

Revision of the subgenus *Chonomantis* (Anura: Mantellidae: *Mantidactylus*) from Madagascar, with description of two new species

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(Accepted 18 June 2002)

A revision of Malagasy frogs of the subgenus *Chonomantis* (genus *Mantidactylus*) led to the recognition of three additional species, increasing their number from four to seven. *Mantidactylus melanopleura* is resurrected from the synonymy of *M. opiparis*. Two new sibling species of *M. albofrenatus*, from mid-altitudes in central eastern Madagascar and from low altitude areas along the east coast, respectively, are described as *M. zipperi* and *M. charlotteae*. Although the neotype of *Mantidactylus aerumnalis* is not completely consistent with the original description of this species, we accept it as the valid name-bearing type and thus the re-definition of *M. aerumnalis* based on its designation. The six *Chonomantis* species for which call recordings were available (all but *M. aerumnalis*) differed markedly in the temporal structure of their advertisement calls. Males of all seven species were easily distinguished by combination of relative tympanum size, relative toe length, amount of webbing, relative hindlimb length, and extension of frenal stripe. A key to all species and completely revised distribution maps are provided. Five of the seven species were found syntopically at a single locality in central eastern Madagascar, indicating that this region is the centre of diversity of the group. *Chonomantis* species diversity was highest at mid-altitude localities (500–1000 m elevation). The recognition of numerous sibling species in *Chonomantis* and other Malagasy anuran groups, which have been fairly well represented in scientific collections for decades, indicates that much revisionary taxonomic work is necessary before rigorous biogeographic analyses of the fauna are possible.

KEYWORDS: Amphibia, Anura, Mantellidae, *Mantidactylus*, *Chonomantis*, *Mantidactylus aerumnalis*, *Mantidactylus albofrenatus*, *Mantidactylus brevipalmatus*, *Mantidactylus opiparis*, *Mantidactylus melanopleura*, *Mantidactylus charlotteae* sp. nov., *Mantidactylus zipperi* sp. nov., Madagascar, taxonomy, biogeography.

Introduction

Among species in the Malagasy anuran genus *Mantidactylus*, representatives of the subgenus *Chonomantis* are characterized by their distinctive larval morphology

(Blommers-Schlösser, 1979; Razarihelisoa, 1974). *Chonomantis* are slender, small to medium-sized, terrestrial and largely diurnal frogs that live along small streams, generally in forested areas. Most species have a sharp border between a light brown back and dark brown flanks (dorsolateral colour border), a more or less distinct white stripe running from forelimb insertion along the upper lip to the eye, sometimes continuing toward the nostril (frenal stripe), and are sexually dimorphic in relative tympanum size and femoral gland size. Their tadpoles occur in streams, generally in slowly flowing parts, and have a specialized funnel-shaped mouth, similar to that of neustonic feeding larvae of some *Microhyla*, *Colostethus*, *Megophrys* and *Phyllomedusa* (Altig and Johnston, 1989; Lamotte and Lescure, 1989). The bizarre mouthparts in *Chonomantis* apparently are used for surface-feeding (Razarihelisoa, 1974). The two *Chonomantis* species investigated for karyotypes had $2n=26$ chromosomes, including acrocentric elements (Blommers-Schlösser, 1978).

Since 1978, the taxonomy of those *Mantidactylus* currently placed in the subgenus *Chonomantis* has been the subject of several revisions. Guibé (1978) listed three valid taxa: *M. albofrenatus*, *M. brevipalmatus* and *M. aerumnalis*. Blommers-Schlösser (1979) resurrected *M. opiparis* from the synonymy of *M. albofrenatus*, and considered *M. brevipalmatus* as a possible synonym of *M. aerumnalis*. She included *M. aerumnalis*, *M. albofrenatus* and *M. opiparis* in her *M. albofrenatus* group (see also Blommers-Schlösser and Blanc, 1991). Gavetti and Andreone (1993) designated a lectotype for *M. opiparis*. Andreone and Gavetti (1994) designated a neotype for *M. aerumnalis* and redefined the species based on specimens collected at An'Ala in central eastern Madagascar. They also resurrected the name *M. brevipalmatus* from the synonymy of *M. aerumnalis*, to refer to a species common at higher altitudes in central Madagascar. Glaw and Vences (1994) erected the subgenus *Chonomantis* for all these species, mainly based on the derived funnel-like tadpole mouthparts which are not known in any other *Mantidactylus*. Andreone and Randriamahazo (1997) noted bioacoustic and chromatic differences between different *M. opiparis* populations and considered the taxon *melanopleura* from south-eastern Madagascar, previously recognized as a synonym of *M. opiparis*, as a subspecies, *M. opiparis melanopleura*.

Ongoing fieldwork, together with the application of bioacoustic methods, indicated that the species diversity of almost all Malagasy anuran groups is much higher than previously thought. In the case of *Chonomantis*, one of us (F. G.) discovered as many as five different species occurring syntopically at one locality (An'Ala). As all these species were morphologically recognizable by distinct characters, we undertook a revision of all preserved *Chonomantis* material available to us (approximately 380 specimens from 12 zoological collections, including those on which previous distributional information was based). Besides describing the new species discovered, we provide completely revised species distribution maps as the basis to discuss biogeographic scenarios, and as a contribution to the assessment of conservation priorities in Malagasy amphibians.

Materials and methods

Specimens were collected during day and night, generally placing special emphasis on the collection of calling males. Vouchers collected by the authors were fixed in 96% ethanol and subsequently stored in 70% ethanol; most specimens examined from the MNHN, MRSN and ZMA collections had been fixed in formalin. Individuals were sexed by examination of femoral glands (more prominent and

larger in males), and/or by gonad dissection. Morphometric measurements were done by M. V. with precision callipers to the nearest 0.1 mm. Measurements taken were: SVL, snout–vent length; HW, maximum head width (generally measured at a point immediately posterior to the eyes); HL, head length (measured from posterior maxillary commissure to snout tip); Eye, horizontal eye diameter; Tym, horizontal tympanum diameter; Eye–Ns, eye–nostril distance; Ns–St, distance between nostril and snout tip; FoL, foot length (measured from foot–tarsus articulation to the tip of longest toe); FoTL, foot length including tarsus (measured from tibiotarsal articulation to the tip of longest toe); HiL, hindlimb length (measured from anus to the tip of longest toe); ForL, forelimb length (measured from axilla to the tip of longest finger); HaL, hand length (measured from carpus–hand articulation to the tip of longest finger); FGD, femoral gland distance (distance between the median central depressions of femoral glands on opposite femurs). Webbing formula follows Blommers-Schlösser (1979) and most subsequent authors who published accounts on Malagasy anurans. Webbing is described relative to subarticular tubercles, which are numbered 1–3, beginning from the disks. Only one subarticular tubercle was recognizable on the second toe of most specimens; no exact webbing value could therefore be given for species in which the webbing did not reach that tubercle. Description of colour patterns follows Vences *et al.* (1999a). The terms femur, tibia, and tarsus, as used in the sections on coloration, do not refer to the skeletal elements but to the external coloration of the corresponding hindlimb sections.

The following institutional abbreviations are used: BMNH (The Natural History Museum, London); FAZC (Franco Andreone Zoological Collection; specimens deposited in MRSN); MNHN (Muséum national d'Histoire naturelle, Paris); MRSN (Museo regionale di Scienze Naturali, Torino); MZUT (Museo Zoologico dell'Università di Torino; specimens currently in MRSN); NMBA (Naturhistorisches Museum Basel); NMBE (Naturhistorisches Museum Bern), SMF (Senckenberg Museum, Frankfurt); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZMA (Zoölogisch Museum, Amsterdam); ZMB (Museum für Naturkunde, Berlin); ZSM (Zoologische Staatssammlung, München). ZMA catalogue numbers refer to specimen series; where appropriate, we therefore give in parentheses also the individual field number to address particular specimens.

Bioacoustic analyses were made by F. G. with the sound analysis system MEDAV Spektrum 3.2. Temporal measurements are given as range, followed by mean, standard deviation and number of measurements in parentheses and number (*n*) of analysed notes respectively calls or intervals. Table 1 gives a summary of longitudes, latitudes, and altitudes of all localities referred to in the text.

Results

Discrimination of species

By a combination of discrete morphological characters and temporal call characteristics, we identified a total of seven different *Chonomantis* species in the field. Plotting the male specimens along only two variables (Tym/Eye ratio, and SVL) allowed separation of most of the previously recognized species (figure 1). Relevant overlap was found between the three species of the *M. albofrenatus* complex (*M. albofrenatus*, *M. zipperi*, *M. charlotteae*; see *Discussion*), between the otherwise very distinct *M. brevipalmatus* and *M. melanopleura*, and between *M. aerumnalis* and *M. charlotteae*. On the other hand, the species of the *M. albofrenatus* complex were

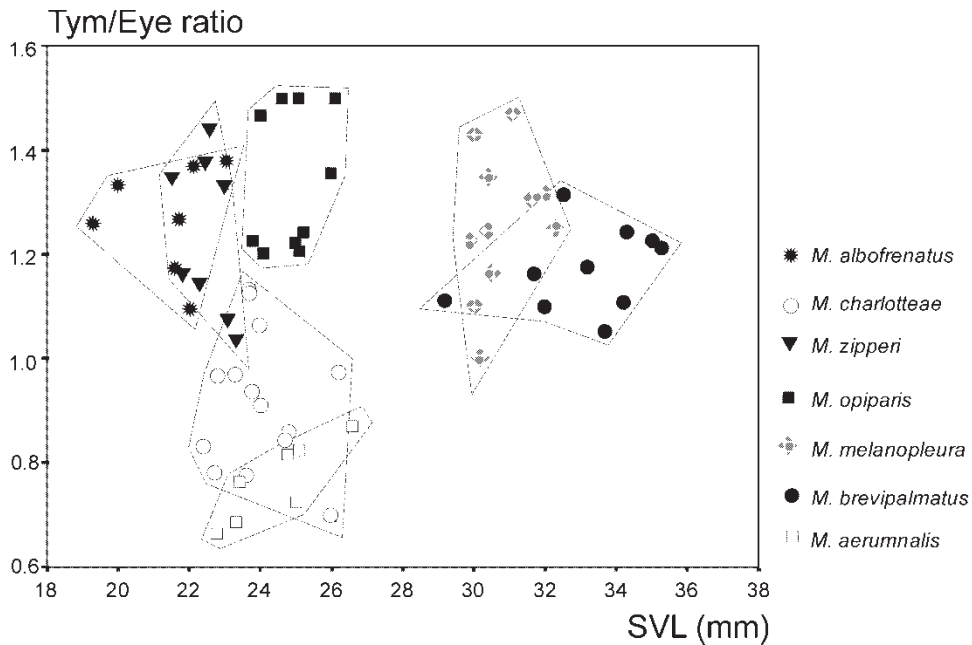


FIG. 1. Scatterplot of snout-vent length (SVL) and relative tympanum size in males of the seven *Chonomantis* species identified. See *Appendix* for list of measured specimens.

especially easily separated by temporal advertisement call parameters (figure 2). Several additional diagnostic morphological and chromatic characters were found for each of the species. The fact that five of these (and four different calls) were sympatrically recorded at a single locality (see *Discussion*) leaves us in no doubt that they all represent well differentiated species within both a biological and an evolutionary species concept. In the following accounts, we summarize knowledge of each of these species (figures 3–6), attribute the existing names in the subgenus *Chonomantis* to them by complete re-analysis of available type material, and describe two species as new. Species are listed in a rough phenetic order: we first provide accounts for two long-legged species of uncertain affinities, *M. brevipalmatus* and *M. aerumnalis*; we then provide accounts for the *M. opiparis* complex (*M. melanopleura* and *M. opiparis*), followed by the *M. albofrenatus* complex (*M. albofrenatus*, *M. zipperi*, *M. charlotteae*).

***Mantidactylus brevipalmatus* Ahl, 1929**
(figures 3a–b, 6a)

Synonyms. *Mantidactylus delormei* Angel, 1938

Although the holotype of *M. delormei* (re-examined by us in June 2000) is in a poor state of preservation, it largely agrees with *M. brevipalmatus* morphologically.

Identity. The holotype of *M. brevipalmatus* was thought to be lost (Guibé, 1978; Blommers-Schlösser and Blanc, 1991) but was rediscovered by Glaw and Vences (1992). We re-examined the specimen in May 2000. It agrees well with the other specimens attributed to this species morphologically: by its light throat with few irregular dark markings, light frenal stripe (clearly visible, although its exact

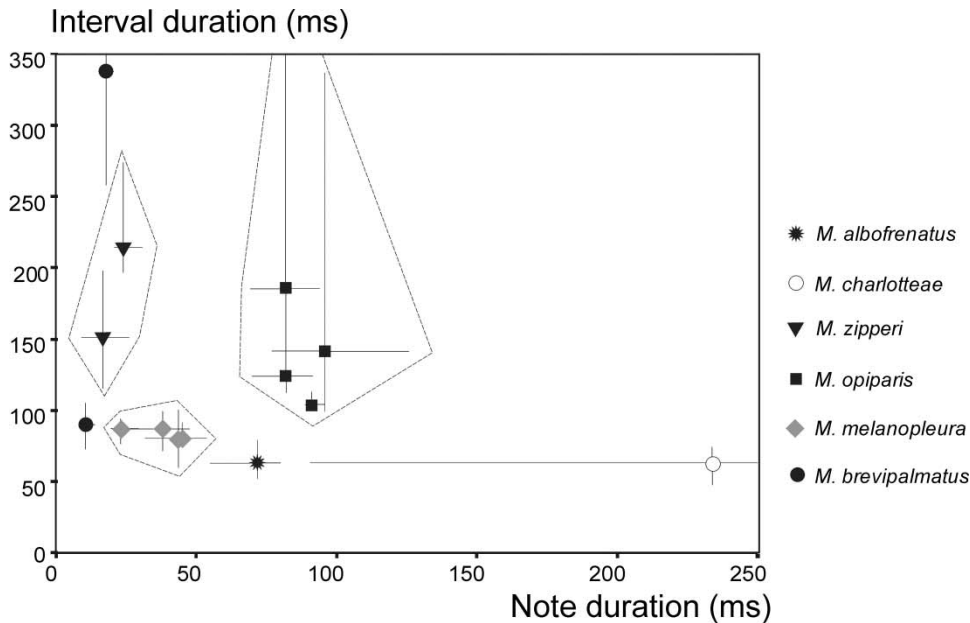


FIG. 2. Scatterplot of duration of notes and intervals between notes of advertisement calls of six *Chonomantis* species. Each symbol represents mean values of one population, except for *Mantidactylus brevipalmatus* in which the two symbols refer to the two note types recorded in the Manjakatampo population. Lines mark minimum and maximum values measured. Note that species with overlapping morphometric values (figure 1), especially, *M. albobrenatus*, *M. zipperi* and *M. charlotteae*, are well separated by bioacoustic characters.

extension is not recognizable due to the partly faded pattern), and the only indistinct colour border between back and flanks.

Diagnosis. The largest *Chonomantis* known. Legs very long (tibiotarsal articulation reaching at least the snout tip, usually widely beyond snout tip). SVL 27.6–35.3 mm in males, 34.8–44.9 mm in females. Third toe distinctly shorter than fifth toe, fourth toe very long. No distinct dorsolateral colour border; back light with different irregular spots and markings, sometimes with a distinct light vertebral stripe. Frenal stripe distinct from forelimb insertion to eye, becoming indistinct towards the nostril. Throat whitish with few irregular markings. Femoral glands of males very large and distinct. Tympanum in males distinctly larger than the eye. Webbing of the foot (based on ZSM 373/2000, male) 1 (1), 2i ($\gg 1$), 2e (1), 3i (2.25), 3e (2), 4i (3), 4e (3), 5 (2). Size of femoral gland (type 3, structure A according to Glaw *et al.*, 2000) in ZSM 373/2000 (SVL 29.6 mm): 5.2 \times 3.1 mm; FGD 9.1 mm.

Material examined. FAZC 7926, 7943, 7948 (Manjakatampo); MNHN 1938.240 (holotype of *M. delormei*; no precise locality according to catalogue but given as Antaranomby, l'Étang des boeufs, in the original description); MNHN 1953.45 (Manjakatampo), MNHN 1953.46 (Vakoana forest, Andringitra); MNHN 1972.1355–1972.1361 (Ambohimirandrana, Ankaratra); MNHN 1972.1362–1972.1364 (Manjavona valley, Ankaratra); MNHN 1972.1365–1972.1396 (Betay forest, Ankaratra); MNHN 1972.1397–1972.1402 (Nosiarivo, Ankaratra); MNHN 1973.756–1973.760 (Ambatomenaloha, Itremo); MNHN 1975.392

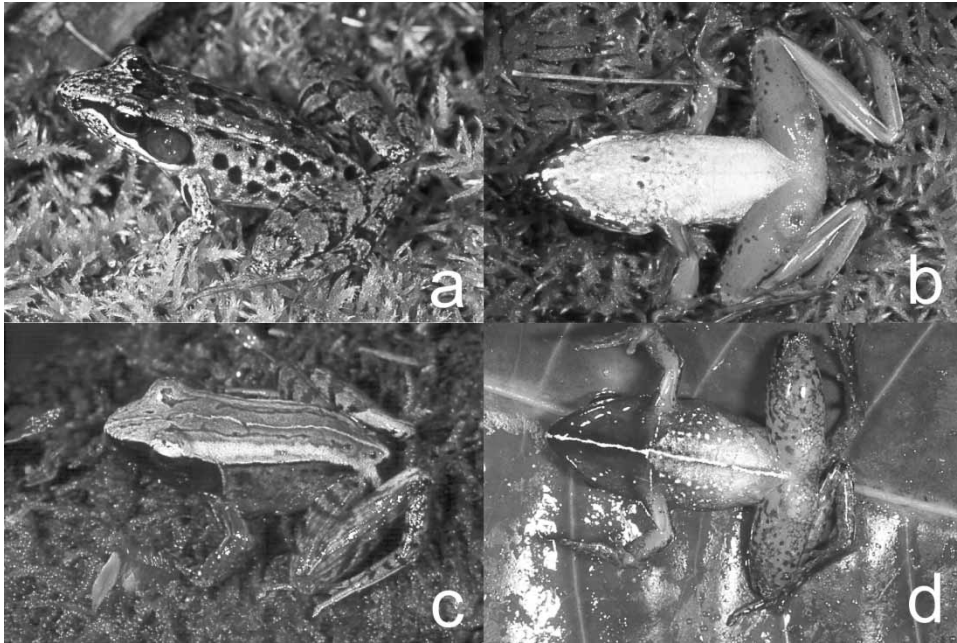


FIG. 3. Photographs of live male specimens (dorsolateral and ventral views) of: (a–b) *Mantisactylus brevipalmatus*, specimen from Manjakatampo (1994); (c–d) *M. aerumnalis*, specimen from An'Ala (1995).

