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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Keywords: Amphibia, Mantellidae, Mantidactylus, subgenus Laurentomantis, Aglyptodactylus, Boophis, Lalosoma, 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 and biogeography of the endemic mantellid frog radiation in Madagascar. Four Laurentomantis species, distinguished by morphology and advertisement calls, are recognized: Mantidactylus (Laurentomantis) boiei (Northern and Northern Western biogeographic regions), M. (L.) westermanni (South-East and East); M. (L.) madagascariensis (East); and the new species M. (L.) soroa (North-East). M. boiei and M. madagascariensis are probably sister species based on homoeocercal and morphological affinities. A tibial gland, so far unknown in mantellids, is described in M. madagascariensis and M. boiei. A phylogenetic analysis of 54 mainly osteological and morphological characters in 35 endemic Malagasy mantellids resulted in a position of Laurentomantis close to species of the subgenus Lepidomantis and Gephyromantis (genus Mantidactylus), in accordance with its enigmatic status. However, the well-established genus Mantella remained to be nested within Mantidactylus, supporting the need of generic partitioning of the latter.

Introduction

Recent phylogenetic studies based on mitochondrial DNA sequences suggested that the endemic Malagasy frogs of the genera Aglyptodactylus, Boophis, Lalosoma (previously Tonomantis), Mantidactylus and Mantella form a monophyletic lineage (Richards and Moore, 1998; Bossuyt and Milminkovitch, 2000; Richards et al., 2000; Venesés et al., 2000), although they had been previously assigned to three different subfamilies in the family Mantellidae (Blennerhassett-Schlüscher, 1993). Based on the genetic evidence, Venesés and Glaw (2001) proposed including representatives of the five genera in a separate family Mantellidae, with three subfamilies (Mantellinae, Boophinae, Lalosomatinae). Molecular studies of 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 Lalosoma are well defined lineages...
with a limited number of species. *Buphis* and *Manducatus* are speciose, with about 40 and 75 nominal species, respectively. Especially *Manducatus*, currently partitioned into 12 subgenera (Glaw and Vences, 1994), contains very diverse frogs 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 *Manducatus* and *Buphis*. To understand how the malleant radiation could give rise to its present extraordinary diversity in Madagascar, it is crucial to gather information on its less-known lineages.

Despite the important recent progress in knowledge on the batschcharinae of Madagascar (Glaw and Vences, 2000), a number of groups remain largely unknown. Such is the case for the frog species classified in *Laurentoniinae*, which at present (Glaw and Vences, 1993) contains 42 species, and few of them are included in a recently published monograph (Glaw and Vences, 2000). In the present paper, we review the *Laurentoniinae* material available to us (more than 45 specimens) and describe three new species. We further undertake a phylogenetic analysis of 33 species, representing all malleant radiation genera, to assess the position of *Laurentoniinae* 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 MEDAS sound analysis system (Spektrum 3.0, M. mandarinus, M. serrana, M. laursonii) or on a PC using the software CopyTalk (System Software Corp. M. hortensis). The following morphological measurements were taken with a callipers to the nearest 0.1 mm: SVL (snout-vent length), HW (head width), HL (head length), TD (total body diameter), ND (nose-dorsal diameter), NN (nose-naral diameter), ND (nose-oral diameter), TD (total body diameter), HD (head diameter), LD (lateral diameter), FF (femoral diameter), LIL (laryngeal length), LIL (laryngeal length), LIL (laryngeal length), LIL (laryngeal length) including a *M. Hortensis*. PTFL, PTFL, PTFL (length and height of inner metatarsal tubercle), TFL (length of first toe).

Additional abbreviations are as follows: BMNH (The Natural History Museum, London), ISG (Franko-Andersson Zoological Collections, preliminary enumeration of specimens which will be deposited in BMNH); FMNH (Field Museum, Chicago), MUSM (Museo Nazionale di Storia Naturale, Paris); MMNS (Museo Regionale di Scienze Naturali, Turin); MZUSP (Museu de Zoologia, São Paulo, Brazil); NZSAM (Zoological Survey of India, Kolkata); SMF (Zoological Museum, Copenhagen).

Statistical analyses were carried out using SPSS for Windows, version 9.0. We performed Mann-Whitney U-tests to assess significance of intersexual and interspecific differences in size and morphometric ratios (relative head length and body width, calcium levels). T-tests were performed to compare the relative size of internal structures, tibia and foot VRSLV; relative size of internal structures, and consequently considered *Laurentoniinae* as a subgenus of *Manducatus*.

