SPIXIANA	48	2	221–302	München, Mai 2026	ISSN 0341-8391

A review of molecular diversity of Malagasy frogs of the subgenera *Chonomantis* and *Ochthomantis* (genus *Mantidactylus*), with descriptions of nine new species

(Amphibia: Anura)

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Vences, M., Köhler, J., Mitze, A. S., Petzold, A., Preick, M., Raselimanana, A. P., Rakotoarison, A., Riemann, J. C., Rödel, M.-O., Wastyn, L., Scherz, M. D. & Glaw, F. 2026. A review of molecular diversity of Malagasy frogs of the subgenera *Chonomantis* and *Ochthomantis* (genus *Mantidactylus*), with descriptions of nine new species (Amphibia: Anura). Spixiana 48 (2): 221-302.

Based on analysis of mitochondrial DNA sequences of over 1900 samples, 331 of which were newly sequenced for this study, we provide an overview of the genetic variation in *Chonomantis* and *Ochthomantis*, two subgenera of the species-rich mantellid genus *Mantidactylus*. Our data confirm the existence of numerous deeply divergent mitochondrial lineages in *Chonomantis* which largely correspond to currently recognized species and previously identified candidate species. Based on concordance of high mitochondrial divergence with uncorrected pairwise distances of >4 % in the mitochondrial 16S rRNA gene, limited haplotype sharing in several nuclear-encoded gene fragments, and subtle but consistent morphological differences between the majority of these lineages, often occurring in close geographical proximity or even syntopy, we conclude that they represent independent evolutionary lineages meriting species status. We furthermore used archival DNA analyses on the type specimens of two *Chonomantis* species, *M. albofrenatus* and *M. charlotteae*, and conclude that the latter is a junior synonym of the former. Our integrative taxonomic revision leads to the formal description of eight new species in the subgenus *Chonomantis* (*M. charlotteianus* sp. nov., *M. chonodus* sp. nov., *M. dichromus* sp. nov., *M. kitrinolaimus* sp. nov., *M. maharira* sp. nov., *M. malokila* sp. nov., *M. temachikus* sp. nov., and *M. ventrilineatus* sp. nov.) and one new species in the subgenus *Ochthomantis* (*M. rabibisoai* sp. nov.), bringing the total species number to 16 in *Chonomantis* and 13 in *Ochthomantis*. Our data also point to the existence of deeply divergent, probably allopatric genetic lineages in numerous of these species (e. g., *M. charlotteianus* sp. nov., *M. dichromus* sp. nov., *M. melanopleura*, and *M. zipperi* in *Chonomantis*; *M. danieli*, *M. femoralis*, *M. majori*, *M. mocquardi*, and *M. tavaratra* in *Ochthomantis*), and to populations with possible morphological or bioacoustic differences (e. g., in *M. albofrenatus*), suggesting a need for future in-depth revision of these species, including new field work to obtain bioacoustic data and additional material for many of them.

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Introduction

The mantellid genus *Mantidactylus* Boulenger, 1895 is one of the most species-rich and ecomorphologically diverse groups of Malagasy anurans, with 65 currently recognized species (Frost 2026). Until 2006 (Guibé 1978, Blommers-Schlösser 1979, Blommers-Schlösser & Blanc 1991, Dubois 1992), *Mantidactylus* was defined spanning an even greater diversity of frogs, containing taxa currently included in the genera *Blommersia* Dubois, 1992, *Boehmantis* Glaw & Vences, 2006, *Gephyromantis* Methuen, 1920, *Guibemantis* Dubois, 1992, and *Spinomantis* Dubois, 1992. After these were split off into separate genera (Glaw & Vences 2006), the genus *Mantidactylus* now primarily contains semi-aquatic or terrestrial species associated with humid forest streams, classified in six subgenera: *Brygoomantis* Dubois, 1992, *Chonomantis* Glaw & Vences, 1994, *Hylobatrachus* Laurent, 1943, *Maitsomantis* Glaw & Vences, 2006, *Mantidactylus* Boulenger, 1895, and *Ochthomantis* Glaw & Vences, 1994, several of which are characterized by highly derived larval morphologies (Blommers-Schlösser 1979, Altig & McDiarmid 2006, Grosjean et al. 2011, Randrianiaina et al. 2011, Schulze et al. 2016). *Mantidactylus* are among the most commonly encountered frogs in Madagascar's rainforests (Glaw & Vences 2007, Strauß et al. 2013, Scherz et al. 2022b). Yet, because their morphology and coloration are typically inconspicuous, many aspects of their pattern are highly variable, their advertisement calls are mostly soft and emitted from concealed positions, and their entire reproductive behaviour is shy and rarely observed, their true species diversity has not been appreciated for a long time.

Only recently, molecular work has revealed the existence of numerous candidate species in *Mantidactylus* (Vieites et al. 2009, Perl et al. 2014, Carné & Vieites 2024), and integrative taxonomic work based on molecular and morphological data has targeted the various subgenera. Specifically, *Brygoomantis* has been the focus of a large and comprehensive revision (Scherz et al. 2022a), *Hylobatrachus* was revised by Scherz et al. (2019), the subgenus *Mantidactylus* was examined by Rancilhac et al. (2020) and *Ochthomantis* by Rabibisoa et al. (2023). However, these considerable efforts have not yet succeeded in fully clarifying the taxonomy of the various *Mantidactylus* subgenera. For instance, the subgenera *Chonomantis*, *Hylobatrachus*, *Mantidactylus*, and *Ochthomantis* still contain candidate species of uncertain status (e. g., Vieites et al. 2009, Scherz et al. 2019, Rancilhac et al. 2020, Carné & Vieites 2024), the relationships and subgeneric allocation of the enigmatic *Mantidactylus majori* Boulenger, 1896, currently in *Ochthomantis* but perhaps deserving its own, separate subgenus is unclarified (Wollenberg et al. 2011, Rabibisoa et al. 2023), and the attribution of candidate species names in *Ochthomantis* (e. g., Vieites et al. 2009, Randrianiaina et al. 2011, Poth et al. 2013, Carné & Vieites 2024) to recently described new species (Rabibisoa et al. 2023) remains unassessed. The focus of the present study is on two of these *Mantidactylus* subgenera, *Chonomantis* and *Ochthomantis*. These are two common and widespread groups of mantellines, typically found on or close to the banks of streams in rainforests across Madagascar.

The subgenus *Chonomantis* currently contains nine species: *Mantidactylus albofrenatus* (Müller, 1892), *M. aerumnalis* (Peracca, 1893), *M. brevipal-*

matus Ahl, 1929, *M. charlotteae* Vences & Glaw, 2004, *M. delormei* Angel, 1938, *M. melanopleura* (Mocquard, 1901), *M. opiparis* (Peracca, 1893), *M. paidroa* Bora, Ramilijaona, Raminosoa & Vences, 2011, and *M. zipperi* Vences & Glaw, 2004. All of these are characterized by a dorsolateral fold separating dorsal and (typically darker) lateral coloration, and by a specific funnel-mouthed tadpole morphology (Blommers-Schlösser 1979, Vences & Glaw 2004, Glaw & Vences 2006, 2007, Bora et al. 2011, Grosjean et al. 2011). *Chonomantis* range between 19–45 mm from snout to vent (SVL) and are rather terrestrial, observed on the ground and low vegetation near streams but usually not in the water (Glaw & Vences 2007). Their larval morphology is remarkably uniform (Grosjean et al. 2011) and therefore not useful for taxonomic conclusions. *Chonomantis* taxonomy is almost exclusively based on distinct and unambiguous bioacoustic and morphological differences between the recognized species, several of which can occur in syntopy which clearly supports their species-level distinctness (Vences & Glaw 2004, Bora et al. 2011). Species of *Chonomantis* differ from each other, among other characters, in body size, relative tympanum size of males, shape and extension of frenal stripe, and dorsal as well as lateral colour.

Ochthomantis, the second focal subgenus of this study, can be seen as slightly more water-dependent than *Chonomantis* (e. g., Glaw & Vences 2007) and currently contains 12 species: *Mantidactylus ambreensis* Mocquard, 1895, *M. ambony* Scherz, Rasolonjatovo, Köhler, Rancilhac, Rakotoarison, Raselimanana, Ohler, Preick, Hofreiter, Glaw & Vences, 2020, *M. catalai* Angel, 1935, *M. danieli* Rabibisoa, Welt & Raxworthy, 2023, *M. femoralis* (Boulenger, 1882), *M. macrotympanum* Rabibisoa, Welt & Raxworthy, 2023, *M. majori* Boulenger, 1896, *M. mocquardi* Angel, 1929, *M. olgae* Rabibisoa, Welt & Raxworthy, 2023, *M. poissoni* Angel, 1937, *M. tavaratra* Rabibisoa, Welt & Raxworthy, 2023, and *M. zolitschka* Glaw & Vences, 2004. Species of *Ochthomantis* range between 29–67 mm in SVL, and females are often much larger than conspecific males (Glaw & Vences 2007, Rabibisoa et al. 2023). *Ochthomantis* are dorsally smooth or rugose with irregular and interrupted rows of tubercles, and many species have a yellow mark in the inguinal region. Their tadpoles show unique morphologies, with different degrees of reduction of keratodonts and presence of enlarged papillae in the oral disk, as well as specialized internal oral structures, probably reflecting trophic specialization (Altig & McDiarmid 2006, Randrianiaina et al. 2011, dos Santos Dias et al. 2024). Furthermore, several species of *Ochthomantis* have also been studied for the content of volatile chemical substances in their femoral glands (Poth et al. 2013). After description of one new species each by Glaw & Vences (2004) and Scherz et al. (2020), *Ochthomantis* have been taxonomically revised by Rabibisoa et al. (2023) who described four new species, resurrected *M. catalai* Angel, 1935 and *M. poissoni* Angel, 1937, and proposed distribution maps of all species based primarily on morphometric examination of a large quantity of preserved voucher specimens.

Here, we review the molecular diversity of *Chonomantis* and *Ochthomantis* based on newly produced DNA barcodes of a great number of samples. We also provide information on the molecular identity of several – though not all – historical type specimens from archival DNA analysis, phylogenetic hypotheses for both subgenera based on DNA sequences of concatenated mitochondrial gene fragments, and information on their variation in up to four nuclear-encoded DNA fragments. Although far from providing a comprehensive taxonomic resolution of the two subgenera, our review allows for the formal description of nine new species, and for a clearer identification of our gaps in knowledge and necessary future research focus to fully comprehend the systematics of these amphibians.

Materials and methods

This study is based on a large number of tissue samples and voucher specimens collected during multiple field expeditions from 1994–2022, combined with DNA sequences of other samples retrieved from GenBank. Specimens were collected in the field mostly via opportunistic day and night searches, sometimes specifically seeking calling males, with the aid of flashlights at night. Collected specimens were anesthetized by immersion in aqueous solutions of tricaine methanesulfonate (MS222), chlorobutanol or lidocaine, and subsequently euthanized by an overdose of the same substances. Before fixation, we took tissue samples from the euthanized specimens and stored them separately in 1.5 ml vials filled with pure ethanol. Vouchers were then fixed in 95 % ethanol or in 4 % formaldehyde solution, preserved in 70 % ethanol, and deposited in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Zoological Museum Amsterdam (ZMA); collection now included in Naturalis, Leiden); Museum für Naturkunde Berlin (ZMB); Natural History Museum Denmark (ZMUC); Zoologische Staatssammlung München (ZSM); and the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale (UADBA). We also discuss historical type specimens from the Naturhistorisches Museum Basel (NMBA), the Muséum national d'Histoire Naturelle, Paris (MNHN), the Museo regionale di Scienze Naturali, Torino (MRSN), and the Museum für Naturkunde Berlin (ZMB). FGZC, FGMV and ZCMV refer to field numbers and catalogue numbers of F. Glaw and M. Vences. APR, JCR, MSZC, and NSH refer to field numbers of Achille P. Raselimanana, Jana C. Riemann, Mark D. Scherz and Serge H. Ndriantsoa, respectively. For additional field number and catalogue number acronyms of sequences taken from GenBank, see the respective publications as retrievable via the respective accession numbers. Geographic regions within Madagascar are named according to Boumans et al. (2007) and Brown et al. (2016). Candidate species are named according to the numbering started by Vieites et al. (2009) and followed (for *Ochthomantis*) by Randrianiaina et al. (2011) and Carné & Vieites (2024), adding a "Ca" before each candidate number as proposed by Padial et al. (2010) and applied by Perl et al. (2014).

Morphometric measurements of voucher specimens were taken by MV with a manual caliper at an accuracy of 0.1 mm, as follows: snout–vent length (SVL); maximum head width (HW); head length from tip of snout to posterior edge of mouth opening (HL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); distance between anterior edge of eye and nostril (END); distance between nostril and tip of snout (NSD); distance between both nostrils (NND); forelimb length, from limb insertion to tip of longest finger (FORL); hand length, from the articulation of the carpus with the radioulna to the tip of the longest finger (HAL); hindlimb length, from the cloaca to the tip of the longest toe (HIL); foot length (FOL); foot length including tarsus (FOTL); and tibia length (TIBL). Foot webbing formula is reported according to Blommers-Schlösser (1979) to ensure comparability with previous species descriptions of Malagasy frogs.

Vocalizations were recorded in the field using various digital recorders and saved in uncompressed wave format, (re-)sampled at 22.05 kHz and 32-bit resolution and analyzed using the software Cool Edit Pro 2.0. Temporal parameters were measured in the oscillograms. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points) at Hanning window function. Spectrograms were produced at Blackman window function with 256 bands resolution. For a clearer graphical presentation, in some cases, careful band-pass filtering was applied to remove background sounds, applied only to frequencies outside the prevalent bandwidths of calls. Temporal measurements are summarized as range with mean ± standard deviation in parentheses. Description, terminology, and methods follow those recommended by Köhler et al. (2017), using the call-centered termnological scheme. Representative sections of new call recordings analyzed were archived in the Zenodo repository at https://doi.org/10.5281/zenodo.15161297.

Genetic divergence between individuals and lineages was assessed using DNA fragments of mitochondrial and nuclear-encoded genes, determined using Sanger sequencing after extracting DNA from tissue samples using a salt-extraction protocol (Bruford et al. 1992) and PCR amplifying the respective DNA fragments with primers and protocols as specified below. PCR products were purified with Exonuclease I and Shrimp Alkaline Phosphatase digestion and sequenced by LGC Genomics (Berlin) on an automated capillary sequencer. Chromatograms were checked for base-calling errors and edited with CodonCode Aligner v 3.7.1 (Codon Code Corporation, Dedham, MA, USA) and newly determined sequences submitted to GenBank (accession numbers PZ059868–PZ059871, PZ066204–PZ066671). All alignments and a spreadsheet with sequence metadata are available from Zenodo (https://doi.org/10.5281/zenodo.15161297). Various different datasets were compiled using the following laboratory and bioinformatic methods:

As a means to assess genetic variation within *Chonomantis* and *Ochthomantis*, we compiled datasets, separately for *Chonomantis* and *Ochthomantis*, of DNA sequences of the 3′-terminal fragment of the 16S rRNA gene (16S) which has often been used for DNA barcoding of Malagasy anurans (e.g., Vieites et al. 2009) and is available for a large number of comparative sequences from previous work (e.g., Randrianiaina et al. 2011, Strauß et al. 2013, Ndriantsoa et al. 2017, Rabibisoa et al. 2023). PCR was carried out using primers 16SAL (5′–CGCCTGTTTATCAAAAACAT–3′) and 16SBH-new (5′–CCTGGATTACTCCGGTCTGA–3′), modified from Palumbi et al. (1991), with cycling protocol 94°C (90 s), [94°C (45 s), 55°C (45 s), 72°C (90 s)] × 33, 72°C (300 s).

From a few crucial specimens, mostly name-bearing types, 16S sequences were also assembled from archival DNA analyses (museomics) and added to the Sanger-sequenced 16S dataset, along with all available 16S sequences of the two subgenera from GenBank. For several type specimens of *Ochthomantis*, archival DNA sequences were already determined and published by Scherz et al. (2022a) using methods described therein. Herein, new sequences were added for the name-bearing types of two *Chonomantis*, the holotype of *Mantidactylus albofrenatus* as well as the holotype and two paratypes of *M. charlotteae*. These specimens (details in the respective Results sections below) were sampled in 2023 for small pieces of thigh muscle tissue after making a small incision and reflecting the ventral skin of the thigh. Sampling was carried out with sterile scalpels and tweezers, and the sample was stored in a vial with pure ethanol that had been previously filled in a laboratory naïve to molecular work on the two focal subgenera of mantellids. Prior to DNA extraction, all samples were weighed and incubated in a Guanidine Thiocyanate (GuSCN)-based extraction buffer solution at 37°C overnight (~18 hours). Subsequently, a total volume of 25 µl genomic DNA per sample was extracted following the protocol of Rohland et al. (2004), following several consecutive steps as described in Straube et al. (2021). The yield in DNA was quantified based on 1 µl DNA of extract using the Qubit dsDNA HS Assay Kit 0.2–100 ng/µl (Life Technologies, Carlsbad, California, US) according to the instructions of the manufacturer's protocol. Single-stranded libraries were prepared following the protocol of Gansauge et al. (2017) using up to 13 ng/µl input DNA per sample. All lab work prior to qPCR was conducted in a dedicated DNA facility at the University of Potsdam, Germany, which meets all requirements for work with historical samples (see Fulton & Shapiro 2019) and extraction and library blanks were run alongside all samples to check for contamination. We assessed final library concentrations and fragment length distributions with a 2200 TapeStation (Aligent Technologies) assay. Sequence data were obtained through shotgun-sequencing of approximately five million 75 bp-long single-end reads on an Illumina Nextseq 500/550 sequencing platform at the University of Potsdam, as described in Paijmans et al. (2017). The quality of the obtained reads

Fig. 1. A–K. Maximum Likelihood tree inferred from a fragment of the mitochondrial 16S rRNA gene (alignment length 535 bp) from 1147 ingroup sequences of species of the subgenus *Chonomantis*. Numbers at nodes are support values in percent from a bootstrap analysis with 500 replicates (not shown if < 50 %). Candidate species numbers according to Vieites et al. (2009) are given for the new species described; for additional candidate numbers, see Table 7. Bold font indicates sequences from name-bearing types (asterisk highlights paratypes of *M. charlotteae*, here considered junior synonym of *M. albofrenatus*).

▶▶

was visualized twice using FastQC (https://www.bioinformatics.babraham.ac.uk), both before and after trimming of custom Illumina adapter sequences and discarding reads shorter than 30 bp with cutadapt v1.12 (Martin 2011). We used local Blast (BLAST+; Camacho et al. 2009) as implemented in BlasTax, a new tool of the iTaxoTools project (Vences et al. 2021, 2026), against a library of 16S sequences of all main mitochondrial lineages of *Chonomantis* plus a selection of additional mantellid genera (*Mantidactylus*, *Spinomantis*, *Blommersia*), and collected the matching reads in a FASTA file. We then used CodonCode Aligner v 3.7.1 (CodonCode Corporation) to map the matching reads to 16S reference sequences of all main *Chonomantis* lineages, verified the resulting assemblies were congruent (thus, no reference bias was introduced), and used final assemblies against sequences of specimens from the locality Betampona (which were placed phylogenetically closest to the sequences obtained by the exploratory assemblies), with missing sections in-between contigs coded by the letter "N".

For the full 16S datasets (from Sanger sequencing, archival DNA sequencing, and sequences compiled for GenBank; separately for the two subgenera) we used the G-INS-i algorithm in MAFFT (Katoh & Standley 2013) as implemented in Concatenator (Vences et al. 2022c) for alignment, determined the substitution models best fitting the data under the Bayesian Information Criterion in MEGA 7 (Kumar et al. 2016) (in both cases, GTR + G models), and inferred Maximum Likelihood (ML) trees in RAxML (Stamatakis 2014) using raxmlGUI v. 2.0 (Edler et al. 2020). Node support was tested with 500 full ("thorough") bootstrap replicates. A sequence of *M. betsileanus* (subgenus *Brygoomantis*) was used as outgroup in the *Chonomantis* phylogeny, and a sequence of *Mantidactylus radaka* (subgenus *Mantidactylus*), was used as outgroup in the *Ochthomantis* phylogeny (see https://doi.org/10.5281/zenodo.15161297 for accession numbers).

Trimmed alignments of 16S (separately for *Chonomantis* and *Ochthomantis*) were prepared for analysis of primary species hypotheses, genetic distances and diagnostic sites, by removing sequences with large numbers of missing data, and trimming the entire alignment to equal length of remaining sequences, making sure that all major lineages were represented. On these alignments, for an algorithmic inference of primary species hypotheses, we used ASAP (Puillandre et al. 2021) as implemented in iTaxoTools (Vences et al. 2021). Pairwise sequence distances between ASAP-inferred lineages were

Table 1. Primers and cycling protocols used for polymerase chain reaction amplification of nuclear markers used in this study. The nested PCR RAG1 sequence was only used for some *Chonomantis* samples.

Marker	Primers (5'–3')	Cycling protocol	Source
RAG1	F: Rag1-Manti-F1: CGTGACAGAGTSAAAGGAGT R: Rag1-Manti-R1: TCAATGATCTCTGGAACGTG	94°C (120s), [94°C (20s), 54°C (50s), 72°C (180s)] x 39, 72°C (600s)	Vences et al. (2018)
RAG1 (nested PCR)	F1: Rag1-Mart Fl1: AGCTGGAGYCARTAYCAYAARATG R1: Rag-1Mart R6: GTGTAGAGCCARTGRTGYTT F2: Rag-1AmpF2: ACNGGNMGICARATCTTYCARCC R2: Rag1-UC-R: TTGGACTGCCTGGCATTCAT	94°C (240s), [94°C (45s), 45°C (40s), 72°C (120s)] x 45, 72°C (600s)	Rakotoarison et al. (2015) and references therein
SACS (nested PCR)	F1: SACSF2: AAYATHACNAAYGCNTGYTAYAA R1: SACSR2: GCRAARTGNCCRTTNACRTGRAA F2: SACSNF2: TGYTAYAAYGAYTGYCCNTGGAT R2: SACSNR2: CKGTGRGGYTTYTTRTARTTRTG	94°C (240s), [94°C (45s), 45°C (40s), 72°C (120s)] x 45, 72°C (600s)	Shen et al. (2012)
KIAA1239 (nested PCR)	F1: KIAA1239-F1: CARCCTTGGGTNTTYCA R1: KIAA1239-R1: CMACAAAYTGGTCRTTR F2: KIAA1239-NF1: GAGCCNGAYATHTTYTTYG R2: KIAA1239-NR1: TTCACRAANCCMCCNG	94°C (240s), [94°C (45s), 45°C (40s), 72°C (120s)] x 45, 72°C (600s)	Shen et al. (2012)
POMC	F: POMC-DRV- F1: ATATGTCATGASCCAYTTYCGCTGGAA R: POMC-DRV- R1: GGCRTTYTTGAAWAGAGTCATTAGWGG	95°C (120s), [(95°C (45s), 62°C (50s), 72°C (80s)] x 9, [(95°C (45s), 52°C (50s), 72°C (80s)] x 30, 72°C (600s)	Vieites et al. (2007)

Fig. 1. Continued.

Fig. 1. Continued.

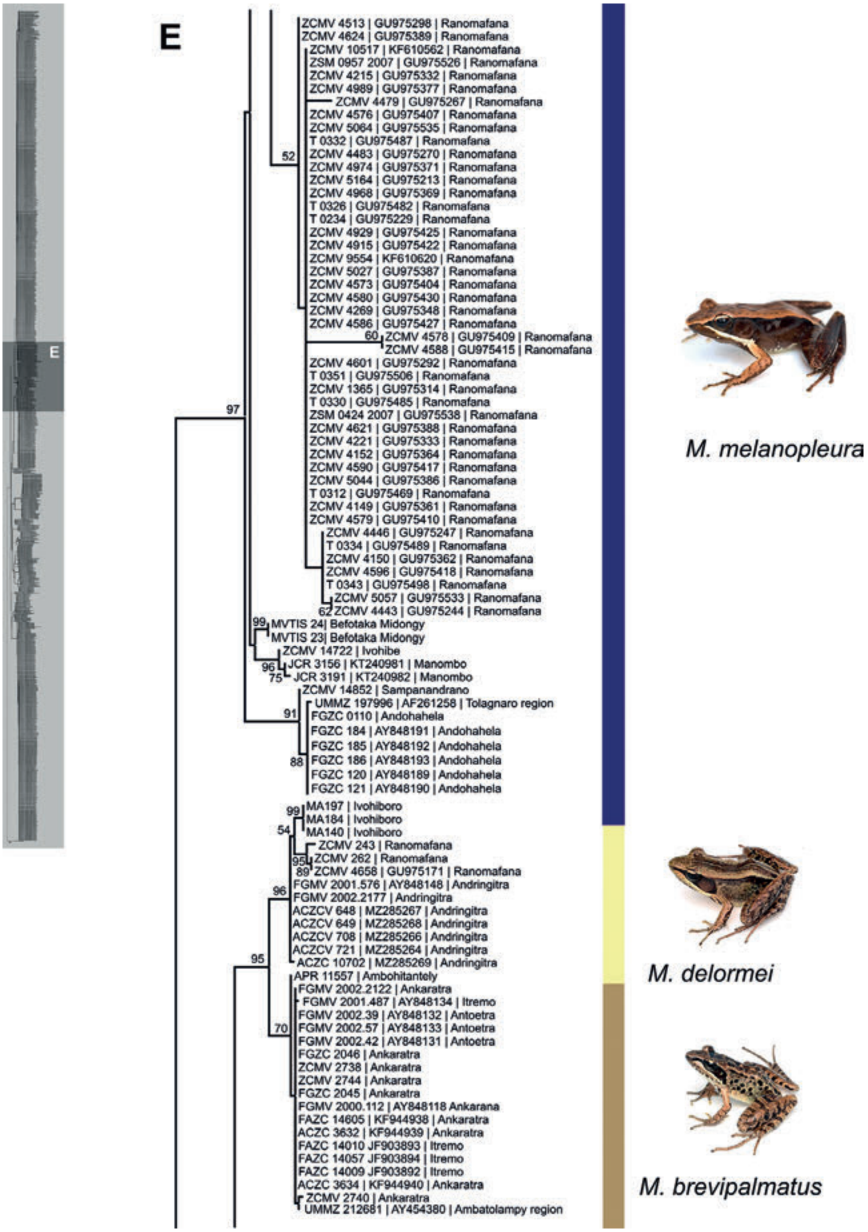


Fig. 1. Continued.

then calculated using the program TaxI2 (Vences et al. 2024b). We complemented the same trimmed 16S datasets with a full-length 16S sequence of *Mantella baroni* (Kurabayashi et al. 2006), to determine molecular diagnostic sites for the inferred species in the two focal subgenera using MolD (Fedosov et al. 2022). The trimmed alignments as well as a table with molecular diagnoses of all species are available from the Zenodo repository, https://doi.org/10.5281/zenodo.15161297).

To more reliably assess the phylogenetic relationships among species-level lineages within *Chonomantis* and *Ochthomantis*, we expanded the mitochondrial multi-gene dataset for *Ochthomantis* of Poth et al. (2013) consisting of DNA sequences of fragments of the genes for cytochrome *b* (COB), cytochrome oxidase subunit I (COI), 12S rRNA (12S), 16S rRNA (16S), and NADH-Dehydrogenase Subunit 1 (ND1), and compiled a similar dataset by sequencing fragments of COI, 12S, and 16S for *Chonomantis*, in order

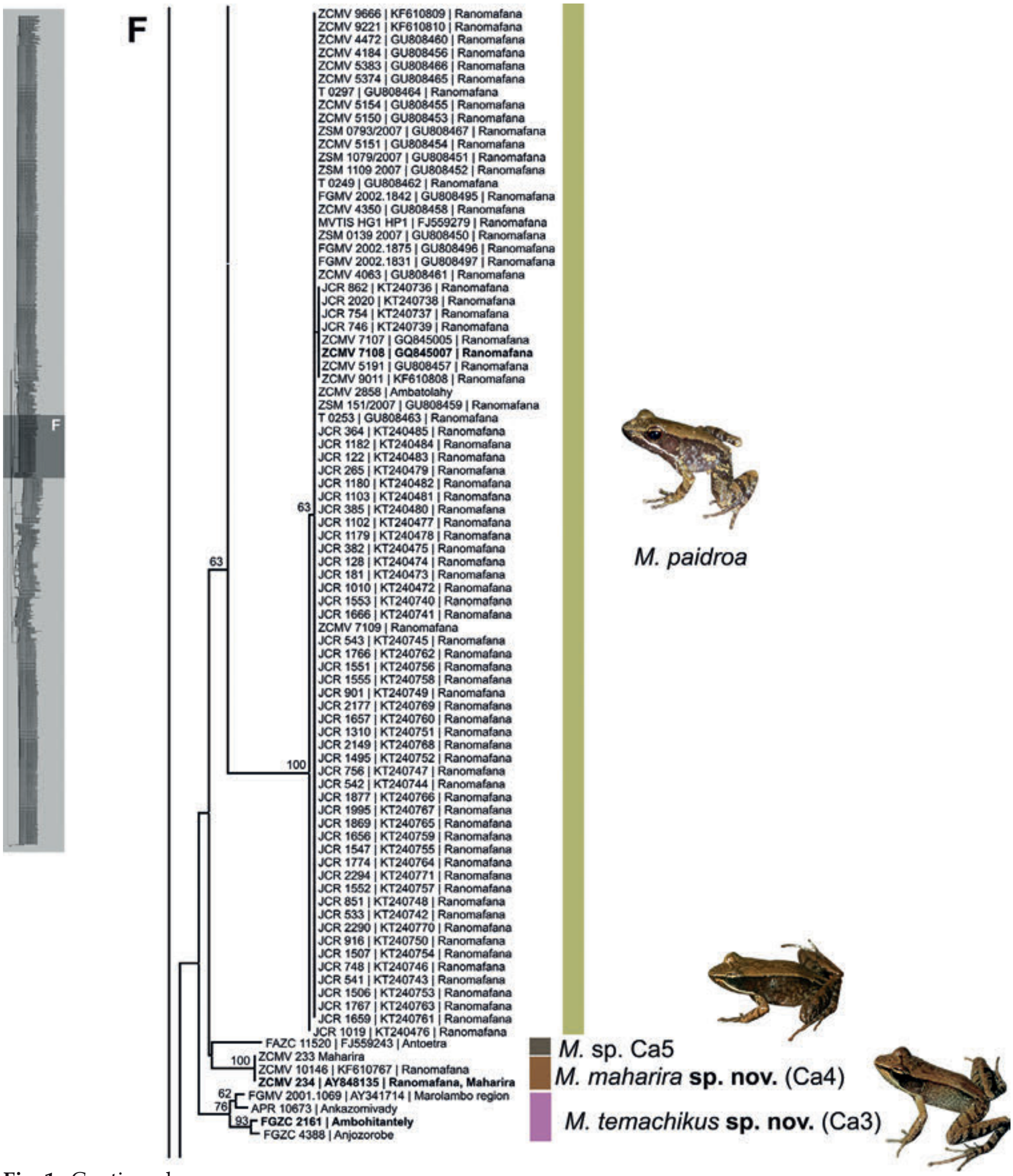


Fig. 1. Continued.

to include sequences of these genes for one representative sample of each species-level lineage. For primers and cycling conditions, see Vences et al. (2003) and Hutter et al. (2018). Sequences were aligned with the MAFFT G-INS-i algorithm (Katoh & Standley 2013), trimmed for positions present in <75 % of taxa, and concatenated in Concatenator (Vences et al. 2022c). From these datasets, ML trees (separately for each subgenus) were inferred using by-gene partitioned searches using IQ-Tree v.2.2.2.6 (Nguyen et al. 2015) after determining substitution models and (for the partitioned analysis) data partitions using ModelFinder (Kalyaanamoorthy et al. 2017) by assessing bootstrap support with 1000 full non-parametric bootstrap replicates. Specifically, for the *Ochthomantis* dataset (3056 bp) a two-partition scheme with a TIM2+F+I+G4 model for 12S+16S and a TPM2+F+ I+G4 model for COI+COB+ND1, and for the *Chonomantis* dataset (2256 bp) a two-partition scheme with a TIM2+F+R3 model for 12S+16S and a GTR+F+I+G4 model for COI were selected and used for ML inference.