(Manjakatampo); MNHN 1984.105 (no locality). NMBE 1046022 (Ambohitantely). ZFMK 59853 (Manjakatampo, Ankaratra); ZFMK 59853, 56163 (Manjakatampo, Ankaratra), ZMB 30530 (holotype of *M. brevipalmatus*, locality given as 'Nord-West-Madagascar', but see comment below); ZSM 371/2000 (plain close to Tsiafajavona summit, Ankaratra); ZSM 372/2000–374/2000 (Manjakatampo); ZSM 751/2001 (Imaitso forest, Andringitra); ZSM 752/2001 (Itremo); ZSM 753/2001 (Ankaratra).

Distribution. Known from: (1) the Ankaratra massif (1a, Ambohimirandana; 1b, Mahiavona valley; 1c, Betay forest; 1d, Nosiarivo; 1e, Manjakatampo, 1f, close to Tsiafajavona summit); (2) Ambatomenaloha (Itremo); (3) the Andringitra massif (3a, Antaranomby; 3b, Vakoana forest; 3c Imaitso forest); (4) Ambohitantely. The localities in the Ankaratra mountains have been spelt in different ways in the pertinent references and in the MNHN catalogue. We here follow the spelling in a recent map ('La station forestiere et piscicole de Manjakatampo' by the Direction des Eaux et Forets, edited 1995 by the Foiben-Taosarintanin'i Madagasikara in co-operation with the Gesellschaft für Technische Zusammenarbeit), and change Mihavona (Blommers-Schlösser and Blanc, 1991) respectively Mahiavona valley (MNHN catalogue) to Manjavona; and Ambomirandrana (MNHN catalogue) to Ambohimirandana. We could not locate the locality 'Betay forest' which also is in the Ankaratra mountain range according to the MNHN catalogue. The species has probably also been recorded from Ankaratra and Andringitra by Raxworthy and Nussbaum (1996a, b) as *M. aerumnalis*. Considering localities with reliably known altitude, the species is known from 1670–2380 m above sea level (table 1).

In addition to the mentioned localities, Blommers-Schlösser and Blanc (1991) give (under the name *M. aerumnalis*) three further localities: Angavokely, Mandraka,

Table 1. Collecting localities which are mentioned in the text, their exact location, and recorded species. Localities are arranged alphabetically. Co-ordinates and altitudes according to: (1) Carleton and Schmidt (1990); (2) Andreone *et al.* (1995); (3) Brygoo (unpubl.); (4) the MNHN catalogue; (5) Andreone and Randriamahazo (1997); (6) Viette (1991); (7) Nicoll and Langrand (1989); (8) personal communication of F. Andreone; (9) Raselimanana (1998). High-altitude refers to an altitude between c. 1000 and 1500 m, mid-altitude to c. 500–1000 m, low altitude to c. 0–500 m. In the Marojejy massif, we assumed that the MNHN catalogue entries ‘300 m’ and ‘600 m’ refer to the campsites I and III sampled by us, which probably had also been used by the expedition of C. P. Blanc and co-workers who collected most of the MNHN material.

Locality name	Altitude	Co-ordinates	Species recorded
Ambatobe	c. 50–200 m	15°15' S/50°26' E	<i>M. charlotteae</i>
Ambohimirandrana	c. 2000 m	19°20' S/47°16' E	<i>M. brevipalmatus</i>
Ambohitantely	1200–1650 m (7)	18°10' S/47°17' E	<i>M. opiparis</i> , <i>M. zipperi</i> , <i>M. brevipalmatus</i>
Ambolokopatrika, Camp 2 (8)	860 m	14°32' S/49°26' E	<i>M. opiparis</i> , <i>M. charlotteae</i>
Ampokafo	c. 200–500 m	15°16' S/50°3' E	<i>M. charlotteae</i>
An'Ala	840 m	18°56' S/48°28' E	<i>M. aerumnalis</i> , <i>M.</i> <i>albofrenatus</i> , <i>M. melanopleura</i> , <i>M. opiparis</i> , <i>M. zipperi</i>
Andasibe (= Perinet)	915 m (1)	18°56' S/48°25' E (1)	<i>M. albofrenatus</i> , <i>M.</i> <i>melanopleura</i> , <i>M. opiparis</i> , <i>M. zipperi</i>
Andohahela	c. 400 m (2)	24°47' S/46°51' E	<i>M. charlotteae?</i> , <i>M. melanopleura</i>
Andrangoloaka	950 m (1)	19°2' S/47°55' E	<i>M. opiparis</i>
Anjanaharibe	mid-altitude	13°37' S/49°36' E (3)	<i>M. opiparis</i> , <i>M. charlotteae</i>
Anjozorobe	c. 1300 m (9)	18°24' S/47°53' E	<i>M. melanopleura</i>
Antsihanaka	mid-altitude	unknown; forest in Lake Alaotra region	<i>M. melanopleura</i> , <i>M. opiparis</i>
Besariaka (8)	850–940 m	14°50' S/49°36' E	<i>M. opiparis</i> , <i>M. charlotteae</i>
Fizoana	low altitude	15°20' S/49°57' E	<i>M. charlotteae</i>
Foulpointe (= Mahavelona)	c. 0–100 m	17°41' S/49°30' E	<i>M. charlotteae</i>
Ifanadiana	450 m	21°18' S/47°38' E	<i>M. melanopleura</i> , <i>M. opiparis</i>
Ilampy (8)	450–500 m	15°23' S/50°2' E	<i>M. melanopleura</i> , <i>M. opiparis</i> , <i>M. albofrenatus</i> complex
Imaitso forest (Andringitra)	1500 m	22°08' S/46°56' E	<i>M. brevipalmatus</i>
Isaka-Eminiminy (Andohahela)	310–430 m (5)	24°45' S/46°51' E	<i>M. melanopleura</i>
Itremo (Ambatomenaloha)	> 1000 m	c. 20°36' S/46°38' E	<i>M. brevipalmatus</i>
Ivohibe (Marovitsika forest)	1000 m (4)	c. 22°29' S/46°55–58' E	<i>M. aerumnalis</i> , <i>M. melanopleura</i>
Mahajebly forest (Morafenobe)	c. 600 m (6)	18°02' S/46°00' E	<i>M. zipperi</i> , <i>M. opiparis</i>
Lac Alaotra (E Imerimandroso)	c. 1000 m	c. 17°25' S/48°50' E	<i>M. opiparis</i>
Manarikoba forest (Tsaratanana)	1000 m	14°03' S/48°47' E	<i>M. opiparis</i>
Mandraka	1220 m (1)	18°55' S/47°56' E (1)	<i>M. opiparis</i>
Manjakatombo (Ankaratra)	1670 m	19°21' S/47°18' E	<i>M. brevipalmatus</i>
Manjavona (Ankaratra)	c. 1800 m	19°21' S/47°16' E	<i>M. brevipalmatus</i> , <i>M. melanopleura?</i>
Mantady	900 m	18°53' S/48°25' E	<i>M. melanopleura</i> , <i>M. zipperi</i>
Marojejy Camp I	300 m	14°26' S/c. 49°46' E	<i>M. charlotteae</i>
Marojejy Camp III	700 m	14°26' S/c. 49°46' E	<i>M. charlotteae</i> , <i>M.</i> <i>melanopleura</i> , <i>M. opiparis</i>

Table 1. (Continued).

Locality name	Altitude	Co-ordinates	Species recorded
Marojejy	1300 m	14°26' S/c.49°46' E	<i>M. opiparis</i>
Masoala Camp 1 (8)	450 m	15°17' S/50°00' E	<i>M. opiparis</i> , <i>M. albofrenatus</i> complex
Masoala Camp 2 (8)	620 m	15°16' S/49°59' E	<i>M. melanopleura</i> , <i>M. opiparis</i>
Masoala Camp 3 (8)	600–700 m	15°18' S/50°01' E	<i>M. melanopleura</i>
Moramanga	c.900–1000 m	18°57' S/48°13' E	<i>M. aerumnalis</i> , <i>M. melanopleura</i>
Nahampoana	c.300 m	24°58' S/46°58' E	<i>M. melanopleura</i>
Navana	c.100–200 m	15°24' S/49°52' E	<i>M. charlotteae</i>
Nosiarivo (Ankaratra)	c.2000 m	19°20' S/47°17' E	<i>M. brevipalmatus</i>
Nosy Boraha	< 50 m	17°00' S/49°51' E	<i>M. charlotteae</i>
Nosy Mangabe	c.0–200 m	15°30' S/49°36' E	<i>M. charlotteae</i>
Nahampoana	c.300 m	24°58' S/46°58' E	<i>M. melanopleura</i>
Niagarakely	mid altitude	19°08' S/48°14' E	<i>M. opiparis</i>
Ranomafana	600 m	21°15' S/47°27' E	<i>M. aerumnalis</i> , <i>M. melanopleura</i> , <i>M. opiparis</i> , <i>M. zipperi</i>
Rantabe	< 100 m	15°42' S/49°38' E	<i>M. charlotteae</i>
Sahafary	c.100–500 m	15°15' S/50°27' E	<i>M. charlotteae</i>
Soavala (= Soavata) (Chaines Anosyennes)	probably low altitude	c.24°13' S/47°12' E (6)	<i>M. melanopleura</i>
Tampoketsa d'Ankazobe	high altitude	18°17' S/47°08' E	<i>M. opiparis</i>
Tolongoina	c.700 m	c.21°28' S/47°33' E	<i>M. aerumnalis</i>
Tsararano (8)	700 m	14°55' S/49°41' E	<i>M. melanopleura</i> , <i>M. opiparis</i>
Tsiafajavona (Ankaratra)	2380 m	19°20' S/47°14' E	<i>M. brevipalmatus</i>
Vohidrazana	730 m	18°57' S/48°30' E	<i>M. melanopleura</i>
Vohiparara	c.1000 m	21°13' S/47°22' E (1)	<i>M. melanopleura</i> , <i>M. opiparis</i>
Voloina	c.100–300 m	15°34' S/49°36' E	<i>M. charlotteae</i>
Vondrozo	700 m	22°49' S/47°20' E	<i>M. aerumnalis</i>
Zahamena	mid-altitude	17°40' S/48°50' E	<i>M. melanopleura</i>

and Nord-Ouest. The locality Angavokely (1600 m altitude) is apparently based on the tadpoles ZMA 7184 (see Blommers-Schlösser, 1979), and their identification requires confirmation. The locality Mandraka (Razarihelisoa, 1974) is also based on tadpoles, which can not be reliably attributed to *M. brevipalmatus* at present. According to the original description (Ahl, 1929), the type locality of *M. brevipalmatus* is 'Nord-West-Madagascar' (erroneously given as 'NE-Madagascar' by Glaw and Vences, 1994). The holotype was collected by Johannes Maria Hildebrandt, who used a special numbering system for his collection. However, obviously erroneous labelling of his collection occurred at least in some instances (Beentje, 1998). Peters (1880) reported on a collection of Hildebrandt made in Nosy Be and north-western Madagascar, which corresponded well with Hildebrandt's travel routes in 1879 and 1880. On 17 January 1881, Hildebrandt collected in the Ankaratra massif, but was forced to leave the region due to heavy rains; shortly after this expedition, he became ill and eventually died in Madagascar on 29 May 1881. We consider it likely that the material not yet mentioned by Peters (1880) but later described by Ahl (1928, 1929) was collected during Hildebrandt's last trip along his 1881 travel route in central and eastern Madagascar (see Beentje, 1998). Among others, this relates to the taxa *Mantidactylus brevipalmatus*, *Rhacophorus brevirostris* (synonym of *Boophis rhodoscelis*), *Rhacophorus callichromus*, *R. fasciolatus*, *R. kanbergi* (all synonyms of *Boophis goudoti*), *Mantidactylus sculpturatus* and *Cophyla tuberculata*

(synonym of *Platypelis grandis*). All these taxa were described as originating from north-western Madagascar but were never collected again in this region. It is therefore likely that these locality data are erroneous. If this hypothesis is true, then the holotype of *M. brevipalmatus* most probably was collected in the Ankaratra massif.

Variation. Of the MNHN sample from Ankaratra (MNHN 1972.1355–1972.1402), 24 of 40 males had a distinct vertebral stripe, whereas the remaining 16 were unstriped. Five of eight females were striped. In the Itremo sample (MNHN 1973.756–1973.760) all specimens were unstriped. All examined male specimens had very distinct and large femoral glands. The Itremo sample differed in their shorter SVL and shorter legs (MNHN 1973.756, male, SVL 28.5 mm, tibiotarsal articulation reaching snout tip; MNHN 1973.758, male, SVL 28.4 mm, tibiotarsal articulation reaching snout tip; MNHN 1973.759, male, SVL 28.3, tibiotarsal articulation reaching nostrils; MNHN 1972.760, male, SVL 27.6 mm, tibiotarsal articulation reaching between nostril and snout tip; MNHN 1973.757, female, SVL 35.5 mm, tibiotarsal articulation reaching snout tip). The femoral glands of the Itremo specimens were located nearer to the cloaca than in most other specimens. In four males, FGD was 7.4 mm (MNHN 1973.756), 8.0 mm (MNHN 1973.758), 6.4 mm (MNHN 1973.759), 7.0 mm (MNHN 1973.760). For comparison, FGD in Ankaratra specimens of only slightly larger SVL was 10.2 mm (MNHN 1972.1360), 8.7 mm (MNHN 1972.1364), 10.7 mm (MNHN 1972.1367), 9.0 mm (MNHN 1972.1368), 9.7 mm (MNHN 1972.1386). According to photographs and examination of ZSM 751/2001, specimens from Andringitra are also distinct; they have a more yellowish venter, more distinct dorsolateral colour border, and a dark median area on the dorsum. However, as no adult males in good state of preservation from Andringitra are known, and no calls can be reliably attributed to this population, its status remains uncertain; the name *M. delormei* is available in case the Andringitra specimens are demonstrated to belong to a distinct species.

Colour photos of *M. brevipalmatus* were published by Glaw and Vences (1992: cp. 77, as *M. aerumnalis*), Blommers-Schlösser and Blanc (1993: plate 18 (figure 89), as *M. aerumnalis*), Andreone and Gavetti (1994: figure 5) and Glaw and Vences (1994: cp. 110).

Cytogenetics. Karyological data were provided by Blommers-Schlösser (1978) under the name *M. aerumnalis* (voucher specimens ZMA 6777, 6779 and 6781 from Manjakatempo).

Tadpoles. Larvae were described by Blommers-Schlösser (1979) under the name *M. aerumnalis*. The description was largely based on tadpoles from Manjakatempo, and the drawings refer to a specimen from this locality (ZMA 7078). As *M. brevipalmatus* is the only or at least by far the most common *Chonomantis* at Manjakatempo, the drawing almost certainly applies to a tadpole of this species. The tadpole description by Razarihelisoa (1974) largely refers to tadpoles from Angavokely and Mandraka, of uncertain attribution.

Habits. Calling males were heard, during day and evening, alongside small streams in the months October, February and March (Blommers-Schlösser, 1979, pers. obs.). We found them both in forest and in high-altitude savanna close to the Tsiafajavona summit. The ventral surface of several specimens was covered with reddish pustules (pers. obs.). One eggmass (ZMA 7079, deposited by a pair from Manjakatempo preserved as ZMA 6777) was deposited on land and contained 30 fertilized eggs, 3.5–4.0 mm in diameter and 8–9 mm including the capsule (Blommers-Schlösser, 1979).

Calls. Recordings made on 13 March 1992 near Manjakatempo have already been briefly described by Glaw and Vences (1994). A new, more detailed analysis resulted in the following description. Two note types could be distinguished. Notes of type 1 were arranged in series. Temporal call parameters: note duration 16–21 ms (18 SD 1 ms, $n=15$), interval duration 262–581 ms (337 SD 91 ms, $n=11$), note repetition rate 3.5/s. Three frequency bands were recognizable: 1050–1750 Hz, 2150–3050 Hz (dominant frequency 2200–2750 Hz), and 3900–4300 Hz. Notes of type 2 (figure 7) were slightly shorter. They were arranged in series of five to seven notes ($n=2$). Temporal call parameters: note duration 9–13 ms (11 SD 1 ms, $n=12$), interval duration 72–105 ms (89 SD 10 ms, $n=10$; distinctly shorter than between notes of type 1), note repetition rate 9–10/s. Frequency was similar to that of notes of type 1.

One specimen emitted distress calls on 13 March 1992 at Manjakatempo. They were arranged in series. One recorded series consisted of eight notes. Temporal call parameters: note duration 137–244 ms (179 SD 34 ms, $n=8$), interval duration 223–340 ms (268 SD 40 ms, $n=7$). Frequency was 1300–5200 Hz, with lower intensity up to 6600 Hz. The notes showed the typical distress call pattern (compare Hödl and Gollmann, 1986) with four to seven frequency bands, which were strongly but irregularly modulated. The distress vocalizations took place with closed mouth, when handling the specimen by its hindlimbs.

Blommers-Schlösser (1979) described the call of the species from Manjakatempo, based on recordings made in October 1971 (22 h), as a series (duration 6–10 s) of 17–25 melodious notes of 80 ms duration, with a dominant frequency of 1200 Hz. Her sonagram shows a note repetition rate of 4–5/s. This description partly agrees with our data of notes of type one; the longer note duration may be due to the measuring method (directly measured on the sonagram).

Mantidactylus aerumnalis (Peracca, 1893)
(figures 3c–d, 6b)

Original name. *Rana aerumnalis* Peracca, 1893

Synonyms. None.

Identity. Andreone and Gavetti (1994), determining that the holotype of *Mantidactylus aerumnalis* was lost, re-defined this species based on three specimens (one male and two females) collected at An'Ala. Their contribution significantly improved our understanding of *Chonomantis* taxonomy as they recognized that the high-altitude species from the Ankaratra and Andringitra massifs was not conspecific with *M. aerumnalis*, and that *M. brevipalmatus* was the oldest available name for this species (*M. delormei* being a junior synonym). Previously, confusion regarding the names *M. aerumnalis* and *M. brevipalmatus* existed, and the descriptions of these taxa by Guibé (1978) and Blommers-Schlösser and Blanc (1991) were contradictory in several respects as they apparently mixed characters typical for either species.