During the last years, numerous additional specimens of *Laurentoniinae* were collected during surveys in several regions of Madagascar. In the present paper we review the *Laurentoniinae* material available to us (over 45 specimens), provide detailed morphological and biochemical data, and describe three new species. We further undertake a phylogenetic analysis of 33 species, representing all malleant radiation genera, to assess the position of *Laurentoniinae* relative to them, and to draw hypotheses on the origin and evolution of this radiation.
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 advertise-
ment calls (13/s vs. 18-40/s). Further distinguished
from M. ventrimaculatus by absence of prominent
dorsal ridges, from M. ventrimaculatus and M.
stratus by a granular belly, and from M. malagascus
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 recogniz-
able in preserved specimens, is single subangular.
Throat and limbs are ventrally smooth, the belly is
granular. A tibial gland is present in all male speci-
mens from Tsaratana (although less prominent
than in M. malagascus), but absent in the single
female from Montagne d'Ambre. Femoral glands
in MNSG 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 diam-
eter 0.8-1.3 mm). The tibial gland in this speci-
men, in internal view, has a structure similar to
that found in femoral glands of type 2 (versus 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 sep-
ate secretion pore (Fig. 3). Size of the tibial gland
is 5.0 x 2.2 mm.

No significant sexual dimorphism in relative
tympanum size and relative size of inner metatar-
sal tubercle was detected in the single female avail-
able. Mean male size was 76% of female size.

Coloration. — In preservative, dorsally greyish brown

Fig. 1. Dorsal and ventral views of species in the subgenus Laurentomantis in life. a-b, Mauderina (Laurentomantis)
horribilis, female ZFMK 57133 from Montagne d'Ambre; c-d, Mauderina (Laurentomantis) malagascus, male from Antsirabe;
e-f, Mauderina (Laurentomantis) stratus, male from Marojejy; g-h, Mauderina (Laurentomantis) ventrimaculatus, male from
Vokatara.

with a very faint and poorly delimited dark pat-
tern which forms 2-3 indistinct broad transverse
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 mark-
ings 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
Nossy Be, (2) Montagne d'Ambre, and (3) Tsara-
tana (altitude 1300 m) (Fig. 5). At Montagne
d'Ambre, the species has also been recorded at an
altitude of 1200 m by Rasamison and Nossazard
(1994). The highest elevation of the island of Nossy
Be is 430 m in the Lokobe reserve. Altitudinal range
is therefore 450 m (probably also lower altitudes
at Nossy Be) to 1300 m. Blommers-Schlösser and
Blanc (1991) listed three further localities: Maroje-
jy, Fenerive and Tampolo. While the latter two lo-
calities both refer to the specimen MNHN 1953:130
which is here assigned to M. malagascus (see sec-
tion on distribution of that species), we did not
find any voucher for the locality Marojejy in the
MNHN and ZMA collections on which the distribu-
tional data of Blommers-Schlösser and Blanc
(1991) were largely based; the Marojejy locality
which possibly refers to M. stratus — is therefore
considered in need of confirmation. The specimen
shown as M. horribilis in Hofrichter (1998) is ac-
Actually a M. ventrimaculatus (NMN 206896, see
below).

Natural history. — On the Tsaratana Massif. M.
horribilis was collected within the primary rainfor-
est of Masoali, which was described by Perrier
de la Bâtie (1927) and characterised by trees heav-
ily covered with mosses and herbaceous under-

Table 2: Measurements (in mm) of Lamprohynus species. See Materials and Methods section for abbreviations of characters. M, male; F, female; SA, subspecies; HT, holotype; PT, paratype; LT, lectotype; PTL, paralectotype; HBL, holotype hindlimb length.) given the position reached by the skeleton articulation when the hindlimbs are addorsed along the body: (3) eye centre; (4) anterior eye centre; (5) between eye and nostril; (6) snout tip; (7) beyond snout tip.

<table>
<thead>
<tr>
<th>ZSMK</th>
<th>Sex</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>5742</td>
<td>M</td>
<td>Lamprohynus</td>
</tr>
<tr>
<td>5743</td>
<td>F</td>
<td>Lamprohynus</td>
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Table 3: Continued.