To confront the primary species hypotheses derived from mitochondrial DNA analysis, we sequenced a series of fragments of nuclear-encoded, single-copy, protein coding genes: recombination activation gene 1 (RAG1),

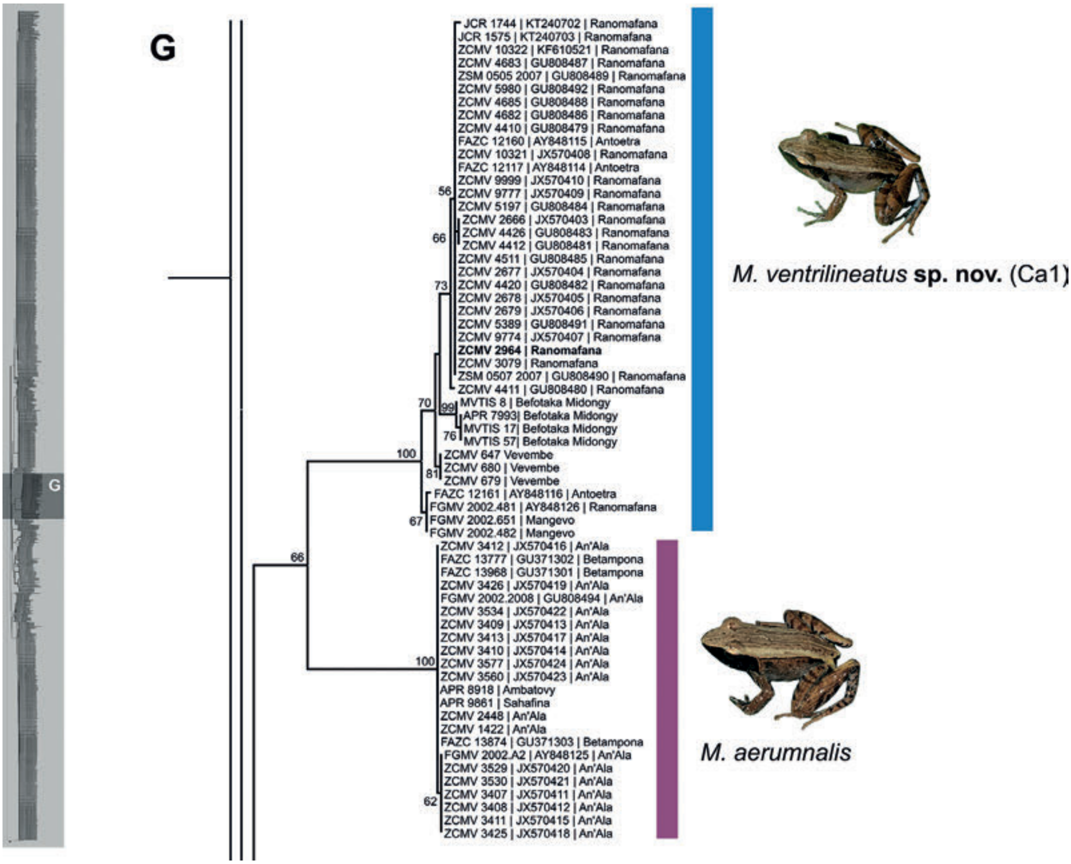


Fig. 1. Continued.

sacsin (SACS), leucine-rich repeat and WD repeat-containing protein (KIAA1239), and pro-opiomelanocortin (POMC), using primers and PCR protocols given in Table 1, with long fragments of RAG1, SACS, and KIAA1239 sequenced using a nested PCR approach (see Shen et al. 2012). The alignments of the nuclear-encoded genes were analyzed independently to understand concordance (or absence thereof) in the differentiation of these three unlinked genetic markers. We used a genealogy visualization approach to graphically represent the relationship among alleles (haplotypes). Haplotypes were estimated with the PHASE algorithm (Stephens et al. 2001), and haplotype genealogies were reconstructed with the Fitchi approach (Matschiner 2016) in Hapsolutely (Vences et al. 2024c; part of iTaxoTools) following the methodological approach of Salzburger et al. (2011).

We follow the general lineage concept (de Queiroz 1998, 2007) in combination with a relaxed biological species criterion, i. e., demanding reproductive isolation indicated by restricted gene flow among lineages (e. g., Speybroeck et al. 2020, Dufresnes et al. 2021). Because reproductive barriers generated through time increase genealogical depth and agreement among unlinked loci (Avise & Wollenberg 1997), we use genealogical concordance (Avise & Ball 1990) between mitochondrial and nuclear loci, especially in populations occurring in sympatry or close geographical proximity, as an indicator for restricted gene flow. Species status is then assigned to lineages based on combined evaluation of genetic, morphological and (where available) bioacoustic evidence (Padial et al. 2010).

Results and discussion

Molecular systematics of the subgenus *Chonomantis*

The ML tree inferred from the full *Chonomantis* 16S dataset (1147 in-group sequences for a total alignment length of 535 bp) revealed a large amount of genetic variation and an uneven distribution of sequences to main lineages. *Mantidactylus melanopleura* and *M. opiparis* were represented by a large number of sequences, mainly due to numerous barcodes from the Ranomafana region (see Strauß

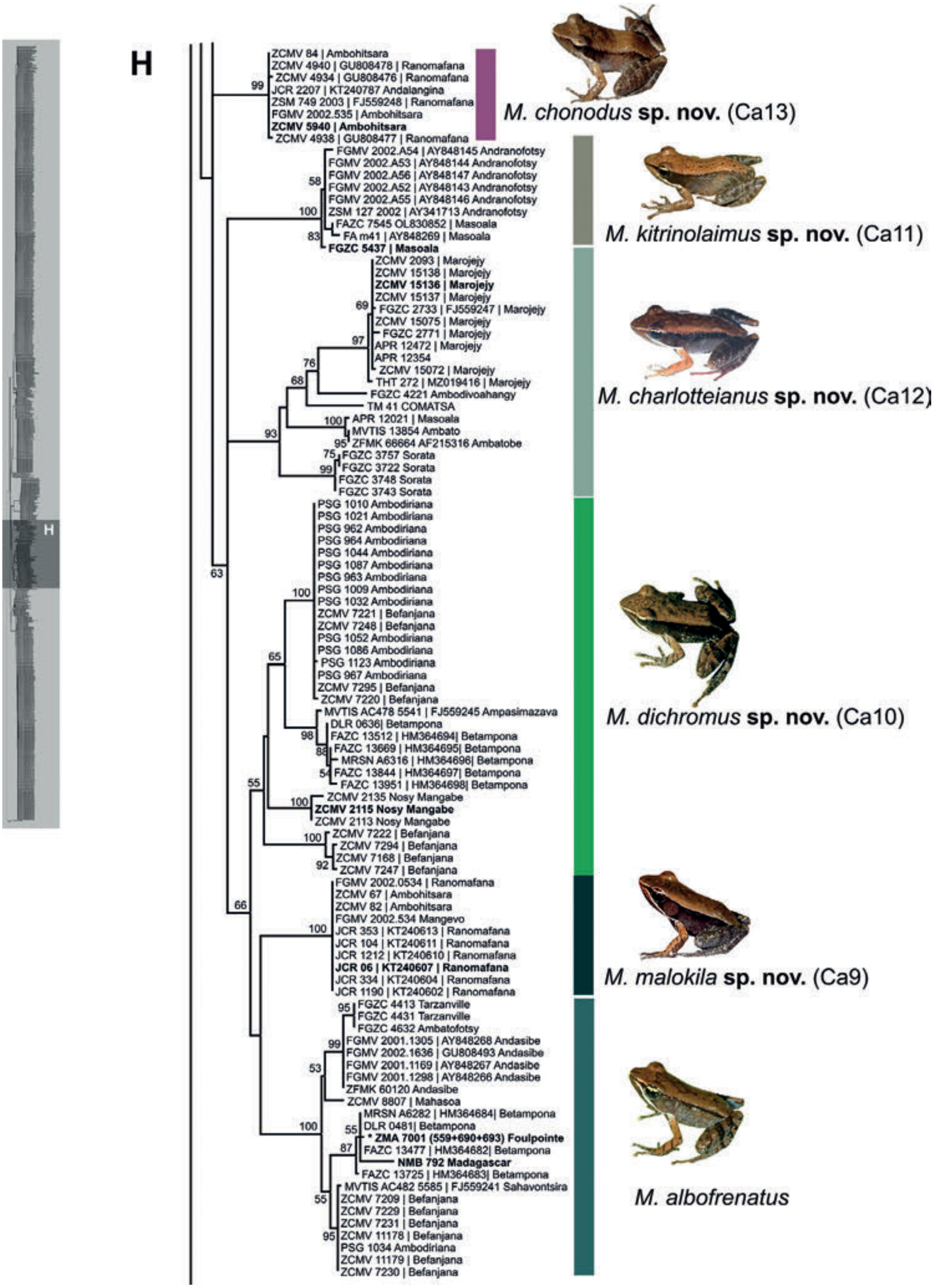
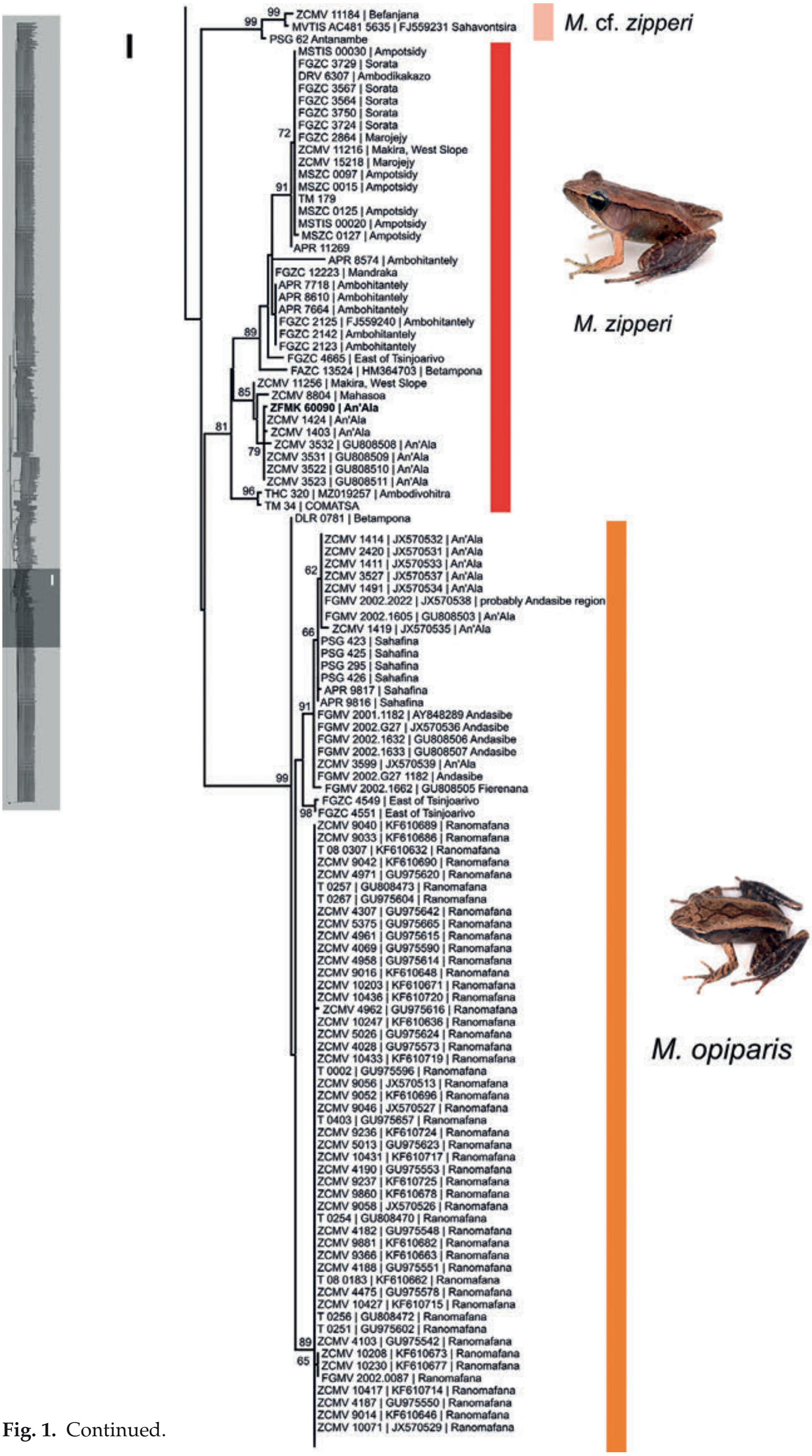


Fig. 1. Continued.

et al. 2013, Ndriantsoa et al. 2017) where these two species were found to be very abundant (Grosjean et al. 2011, Strauß et al. 2013). However, both species were also found at many other sites and therefore can be considered to be both widespread and locally common. In contrast, several other main lineages were represented by only a few sequences from single or few localities. The tree shows high genetic



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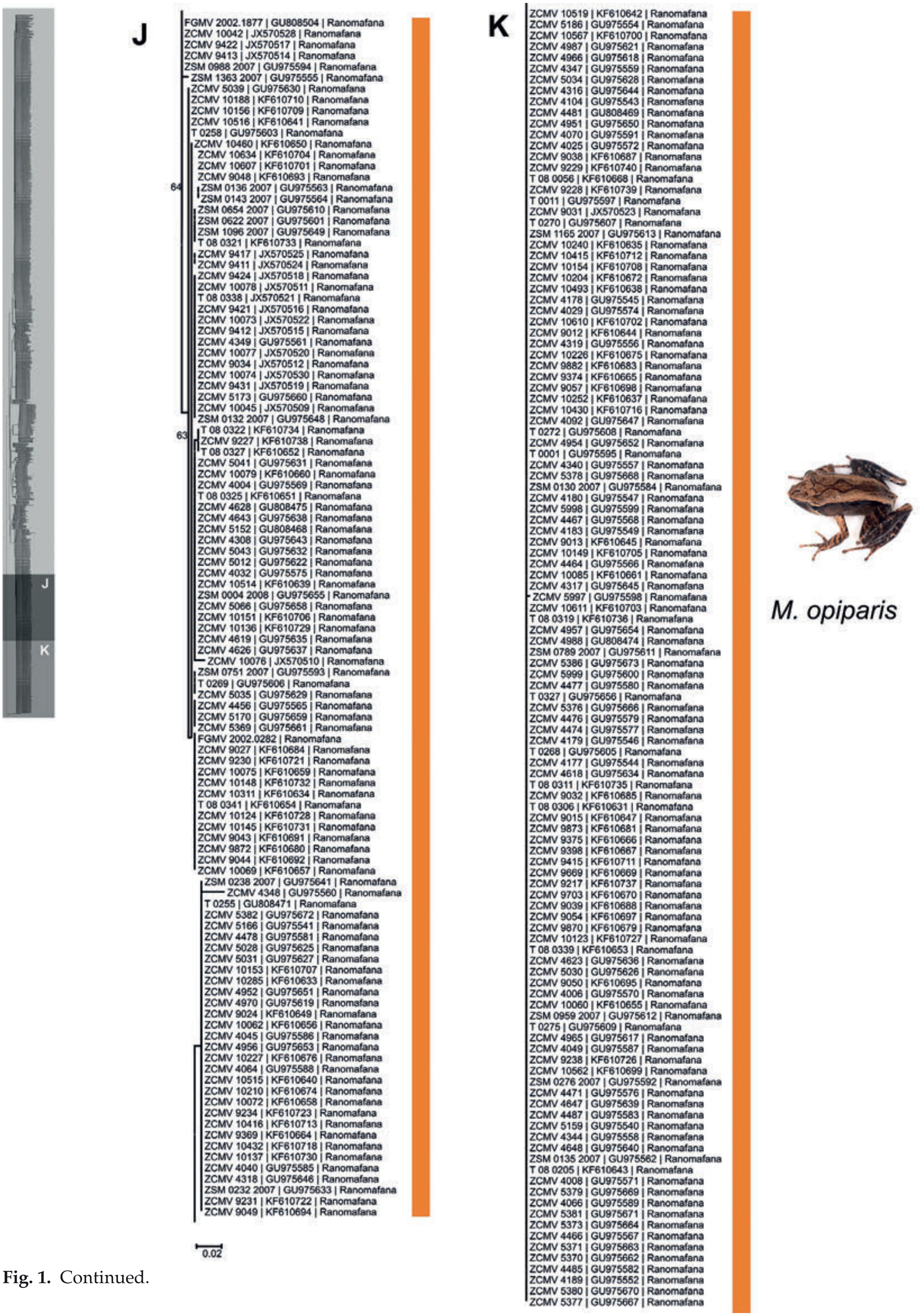


Fig. 1. Continued.

structure, with several deep lineages with strong bootstrap support, of which, however, several were themselves further structured into sublineages of substantial genetic divergence.

The trimmed 16S alignment contained 595 sequences for 476 nucleotides (*Chonomantis*) and its analysis by ASAP confirmed the existence of a striking number of genetically divergent mitochondrial

Table 2. Mean, minimum, and maximum uncorrected pairwise distances calculated from DNA sequences of a fragment of the mitochondrial 16S rRNA gene in species of the subgenus *Chonomantis* in the genus *Mantidactylus*. Values are given as mean, with minimum and maximum in parentheses.

	M. aerumnalis	*M. albofrenatus*	*M. brevipalmatus*	*M. delormei*	*M. melanopleura*	*M. opiparis*	*M. paidroa*	*M. charlotteianus* sp. nov. (Ca12)	*M. ventrilineatus* sp. nov. (Ca1)	*M. kitrinolaimus* sp. nov. (Ca11)	*M. dichromus* sp. nov. (Ca10)	*M. maharira* sp. nov. (Ca4)
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	0.1 (0.0–0.2)											
2	9.7 (9.4–10.7)	1.7 (0.0–3.9)										
3	8.3 (7.9–8.7)	8.7 (8.1–9.5)	0.1 (0.0–0.4)									
4	9.4 (9.0–9.8)	9.5 (8.5–10.3)	2.6 (2.0–3.5)	0.7 (0.0–1.6)								
5	9.8 (8.9–10.5)	9.7 (8.7–11.3)	7.8 (7.4–9.2)	8.2 (7.4–9.6)	0.9 (0.0–5.0)							
6	11.6 (10.9–12.2)	10.9 (10.2–12.0)	8.8 (7.9–9.7)	9.2 (8.1–10.3)	10.0 (7.8–11.1)	0.7 (0.0–3.5)						
7	10.2 (10.0–10.5)	9.4 (8.8–10.1)	6.0 (5.9–6.4)	6.9 (6.4–7.7)	9.5 (8.5–10.7)	8.5 (8.1–9.2)	0.1 (0.0–0.2)					
8	10.7 (9.8–11.4)	9.3 (7.9–10.5)	9.2 (8.8–10.1)	9.2 (8.1–9.9)	10.3 (8.1–11.6)	10.8 (9.8–12.4)	10.0 (9.4–11.0)	4.1 (0.0–7.2)				
9	9.9 (8.9–10.5)	9.7 (9.2–10.9)	10.0 (9.2–10.5)	10.2 (8.8–10.8)	10.7 (9.0–12.0)	11.3 (10.0–12.2)	11.3 (10.5–11.8)	10.8 (9.2–11.6)	0.8 (0.0–2.4)			
10	10.3 (10.1–10.7)	8.2 (7.7–8.8)	9.0 (8.8–9.5)	9.7 (9.0–10.4)	9.7 (8.3–10.3)	9.4 (8.3–10.7)	9.0 (8.8–9.9)	8.6 (7.7–9.5)	9.5 (8.8–10.3)	0.4 (0.0–1.3)		
11	10.1 (9.6–11.1)	6.6 (5.9–8.9)	8.5 (8.1–9.2)	8.9 (7.5–9.9)	9.7 (7.9–11.1)	9.7 (8.5–11.1)	9.0 (8.5–10.1)	8.7 (7.9–9.6)	10.7 (9.6–12.2)	7.0 (6.1–8.1)	2.8 (0.0–6.3)	
12	9.7 (9.6–9.8)	8.9 (8.7–9.2)	5.1 (5.0–5.3)	4.5 (3.9–5.0)	7.9 (7.2–8.5)	9.5 (8.3–10.0)	6.8 (6.8–7.0)	8.8 (7.9–9.6)	9.9 (9.0–10.5)	9.1 (9.0–9.4)	8.0 (7.0–9.2)	0.0 (0.0–0.0)
13	8.8 (8.7–9.0)	9.3 (8.5–9.8)	5.5 (5.5–5.7)	6.0 (5.5–6.5)	7.9 (7.0–8.3)	8.5 (7.6–9.2)	7.3 (7.2–7.5)	8.6 (7.2–9.4)	9.6 (8.7–10.0)	7.6 (7.5–7.9)	7.8 (7.2–8.1)	4.1 (4.1–4.1)
14	11.0 (10.9–11.1)	7.1 (6.8–7.4)	9.7 (9.6–9.9)	9.5 (9.0–9.9)	9.2 (8.7–10.0)	9.9 (9.4–10.5)	9.3 (9.2–9.4)	8.1 (7.7–8.6)	10.9 (10.0–11.4)	7.3 (7.2–7.7)	5.9 (5.5–6.6)	7.7 (7.7–7.7)
15	9.5 (9.4–9.8)	8.9 (8.7–9.4)	8.0 (7.9–8.4)	8.5 (7.9–9.2)	6.7 (6.3–8.3)	8.8 (7.4–9.6)	9.0 (9.0–9.4)	7.9 (7.6–8.3)	8.9 (8.3–9.6)	6.9 (6.8–7.4)	7.7 (6.3–8.5)	7.0 (7.0–7.2)
16	9.6 (9.2–10.0)	8.8 (8.3–9.4)	5.6 (5.1–5.9)	6.8 (6.1–7.5)	7.7 (6.3–8.1)	6.7 (4.8–7.9)	6.2 (5.5–6.8)	8.5 (7.7–9.2)	9.1 (8.3–9.8)	7.6 (6.8–8.3)	7.6 (6.3–8.7)	5.1 (4.6–5.5)
17	9.3 (9.2–9.6)	9.2 (8.5–9.8)	7.9 (7.0–8.6)	8.6 (7.0–9.6)	9.1 (7.2–10.2)	8.5 (6.5–9.8)	8.9 (8.3–9.4)	9.4 (7.4–10.9)	10.7 (10.5–11.1)	8.6 (7.9–9.4)	9.2 (8.1–10.5)	7.8 (7.0–8.3)
18	10.4 (9.2–11.1)	9.5 (8.3–10.5)	7.8 (6.1–8.4)	8.1 (6.3–8.8)	7.5 (5.4–8.3)	8.2 (6.3–9.4)	8.5 (7.7–9.0)	9.0 (7.4–10.5)	9.9 (9.0–10.7)	7.2 (6.6–7.9)	8.6 (7.2–9.6)	6.6 (6.3–7.2)

lineages in *Chonomantis*. The preferred partition with an ASAP score of 1.5 distinguished as many as 24 different species-level subsets (see https://doi.org/10.5281/zenodo.15161297 for full ASAP results). Other partitions ranged over 14–44 subsets. None of these were fully concordant with taxonomic knowledge (Vences & Glaw 2004) as they either split species known to be morphologically and bioacoustically uniform into separate (geographical) subsets, or merged subsets known to be distinct bioacoustically and morphologically, and occurring in syntopy, into the same subsets. We therefore chose a custom partition containing 18 subsets, taking into account the various partitions from ASAP and making sure that (i) lineages occurring in syntopy and with different morphologies and/or advertisement calls were always considered as different subsets, (ii) geographically separated lineages currently considered as different species, even if poorly divergent genetically (e. g., *M. brevipalmatus* and *M. delormei*) were considered as separate subsets (but later submitted to further scrutiny; see below), (iii) other lineages (newly recognized or corresponding to previously defined candidate species: Vieites et al. 2009) were generally considered as distinct subsets if their uncorrected pairwise 16S distance to other subsets was >4 %, and (iv) in three cases, we conservatively merged geographically separate samples diverging >4 % into the same subsets when these were known to be morphologically uniform (in the case of the extremely widespread *M. melanopleura)* or too few morphological or bioacoustic data were available for an integrative assessment. This approach is much more conservative than that used by Carné & Vieites (2024), which is based largely on genetics alone, and therefore proposed to recognize more species-level lineages in this and other Malagasy anuran taxa. The resulting species partition is shown by differently coloured subsets in Fig. 1, and uncorrected pairwise distances between samples of all subsets are summarized in Table 2. MolD found diagnostic nucleotide combinations for each of the 18 species-level lineages (subsets) of our preferred partition (details in dataset https://doi.org/10.5281/zenodo.15161297).

M. sp. Ca5	*M. malokila* sp. nov. (Ca9)	*M. chonodus* sp. nov. (Ca13)	*M. temachikus* sp. nov. (Ca3)	*M.* sp. cf. *zipperi*	*M. zipperi*
13	**14**	**15**	**16**	**17**	**18**
0.0 (0.0–0.0)					
7.7 (7.7–7.7)	0.0 (0.0–0.0)				
5.7 (5.7–5.9)	6.8 (6.8–7.0)	0.1 (0.0–0.2)			
4.9 (4.8–5.0)	8.0 (7.7–8.3)	6.1 (5.7–6.6)	1.1 (0.0–2.2)		
6.6 (5.5–7.2)	10.5 (9.4–11.1)	8.3 (7.4–8.9)	5.7 (4.8–6.6)	1.0 (0.0–2.0)	
5.4 (4.6–6.8)	8.5 (8.1–8.8)	6.9 (6.3–7.6)	5.6 (5.2–6.3)	6.4 (5.2–7.4)	2.1 (0.0–4.6)

The haplotype genealogy of RAG1 sequences of 1291 bp of 30 samples, after phasing, led to a network representation separating all included mitochondrial lineages, without any haplotype sharing among them (Fig. 2). Moreover, the majority of lineages formed distinct phylogroups, i. e., alleles of each lineage clustered together and apart from those of other lineages. In contrast, the genealogy representation of the entire dataset of shorter RAG1 sequences (411 bp; 116 samples; not shown but dataset and network available at https://doi.org/10.5281/zenodo.15161297) was much less structured; although haplotype sharing was observed only in seven out of 116 alleles, the alleles in general did not form lineage-specific phylogroups. Subsets of these shorter RAG1 sequences were analyzed separately for species delimitation in particular species complexes; see below. The genealogies of SACS (47 samples; 686 bp) and KIAA1239 (78 samples; 749 bp) each contained

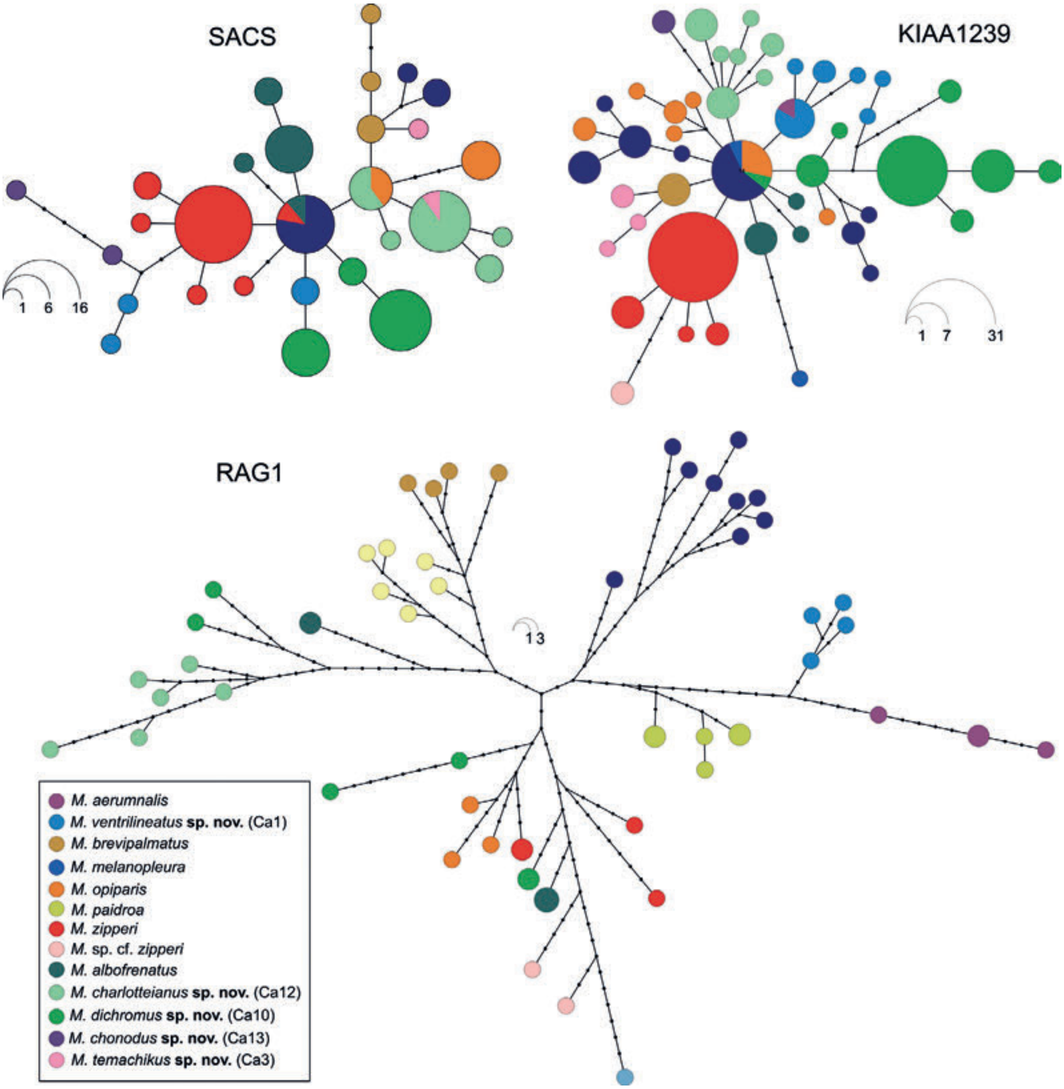


Fig. 2. Haplotype genealogies from sequences of three nuclear-encoded gene fragments from species in the subgenus *Chonomantis*: SACS (686 bp, 47 samples), KIAA1239 (749 bp, 78 samples); RAG1 (1291 bp, 30 samples). No data of these gene fragments were available for *M. delormei*, *M.* sp. Ca5, or the three new species *M. kitrinolaimus* sp. nov., *M. maharira* sp. nov. and *M. malokila* sp. nov. All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

a central allele shared by three and four lineages, respectively, while in general, alleles of the different lineages clustered apart from each other, with limited haplotype sharing, and sometimes forming separate lineage-specific phylogroups. Details will be discussed in the following in the context of particular species delimitation questions.

The ML tree inferred from partitioned analysis of the concatenated sequences of the 12S, 16S and COI mitochondrial gene fragments (Fig. 3) confirmed substantial genetic differentiation (as indicated by long branches) for all species and candidate species of *Chonomantis* included. Phylogenetic relationships were poorly resolved, with most basal nodes receiving bootstrap support < 50 %. Among the well-resolved relationships were the expected sister group relationships of (1) *M. brevipalmatus* and *M. delormei* (bootstrap support BS = 100 %)

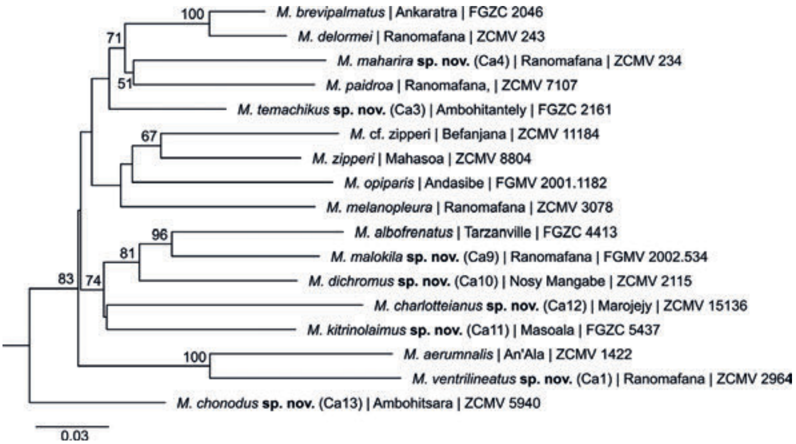


Fig. 3. Maximum Likelihood tree inferred from 2256 bp of concatenated DNA sequences of the mitochondrial genes for 12S rRNA, 16S rRNA, and Cytochrome Oxidase Subunit 1, showing evolutionary relationships of species within the subgenus *Chonomantis*, *Mantidactylus* sp. Ca5 not included. Numbers at nodes are support values in percent from a bootstrap analysis (1000 replicates; not shown if <50 %). *Mantidactylus femoralis* (subgenus *Ochthomantis*) was used as the outgroup (graphically removed to better illustrate branch lengths within the ingroup).

and (2) *M. aerumnalis* and *M.* sp. Ca1 (BSS = 100 %). Furthermore, (3) a clade grouping *M. paidroa* and *M.* sp. Ca4 with *M. brevipalmatus* and *M. delormei* received BS = 71 %, (4) a clade containing *M. zipperi* and a deep genetic lineage from Befanjana received BS = 67 %, (5) a clade containing *M. albofrenatus*, its sister species *M.* sp. Ca9, as well as *M.* sp. Ca10, Ca11 and Ca12 was well supported (BS = 74 %) and also featured strong support for several internal nodes. Finally a clade containing all lineages except for *M.* sp. Ca13 was supported by 83 %; although the rather long branch separating this lineage from the next basalmost node in the subgenus is surprising, no artifactual origin of this placement could be identified examining exploratory single-gene trees, and *M.* sp. Ca13 thus might represent the sister clade to all other *Chonomantis*; it is herein described as new species, *M. chonodus* sp. nov.

Identity of *Mantidactylus albofrenatus* and *M. charlotteae*

Originally described as *Rana albofrenata* Müller, 1892, the definition of *Mantidactylus albofrenatus* has changed over the years (e. g., Guibé 1978, Blommers-Schlösser 1979, Blommers-Schlösser & Blanc 1991). The species is based on the holotype specimen NMBA 792, which by the year 2000 had almost completely faded colour pattern (see redescription of type specimen in Vences & Glaw 2004). The species has no precise information on collector or collecting locality, besides the general provenance “Madagascar”. Based on colour pattern in the original description (Müller 1892), i. e., in particular a white stripe that began at the forelimb insertion, passed underneath the eye, and extended to the nostril, and the small size of the (female) holotype (SVL 27.1 mm), Vences & Glaw (2004) considered the *albofrenatus* type as conspecific with a lineage of small *Chonomantis* collected near Andasibe in the northern Central East of Madagascar.