Andreone and Gavetti (1994) argued that their specimens from An'Ala agreed with the original description of *M. aerumnalis* (Peracca, 1893) in having: (a) shorter hindlegs than *M. brevipalmatus* (tibiotarsal articulation not reaching beyond snout tip); and (b) agreeing in body size with the original *M. aerumnalis* description. Accordingly, they designated the female MRSN A72 as neotype of *M. aerumnalis*. A thorough revision of the characters of *M. aerumnalis* as described by Peracca (1893) demonstrated, however, that the original description does not correspond with Andreone and Gavetti's (1994) species in a number of characters: according

to Peracca (1893) the lost holotype had: (a) short hindlegs, the tibiotarsal articulation reaching the nostrils ('...l'articolazione tibio-tarsale raggiunge le narici'); (b) a light frenal stripe at least between forelimb insertion and eye ('...una striscia biancogrigiastra che contorna inferiormente l'occhio ed il timpano per perdersi sulla spalla'), although the notion that it is fading on the back ('sulla spalla') does not agree with frenal stripes in *Chonomantis*; (c) a large tympanum, its diameter larger than that of the eye, equalling that of the eye–snout tip distance ('Timpano molto visibile, più grande dell'occhio. Il suo diametro orizzontale eguaglia la distanza che intercede tra l'angolo antero-interno dell'occhio e la punta del muso'); and (d) rudimentary webbing ('Palmatura delle dita rudimentale'). In contrast, the species defined as *M. aerumnalis* by Andreone and Gavetti (1994) usually has long legs (the tibiotarsal articulation reaches the snout tip in two out of 11 specimens, beyond snout tip in eight out of 11 specimens), a tympanum smaller than the eye in males, and no frenal stripe. Nevertheless, the neotype designation of Andreone and Gavetti (1994) was, apparently, in accordance with the requirements of the International Code of Zoological Nomenclature, third edition (Anonymous 1985) as in force in 1994. According to Article 75 (d) (1), a neotype must be 'consistent with what is known of the former name-bearing type from the original description'. Actually, of the differences mentioned above, the first (hindlimb length) does not apply, as the neotype has exceptionally short legs, thus agreeing with the original description; the tympanum size difference does not apply as the neotype is a female (females always having a small tympanum in *Chonomantis*), and the frenal stripe is not described unambiguously in the original description. We therefore propose to accept Andreone and Gavetti's (1994) neotype designation as valid and herein follow their definition of the species *M. aerumnalis*.

Diagnosis. A medium-sized *Chonomantis* with long legs (tibiotarsal articulation always reaching beyond nostrils, usually beyond snout tip). SVL 22.8–26.6 mm in males, 25.3–31.0 mm in females. Third toe of same length, or slightly shorter or longer than fifth toe. Back beige, with a distinct dorsolateral colour border and more or less distinct longitudinal patterns or a diamond-shaped marking. Head laterally uniformly dark, no trace of a frenal stripe. Throat dark with a light median line which is continued onto the venter, and which does not begin as enlarged white marking close to the snout tip. Femoral glands of males prominent and very distinct. Tympanum of males and females smaller than the eye. Webbing of the foot (based on ZFMK 62248, male, and 60094, female) 1 (1), 2i (1.5), 2e (1), 3i (1.25–2), 3e (1–1.5), 4i (2.25–2.75), 4e (2.25), 5 (0.75–1). Size of femoral gland (type 3, structure A according to Glaw *et al.*, 2000) in ZFMK 62248 (SVL 25.0 mm): 3.7 × 2.6 mm; FGD 5.0 mm.

Material examined. MNHN 1930.415 (Vondrozo); MNHN 1972.542 (Col Ivohibe, Marovitsika forest); MNHN 1975.373 (Ranomafana); MNHN 1975.382 (Ranomafana); MNHN 1989.3579 (formerly 1930.412D, Moramanga); ZFMK 47254 (Tolongoina); MRSN A72 (neotype; An'Ala), MRSN A74.1–74.2 (An'Ala); ZFMK 60092–60094, 62248 (An'Ala); ZMA 6998 (field numbers 125–128, 148, 192; specimens 147 and 214, also belonging to the series according to jar label, are apparently lost and were not examined).

Distribution. Known from: (1) Moramanga; (2) An'Ala; (3) Ranomafana; (4) Tolongoina; (5) Ivohibe; (6) Vondrozo. We do not consider here the original type locality Andrangoloaka, as the identity of the former name-bearing specimen (the lost holotype) is uncertain. Raxworthy and Nussbaum (1996a, b) recorded

M. aerumnalis from high elevation areas of the Andringitra and Ankaratra massifs, but did not list *M. brevipalmatus*. Therefore, it is likely that these authors followed the species definition of Blommers-Schlösser and Blanc (1991) who considered *M. brevipalmatus* to be a synonym of *M. aerumnalis*. Similarly, the localities Ankaratra, Manjakatempo, Nosiarivo, Mihavona (= Manjavona), Itremo, and Antaranomby given by Blommers-Schlösser and Blanc (1991) actually refer to *M. brevipalmatus* specimens. The localities Mandraka and Angavokely (Blommers-Schlösser and Blanc, 1991) are based on tadpoles and therefore can not be reliably assigned to a *Chonomantis* species. Considering localities with reliable altitudinal data, the species is known from 600–950 m above sea level (table 1).

Variation. All specimens from An'Ala are rather uniform in coloration and morphology. Specimens from the other localities are in relatively poor condition, and their determination was sometimes difficult. Few conclusions are therefore possible regarding geographical variation of morphology or coloration. However, by combination of relative toe length, hindlimb length, and lack of frenal stripe, reliable designation of all specimens was possible. Colour photos of the neotype were published by Andreone and Gavetti (1994: figure 10 and 11) and Glaw and Vences (1994: cp. 111).

Cytogenetics. Blommers-Schlösser (1978) described the karyotype of specimens (ZMA 6998) which were attributed to *Mantidactylus opiparis*. Re-examination showed that the vouchers are subadults; they are characterized by: (a) absence of frenal stripe on the uniformly dark sides of the head; (b) a thin median white line of continuous width on the uniformly dark throat; (c) a variable toe length (fifth toe slightly longer than third toe in four specimens, slightly shorter in two specimens); (d) a diamond-shaped marking and a thin light vertebral line on the back; (e) long hindlimbs (tibiotarsal articulation reaching snout tip or beyond); and (f) a pattern of a line of few white spots on the throat which is directed from the lips centroposteriorly towards the light median throat line. Although the possible continuation of the median throat line onto the belly cannot be assessed (ventral skin largely removed for dissection), these character states are typical for *M. aerumnalis*. The lack of a frenal stripe is diagnostic, and the shape of the throat line (not forming an enlarged white marking close to the snout tip) is a further clear difference from most *M. opiparis*. We thus consider the karyotype description published by Blommers-Schlösser (1978) under the name *M. opiparis*, subsequently also reproduced by Blommers-Schlösser and Blanc (1991), as referring to *M. aerumnalis*.

Habits and calls. The species was observed several times at An'Ala in February and March, but its calls were never heard. The descriptions of eggs and tadpoles in Blommers-Schlösser (1979), Blommers-Schlösser and Blanc (1991) and Glaw and Vences (1992), as well as the call description by Glaw and Vences (1992), referred to *M. brevipalmatus* (see below).

Mantidactylus opiparis (Peracca, 1893)
(figures 4a–b, 6c)

Original name. *Rana opiparis* Peracca, 1893

Synonyms. None.

Identity. The syntypes were once thought to be lost (Guibé, 1978; Blommers-Schlösser and Blanc, 1991), but were rediscovered by Gavetti and Andreone (1993) who designated a lectotype (MZUT An730.1), a female specimen in mediocre state

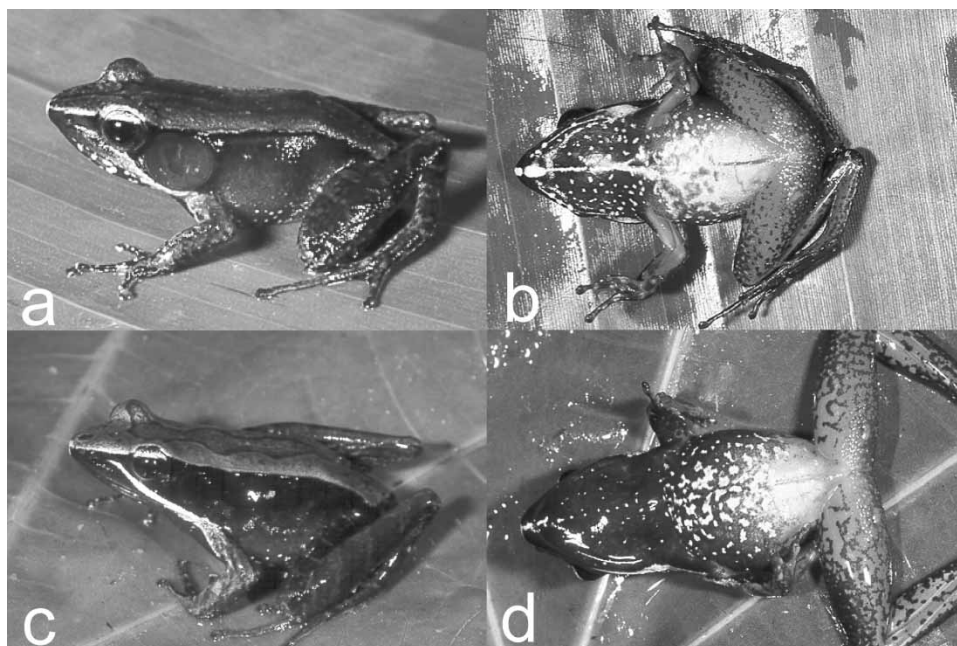


FIG. 4. Photographs of live male specimens (dorsolateral and ventral views) of the *Mantidactylus opiparis* complex: (a–b) *M. opiparis*, specimen from Mandraka (1994); (c–d) *M. melanopleura*, specimen from Andasibe (1996).

of preservation. Gavetti and Andreone (1993) described that ‘a white frenal stripe runs from the armpit along the upper lip, curved upwards behind the eye’. Upon re-examination of the specimen in June 2000, we conclude that it is conspecific with the small *M. opiparis*-like species without distinct frenal stripe anterior to the eye (see ‘Identity’ of *M. melanopleura*). Actually, a distinct white stripe was present between forelimb insertion and eye. This stripe became broader towards the eye, giving the impression of an upward curve. However, no stripe at all was recognizable between eye and nostril, the state typical for the small *M. opiparis*-like species. As the stripe was well recognizable between forelimb and eye, its absence between eye and nostril cannot be attributed to a general fading of pattern. Other colour patterns also were in agreement with the re-definition of *M. opiparis*. Dorsal coloration was light with a distinct diamond-shaped marking and a thin light median line. It extended onto the snout and gave the impression of a light spot on the snout tip. A clear dorsolateral colour border was present. The throat was dark with a narrow light median line. The two paralectotypes agreed in morphology and coloration with the lectotype (see also Gavetti and Andreone, 1993).

Diagnosis. A medium-sized species with long legs (tibiotarsal articulation generally reaching at least nostril, often beyond snout tip). SVL 23.8–26.1 mm in males, 27.0–33.2 mm in females. Third toe slightly shorter than fifth toe. Frenal stripe between forelimb insertion and eye, not between eye and nostril. Dorsolateral colour border present. Back often with diamond-shaped marking. Throat mostly dark, generally with a thin median white line which often begins as a rather broad white marking close to the snout tip. Femoral glands of males small and indistinct. Tympanum in males distinctly larger than eye. Webbing of the foot (based on the

males ZFMK 60095 and 60097) 1 (1), 2i ($\gg 1$), 2e (1), 3i (2.25), 3e (1.5), 4i (2.75), 4e (2.75), 5 (1). Size of femoral gland (type 3, structure A according to Glaw *et al.*, 2000) in ZFMK 60097 (SVL 25.1 mm): 2.3×1.5 mm; FGD 6.3 mm.

Material examined. BMNH 1925.7.2.23–25 (not individually labelled, in series with three *M. melanopleura*; Antsihanaka); BMNH 1952.1.1.96–97 (20 miles E Imerimandroso, Lac Alaotra); FAZC 1032, 1038, 1069 (Besariaka-Amponaomby); FAZC 6768, 6789, 6791, 6831, 7118, 7350–7351 (Ambolokopatrika); FAZC 7336, 7358, 7379, 7386, 7387 (Masoala, Camp 1); FAZC 7526, 7600, 7647 (Masoala, Camp 2); FAZC 10011, 10012, 10025, 10027, 10070, 10114, 10256, 10259, 10268 (Ilampy); MNHN 1972.549 (Ambohitantely); MNHN 1975.375 (Marojejy, 1300 m altitude); MNHN 1975.377 (Marojejy 600 m); MNHN 1989.3586 (formerly 1953.101, Morafenobe, Mahajeby forest); MRSN A284, A421.1–A421.4, A227.2–227.3, A334.1–334.2 (Andasibe); MRSN A298 (two female specimens; Anjaimba forest, Vohiparara); MRSN A329.1 (An'Ala); MRSN A407.2 (near Ifanadiana); MRSN A1923 (Tsararano, Camp 1); MRSN uncatalogued (four specimens; Analabe-Anjanaharibe, Camp A); MZUT An730.1 (lectotype of *M. opiparis*; Andrangoloaka); MZUT An730.2–An730.3 (paralectotypes of *M. opiparis*; Andrangoloaka); ZFMK 14183 (Niagarakely); ZFMK 52697, 53680, 60061, 60066 (Andasibe); ZFMK 59817–59818 (Mandraka); ZFMK 60095–60097 (An'Ala); ZFMK 60117, 62320 (An'Ala); ZFMK 60138 (Ambohitantely); ZFMK 62286 (Vohiparara); ZMA 7035 (field number 483; Mandraka); ZMA 6996 (field numbers 386, 387; Mandraka); ZMA 6997 (field numbers 281, 485; Tampoketsa d'Ankazobe); ZSM 641/2001 (Manarikoba forest, Tsaratanana massif).

Distribution. The species is known from: (1) the Tsaratanana massif; (2) the Marojejy massif, 600–1300 m altitude; (3) the Tsararano chain; (4) Besariaka; (5) Anjanaharibe; (6) Ambolokopatrika corridor; (7) Masoala; (8) Ilampy; (9) Antsihanaka; (10) Lac Alaotra; (11) Mahajeby forest; (12) Tampoketsa d'Ankazobe; (13) Ambohitantely; (14) Mandraka; (15) the type locality Andrangoloaka; (16) Andasibe, including the Analamazaotra reserve; (17) An'Ala; (18) Niagarakely; (19) Vohiparara; (20) Ifanadiana; and (21) Ranomafana National Park (call recordings). The locality Ambalamarina (Andringitra) was listed by Glaw and Vences (1994) based on call recordings; as no voucher specimens can be attributed to *M. opiparis*, this locality is not considered here. Of the remaining localities listed by Blommers-Schlösser and Blanc (1991), Mihavona (=Manjavona), Marovitsika (Ivohibe), Chaines Anosyennes, Ambana, Soavala, Isaka-Ivondro, and Fort Dauphin (=Tolagnaro) refer to *M. melanopleura*, whereas Tolongoina and Vondrozo refer to *M. aerumnalis*. The localities Bekazaha and Anosibe (Blommers-Schlösser and Blanc, 1991) are in need of confirmation as we did not locate voucher specimens. The same is true for the locality Nosy Mangabe (Andreone, 1993). The locality Nahampoana (Andreone, 1993; Glaw and Vences, 1992, 1994) refers to *M. melanopleura*. The Ivohibe record in Raselimanana (1999) possibly refers entirely or partly to *M. melanopleura* which is known from this locality, and is thus in need of confirmation. The same regards records from Andohahela (Nussbaum *et al.*, 1999) and Andringitra (Raxworthy and Nussbaum, 1996a). Most localities are at mid-elevations, although the species appears to reach lower elevations in the north-eastern part of its distribution. Considering localities with reliably known elevation, the species is known from 450–1300 m above sea level.

Variation. Specimens from the north-east (Marojejy-Masoala area) appeared to be slightly larger than those from the central-east (Andasibe area). The typical

colour pattern, especially the extension of the frenal stripe, was very uniform among all specimens examined. A colour photo of *Mantidactylus opiparis* was published by Glaw and Vences (1994: cp. 112, specimen on the left of the photograph). The photo in Andreone (1993, figure 7) does not show *Mantidactylus opiparis*, but a species of the subgenus *Gephyromantis*.

Tadpoles. Blommers-Schlösser (1979) described tadpoles of *Mantidactylus opiparis* based on reared specimens from Mandraka and Andasibe. The tadpoles from Mandraka (one specimen of the series ZMA 7031 was illustrated) may actually belong to *M. opiparis*, as this species appears to be common at Mandraka. However, considering the high species diversity of *Chonomantis* in central-eastern Madagascar, the specific attribution of these tadpoles must be considered tentative.

Habits. Calling males were observed in all months between December and April, indicating prolonged breeding activity in this species. They were found mostly during the day along brooks in primary rainforest and were calling either from the ground or up to 50 cm high from elevated positions. Distance from the brook was up to 10 m. At night, calling specimens were found on leaves up to 1 m above the ground. During the day, *Mantidactylus opiparis* and *M. melanopleura* were often calling at the same time in mixed choruses, but calling activity was not continuous in both species. After some time of silence, boosts of calls were emitted, stimulating neighbouring males to call. Calling activity was thus running along the brook in a wave-like manner. This made localization of calling males somewhat difficult. Three females (MNHN 1972.549, 1975.375 and 1975.377) contained 22–43 yellowish oocytes with a dark pole of up to 2 mm diameter (Vences *et al.*, 1999b).

Calls. Recordings were made at An'Ala on 11 February 1995, c.17 h, at 22°C air temperature. Calls consisted of series of 23–35 notes and lasted up to 10,300 ms. At the beginning of a call, the intervals between notes were longest; they decreased during the call and reached a value which corresponded to a note repetition rate of 5/s. Notes consisted of 13–18 (15.3 SD 1.6; $n=25$) pulses. Temporal call parameters: note duration 88–96 ms (91 SD 3 ms, $n=10$), interval duration in a quickly repeated section 100–113 ms (104 SD 4 ms, $n=9$). Frequency was between 1550–4400 Hz, with a 'frequency gap' between 2100–2700 Hz and a dominant frequency of c.3500 Hz. Calls recorded at Andasibe on 28 February 1994, at 21°C air temperature were similar: note duration 77–126 ms (96 SD 11 ms, $n=27$), interval duration 98–336 ms (142 SD 57 ms, $n=26$). Calls recorded at Ranomafana National Park on 1 March 1996, at c.23°C air temperature were also similar (figure 8). They contained up to 30 notes. Notes consisted of c.13 pulses ($n=3$). Temporal call parameters: note duration 69–94 ms (82 SD 5 ms, $n=29$), interval duration 113–637 ms (186 SD 126 ms, $n=28$), note repetition rate c.5/s. Frequency was 1400–3500 Hz, dominant frequency 3000–3300 Hz.