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<th>Sex</th>
<th>Locality</th>
</tr>
</thead>
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<td>M</td>
<td>Ardabir</td>
</tr>
<tr>
<td>60039</td>
<td>M</td>
<td>Ardabir</td>
</tr>
<tr>
<td>72400</td>
<td>F</td>
<td>Vehilazara</td>
</tr>
</tbody>
</table>

M. marausah

<table>
<thead>
<tr>
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<th>Sex</th>
<th>Locality</th>
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</thead>
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<td>5982000000</td>
<td>M</td>
<td>Manoj</td>
</tr>
<tr>
<td>76711</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>77967</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>78400</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>78515</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>78775</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>78926</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>79185</td>
<td>F</td>
<td>Manoj, Comp 3</td>
</tr>
<tr>
<td>82299</td>
<td>F</td>
<td>Ilamuy, Mascuri</td>
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<tr>
<td>83103</td>
<td>F</td>
<td>Ilamuy, Mascuri</td>
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<tr>
<td>83708</td>
<td>F</td>
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<td>84270</td>
<td>F</td>
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</tr>
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<td>84313</td>
<td>F</td>
<td>Tavarnara</td>
</tr>
<tr>
<td>85341</td>
<td>F</td>
<td>Tavarnara</td>
</tr>
<tr>
<td>85512</td>
<td>F</td>
<td>Tavarnara</td>
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<tr>
<td>85761</td>
<td>F</td>
<td>Tavarnara</td>
</tr>
<tr>
<td>85910</td>
<td>F</td>
<td>Tavarnara</td>
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</table>
Table II. Differential characters of *Laurentomantis* species. Morphometric ratios were calculated from data in Table I. TT is used as abbreviation for tibial tubercle.

<table>
<thead>
<tr>
<th>Species</th>
<th>M. cornelii</th>
<th>M. ventromaculatus</th>
<th>M. malagasi</th>
<th>M. striata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male SVL</td>
<td>262.25-21.5 mm</td>
<td>22.02-25.0 mm</td>
<td>20.32-0.6 mm</td>
<td>22.223.8 mm</td>
</tr>
<tr>
<td>Female SVL</td>
<td>27.91 mm</td>
<td>22.02-25.0 mm</td>
<td>21.52-7 mm</td>
<td>22.223.8 mm</td>
</tr>
<tr>
<td>Head width</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
</tr>
<tr>
<td>Temporals</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
<td>0.87 (0.86-1.05)</td>
</tr>
<tr>
<td>Fingers [L]</td>
<td>0.90 (0.85-0.95)</td>
<td>0.90 (0.85-0.95)</td>
<td>0.90 (0.85-0.95)</td>
<td>0.90 (0.85-0.95)</td>
</tr>
<tr>
<td>Head length</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
</tr>
<tr>
<td>Tibial gland</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
<td>Present in males and females</td>
</tr>
<tr>
<td>Granules in dorsal glands</td>
<td>3-5</td>
<td>3-5</td>
<td>3-5</td>
<td>3-5</td>
</tr>
<tr>
<td>Dorsal skin texture</td>
<td>Granular</td>
<td>Granular</td>
<td>Granular</td>
<td>Granular</td>
</tr>
<tr>
<td>Ventral skin texture</td>
<td>Granular</td>
<td>Granular</td>
<td>Granular</td>
<td>Granular</td>
</tr>
<tr>
<td>Color on hindlimbs</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
</tr>
<tr>
<td>Color in life</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
<td>Brown/yellow</td>
</tr>
<tr>
<td>Ventral groove</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Hindlimb length</td>
<td>1271-351 mm</td>
<td>1271-351 mm</td>
<td>1271-351 mm</td>
<td>1271-351 mm</td>
</tr>
<tr>
<td>Pulse repetition rate in advertisement calls</td>
<td>0.21-24.5</td>
<td>0.21-24.5</td>
<td>0.21-24.5</td>
<td>0.21-24.5</td>
</tr>
</tbody>
</table>

Original name: *Trachyomantis malagasius* var. *ventromaculatus* Angol, 1935.

Identity. The morphological and chromatic characters of the type (light marbling on ventral, relatively long hindlimbs; dorsal ridges) leave little doubt on the correct attribution of the Vohitranana and Andasibe specimens to *M. ventromaculatus*.

Diagnosis. - Distinguished from other known *Laurentomantis* by short note duration in advertisement calls (407-455 ms vs. 440-2521 ms). Further distinguished from *M. cornelii* by smaller body size (male SVL 23-25 mm vs. 28-28 mm), smooth belly, and higher pulse repetition rate in advertisement calls (21.24 vs. 13.5); and from *M. striatus* and *M. malagasi* by dark belly with distinct light markings (which are blurred 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 NMBF and ZAIM material, both in the males and in the subadult (female) specimens. Ventral 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 ZAIM 31263, the ovary 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 NMBF 31269 (Fig. 3), in which the gland measures 5 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 preserved, dorsally greyish brown with two indistinct, faintly recognizable dark crossbands which are largely discontinuous dorsally but rather distinct on the flanks. Spurs with distinct and regular crossbands; 2-3 on femur, 3 on tibia.