Based especially on a very distinct advertisement call recorded by Blommers-Schlösser (1979), specimens of *Chonomantis* from the east coast locality Foulpointe were described by Vences & Glaw (2004) as a distinct species, *M. charlotteae.* The collection of R. Blommers-Schlösser from Foulpointe consists of two series of specimens: ZMA 7000 (one male and one female, field numbers 559–560, collected on 12 February 1972) and ZMA 7001 (field numbers 337, 688-691-694, six males and two females, collected on 13 October 1971). The call published by Blommers-Schlösser (1979) and re-analyzed by Vences & Glaw (2004) was recorded from an unspecified male of series ZMA 7001 in a terrarium. The specimen with field number 692 from the series ZMA 7001 was chosen as holotype of *M. charlotteae* by Vences & Glaw (2004). *Mantidactylus charlotteae* was considered to be widespread along mainly low-elevation sites in the northern Central East and North East of Madagascar (Glaw & Vences 2007). In comparison to the lineage from Andasibe (also occurring at other sites such as Anosibe An’Ala; see Fig. 4) considered as *M. albofrenatus*, the type specimens of *M. charlotteae* differed mainly by a larger body size (SVL 22.7–

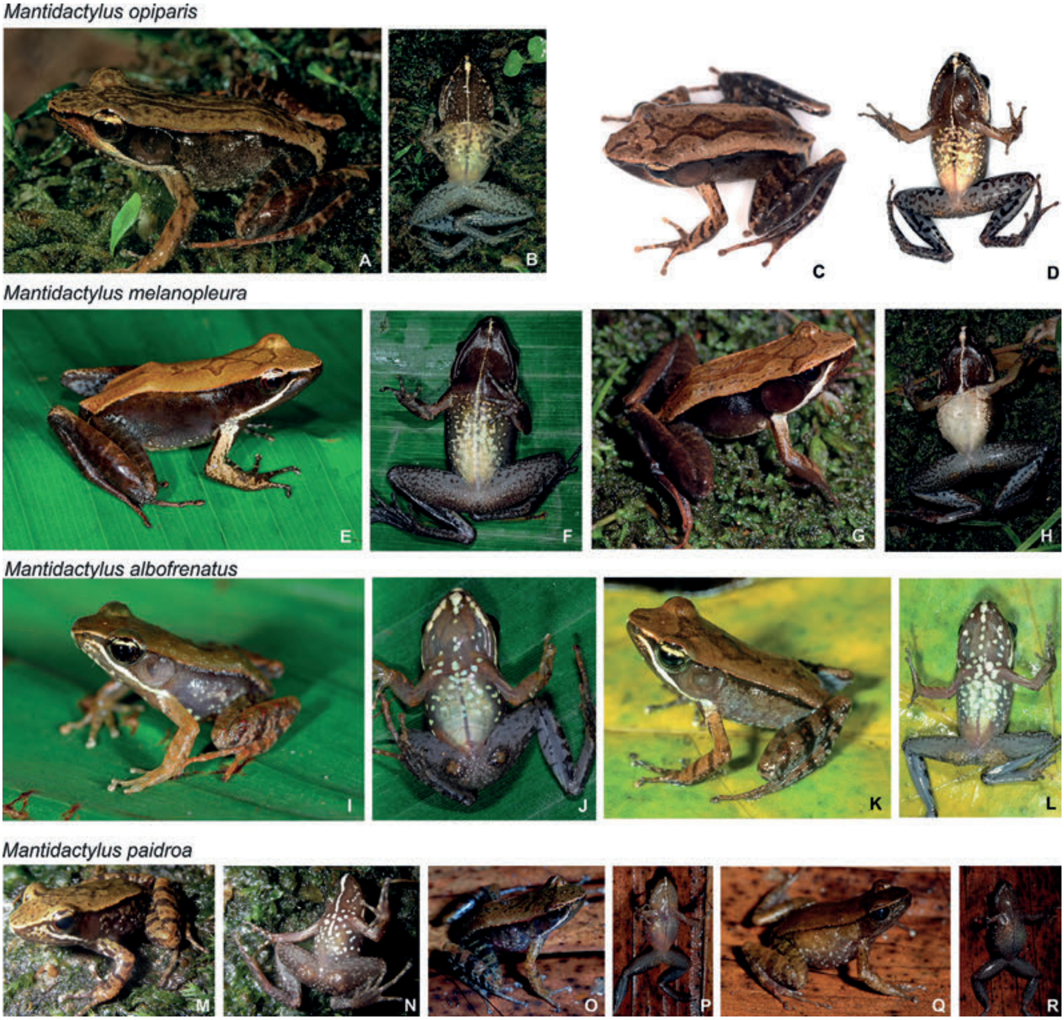


Fig. 4. Photos of representative individuals of four species of *Mantidactylus* (subgenus *Chonomantis*) in life, in dorsolateral and ventral views. All photos except those of *M. opiparis* and *M. albofrenatus* K-L show specimens identified by mitochondrial DNA sequences. **A–B.** Male of *M. opiparis* from An'Ala (not assignable to a voucher specimen), **C–D.** Male of *M. opiparis* from Andasibe, specimen photographed in 2022 (not collected). **E–F.** *M. melanopleura* from Anosibe An'Ala, specimen ZSM 378/2010 (FGZC 4450). **G–H.** *M. melanopleura*, specimen from Ranomafana (JCR 112). **I–J.** *M. albofrenatus* from Anosibe An'Ala, specimen ZSM 357/2010 (FGZC 4431). **K–L.** *M. albofrenatus* from Andasibe (not assignable to a voucher specimen). **M–N.** *M. paidroa* from Ranomafana, holotype ZSM 1777/2008 (from Bora et al. 2011). **O–P.** *M. paidroa*, male from Ranomafana (JCR 128). **Q–R.** *M. paidroa*, female from Ranomafana (JCR 122).

24.8 mm in males, females from the type locality Foulpointe unknown, vs. 19.3–23.0 mm in males, 25.3 in one female), by a smaller relative tympanum size in males (TD/ED 0.77–0.91 vs. 1.10–1.38) and especially, by a different advertisement call (note duration 91–304 ms vs. 56–80 ms). A specimen from Betampona genetically agreeing with the Foulpointe specimens is shown by Rosa et al. (2012) on their fig. 5q; it has a frenal stripe becoming somewhat faded towards the nostril, a reddish colour on the dorsolateral fold, and rather dark flanks.

Archival DNA sequencing from three paratopotypes of *M. charlotteae*, ZMA 7000[559], ZMA 7001[690], and ZMA 7001[693] (accession numbers PZ059868–PZ059871), yielded congruent 16S sequences of all three samples; in the phylogenetic tree (Fig. 1), these were placed in the same cluster as sequences from Betampona, and indeed were fully identical to three of these (accession numbers HM364682 and HM364684, and the new sequence DLR 481) in the entire 16S stretch covered. This is phylogeographically plausible because Betampona is close to the type locality Foulpointe. Although we did not obtain sequences from the *M. charlotteae* holotype, it is extremely unlikely that this specimen is not conspecific with the three paratypes, given the great morphological uniformity of the entire series, including variables such as body size, relative tympanum size, relative toe length or relative hindlimb length (see measurements in Vences & Glaw 2004 and in dataset https://doi.org/10.5281/zenodo.15161297). Surprisingly, the archival DNA sequence assembled from the holotype of *M. albofrenatus* showed basically no difference to the *M. charlotteae* types (0.6 % sequence divergence, caused by seven mutations at positions directly adjacent to missing data which very likely represent sequence errors). Although we initially suspected a contamination, we now think that this genetic placement of the *M. albofrenatus* is likely correct because (i) the sequence consists of numerous contiguous reads, making up altogether 493 bp after exclusion of only short stretches of missing data, which is untypical for sample contamination which usually yields only a few target reads, and (ii) the provenance of the *M. albofrenatus* type is also plausible based on associated collections as discussed in the following. In the original description of *M. albofrenatus*, Müller (1892) among other species also reported specimens of *Aglyptodactylus madagascariensis*, *Heterixalus madagascariensis*, and *Plethodontohyla notosticta* which all occur in Betampona (Rosa et al. 2012), and described *Anodonthyla boulengerii* which, according to our own yet-unpublished archival DNA sequences of the holotype, also corresponds to the *Anodonthyla* lineage from Betampona (M. D. Scherz, A. Petzold, study in progress). It therefore is likely that the holotype of *M. albofrenatus* was collected in the same geographical area.

To complicate the issue further, the lineage from Andasibe previously considered as *M. albofrenatus* forms a clade with the Foulpointe/Betampona lineage (thus, with the true *M. albofrenatus*) and differs by only up to 3.1 % uncorrected pairwise distance in 16S (Table 2), despite the purportedly highly distinct advertisement calls of these populations and the morphological differences e. g. in SVL and relative tympanum size (Vences & Glaw 2004). To verify this finding, we used archival DNA analysis to sequence the call voucher from Andasibe on which the results of Vences & Glaw (2004) were based (ZFMK 60120), and found it to conform genetically to other specimens assigned to *M. albofrenatus* from Andasibe (Fig. 1). Blommers-Schlösser (1979) stated that “sometimes the call starts with a few very short notes (0.02–0.07 sec.)”, which could perhaps partly explain the differences between the call data, although the available data remain mysterious and difficult to interpret. For the time being, we thus suggest to consider *M. charlotteae* Vences & Glaw, 2004 as a junior synonym of *M. albofrenatus* (Müller, 1892). We stress the need to obtain and analyze advertisement calls of additional genotyped specimens from Betampona/Foulpointe and Andasibe to understand the taxonomy of these *Chonomantis* populations. This revised definition also subsumes *M.* sp. Ca2 from Sahavontsira as identified by Vieites et al. (2009) and expanded to include specimens from Betampona by Carné & Vieites (2024).

New species in the *Mantidactylus albofrenatus* complex

After redefining *M. albofrenatus* and synonymizing *M. charlotteae*, several deep mitochondrial lineages of *Chonomantis*, most of them previously defined as candidate species (Vieites et al. 2009, Carné & Vieites 2024), require taxonomic revision. Four of these are mainly distributed in lowland localities and not found at >1000 m a. s. l., appear to be morphologically similar and perhaps phylogenetically related to *M. albofrenatus* (according to the multigene tree: Fig. 3) and are therefore together with that species here considered as the *M. albofrenatus* complex:

(i) The candidate species *M.* sp. Ca10 occurs in several east coast localities (Ampasimazava, Ambodiriana, Befanjana, Nosy Mangabe) as well as in Betampona where it is sympatric with *M. albofrenatus*. A specimen of this lineage was used as the genetic voucher representing *M. charlotteae* by Vieites et al. (2009) and Carné & Vieites (2024), which we have shown here is incorrect. It does not share alleles with *M. albofrenatus* in the long RAG1 fragment, KIAA1239 nor SACS, has only limited haplotype sharing in the short RAG1 fragment, and differs from that species by a remarkably high uncorrected pairwise distance in 16S (5.9–8.9 %). We therefore consider it as a distinct species, *M. dichromus* sp. nov., described below;

(ii) The candidate species *M.* sp. Ca11 occurs in Andranofotsy and Masoala in the North East. Its distribution abuts that of *M.* sp. Ca10 which is present on Nosy Mangabe, an offshore islet very close to Andranofotsy, and it does not share RAG1 alleles with *M.* sp. Ca10 or *M. albofrenatus* (Fig. 5; but only one sample was sequenced), and differs from these species by a 16S distance of 6.1–8.8 %, and a unique

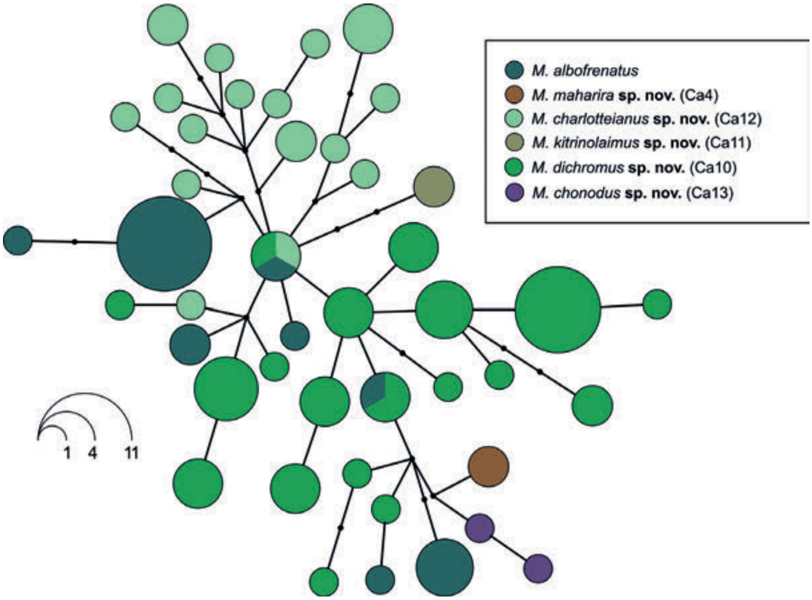


Fig. 5. Haplotype genealogies from sequences of a short fragment of the nuclear-encoded RAG1 gene (410 bp, 47 samples) in species in the subgenus *Chonomantis* related to *M. albofrenatus,* plus *M. chonodus* sp. nov. and *M. maharira* sp. nov. All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

ventral colour pattern. We therefore also consider this lineage as a distinct species, *M. kitrinolaimus* sp. nov., described below;

(iii) The candidate species *M.* sp. Ca12 is found in Ambatobe, Masoala, Marojejy and Sorata. At Masoala, it occurs in sympatry with *M.* sp. Ca11, but does not share alleles in KIAA1239, SACS or the long RAG1 fragment with *M. albofrenatus, M.* sp. Ca10, *M.* sp. Ca11 or *M.* sp. Ca12; in the short RAG1 fragment, only the central allele is shared with *M. albofrenatus* and *M.* sp. Ca10. There is little doubt that this lineage represents a distinct species, *M. charlotteianus* sp. nov., described below;

Finally, (iv) the candidate species *M.* sp. Ca9, known from Ranomafana, Ambolo and Ambohitsara in the southern Central East, is the sister species of *M. albofrenatus*. It differs from its sister species by 6.8–7.4 %, and from all other lineages by >5 % uncorrected pairwise distance. This lineage also differs bioacoustically: Advertisement calls of *M.* sp. Ca9 differ from those of *M. albofrenatus* recorded at An'Ala in 1995 (Vences et al. 2006, CD2, track 79) by slightly shorter call duration (45–55 vs. 54–73 ms), lower number of pulses per call (7–8 versus 10–16), distinctly lower pulse repetition rate (142–167 vs. 214–250 pulses/s), and distinctly lower dominant

Table 3. Comparison of call parameters of one male of *Mantidactylus malokila* sp. nov. and one male of its sister species *M. albofrenatus*. Call repetition rate is calculated within regular call series; pulse repetition rate is calculated within calls.

	M. malokila sp. nov. Ambolo	*M. albofrenatus* An'Ala
recorded by	J. C. Riemann	F. Glaw
recording date	09.03.2010	12.02.1995
temperature [°C]	not available	not available
call duration (= note duration) [ms]	45–55 (51.6 ± 3.0)	54–73 (64.7 ± 5.0)
pulses/call	7–8 (7.3 ± 0.5)	10–16 (13.5 ± 1.5)
pulses/second	142–167 (155.4 ± 9.9)	214–250 (232.4 ± 12.0)
calls/minute	ca. 580	ca. 500
dominant frequency [Hz]	1614–2201 (1813 ± 224)	3970–4254 (4145 ± 97)

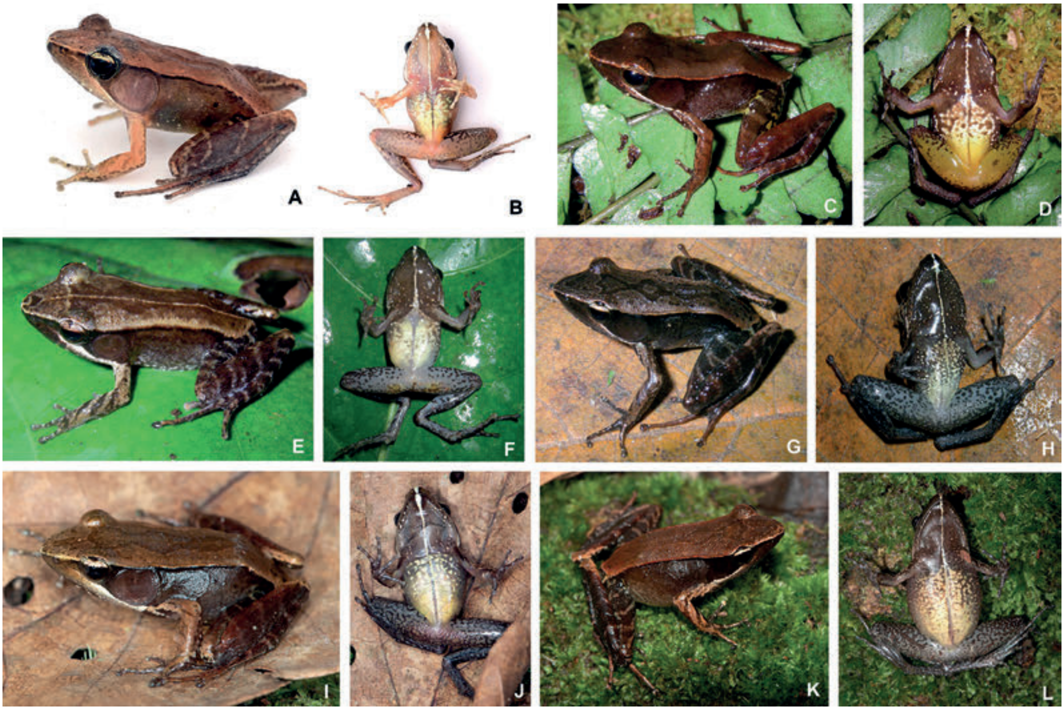


Fig. 6. Photos of representative individuals of *Mantidactylus* (*Chonomantis*) *zipperi* in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences, and include mitochondrial clades previously assigned to the candidate species *M.* sp. Ca3 (e.g., Vieites et al. 2009, Carné & Vieites 2024) but here subsumed within *M. zipperi* in a preliminary way. **A–B.** Male (FGZC 12223) from Mandraka (Vallombre Natiora), photographed 2024. **C–D.** Male from Mahasoa forest, specimen ZSM 1795/2008 (ZCMV 8804), photographed 2008. **E–F.** Specimen from the western slope of the Makira Reserve, ZSM 554/2009 (ZCMV 11256), photographed 2009. **G–H.** Specimen from the western slope of the Makira Reserve, ZSM 561/2009 (ZCMV 11216), photographed 2009. **I–J.** Specimen ZSM 99/2016 (MSZC 127) from Ampotsidy. **K–L.** Specimen UADBA-A 62295 (MSZC 125) from Ampotsidy.

frequency (1614–2201 vs. 3970–4254 Hz) (Table 3). Although nuclear gene data are missing for this taxon, we here also consider it as a separate species, *M. malokila* sp. nov., described below, based on its strong mitochondrial divergence, distinct bioacoustic differentiation, as well as faint but consistent morphological differences described in its diagnosis below.

In addition, two further deep mitochondrial lineages known only from highland localities may bear some similarity to *M. albofrenatus* based on superficial morphological similarity but are phylogenetically distant: *M.* sp. Ca4 from Ranomafana and probably *M.* sp. Ca5 from Antoetra in the southern Central East. These two candidate species are highly divergent, with 16S distances between 4.8–10.5 % to other *Chonomantis*, and differ from each other by 4.1 %. No material was available to us for *M.* sp. Ca5 which remains known from only one 16S sequence, and the status of this candidate species thus remains pending further study. For *M.* sp. Ca4 more data could be gathered herein, and in the multigene phylogeny this lineage turned out to be related to the sympatric *M. paidroa* and the *M. brevipalmatus*/*M. delormei* clade. We therefore consider *M.* sp. Ca4 as a distinct species, *M. maharira* sp. nov., based on a lack of allele sharing in RAG1 from all other *Chonomantis* studied, including *M. paidroa*, and its otherwise isolated phylogenetic position in the multigene tree. For more details and images of these new species, see species accounts below.

Molecular variation and new species in *Mantidactylus zipperi* and two unnamed lineages

Mantidactylus zipperi was described by Vences & Glaw (2004) based on holotype ZFMK 60090 from An'Ala, and these authors also included voucher specimens from Ambohitantely, Ranomafana and

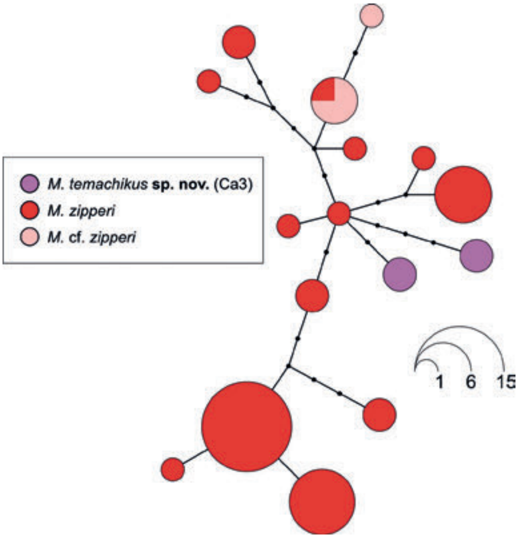


Fig. 7. Haplotype genealogies from sequences of a short fragment of the nuclear-encoded RAG1 gene (410 bp, 25 samples) in *Mantidactylus* (*Chonomantis*) *zipperi*, a deep mitochondrial lineage here considered as *M.* cf. *zipperi*, and the new species *M. temachikus* sp. nov. All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

other localities as paratypes. This *Chonomantis* species is characterized by a very large tympanum in males and an indistinct frenal stripe fading anterior to the eye. In this character it is reminiscent of *M. opiparis* but differs from that species by relative toe length with the third toe being slightly longer than fifth (vs. fifth longer than third), and by an advertisement call with notes of very short duration (21–31 ms vs. 69–126 ms). The multigene tree suggests that *M. zipperi* may indeed be related to *M. melanopleura* and *M. opiparis*, but the respective clade received no bootstrap support. In the following we discuss the relationships of *M. zipperi* with two other unnamed mitochondrial lineages, one of which, however, is probably not closely related to it.

The 16S phylogeny includes samples here assigned to *M. zipperi* from a large number of sites, ranging from Sorata in the North East to Tsinjoarivo in the northern Central East. We also obtained DNA sequences of the *M. zipperi* holotype from An'Ala (ZFMK 60090) which confirmed the assignment of the nomen to this genetic lineage (Fig. 1). The lineage, however, is highly phylogeographically structured, with mitochondrial subclades from numerous localities having distances of up to 4.6 % to each other. Some of the photographed and genotyped specimens of *M. zipperi* have yellowish colour on the ventral side as described for the type series (Vences & Glaw 2004) while others do not (Fig. 6). Advertisement calls from Ampotsidy in northern Madagascar were rather similar to those from the type locality An'Ala, thus not immediately hinting at species-level divergence within the genetically diverse lineage (Appendix 1).

The SACS and KIAA1239 haplotype networks show most samples of the complex clustering closely together (and most having the same haplotype), but in these datasets, the lineage containing *M. zipperi* from the type locality is underrepresented (only one sample from Tsinjoarivo in the SACS network). We consider all these samples as belonging to *M. zipperi* for the time being but stress that further effort is needed to gather morphological, bioacoustic and genomic data of the different populations, and possibly subdivide *M. zipperi* into different subspecies or species.

Vieites et al. (2009) and Perl et al. (2014) defined an unconfirmed candidate species *M.* sp. Ca3, based on a specimen (FGZC 2161) from Ambohitantely, purportedly sister to *M. zipperi* in the 16S phylogeny (but not in the COI phylogeny; Perl et al. 2014) and differing by a 16S distance of 2.8 %. We here resequenced the same sample (FGZC 2161) and found the sequence in GenBank (also used by Vieites et al. 2009) was confused with that from another specimen from the same locality (FGZC 2125). Based on the corrected sequences, FGZC 2161 in our tree is placed in a separate lineage corresponding to the true *M.* sp. Ca3 that includes five samples from Ambohitantely, Anjozorobe, Ankazomivady and Marolambo, has an isolated position in the multigene tree (Fig. 3), and differs from *M. zipperi* by 5.2–6.3 % uncorrected pairwise distance. This suggests that the definition of *M.* sp. Ca3 as candidate species (Vieites et al. 2009) was correctly based on FGZC 2161 from Ambohitantely, but the phylogenetic tree, associated genetic distance calculation of these authors was erroneously based on a *M. zipperi* sequence from the same locality (FGZC 2125). In the framework of this study, we have requested the correction of the two sequences in GenBank to avoid future confusion.

In the nuclear gene networks, the alleles of *M.* sp. Ca3 are placed apart from those of *M. zipperi* in SACS, KIAA1239, and RAG1 (Fig. 2; but not with the short RAG1 fragment: Fig. 7). Because *M.* sp. Ca3 and *M. zipperi* occur in syntopy in Ambohitantely, we consider *M.* sp. Ca3 as distinct species *M. temachikus* sp. nov., based on high mitochondrial sequence divergence, lack of haplotype sharing in nuclear DNA, and differences in morphology as detailed in the diagnosis below. For more details on, and images of, the new species, see the species account below.

Three samples from three rather low-elevation localities in the northern Central East (Sahavontsira, Befanjana and Antanambe) which previously (Vieites et al. 2009) had been included as deep conspecific lineage in *M. albofrenatus* based on a sample labeled MVTIS-AC481/FAZC 5635 from Sahavontsira (accession number FJ559231; given candidate number *M.* sp. Ca70 by Carné & Vieites 2024), clustered close to *M. zipperi* in our 16S tree, albeit without bootstrap support. The multigene tree (Fig. 3) confirms that this lineage is indeed the sister to *M. zipperi.* Its 16S uncorrected pairwise distance is 5.2–7.4 % to *M. zipperi* and 8.5–9.8 % to *M. albofrenatus*. Nuclear genetic data are available only for KIAA1239 and RAG1. In the KIAA1239 network, the allele of the Antanambe sample differed by four mutations from the most common *M. zipperi* haplotype, whereas in the (long) RAG1 fragment, the Befanjana sample clustered closer to *M. albofrenatus* but with several mutational differences. Due to the high mitochondrial divergence to other *Chonomantis*, and concordant differentiation in mitochondrial and nuclear genes, it is likely that this lineage is distinct from its sister lineage, *M. zipperi*, at the species level. However, due to the extreme scarcity of available material and the phylogenetic position sister to *M. zipperi* in the multigene tree, we here refrain from formally naming this new species and postpone taxonomic decisions to a future revision that should comprehensively assess the status of this lineage along with the various deep mitochondrial lineages that we identified within *M. zipperi.*

Differentiation in the *Mantidactylus aerumnalis* complex

The species *M. aerumnalis* was originally described as *Rana aerumnalis* by Peracca (1893) from "Andrangoloka e dalla vicina valle dell'Umbi" (p. 1). Because the holotype was not found in the collection of the Turin museum (see also Gavetti & Andreone 1993), the identity of this species was discussed by Andreone & Gavetti (1994) based on the original description, and a neotype designated from a population of *Chonomantis* from An'Ala, distinguished by a characteristically uniform dark brown colour on the side of the head and tympanic region, without frenal stripe. Despite some doubts that this population really is conspecific with the lost holotype of *M. aerumnalis*, the neotype designation has been accepted (Vences & Glaw 2004) and this definition of *M. aerumnalis* been followed ever since.

Vieites et al. (2009) and Perl et al. (2014) reported a confirmed candidate species *M.* sp. Ca1 from Ranomafana, sister to *M. aerumnalis* but differing by "constant colour differences" (Vieites et al. 2009). *M.* sp. Ca1 (from Antoetra, Befotaka-Midongy, and Ranomafana), differs from *M. aerumnalis* (from An'Ala, Betampona, and Sahafina) by a high 16S divergence of 8.9–10 % uncorrected pairwise distance. Furthermore, we here confirm the existence of differences in coloration, and probable differences in body size between the specimens from An'Ala (provenance of the neotype) and Ranomafana. Alleles of the two lineages are quite distant from each other in the SACS network, while they do cluster in one phylogroup in the network of the full RAG1 sequences, but without haplotype sharing. In the KIAA1239 network one allele of one specimen of *M. aerumnalis* (APR 9861 from Sahafina) is shared with *M.* sp. Ca1, and in the network of the short RAG1 sequences, (Fig. 8), one allele of one specimen of *M.* sp. Ca1 (ZCMV 3079 from Ranomafana) is shared with *M. aerumnalis* (but this same individual does not share alleles with *M. aerumnalis* in the longer RAG1 dataset). Given the exceedingly high mitochondrial divergence and very limited nuclear haplotype sharing, we consider the southern populations (candidate species *M.* sp. Ca1) as a separate species which is formally described below (see diagnosis for more details on morphological differentiation). For images of *M. aerumnalis* and the new species (described herein as *M. ventrilineatus* sp. nov.), see the respective species accounts below.

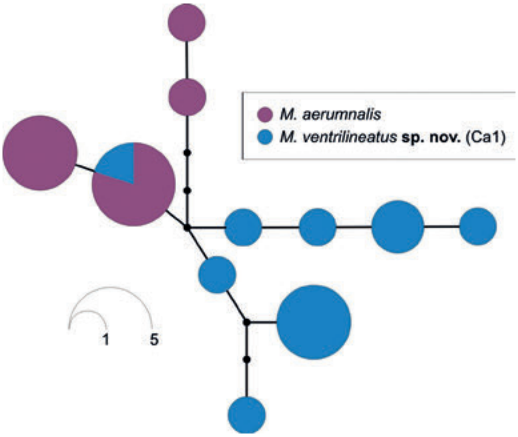


Fig. 8. Haplotype genealogies from sequences of a short fragment of the nuclear-encoded RAG1 gene (410 bp, 11 samples) in *Mantidactylus* (*Chonomantis*) *aerumnalis* and its sister species, *M. ventrilineatus* sp. nov. All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

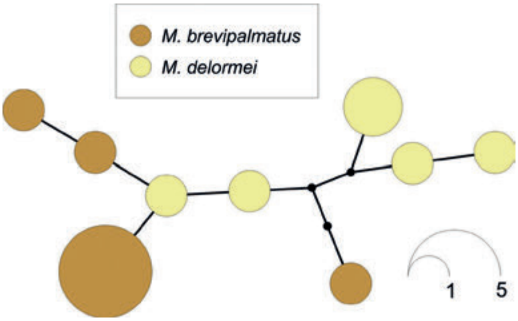


Fig. 9. Haplotype genealogies from sequences of a short fragment of the nuclear-encoded RAG1 gene (410 bp, 7 samples) in *Mantidactylus* (*Chonomantis*) *brevipalmatus* and its sister taxon, *M.* (*C.*) *delormei.* All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

Differentiation in the *Mantidactylus brevipalmatus*/*M. delormei* complex

Mantidactylus brevipalmatus Ahl, 1929 and *M. delormei* Angel, 1938 are closely related lineages of *Chonomantis* that in the past have been considered to be synonyms (Vences & Glaw 2004). According to Ahl (1929), the holotype of *M. brevipalmatus* (ZMB 30530) originates from "Nord-West Madagascar", but this is probably in error, as morphologically, the holotype agrees well with long-legged *Chonomantis* specimens from Madagascar's highlands, e.g., the Ankaratra Massif (Vences & Glaw 2004).

Mantidactylus delormei was described based on the holotype MNHN 1938.240 from "Andringitra: Antaranomby (Etang de Boeufs)" (Angel 1938). Glaw & Vences (2006) resurrected *M. delormei* as distinct species based on some colour differences (a more distinct dorsolateral colour border, a dark median area on the dorsum, and a more yellowish venter), genetic differences in the 16S gene, and a possible ecological separation, not occurring in montane habitats in open area outside of forest as is typical for *M. brevipalmatus.* Our extended genetic dataset includes samples of *M. brevipalmatus* from Ambohitantely, Ankaratra, Antoetra, and Itremo, and samples of *M. delormei* from the type locality Andringitra, as well as Ranomafana and Ivohiboro. The genetic divergence between these two taxa is quite low (uncorrected pairwise 16S divergence of 2.0–3.5 %) while the populations assigned to *M. delormei* differ by up to 1.6 % from each other. The two species were not identified as separate species-level subsets in the ASAP analysis, but on the other hand, we did not observe haplotype sharing in RAG1 (Fig. 9) and the two taxa apparently show consistent differences in coloration (Fig. 10).