Similar calls were also recorded at Marojejy (near Camp 1, on 29 March 1995, 1330 h, 26°C air temperature), but the calling specimens could not be captured. We refer these calls to *M. opiparis*, as the species appears to occur at Marojejy based on three MNHN specimens. The calls were series of up to 30 unharmonious notes and lasted up to 8000 ms. Intervals between the first notes of a call are rather long (500–1000 ms), but decrease successively and reach a stable value. At the end of a call (having reached a regular note repetition rate), temporal call parameters were as follows: note duration 70–92 ms (82 SD 5 ms, $n=26$), interval duration 113–139 ms (124 SD 7 ms, $n=19$), note repetition rate c.5/s. Notes consisted of 12–16 pulses (15 SD 1, $n=21$). Frequency was 1900–4600 Hz, dominant frequency

3500–4200 Hz. Glaw and Vences (1994) reported on *M. opiparis* calls from Andringitra, which consisted of about 20 notes (call duration 3500 ms, frequency between 1500 and 3000 Hz) and had a note repetition rate of 6/s (temperature 19°C).

Mantidactylus melanopleura (Mocquard, 1901)
(figures 4c–d, 6d)

Original name. *Rhacophorus melanopleura* Mocquard, 1901

Synonyms. *Mantidactylus frenatus* Boettger, 1913

Identity. *Mantidactylus melanopleura* has previously been considered as a synonym (Blommers-Schlösser and Blanc, 1991) or a subspecies (Andreone and Randriamahazo, 1997) of *M. opiparis*. Our fieldwork revealed the existence of two *M. opiparis*-like species, a small one without frenal stripe anterior to the eye, and a larger one with such a frenal stripe. Since both occur syntopically and have distinct advertisement calls, there is no doubt about their differentiation at the species level. As the *M. opiparis* lectotype is small and has no frenal stripe anterior to the eye (see above), this name is not available for the large species with frenal stripe anterior to the eye. *Rhacophorus melanopleura* Mocquard, 1901 is the oldest available name for the *M. opiparis*-like species with frenal stripe anterior to the eye. The holotype is probably a subadult female (small femoral glands, small tympanum size). Although the lateral anterior part of the head is largely faded (pigmentless), the borders of a distinct frenal stripe are still recognizable. Especially anterior to the eye, a dark triangle is sharply bordered by the frenal stripe (below) and the dorsal colour (above), a pattern not observed in *M. opiparis*. Furthermore, only the *M. opiparis*-like species with frenal stripe anterior to the eye is known from extreme south-eastern Madagascar where the *M. melanopleura* type was collected.

The large size of the *M. frenatus* holotype and the extension of its distinct frenal stripe extending anteriorly of the eye (also reflected by the specific name), leaves no doubt on its attribution to *M. melanopleura*.

Diagnosis. A relatively large *Chonomantis* with long legs (tibiotarsal articulation reaching at least the nostril, often clearly beyond snout tip). SVL 29.9–39.5 mm in males, 32.3–40.5 mm in females. Third toe slightly shorter than fifth toe. Distinct frenal stripe present, extending between forelimb insertion and nostril. Distinct dorsolateral colour border present; diamond-shaped marking on the back mostly present. Throat generally dark with a median white line. Femoral glands of males small and indistinct. Tympanum in males distinctly larger than the eye. Webbing of the foot (based on ZFMK 53681 and 60060, males) 1 (1), 2i (>>1), 2e (1), 3i (2), 3e (1.25), 4i (2.5), 4e (2.25), 5 (1). Size of femoral gland (type 3, structure A according to Glaw *et al.*, 2000) in ZFMK 53681 (SVL 32.3 mm): 3.3 × 2.1 mm; FGD 8.7 mm.

Material examined. BMNH 1896.10.9.34 (Ivohimanitra); BMNH 1892.3.7.42 (Sahambendrana); BMNH 1925.7.2.26–28 (in a series with three *M. opiparis*; Antsihanaka); BMNH 1952.1.1.98 (Ivohibe, 4000 ft); BMNH 1986.4 (Zahamena, Camp 5). FAZC 7411 (Andasibe); FAZC 7563, 7644, 7646 (Masoala, Camp 2); FAZC 7821, 7844 (Masoala, Camp 3); FAZC 10012, 10208, 10212, 10213, 10316 (Ilampy); MNHN 1901.226 (holotype of *M. melanopleura*; Fort Dauphin (=Tolagnaro)); MNHN 1930.411 (Vondrozo); MNHN 1930.412 (Moramanga); MNHN 1935.154 (Isaka-Ivondro), 1935.156–1935.157 (Isaka-Ivondro); MNHN 1935.158 (Bezavona forest); MNHN 1946.362 (Sandrangato forest, S Moramanga); MNHN 1953.98 (Ampasy forest, E Ivohibe); MNHN 1953.100 (Andasibe); MNHN

1972.536 (Col Ivohibe, Marovitsika forest); MNHN 1972.537 (Moramanga forest); MNHN 1972.538–1972.541, 1972.543–1972.545 (Col Ivohibe, Marovitsika forest); MNHN 1972.547–1972.548 (Soavala); MNHN 1972.1328 (Bekazaha, Chaines Anosyennes); MNHN 1972.1329 Vallee Manjavona (Ankaratra); MNHN 1972.1330–1972.1343 (Ambana-Soavala, Chaines Anosyennes); MNHN 1972.1344, 1972.1345, 1972.1346, 1972.49, 1972.1351, 1972.1353, 1972.1354 (all Camp IV and III bis, Chaines Anosyennes); MNHN 1975.367–1975.370 (without locality data); MNHN 1975.371 (Marojejy 600 m); MNHN 1975.374 (without locality data); MNHN 1975.376 (Andasibe); MNHN 1989.3576–1989.3578, 1989.3580 (formerly 1930.412; Moramanga); MNHN 1989.3581–1989.3582 (formerly 1953.98; Ampasy forest, E Ivohibe); MNHN 1989.3585 (formerly 1953.100 C; Andasibe); MRSN A227.1 (Andasibe); MRSN A236 (Nahampoana); MRSN A244.1–244.2 (Nahampoana); MRSN A298 (three unlabelled males; Anjaimba forest, Vohiparara); MRSN A407.1 (near Ifanadiana); MRSN 429.1–429.2 (Anjozorobe); MRSN A624.1–624.4 (Col de Tanatana, Andohahela); MRSN A734.1–734.2 (Isaka-Eminiminy, Andohahela); MRSN A745.1 (Ifanadiana); MRSN A1944–A1945 (Tsararano, Camp 1); SMF 6734 (holotype of *M. frenatus*; Moramanga); ZFMK 8873 (Andasibe); ZFMK 18957 (Moramanga); ZFMK 25372 (Andasibe); ZFMK 52695 (Nahampoana); ZFMK 53681, 60060, 60062–60065 (Andasibe); ZFMK 60098–60099 (An'Ala); ZFMK 62241 (Mantady); ZMA 6999 (field number 644; Andasibe); ZMA 7030 (field number 572; Andasibe); ZSM 306/2000 (Vohidrazana).

Distribution. Known from: (1) Marojejy; (2) Tsararano; (3) Masoala; (4) Ilampy; (5) Antsihanaka; (6) Zahamena; (7) Anjozorobe; (8) Mantady; (9) Andasibe; (10) An'Ala; (11) Vohidrazana; (12) Moramanga; (13) Ankaratra (Manjavona); (14) Vohiparara; (15) Ifanadiana; (16) Ranomafana National Park (call recordings); (17) Ivohibe (Ampasy and Marovitsika forests); (18) Chaines Anosyennes (18a, Bekazaha; 18b, Ambana-Soavala; 18c, Soavala; 18d, Camp IV and III bis); (19) Andohahela (19a, Isaka-Ivondro; 19b, Col de Tanatana; 19c, Isaka-Eminiminy); and (20) Nahampoana. The Ankaratra locality (original catalogue entry: Mahiavona valley, Mihavona according to Blommers-Schlösser and Blanc, 1991; see section of *Mantidactylus brevipalmatus*) is based on a single specimen (MNHN 1972.1329). No further *Chonomantis* specimens other than *M. brevipalmatus* have so far been found in this region. We accept this locality in a preliminary way, but consider it as in need of confirmation. A further record (Bezavona forest) could not be located on the available maps. Similarly, the records from Sahambendrana (=Sahembendrana, near Akkoraka) and Ivohimanitra (Tanala region) can not be reliably located and are thus not further regarded here. Considering localities with reliably known elevation, the species is known from 300 to more than 1000 m above sea level (up to 1800 m if the Ankaratra locality is included).

Variation. Relative toe length was very uniform among examined specimens. Of 61 MNHN specimens, only MNHN 1946.362 had a (slightly) longer third toe as compared to the fifth toe, and in two other specimens (MNHN 1953.99 and the juvenile MNHN 1975.371) length of both toes was similar; all remaining 58 specimens had at least a slight tendency of the fifth toe to be longer than the third.

Colour photos of *Mantidactylus melanopleura* were published by Glaw and Vences (1992: cp. 76, as *M. opiparis*), Blommers-Schlösser and Blanc (1993: planche 18 (figure 88), as *M. opiparis*), Andreone and Gavetti (1994: figure 13, as *M. opiparis*), Glaw and Vences (1994: cp. 112 (specimen on the right side of the

photograph), as *M. opiparis*), and Andreone and Randriamahazo (1997: figures 47 and 48, as *M. opiparis melanopleura*).

Habits. Calling males were observed regularly in all months between December and April, indicating prolonged breeding activity in this species. They were mostly found during the day along brooks in primary rainforest and were calling either from the ground or from elevated positions (up to 50 cm high). Their distance from the brook was up to 10 m. Five females from the MNHN collection contained 21–73 oocytes up to 3 mm diameter. They were yellowish with a dark pole, beige or nearly black (Vences *et al.*, 1999b).

Calls. A re-analysis of recordings from Nahampoana (from 30 December 1991) resulted in the following description: calls were series of 4–26 notes ($n=13$). Note duration was 19–29 ms (23 SD 2 ms, $n=26$), interval duration 76–94 ms (87 SD 5 ms, $n=25$), note repetition rate 9/s, frequency 1350–3950 Hz (figure 9). Andreone and Randriamahazo (1997) reported on calls from Andohahela (under the name *Mantidactylus opiparis melanopleura*; temperature 19°C) with a note repetition rate of 8.9/s, which agrees well with our data. Re-analysis of the respective recordings yielded a note duration of 39–49 ms (44 SD 3 ms, $n=27$) and an interval duration of 59–100 ms (80 SD 11 ms, $n=25$).

Calls from Andasibe were recorded on 18 December 1994, 1920 h, at 20°C air temperature. They consisted of up to 28 notes. Temporal call parameters: note duration 23–48 ms (38 SD 7 ms, $n=28$), interval duration 72–98 ms (87 SD 6 ms, $n=27$), note repetition rate 8/s. Frequency was 1600–3800 Hz, with a ‘frequency gap’ at 2000–2500 Hz, dominant frequency was 3300 Hz.

Calls from An’Ala were recorded on 11 February 1995, at 22°C air temperature. They consisted of 12–23 notes. Temporal call parameters: note duration 32–54 ms (45 SD 5 ms, $n=24$), interval duration 73–90 ms (80 SD 5 ms, $n=21$), note repetition rate 8/s. Frequency was 1500–5000 Hz, dominant frequency 3200 Hz.

Mantidactylus albofrenatus (Müller, 1892)
(figures 5a–b, 6e)

Original name. *Rana albofrenata* Müller, 1892

Synonyms. None.

Identity. According to the original description (Müller, 1892), the holotype had a distinct white stripe that began at the forelimb insertion, passed underneath the eye, and extended to the nostril. The exact shape of this stripe was documented in figure 1a of Müller (1892), a profile drawing of the head. A second drawing (figure 1 in the original description) showed the dorsal pattern. According to description and drawing, the back was brown, with a distinct dorsolateral colour border, and dark brown flanks. No conspicuous dorsal pattern (e.g. a diamond-shaped marking) was mentioned. In the drawing, three dark continuous crossbands are recognizable on the tibia, and two crossbands on the tarsus. The ventral side was described as greyish brown, with a few white spots on the throat and many such spots on the chest.

In May 2000, the holotype (NMBA 792), a female as recognizable by presence of immature oocytes, was almost uniformly greyish and brownish, with no recognizable pattern except the contrast between dark flanks and lighter back. However, the pattern mentioned in the original description, together with morphology and size of the specimen, allows a rather reliable designation. Webbing of the holotype is 1 (1), 2i (1.5), 2e (1), 3i (2), 3e (1.5), 4i (3), 4e (3), 5 (1.5) on the right foot (less on the

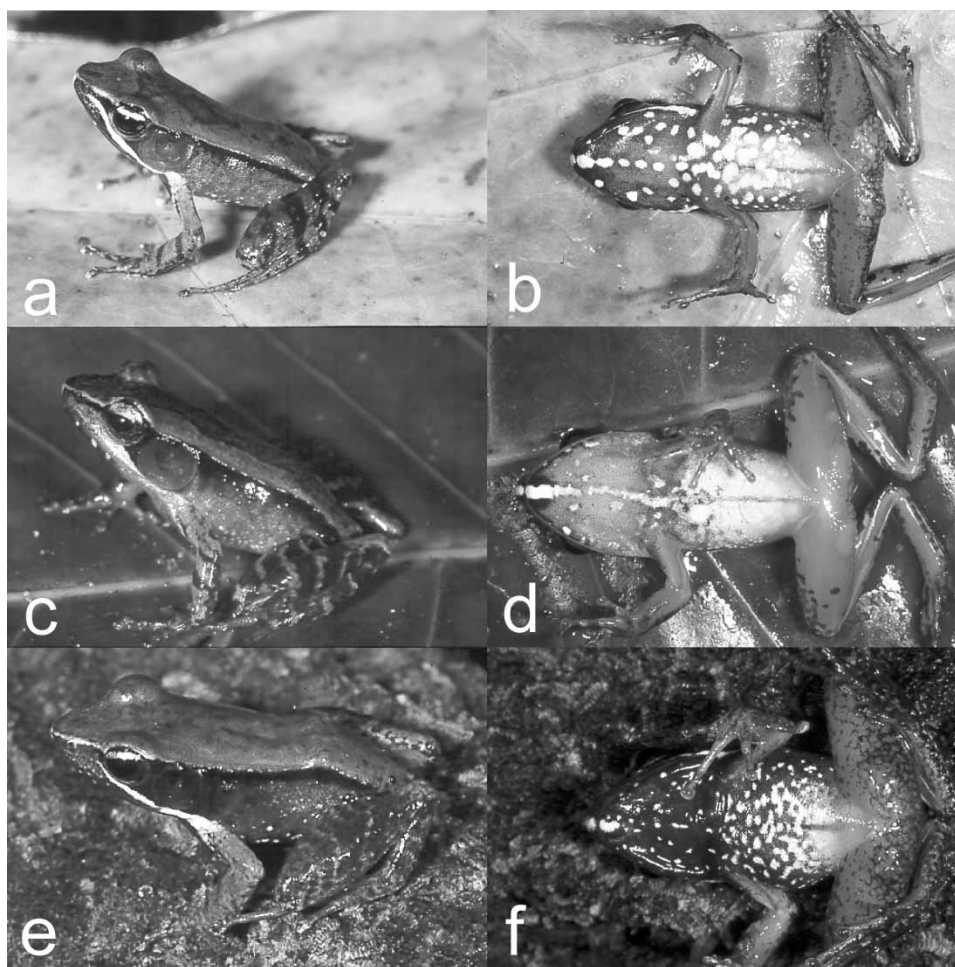


FIG. 5. Photographs of live male specimens (dorsolateral and ventral views) of the *Mantidactylus albofrenatus* complex: (a–b) *M. albofrenatus*, specimen from Andasibe (1995); (c–d) *M. zipperi*, specimen from An'Ala (1995); (e–f) *M. charlotteae*, specimen from Marojejy (1995).

left foot, probably due to bad state of preservation). The short hindlimbs and long third toe found in the holotype are diagnostic for three species recognized by us and previously all subsumed under *M. albofrenatus*. Female specimens of the new species *M. charlotteae* (described below) are generally larger, their frenal stripe does not reach the nostril, and they often have a conspicuous dark ventral colour (especially on the throat), which would certainly have been mentioned by Müller (1892) if it had been present in the holotype of *M. albofrenatus*. Female specimens of *M. zipperi* do not have distinct white spots on the venter as described for the *M. albofrenatus* holotype (but a more marbled pattern), and they have no distinct frenal stripe anterior to the eye; furthermore, they generally have more narrowly spaced crossbands on the hind limb, with four to five (often incomplete) bands visible on the tibia. The characters mentioned apply to males and females of the two species, respectively, and appear to be diagnostic. In contrast, the species here attributed to

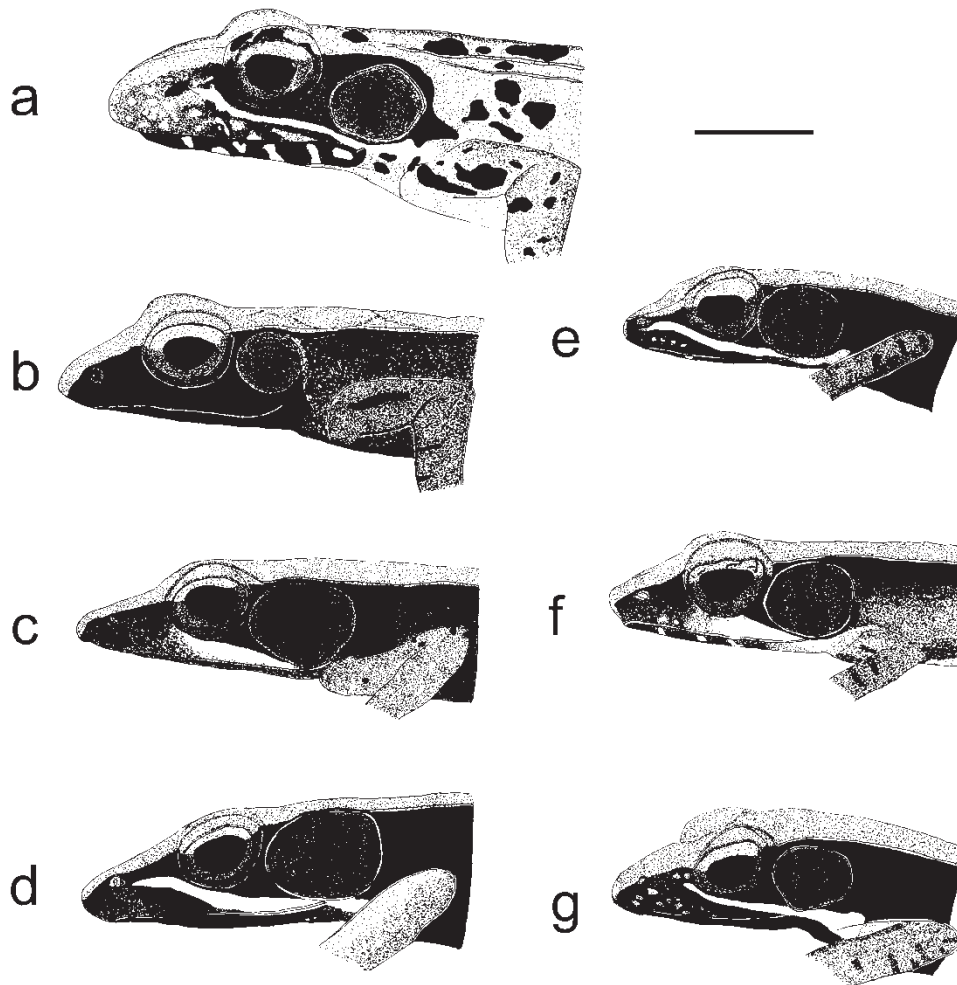


FIG. 6. Schematic drawings of heads (lateral views, showing shape and extension of frenal stripe and relative tympanum size) of representative male specimens of: (a) *Mantidactylus brevipalmatus* (ZSM 372/2000); (b) *M. aerumnalis* (ZFMK 62248); (c) *M. opiparis* (ZFMK 60066); (d) *M. melanopleura* (ZFMK 60065); (e) *M. albofrenatus* (ZFMK 60051); (f) *M. zipperi* (ZFMK 60090); (g) *M. charlotteae* (ZFMK 59919). Scale bar = 5 mm.