Distribution. - Known from (1) the type locality Isaka-Ivondro (at an altitude of 700 m according to original description), (2) Vohitranana, and (3) Andasibe (Fig. 3). Altitudinal range 700-1000 m.
Natural history. — A single calling male was heard from near the ground at night in forest at Vohibaranana, at a distance of more than 10 m from a brook.

Calls. — Recorded at Vohibaranana on 27 February 1991. Calls were series of unharmonious notes (Fig. 4a). Note duration was 407-452 ms (442 ± 19 ms, n = 7), duration of intervals between notes was 267-627 ms (3452 ± 1281 ms, n = 7), duration of intervals between pulses was 28-48 ms (36 ± 4 ms, n = 66), Pulse repetition rate was 21-24 (22 ± 1.7) pulses per second. Frequency ranged between 2000-5750 Hz, the poorly defined dominant frequency between 2300-2500 Hz.

Mandibulatus (Laurentianis) malagassius (Methuen and Hewitt, 1913)

Fig. 1c-d


Original name. — Microphyletus malagassius Methuen and Hewitt, 1913

Fig. 5. Distribution map of species in the subgenus Laurentianis. Positions of localities in the maps is in part only approximate. Numbers of localities correspond to those given in the "Distribution" sections of each species.

Identity. — The male holotype is characterized by a coarsely granular dorsal skin, with two ridge-like granules in the shoulder region and two larger rounded granules on the anterior dorsal; throat and chest are smooth, ventral and ventral surface of femur are slightly granular, Femoral glands are prominent. The gland on the left femur consists of one single enlarged granule, diameter ca. 1.5 mm; the gland on the right femur consists of two granules (see also Methuen and Hewitt, 1920). There are no tubal glands. Color (after about 90 years in preservative) has largely faded into an almost uniform light brown. According to the original description, "hidden surface of the thighs and tibiae with large white blotches" which almost certainly correspond to the unpigmented areas (red in life) typical for this species. Furthermore, the general morphology, size, and structure of the femoral gland (composed of 1-2 granules) indicate that the name malagassius is correctly applied to the red-legged Laurentianis species from eastern Madagascar.

Diagnosis. — Distinguished from other known Laurentianis by red color on posterior and ventral surface of limbs (appearing pigmented in preservative vs. pigmented brown-gray in the other species). Further distinguished from M. horridus by shorter note duration (768-1468 ms vs. 1271-2521 ms) and higher pulse repetition rate in advertisement calls (18-36/s vs. 13/s), and smaller body size (male SW, 20-24 vs. 26-28 mm; female SVI, 23-26 mm vs. 35 mm); from M. ventrimaculatus by absence of regular light marking (blush in life) on a dark ventral, and longer note duration in advertisement calls (768-1468 ms vs. 407-455 ms). For a distinction from M. striatus, see diagnosis of that species below.

Remark. — The specimen MNHN 1976-250 differs in general appearance and femoral gland morphology from the remaining specimens; it is only tentatively assigned to M. malagassius, and not considered in the morphometric calculations.

Morphology. — For measurements see Tables I and II. The dorsum is moderately granular, the granules only occasionally brown-ridge-like structures which, however, are never very prominent. The throat is smooth, the belly slightly to moderately granular. Very distinct and prominent tibial glands are present in the males from Andasibe and Ambatozofia as well as in the females from Andasibe (ZFMK 57434). They are also present in the dubious specimen MNHN 1976-250, but absent in the male holotype and in specimens from Ambatovocia and Andrano (Masoala). This may indicate a constant difference between mid-altitude and low altitude localities, but more material is necessary to assess whether it may bear taxonomic relevance. In ZFMK 57434, the tibial gland measures 7.1 x 1.4 mm and consists of (internal view) of about 75 granules (0.2-0.4 mm in diameter). The external poms of the gland are clearly visible.

Femoral glands are present in males; on each femur, the gland generally consists of two large granules (a single granule in the holotype).
in BMNH 1988.590 from Ambatohy, the gland on each tergum consists of two groups of two granules each (total number of granules on both female eight). Femoral gland size in SME 233.96 is 3.1 x 1.4 mm in external view (diameter of each granule in internal view of 1.2 mm).

No significant sexual dimorphism in relative tympanum size and relative size of inner metatarsal tubercle was detected. Mean male size was 92% of mean female size.