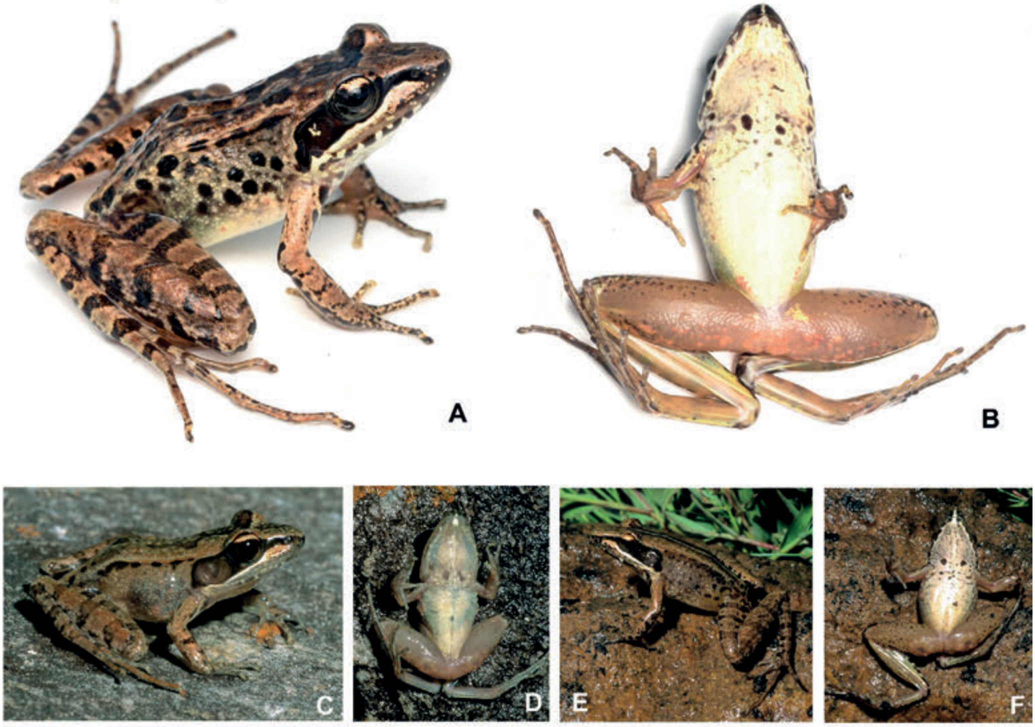
The advertisement call of *M. brevipalmatus* has been described by Blommers-Schlösser (1979) and Vences & Glaw (2004), and calls of *M. brevipalmatus*

Fig. 10. Photos of representative individuals of *Mantidactylus* (*Chonomantis*) *brevipalmatus* and *M.* (*C.*) *delormei* in life, in dorsolateral and ventral views. **A–B.** Female of *M. brevipalmatus* from Ankaratra, photographed 2023 (not collected). **C–D.** Male specimen ZSM 752/2001 (FGMV 2001.487) of *M. brevipalmatus* from Itremo, photographed 2001. **E–F.** Male specimen of *M. brevipalmatus* from Antoetra (photos not reliably assignable to a voucher specimen). **G–H.** Female specimen ZSM 751/2001 (FGMV 2001.576) of *M. delormei* from Imaitso forest, Andringitra, photographed 2002. **I–J.** Male specimen of *M. delormei* from Imaitso forest, Andringitra, photographed 2023 (not collected). **K.** Male specimen ZSM 387/2004 (ZCMV 262) of *M. delormei* from Maharira, Ranomafana, photographed 2004. ▶

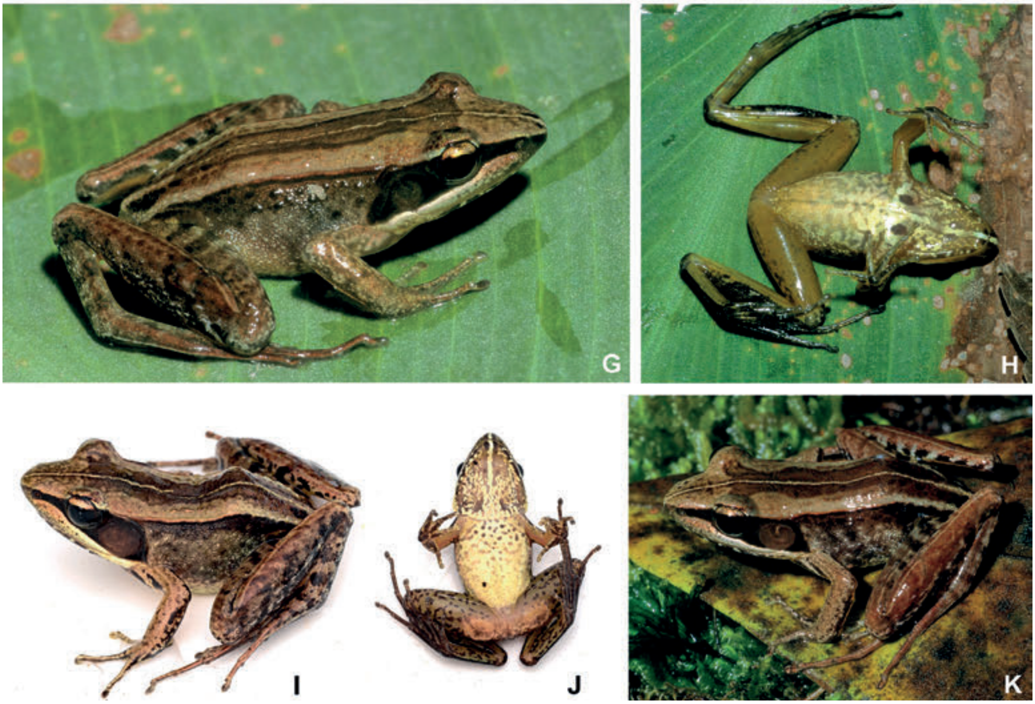
Table 4. Comparison of call parameters of two males of *Mantidactylus delormei* and two males of *M. brevipalmatus*. Duration of calls and of inter-call intervals is given as range, with mean ± standard deviation in parentheses; call duration = note duration.

	M. delormei Maharira	*M. delormei* Andringitra	*M. brevipalmatus* Antoetra	*M. brevipalmatus* Manjakatompo
recorded by	M. Vences	F. Glaw & M. Vences	M. Vences	R. Blommers-Schlösser
recording date	24.01.2004	16.01.1994	21.01.2003	October 1971
temperature [°C]	18.4	ca. 19.0	18.9	not available
call duration [ms]	25–34 (30.1 ± 2.4)	26–40 (33.0 ± 5.4)	32–40 (35.1 ± 3.2)	32–45 (37.6 ± 3.4)
inter-call interval [ms]	118–166 (131.4 ± 14.7)	127–164 (140.5 ± 13.5)	152–294 (203.5 ± 53.2)	168–185 (175.6 ± 4.9)
calls/minute	ca. 400	ca. 350	ca. 230–290	ca. 280
dominant freq. [Hz]	1304–1431 (1388 ± 42)	1340–1431 (1367 ± 40)	1436–1497 (1455 ± 20)	1329–1452 (1375 ± 37)
character	tonal	tonal	pulsatile	pulsatile
freq. modulation	downward sweep	downward sweep	no	no

Mantidactylus brevipalmatus



Mantidactylus delormei



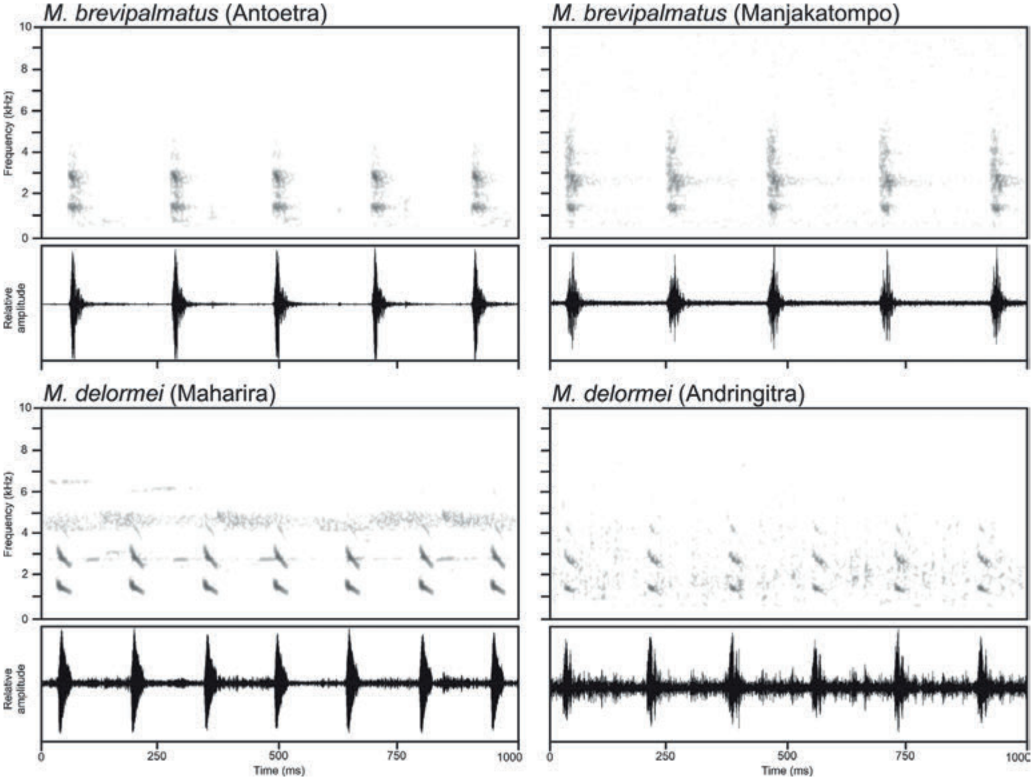


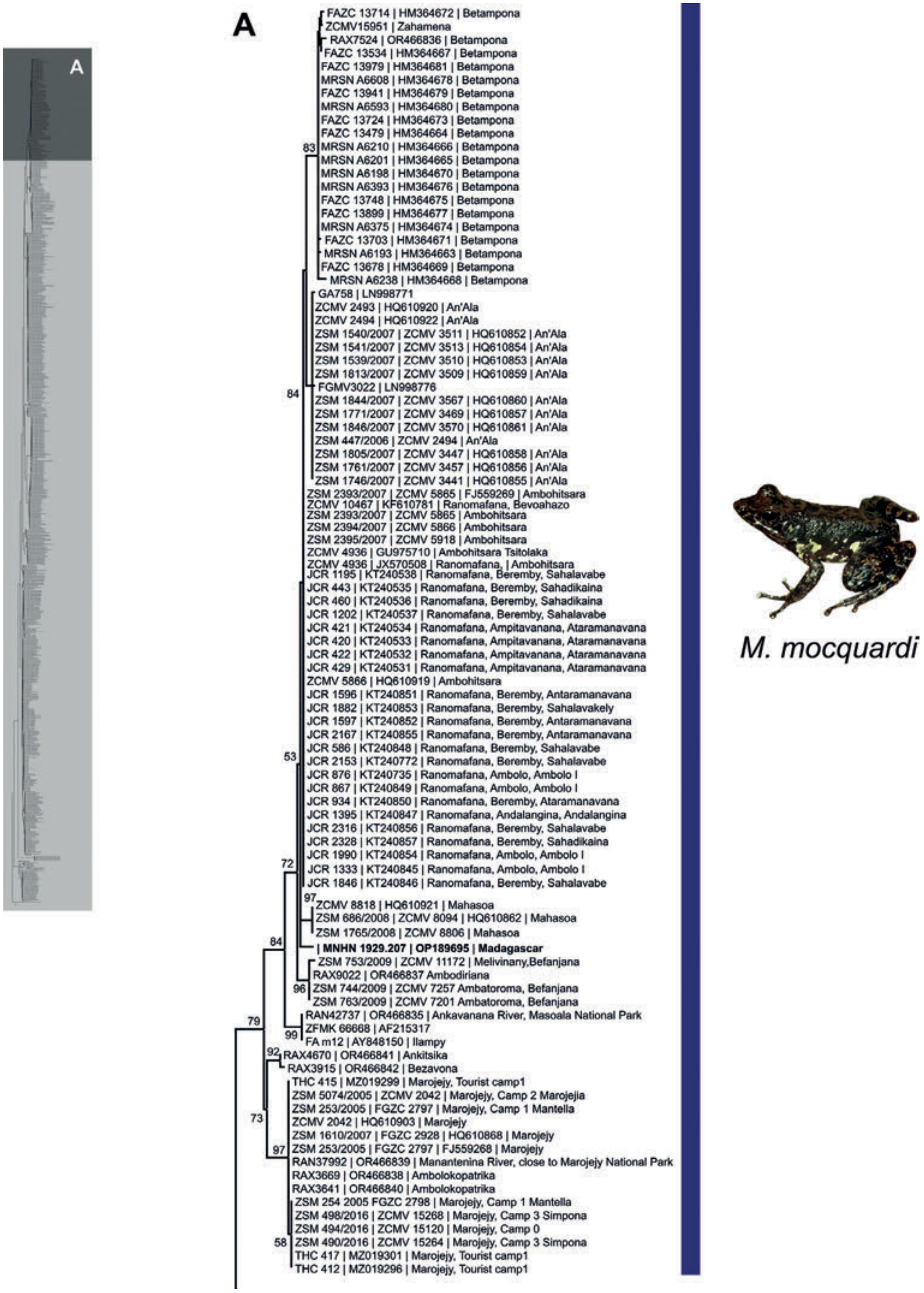
Fig. 11. Audiospectrograms and corresponding oscillograms of the advertisement calls of *Mantidactylus* (*Chonomantis*) *brevipalmatus* and *M.* (*C.*) *delormei* from two localities each, displayed at the same time scale (1000 ms).

and *M. delormei* were included in the audio CD of Vences et al. (2006) but not yet comparatively analyzed. Following the call-centered description scheme (Köhler et al. 2017), the calls of both species consist of series of short one-note calls (series of notes in the note-centered scheme followed by Vences & Glaw 2004). However, despite similarly low recording temperatures, the inter-note intervals are longer, and call rate thus slower, in *M. brevipalmatus* as compared to *M. delormei*, from two localities each (Table 4). More importantly, the calls of *M. delormei* are of nearly tonal character and exhibit a distinct downward frequency modulation, while those of *M. brevipalmatus* are pulsatile and lack such distinct frequency modulation, as can also be recognized in the respective spectrograms and oscillograms (Fig. 11), thus showing qualitative differences in call traits (sensu Köhler et al. 2017).

Despite the low genetic divergence, which may argue for a subspecific classification of *delormei* within *M. brevipalmatus*, for the time being and despite the limited amount of available data, we regard both taxa as separate at the species-level given the limited amount of data on variation, and the apparent concordant pattern of (weak) genetic, morphological, bioacoustic, and possible ecological differentiation.

Fig. 12. A–I. Maximum Likelihood tree inferred from a fragment of the mitochondrial 16S rRNA gene (alignment length 527 bp) from 785 ingroup sequences of species of the subgenus *Ochthomantis*. Numbers at nodes are support values in percent from a bootstrap analysis with 500 replicates (not shown if <50 %). The candidate species numbers according to Randrianiaina et al. (2011) is given for the new species described; for additional candidate numbers, see Table 7. Bold font indicates sequences from name-bearing types and (marked with asterisks) paratypes of *M. charlotteae*.

▶▶


A
A
FAZC 13714 | HM364672 | Betampona
ZCMV15951 | Zahamena
RAX7524 | OR466836 | Betampona
FAZC 13534 | HM364667 | Betampona
FAZC 13979 | HM364681 | Betampona
MRSN A6608 | HM364678 | Betampona
FAZC 13941 | HM364679 | Betampona
MRSN A6593 | HM364680 | Betampona
FAZC 13724 | HM364673 | Betampona
FAZC 13479 | HM364664 | Betampona
83
MRSN A6210 | HM364666 | Betampona
MRSN A6201 | HM364665 | Betampona
MRSN A6198 | HM364670 | Betampona
MRSN A6393 | HM364676 | Betampona
FAZC 13748 | HM364675 | Betampona
FAZC 13899 | HM364677 | Betampona
MRSN A6375 | HM364674 | Betampona
FAZC 13703 | HM364671 | Betampona
MRSN A6193 | HM364663 | Betampona
FAZC 13678 | HM364669 | Betampona
MRSN A6238 | HM364668 | Betampona
GA758 | LN998771
ZCMV 2493 | HQ610920 | An'Ala
ZCMV 2494 | HQ610922 | An'Ala
ZSM 1540/2007 | ZCMV 3511 | HQ610852 | An'Ala
ZSM 1541/2007 | ZCMV 3513 | HQ610854 | An'Ala
ZSM 1539/2007 | ZCMV 3510 | HQ610853 | An'Ala
ZSM 1813/2007 | ZCMV 3509 | HQ610859 | An'Ala
FGMV3022 | LN998776
84
ZSM 1844/2007 | ZCMV 3567 | HQ610860 | An'Ala
ZSM 1771/2007 | ZCMV 3469 | HQ610857 | An'Ala
ZSM 1846/2007 | ZCMV 3570 | HQ610861 | An'Ala
ZSM 447/2006 | ZCMV 2494 | An'Ala
ZSM 1805/2007 | ZCMV 3447 | HQ610858 | An'Ala
ZSM 1761/2007 | ZCMV 3457 | HQ610856 | An'Ala
ZSM 1746/2007 | ZCMV 3441 | HQ610855 | An'Ala
ZSM 2393/2007 | ZCMV 5865 | FJ559269 | Ambohitsara
ZCMV 10467 | KF610781 | Ranomafana, Bevoahazo
ZSM 2393/2007 | ZCMV 5865 | Ambohitsara
ZSM 2394/2007 | ZCMV 5866 | Ambohitsara
ZSM 2395/2007 | ZCMV 5918 | Ambohitsara
ZCMV 4936 | GU975710 | Ambohitsara Tsitolaka
ZCMV 4936 | JX570508 | Ranomafana, | Ambohitsara
JCR 1195 | KT240538 | Ranomafana, Beremby, Sahalavabe
JCR 443 | KT240535 | Ranomafana, Beremby, Sahadikaina
JCR 460 | KT240536 | Ranomafana, Beremby, Sahadikaina
JCR 1202 | KT240537 | Ranomafana, Beremby, Sahalavabe
JCR 421 | KT240534 | Ranomafana, Ampitavanana, Ataramanavana
JCR 420 | KT240533 | Ranomafana, Ampitavanana, Ataramanavana
JCR 422 | KT240532 | Ranomafana, Ampitavanana, Ataramanavana
JCR 429 | KT240531 | Ranomafana, Ampitavanana, Ataramanavana
ZCMV 5866 | HQ610919 | Ambohitsara
JCR 1596 | KT240851 | Ranomafana, Beremby, Antaramanavana
JCR 1882 | KT240853 | Ranomafana, Beremby, Sahalavakely
JCR 1597 | KT240852 | Ranomafana, Beremby, Antaramanavana
JCR 2167 | KT240855 | Ranomafana, Beremby, Antaramanavana
JCR 586 | KT240848 | Ranomafana, Beremby, Sahalavabe
53
JCR 2153 | KT240772 | Ranomafana, Beremby, Sahalavabe
JCR 876 | KT240735 | Ranomafana, Ambolo, Ambolo I
JCR 867 | KT240849 | Ranomafana, Ambolo, Ambolo I
JCR 934 | KT240850 | Ranomafana, Beremby, Ataramanavana
JCR 1395 | KT240847 | Ranomafana, Andalangina, Andalangina
JCR 2316 | KT240856 | Ranomafana, Beremby, Sahalavabe
JCR 2328 | KT240857 | Ranomafana, Beremby, Sahadikaina
JCR 1990 | KT240854 | Ranomafana, Ambolo, Ambolo I
72
JCR 1333 | KT240845 | Ranomafana, Ambolo, Ambolo I
JCR 1846 | KT240846 | Ranomafana, Beremby, Sahalavabe
97
ZCMV 8818 | HQ610921 | Mahasoa
ZSM 686/2008 | ZCMV 8094 | HQ610862 | Mahasoa
ZSM 1765/2008 | ZCMV 8806 | Mahasoa
84
| MNHN 1929.207 | OP189695 | Madagascar
ZSM 753/2009 | ZCMV 11172 | Melivinany,Befanjana
RAX9022 | OR466837 Ambodiriana
96
ZSM 744/2009 | ZCMV 7257 Ambatoroma, Befanjana
ZSM 763/2009 | ZCMV 7201 Ambatoroma, Befanjana
RAN42737 | OR466835 | Ankavanana River, Masoala National Park
79
ZFMK 66668 | AF215317
99
FA m12 | AY848150 | Ilampy
92
RAX4670 | OR466841 | Ankitsika
RAX3915 | OR466842 | Bezavona
THC 415 | MZ019299 | Marojejy, Tourist camp1
ZSM 5074/2005 | ZCMV 2042 | Marojejy, Camp 2 Marojejia
ZSM 253/2005 | FGZC 2797 | Marojejy, Camp 1 Mantella
73
ZCMV 2042 | HQ610903 | Marojejy
ZSM 1610/2007 | FGZC 2928 | HQ610868 | Marojejy
97
ZSM 253/2005 | FGZC 2797 | FJ559268 | Marojejy
RAN37992 | OR466839 | Manantenina River, close to Marojejy National Park
RAX3669 | OR466838 | Ambolokopatrika
RAX3641 | OR466840 | Ambolokopatrika
ZSM 254 2005 FGZC 2798 | Marojejy, Camp 1 Mantella
ZSM 498/2016 | ZCMV 15268 | Marojejy, Camp 3 Simpona
ZSM 494/2016 | ZCMV 15120 | Marojejy, Camp 0
58
ZSM 490/2016 | ZCMV 15264 | Marojejy, Camp 3 Simpona
THC 417 | MZ019301 | Marojejy, Tourist camp1
THC 412 | MZ019296 | Marojejy, Tourist camp1
M. mocquardi

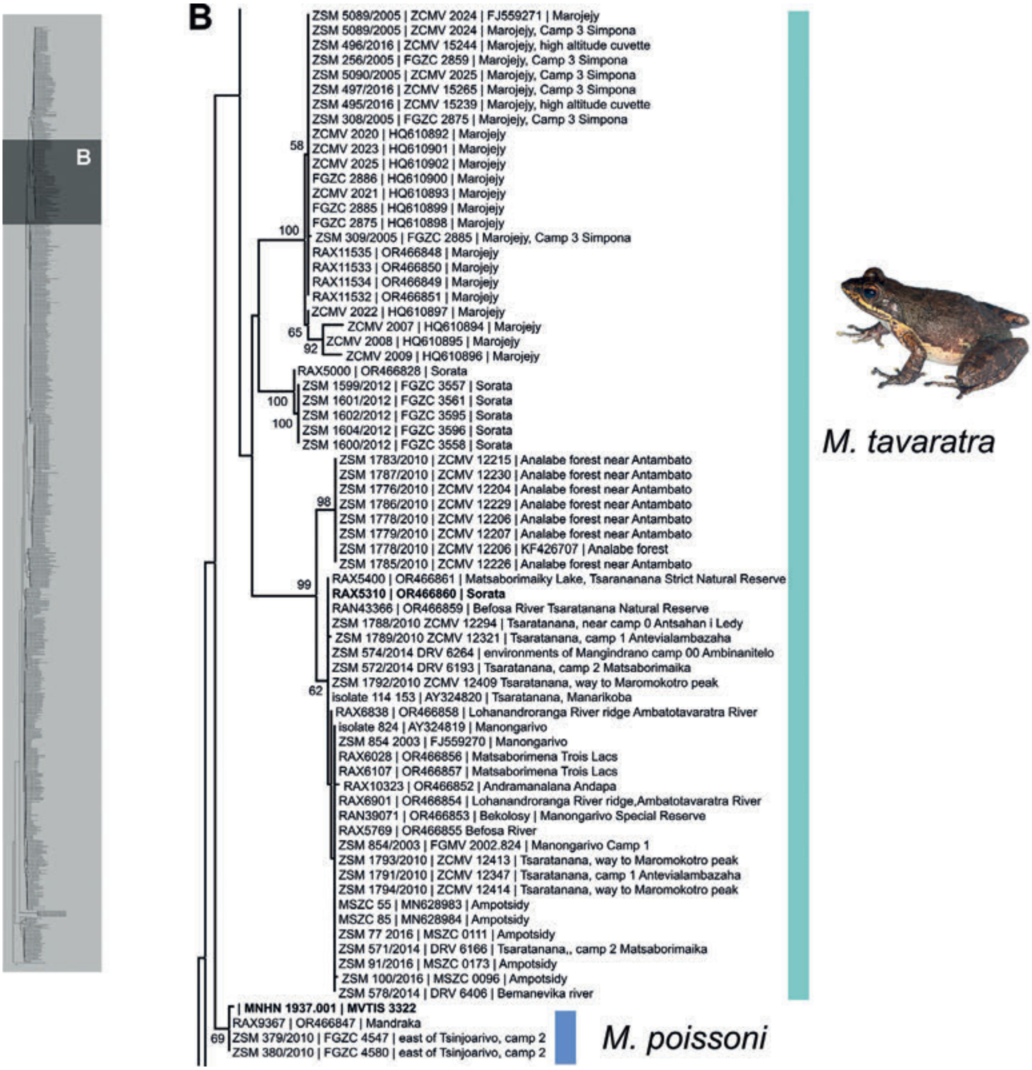


Fig. 12. Continued.

Molecular systematics of the subgenus *Ochthomantis*

The ML tree inferred from the *Ochthomantis* 16S dataset (Fig. 12) contained 785 ingroup sequences for an alignment length of 527 bp. The tree contained several deep clades that largely corresponded to the currently recognized species in the subgenus (Rabibisoa et al. 2023). Several of these were represented by large numbers of samples, often reflecting their widespread and/or common occurrence (e.g., *M. femoralis*, *M. tavaratra*), or an intensive sampling effort in particular areas, such as Montagne d'Ambre for *M. ambreensis* and *M. ambony* (Rasolonjatovo et al. 2020, Scherz et al. 2020, 2023) or Ranomafana for *M. catalai*, *M. femoralis*, *M. majori*, and *M. mocquardi* (e.g., Strauß et al. 2013, Ndriantsoa et al. 2017). Several of the species show a deep phylogeographic structure, in particular *M. femoralis*, *M. mocquardi*, and *M. tavaratra*. Comparison of 16S sequences also allowed us to assess the identity of previously defined candidate species (Vieites et al. 2009, Randrianiaina et al. 2011, Perl et al. 2014, Carné & Vieites 2024) with more recently described or resurrected species: *M. catalai* corresponds to *M.* sp. Ca47; *M. danieli* corresponds to *M.* sp. Ca42 from

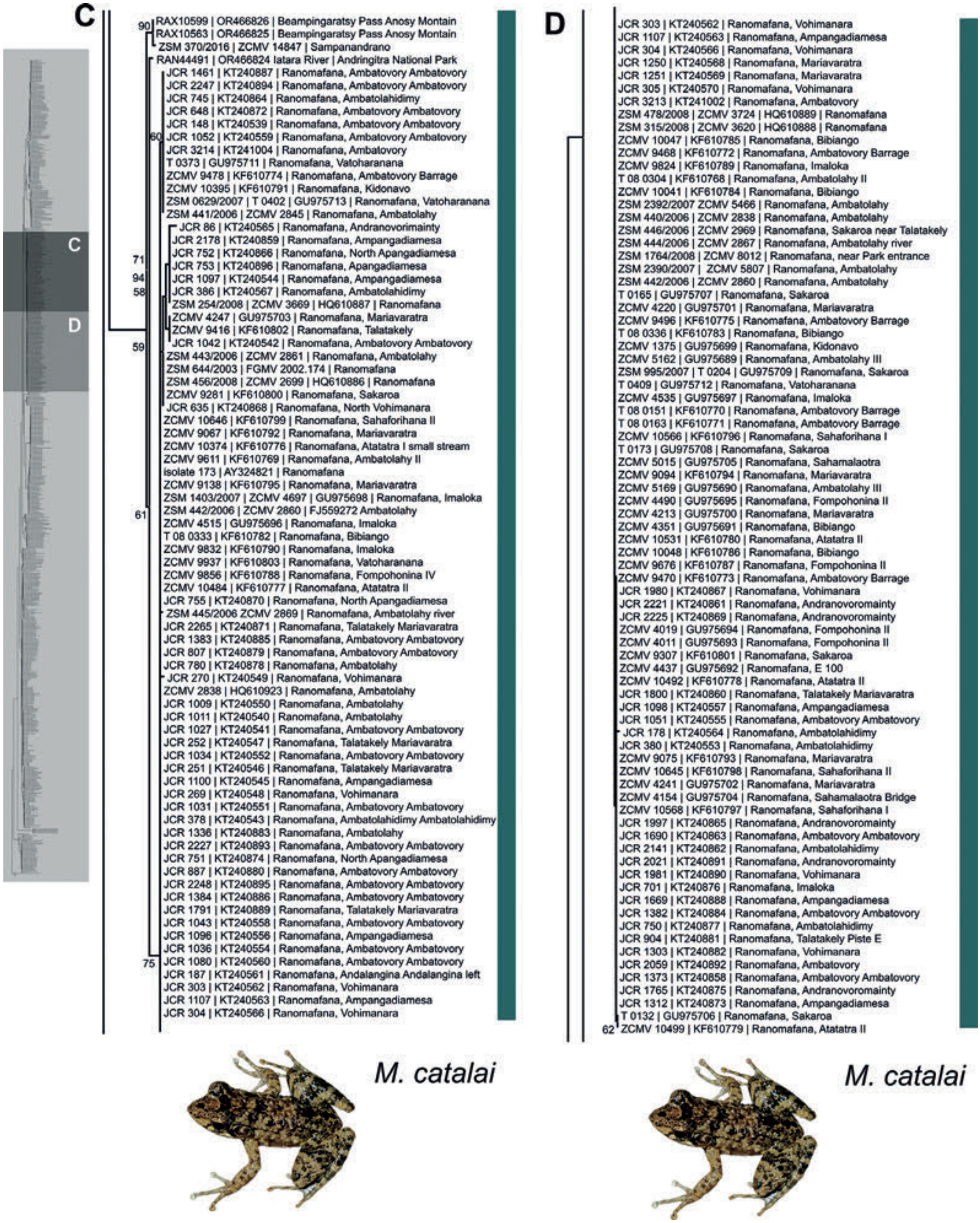


Fig. 12. Continued.

Montagne d'Ambre and other sites, and according to Rabibisoa et al. (2023) would also include *M.* sp. Ca61 from Marojejy and other sites; and *M. tavaratra* corresponds to a mitochondrial lineage only known from its type locality Sorata, but to a more inclusive lineage encompassing *M.* sp. Ca62 from Marojejy and *M.* sp. Ca63 from Tsaratanàna, Manongarivo, and nearby sites. Furthermore, we here conservatively

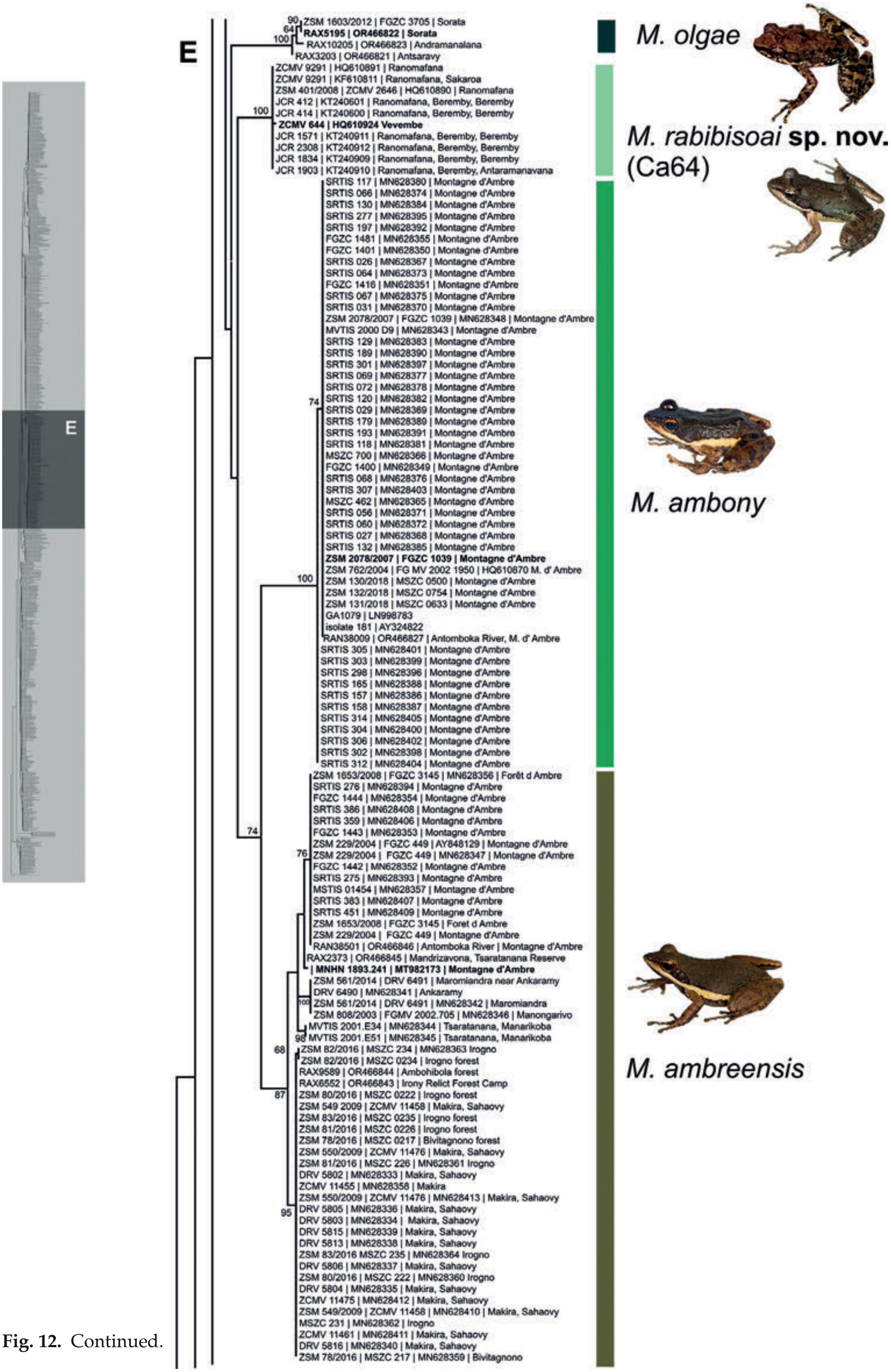


Fig. 12. Continued.

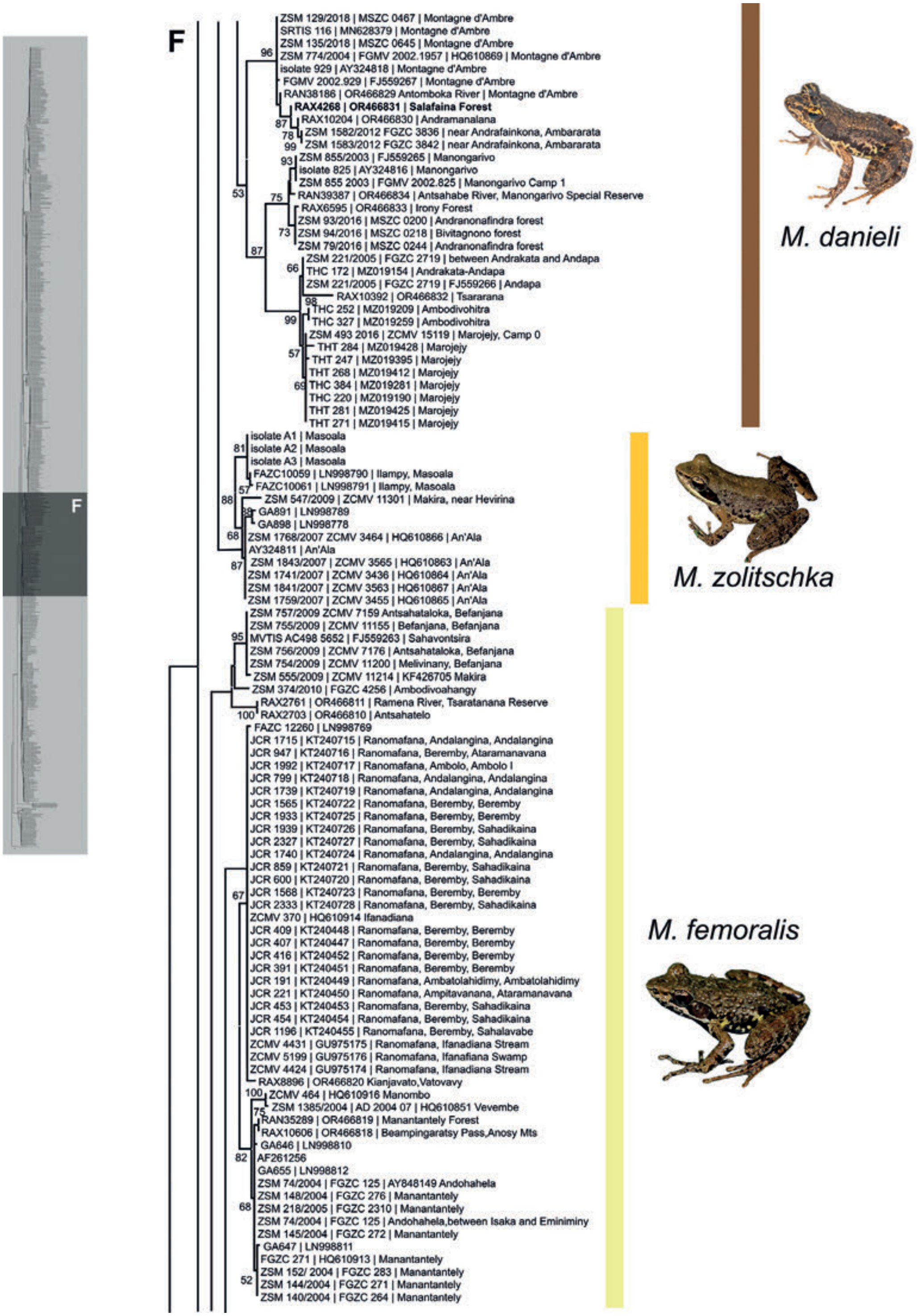


Fig. 12. Continued.