M. albofrenatus agrees with the holotype regarding: (a) size of females; (b) presence of distinct white spots on throat and breast; (c) widely spaced crossbands on hindlimbs (three bands on tibia); (d) distinct frenal stripe running to nostril; and (e) low amount of webbing (web on fourth toe not reaching beyond the third subarticular tubercle).

Diagnosis. The smallest *Chonomantis* known. SVL 19.3–23.0 mm in males, 25.3–27.1 mm in females (only specimens from Andasibe and type considered). Legs short; tibiotarsal articulation reaches to a point between the anterior eye corner and the nostril. Third toe distinctly longer than fifth toe. Distinct dorsolateral colour border present. Back generally without distinct diamond-shaped marking (but with such a marking in some specimens, e.g. ZFMK 60051). Distinct frenal stripe present, reaching or nearly reaching to the nostril. Throat dark grey; throat and venter with

a distinct pattern of white spots, which form a median row on the throat. Femoral glands of males distinct. Tympanum in males distinctly larger than the eye. Webbing of the foot (based on ZFMK 60050, male, and ZFMK 59880, female): only traces of web between most toes; 4i (3), 4e (3), 5 (2). Size of femoral gland (type 3, structure A according to Glaw *et al.*, 2000) in ZFMK 60050 (SVL 22.1 mm) 3.1×2.2 mm, FGD 4.1 mm. Males of *Mantidactylus albofrenatus* are furthermore recognizable by the much reduced webbing, which does not extend beyond the second subarticular tubercle of the fifth toe, and the partly connected lateral metatarsalia (less distinctly expressed in females).

Material examined. NMBA 792 (holotype of *M. albofrenatus*); ZFMK 59879–59880 (Andasibe); ZFMK 60048–60052 (Andasibe); ZFMK 60120 (Andasibe).

Distribution. Known from: (1) Andasibe; and (2) An'Ala (call records only). The localities Foulpointe (Blommers-Schlösser and Blanc, 1991), as well as Sahafary, Ampokafo, Fizoana, Navana, Nosy Mangabe, Voloina (Glaw and Vences, 1992, 1994; Andreone, 1993) refer to the new species *M. charlotteae* (see below). The locality Mandraka (Glaw and Vences, 1994) refers to *M. opiparis*. Attribution of the locality Moramanga (Blommers-Schlösser and Blanc, 1991) is uncertain as we did not find the corresponding voucher specimen(s) in the MNHN or ZMA collections. The record from the Andranomay forest, Anjozorobe (Raselimanana, 1998) may refer to *M. albofrenatus* or to *M. zipperi* (see below), and is therefore not included here. The records from Anjanaharibe-Sud and Tsaratanana (Raxworthy *et al.*, 1998) possibly refer to *M. charlotteae* (see below). Considering localities with reliably known elevation, the species is known from 840–915 m above sea level (table 1).

Habits. Calling specimens were observed at An'Ala and Andasibe during the day in the immediate proximity of small brooks in primary rainforest. Each note was one expiration. Vocal sacs did not remain inflated between notes. MNHN 1953.101 from Mahajebby contained 24 oocytes, which measured up to 2 mm in diameter and were yellowish with a dark pole (Vences *et al.*, 1999b). The egg and tadpole descriptions in Blommers-Schlösser (1979), Blommers-Schlösser and Blanc (1991) and Glaw and Vences (1992, 1994) refer to the new species *M. charlotteae* (see below).

Calls. Recordings were made at Andasibe on 14 February 1995, 0855 h, at 23°C air temperature. Calls consisted of 31–36 unharmonious notes (figure 10) and lasted 3362–5320 ms ($n=2$). Intensity was high at the beginning of each note and decreased towards the end of the note. Each note consisted of 10–17 (14 SD 3, $n=8$) pulses. Temporal call parameters: note duration 56–80 ms (72 SD 7 ms, $n=36$), interval duration 53–78 ms (63 SD 5 ms, $n=35$), note repetition rate 6.8/s. Frequency was 2500–5600 Hz, dominant frequency 3800–4600 Hz. Below 3500 Hz and above 4900 Hz, a 'frequency gap' was noted.

***Mantidactylus zipperi* sp. nov.**
(figures 5c–d, 6f)

Diagnosis. A relatively small species that can be distinguished from all other *Chonomantis* by combination of the following characters: SVL 21.5–23.6 mm in males, 29.5 mm in a female. Legs short (tibiotarsal articulation generally not reaching beyond nostrils). Third toe slightly longer than fifth toe. Dorsolateral colour border present but rather indistinct, flanks often only distinctly dark in their dorsal part.

Back often with dark markings. Frenal stripe between forelimb insertion and eye, not between eye and nostril. Venter largely without pattern; throat grey with a rather broad median white stripe. Femoral glands in males distinct. Tympanum in males distinctly larger than the eye.

The species is distinguished from *M. melanopleura* and *M. opiparis* by the different relative toe length (third toe slightly longer than fifth vs. fifth longer than third); from *M. aerumnalis* by presence of a frenal stripe between forelimb insertion and eye and the much larger tympanum in males (vs. frenal stripe absent and tympanum smaller than eye in males); from *M. brevipalmatus* by smaller size and shorter hindlimbs (males smaller than 24 mm vs. longer than 27 mm; tibiotarsal articulation not reaching beyond nostril vs. generally reaching at least snout tip), as well as different coloration; and from *M. albofrenatus* by the absence of a distinct frenal stripe between eye and nostril (vs. presence of such a stripe). The calls of *M. zipperi* consist of notes of a very short duration (21–31 ms), differing from the longer note durations in *M. albofrenatus* (56–80 ms) and *M. opiparis* (69–126 ms).

Etymology. This species is dedicated on behalf of Viola Zimmermann to Claus Zimmermann (nickname ‘Zipper’), in recognition of financial support for biodiversity research and nature conservation through the BIOPAT program.

Material. HOLOTYPE. ZFMK 60090, adult male, collected by F. Glaw on 11–12 February 1995 at An’Ala eastern Madagascar (180°56’S, 48°28’E, 840 m above sea level).

PARATYPES. ZSM 1216/2001 (originally ZFMK 60091), adult male, same collection data as holotype; ZFMK 60135–60137 three males, collected by F. Glaw and D. Vallan on 6 April 1995 at Ambohitantely; ZFMK 60118, female, collected by F. Glaw in February or March 1995 at An’Ala; ZFMK 62238, male, collected by F. Glaw on 10 February 1996 at Mantady; ZFMK 62301, collected by F. Glaw, D. Rakotomalala and F. Ranaivojaona on 2 March 1996 at Ranomafana National Park; MRSN A329.2, adult male, and MRSN A332, adult female, collected by F. Andreone on 8 August 1992 at An’Ala.

Further material. MNHN 1953.101 (Morafenobe, Mahajeby forest); ZFMK 50655 (Andasibe); ZMA 7036, two males (field numbers 907 and 909, both from Andasibe), the third specimen of the series, field number 908, is probably a subadult female of *M. opiparis*. Not included as paratypes because of tentative determination and partly poor state of preservation.

Description of holotype. SVL 23.6 mm. Body slender; head longer than wide, slightly wider than body; snout slightly pointed in dorsal and lateral views; nostrils directed laterally, very slightly protuberant, nearer to tip of snout than to eye; canthus rostralis rather distinct, straight; loreal region slightly concave; tympanum distinct, elliptical (wider than high), 138% of eye diameter; supratympanic fold absent; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae; choanae small, rounded. Arms slender, subarticular tubercles single; inner metacarpal tubercle present but indistinct, no outer metacarpal tubercle; fingers without webbing; comparative finger length $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth finger; finger disks slightly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches between eye and nostril; lateral metatarsalia not connected; comparative toe length $1 < 2 < 5 < 3 < 4$; third toe distinctly longer than fifth toe on left foot, slightly longer on right foot; inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable; webbing formula between toes 1(1), 2i(<<1), 2e (1), 3i (>2), 3e (2),

4i (3), 4e (3), 5 (1.5). Skin on the upper surface smooth; back with distinct dorsolateral folds; no distinct tubercles in the cloacal region; ventral skin smooth, slightly granular in the cloacal region. Femoral glands distinct (structure A, 2.8×1.9 mm; FGD 5.8 mm), of type 3 *sensu* Glaw *et al.* (2000).

In preservative, back light brown, with an indistinct brown diamond-shaped marking. Sharp dorsolateral colour border, but dark brown flank coloration only present in the upper third of the flanks, fading into yellow-beige towards the venter. On the anterior head, colour border reduced to a black streak along the canthus rostralis. Indistinct light frenal stripe from forelimb insertion to eye, but no traces of such a stripe between eye and nostril. Hindlimbs dorsally brown with five dark brown crossbands on the femur, four crossbands on tibia, and five crossbands on tarsus and foot. Venter uniformly beige, a very fine brown shade on the throat, irregular brown marbling on chest. Few irregular white spots on throat. A median white line on the throat, starting anteriorly in a distinct central light spot, bordered by dark brown; in connection with a white spot on the upper snout tip. Fore- and hindlimbs uniformly yellowish-beige without dark pattern.

Colour in life. Based on photographs of several specimens from An'Ala. Similar to colour in preservative. General appearance not colourful. Back brown, with a dark brown diamond shape marking. Flanks blackish grey in their upper part, fading into light grey towards the venter. Throat grey, venter silvery yellowish. Ventral side of legs yellowish without further pigments.

Variation. In life, yellow colour was present ventrally on the hindlimbs of specimens from the An'Ala and Mantady populations, but absent in specimens from Ambohitantely.

Distribution. Known from: (1) An'Ala; (2) Andasibe; (3) Mantady; (4) Ambohitantely; (5) Mahajebby forest; and (6) Ranomafana National Park. Considering localities with reliably known elevation, the species is known from 840 to more than 1000 m.

Habits. Calling males were observed during the day at An'Ala and Ambohitantely in December, February and April, indicating prolonged breeding activity of this species. Individuals were sitting on the ground near small brooks in primary rainforest. Each note was one expiration. Vocal sacs did not remain inflated between notes.

Calls. Recordings were made at An'Ala on 11 February 1995, 13–14 h, at 23.5°C air temperature. A call consisted of a series of up to 33 unharmonious notes (figure 11) and lasted up to 5338 ms. Temporal call parameters: note duration 9–22 ms (17 SD 3 ms, $n=24$), interval duration 120–197 ms (151 SD 21 ms, $n=23$), note repetition rate 6.2/s. Intensity was high at the beginning of each note and decreased towards the end of the note. Two frequency bands were recognizable, at 1700–2100 Hz, and 3150–4600 Hz; dominant frequency was 4100 Hz.

Recordings from Ambohitantely (7 April 1995, 1630 h) were similar, but note repetition rate was lower (probably caused by a lower recording temperature). Calls consisted of 19–27 notes ($n=3$) and lasted up to 7000 ms. Note duration was 21–31 ms (24 SD 3 ms, $n=17$). Intervals between notes were long and irregular at the beginning of each call, and became shorter towards the end of the call. At the end of the call, interval duration was 196–274 ms (214 SD 21 ms, $n=16$). The interval between the ultimate and penultimate note was sometimes longer. Note repetition rate was 4.3/s. Frequency was similar to that in the recordings from An'Ala.

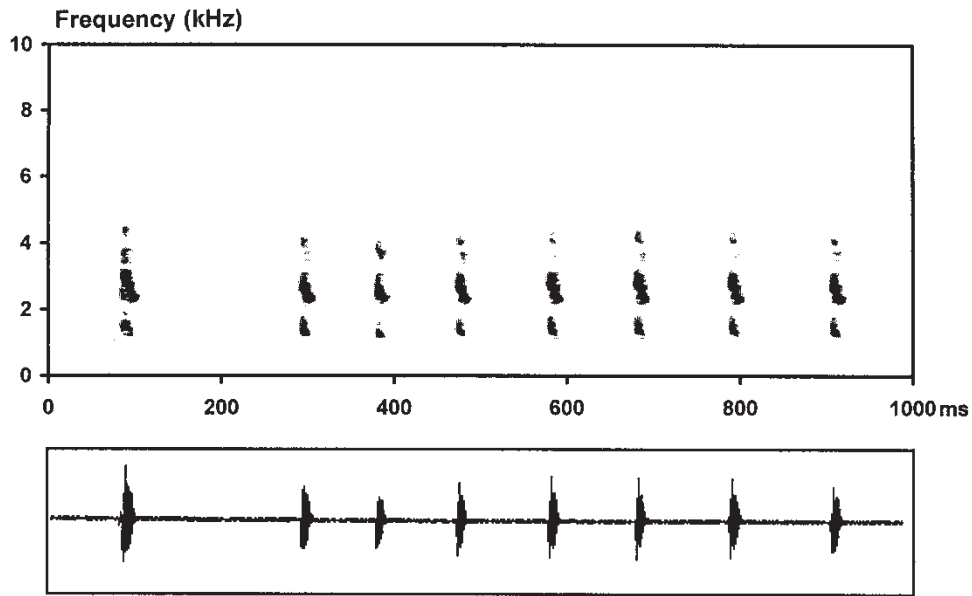


FIG. 7. Sonogram and oscillogram of a series of notes of type two of *Mantidactylus brevipalmatus* from Manjakatempo. Recorded on 13 March 1992.

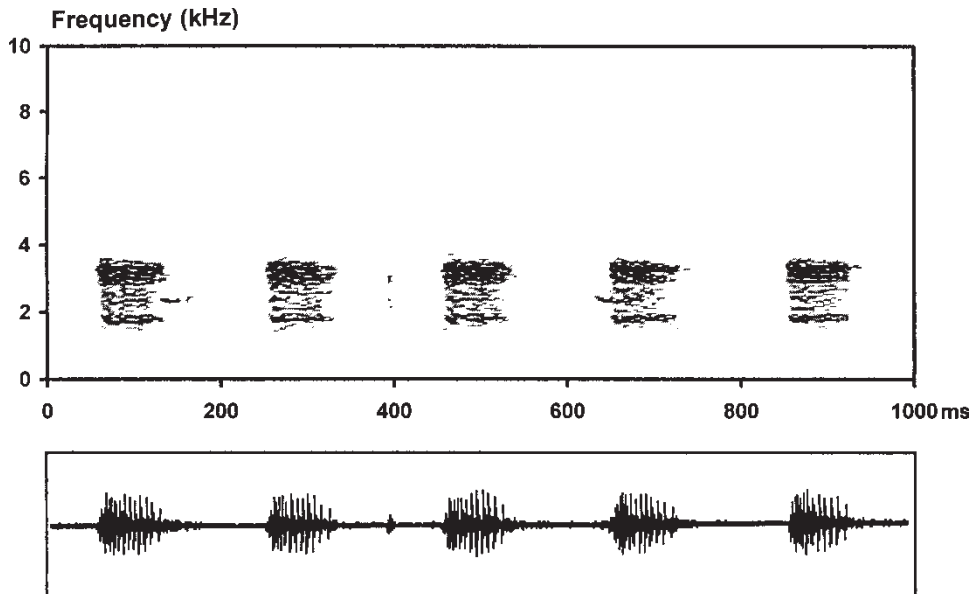


FIG. 8. Sonogram and oscillogram of a series of five notes of *Mantidactylus opiparis* from Ranomafana. Recorded on 1 March 1996 at *c.* 23°C air temperature.

One specimen uttered short notes when caught, which were not unequivocally recognizable as distress calls. As release calls are so far unknown in *Mantidactylus*, we tentatively consider these calls (which had a broad frequency band between 1000 Hz and 8000 Hz) as distress calls.

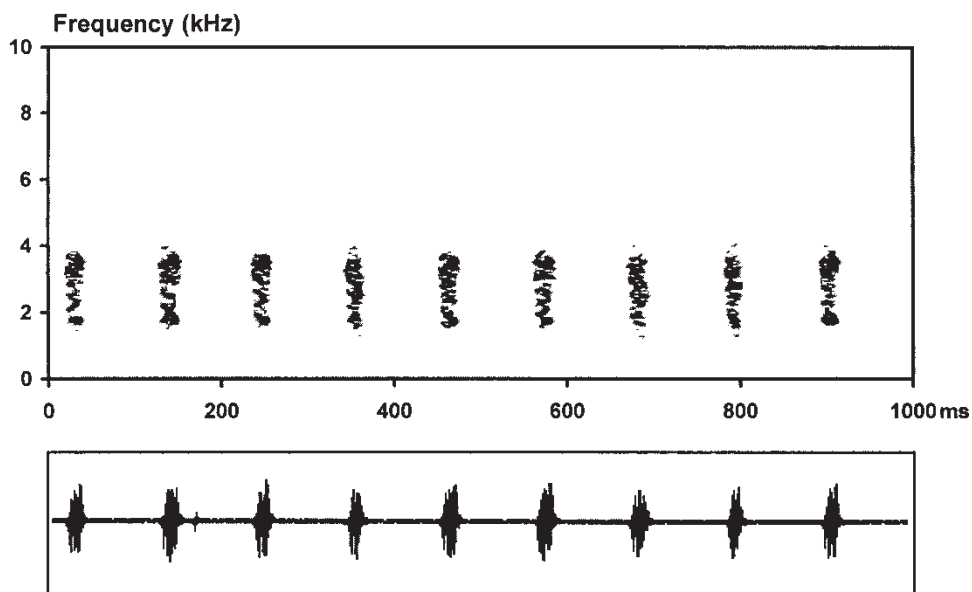


FIG. 9. Sonogram and oscillogram of a series of nine notes of *Mantidactylus melanopleura* from Nahampoana. Recorded on 30 December 1991.