Coloration. - In preservative, dorsally greyish brown, with indistinct dark pattern. Except short brown crossbands on femur, 4-5 on tibia, 5-10 on tarsus and foot, 6-7 on radius and hand; no distinct bands are seen on humerus. Venuly grey-brown on thorax, chest and anterior belly, pigmentation cream on posterior belly. A pattern of small white spots, partly forming aggregations, is present on the dark ventral areas. On the belly, each of these spots coincides with a single granule. Along the lower lip, the light spots sometimes form crossbands (cf. ZFMK 59786). Ventral side of foreleg and legs with light spots. Ventral venule pigmentless cream, tibia cream with brown markings. In life, the posterior and ventral surfaces of the femur are deep red, as is the inferio r region and of a small area around the foreleg insertion. The femurs and posterior belly are more or less intensely shaded red. The iris is orange brown in its upper part, greys in its lower part. The dorsal surface can have a olive-greenish shade.

Distribution. - The species is known from (1) the type locality Folohy, (2) Andrambe (Masoala), (3) Masoala (other localities), (4) Ambatohy, (5) Fenerivo, (6) Andasibe, (7) Ankanahery, (8) Vohidrabe, (9) Anosy (Arabolite) (Fig. 3). The known altitudinal range is 300-900 m.

The specimens BMNH 1982.9.13.13 (Brickell; punch Rose) and BMNH 1982.7.9.2 (Masi hajaka; punch Rosen) were not available at the time of our study and cannot be confirmed as M. madagascarii until examined. The specimen from Fenerive (MNHN 1953.130) is subadult (SVL 15.2 mm); traces of femoral glands recognizable and in mediotic state of preservation. It was considered as M. horridus by Bemmels-Schönherr and Blanc (1991). Despite its short hindlimbs (tibial articulation reaching anterior eye corner) we consider it as M. madagascarii because on the posteroero part of the femur, unpigmented areas are recognizable (which probably correspond to the real life color typical for this species). The dorsum of the specimen is covered by a dense, brownish, granular layer without ridge elements. According to the MNHN catalogue, two specimens were originally granted the number MNHN 1953.130; the locality information reads "Fenerive, Tamajo Est". Blommers-Schönherr and Blanc (1991) apparently interpreted this as separate populations for the two specimens, and correspondingly plotted two localities on their distribution map, one for Fenerive, a second one for Tamajo Est. There are at least two localities named Tamajo along the eastern coast of Madagascar, one close to Manarana and north of Fenerive (Fenerive), a second one south of Tanondro near Tamajo (Tamajo). As specimens from different localities generally were not catalogued under the same number in the MNHN, we treat "Fenerive" as added to indicate that "Tamajo Est" refers to the locality north of Fenerive.

Natural history. - Calling males were observed at night in forest vegetation, 5-50 cm above the ground, not concentrated around water bodies. The vocal sac was single salivary and only slightly distensible.

Calls. - Recorded at Ankeniheny at 23.5°C air temperature and at Andasibe. Series of unharmonious notes (Fig. 4b). Note duration was 934-1468 ms (1169 - 2015 ms, n = 6) at Andasibe and 259-995 ms (864 - 72 ms, n = 12) at Ankeniheny. Duration of intervals between notes was 769-1049 ms (876 - 108 ms, n = 5) at Andasibe, and 1126-1636 ms (1353 - 208 ms, n = 11) at Ankeniheny. Each note consisted of 22-43 (5 - 9, n = 6) pulses, duration of intervals between pulses at the localities were 30-80 ms. Pulse repetition rate was 23-36 (30 - 5, n = 6) respectively 18-22 (20 - 11, n = 13) pulses per second. Frequency was 2500-4500 respectively 2650-4000 Hz.

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Mantidactylus (Laurentianus) striatus n. sp. Fig. 1-2