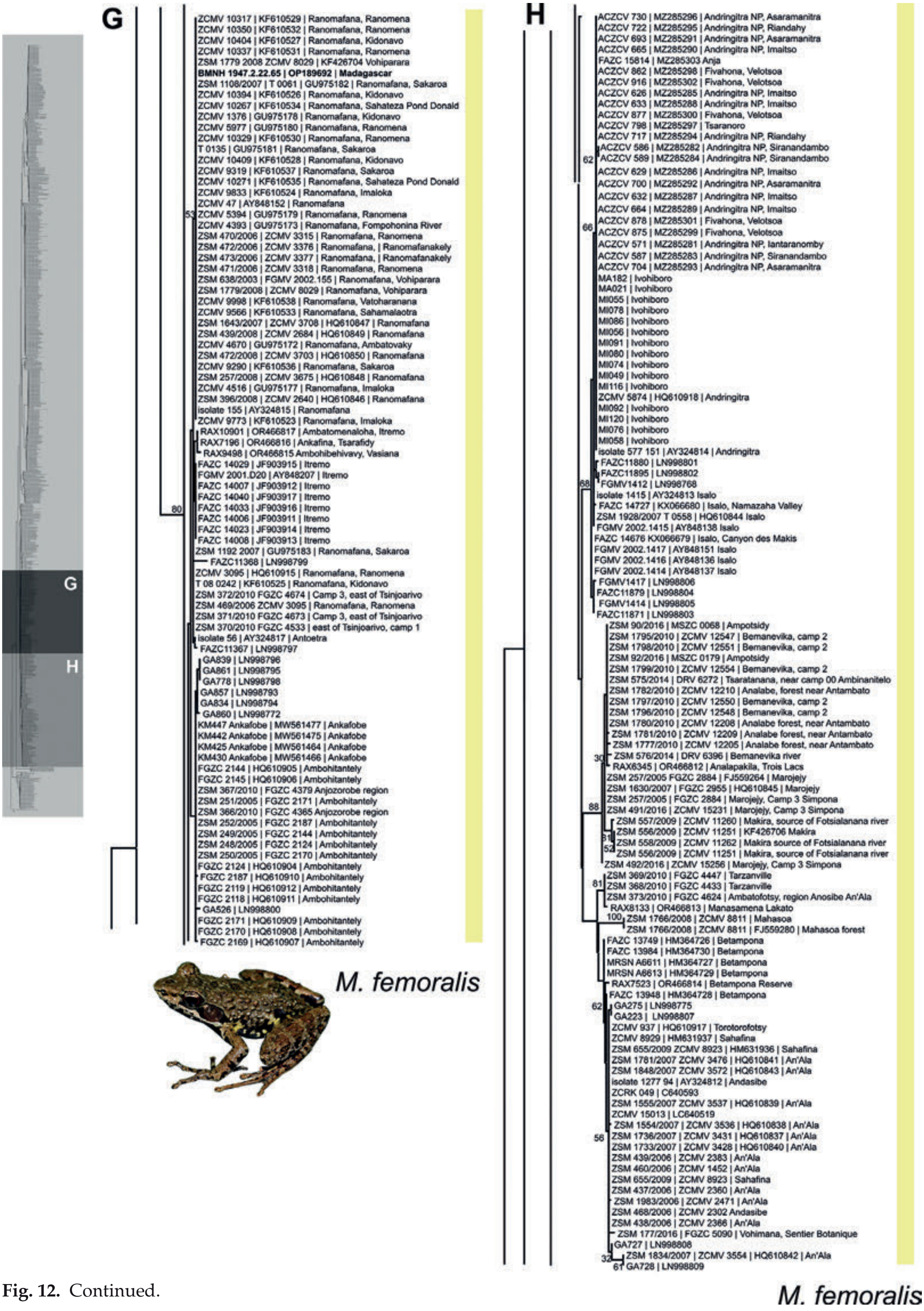


Fig. 12. Continued.

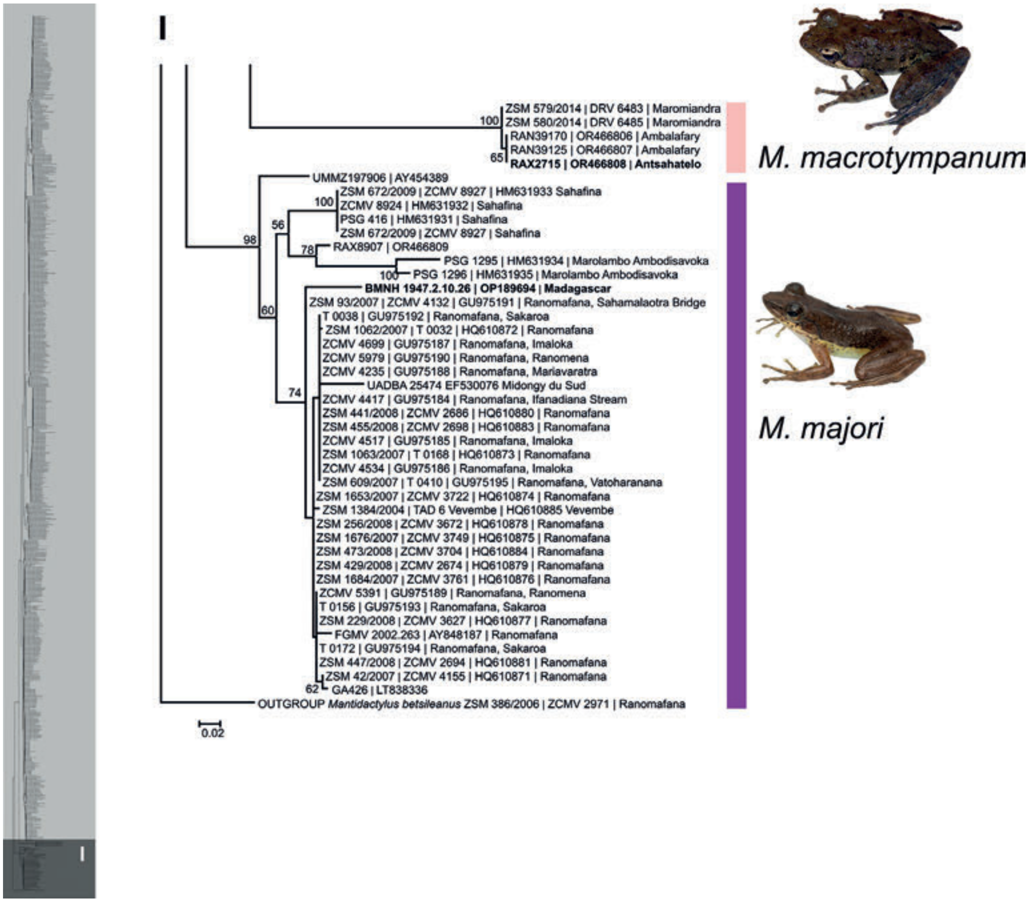


Fig. 12. Continued.

consider *M.* sp. Ca43 as belonging to *M. mocquardi* to which it is sister in the mitochondrial phylogeny.

The trimmed alignment contained 359 16S sequences for an alignment length of 510 nucleotides. ASAP suggested species partitions with 19–52 subsets where the partition with the best (lowest) ASAP score of 5.5 corresponded to a 39 subset-partition. This almost certainly reflects oversplitting due to high geographically structured genetic variation. The partition with the lowest number of subsets (19) ranked fourth, with an ASAP score of 8.5. It separated all currently known species (Rabibisoa et al. 2023) plus one candidate species (*M.* sp. Ca64: Randrianiaina et al. 2011) into distinct subsets, but split several of these further: *M. tavaratra* was split into five subsets, and *M. danieli*, *M. catalai* and *M. majori* into two subsets, respectively, always corresponding to geographically separated sublineages and in the case of *M. danieli* and *M. tavaratra*, largely corresponding to candidate species defined by Randrianiaina et al. (2011). Uncorrected pairwise 16S distances between nominal species of *Ochthomantis* ranged from 4.3–14.1 % (Table 5). The two most divergent species were *M. majori* and *M. macrotympanum* which differed from all other species by 10.4–13.9 % and from each other by 13.4–14.1 %. Excluding these two species, inter-species distances in the subgenus ranged from 4.3–11.0 %. The species split by ASAP into various subsets contained a substantial amount of genetic variation: up to 7.3 % in *M. tavaratra*, 5.3 % in *M. danieli*, 1.8 % in *M. catalai*, and 5.9 % in *M. majori*. However, other species also contained highly distinct lineages: *M. ambreensis* up to 2.6 %, *M. femoralis* up to 6.1 %, *M. mocquardi* up to 5.7 %, and *M. zolitschka* up to 2.8 %.

The genealogies reconstructed from the two nuclear-encoded gene fragments RAG1 (139 samples; 398 bp) and POMC (98 samples; 403 bp) provide a complex picture (Fig. 13), with multiple instances of haplotype sharing between species, and some species separated into phylogroups in different parts of the networks. Both networks contained central haplotypes shared by 4–5 species: In the RAG1 network, one allele with 56 sequences was shared by *M. catalai*, *M. femoralis*, *M. mocquardi* and *M. poissoni*; one allele with 37 sequences by *M. danieli*, *M. femoralis*, *M. mocquardi*, and *M. zolitschka*; one allele with 24 sequences by *M. danieli*, *M. femoralis*, *M. mocquardi*, and *M. tavaratra*; and one allele with eight sequences by *M. ambreensis*, *M. femoralis*, *M. mocquardi*, and *M. olgae*. In POMC, the central allele with 28 sequences was shared by *M. femoralis*, *M. mocquardi*, *M. olgae*, *M. danieli*, and *M. tavaratra*.

The two networks congruently place the alleles of *M. macrotympanum* apart from those of all other species, separated by seven (RAG1) and five (POMC) mutational steps, thus confirming the high and unambiguous divergence of that species. Similarly, in RAG1, the included sequence of *M. majori* (not included in the POMC network) differed from all other sequences by a minimum of five mutations. As in Rasolojantovo et al. (2020) and Scherz et al. (2020), the sympatric sister species *M. ambony* and *M. ambreensis* did not share alleles, confirming their species-level distinctness. Species whose sequences show up in quite different areas of the networks, partly forming distinct phylogroups, include *M. tavaratra*, *M. femoralis*, and *M. catalai*.

The ML tree inferred from partitioned analysis of the concatenated sequences of the 12S, 16S, COB, COI, and ND1 mitochondrial gene fragments confirmed substantial genetic differentiation (as indicated by long branches) for all species and candidate species of *Ochthomantis* included (Fig. 14). As in previous analyses of similar datasets (Poth et al. 2013, Rasolonjatovo et al. 2020), most nodes in the phylogeny received substantial bootstrap support

Table 5. Mean, minimum and maximum uncorrected pairwise distances calculated from DNA sequences of a fragment of the mitochondrial 16S rRNA gene in species of the subgenus *Ochthomantis* in the genus *Mantidactylus*. Values are given as mean, with minimum and maximum in parentheses.

	M. ambony	*M. ambreensis*	*M. catalai*	*M. danieli*	*M. femoralis*	*M. macrotympanum*	*M. majori*	*M. mocquardi*	*M. olgae*
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	0.1 (0.0–0.4)								
2	6.3 (5.9–6.7)	1.3 (0.0–2.6)							
3	7.7 (7.7–7.9)	7.3 (6.7–8.1)	0.2 (0.0–1.8)						
4	7.6 (6.5–8.9)	6.6 (5.9–8.1)	6.4 (5.9–7.5)	3.1 (0.0–5.3)					
5	8.6 (7.1–9.9)	7.9 (7.1–9.1)	6.7 (5.1–8.3)	7.0 (5.1–9.3)	2.4 (0.0–6.1)				
6	13.1 (13.0–13.2)	11.9 (11.8–12.2)	12.2 (12.0–12.4)	11.9 (11.6–12.6)	11.5 (10.8–12.4)	0.0 (0.0–0.0)			
7	12.3 (12.0–12.7)	10.9 (10.4–11.6)	12.3 (11.8–13.0)	11.5 (10.4–13.1)	11.5 (10.4–13.1)	13.8 (13.4–14.1)	3.0 (0.0–5.9)		
8	8.0 (6.9–9.1)	7.0 (6.1–8.5)	5.9 (5.1–6.7)	6.4 (5.3–8.4)	8.5 (6.7–10.4)	12.3 (11.0–12.8)	11.9 (10.6–13.4)	2.2 (0.0–5.7)	
9	7.6 (7.5–7.7)	8.4 (8.1–9.4)	6.9 (6.9–7.1)	7.7 (6.9–8.6)	9.3 (7.9–11.0)	13.3 (13.3–13.3)	13.1 (12.7–13.5)	7.6 (6.7–8.4)	0.0 (0.0–0.0)
10	6.2 (5.9–6.3)	5.9 (5.5–6.7)	4.1 (4.1–4.3)	5.2 (4.7–5.9)	5.7 (4.3–7.1)	11.0 (11.0–11.0)	10.5 (10.2–10.8)	5.2 (4.9–5.5)	6.1 (6.1–6.1)
11	7.1 (7.1–7.1)	5.5 (5.1–6.7)	4.1 (4.1–4.5)	5.7 (5.1–6.7)	7.3 (5.9–8.9)	12.0 (12.0–12.0)	11.5 (11.2–11.8)	5.5 (5.1–6.3)	6.7 (6.7–6.7)
12	8.1 (7.5–8.5)	8.1 (7.3–9.4)	7.1 (5.5–8.1)	7.2 (5.5–8.5)	7.7 (5.7–9.8)	12.6 (11.6–13.9)	12.1 (10.4–13.5)	6.8 (4.9–8.5)	7.8 (6.7–9.2)
13	7.3 (7.1–7.9)	6.7 (6.1–7.9)	6.1 (5.5–7.3)	5.4 (4.7–7.5)	5.2 (4.3–7.5)	11.8 (11.2–12.8)	11.4 (10.6–12.8)	7.4 (6.5–8.3)	7.9 (7.3–8.6)

and the relationships among species of *Ochthomantis* can therefore be considered as relatively well resolved. As in previous studies (e. g., Wollenberg et al. 2011), *M. majori* was placed away from all other *Ochthomantis*, and this species may not even belong to the subgenus (Rabibisoa et al. 2023). The recently described *M. macrotympanum* also had an isolated phylogenetic position in the tree inferred from the concatenated multi-gene dataset, as well as in exploratory single-gene trees; in the multi-gene tree, it was even characterized by a conspicuously long branch (Fig. 14) suggesting that the phylogenetic relationships of this species, plus *M. majori* and *Mantidactylus* (*Maitsomantis*) *argenteus* which was herein used as outgroup, deserve future study with more comprehensive, phylogenomic datasets. Among the intrageneric clades identified we highlight (1) a clade containing the morphologically similar sister species *M. ambony* and *M. ambreensis* (BS = 93 %), (2) a clade containing *M. catalai*, *M. poissoni* and *M.* sp. Ca64 (BS = 98 %), three species rather strongly differing from each other morphologically, (3) a clade containing *M. femoralis*, its sister species *M. zolitschka*, and *M. danieli* (BS = 99 %) which all are morphologically rather similar to each other, and (4) a clade containing *M. mocquardi* and *M. tavaratra* (BS = 95 %).

M. poissoni	*M. rabibisoai* sp. nov. (Ca64)	*M. tavaratra*	*M. zolitschka*
10	**11**	**12**	**13**
0.0 (0.0–0.0)			
4.5 (4.5–4.5)	0.0 (0.0–0.0)		
5.1 (4.5–5.9)	7.0 (6.1–7.7)	3.8 (0.0–7.3)	
4.6 (4.3–5.1)	6.8 (6.3–7.7)	6.1 (5.3–7.5)	1.2 (0.0–2.8)

Given the high intraspecific mitochondrial variation, substructuring suggested by ASAP, and different phylogroups in the nuclear gene genealogies, it is likely that several species in *Ochthomantis* require future taxonomic scrutiny. Especially, we suspect that *M. tavaratra* merits being split into different species. At present, we lack data to investigate these splits in further detail, and we do not suggest any taxonomic changes or splits for the currently accepted species, all of which form monophyletic groups in the mitochondrial phylogeny. For instance, the sequences available from GenBank from the study of Rabibisoa et al. (2023) lack a section corresponding to a central hypervariable region of the gene, which was probably removed prior to analysis; the trimmed sequences were erroneously then submitted to GenBank instead of the full sequences. Although these incomplete sequences could be unambiguously assigned to mitochondrial clades, it complicates the computation of species partitions and genetic distances (these sequences were excluded from our ASAP and distance analysis), and the genetic information is therefore incomplete for several collecting locations not sampled by us.

It is also worth mentioning that through earlier archival DNA analyses (Scherz et al. 2020, 2022a), DNA data are available for the name-bearing types of several of these species, specifically *M. ambreensis*, *M. catalai*, *M. femoralis*, and *M. mocquardi*. Furthermore, more recent species descriptions (Scherz et al. 2020, Rabibisoa et al. 2023) have included DNA sequences of the holotypes of new species, i. e., *M. ambony*, *M. danieli*, *M. macrotympanum*, *M. olgae*, and of a paratype of *M. tavaratra*. Therefore, the nomenclatural identity of only two species is at present not confirmed by molecular data: a DNA analysis of the type of *M. catalai* by Scherz et al. (2022a) did not yield informative reads, but the identity of this species is rather reliable due to morphological analysis (Rabibisoa et al. 2023) and geographical provenance of the type from the South East of Madagascar; and *M. zolitschka* which is a morphologically easily identifiable species, and of which several 16S sequences from its type locality An'Ala are included in our dataset. By summarizing genetic variation within and between species, and photographically illustrating morphological appearance and colour variation for a set of genotyped specimens of all species (Figs 15–22), this study thus sets the stage for future in-depth revisionary work on the taxonomic diversity of species of *Ochthomantis*.

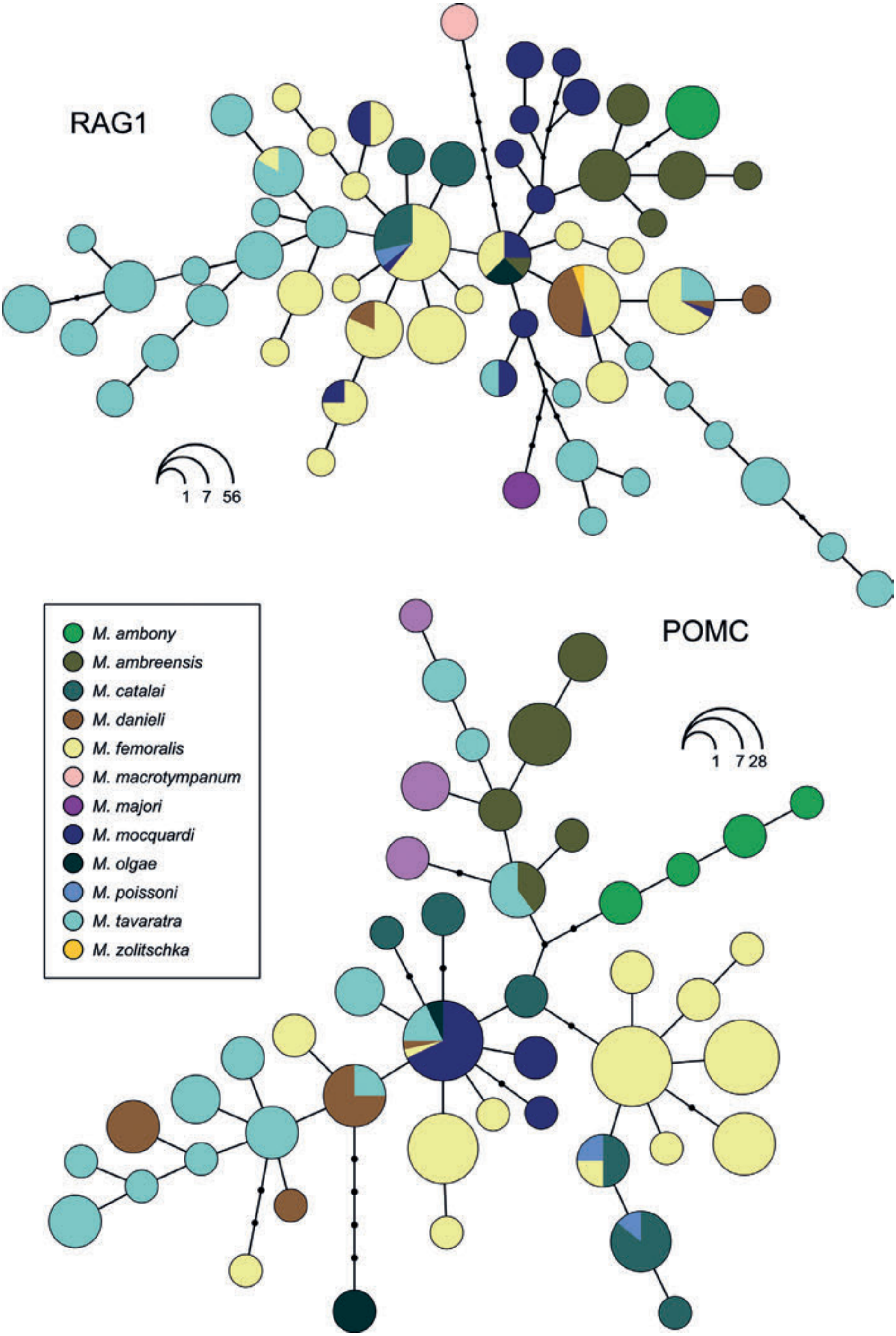


Fig. 13. Haplotype genealogies from sequences of two nuclear-encoded gene fragments from species in the subgenus *Ochthomantis*: RAG1 (139 samples; 398 bp) and POMC (98 samples; 403 bp). *Mantidactylus rabibisoai* sp. nov. is not shown. All sequences were phased before the analysis. Small dots represent additional mutational steps or unsampled alleles.

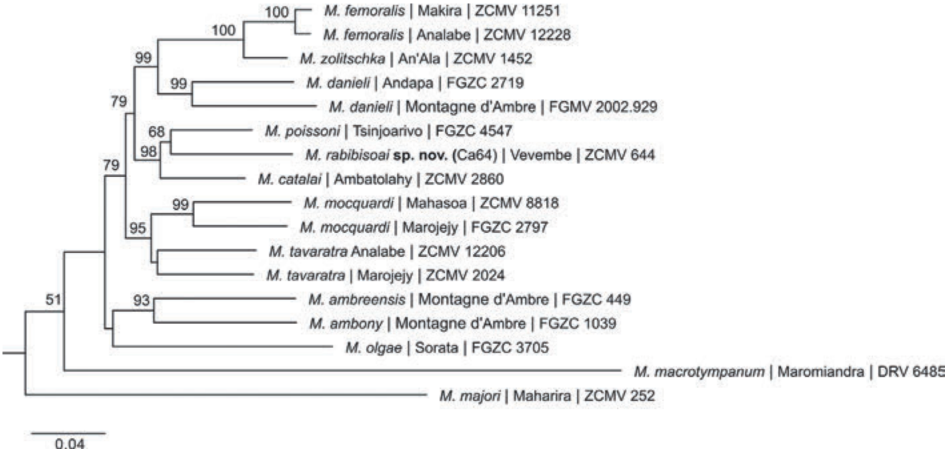


Fig. 14. Maximum Likelihood tree inferred from 3056 bp of concatenated DNA sequences of the mitochondrial genes for 12S rRNA, 16S rRNA, Cytochrome *b*, Cytochrome Oxidase Subunit 1, and NADH Dehydrogenase Subunit 1, showing evolutionary relationships of species within the subgenus *Ochthomantis*. Numbers at nodes are support values in percent from a bootstrap analysis (1000 replicates; not shown if < 50 %). *M. argenteus* (subgenus *Maitsomantis*) was used as the outgroup (graphically removed to better illustrate branch lengths within the ingroup).

Fig. 15. Photos of representative individuals of two species of *Mantidactylus* (subgenus *Ochthomantis*). **A.** *M. majori* from Manombo, specimen ZMUC-H005219 (MSZC 0947) from Manombo, photographed 2024. **C–D.** *M. macrotympanum*, male specimen ZSM 580/2014 (DRV 6485) from Maromiandra near Ankaramy, photographed 2010. These two species are the phylogenetically most divergent lineages in the subgenus, and the assignment of *M. majori* to *Ochthomantis* is in need of revision.

Fig. 16. Photos of representative individuals of three species of *Mantidactylus* (subgenus *Ochthomantis*) from northern Madagascar. **A–B.** *M. ambreensis*, male specimen ZSM 229/2004 from Montagne d'Ambre, photographed 2004. **C–D.** *M. ambony*, female holotype ZSM 2078/2007 from Montagne d'Ambre, photographed 2007. **E–F.** *Mantidactylus olgae*, male specimen ZSM 1603/2012 (FGZC 3705) from Sorata, photographed 2012.

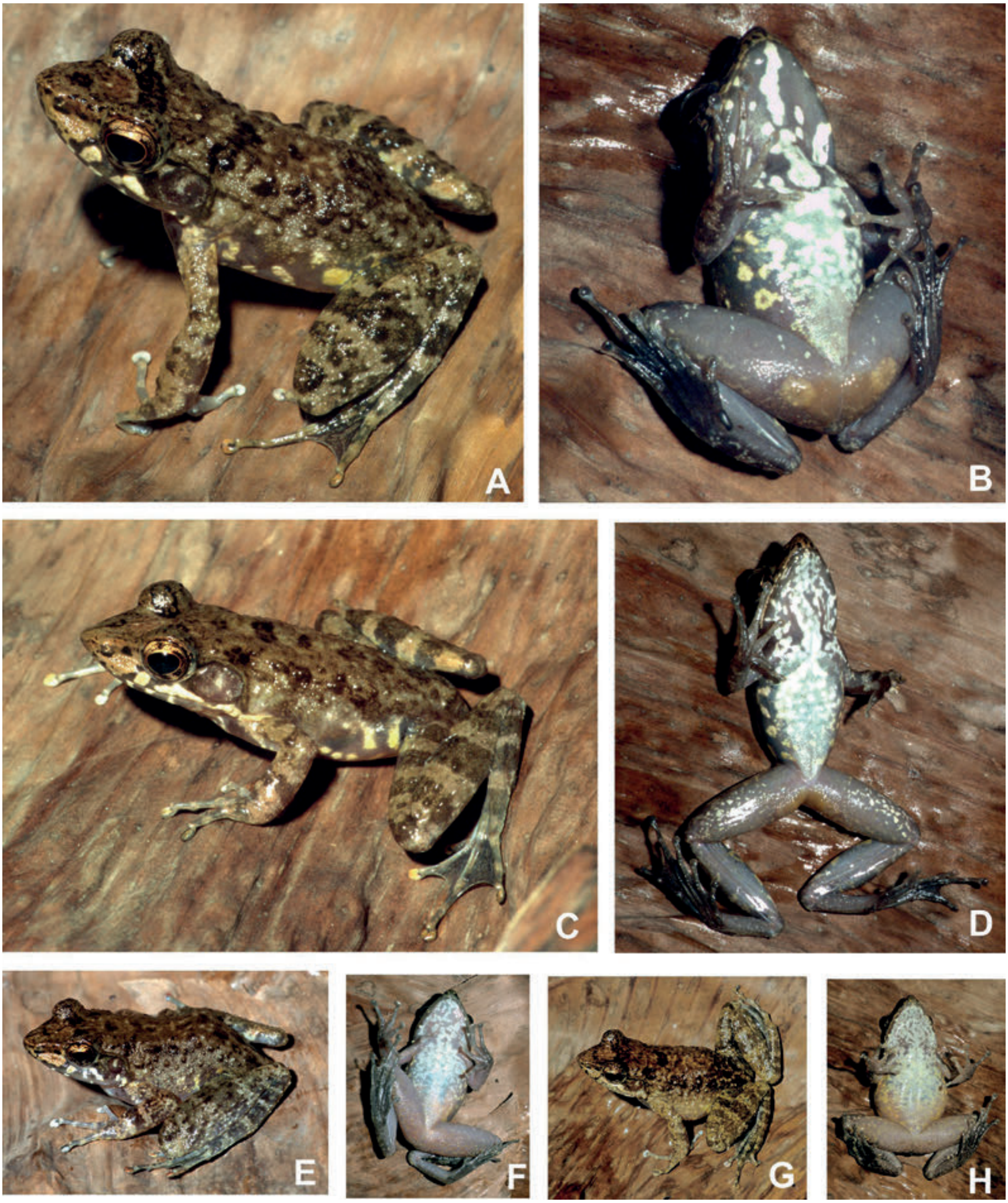


Fig. 17. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *catalai* in life, in dorsolateral and ventral views. All specimens from Ambatolahy near Ranomafana, photographed 2006. **A–B.** Male specimen ZSM 442/2006 (ZCMV 2860). **C–D.** Male specimen ZSM 443/2006 (ZCMV 2861). **E–F.** and **G–H.** Two female specimens (photos not reliably assignable to a voucher specimen).

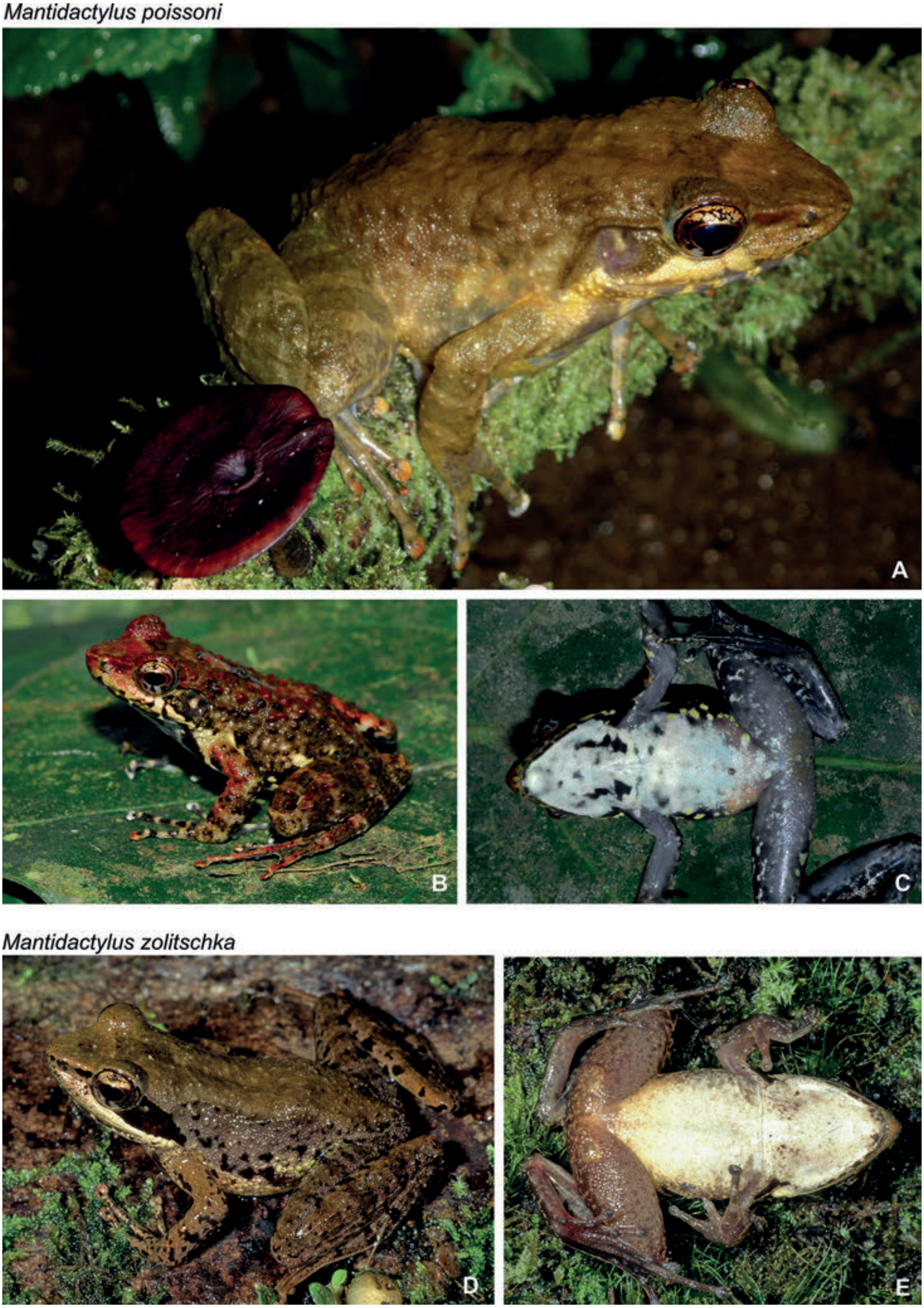


Fig. 18. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *poissoni* and *Mantidactylus* (*Ochthomantis*) *zolitschka* in life, in dorsolateral and ventral views. **A.** *M. poissoni* female ZSM 379/2010 (FGZC 4547) from Tsinjoarivo, photographed 2010. **B–C.** Male from Tsinjoarivo, photographed 2010, tentatively assigned to *M. poissoni* (photos not reliably assignable to a voucher specimen). **D–E.** Specimen of *M. zolitschka* from An'Ala (photos not reliably assignable to a voucher specimen).