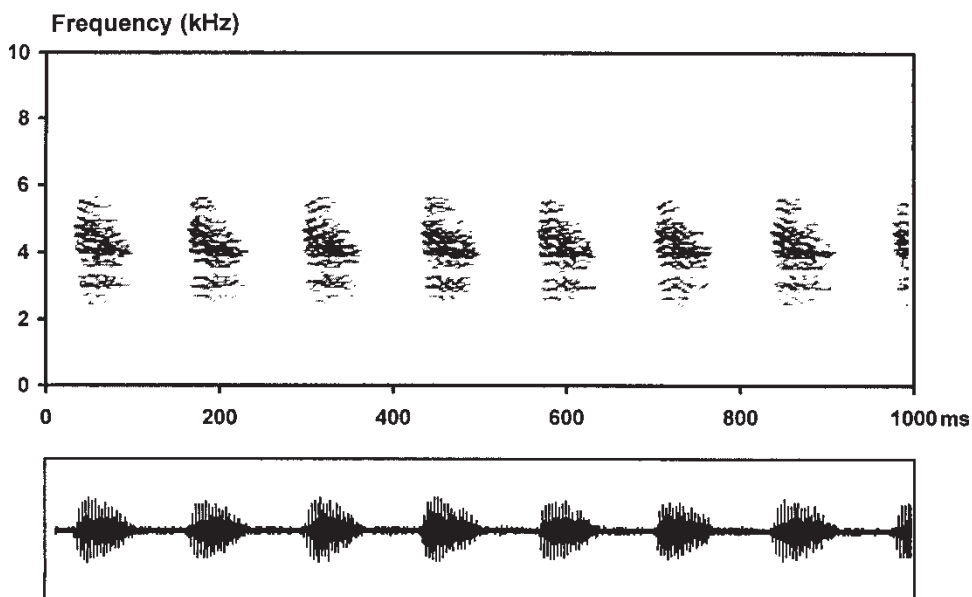


FIG. 10. Sonogram and oscillogram of a series of eight notes of *Mantidactylus albofrenatus* from Andasibe. Recorded on 14 January 1995 at 23°C air temperature.

Mantidactylus charlotteae sp. nov.
(figures 5e–f, 6g)

Diagnosis. A medium-sized species which can be distinguished from all other *Chonomantis* by combination of the following characters: SVL 22.4–26.2 mm in

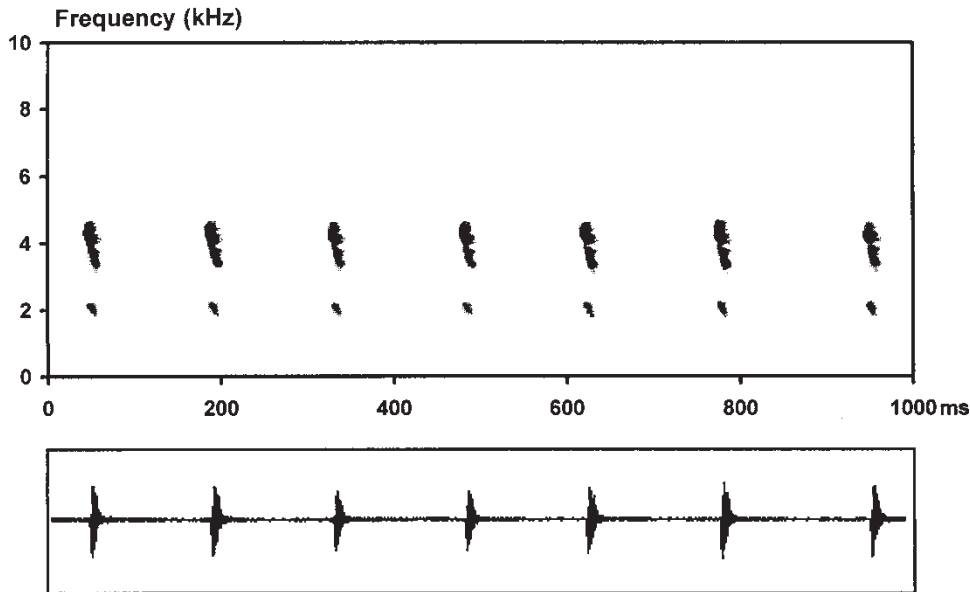


FIG. 11. Sonogram and oscillogram of a series of seven notes of *Mantidactylus zipperi* from An'Ala. Recorded on 11 February 1995 at 23.5°C air temperature.

males, 26.3–32.2 mm in females. Legs rather short (tibiotarsal articulation generally not reaching beyond nostrils). Third toe distinctly longer than fifth toe in most specimens. Dorsolateral colour border present. Back generally without dark markings. Frenal stripe between forelimb insertion and eye, extends as thin, distinct line to a point between eye and nostril and ends abruptly. Throat usually black with a light median line, sometimes consisting of a row of small light spots. Femoral glands in males indistinct. Tym/Eye ratio in males 0.70–1.13. The species is distinguished from *Mantidactylus melanopleura* and *M. opiparis* by the different relative toe length (third toe longer than fifth vs. fifth longer than third) and shorter hindlegs; from *M. aerumnalis* and *M. zipperi* by presence of a distinct frenal stripe between forelimb insertion and a point anterior to the eye (vs. total absence of frenal stripe in *M. aerumnalis*, and absence of stripe anterior to the eye in *M. zipperi*); from *M. brevipalmatus* by smaller size and shorter hindlimbs (males smaller than 27 mm vs. larger than 27 mm; tibiotarsal articulation generally not reaching beyond nostril vs. generally reaching at least snout tip), as well as different coloration; from *M. albofrenatus* by the condition of the frenal stripe which ends far from the nostril (vs. reaching at least close to the nostril). Furthermore, the new species differs from all species except *M. aerumnalis* in the relatively small tympanum of males (usually smaller, occasionally slightly larger than the eye; mean ratio Tym/Eye 0.92 versus 1.17–1.34). The calls of *M. charlotteae* consist of notes of a very long duration (91–304 ms, mean 234 ms), differing from the shorter note durations in *M. albofrenatus* (56–80 ms), *M. brevipalmatus* (9–21 ms), *M. melanopleura* (19–54 ms), and *M. zipperi* (21–31 ms), with some overlap of duration values only in the comparison with *M. opiparis* (69–126 ms). In addition, *M. charlotteae* is unique among *Chonomantis* species in that the note duration is longer than the interval between two notes of a series.

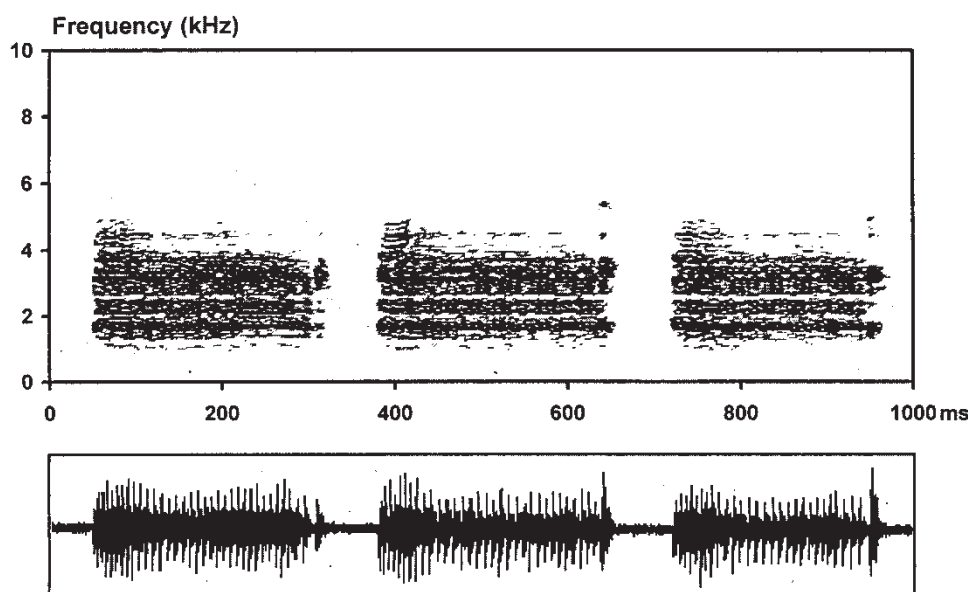


FIG. 12. Sonogram and oscillogram of a series of three notes of *Mantidactylus charlotteae* from Foulpointe. Recorded by R. Blommers-Schlösser, March 1972.

Etymology. Dedicated to Charlotte Richter-Pfeil in recognition of financial support to biodiversity research through the BIOPAT program.

Material. HOLOTYPE. ZMA 7001 (field number 692), adult male, collected by R. Blommers-Schlösser on 13 October 1971 at Foulpointe (17°41'S, 49°30'E, less than 100 m above sea level), eastern Madagascar. Chosen as holotype as the call recordings of Blommers-Schlösser (1979), diagnostic for the new species, refer to a male of the ZMA 7001 series; from this series, the state of preservation of the specimen with the field number 692 allowed recognition of most morphological and coloration characters.

PARATYPES. ZMA 7001 (field numbers 337, 688–691, 693–694), five males and two females, same locality and collection data as holotype; ZMA 7000 (field numbers 559–560), one male and one female, collected by R. Blommers-Schlösser on 12 February 1972 at Foulpointe; ZFMK 46001–46003, one male and two females, collected by F. W. Henkel 1987 at Nosy Boraha; ZFMK 47211–47212, one male and one female, collected by F. Glaw on 24–25 October 1987 at Nosy Mangabe; ZFMK 47214–47215 and 47217, two males and one female, collected by F. Glaw on 4 November 1987 at Sahafary; ZFMK 52693, male, collected by F. Glaw and M. Vences on 19 March 1991 at Voloina; ZFMK 52694, female, collected by F. Glaw and M. Vences on 12 March 1991 at Nosy Mangabe; ZFMK 59918–59921, three males and one female, collected by F. Glaw and O. Ramilison on 24 February 1995 at the Marojejy massif (camp I); ZFMK 59922, female, collected by F. Glaw and O. Ramilison on 26 February 1995 at the Marojejy massif (camp III); ZFMK 66664, collected by K. Schmidt at Ambatobe; ZSM 934/2000 (originally ZFMK 47210), collected by F. Glaw on 24–25 October 1987 at Nosy Mangabe.

Further material. BMNH 1892.3.7.43–46 (Sahambendrana); BMNH 1952.1.1.78–79 (Rantabe, Antongil bay); BMNH 1955.1.1.80 (Nosy Mangabe). FAZC 001 (Anjanaharibe, eastern slope); FAZC 002 (Ambanizana); FAZC 1032,

1038, 1069 (Besariaka-Amponaomby); FAZC 6623 (Ambolokopatrika); FAZC 7359, 7415 (Masoala, Camp 1); FAZC 10024, 10267 (Ilampy); MNHN 1975.372, 1975.384 (Marojejy, 600 m altitude); MNHN 1975.378 (Marojejy, 300 m); MNHN 1975.380, 1975.381, 1975.386 (no locality data); MNHN 1975.383 (Massif d'Andohahelo (=Andohahela)); MNHN 1975.387 (Marojejy, 300 m altitude); ZFMK 17610 (Maroantsetra). Not included as paratypes due to tentative determination and partly uncertain or doubtful locality data. Photographs of specimens captured by us (no vouchers collected) were further available from Ampokafo, Fizoana, and Navana.

Description of the holotype. SVL 24.5 mm. Body relatively slender; head longer than wide, of same width as body; snout rounded in dorsal and lateral views; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis rather indistinct, straight; loreal region slightly concave; tympanum distinct, rounded, 81% of eye diameter; supratympanic fold absent; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae; choanae small, rounded. Arms slender, subarticular tubercle single; inner metacarpal tubercle present but indistinct, outer metacarpal tubercle not recognizable; fingers without webbing; comparative finger length $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth finger; finger disks slightly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches between eye and nostril; lateral metatarsalia not connected; comparative toe length $1 < 2 < 3 < 5 < 4$; third toe distinctly longer than fifth toe; inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable; webbing formula between toes 1(1), 2i(\ll 1), 2e(1), 3i(2), 3e(1.5), 4i(3), 4e(2.75), 5(1.25). Skin on the upper surface smooth; back with distinct dorsolateral folds; no distinct tubercles in the cloacal region; ventral skin smooth, slightly granular in the cloacal region. Femoral glands rather small and indistinct (structure A, 2.0×1.5 mm; FGD 5.2 mm), of type 3 *sensu* Glaw *et al.* (2000).

After almost 30 years in preservative, back brown, with sharp dorsolateral colour border. Flanks dark brown. Traces of a frenal stripe running from forelimb insertion to eye, but the pattern contrast largely faded. No further dorsal pattern. Hindlimbs dorsally brown with three to four dark crossbands on femur, three on tibia, and four to five on tarsus and foot. Ventrally brown, more intensive on throat than on belly. A median row of small white spots on throat faintly recognizable. Hindlimbs ventrally beige with brown marblings.

Colour in life. Description according to figure 87 in Blommers-Schlösser and Blanc (1993), showing a specimen from the ZMA 7001 series: back reddish brown without markings. Dorsolateral glandular ridges reddish. Flanks blackish, with sharp dorsolateral colour border. Forelimbs light brown, hindlimbs dark brown. Frenal stripe white and very distinct, running from the forelimb insertion towards the eye, curving upwards but ending immediately anterior to the eye. Specimens from other localities agree well with this description. In specimens from Nosy Mangabe and Marojejy, the ventral side is posteriorly bluish-grey with black marbling, especially on the hindlimbs. The anterior half of the venter and the throat are black with white spots; these are especially intense on the anterior half of the venter. On the throat they form a median row which sometimes fuses to form a white line.

Variation. The ZMA paratypes agree very well with the holotype in morphology and coloration. In the specimen with the field number 690, femoral glands have been removed for histological examination. All specimens have a ventral pattern

of small white spots, with a median row of spots on the throat. No distinct diamond-shaped marking is recognizable in any specimen. In ZFMK 66664, the frenal stripe runs almost to the nostril, similar to *Mantidactylus albofrenatus*. The specimen MNHN 1975.383 from Andohahela; (the only specimen of the *M. albofrenatus* complex known from southern Madagascar) is an adult male with a distinct frenal stripe anterior to the eye (not reaching nostril) and a line of small light spots on the throat. Its tympanum is larger than in most *M. charlotteae* (c.120% of eye diameter). We here tentatively accept the Andohahela locality, although it was not confirmed by Andreone and Randriamahazo (1997) nor by Nussbaum *et al.* (1999). Colour photos of *M. charlotteae* were published by Blommers-Schlösser and Blanc (1993: planche 18 (figure 87), as *M. albofrenatus*), Andreone and Gavetti (1994: figure 14, as *M. albofrenatus*), and Glaw and Vences (1994: cp. 113, as *M. albofrenatus*).

Distribution. Known from: (1) Marojejy; (2) Ambolokopatrika; (3) Besariaka; (4) Anjanaharibe; (5) Ambatobe; (6) Ampokafo; (7) Fizoana; (8) Navana; (9) Sahafary; (10) Ilampy; (11) Masoala; (12) Ambanizana; (13) Nosy Mangabe; (14) Maroantsetra; (15) Voloina; (16) Rantabe; (17) Nosy Boraha; (18) Foulpointe; and probably (19) Andohahela. The record from Sahambendrana (=Sahembendrana, near Akkoraka) can not be precisely located and is therefore not further considered here. Considering localities with reliably known altitude, the species is known from near sea level up to 860 m.

Tadpoles. Blommers-Schlösser (1979) described tadpoles (ZMA 7044, as *M. albofrenatus*) which were collected at Foulpointe, in the brook along which adults were collected. As no other *Chonomantis* is so far known from low altitudes along the east coast, these tadpoles can be tentatively attributed to *M. charlotteae*.

Habits. Blommers-Schlösser (1979) found this species along a brook in forest during the day; the males were calling in dense vegetation. At Nosy Mangabe, Voloina, in the Masoala peninsula and in Marojejy, we observed specimens during the day on the forest floor in the vicinity of brooks. In captivity, eggs of 2.5 mm diameter (ZMA 7043) were deposited out of the water on the bottom of the vivarium (Blommers-Schlösser, 1979). MNHN 1975.372 from Marojejy contained 31 oocytes (Vences *et al.*, 1999b).

Calls. Recordings of a specimen from Foulpointe (ZMA 7001) were made by R. Blommers-Schlösser in March 1972, 20 h, in a terrarium (see Blommers-Schlösser, 1979). A re-analysis of these recordings resulted in the following description. Calls consisted of a series of 16–21 unharmonious notes (figure 12) and lasted up to 5000 ms. Notes consisted of 9–38 (30 SD 7, $n = 16$) pulses. Temporal call parameters: note duration 91–304 ms (234 SD 52 ms, $n = 16$), interval duration 48–71 ms (63 SD 7 ms, $n = 16$), note repetition rate 3–4/s. Frequency ranged from 1300–4800 Hz, with dominant frequencies at 1300–1800 Hz and 2600–3200 Hz.