Description of holotype. - Adult male. SVL 23.8 mm. For measurements, see Table 1. Body slender; head longer than wide, slightly wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protruding, much nearer to tip of snout than to eye; canthus rostralis indistinct, concave; loreal region concave; tympanum small, distinct on left side of head, indistinct on right side, rounded, 42% of eye diameter; supraorbital fold wide, indistinct and rather irregular, not clearly curved; tongue oval, distally bifid; posteriorly vomerine teeth not visible on the buccal roof, but present under the mucous skin, chytrine small, rounded. Arms slender, subarticular tubercles single; two outer, and one inner metatarsal tubercles present; fingers without webbing; relative length of fingers 1-2-4-3-2, finger 2 distinctly shorter than finger 4, only slightly shorter than finger 1; finger disks distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibial articulation reaches between eye and nostril; lateral metatarsal tubercle connected; inner metatarsal tubercle distinct, outer metatarsal tubercle present; only traces of webbing between toes; relative toe length 1-2-5-4-3, toe 3 distinctly longer than toe 5. Skin on the upper surface coarsely granular; granules are arranged asymmetrically except for the anterior back and head regions, where some symmetrical larger tubercles and short ridges are present; a number of granules also above the eyes; no distinct enlarged tubercles in the cloacal region; ventral skin smooth. Femoral glands very distinct and prominent. On the right femur, in internal view (after reflection of skin), four large granules are visible, two of which are arranged symmetrically, apparently encircling a weakly marked external cephalic depression. Tibial glands absent. The folded vocal sac marks two distinct longitudinal lateral folds on the posterior throat.

Species is found in head width (U-test of ratio W/SV, P = 0.001; P = 0.005 considering males only, although some range overlap in this character exists. On the Masoala peninsula, the two species come into close contact and even syntypy, while only M. striatus was collected at Tamajo and only M. madagascarii at Andrambe, at Campagne 2 both species were captured.
After six years in preservation, dorsal coloration is uniformly greyish brown, with some darker coloration bordering the dorsal tubercles and granules. The limbs are light brown with indistinct dark brown crossbands (3-5 mm) on femur, 3-4 mm on tibia, 6-7 mm on tarsus and foot, 1-2 mm on humerus, 6-7 mm on radius and hand. A short (2-5 mm) beige ventral stripe starts on the posterior back and ends at the cloaca. Lower leg with indistinct dark and light crossbands. Ventrally uniformly greyish brown, with a few small light spots on chest.

Variation. The vertebral stripe on the posterior dorsal can be very short as in the holotype, or run along the whole posterior half of the dorsum (e.g., ZMK S9935, stripe length 12.5 mm). It is absent in only a single specimen (MRSN A19397) examined. Limb crossbands are 2-4 mm on femur, 3-4 mm on tibia, 6-8 mm on tarsus and foot, 1-2 mm on humerus, 7-8 mm radius and hand. Indistinct brown patches are generally present behind the forelimb insertion and in the inguinal region. ZMK S9936 is exceptionally light colored but agrees in pattern. The ventral ground color is always a diffuse and uniform greyish brown. In the female ZMK S9931, the throat is a darker brown shade than the ventral. A number of white markings can be present on the clavicle and on the throat along the lower lip. The hindlimbs are ventrally uniformly diffuse grey-brown. Dorsum coarsely granular, the granules generally not forming ridges (holotype showing an exceptional state). The belly skin is smooth in all specimens. The femoral glands measure between 3.8-1.8 mm (FAZC 10378) and 4.8-2.1 mm (MRSN A1938). They consist of 3 (FAZC 7905) to 5-6 granules per gland (MRSN A1938). Granule diameter is 0.8-1.2 mm.

No significant sexual dimorphism in relative tympanum size was detected, but the inner metatarsal tubercle was significantly higher in males (U-test, P<0.005), and possibly also had a tendency of being larger in males (U-test, P=0.09). Mean male size was 92% of mean female size.

In life, the color was similar to that in preservative. The iris was reddish in its upper part, brown in its lower part. The vertebral stripe was generally orange. The ventral side was dark to light grey, without any trace of red of reddish color.

Distribution. Known from (1) the Marojejy Massif, (2) Tsarano, (3) Masoala (Campére), (4) Hamidy (Fig. 3). Known altitudinal range 200-700 m.

Natural history. At Marojejy, calling males were found along small streams, at a maximum distance of 5 m from the water. FAZC 10311 contained two very large unpigmented oocytes (diameter 4 mm) and two smaller unpigmented oocytes (diameter 3 mm).

Calls. Recorded at Marojejy. Series of harmonious notes (Fig. 4c). Note duration was 400-1200 ms (932-324 ms, n=14). Duration of intervals between notes was 162-432 ms (238-72 ms, n=13). Number of pulses per note was 15-39 (28-9, n=14). Intervals between pulses lasted 21-23 ms (n=5). Pulse repetition rate was 29-40 (35-14, n=14) pulses per note. Frequency was 3000-4500 Hz. Exceptionally, a very long note type (duration ca. 2000 ms, consisting of 75 pulses) was heard.