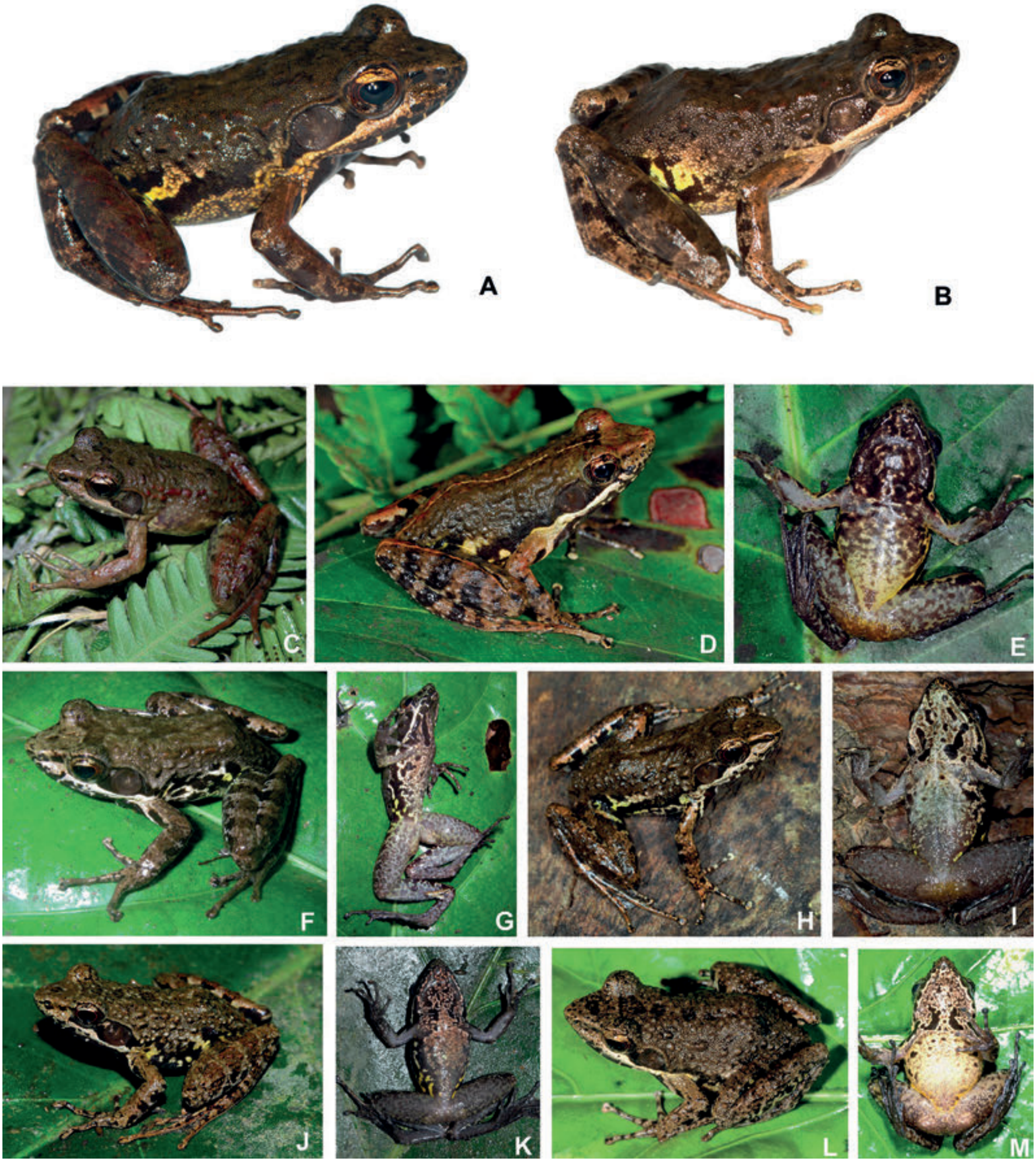


Fig. 19. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *femoralis* from across the species' range in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A.** Male specimen ZSM 92/2016 (MSZC 0179) from Ampotsidy. **B.** Male specimen UADBA-A 62278 (MSZC 0143) from Ampotsidy. **C.** Male specimen ZSM 1795/2010 (ZCMV 12547) from Bemanevika, photographed 2010. **D–E.** Male specimen ZSM 374/2010 (FGZC 4256) from Ambodivoangy, photographed 2010. **F–G.** Male specimen ZSM 558/2009 (ZCMV 11262) from the western slope of Makira Reserve, photographed 2009. **H–I.** Male specimen ZSM 366/2010 (FGZC 4365) from Anjozorobe, photographed 2010. **J–K.** Male specimen ZSM 370/2010 (FGZC 4533) from Tsinjoarivo, photographed 2010. **L–M.** Male specimen ZSM 144/2004 (FGZC 271) from Manantantely, photographed 2004.

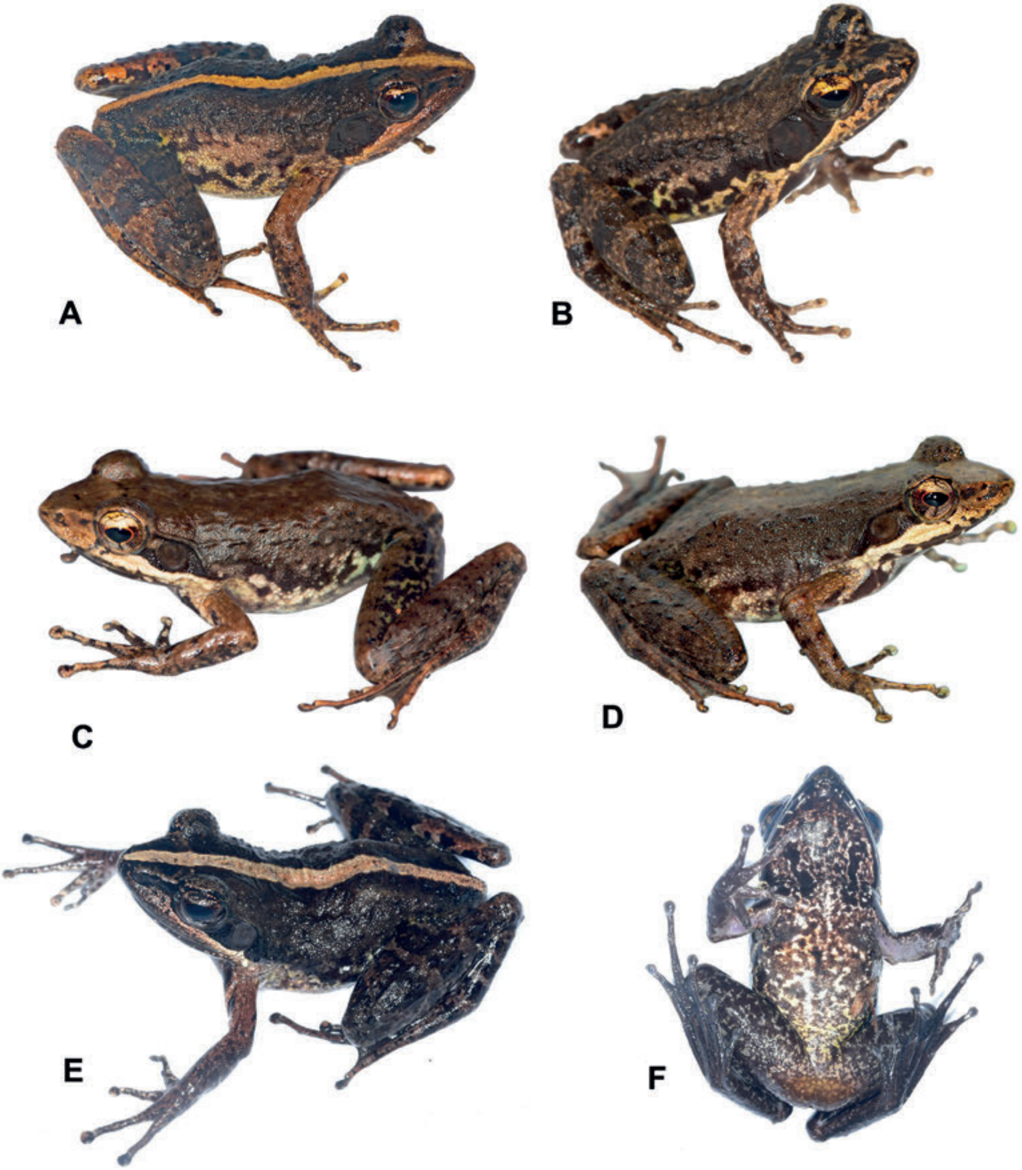


Fig. 20. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *danieli* in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A.** Specimen ZSM 136/2018 (MSZC 0669) from Montagne d'Ambre. **B.** Specimen ZSM 129/2018 (MSZC 0467) from Montagne d'Ambre. **C.** Specimen UADBA-A 62285 (MSZC 0215) from Bealanana. **D.** Male specimen ZSM 93/2016 (MSZC 0200) from Ampotsidy. **E–F.** Specimen ZSM 493/2016 (ZCMV 15119) from Marojejy.

Because the genetically divergent subsets in species such as *M. femoralis*, *M. catalai*, *M. danieli*, *M. majori*, and especially *M. tavaratra*, all appear allopatrically distributed, such future studies should focus on identifying their contact zones and ideally, apply phylogenomic analyses of hybrid zones (Dufresnes et al. 2021) to understand their taxonomic status.

Fig. 21. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *mocquardi* in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A–B.** Male specimen ZSM 253/2005 (FGZC 2797) from Marojejy, photographed 2005. **C–D.** Specimen ZSM 494/2016 (ZCMV 15120) from Marojejy, photographed 2016. **E–F.** Female specimen ZSM 2394/2007 (ZCMV 5866) from Ambohitsara, photographed 2007. **G.** Specimen ZSM 2393/2007 (ZCMV 5865) from Ambohitsara, photographed 2007.

Delimiting a new species of *Ochthomantis* from the southern Central East

Our mitochondrial dataset includes the same main lineages (= species) also reported by Rabibisoa et al. (2023), plus one further candidate species from the northern Central East and North East of Madagascar that was defined as *M.* sp. 64 (herein *M.* sp. Ca64) by Randrianiaina et al. (2011) based on tadpoles from the Namorona River in Ranomafana, and one further sequence from Vevembe. Here, we include eight additional 16S sequences of this candidate species, all from Ranomafana, and morphological data of two adult voucher specimens (see species account below). *Mantidactylus* sp. Ca64 was delimited as a separate subset by ASAP and differs by > 4 % 16S uncorrected pairwise distance from all other *Ochthomantis*, and specifically, by 4.1–4.5 % from its sister lineage, *M. catalai*. Unfortunately, no sequences of the nuclear encoded gene fragments could be generated for this candidate species. However, its tadpole morphology reported by Randrianiaina et al. (2011) allows a clear delimitation from several species occurring syntopically in Ranomafana. Among other characters its absence of keratodonts and of a dorsal gap of marginal papillae is a clear difference from *M. femoralis* (and also from *M. catalai*, reported as *M.* sp. 47 by Randrianiaina et al. 2011), and several details of morphology constitute differences to *M. mocquardi* (see Randrianiaina et al. 2011).

Based on high mitochondrial divergences and tadpole morphology, there are thus two *Ochthomantis* species restricted to the southern Central East and South East, which phylogenetically are sister to each other: One of these was defined as *M. catalai* by Rabibisoa et al. (2023) based on morphological examination of the types, and the respective genetic lineage includes samples from the Anosy mountains, close to the *catalai* type locality Isaka-Ivondro (see Angel 1935; holotype MNHN 1935.153). The second one is the candidate species *M.* sp. Ca64 defined by Randriainaina et al. (2011). Based on morphological examination of the holotype of *M. catalai* we here confirm the species definition as given in Rabibisoa et al. (2023). Both *M. catalai* and *M.* sp. Ca64 are rather large: in the Ambatolahy population of *M. catalai*, three female specimens ZCMV 2838, ZCMV 2845 an ZCMV 2867 measured 61.1–65.2 mm and three males ZCMV 2860, ZCMV 2861 and ZCMV 2869 measured 40.3–45.1 mm, while the three available males of *M.* sp. Ca64 (Table 6) measure 43.4–47.3 mm in SVL. However, *M. catalai* has a highly tubercular skin and lacks a distinct uninterrupted frenal stripe, whereas a smooth skin and frenal

Table 6. Morphological measurements (all in mm) of type specimens of the new species described herein in the *Mantidactylus* subgenera *Chonomantis* and *Ochthomantis*. Additional abbreviations: HT, holotype; PT, paratype; M, male; F, female; SVL, snout–vent length; HW, head width; HL, head length; TD, tympanum diameter; ED, eye diameter; END, eye to nostril distance; NSD, nostril to snout tip distance; NND, nostril to nostril distance; FORL, forelimb length; HAL, hand length; HIL, hindlimb length; FOL, foot length; FOTL, foot length including

Specimen-voucher	Field number	Locality	Status	Sex	SVL	HW	HL
M. charlotteianus sp. nov. (Ca12)							
ZSM 225/2005	FGZC 2733	Marojejy	PT	F	28.5	9.1	10.5
ZSM 226/2005	FGZC 2771	Marojejy	PT	F	29.6	9.0	11.3
ZSM 5067/2005	ZCMV 2093	Marojejy	PT	F	30.7	9.9	11.4
ZSM 365/2010	FGZC 4221	Ambodivoangy	PT	F	29.1	9.2	10.9
ZSM 487/2016	ZCMV 15136	Marojejy	HT	F	30.1	9.5	11.8
ZSM 488/2016	ZCMV 15138	Marojejy	PT	M	21.9	7.2	9.0
M. chonodus sp. nov. (Ca13)							
ZSM 2383/2007	ZCMV 5940	Ambohitsara	HT	M	21.6	7.5	9.1
ZSM 749/2003	FGMV 2002.535	Ambohitsara	PT	M	26.7	9.0	10.1
ZMA 20036	ZCMV 84	Ambohitsara	PT	M	20.1	6.8	8.7
M. dichromus sp. nov. (Ca10)							
ZSM 5069/2005	ZCMV 2113	Nosy Mangabe	PT	F	30.6	9.5	11.7
ZSM 5071/2005	ZCMV 2135	Nosy Mangabe	PT	F	30.1	9.7	11.8
ZSM 5068/2005	ZCMV 895	Nosy Mangabe	PT	M	24.7	8.5	10.4
ZSM 5070/2005	ZCMV 2115	Nosy Mangabe	HT	M	25.5	8.7	10.5
ZSM 729/2009	ZCMV 7221	Befanjana	PT	M	22.3	7.1	9.0
M. kitrinolaimus sp. nov. (Ca11)							
ZSM 267/2016	FGZC 5437	Masoala	HT	M	24.7	8.3	10.3
ZSM 128/2002	FGMV 2001.1426	Andranofotsy	PT	F	29.5	9.4	11.7
ZSM 127/2002	FGMV 2001.1382	Andranofotsy	PT	M?	24.7	7.9	10.4
M. maharira sp. nov. (Ca4)							
ZMA 20038	ZCMV 234	Maharira, Ranomafana	HT	F	28.5	8.6	10.9
ZMA 20039	ZCMV 233	Maharira, Ranomafana	PT	M	22.1	6.9	8.5
M. malokila sp. nov. (Ca9)							
ZMB 81915	JCR 6	Ranomafana	HT	M	25.8	8.8	10.5
ZSM 748/2003	FGMV 2002.534	Ranomafana	PT	F	30.1	9.2	11.3
ZMA 20035	ZCMV 82	Ambohitsara	PT	F	31.7	10.4	12.6
ZMA 20037	ZCMV 67	Ambohitsara	PT	F	29.5	9.2	11.4
M. temachikus sp. nov. (Ca3)							
ZSM 324/2005	FGZC 2161	Ambohitantely	HT	M	22.2	7.3	9.4
ZSM 381/2010	FGZC 4388	Anjozorobe	PT	M	23.0	8.1	9.3
M. sp. cf. *zipperi*							
ZSM 696/2009	ZCMV 11184	Befanjana, Melivinany	HT	F	28.2	9.6	11.4
M. ventrilineatus sp. nov. (Ca1)							
ZSM 378/2006	ZCMV 3079	Ranomafana	PT	F	25.9	8.1	11.2
ZSM 411/2006	ZCMV 2964	Ranomafana	HT	M	23.3	8.3	10.3
ZSM 179/2006	BOR 1025	Midongy du Sud	PT	M	23.3	8.8	10.1
ZMA 20112	ZCMV 679	Vevembe	PT	F	31.8	11.1	13.4
ZMA 20111	ZCMV 647	Vevembe	PT	F	31.6	11.1	13.3
ZMA 19404	FGMV 2002.481	Mangevo, Ranomafana	PT	F	32.0	11.1	13.0
ZMA 19405	FGMV 2002.482	Mangevo, Ranomafana	PT	M	26.0	9.3	11.0
M. rabibisoai sp. nov. (Ca64)							
ZMA 20143	ZCMV 644	Vevembe	HT	M	47.3	15.6	18.7
ZMA 20222	ZCMV 9	Ranomafana	PT	M	43.4	15.6	17.2
ZMB 81952	NSH 1571	Ranomafana	PT	M?	47.3	15.6	17.5

tarsus; TIL, tibia length; FGL and FGW, length and width of femoral gland. See Materials and Methods for additional details on morphometric measurements. For a table with a full set of measurements, including other nominal species of *Chonomantis* and additional non-type specimens assigned to the new species, see https://doi.org/10.5281/zenodo.15161297.

TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIL	FGL	FGW
3.1	3.8	2.8	2.2	3.5	17.7	7.9	45.6	20.4	13.4	14.7		
3.3	3.8	2.6	2.0	3.6	18.3	8.7	50.5	22.3	14.7	15.5		
3.6	4.1	3.0	2.0	3.4	18.9	8.8	49.5	21.4	14.1	15.9		
2.3	4.2	2.4	2.0	3.4	19.0	8.2	50.1	21.9	14.0	15.8		
3.3	4.1	2.9	2.0	3.7	20.2	9.2	49.3	22.5	14.5	15.7		
2.7	3.6	2.2	1.7	2.9	14.7	6.9	37.0	16.8	10.8	11.5	3.6	2.0
2.3	3.2	2.2	1.7	2.8	13.3	5.9	36.3	16.4	10.8	11.2	2.8	1.6
2.6	3.9	2.2	1.9	3.0	16.4	7.0	43.5	19.5	12.7	13.6	2.7	1.2
2.5	2.6	2.0	1.5	2.5	13.2	6.0	36.1	16.2	10.5	10.9	4.0	2.0
3.3	4.1	3.3	2.2	3.6	19.2	9.0	46.3	22.1	14.6	14.5		
3.4	4.5	2.9	2.1	3.9	20.1	8.5	48.7	22.1	14.6	15.1		
4.0	4.0	2.8	2.2	3.4	16.5	7.6	39.9	19.2	12.7	12.2	3.8	2.0
3.8	3.6	3.0	2.1	3.2	17.2	7.7	43.5	20.0	13.0	13.0	3.4	2.0
3.1	3.6	2.0	1.3	3.0	15.8	6.0	35.5	15.3	10.1	11.1	3.3	2.5
3.8	3.8	2.6	2.1	3.5	16.2	7.7	40.6	18.8	12.2	12.8	3.3	1.9
2.9	4.3	2.6	1.9	3.8	20.0	9.2	49.2	22.7	14.8	15.4		
3.2	3.7	2.2	2.1	3.0	16.7	7.6	40.1	18.6	12.1	12.5	3.0	1.8
2.8	3.9	2.4	1.8	2.6	17.9	8.0	48.3	21.7	13.7	14.6		
3.0	3.2	2.3	1.3	2.0	14.8	6.3	39.2	17.9	11.6	11.6	3.9	2.6
3.8	4.2	2.6	2.0	3.5	17.0	7.3	38.8	18.6	11.8	12.7	3.8	2.6
3.3	4.0	2.9	2.0	3.4	19.3	8.8	46.9	21.3	14.1	14.9		
3.5	4.2	2.6	2.0	3.6	21.8	8.9	51.8	23.8	15.6	15.7		
3.0	4.0	2.6	1.8	3.0	20.6	8.6	45.7	18.7	11.5	14.7		
4.2	3.5	2.4	1.8	2.9	15.1	6.7	39.6	17.2	11.3	12.2	3.2	2.1
3.8	3.4	2.2	1.8	2.7	16.0	7.5	41.3	18.2	12.3	12.9	3.2	1.5
2.9	3.9	2.8	2.2	3.7	18.6	8.1	49.1	22.7	14.6	16.1		
2.5	3.6	2.5	2.0	2.9	16.9	7.0	46.4	21.7	13.9	15.5		
3.0	3.4	2.5	2.0	3.2	15.5	7.3	43.9	20.2	13.4	14.2	3.5	2.1
2.7	3.4	2.1	1.8	3.1	14.6	6.1	44.0	19.6	12.6	14.1	3.6	2.1
3.0	4.6	2.7	1.9	3.0	18.9	8.9	59.0	26.4	17.5	18.9	1.6	1.0
2.7	5.0	2.8	2.2	3.2	20.2	9.3	59.7	26.4	17.3	18.7	1.8	1.3
2.5	4.8	3.2	1.8	2.9	20.0	8.8	57.3	25.4	16.6	18.5	2.0	1.3
3.2	4.2	2.2	1.7	2.6	15.4	7.9	46.5	21.2	14.3	15.4	3.4	2.5
5.4	6.4	4.3	2.6	4.5	31.6	13.7	85.4	40.0	26.5	26.2	5.3	2.9
5.4	6.3	4.2	2.5	4.2	27.8	12.7	79.1	35.4	23.7	24.9	5.1	3.3
5.1	5.9	3.7	2.5	4.6	26.6	12.3	78.2	36.6	24.2	27.6		

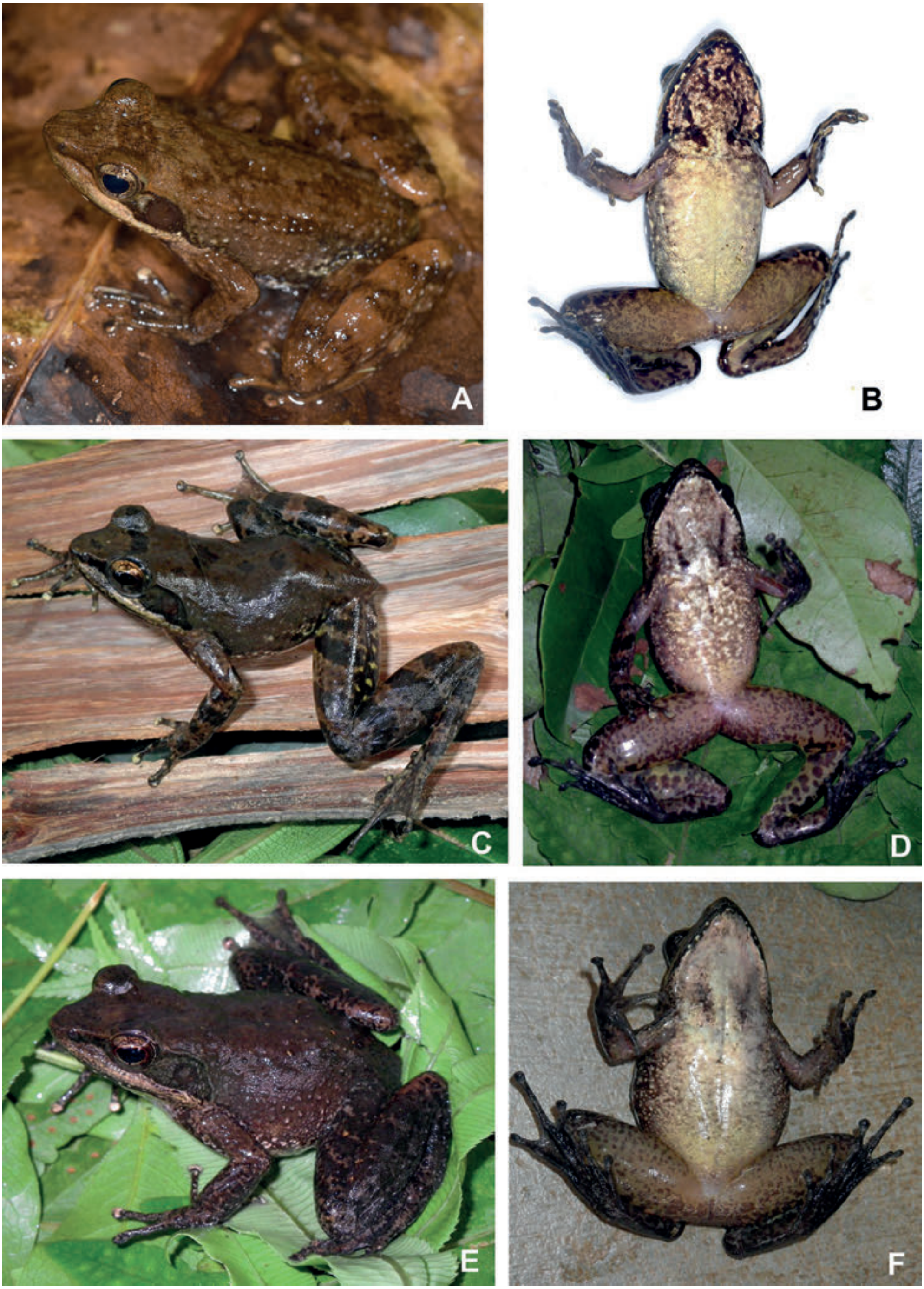


Fig. 22. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *tavaratra* in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A–B.** Specimen ZSM 495/2016 (ZCMV 15239) from Marojejy, photographed 2016. **C–D.** Specimen ZSM 1775/2010 (ZCMV 12203) from Analabe, photographed 2010. **E–F.** Specimen ZSM 1776/2010 (ZCMV 12204) from Analabe, photographed 2010.

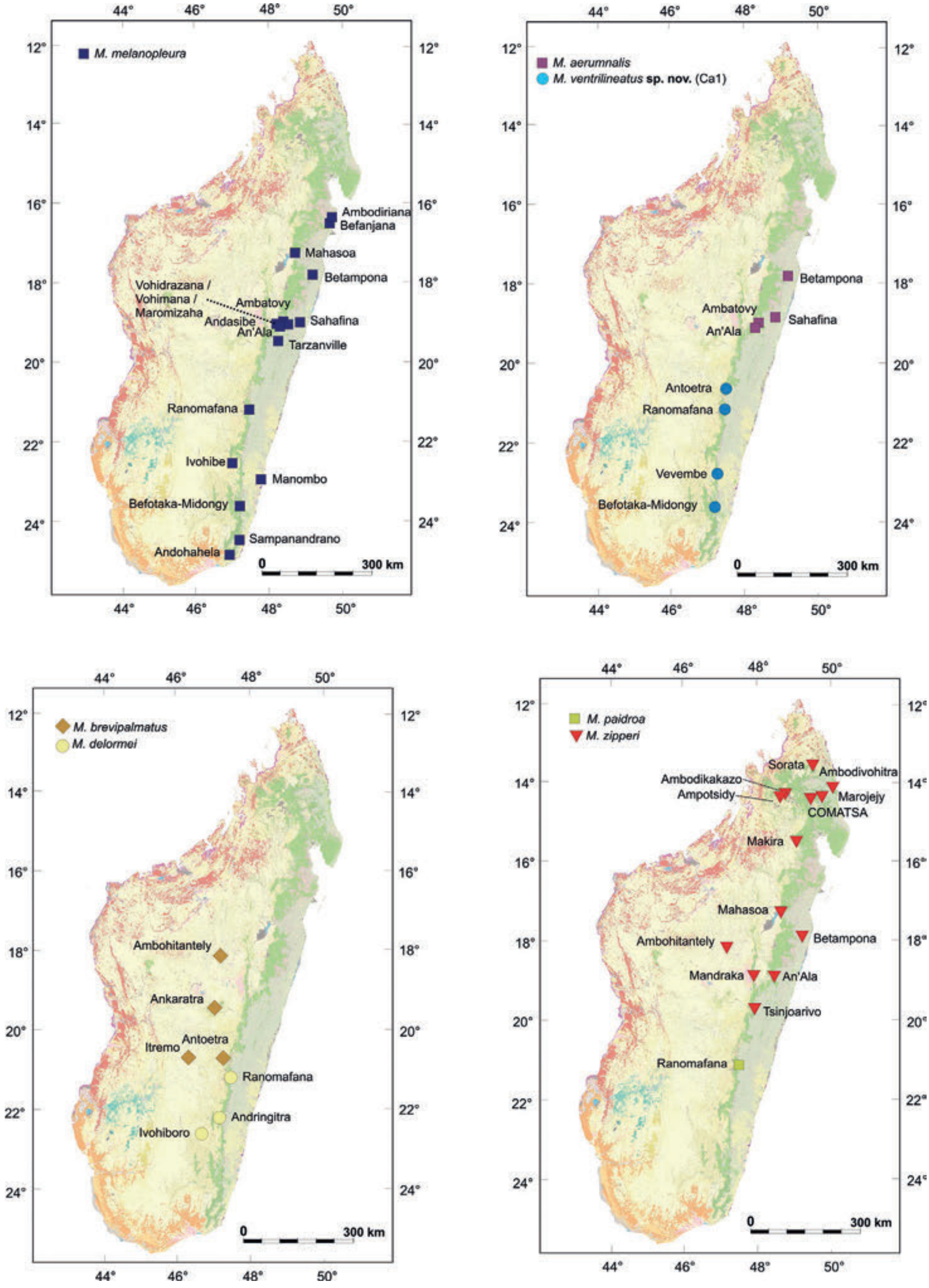


Fig. 23. Distribution maps of seven species in the subgenus *Chonomantis*, only showing sites confirmed by DNA sequencing. The base map shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; available at https://web.archive.org/web/20180419112513/, http://www.vegmad.org/). Vegetation is coloured as follows: green, humid forest (rainforest); red, western dry deciduous forest; pink, mangroves; orange, spiny forest-thicket; greenish blue, western subhumid forest; yellow, sclerophyllous woodland; grey, water bodies.

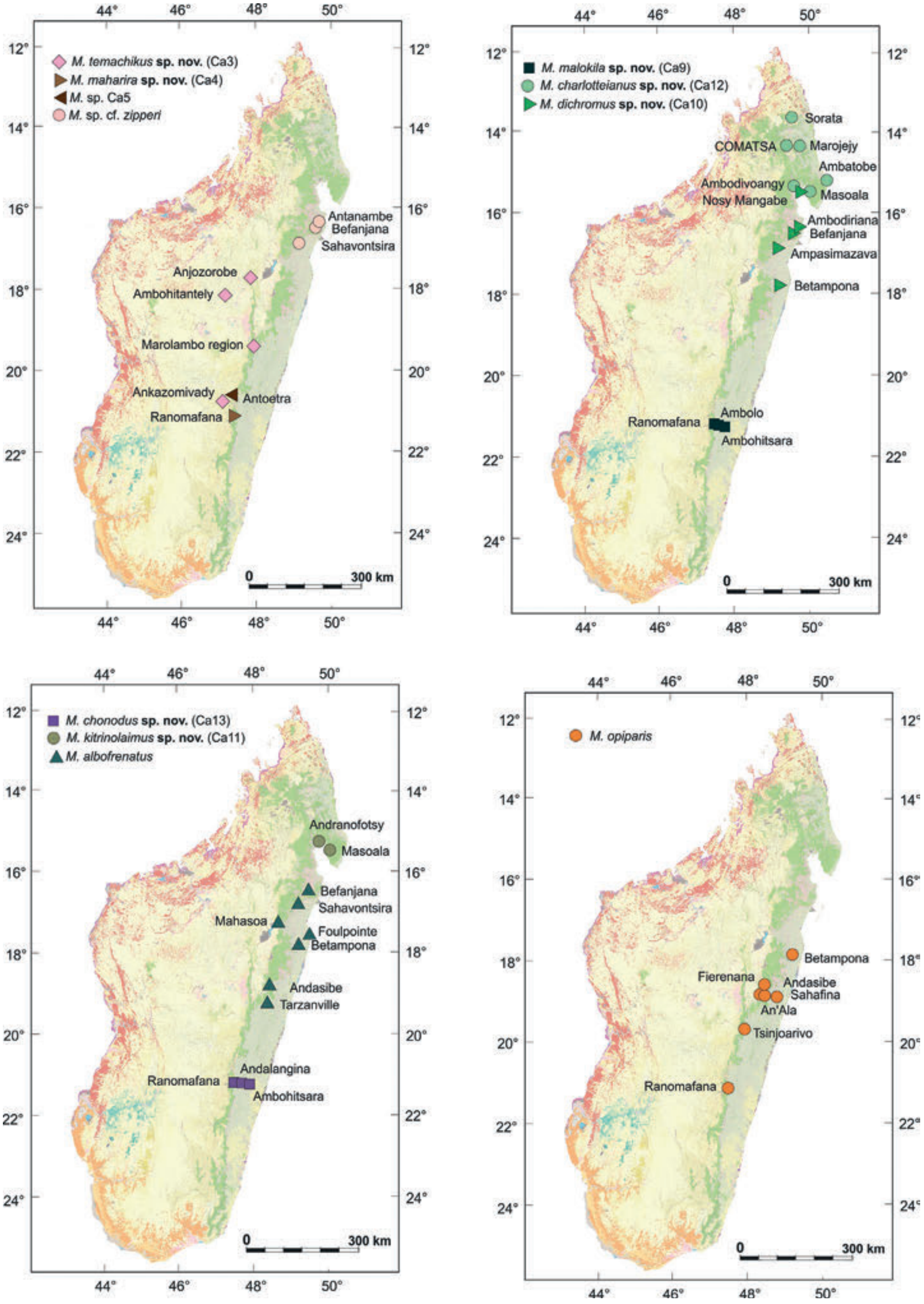


Fig. 24. Distribution maps of ten species and one candidate species in the subgenus *Chonomantis*, only showing sites confirmed by DNA sequencing. The base map shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; available at https://web.archive.org/web/20180419112513/, http://www.vegmad.org/). Vegetation is coloured as follows: green, humid forest (rainforest); red, western dry deciduous forest; pink, mangroves; orange, spiny forest-thicket; greenish blue, western subhumid forest; yellow, sclerophyllous woodland; grey, water bodies.