Identification key to *Chonomantis* species

- 1 Flanks distinctly darker than back, at least in its upper part; SVL up to 32 mm in males and 41 mm in females (but generally smaller); back always without a light vertebral stripe (a thin line can be present) 2
- Flanks not distinctly darker than back; tibiotarsal articulation reaches beyond snout tip; largest species, SVL 28–35 mm in males, 35–45 mm in females, back with or without a light vertebral stripe *M. brevipalmatus*
- 2 Head uniformly black laterally (no trace of light frenal stripe from the insertion of

- arms to the eye); small tympanum size in males (tympanum diameter 67–87% of eye diameter); a white median line on the throat continues onto the venter *M. aerumnalis*
- Head not uniformly black laterally, a more or less distinct light frenal stripe is present from insertion of arms to the eye or beyond; larger tympanum size in males (tympanum diameter 70–150% of eye diameter); the white median line on the throat, if present, does not continue onto the venter 3
- 3 Fifth toe generally at least slightly longer than third toe; tibiotarsal articulation usually reaches snout tip or beyond; back generally with distinct diamond-shaped markings; males with small and indistinct femoral glands 4
- Fifth toe generally at least slightly shorter than third toe; tibiotarsal articulation at most reaches snout tip; back generally with indistinct or without diamond-shaped markings; males usually with large and distinct femoral glands 5
- 4 Frenal stripe from foreleg insertion to eye, fading anterior to the eye; smaller species (SVL 24–29 mm in males, 31–33 mm in females); note duration of advertisement calls 69–126 ms, note repetition rate 5–6/s *M. opiparis*
- Frenal stripe from foreleg insertion to eye, curves upwards anterior to the eye and reaches or nearly reaches nostril, remaining very distinct along its entire length; larger species (SVL 30–32 mm in males, 32–40 mm in females); note duration of advertisement calls 19–54 ms, note repetition rate 8–9/s *M. melanopleura*
- 5 Tympanum in males large (ratio Tym/Eye 1.03–1.44); no frenal stripe between eye and nostril; venter largely without pattern, throat grey with a rather broad median white stripe; webbing moderately reduced, reaching beyond second subarticular tubercle on fifth toe; notes of advertisement calls short (21–31 ms), shorter than interval duration *M. zipperi*
- Tympanum in males large (ratio Tym/Eye 1.10–1.38); distinct frenal stripe between eye and nostril present; throat and venter with a distinct pattern of rather large white spots, which form a median row on the throat; webbing much reduced, not reaching beyond second subarticular tubercle on fifth toe; notes of advertisement calls of moderate duration (56–80 ms), shorter than interval duration *M. albofrenatus*
- Tympanum in males usually small (ratio Tym/Eye 0.70–1.13); frenal stripe present anterior to eye, but abruptly ending close to the eye in most specimens; venter black anteriorly with a pattern of small white spots forming a median row or line on the throat; webbing moderately reduced, reaching beyond second subarticular tubercle on fifth toe; notes of advertisement calls long (91–304 ms), longer than interval duration *M. charlotteae*

Discussion

Morphometric differentiation and relationships among Chonomantis species

Morphometric data for 119 adult *Chonomantis* specimens (the types of *M. aerumnalis*, *M. brevipalmatus*, *M. delormei*, *M. melanopleura*, *M. frenatus* and *M. opiparis* were not considered because the specimens were unavailable or in a poor state of preservation) as presented in table 2 allow for a number of analyses. Mean SVL of males was 76–83% of mean female SVL (*M. aerumnalis* 81%; *M. albofrenatus* 82%; *M. brevipalmatus* 80%; *M. melanopleura* 83%; *M. opiparis* 83%; *M. zipperi* 76%; *M. charlotteae* 82%). These values agree with those observed in other brook-dwelling subgenera (e.g. *Brygoomantis*, *Ochthomantis*, *Hylobatrachus*), while in other *Mantidactylus* (e.g. subgenera *Guibemantis*, *Blommersia*, *Gephyromantis*), females are of similar size or only slightly larger than males (pers. obs.).

Relative male tympanum size was larger than relative female tympanum size (tables 2–3), as also known in other subgenera, such as *Brygoomantis*, *Ochthomantis*, *Hylobatrachus*, and some species of *Phylacomantis* and *Blommersia* (Glaw and Vences, 1994). Relative male tympanum size varies substantially among closely

Table 2. Morphometric measurements of *Chonomantis* species. See Materials and Methods for abbreviations. Values are given separately for name-bearing types, and for males and females of each species (as mean SD standard deviation and range in parentheses, *N*, number of specimens measured). Values for relative hindlimb length (RHL) are coded as follows: 0, posterior eye margin; 1, eye centre; 2, anterior eye margin; 3, between eye and nostril; 4, nostril; 5, snout tip; 6, slightly beyond snout tip; 7, distinctly beyond snout tip; 8, widely beyond snout tip. Values for relative toe length (RTL) are coded as follows: 0, fifth toe distinctly longer than third toe; 1, fifth toe slightly longer than third toe; 2, fifth toe of same length as third toe; 3, fifth toe slightly shorter than third toe; 4, fifth toe distinctly shorter than third toe. Sex of types is given in parentheses (M, male; F, female). Junior synonyms are written in parentheses. See *Appendix* for list of specimens measured.

	<i>N</i>	SVL	HW	HL	Tym	Eye	Eye–Ns	Ns–St	ForL	HaL	HiL	FoTL	FoL	RTL	RHL
<i>M. brevipalmatus</i> holotype (F)	1	37.0	11.7	14, 5	2, 7	4, 1	4, 0	3, 3	24, 5	11, 6	76, 8	38, 7	25, 0	0	8
(<i>M. delormei</i> holotype) (F)	1	38.9	12.0	14.5	2.8	4.2	3.6	2.7	21.3	11.7	69.8	36.8	25.0	0	–
<i>M. brevipalmatus</i> males	10	33.1 SD 1.8 (29.2–35.3)	10.8 SD 0.5 (10.3–12.0)	13.0 SD 0.6 (12.1–14.4)	4.4 SD 0.3 (4.0–4.9)	3.8 SD 0.2 (3.4–4.1)	3.0 SD 0.2 (2.7–3.3)	2.4 SD 0.4 (2.0–3.3)	20.4 SD 1.1 (18.8–22.2)	10.0 SD 0.6 (9.3–10.9)	66.0 SD 3.2 (61.1–71.0)	32.0 SD 1.7 (29.6–34.3)	22.2 SD 1.4 (20.1–24.0)	0	5–8
<i>M. brevipalmatus</i> females	9	41.6 SD 3.3 (34.8–44.9)	13.2 SD 1.3 (10.7–15.0)	15.6 (13.3–16.7)	3.7 SD 0.6 (2.6–4.3)	4.5 SD 0.4 (3.7–5.0)	3.4 SD 0.3 (2.7–3.7)	2.9 SD 0.4 (2.2–3.6)	25.0 SD 2.3 (22.0–29.1)	11.9 SD 0.6 (10.7–13.0)	80.5 SD 3.9 (73.9–85.9)	41.4 SD 4.6 (36.8–48.7)	27.0 SD 1.5 (24.3–29.1)	0	5–8
<i>M. aerumnalis</i> males	7	24.4 SD 1.3 (22.8–26.6)	8.8 SD 0.9 (7.2–9.9)	10.4 SD 0.8 (8.9–11.2)	2.5 SD 0.3 (1.8–2.8)	3.2 SD 0.3 (2.7–3.5)	2.3 SD 0.1 (2.1–2.4)	2.0 SD 0.2 (1.8–2.2)	15.8 SD 1.4 (14.0–17.2)	7.1 SD 0.6 (6.1–7.6)	46.8 SD 3.6 (40.5–49.0)	21.0 SD 1.8 (17.9–22.3)	14.0 SD 1.4 (11.7–15.1)	1–3	5–8
<i>M. aerumnalis</i> females	6	29.4 SD 2.0 (25.8–31.0)	10.4 SD 0.5 (9.6–11.0)	11.9 SD 0.6 (10.6–12.3)	2.5 SD 0.2 (2.2–2.8)	3.5 SD 0.3 (3.0–3.8)	2.6 SD 0.2 (2.4–2.9)	2.1 SD 0.1 (2.0–2.3)	18.2 SD 1.2 (16.3–19.7)	8.4 SD 0.6 (7.2–9.0)	54.9 SD 4.8 (46.4–60.3)	24.9 SD 1.7 (21.6–26.2)	16.3 SD 1.0 (14.3–17.2)	1–3	4–8
<i>M. opiparis</i> lectotype (F)	1	23.1	7.6	9.1	2.0	3.0	2.0	1.8	14.7	6.4	45.3	20.7	13.5	0	7
<i>M. opiparis</i> males	10	24.9 SD 0.8 (23.8–26.1)	8.8 SD 0.4 (8.0–9.3)	10.3 SD 0.4 (9.7–10.9)	4.1 SD 0.4 (3.3–4.5)	3.1 SD 0.2 (2.7–3.4)	2.3 SD 0.2 (2.1–2.5)	1.8 SD 0.2 (1.4–2.0)	15.6 SD 0.3 (15.0–16.1)	7.2 SD 0.3 (6.9–7.7)	44.4 SD 1.6 (42.1–47.9)	19.9 SD 0.9 (18.3–21.6)	13.7 SD 1.3 (12.3–16.2)	0–1	4–8

Table 2. (Continued).

<i>M. opiparis</i> females	11	30.1 SD 2.0 (27.0–33.2)	9.8 SD 0.9 (8.2–10.9)	11.8 SD 0.8 (10.4–12.8)	3.2 SD 0.4 (2.7–4.1)	3.9 SD 0.5 (3.2–4.5)	2.6 SD 0.2 (2.2–3.0)	2.1 SD 0.2 (1.8–2.5)	18.8 SD 1.3 (16.7–20.7)	8.8 SD 0.6 (8.1–9.8)	54.3 SD 2.2 (50.5–57.0)	25.0 SD 0.8 (23.5–25.9)	16.3 SD 0.7 (14.9–17.1)	0–1	3–8
<i>M. melanopleura</i> holotype (F?)	1	26.2	8.4	10.8	3.1	3.6	2.7	1.6	14.9	7.4	48.0	20.8	13.8	0	8
(<i>M. frenatus</i> holotype)(F)	1	38.4	12.6	15.0	3.9	3.8	3.5	2.3	23.7	11.4	69.5	31.4	20.8	0	5
<i>M. melanopleura</i> males	13	31.5 SD 2.5 (29.9–39.5)	10.9 SD 0.9 (9.5–13.3)	12.6 SD 0.9 (12.0–15.4)	4.7 SD 0.5 (3.8–5.4)	3.8 SD 0.3 (3.4–4.3)	2.8 SD 0.3 (2.4–3.4)	2.3 SD 0.3 (1.9–2.7)	19.0 SD 1.7 (17.2–23.8)	8.7 SD 0.8 (7.7–11.0)	56.1 SD 5.0 (49.1–70.4)	25.4 SD 2.2 (22.5–31.4)	17.4 SD 2.4 (15.3–24.0)	0	4–8
<i>M. melanopleura</i> females	9	38.0 SD 2.5 (32.3–40.5)	12.1 SD 0.66 (11.0–13.2)	14.4 SD 0.8 (12.9–15.3)	3.5 SD 0.3 (3.1–4.0)	4.4 SD 0.5 (3.8–5.2)	3.3 SD 0.3 (2.8–3.8)	2.7 SD 0.4 (2.1–3.1)	23.0 SD 1.5 (20.2–25.0)	10.3 SD 0.6 (9.4–11.2)	69.4 SD 5.3 (57.3–74.0)	31.3 SD 2.5 (26.0–34.2)	20.2 SD 1.7 (16.7–22.1)	0	4–8
<i>M. albofrenatus</i> holotype (F)	1	27.1	9.0	10.9	2.5	3.4	2.7	1.9	20.7	7.5	44.9	19.4	12.3	4	4
<i>M. albofrenatus</i> males	7	21.4 SD 1.3 (19.3–23.0)	7.2 SD 0.5 (6.7–8.3)	8.6 SD 0.5 (7.9–9.3)	3.7 SD 0.3 (3.4–4.1)	2.9 SD 0.2 (2.7–3.1)	1.9 SD 0.2 (1.5–2.0)	1.3 SD 0.2 (1.0–1.6)	14.2 SD 0.7 (13.0–14.8)	6.2 SD 0.5 (5.5–6.9)	34.7 SD 2.0 (31.3–36.7)	16.2 SD 0.9 (14.7–17.4)	10.9 SD 1.4 (9.3–13.7)	4	2–4
<i>M. albofrenatus</i> female	1	25.3	8.1	9.5	2.2	3.0	2.3	1.3	16.1	7.3	41.3	19.0	12.5	4	2
<i>M. zipperi</i> holotype (M)	1	23.6	8.2	9.6	4.0	2.9	2.2	1.5	13.8	5.9	38.1	17.0	11.0	4	2
<i>M. zipperi</i> males	8	22.5 SD 0.7 (21.5–23.4)	7.6 SD 0.3 (7.2–8.1)	9.3 SD 0.6 (8.6–10.5)	3.4 SD 0.4 (2.8–4.0)	2.8 SD 0.4 (2.4–3.5)	2.1 SD 0.2 (1.8–2.3)	1.5 SD 0.2 (1.2–1.8)	14.7 SD 0.7 (13.5–15.5)	6.9 SD 0.4 (6.1–7.4)	39.3 SD 1.7 (36.4–40.6)	18.1 SD 0.7 (17.1–19.4)	11.9 SD 0.6 (11.0–12.4)	2–4	2–8
<i>M. zipperi</i> female	1	29.5	9.4	11.6	3.0	3.8	2.3	2.0	17.8	7.9	47.6	22.0	14.0	3	3
<i>M. charlotteae</i> holotype (M)	1	24.5	8.8	9.5	2.7	3.3	2.4	1.6	14.8	7.3	40.3	18.7	12.5	4	2
<i>M. charlotteae</i> males	14	24.0 SD 1.1 (22.4–26.2)	8.2 SD 0.4 (7.4–8.9)	10.0 SD 0.4 (9.3–10.7)	2.9 SD 0.4 (2.3–3.5)	3.2 SD 0.2 (2.9–3.5)	2.4 SD 0.3 (2.0–2.9)	1.7 SD 0.2 (1.3–2.0)	15.9 SD 1.0 (14.7–18.0)	7.1 SD 0.4 (6.3–7.9)	40.2 SD 2.7 (37.0–47.4)	18.4 SD 1.0 (17.0–20.3)	11.9 SD 0.9 (10.7–13.3)	2–4	0–4
<i>M. charlotteae</i> females	11	29.3 SD 2.1 (26.3–32.2)	9.6 SD 0.8 (8.5–10.7)	11.2 SD 0.6 (10.2–12.0)	2.8 SD 0.3 (2.3–3.2)	3.7 SD 0.3 (3.1–4.3)	2.7 SD 0.2 (2.4–3.0)	1.9 SD 0.3 (1.4–2.3)	18.9 SD 1.4 (16.4–20.8)	8.4 SD 0.5 (7.7–9.2)	47.1 SD 2.9 (41.6–51.1)	21.8 SD 1.0 (20.0–22.9)	14.1 SD 0.8 (12.5–15.2)	2–4	1–4

related *Chonomantis* species, and distinguishes *Mantidactylus aerumnalis* and *M. charlotteae* (characterized by a small tympanum) from all other species. However, these differences were much less distinct in females. *Mantidactylus aerumnalis* females have the lowest relative tympanum size values, corresponding to the situation in males, but *M. charlotteae* females appear to have larger relative tympani than *M. albofrenatus*, in which males have the second highest values. Actually, no significant correlation was found between mean male and female values (Spearman rank correlation, $r_s=0.378$, $P>0.4$).

As also a second important character, femoral glands, are weakly expressed in females, their determination is much more difficult. The fact that six out of eight name-bearing types (including synonyms) are female specimens enhances the difficulties of correct assessment of specific identities, and explains much of the past taxonomic confusion in the subgenus. In future species descriptions or lecto- or neotype designations in *Mantidactylus* species, we recommend adult males to be selected as name-bearing types whenever possible.

The available data are an insufficient basis for a comprehensive phylogenetic analysis of species in the subgenus *Chonomantis*. Several characters which may be important for species recognition (frenal stripe, advertisement calls) appear to diagnose species that are difficult to distinguish morphologically. Using relative toe length, relative hindlimb length, and prominence of femoral glands, two phenetic clusters can be identified: (a) the *M. opiparis* complex (containing *M. melanopleura* and *M. opiparis*) differs from other *Chonomantis* in the presence of small, indistinct femoral glands in males (although some *M. charlotteae* approach this state). As most representatives of the probably closely related subgenera *Hylobatrachus*, *Ochthomantis* and *Brygoomantis* have distinct femoral glands, the reduced state in the *M. opiparis* complex may be seen as synapomorphy. (b) The *M. albofrenatus* complex (*M. albofrenatus*, *M. zipperi*, *M. charlotteae*). These three species are characterized by distinct femoral glands (probably symplesiomorphic), short legs, and a long third toe. The latter two characters are difficult to polarize as both states occur in the potential outgroup. Relationships of *M. brevipalmatus* and *M. aerumnalis* to other *Chonomantis* species are not obvious. Their long hindlegs suggest that they may be closely related to one another and to the *M. opiparis* complex, whereas their large and distinct femoral glands are more similar to those characteristic of the *M. albofrenatus* complex.

Species diversity

We recognize seven species in the subgenus *Chonomantis*, as opposed to earlier workers who recognized three (Blommers-Schlösser and Blanc, 1991; Guibé, 1978) or four (Andreone and Gavetti, 1994; Glaw and Vences, 1994) species. Several specimens of the *M. albofrenatus* complex collected by F. Andreone and J. Randrianirina in the Masoala peninsula, and on the Anjanaharibe and Tsararano chains, could not be reliably assigned to one of the species recognized herein, suggesting the existence of an additional species of *Chonomantis* in north-eastern Madagascar. Similarly, the status of the *M. charlotteae*-like population from southern Madagascar (Andohahela), and the differentiation between the allopatric populations of *M. brevipalmatus* (Ankaratra, Itremo, Andringitra) are not well understood and await further fieldwork in these areas.

The validity of the seven species recognized herein is confirmed by the extraordinary degree of syntopic occurrence. The two species previously subsumed under

Table 3. Morphometric ratios and distinctive morphological and bioacoustic characters in *Chonomantis*. Ratios were calculated using data from specimens mentioned in table 1 (types of *brevipalmatus*, *delormei*, *melanopleura*, *frenatus*, and *opiparis* not considered due to subadult state or bad state of preservation). SVL ratios of *brevipalmatus* include specimens from Itremo (see corresponding section) which were not used in table 1. The abbreviation TT is used for tibiotarsal articulation.

