 7910 (PT) | M | Masoala, Camp 3 | 22.2 | 8.4 | 8.3 | 1.3 | 2.5 | 2.6 | 1.6 | 1.9 | 16.3 | 7.3 | 38.3 | 16.4 | 10.9 | 2 | 2.3 | 0.8 | 0.5 |
| FAZC 10299 (PT) | F | Ilampy, Masoala | 25.1 | 7.2 | 9.1 | 1.3 | 2.5 | 2.5 | 1.8 | 2.0 | 19.0 | 8.1 | 43.5 | 19.4 | 11.8 | 3 | 2.6 | 0.7 | 0.4 |
| FAZC 10313 (PT) | F | Ilampy, Masoala | 25.4 | 8.0 | 9.6 | 1.4 | 3.0 | 2.8 | 1.6 | 2.1 | 18.8 | 8.3 | 43.5 | 18.5 | 11.3 | 3 | – | – | – |
| FAZC 10378 (PT) | M | Ilampy, Masoala | 22.5 | 7.5 | 8.9 | 1.4 | 2.7 | 2.6 | 1.2 | 2.0 | 16.1 | 7.3 | 37.8 | 16.8 | 10.6 | 2 | 2.4 | 1.1 | 0.5 |
| FAZC 10424 (PT) | F | Ilampy, Masoala | 24.9 | 8.0 | 8.8 | 1.3 | 2.8 | 2.3 | 2.1 | 2.1 | 18.4 | 8.9 | 44.6 | 19.3 | 12.0 | 4 | – | – | – |
| FAZC 10441 (PT) | F | Ilampy, Masoala | 25.0 | 8.2 | 9.2 | 2.0 | 2.6 | 2.8 | 1.3 | 2.2 | 17.5 | 8.2 | 42.9 | 19.8 | 12.3 | 2 | 2.8 | 0.6 | 0.4 |
| MRSN A1937.1 (PT) | M | Tsararano | 23.4 | 7.9 | 9.1 | 1.3 | 3.0 | 2.8 | 1.4 | 2.1 | 18.7 | 8.6 | 42.0 | 18.3 | 11.3 | 5 | 2.9 | 0.9 | 0.5 |
| MRSN A1937.2 (PT) | F | Tsararano | 26.9 | 8.6 | 10.0 | 1.5 | 3.2 | 3.1 | 2.0 | 2.1 | 19.8 | 9.0 | 43.0 | 19.3 | 12.3 | 2 | 2.9 | 0.9 | 0.5 |
| MRSN A1938 (PT) | M | Tsararano | 23.8 | 7.8 | 9.1 | 1.3 | 2.8 | 2.8 | 1.7 | 1.8 | 19.1 | 8.6 | 44.4 | 19.1 | 12.3 | 5 | 3.0 | 0.9 | 0.6 |
| ZFMK 57437 (PT) | M | Marojejy | 22.8 | 7.6 | 8.8 | 1.3 | 3.2 | 2.3 | 1.2 | 2.0 | 17.0 | 8.1 | 39.6 | 18.3 | 11.7 | 4 | 2.4 | 1.2 | 0.5 |
| ZFMK 57438 (PT) | M | Marojejy | 23.4 | 8.0 | 8.9 | 1.2 | 3.3 | 2.4 | 1.2 | 2.1 | 18.6 | 8.8 | 42.7 | 18.5 | 12.2 | 5 | 2.4 | 1.0 | 0.6 |
| ZFMK 59930 (PT) | M | Marojejy | 23.6 | 8.3 | 9.0 | 1.5 | 3.2 | 2.6 | 1.5 | 2.2 | 19.4 | 8.5 | 42.2 | 18.7 | 11.9 | 5 | 2.5 | 1.2 | 0.5 |
| ZFMK 59931 (PT) | F | Marojejy | 24.8 | 8.7 | 9.4 | 1.3 | 3.4 | 2.7 | 1.4 | 2.1 | 18.4 | 8.0 | 44.0 | 18.6 | 11.4 | 5 | 2.1 | 1.1 | 0.5 |

*Table II.* Differential characters of *Laurentomantis* species. Morphometric ratios were calculated from data in Table I. TT is used as abbreviation for tibiotarsal articulation.