Key to species of Laurentomantis (see also table II)

1. Larger species, male SVL 26-28 mm, female SVL 25 mm. Hindlimbs mostly shorter than, adapted along body, hindlimbs not reaching the ground, inmost. Pulse repetition rate in notes of advertisement calls low (1-3/5 s), note duration long (1-2.5 s) ... *Mantidactylus (Laurentomantis) brevipes* (B) Smaller species, male SVL up to 25 mm, female SVL up to 25 mm. Hindlimbs mostly longer, adapted along body, hindlimb orientation reaches at least mid, often short to beyond. Pulse repetition rate in notes of advertisement calls higher (5-8/5 s), note duration mostly shorter (0.4-1.5 s) ... *Mantidactylus (Laurentomantis) varium* sp. n.

Phylogenetic analysis

We analysed a total of 54 osteological, morphological, etho-ecological and karyological characters as listed in Appendix 1. Osteological data are based on cleared and stained specimens listed in Table III, and on informations published previously (Glaw et al., 1998; Vences et al., 1998). Non-osteological data were taken from the information summarized in Glaw et al. (1998) and Glaw and Vences (1998). Three species of *Heterixalus* (family Hyperoliidae) were used as outgroup.

The maximum parsimony analysis (Fig. 6) failed to place *Boophis* as monophyletic; all *Boophis* species were paraphyletically arranged along the lineage leading to *Mantidactylus* and *Mantidactylus* and *Mantella* together formed a monophyletic group. The two *Laurentomantis* included were sister taxa nested within *Mantidactylus*. A cluster of three species of the subgenus *Cephalotus* were the sister group of *Laurentomantis*. *Mantella* was also nested within *Mantidactylus*, with a species of the subgenus *Galerhtius* (M. libery) as sister group. *Lithostoma* and *Aegyptophyton* were sister taxa. Bootstrap support for most groupings was low, indicating their relatively low reliability.
Discussion

Phylogenetic relationships of Laurentomantis

Phylogenetic analysis placed the two Laurentomantis species as sister species deeply nested within the genus Mantidae. The phylogenetic positioning of Mantella and Laurentomantis, nested within Mantidae, agrees with the (much better supported) results of the molecular study of Richards et al. (2000). Based on these data, we continue to use Laurentomantis as a subgenus of Mantidae rather than as a valid genus. On the other hand, Mantidae appears to be paraphyletic, because the well-established genus Mantella resulted to be more phylogenetically related to the subgenus Blommersia and Gephyromantis. The monophyly of Laurentomantis as defined here appears to be ascertained considering the similar advertisement calls (long notes of widely spaced short pulses) and similar morphology of the four included species. Within Laurentomantis, M. madagascar and M. striatus almost certainly are sister species based on their similarities in morphology and advertisement calls.

Due to the derived mating behavior (absence of strong mating amplexus), sexual dimorphism in Mantidae affects different character complexes in comparison to most other frogs. As in other Mantidae, males of the subgenus Laurentomantis lack nuptial pads. Sexual size dimorphism appears to be rather pronounced in at least two species, M. hoffmanni and M. verruculatus, in which male size is 76-92% of female size. In contrast, it is faint in M. madagascar and M. striatus (male size 80-90% of female size). At least in M. striatus, males have a (slightly) larger inner metatarsal tubercle, a state shared with species of the subgenus Phelcomantis and Gephyromantis; a survey of this character in more sister genera of Mantidae is necessary to assess its phylogenetic value.

Biogeography

The distribution patterns of the four Laurentomantis species as revised herein provide some information on the biogeographic regions within Madagascar defined by Angel (1942), Glaw and Vences (1994) and Rick et al. (1985). The presence of M. verruculatus at Iaka-Ivandry in the South-East and at Andasibe in the Central East (distance between both localities ca. 675 km) provides a further example of a species occupying a large and probably more or less continuous distribution area along the eastern rainforests. On the other hand, the sharp distribution barrier between M. madagascar and M. striatus is a further example of the faunal turnover between the Eastern and North-Eastern regions which at least partly takes place in the Masoala- Tsaratanana-Ankaranamba corridors (Vences et al. 1999), without conspicuous recent distribution changes. Finally, the presence of M. hoffmanni in Sanmarino (Masoala), the Central North (Tsaratanana) and the North (Montagne d'Amber) emphasizes the similarities between the herpetofaunas occurring in these regions.