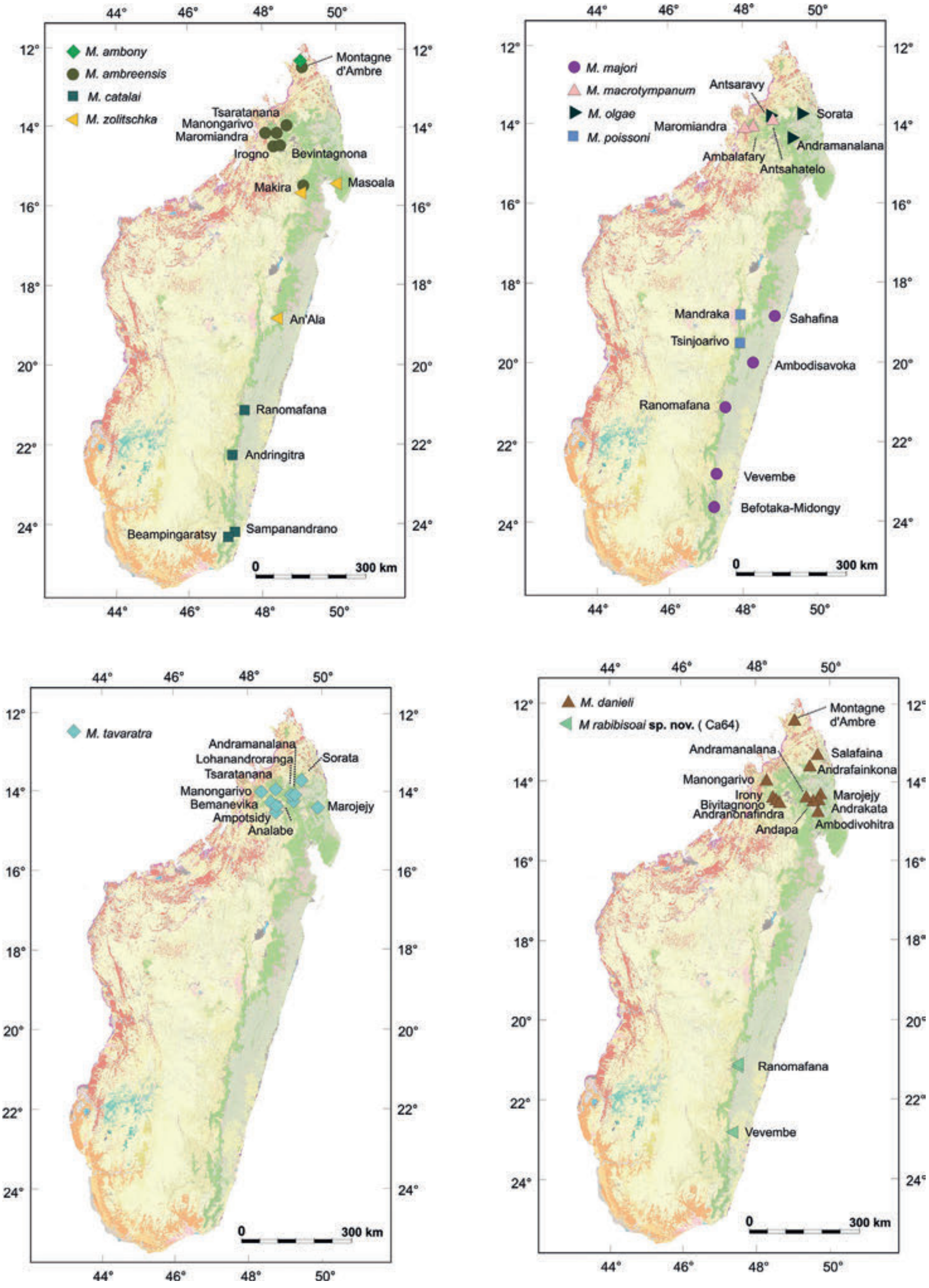


Fig. 25. Distribution maps of eleven species in the subgenus *Ochthomantis*, only showing sites confirmed by DNA sequencing. The base map shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; available at https://web.archive.org/web/20180419112513/, http://www.vegmad.org/). Vegetation is coloured as follows: green, humid forest (rainforest); red, western dry deciduous forest; pink, mangroves; orange, spiny forest-thicket; greenish blue, western subhumid forest; yellow, sclerophyllous woodland; grey, water bodies.

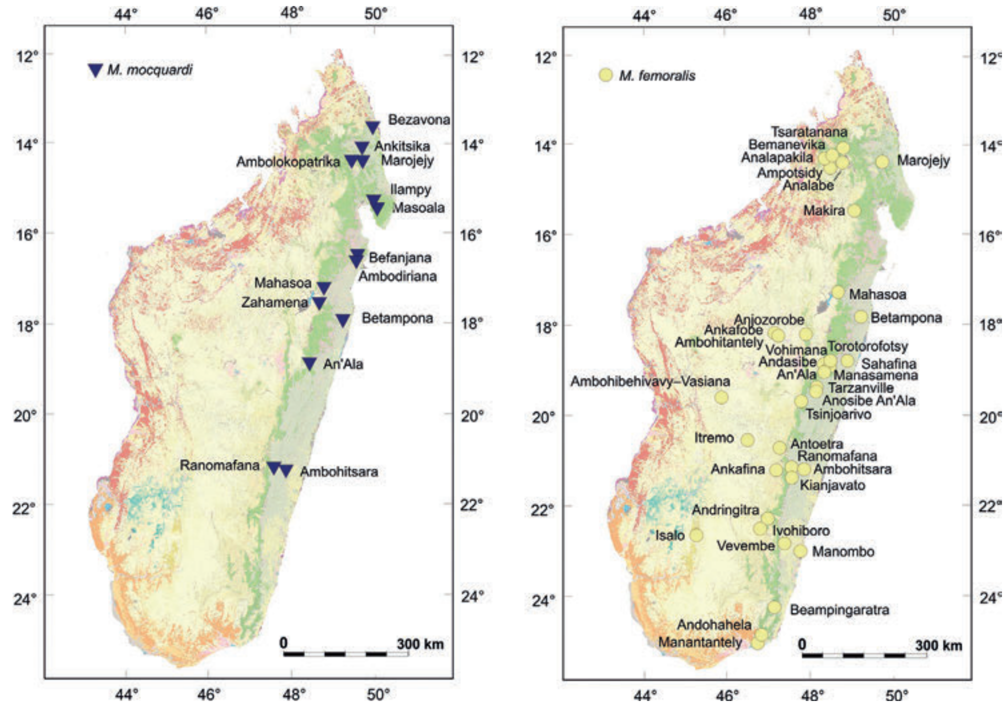


Fig. 26. Distribution maps of two widespread species in the subgenus *Ochthomantis*, only showing sites confirmed by DNA sequencing. The base map shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; available at https://web.archive.org/web/20180419112513/, http://www.vegmad.org/). Vegetation is coloured as follows: green, humid forest (rainforest); red, western dry deciduous forest; pink, mangroves; orange, spiny forest-thicket; greenish blue, western subhumid forest; yellow, sclerophyllous woodland; grey, water bodies.

stripe are typical for *M.* sp. Ca64. Therefore, in the following taxonomic accounts we will proceed by describing *M.* sp. Ca64 as a new species, *M. rabibisoai* sp. nov.

Distribution and biogeography of the subgenera *Chonomantis* and *Ochthomantis*

Under the assumption that the mitochondrial data correctly assigned individuals to evolutionary lineages (i.e., no introgression), our dataset provides molecular identification of 1147 samples of *Chonomantis* and 785 samples of *Ochthomantis*. Summarizing some sites (e.g., all specific sites from Ranomafana, Marojejy, or Sorata), the dataset includes approximately 60 unique locations for *Chonomantis*, and 87 unique localities for *Ochthomantis* (at several of these, multiple species of either subgenus occur) (Figs 23–26). Previous work (e.g., Blommers-Schlösser & Blanc 1991, Vences & Glaw 2004, Glaw & Vences 2007, Goodman et al. 2018, Rabibisoa et al. 2023) reported numerous additional localities based on the morphological examination of voucher specimens. However, given the many morphologically cryptic new species described from both subgenera in recent years (Vences & Glaw 2004, Bora et al. 2011, Scherz et al. 2020, Rabibisoa et al. 2023, and herein), it is obvious that many of these records are inaccurate and based on either outdated taxonomy or misidentification. The distribution maps proposed here therefore are only based on records confirmed by molecular data.

In both subgenera, there are clear biogeographical patterns already known from the Malagasy herpetofauna. Not surprisingly, there is elevational segregation, with some species occurring mainly or exclusively at highland sites (e.g., *M. brevipalmatus* in *Chonomantis*), and others specialized to lowland localities (e.g., *M. malokila* sp. nov. [=Ca9], *M. dichromus* sp. nov. [=Ca10], *M. kitrinolaimus* sp. nov. [=Ca11], *M. charlotteianus* sp. nov. [=Ca12]). Several species appear to be both widespread and locally common (e.g., *M. melanopleura* and *M. opiparis* in *Chonomantis*; *M. femoralis* and *M. mocquardi* in *Ochthomantis*), while others appear to be both restricted to smaller ranges and rather rare (e.g., *M. temachikus* sp. nov. [=Ca3], *M. malokila* sp. nov. [=Ca9], *M. chonodus* sp. nov. [=Ca13] in *Chonomantis*; *M. macrotympanum*, *M. poissoni*, and *M. rabibisoai* sp. nov. [=Ca64] in *Ochthomantis*). Among the relevant range extensions revealed or confirmed by our molecular dataset is the occurrence of *M. zolitschka* (previously only known from the type locality) from Makira and Masoala based on own data and sequences from Rakotozafy et al. (2025), and a new locality of *M. poissoni* at Tsinjoarivo.

New species descriptions

Altogether, our review revealed eight new species in the subgenus *Chonomantis* and one new species in the subgenus *Ochthomantis* with sufficient data for formal description and naming. At least two candidate species remain in *Chonomantis*, with insufficient material currently available for a formal description, and numerous mitochondrial lineages are here considered as deep intraspecific lineages and merit future investigation. For a full table with the species recognized in the two subgenera and their correspondence with previously used candi-

Table 7. Updated classification at the species level in the subgenera *Chonomantis* and *Ochthomantis* (in the genus *Mantidactylus*), following the present revision. Two additional deep genetic lineages of *Chonomantis* (*M.* sp. Ca5 and a deep lineage sister to *M. zipperi* defined as *M.* sp. Ca70 by Carné & Vieites (2024)) are not listed. Previous candidate species names refer to Vieites et al. (2009), Randrianiaina et al. (2011) and Carné & Vieites (2024) and may not list all names applied in various publications, in part due to confusion of sequences. * candidate species included in species as currently defined.

Species name	Species authors	Previous candidate species name	Type locality
Subgenus *Chonomantis*			
M. (*C.*) *aerumnalis*	(Peracca, 1893)		An'Ala
M. (*C.*) *albofrenatus*	(Müller, 1892)	Ca2*	Madagascar
M. (*C.*) *brevipalmatus*	Ahl, 1929		"Nord-West-Madagascar"
M. (*C.*) *delormei*	Angel, 1938		Antaranomby, Andringitra
M. (*C.*) *melanopleura*	(Mocquard, 1901)		Tolagnaro
M. (*C.*) *opiparis*	(Peracca, 1893)	Ca58	Andrangoloaka
M. (*C.*) *paidroa*	Bora et al., 2011	Ca59	Ankerana, Ranomafana
M. (*C.*) *zipperi*	Vences & Glaw, 2004	(Ca3 as wrongly defined)*	An'Ala
M. (*C.*) *charlotteianus*	new species	Ca12 A	Marojejy
M. (*C.*) *chonodus*	new species	Ca13 E	Ambohitsara
M. (*C.*) *dichromus*	new species	Ca10 C	Nosy Mangabe
M. (*C.*) *kitrinolaimus*	new species	Ca11 B	Masoala
M. (*C.*) *maharira*	new species	Ca4	Maharira, Ranomafana
M. (*C.*) *malokila*	new species	Ca9 D	Ranomafana
M. (*C.*) *temachikus*	new species	Ca3 F	Ambohitantely
M. (*C.*) *ventrilineatus*	new species	Ca1	Ranomafana
Subgenus *Ochthomantis*			
M. (*O.*) *ambony*	Scherz et al., 2020		Montagne d'Ambre
M. (*O.*) *ambreensis*	Mocquard, 1895		Montagne d'Ambre
M. (*O.*) *catalai*	Angel, 1935	Ca47	Isaka–Ivondro
M. (*O.*) *danieli*	Rabibisoa et al., 2023	Ca42, Ca61	Salafaina Forest
M. (*O.*) *femoralis*	(Boulenger, 1882)		East Betsileo
M. (*O.*) *macrotympanum*	Rabibisoa et al., 2023		Antsahatelo, Tsaratanàna
M. (*O.*) *majori*	Boulenger, 1896		Ivohimanita
M. (*O.*) *mocquardi*	Angel, 1929	Ca43*	Rogez, Moramanga District
M. (*O.*) *olgae*	Rabibisoa et al., 2023		Sorata
M. (*O.*) *poissoni*	Angel, 1937		Mandraka
M. (*O.*) *tavaratra*	Rabibisoa et al., 2023	Ca62, Ca63	Sorata
M. (*O.*) *zolitschka*	Glaw & Vences, 2004		An'Ala
M. (*O.*) *rabibisoai*	new species	Ca64	Vevembe

date species names, see Table 7. For a summary of the main diagnostic characters in *Chonomantis*, see Table 8. In the following, we proceed with naming and describing the nine new species revealed by the present study.

***Mantidactylus* (*Chonomantis*) *charlotteianus* sp. nov.**

Figs 27–28

Remark. Corresponds to *M.* sp. 12 (Vieites et al. 2009, Carné & Vieites 2024) and *M.* sp. Ca12 (Perl et al. 2014).

Holotype: ZSM 487/2016 (field number ZCMV 15136), adult female, collected on 16 November 2016 at Camp 1 “Mantella”, Marojejy, National Park, North East of Madagascar (geographical coordinates 14.4377° S, 49.7756° E, 456 m a.s.l.), by M. D. Scherz, A. Rakotoarison, M. C. Bletz, M. Vences, and J. Razafindraibe.

Paratypes: Five specimens: ZSM 488/2016 (ZCMV 15138), male, with same collection data as holotype. ZSM 225/2005 (FGZC 2733) and ZSM 226/2005 (FGZC 2771), two females, collected on 14 February 2005 at the type locality by F. Glaw, M. Vences, and R. D. Randrianiaina. ZSM 5067/2005 (ZCMV 2093), female, collected on 19 February 2005 to the type locality in Marojejy National Park (between Camp 1 “Mantella” and National Park entrance; precise geographical coordinates not recorded), by F. Glaw, M. Vences, and R. D. Randrianiaina. ZSM 365/2010 (FGZC 4221), female, collected on 31 March 2010 at Ambodivoangy, adjacent to Makira Reserve, North East of Madagascar (15.2899° S, 49.6203° E, ca. 100 m a.s.l.), by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, and F. M. Ratsoavina.

Additional material. One specimen from Sorata is assigned to this species but not included in the type series due to a substantial genetic differentiation: ZSM 1596/2012 (FGZC 3748), collected on 30 November 2012 at Sorata, in a bamboo forest above the campsite (near geographical coordinates 13.6752° S, ca. 49.4410° E, ca. 1485 m a.s.l.), by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F. M. Ratsoavina, and A. Razafimanantsoa. Several additional specimens probably belong to this species (measurements in supplementary data) but are not included in the paratype series because no molecular data are available: ZFMK 59918–59920 and ZFMK 59921 (from the type locality), ZFMK 59922 (from Camp 3 in Marojejy National Park), MNHN 1975.378 and MNHN 1975.387 (from the Marojejy Massif at 300 m elevation), and MNHN 1975.372 and MNHN 1975.384 (from the Marojejy Massif at 600 m elevation). See Vences & Glaw (2004) for detailed collection data of these specimens.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and

Table 8. Selected diagnostic characters among species of the subgenus *Chonomantis*. Morphometric values and ratios are based on measurements of specimens herein considered to be reliably identified (typically by DNA sequences, type status, or collected from type localities) as presented in Table 6 and https://doi.org/10.5281/zenodo.15161297. Morphometric ranges for some established species thus differ from those previously reported (Vences & Glaw 2004) as only a selection of reliably identified specimens was considered here. Character states of colour characters are simplified and exceptions may occur in some specimens. For *M. albofrenatus*, morphometric values are placed in parentheses as they reflect the high morphological variation among populations assigned to this species by mitochondrial DNA (see Results).

Species	Toe length V vs. III	Frenal stripe reach	Throat colour
M. brevipalmatus	larger	distinct until nostril	light
M. delormei	larger	fades between eye and nostril	marbled with dark pigment
M. aerumnalis	about equal	absent	uniformly dark brown
M. ventrilineatus sp. nov.	about equal	absent	uniformly dark brown
M. melanopleura	larger	distinct until nostril	uniformly dark brown
M. opiparis	larger	fades anterior to eye	uniformly dark brown
M. albofrenatus	smaller	distinct until nostril	dark brown with larger light spots
M. malokila sp. nov.	smaller	distinct until nostril	dark brown with larger light spots
M. charlotteianus sp. nov.	smaller	fades between eye and nostril	dark brown with larger light spots
M. dichromus sp. nov.	smaller	fades between eye and nostril	dark brown with larger light spots
M. kitrinolaimus sp. nov.	smaller	fades between eye and nostril	marbled with dark pigment
M. paidroa	smaller	distinct until nostril	dark brown with larger light spots
M. zipperi	smaller	fades anterior to eye	dark brown with small light spots
M. chonodus sp. nov.	smaller	absent	dark brown with larger light spots
M. maharira sp. nov.	about equal	distinct until nostril	dark brown with larger light spots
M. temachikus sp. nov.	smaller	fades between eye and nostril	irregular light marbling on brown

subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female (see Glaw et al. 2000, Vences et al 2007), (c) sharp dorsolateral colour border between dorsal and lateral coloration along continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 21.9–30.7 mm), and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V < III (vs. V > III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), largely uniform dorsum (vs. presence of dorsolateral light bands), toe V < III (vs. V = III) and throat centrally with an irregular series of light spots (vs. continuous line); from *M. melanopleura* and *M. opiparis* by toe V < III (vs. V > III), shorter limbs (ratio HIL/SVL in males 1.51–1.70 vs. 1.73–1.89), and throat centrally with an irregular series of light spots (vs. continuous line); from *M. paidroa* by throat centrally with an irregular series of light spots (vs. usually continuous line), frenal stripe running until a point between eye and nostril (vs. running to nostril), and smaller tympanum (TD eye ratio < 1.2 vs. > 1.4); from *M. zipperi* by presence of a distinct frenal stripe running until a point between eye and nostril (vs. faded anterior to eye), and throat centrally with an irregular series of light spots (vs. continuous line); phylogenetically, in a clade with *M. albofrenatus* which according to the definition herein is morphologically quite variable, it can be distinguished from highland populations of that species, and perhaps also coastal populations, by frenal stripe not reaching the nostril (vs. reaching nostril). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "T" at site 1105, "A" at site 1107, "T" at site 1108, and "A" at site 1115 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult female in a very good state of preservation (Fig. 27). Part of muscle tissue and skin from right thigh removed as tissue sample for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, as wide as body. Snout long and subacuminate in dorsal and lateral view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, slightly concave, loreal region concave. Tympanum distinct, smaller than eye, oval, horizontal diameter of tympanum 81 % of horizontal eye diameter. Supratympanic fold weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye, then indistinct, bending towards forelimb insertion and running directly adjacent to tympanum. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two distinct rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct but recognizable. Fingers without webbing. Relative length of fingers: I < II = IV < III, fourth finger of same length as second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (92 %). Lateral metatarsalia

Throat line	Male femoral glands	Male SVL (mm)	Male TD/ED	Male HIL/SVL
indistinct, sometimes broad line	large, very prominent	27.6–35.3	1.05–1.38	1.82–2.10
indistinct, sometimes broad line	large, very prominent	NA	NA	NA
continuous line	large, very prominent	24.5–26.9	0.68–0.87	1.80–1.96
continuous line	large, very prominent	22.8–26.0	0.67–0.88	1.78–1.89
continuous line	small, indistinct	29.9–32.3	1.00–1.47	1.74–1.89
continuous line	small, indistinct	25.0–25.2	1.21–1.24	1.73–1.78
line of large spots	large	(19.3–26.0)	(0.70–1.38)	(1.52–1.98)
line of large spots	large	25.8	0.90	1.50
irregular line of spots	large	23.7–25.5	1.06–1.15	1.51–1.70
line of large spots	large	22.3–26.2	0.86–1.06	1.58–1.71
marbling forming indistinct broad line	medium-sized	24.7	0.86–1.00	1.62–1.64
continuous line	large	22.0–22.3	1.43–1.50	1.57–1.64
continuous line	medium-sized	23.0–23.6	1.33–1.38	1.58–1.61
continuous line	large	20.1–26.7	0.67–0.96	1.63–1.80
continuous line	large	22.1	0.94	1.77
marbling forming indistinct broad line	large	22.2–23.0	1.12–1.20	1.78–1.80

M. chonodus **sp. nov.** (Ca13)
ZSM 2383/2007 (ZCMV 5940)
Ambohitsara

M. temachikus **sp. nov.** (Ca3)
ZSM 324/2005 (FGZC 2161)
Ambohitantely

M. malokila
sp. nov. (Ca9)
ZMB 81915 / JCR6
Ranomafana

M. kitrinolaimus **sp. nov.** (Ca11)
ZSM 267/2016 (FGZC 5437)
Masoala

M. charlotteianus **sp. nov.** (Ca12)
ZSM 487/2016 (ZCMV 15136)
Marojejy

M. ventrilineatus **sp. nov.** (Ca1)
ZSM 411/2006 (ZCMV 2964)
Ranomafana

M. maharira **sp. nov.** (Ca4)
ZMA 20038 (ZCMV 234)
Ranomafana (Maharira)

M. dichromus **sp. nov.** (Ca10)
ZSM 5070/2005 (ZCMV 2115)
Nosy Mangabe

◀ **Fig. 27.** Photographs of the preserved holotypes of the eight new species of the subgenus *Chonomantis* described herein, in dorsal and ventral views.

Fig. 28. Photos of representative individuals of *Mantidactylus* (*Chonomantis*) *charlotteianus* sp. nov. (Ca12) in life, in dorsolateral and ventral views. All photos except D, E, G and H show specimens identified by mitochondrial DNA sequences. **A–B.** Female paratype ZSM 365/2010 (FGZC 4221) from Ambodivoangy, photographed 2010. **C.** Paratype ZSM 225/2005 (FGZC 2733) from Marojejy, photographed 2005. **D–E.** Male specimen from Marojejy, photographed in 1995. **F.** Paratype specimen ZCMV 15075 from Marojejy, photographed 2016. **G–H.** Specimen from Marojejy, photographed 2016 (photos not reliably assignable to a voucher specimen).

largely separated by webbing. Inner and (small) outer metatarsal tubercle distinct. Foot webbing formula: 1 (1), 2i (2), 2e (1), 3i (2.5), 3e (1.75), 4i (3), 4e (3), 5 (1.25). Relative length of toes: I < II < V < III < IV, third toe longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Rudimentary femoral glands present.

Colour after eight years in preservative dorsally uniformly light brown. Dorsolateral folds constitute a very marked colour border to the uniformly dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis. A distinctly marked frenal stripe runs from forelimb insertion to the anterior part of the eye where it bends upwards and finishes slightly anteriorly to the eye. Forelimbs light brown with thin dark crossbands, hindlimbs dorsally and posterodorsally almost uniformly dark so that no crossband pattern can be recognized, with only some light markings or spots. Ventrally dark brown on throat, chest and anterior belly, with a central line of ca. 10 small white spots forming an interrupted longitudinal line on throat; a few more small white spots laterally on throat. Larger and denser white spots on chest and anterior belly; posterior belly and hindlimbs light with brown spots and speckles.

Variation. For measurements of the type series, see Table 6; all measurements of specimens assigned to this species are available from https://doi.org/10.5281/zenodo.15161297. The paratypes from the type locality all agree with the holotype in general morphology and coloration, e. g., by having a dark throat with a central line of light spots and a relatively uniform light brown dorsum without symmetrical darker pattern as is typical for e. g. *M. melanopleura*, *M. opiparis* or *M. zipperi*. In the paratype ZSM 365/2010 from Ambodivoangy, the light spots on the throat are sparse and a continuous central line of spots is barely discernible. Males are smaller than females and have a relatively larger tympanum; in reliably sexed specimens, SVL is 23.7–25.5 mm in males and 28.5–30.7 mm in females and TD/ED ratio is 1.06–1.15 in males and 0.55–0.88 in females.

Etymology. The species epithet is a patronym honoring Charlotte Richter-Peill in recognition of her support to biodiversity research and nature conservation through the BIOPAT initiative.

Natural history. Poorly known. Specimens were collected along streams in rainforest. They were found on the forest floor, on wet leaf litter or on herbaceous plants, very active at night after a rain late in the afternoon. Advertisement call and tadpole not recorded.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from six localities in the North East and the boundary between that region and the northern Central East of Madagascar at relatively low elevations (Fig. 24): (1) the type locality, Marojejy, (2) a nearby site in the Tsaratanàna-Marojejy Corridor Protected Area (COMATSA), (3) Ambatobe, (4) Masoala, (5) Ambodivoangy, and (6) Sorata, this latter population being the genetically most divergent one. The reliably known elevational range is 100–456 m a. s. l.; the genetically divergent Sorata population was found at 1485 m a. s. l.

Mantidactylus (*Chonomantis*) *chonodus* sp. nov.
Figs 27, 29

Remark. Corresponds to *M.* sp. 13 (Vieites et al. 2009, Grosjean et al. 2011, Carné & Vieites 2024) and *M.* sp. Ca13 (Perl et al. 2014).

Holotype: ZSM 2383/2007 (field number ZCMV 5940), adult male, collected on 3 March 2007 at Ambohitsara (geographical coordinates 21.3572° S, 47.8157° E, 294 m a. s. l.), southern Central East of Madagascar, by M. Vences, K. C. Wollenberg, and E. Rajeriarison.

Paratypes: Two specimens: ZSM 749/2003 (FGMV 2002.535), male, collected on 24 January 2003 at the type locality, by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas, and D. R. Vieites. ZMA 20036 (ZCMV 84), male, collected on 21 January 2004 at the type locality by D. R. Vieites and I. de la Riva.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female, (c) sharp dorsolateral colour border between dorsal and lateral coloration along continuous dorsolateral folds, (d) smooth dorsal skin, (e) relatively small size (adult SVL 20.1–26.7 mm), (f) specialized funnel-mouth tadpole, and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V < III (vs. V > III), presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by largely uniform dorsum (vs. presence of dorsolateral light bands), toe V < III (vs. V = III); from *M. melanopleura* and *M. opiparis* by toe V < III (vs. V > III), and tympanum in males smaller than eye (vs. larger); from *M. paidroa* by absence of a distinct frenal stripe (vs.

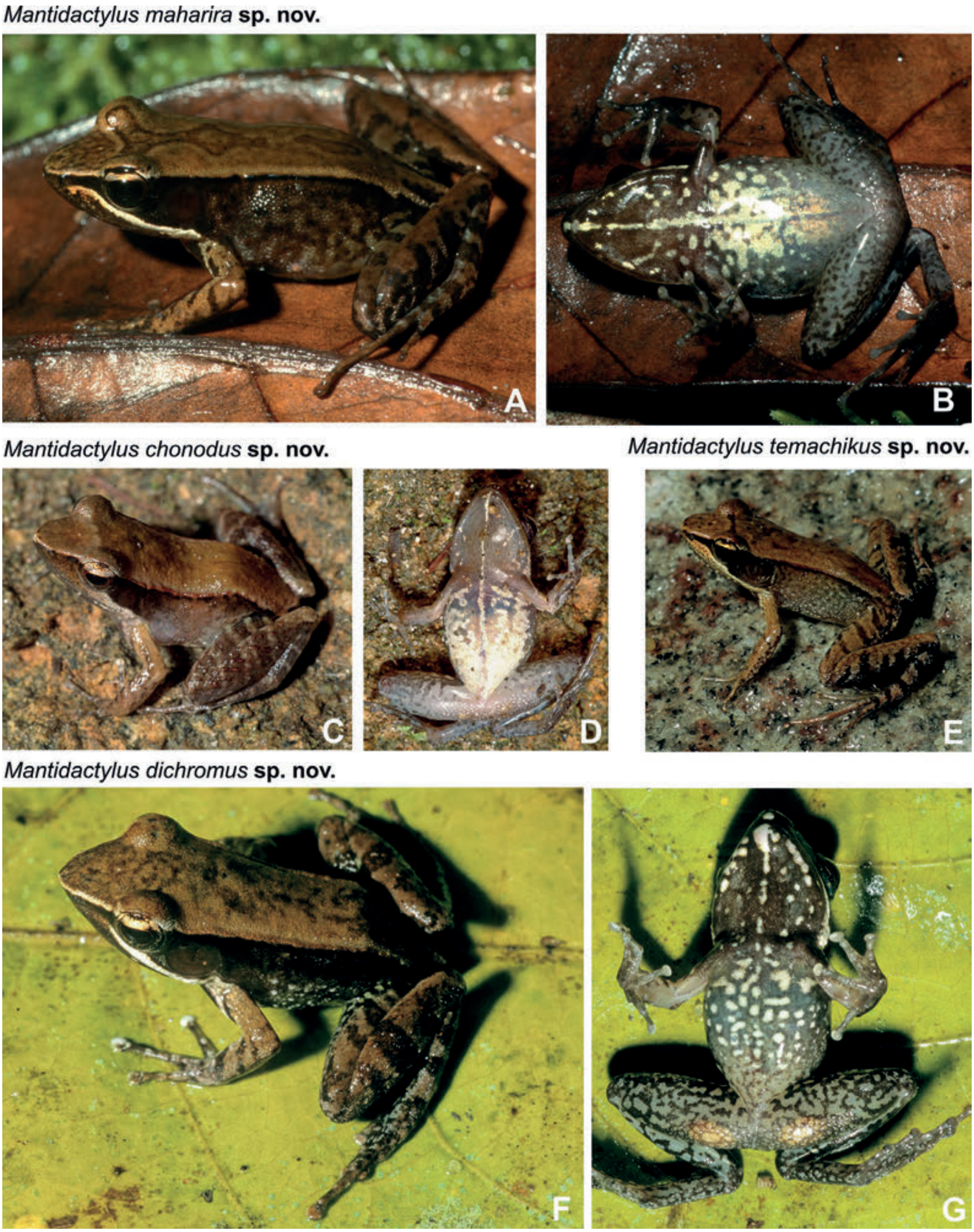


Fig. 29. Photos of representative individuals of three newly described species of *Mantidactylus* (subgenus *Chonomantis*) in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A–B.** *M. maharira* sp. nov. (Ca4), female holotype ZMA 20038 (ZCMV 234) from Maharira, Ranomafana, photographed 2004. **C–D.** *M. chonodus* sp. nov. (Ca9), ZSM 749/2003 (FGMV 2002.535), male paratype from Ambohitsara, photographed 2003. **E.** *M. temachikus* sp. nov. (Ca3), male holotype ZSM 324/2005 (FGZC 2161) from Ambohitantely, photographed 2005. **F–G.** *M. dichromus* sp. nov. (Ca10), male paratype ZSM 5068/2005 (ZCMV 895) from Nosy Mangabe, photographed 2005.

presence, running until nostril), and tympanum in males smaller than eye (vs. larger); from *M. zipperi* by tympanum in males smaller than eye (vs. larger); from *M. albofrenatus* and *M. charlotteianus* by absence of a distinct frenal stripe (vs. presence, running until nostril or to a point between eye and nostril), and continuous light stripe on throat (vs. series of light spots). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "T" at site 1086, "C" at site 1096, and "C" at site 1309 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult male in a good state of preservation (Fig. 27). Some muscle tissue removed from right thigh for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, wider than body. Snout long and subacuminate in dorsal and lateral view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, slightly concave, loreal region concave. Tympanum distinct, smaller than eye, oval, horizontal diameter of tympanum 72 % of horizontal eye diameter. Supratympanic fold basically absent or very weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct, not clearly visible. Fingers without webbing. Relative length of fingers: I < II < IV < III, fourth finger slightly longer than second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (96 %). Lateral metatarsalia largely separated by webbing. Inner and outer metatarsal tubercle distinct. Foot webbing formula: 1 (1), 2i (2), 2e (1), 3i (2), 3e (1.25), 4i (2.75), 4e (2.75), 5 (1). Relative length of toes: I < II < V < III < IV, third toe slightly longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Femoral glands prominent, with clearly visible central depression.

Colour after 17 years in preservative dorsally uniformly light brown with a very weakly contrasted darker symmetrical marking on the anterior dorsum. Dorsolateral folds constitute a very marked colour border to the dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis. A weakly marked frenal stripe runs from forelimb insertion to central part of the eye. Limbs dorsally brownish with sharply delimited dark brown crossbands; approximately five such crossbands visible on thigh. Posterodorsal surface of thighs dark brown with light spots and markings. Throat, chest, and anterior belly dark brown with a distinct central longitudinal light stripe and some light spots. Posterior belly uniformly cream, limbs ventrally cream with fine brown spotting.