| | *M. horridus* | *M. ventrimaculatus* | *M. malagasius* | *M. striatus* |
|---|---|---|---|---|
| Male SVL | 26.0-28.1 mm | 23.0-25.0 mm | 20.2-24.0 mm | 22.2-23.8 mm |
| Female SVL | 35.4 mm | 29.1 mm | 23.2-25.7 mm | 23.9-26.9 mm |
| Head width (ratio HW/HL) | 0.97±0.03 (0.92-1.02) | 1.00±0.05 (0.95-1.06) | 0.98±0.03 (0.94-1.04) | 0.90±0.06 (0.79-1.01) |
| Tympanum size (ratio TD/SVL) | 0.057±0.008 (0.050-0.073) | 0.067±0.008 (0.050-0.075) | 0.061±0.010 (0.047-0.080) | 0.057±0.007 (0.047-0.080) |
| Hindlimb length | short (TT reaching at most nostril) | long (TT reaching up to beyond snout tip) | mostly long (TT reaching sometimes beyond snout tip) | mostly long (TT reaching sometimes beyond snout tip) |
| Tibial gland | present in males, absent in the single known female | absent in males and females | present in males and females of some populations, absent in males and females of other populations | absent in males and females |
| Granules in femoral glands (per femur) | 5-6 | 9 | 1-4 | 3-6 |
| Dorsal skin texture | strongly granular, but without ridge elements on anterior dorsum | strongly granular, mostly with ridge elements on anterior dorsum | moderately to strongly granular, without or with only weak ridge elements on anterior dorsum | slightly to moderately granular, without or with only weak ridge elements on anterior dorsum |
| Ventral skin texture | granular | smooth | slightly granular | largely smooth |
| Red color on hindlimbs | absent | absent | present | absent |
| Ventral color in life | dark/grey marbling | brown/blue marbling | brown/light marbling (with small white spots) | uniformly dark grey-brown with few lighter markings |
| Vertebral stripe | absent or very indistinct | absent | absent | present and distinct |
| Note length in advertisement calls | 1271-2521 ms | 407-455 ms | 768-1468 ms | 440-1266 ms |
| Pulse repetition rate in advertisement calls | 13/s | 21-24/s | 18-36/s | 29-40/s |

growth. The physionomy of this unspoilt forest is also marked by the presence of high numbers of tree ferns (*Cyathea*) and *Pandanus*. During the study period (15-22 February 1997), which occurred in the peak of the rainy season, only calling males were observed: they were spotted at night on bushes at 50-150 cm from the ground in the vicinity of a mountain stream. The female from Montagne d'Ambre was found hidden under deadwood in primary forest (Glaw and Vences, 1994).

Calls. – Recorded on the Tsaratanana Massif on 17 February 1997, at 17.5°C air temperature. Calls were series of long notes with widely spaced pulses (Fig. 4a). Note duration was 1271-2521 ms (2116± 440 ms, n=7), duration of intervals between notes was 1271-3113 ms (1846±589 ms, n=7). Each note consisted of 16-33 (27.3±5.9; n=7) pulses. Pulse duration was 11-17 ms (14±2 ms, n=15), duration of intervals between pulses was 52-64 ms (58± 4 ms, n=15). Pulse repetition rate was 12.6-13.3 (12.9±0.3; n=7) per second. Pulse intensity increased at the beginning of one note, and decreased again towards its end. Frequency was 2300-4300 Hz, dominant frequency 2300-3300 Hz.

*Mantidactylus* (*Laurentomantis*) *ventrimaculatus* (Angel, 1935)
Fig. 1g-h

Material. MNHN 1935.173 (lectotype) and MNHN 1935.172 (paralectotype), both from Isaka-Ivondro, collected by R. Catala; ZFMK 62273 and 62281 (Vohiparara; F. Glaw, D. Rakotomalala and F. Ranaivojaona, 27 February 1996); NMBE 268/96 (Andasibe-Analamazaotra; D. Vallan, 25 January 1996).



Original name. – *Trachymantis malagasia* var. *ventrimaculatus* Angel, 1935

Identity. – The morphological and chromatic characters of the types (light marbling on venter; relatively long hindlimbs; dorsal ridges) leave little doubts on the correct attribution of the Vohiparara and Andasibe specimens to *M. ventrimaculatus*.