	<i>M. brevipalmatus</i>	<i>M. aerumnalis</i>	<i>M. opiparis</i>	<i>M. melanopleura</i>	<i>M. albofrenatus</i>	<i>M. zipperi</i>	<i>M. charlotteae</i>
SVL males	27.6–35.3 mm	22.8–26.6 mm	23.8–26.1 mm	29.9–39.5 mm	19.3–23.0 mm	21.5–23.4 mm	22.4–26.2 mm
SVL females	34.8–44.9 mm	28.3–31.0 mm	27.0–33.2 mm	32.3–40.5 mm	25.3–27.1 mm	29.5 mm	26.3–32.2 mm
Tym/Eye ratio males	1.17 SD 0.08 (1.05–1.31)	0.77 SD 0.08 (0.67–0.87)	1.34 SD 0.14 (1.20–1.50)	1.24 SD 0.16 (0.93–1.47)	1.27 SD 0.10 (1.10–1.38)	1.24 SD 0.16 (1.03–1.44)	0.92 SD 0.13 (0.70–1.13)
Tym/Eye ratio females	0.82 SD 0.07 (0.70–0.91)	0.68 SD 0.05 (0.61–0.74)	0.81 SD 0.09 (0.62–0.91)	0.80 SD 0.03 (0.76–0.85)	0.73–0.74	0.79	0.75 SD 0.08 (0.62–0.84)
FoL/SVL ratio	0.66 SD 0.04 (0.60–0.71)	0.56 SD 0.03 (0.51–0.60)	0.54 SD 0.04 (0.49–0.62)	0.54 SD 0.06 (0.51–0.80)	0.51 SD 0.05 (0.46–0.63)	0.52 SD 0.03 (0.47–0.55)	0.49 SD 0.03 (0.45–0.56)
HaL/SVL ratio	0.30 SD 0.02 (0.27–0.32)	0.29 SD 0.01 (0.27–0.32)	0.29 SD 0.02 (0.25–0.32)	0.27 SD 0.01 (0.25–0.31)	0.29 SD 0.02 (0.27–0.31)	0.30 SD 0.02 (0.27–0.33)	0.29 SD 0.01 (0.27–0.33)
RHL of most specimens	TT reaches beyond snout tip	TT reaches snout tip or beyond	TT reaches snout tip or beyond	TT reaches beyond snout tip	TT reaches at most nostril	TT does not reach snout tip	TT reaches at most nostril
RTL of most specimens	fifth toe longer than third toe	fifth toe of similar length (slightly longer or shorter) as third toe	fifth toe longer than third toe	fifth toe longer than third toe	fifth toe shorter than third toe	fifth toe slightly shorter than third toe	fifth toe shorter than third toe
Webbing of toe 5	2	0.75–1	1	1	1.5–2	1.5	1.25
femoral glands in males	large, very prominent	large, prominent	small, indistinct	small, indistinct	large, prominent	large, not very prominent	small to large, not very prominent

Table 3. (Continued).

frenal stripe between forelimb and eye	present	absent	present	present	present	present	present
frenal stripe between eye and nostril	present, reaches close to nostril	absent	absent	present, reaches nostril or close to it	present, reaches nostril or close to it	absent	present, stops close to the eye in most specimens
throat coloration	light with indistinct, weak darker marbling	black with a distinct white stripe which is continued onto the venter	black or dark brown, with a median line or row of spots	black or dark brown, with a median line or row of spots	grey with large white spots forming a median row	light grey- yellowish, with a rather broad light median stripe which begins as distinct white spot close to the lip	blackish, with small white spots which form a median row, sometimes fusing to a median stripe
note duration of advertisement calls	9–21 ms	unknown	69–126 ms	19–54 ms	56–80 ms	21–31 ms	91–304 ms

M. opiparis (*M. melanopleura* and *M. opiparis*) occur sympatrically from Marojejy to the Ranomafana region, but maintain their characteristic colour patterns and advertisement call throughout their collective range (known from Nahampoana to Andasibe in *M. melanopleura*, and from Ranomafana to Tsaratanana in *M. opiparis*). As many as five different species (*M. aerumnalis*, *M. albofrenatus*, *M. zipperi*, *M. melanopleura*, *M. opiparis*) were found along a brook at a single locality (An'Ala) in an area of less than 1 ha. Considering this high degree of syntopy, *Chonomantis* may be a fruitful system for ecological studies. We believe that differences in advertisement calls, and possibly body size, allow these closely related species to occur in syntopy. It is also striking that the condition of the frenal stripe is invariant within these largely diurnal frog species, and it may be hypothesized that this pattern bears a significant optical signal for species recognition. This is especially likely for the two syntopic species pairs *M. opiparis* (no distinct frenal stripe anterior to the eye)/*M. melanopleura* (distinct frenal stripe anterior to the eye) and *M. zipperi* (no distinct frenal stripe anterior to the eye)/*M. albofrenatus* (distinct frenal stripe anterior to the eye).

The recognition of numerous sibling species in *Chonomantis* and other Malagasy anuran groups, which have partly been well represented in scientific collections for decades, demonstrates that much revisionary taxonomic work is still necessary before high resolution biogeographic analyses of Malagasy anurans will be possible. Many recent herpetofaunal surveys and preliminary biogeographic analyses in Madagascar were only based on lists of taxa without information on reference specimens (e.g. Nussbaum *et al.*, 1999; Raselimanana, 1998, 1999; Raxworthy *et al.*, 1998; Raxworthy and Nussbaum, 1996a, b). Also Blommers-Schlösser and Blanc (1991) gave distribution maps for all Malagasy amphibian species without data on vouchers. In some cases, such distributional information can be extremely difficult to assign properly when subsequent revisions reveal the existence of previously unrecognized sibling species. For this reason we strongly suggest that reference specimens for each species should be mentioned in publications of faunistic surveys.

Ecology and conservation

In some areas in Madagascar, *Chonomantis* are among the most abundantly encountered frogs during the day, but they appear to be relatively restricted to environments with running water and at least a small area of forest cover. The only *Chonomantis* regularly found far from forested areas is *M. brevipalmatus*, which occurs along brooks in high-altitude savanna in the Ankaratra mountains (pers. obs.). *Chonomantis* specimens were often found on the forest floor at some distance from water, but calling males were generally observed along the brooks. Conservation of *Chonomantis* thus depends strictly on the conservation of at least small forest fragments including lotic waterbodies. However, all except *M. albofrenatus*, *Chonomantis* species are more or less widespread. In most other Malagasy amphibian and reptile groups, species which appear to be local endemics were found more or less regularly in other regions when intensive surveys were carried out. Among *Chonomantis*, all species are furthermore known from at least one protected area: *M. aerumnalis*, Ranomafana, Ivohibe; *M. albofrenatus*, Andasibe-Analamazoatra*; *M. brevipalmatus*, Andringitra; *M. melanopleura*, Andohahela*, Ivohibe, Ranomafana*, Andasibe-Analamazoatra*, Mantady*, Masoala*, Marojejy; *M. opiparis*, Ranomafana, Andasibe-Analamazoatra*, Masoala*,

Anjanaharibe, Marojejy, Tsaratanana*; *M. zipperi*, Ranomafana, Andasibe-Analamazoatra, Mantady*; *M. charlotteae*, Nosy Mangabe*, Masoala*, Andohahela?, Anjanaharibe*, Marojejy* (records marked with an asterisk were within the reserve boundaries according to our personal observations or to other reliable sources). Their survival thus seems assured as long as these reserves are effectively protected.

Biogeography

The recognition of three additional species in the subgenus made it necessary to revise completely the distribution maps provided by Blommers-Schlösser and Blanc (1991). According to the new maps presented here (figure 13), *Chonomantis* are widely distributed along the eastern rainforest belt, from Nahampoana in extreme southeast to Marojejy in the northeast. They have not been recorded from: (a) extreme northern Madagascar (Montagne d'Ambre); (b) the Sambirano region (low-altitude regions of northwestern Madagascar); and (c) the humid relict forests of Isalo and Tsingy de Bemaraha in western Madagascar. At least their absence at Montagne d'Ambre and Nosy Be appears to be well supported by several recent surveys at these sites (Raxworthy and Nussbaum, 1994; Andreone *et al.*, in press). Presence of at least two *Chonomantis* (*M. opiparis* and *M. zipperi*) in the Mahajaby forest (Morafenobe) is corroborated by MNHN vouchers. From this locality, also, other brook-dwelling species such as *Boophis erythroductylus* have been collected (Guibé, 1953), but no recent observations are available. Blommers-Schlösser and Blanc (1991) plotted Mahajaby in western Madagascar, at the approximate coordinates of Morafenobe. However, Viette (1991) indicates that Mahajaby is located one to two days walking distance east of Morafenobe, at an altitude of *c.* 600 m. According to the available maps, the first hills with an altitude of more than 500 m are found about 40 km east of Morafenobe. Approximately 110 km east of Morafenobe, a village with the name Mahajaby exists, which probably fits into the 600 m altitude estimate. We suppose that the collecting locality was close to this village, which reduces the distance to the next westernmost locality (Tampoketsa d'Ankazobe) to *c.* 150 km. The site thus may better be considered as a part of the central highland region than of the western region of Madagascar. Hence, we tentatively consider the subgenus *Chonomantis* as absent from the western biogeographic region of Madagascar.

Among the recognized *Chonomantis*, *Mantidactylus melanopleura* appears to be the most widespread species, occurring from Nahampoana in the south-east to Marojejy in the north-east. *Mantidactylus opiparis* is also rather widespread, but is not reliably known from sites south of the Ranomafana region. *Mantidactylus melanopleura* was the only *Chonomantis* found in the southern Andohahela reserve (Andreone and Randriamahazo, 1997) and would appear to be the only species of the subgenus known from an area south of Andringitra/Ivohibe, if there were not a single voucher specimen (MNHN 1975.383) from Andohahela which clearly represents *M. charlotteae* or a related species. *Mantidactylus opiparis* reaches relatively low altitudes in the Masoala peninsula; the same is true for *M. melanopleura* both in the south-east and on the Masoala peninsula. Nevertheless, both species are best characterized as mid-altitude forms. The same applies to *M. zipperi*, *M. aerumnalis* and probably also to *M. albofrenatus*. *Mantidactylus charlotteae*, in contrast, appears to be a coastal species, although it reaches mid-altitudes in the Marojejy

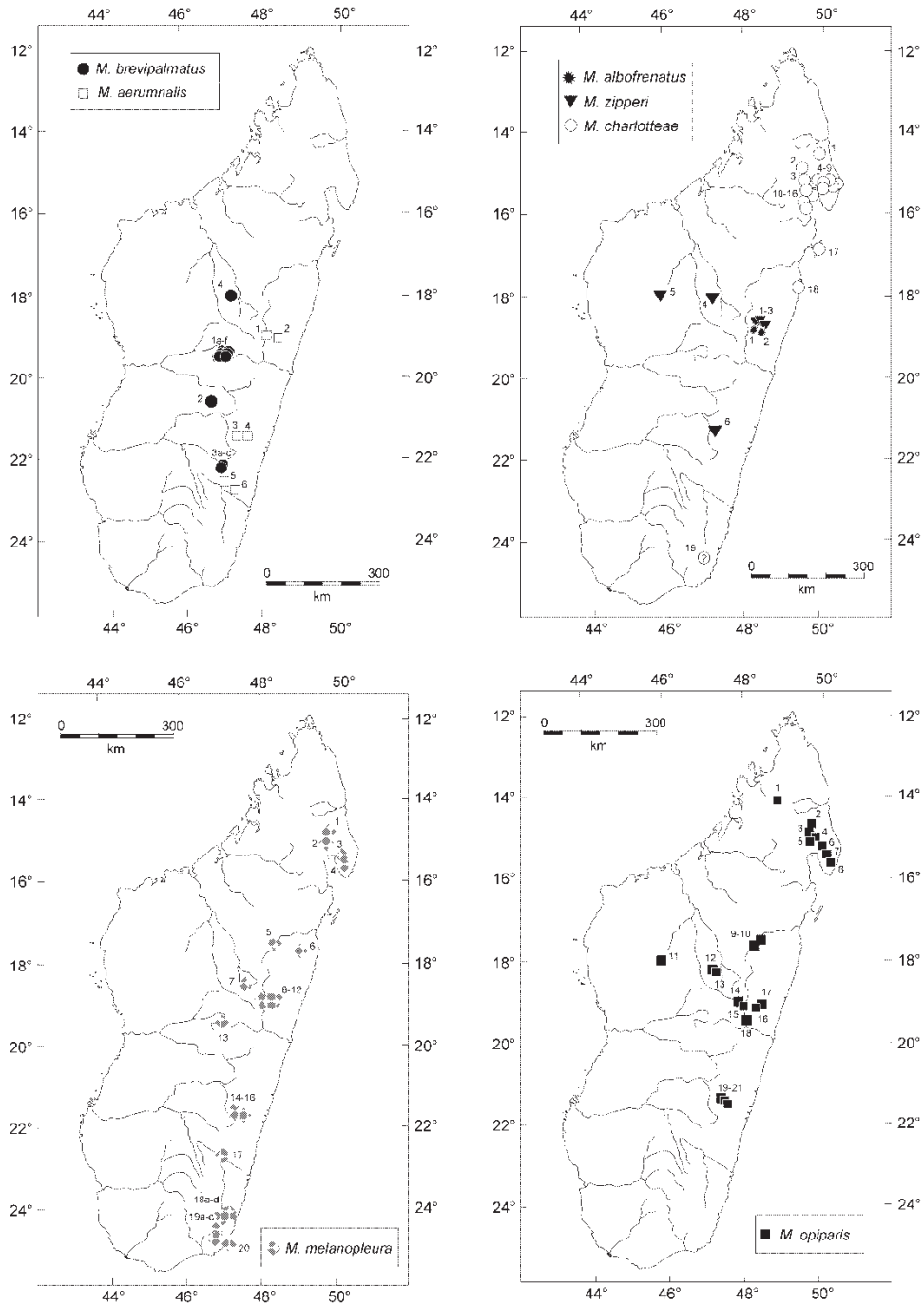


FIG. 13. Distribution maps of species in the subgenus *Chonomantis*. Positioning of localities on the maps is approximate; refer to table 1 for co-ordinates. Numbers of localities correspond to those given in the *Distribution* sections of each species.

massif. *Mantidactylus brevipalmatus*, finally, is a high-altitude specialist, only known reliably from localities of more than 1500 m.

The altitude of many collecting localities is not reliably known (table 1). Even if altitudes of some sites could be assessed more precisely, this would not necessarily lead to a more precise knowledge of the exact collecting localities. Especially in the past, collectors often mentioned nearby villages or towns (e.g. Moramanga, Maroantsetra, Fort Dauphin) as reference for collecting localities which may have been several kilometres away, and possibly at rather different altitudes. Assigning the localities listed in table 1 to low altitude (0–500 m; 20 localities), mid-altitude (500–1000 m; 22 localities), high-altitude and montane localities (> 1000 m; 13 localities) is nevertheless possible. Recorded *Chonomantis* species diversity is distinctly higher at mid-altitude sites (mean value 2.0 species per site) as compared to high-altitude (1.3) and low-altitude (1.2) localities.

The diversity of *Chonomantis* appears to be highest in central eastern Madagascar, coinciding with the syntopic occurrence of five species at An'Ala and four species at Andasibe. Towards the south, species diversity clearly decreases gradually. This pattern appears to be less distinct towards the north; here, at least three species reach the Marojejy massif. Despite the possible future identification of at least one additional *Chonomantis* in north-eastern Madagascar, our data indicate that the high species diversity in central-eastern Madagascar (especially at mid-altitude localities) as described by Lees (1996) is not a sampling artefact but represents the actual diversity pattern of the subgenus *Chonomantis*.

Acknowledgements

We are indebted to Franco Andreone and Jasmin Randrianirina who allowed examination of material collected by them in northern Madagascar, and of specimens deposited at the MRSN. Furthermore we thank Wolfgang Böhme (ZFMK), Barry Clarke and Colin McCarthy (BMNH), Kurt Grossenbacher (NMBE), Rainer Günther (ZMB), Gunther Köhler (SMF), Eugen Kramer (NMBA), Annemarie Ohler and Alain Dubois (MNHN), and Bertus van Tuijl (ZMA) for enabling us to examine specimens held in their care. Andreas Elend, Joachim Müller-Jung, Nirhy Rabibisoa, Domoina Rakotomalala, Olivier Ramilison, Noro Raminosoa, Fara Ranaivojaona, Denis Vallan, and David R. Vieites assisted in the field. Rose Blommers-Schlösser and Franco Andreone supplied call recordings for re-analysis. Alain Dubois and Martin Spies gave useful comments on the neotype problem and Moritz Grubenmann brought our attention to the paper of Beentje (1998). We are grateful to the Malagasy authorities for research authorizations, and collecting and export permits. The work in Madagascar was made possible by cooperation between the Departement de Biologie Animale, Université d'Antananarivo and the Zoologisches Forschungsinstitut und Museum A. Koenig (Bonn) and the Zoologische Staatssammlung (München). We acknowledge the financial support of the Deutscher Akademischer Austauschdienst (DAAD) to the fieldwork of F.G., and to the work of M.V. by a postdoc grant.

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Appendix

Morphometric values and ratios as given in tables 2 and 3 are based on the following specimens: (a) Males: *M. aerumnalis*, MRSN A74.1, ZFMK 60092–60093, 62248, MNHN 1930.415, 1972.542, 1975.373; *M. albofrenatus*, ZFMK 59879, 60048–60052, 60120; *M. brevipalmatus*, MNHN 1972.1356, 1972.1358, 1972.1364, 1972.1379, 1972.1380, 1972.1382, 1972.1390, 1972.1394, 1972.1397, ZFMK 59853; *M. melanopleura*, MNHN 1972.1338, 1972.1339, 1972.1353, 1975.368, 1975.370, ZFMK 53681, 60060, 60063–60065, 60098, 62241, ZMA 7030 (572); *M. opiparis*,

ZFMK 59817, 59818, 60066, 60095–60097, 60117, 62286, 62320, ZMA 7035 (483); *M. zipperi*, ZFMK 60135–60137, 60091, 62238, 62301, ZMA 7036 (907, 909); *M. charlotteae*, ZFMK 46003, 47212, 47215, 47217, 52693, 59918–59920, ZMA 7000 (560), 7001 (337, 689–693). (b) Females: *M. aerumnalis*, MRSN A72, A74.2, ZFMK 47254, 60094, MNHN 1975.382, 1989.3579; *M. albofrenatus*, ZFMK 59880; *M. brevipalmatus*, MNHN 1972.1361, 1972.1373, 1972.1374, 1972.1377, 1972.1398–1972.1401; *M. melanopleura*, MNHN 1972.547, 1972.1335, 1972.1345, 1972.1349, 1972.1351, ZFMK 52695, 60062, 60099, ZMA 6999 (644); *M. opiparis*, MNHN 1972.549, 1975.375, 1975.377, 1989.3586; ZFMK 52697, 53680, 60061, 60138, ZMA 6996 (386–387), 6997 (485); *M. zipperi*, ZFMK 60118; *M. charlotteae*, ZFMK 46001, 46002, 47211, 47214, 52694, 59921, 59922, ZMA 7000 (559), 7001 (688, 694), ZSM 934/2000