Relationships and origins of mantellids

Our results corroborate that the two genera Boophis and Mantidae (classified in two separate subfamilies, Boophinae and Mantellidae; Vences & Glaw, 2001) belong to a monophyletic lineage endemic to Madagascar and adjacent islands (Richards and Moens, 1999; Boaz et al., 2000; Vences et al., 2000) which has been defined as family Mantellidae (Vences and Glaw, 2001). A major difference between the two genera is the apomorphic loss of the anterolateral process of the hyoid plate in most Boophis (Glaw et al., 1998), but this process is present in B. tephrasoma according to the new data presented herein (Tables III and IV). We also ascertained that the number of tarsals, previously used to distinguish both genera (Blommers-Schilts, 1993; Glaw et al., 1998) is variable within Boophis (a small but distinct third free tarsal in B. tephrasoma and B. gotheti; only two tarsals in the remaining species examined) and possibly also in Mantidae (if our observation of only two tarsals in M. hoffmannii is not an artifact caused by poor taphonomic processes in the often carnotaneous third tarsal). This also stresses that the value of osteology and morphology to assess
phylogenetic relationships among frogs is limited by the high degree of homoplasy affecting many characters.

Vences et al. (2000) noted that basal relief groups among Malagasy anurans mainly occur in dry western Madagascar, and hypothesized that the ancestors of extant rainforest frogs in Madagascar were adapted to arid conditions. In contrast, specialization to constant humid conditions is probably found in the Mantidactylus species without free-swimming larvae: direct development is known in the subgenus Geopomantis, and is probable at least in some Leurostomatini based on the data presented in the present paper (large eggs, calling largely independent from water bodies). As no terrestrial Tertiary fossils are known from Madagascar, the classification of the Late Cretaceous remains as described by Asher and Krause (1998) is of importance to reconstruct the timing of these adaptive radiations in rainforest environments. The main fragments - an atlas and a sacrum - belong to large frogs characterized by a procumbent vertebral column and narrowly separated abdominal coxyles. Mantellid fossils are generally characterized as diplacodonts and having widely separated coxyles. Asher and Krause (1998) concluded that the fossils were related to the more basal Pelobatidae (which has no extant representatives in Madagascar and Subsaharan Africa). This conclusion is sound, taking into account the overall archaic Cretaceous fauna of Madagascar (Krause et al., 1997). However, it must be noted that one of the largest extant endemic Malagasy frogs, Mantidactylus guttulatus, is characterized by procumbent (Gümbel, 1978).

According to data presented here, this species and the closely related M. grandis and M. guttulatus, as well as Ahytobate guttulatus and Laliostoma, also have narrowly separated coxyles. In these species, the space between coxyles is slightly larger than the width of one coxyle, agreeing with the state shown by Asher and Krause (1998) in their fossil specimen FMNH PR-161. The hypothesis that the remains belong to Mantellid frog species and that they were already present on Madagascar during the Late Cretaceous can thus not be ruled out at the present state.

Acknowledgements

We are indebted to N. Rabihc, C. Ravez, P. Ramia, C. R. Ramilison, and J. E. Randriamany for their help in the field. W. Belardi (Jena), A. C. Clarke and M. Claudio (London), B. van Lijt (Amsterdam), D. Vaillant and K. Gröben (Brook) and T. De Vries and G. Doria (Genoa) and A. De Vries and A. Otten (Paris) allowed examination and part or all of the specimens held in their care. W. Belardi additionally allowed the exchange of the holotype of M. reticulatus in the USNM. M. Matsui and B. Schaller carried out part of the osteological examinations. We are grateful to the Malagasy authorities for their assistance and permission to work. The research was made possible by a cooperation accord between the Department de Biologie Animale, Université d'Antananarivo and the Zoologische Forschungsinstitut und Museum Alexander Koenig, Bonn, and financially supported by the Deutsche Akademie der Wissenschaften zu Berlin. The survey work of FA at Mananjaka was carried out within a project in cooperation with the Parc Biologique de la Vallée de Taolanaro (Antananarivo), supported by the Wildlife Conservation Society (WCS) (Antananarivo) and the Museo Regional de Ciencias Naturales (Cerco) aimed at monitoring some rainforest areas in southern Madagascar. For their assistance, he is very grateful to the WCS staff at Antananarivo, especially M. Hardy, and to all the people of WES at Madagascar.

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clearly differing from general ventral coloration. (1) Black, (2) white.

**Character 58.** Vocal sac inflation: (0) vocal sac slightly distensible, (1) vocal sac largely distensible.

**Character 59.** Dorsal skin: (0) smooth, (1) slightly granular, (2) moderately to coarsely granular.

**Character 57.** Cellular DNA content: (0) around modal value, (1) distinctly lower than modal value.

**Character 55.** Karyotype: (0) 2n = 26 chromosomes, (1) 2n = 24 chromosomes.

**Character 54.** Acrocentric chromosomes: (0) absent, (1) present.