Diagnosis. – Distinguished from other known *Laurentomantis* by short note duration in advertisement calls (407-455 ms vs. 440-2521 ms). Further distinguished from *M. horridus* by smaller body size (male SVL 23-25 mm vs. 26-28 mm), smooth belly, and higher pulse repetition rate in advertisement calls (21-24/s vs. 13/s); and from *M. striatus* and *M. malagasius* by dark belly with distinct light marblings (which are bluish in life).

Morphology. – For measurements see Tables I and II. The skin of the dorsum is strongly granular. Tubercles on the posterior head and anterior dorsum fuse to form a symmetrical pattern of ridges. These ridges are prominent in most specimens, rigid and of a sharp appearance. A tibial gland is absent in NMBE and ZFMK material, both in the males and in the subadult (female) specimens. Venter and throat are smooth, very slightly granular areas are present on the belly close to the inguinal region. Femoral glands are very distinct and prominent; in ZFMK 62281, the ovoid gland consists of 9 large granules which in internal view are regularly packed but in external view appear to enclose two median depressions. This external configuration is even better visible in NMBE 268/96 (Fig. 5), in which the gland measures 5.6 x 3.0 mm. Diameter of single granules is 0.9 mm.

No significant sexual dimorphism in relative tympanum size and relative size of inner metatarsal tubercle was detected. Mean male size was 82% of mean female size (only adult specimens considered).

Coloration. – In preservative, dorsally greyish brown with two indistinct, faintly recognizable dark crossbands which are largely discontinuous dorsally but rather distinct on the flanks. Limbs with distinct and regular crossbands: 2-3 on femur, 3 on tibia, 7 on tarsus and foot, 1-2 on humerus, 6 on radius and hand. Ventral side dark brown, distinctly marbled with grey. In life, the dorsum was reddish brown and the ventral light marbling was light blue on a deep black venter and throat. The iris was greyish brown, with a narrow vertical black streak in its lower part. The crossbands on the flanks were deep black.

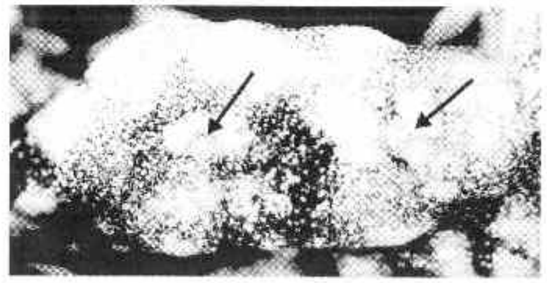


*Fig. 2.* Femoral gland of *Mantidactylus* (*Laurentomantis*) *ventrimaculatus* (NMBE 268/96) in ventral (external) view. Arrows indicate the apparent external central depressions which may be used by the surrounding gland granules for secretion.

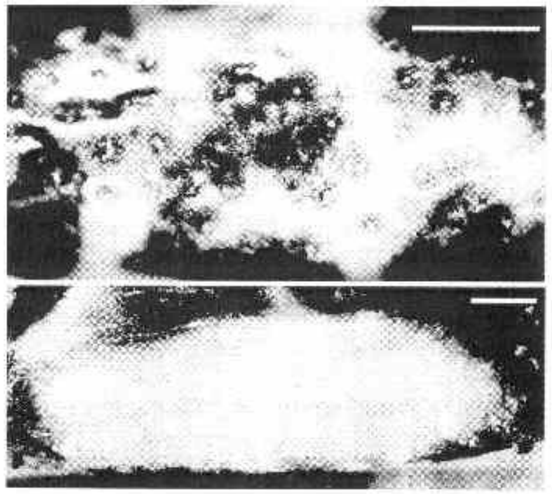


*Fig. 3.* Tibial gland of *Mantidactylus* (*Laurentomantis*) *horridus* (MSNG 49125C) in external view (above) and internal view (below). Note the large number of small secretion pores in external view. Scale bars = 1 mm.

Distribution. – Known from (1) the type locality Isaka-Ivondro (at an altitude of 700 m according to original description), (2) Vohiparara, and (3) Andasibe (Fig. 3). Altitudinal range 700-1000 m.