Variation. Morphometric measurements of the full type series are given in Table 6 and a detailed description of the male paratype ZMA 20036 (ZCMV 84) is available from https://doi.org/10.5281/zenodo.15161297. Holotype and the two paratypes, all of them males collected from the type locality, span a relatively large size range (SVL 21.6–26.7) but share a relatively small tympanum (TD/ED ratio 0.67–0.96), a dark throat with continuous light central line, and lack of distinct frenal stripe anterior to eye.

Etymology. The species epithet is a Latinized adjective derived from the Ancient Greek χώνη (chōnē) meaning "funnel-shaped vessel" and the -ώδης (-ōdēs) suffix meaning "resembling", referring to the typical funnel-shaped tadpole mouthparts of this and other species in the subgenus *Chonomantis*.

Natural history. Poorly known. Specimens were collected along streams in rainforests. Advertisement call not recorded. The tadpole, with the funnel-shaped morphology of the oral disc typical for *Chonomantis*, was described by Grosjean et al. (2011) under the name *M.* sp. 13.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from three localities in the southern Central East of Madagascar (Fig. 24): (1) the type locality, Ambohitsara, (2) Ranomafana National Park (at Tsitolaka), and (3) Andalangina near Ifanadiana. The reliably known elevational range is 294 m a. s. l. at Ambohitsara to ca. 500 m a. s. l. at Andalangina.

***Mantidactylus* (*Chonomantis*) *dichromus* sp. nov.**

Figs 27, 29

Remark. Corresponds to *M.* sp. 10 (Vieites et al. 2009, Carné & Vieites 2024); the species was not included in Perl et al. (2014).

Holotype: ZSM 5070/2005 (ZCMV 2115), adult male, collected on 22 February 2005 on Nosy Mangabe islet off Maroantsetra, North East of Madagascar (geographical coordinates 15.4959° S, 49.7693° E, ca. 50–100 m a. s. l.), by F. Glaw, M. Vences, and R. D. Randrianiaina.

Paratypes: Four specimens: ZSM 5068/2005 (ZCMV 895), ZSM 5069/2005 (ZCMV 2113), ZSM 5071/2005 (ZCMV 2135), one male and two females, with same collection data as the holotype. ZSM 729/2009, (ZCMV 7221), male collected on 19 May 2009 at Ambatoroma "S II", Befanjana Forest (Manompana), precise geographical coordinates not recorded but in the vicinity of ca. 16.66° S, 49.59° E, by J. E. Randrianirina.

Additional material: Four specimens from the ZFMK collection (ZFMK 47210–47212 and ZFMK 52694), all originating from the type locality Nosy Mangabe, are here considered as belonging to this species, but are not included in the paratype series due to the lack of molecular confirmation. See Vences & Glaw (2004) for detailed collection data of these specimens.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female, (c) sharp dorsolateral colour border between dorsal and lateral coloration marked by continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 22.3–32.2 mm), and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V < III (vs. V > III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), largely uniform dorsum (vs. presence of dorsolateral light bands), toe V < III (vs. V = III) and throat centrally with a series of light spots (vs. continuous line); from *M. melanopleura* and *M. opiparis* by toe V < III (vs. V > III), shorter limbs (ratio HIL/SVL in males 1.58–1.71 vs. 1.73–1.89), and throat centrally with a series of light spots (vs. continuous line); from *M. paidroa* by throat centrally with a series of light spots (vs. usually continuous line), frenal stripe fading between eye and nostril (vs. running to nostril), and smaller tympanum (male TD/ED ratio < 1.1 vs. > 1.4); from *M. zipperi* by presence of a distinct frenal stripe running until a point between eye and nostril (vs. faded anterior to eye), throat centrally with a series of light spots (vs. continuous line), and smaller tympanum (male TD/ED ratio < 1.1 vs. > 1.3); from *M. chonodus* by throat centrally with a series of light spots (vs. continuous line) and presence of a distinct frenal stripe running until a point between eye and nostril (vs. absent or faded anterior to eye). Phylogenetically, the species is in a clade with *M. albofrenatus* and *M. charlotteianus*. From *M. albofrenatus*, which according to the definition herein is morphologically quite variable, it can be distinguished at least from highland populations, and perhaps also coastal populations, by frenal stripe not reaching the nostril (vs. reaching nostril); from *M. charlotteianus* by throat with a line of regular and relatively large spots (vs. smaller, irregular spots), and slightly smaller tympanum (male TD/ED ratio 0.86–1.06 vs. 1.06–1.15). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "T" at site 1091, "A" at site 1144, and "C" at site 1361 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult male in a good state of preservation (Fig. 27). Tissue and skin removed ventrally from right thigh for collection of tissue for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, slightly wider than body. Snout rather long, rounded in lateral view and slightly pointed in dorsal view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, slightly concave, loreal region concave. Tympanum distinct, slightly larger than eye, oval, horizontal diameter of tympanum 110 % of horizontal eye diameter. Supratympanic fold weakly expressed, not clearly recognizable. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two small but distinct rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle distinct. Fingers without webbing. Relative length of fingers: I < II = IV < III, fourth finger of same length as second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot of same length as tibia (100 %). Lateral metatarsalia largely but not completely separated by webbing. Inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable. Feet with very little, almost rudimentary webbing. Foot webbing formula: 1 (1), 2i (2), 2e (1), 3i (2.5), 3e (2), 4i (3), 4e (3), 5 (2). Relative length of toes: I < II < V < III < IV, third toe longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Femoral glands distinct.

Colour after 20 years in preservative dorsally uniformly brown with a somewhat darker tint centrally. Dorsolateral folds constitute a very marked colour border to the dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis up to the nostril. A distinctly marked frenal stripe runs from forelimb insertion to the area underneath the eye, then becoming less distinct towards the nostril, clearly bending upwards and leaving a light brown area on the upper lip underneath. Hindlimbs dorsally brownish with distinct crossbands: four on thigh, four on shank, and three to four on tarsus and foot; forelimbs light brown without distinct crossbands. Posterodorsal surface of thighs dark brown with irregular light spots. Throat, chest, and anterior belly dark brown; throat with a central longitudinal series of light spots, flanked by several more light spots on the throat and chest. Anterior belly with larger light dots and posterior belly cream with irregular dark spots and marbling. Limbs ventrally cream, with dense vermiculated dark brown pattern on hindlimbs.

Variation. Morphometric measurements of the full type series are given in Table 6, and a table with measurements of all specimens assigned to this species is available from https://doi.org/10.5281/zenodo.15161297. All specimens share a rather similar dorsal and ventral colour pattern; ventrally, the dark brown colour with light dots on the throat also extends onto chest and anterior belly, in ZSM 5068/2005 also onto posterior belly. Rosa et al. (2012) show a specimen from Betampona on their fig. 5r in dorsolateral view which agrees well with specimens from Nosy Mangabe (Fig. 29) in its frenal stripe fading between eye and nostril.

Males are smaller than females and have a relatively larger tympanum; in reliably sexed specimens, SVL is 22.3–26.2 mm in males and 30.1–32.2 mm in females and TD/ED ratio is 0.86–1.06 in males and 0.72–0.84 in females.

Etymology. The species epithet is a Latinized adjective derived from Ancient Greek διχρωμος (dikhromos) meaning "two-coloured". It refers to the typical colour border between light dorsal and dark lateral colour characterizing this and many other species in the subgenus *Chonomantis*.

Natural history. Poorly known. Specimens were collected along streams in low-elevation rainforest. Advertisement call and tadpole not recorded.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from four lowland localities at relatively low elevations in the northern Central East of Madagascar (Fig. 24): (1) the type locality Nosy Mangabe, (2) Ambodiriana, (3) Befanjana, (4) Ampasimazava, and (5) Betampona. The reliably known elevations are ca. 50–100 m a.s.l. (Nosy Mangabe) and 53 m a.s.l. at Ambodiriana (Gehring et al. 2010), but the species certainly also occurs at higher elevations at Befanjana (elevation not recorded) and Betampona.

Mantidactylus (*Chonomantis*) *kitrinolaimus* sp. nov.

Figs 27, 30

Remark. Corresponds to *M.* sp. 11 (Vieites et al. 2009, Carné & Vieites 2024); not included in Perl et al. (2014).

Holotype: ZSM 267/2016 (field number FGZC 5437), adult male, collected on 12 August 2016 near the hotel "Eco Lodge chez Arol", Masoala Peninsula, North East of Madagascar (geographical coordinates 15.712° S, 49.9640° E, ca. 21 m a.s.l.), by F. Glaw, D. Prötzel, J. Forster, K. Glaw, and T. Glaw.

Paratypes: Two paratypes: ZSM 127/2002 (FGMV 2001.1382) and ZSM 128/2002 (FGMV 2001.1426), male and female, collected on 17 December 2001 in a forest fragment near Andranofotsy, North East of Madagascar (geographical coordinates 15.4353° S, 49.8439° E, 85 m a.s.l.), by M. Vences and A. Sarovy.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands, (c) sharp dorsolateral colour border between dorsal and lateral coloration along continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 24.7–29.5 mm), and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V < III (vs. V > III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), largely uniform dorsum (vs. presence of dorsolateral light bands), toe V < III (vs. V = III) and throat relatively light with indistinct broad line (vs. distinct narrow line); from *M. melanopleura* and *M. opiparis* by toe V < III (vs. V > III), shorter hindlimbs (ratio HIL/SVL in males 1.62–1.64 vs. 1.73–1.89), and throat relatively light with indistinct broad line (vs. distinct narrow line); from *M. paidroa* by throat relatively light with indistinct broad line (vs. dark with distinct line), frenal stripe fading between eye and nostril (vs. running to nostril), and smaller tympanum (male TD/ED ratio ≤ 1.0 vs. > 1.4); from *M. zipperi* by presence of a distinct frenal stripe running until a point between eye and nostril (vs. faded anterior to eye), throat relatively light with indistinct broad line (vs. distinct narrow line), and smaller tympanum (male TD/ED ratio ≤ 1.0 vs. > 1.3); from *M. chonodus* by throat relatively light with indistinct broad line (vs. distinct line), and presence of a distinct frenal stripe

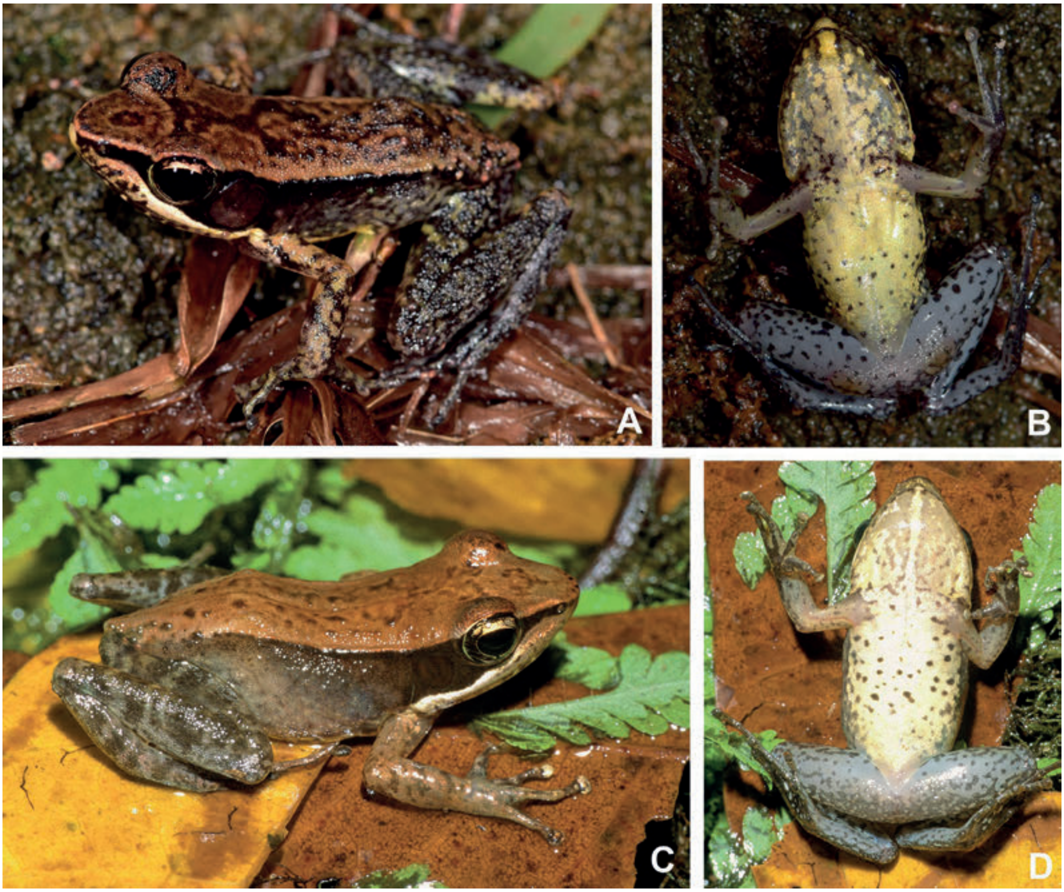


Fig. 30. Photos of representative individuals of *Mantidactylus* (*Chonomantis*) *kitrinolaimus* sp. nov. (Ca11) in life, in dorsolateral and ventral views. All photos show specimens identified by mitochondrial DNA sequences. **A–B.** Male holotype ZSM 267/2016 (FGZC 5437), photographed 2016. **C–D.** Female specimen from Andranofotsy (photos not reliably assignable to a voucher specimen, but belonging to same series collected with paratypes from this site).

running until a point between eye and nostril (vs. absent or faded anterior to eye). Phylogenetically, the species is in a clade with *M. albofrenatus*, *M. charlotteianus* and *M. dichromus* but differs from these species by throat relatively light with indistinct broad line (vs. dark with series of light spots) and yellowish colour on ventral side (vs. absence). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "G" at site 1104, and "C" at site 1406 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult male in a very good state of preservation (Fig. 27). Tongue removed as tissue sample for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, slightly wider than body. Snout long and truncate in dorsal and lateral view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, slightly concave, loreal region concave. Tympanum distinct, of same size as eye, oval, horizontal diameter of tympanum 100 % of horizontal eye diameter. Supratympanic fold weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye, then bending towards forelimb insertion and running directly adjacent to tympanum. Tongue missing. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct, not clearly visible. Fingers without webbing. Relative length of fingers: I < II < IV < III, fourth finger longer than second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (95 %). Lateral metatarsalia partly connected by tissue (only partly separated by webbing). Inner and outer metatarsal tubercle distinct. Foot webbing formula: 1 (1), 2i (2), 2e (1), 3i (2.5), 3e (2), 4i (3), 4e (3), 5 (1.75). Relative length of toes: I < II < V < III < IV, third toe distinctly longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Femoral glands large and prominent, with clearly visible central depression.

Colour after eight years in preservative dorsally light brown with a quite contrasted dark brown symmetrical marking on the anterior dorsum, somewhat hourglass-shaped, and some dark speckles on posterior dorsum. Dorsolateral folds constitute a very marked colour border to the dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis but is washed with lighter marbling on the flanks, particularly in their posterior half towards the inguinal region. A distinctly marked frenal stripe runs from forelimb insertion to the anterior part of the eye where it bends upwards and is recognizable up to a point underneath the nostrils. The upper lip, underneath the frenal stripe, is light with dark speckles. Limbs dorsally and posterodorsally dark brown with light markings or spots which only faintly aggregate to form crossbands. Ventrally light, with silvery white tint on throat, chest and anterior belly, with a more yellowish-beige tint on posterior belly and limbs. Indistinct and weakly expressed symmetrical dark marbling on the throat, some brown spots on belly, dense brown speckles on hindlimbs.

Variation. Morphometric data of the entire type series are given in Table 6. All three specimens share the typical ventral colour pattern, but in the two paratypes of Andranofotsy the dark marbling on the throat is of a higher density and the abdomen has a silvery appearance. The two males are smaller than the female (SVL 24.7 mm vs. 29.5 mm) and have a larger tympanum (TD/ED 0.86–1.00 vs. 0.67).

Etymology. The species epithet is a Latinized adjective formed from the Ancient Greek terms κίτρινος (kítrinos) meaning "yellowish" and λαιμός (laimós) meaning "throat", and refers to the yellowish colour on the throat (and venter) typical for several specimens of this species.

Natural history. Poorly known. Specimens were collected along streams in disturbed low-altitude rainforest. Advertisement call and tadpole not recorded.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from two lowland localities at the border between the northern Central East and North East regions of Madagascar (Fig. 24): (1) the type locality on the Masoala Peninsula, and (2) Andranofotsy. The known elevational range is 21–85 m a. s. l.

Mantidactylus (*Chonomantis*) *maharira* sp. nov.

Figs 27, 29

Remark. Corresponds to *M.* sp. 4 (Vieites et al. 2009, Carné & Vieites 2024) and *M.* sp. Ca4 (Perl et al. 2014).

Holotype: ZMA 20038 (ZCMV 234), adult female, collected on 24 January 2004 at the base camp of Maharira Mountain, Ranomafana National Park, southern Central East of Madagascar (geographical coordinates 21.3258° S, 47.4025° E, approximately 1248 m a. s. l.), by M. Vences, I. de la Riva, E. Rajeriarison, and T. Rajoafiarison.

Paratype: ZMA 20039 (ZCMV 233), adult male, with the same collection data as holotype.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female, (c) sharp dorsolateral colour border between dorsal and lateral coloration marked by continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 22.1–28.5 mm), and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V = III (vs. V > III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), and largely uniform dorsum (vs. presence of dorsolateral light bands); from *M. melanopleura* and *M. opiparis* by toe V = III (vs. V > III), and smaller tympanum (male TD/SVL < 1 vs. ≥ 1.0); from *M. paidroa* by toe V = III (vs. V < III), and smaller tympanum (male TD/SVL < 1 vs. ≥ 1.4); from *M. zipperi* by presence of a distinct frenal stripe running to nostril (vs. faded anterior to eye), toe V = III (vs. V < III), and smaller tympanum (male TD/ED ratio < 1.0 vs. > 1.3); from *M. chonodus* by frenal stripe running to nostril (vs. absent or faded anterior to eye) and by toe V = III (vs. V < III); from *M. kitrinolaimus* by toe V = III (vs. V < III) and throat dark brown with spots and distinct dark line (vs. relatively light with indistinct broad line); from *M. albofrenatus*, *M. charlotteianus*, and *M. dichromus* by toe V = III (vs. V < III), and throat dark brown with continuous light line (vs. series of spots). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "G" at site 1044, and "T" at site 1186 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult female in a good state of preservation (Fig. 27). Part of muscle tissue and skin from right thigh removed as tissue sample for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, as wide as body. Snout moderately long and subacuminate in dorsal and lateral view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, very slightly concave, loreal region concave. Tympanum distinct, smaller than eye, oval, horizontal diameter of tympanum 72 % of horizontal eye diameter. Supratympanic fold weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye, then indistinct, bending towards forelimb insertion and running directly adjacent to tympanum. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two weakly developed oval aggregations, positioned directly posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct but recognizable. Fingers without webbing. Relative length of fingers: I < II = IV < III, fourth finger of same length as second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (94 %). Lateral metatarsalia largely separated by webbing. Inner and (small) outer metatarsal tubercle distinct. Webbing between toes weakly expressed; foot webbing formula: 1 (-), 2i (-), 2e (1), 3i (2.5), 3e (2), 4i (3), 4e (3), 5 (2). Relative length of toes: I < II < V = III < IV, third toe of same length as fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Rudimentary femoral glands present.

Colour after 21 years in preservative dorsally uniformly brown with a symmetrical diamond-shaped dark marking centrally on dorsum which connects to a dark band between eyes. Dorsolateral folds constitute a very marked colour border to the dark brown lateral colour that encompasses flanks, and especially, tympanic region and sides of the head ventral to the canthus rostralis up to the nostril. Along the flanks the darker brown colour is interrupted by irregular and poorly delimited lighter marbling. A distinct white frenal stripe runs from forelimb insertion to lower edge of eye, and from there to nostril. Hindlimbs with distinct dark brown crossbands: three on thigh, two or three on shank, and four on tarsus and foot. Forelimbs with a few dark patches but no regular crossbands. Ventrally, throat and chest dark brown interrupted by a median light band and several light dots arranged in a rather symmetrical pattern. Abdomen mostly cream with brown vermiculation; limbs ventrally cream with brown spots and markings.

Variation. Morphometric data of holotype and paratype are given in Table 6, and a detailed description of the male paratype is provided in Appendix 2 (https://doi.org/10.5281/zenodo.15161297). The male is smaller than the female (SVL 22.1 mm vs. 28.5 mm) and has a larger tympanum (TD/ED 0.94 vs. 0.72).

Etymology. The species epithet is a noun in apposition referring to Maharira, a mountain in Ranomafana National Park, where this species has been collected.

Natural history. Poorly known. Specimens were collected along streams in rainforest. Advertisement call and tadpole not recorded.

Distribution. This species is so far only known from its type locality, the forests surrounding Maharira Mountain in Ranomafana National Park, at 1248 m a. s. l. (Fig. 24).

Mantidactylus (*Chonomantis*) *malokila* sp. nov.

Figs 27, 31

Remark. Corresponds to *M.* sp. 9 (Vieites et al. 2009, Carné & Vieites 2024) and *M.* sp. Ca9 (Perl et al. 2014).

Holotype: ZMB 81915 (JCR 6), adult male, collected on 9 March 2010 at Ambolo, east of Ranomafana (geographical coordinates 21.2636° S, 47.5092° E, ca. 600 m a. s. l.), Madagascar, by J. C. Riemann and S. H. Ndriantsoa.

Paratypes: Three specimens: ZSM 748/2003 (FGMV 2002.534), adult female, collected on 24 January 2001 at Mangevo, Ranomafana National Park (21.3872° S, 47.4550 °E, ca. 590 m a. s. l.), by F. Rabemananjara, P. Bora, and E. Rajeriarison. ZMA 20035 (ZCMV 82) and ZMA 20037 (ZCMV 67), two females, collected on 21 January 2004 at Ambohitsara (geographical coordinates 21.3572° S, 47.8157° E, 294 m a. s. l.), southern Central East of Madagascar, by D. R. Vieites and I. de la Riva.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female, (c) sharp dorsolateral colour border between dorsal and lateral coloration along continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 25.8–31.7 mm), and (g) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V<III (vs. V>III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), largely uniform dorsum (vs. presence of dorsolateral light bands), toe V<III (vs. V=III) and throat centrally with a series of light spots (vs. continuous line); from *M. melanopleura* and *M. opiparis* by toe V<III (vs. V>III), shorter hindlimbs (ratio HIL/SVL in males 1.50 vs. 1.73–1.89), smaller tympanum (male TD/ED ratio 0.90 vs. ≥1.0), and throat centrally with a series of light spots (vs. continuous line); from *M. paidroa* by throat centrally with a series of light spots (vs. usually continuous line), and smaller tympanum (male TD/ED ratio 0.90 vs. >1.4); from *M. zipperi* by presence of a distinct frenal stripe running to nostril (vs. faded anterior to eye), throat centrally with a series of light spots (vs. continuous line), and smaller tympanum (male TD/ED ratio 0.90 vs. >1.3); from *M. chonodus* by throat centrally with a series of light spots (vs. continuous line) and presence of a distinct frenal stripe running to nostril (vs. absent or faded anterior to eye); from *M. maharira* by throat centrally with a series of light spots (vs. continuous line) and toe V<III (vs. V=III).

Phylogenetically, the species is in a clade with *M. albofrenatus*, *M. charlotteianus*, *M. dichromus*, and *M. kitrinolaimus*. It differs from *M. kitrinolaimus* by dark throat centrally with a series of light spots (vs. throat relatively light with indistinct broad line); from *M. charlotteianus*, *M. dichromus*, and *M. kitrinolaimus* by frenal stripe running to nostril (vs. fading between eye and nostril). No reliable morphological or chromatic differences are known to its direct sister species *M. albofrenatus*, which, according to the definition herein, is morphologically quite variable; it can however be distinguished from the mid-elevational populations of *M. albofrenatus* (i.e., Andasibe and nearby sites) by a smaller tympanum (TD/ED ratio 0.90 vs. ≥1.0), fewer and smaller white spots on throat and chest, and from all measured specimens of *M. albofrenatus* by shorter hindlimbs (male ratio HIL/SVL=1.50 vs. 1.52–1.98). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of “C” at site 957, “A” at site 1145, and “G” at site 1311 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

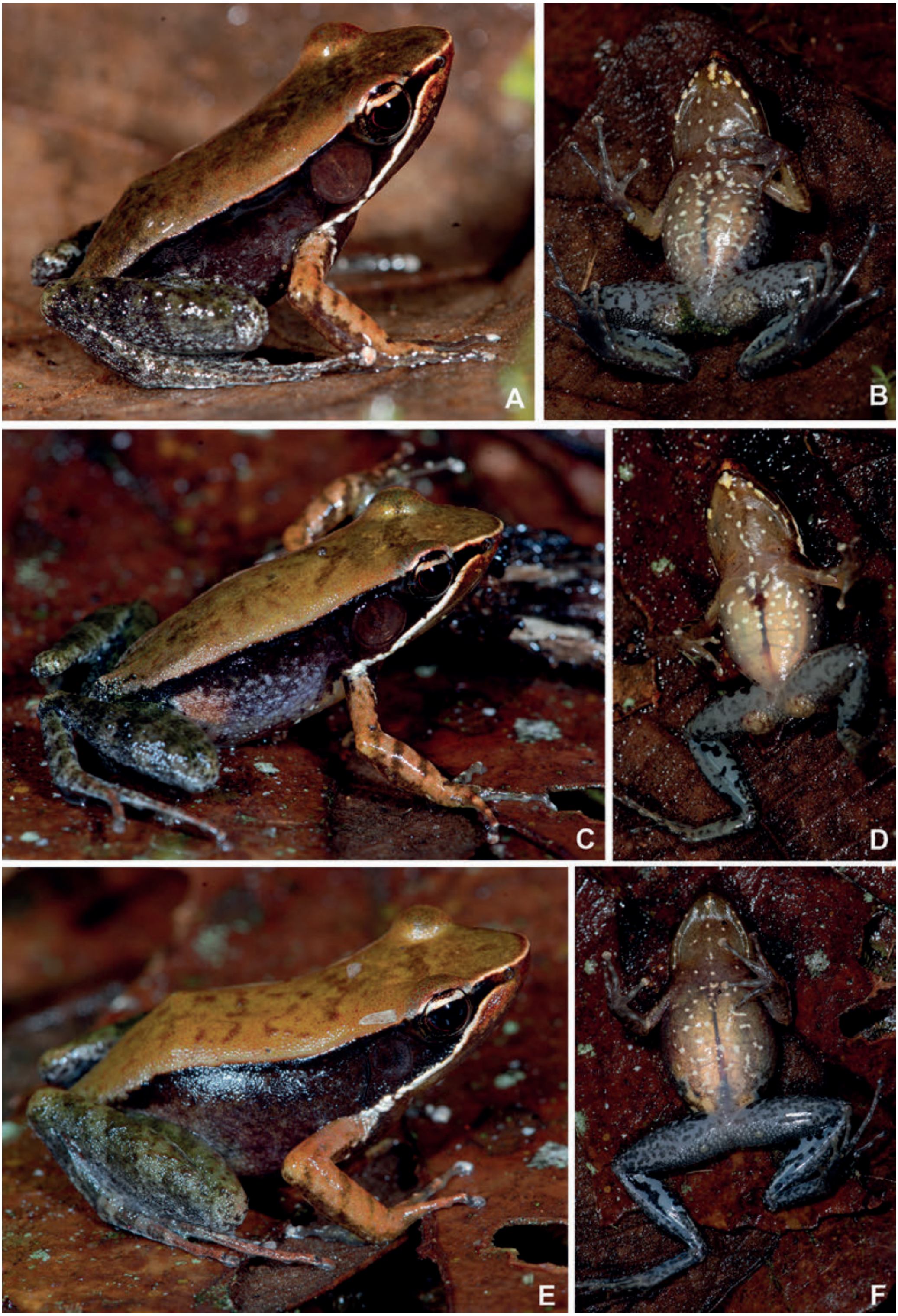
Description of the holotype

Adult male in a good state of preservation (Fig. 27). There is a small incision on the left side of the venter through which a part of liver has been removed for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, slightly wider than body. Snout rather long, and subacuminate in lateral view and round in dorsal view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, slightly concave, loreal region concave. Tympanum distinct, slightly smaller than eye, oval, horizontal diameter of tympanum 91 % of horizontal eye diameter. Supratympanic fold weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye, then indistinct, bending towards forelimb insertion and running directly adjacent to tympanum. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two distinct rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct but recognizable. Fingers without webbing. Relative length of fingers: I<II=IV<III, fourth finger of same length as second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (93 %). Lateral metatarsalia largely separated by webbing. Inner and (small) outer metatarsal tubercle distinct. Feet with very little, almost rudimentary webbing. Foot webbing formula: 1 (1), 2i (2.5), 2e (1.25), 3i (2), 3e (2), 4i (3), 4e (3), 5 (2). Relative length of toes: I<II<V<III<IV, third toe longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Femoral glands distinct, with clearly visible central depression.

Colour after 12 years in preservative dorsally uniformly brown with some weakly contrasted irregular darker and lighter colour. Dorsolateral folds constitute a very marked colour border to the dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis up to the nostril. A distinctly marked frenal stripe runs from forelimb insertion to the nostril, clearly bending upwards and leaving

Fig. 31. Photos of *Mantidactylus* (*Chonomantis*) *malokila* sp. nov. from Ambolo in life, in dorsolateral and ventral views. **A–B.** Male holotype ZMB 81915 (JCR 6). **C–D.** Additional male specimen (not collected, probably corresponding to JCR 8). **E–F.** Female specimen (not collected; JCR 7).

▶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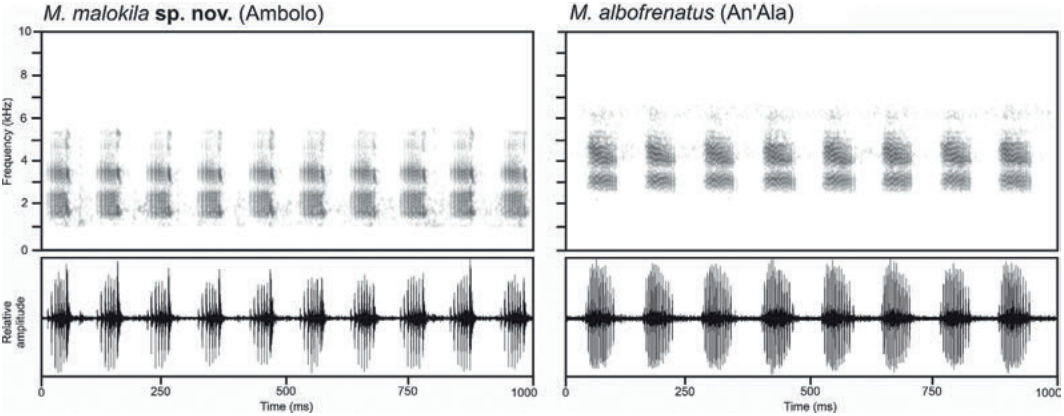

Fig. 32. Audiospectrograms and corresponding oscillograms of the advertisement calls of *Mantidactylus* (*Chonomantis*) *malokila* sp. nov. recorded from the holotype ZMB 81915 on 9 March 2010, and *M.* (*C.*) *albofrenatus* from a recording made on 12 February 1995, 13:30 h, at An'Ala (Vences et al. 2006), displayed at the same time scale (1000 ms).

a light brown area on the upper lip underneath. Hindlimbs dorsally brownish with weakly defined crossbands; forelimbs light brown with about five dark crossbands on lower arm. Posterodorsal surface of thighs dark brown with irregular light speckles and dots. Throat, chest and belly dark brown with a central longitudinal series of four light spots, and more irregular spots on throat, chest and belly which become more vermiculated on the posterior belly. Limbs ventrally cream, with loose vermiculated dark brown pattern on hindlimbs.

Variation. Morphometric data of the entire type series are given in Table 6. Two additional specimens (JCR 7 and JCR 8), one male and one female, observed and photographed along with the holotype at Ambolo, very closely matched the holotype in dorsal and ventral colour and pattern. The three female paratypes ZMA 20035, ZMA 20037 and ZSM 748/2003 agree with the female JCR 7 in having very faint light dots on the throat which even appear to be absent or faded in the preserved ZMA 20037 and ZSM 748/2003. The male holotype is smaller than the three female paratypes (SVL 25.8 mm vs. 29.5–31.7 mm) and has a larger tympanum size (TD/ED 0.90 vs. 0.75–0.83).

Etymology. The species epithet is a noun in apposition derived from the Malagasy words *maloka* (dark) and *ila* or *ilany* (side, flank), The name refers to the dark lateral colour, separated by a sharp dorsolateral colour border from the lighter dorsal colour, which characterizes this and many other species in the subgenus *Chonomantis*.

Natural history. Poorly known. Specimens were collected along streams in rainforest. ZMB 81915 was found on rocky surface on the stream bank. Tadpole not known.

Advertisement call. The advertisement call of *M. malokila* (Fig. 32) recorded from the holotype on 9 March 2010 at Ambolo (air temperature not recorded) consists of a short, distinctly pulsed note emitted at regular intervals in call series consisting of 3–20 calls (n = 6), with the longest series lasting for 2043 ms. Each call, apart from the distinctly separated pulses, shows some clear amplitude modulation with call energy being lowest the first pulse of each call. The terminal pulse of each call is of slightly longer duration (ca. 7 ms) compared to preceding pulses (ca. 3–4 ms). Call energy is distributed within a relatively broad frequency band. Numerical call parameters of 32 analyzed calls are as follows: call duration (= note duration) 45–55 ms (51.6 ± 3.0 ms); pulses/call 7–8 (7.3 ± 0.5); pulses/second within calls 142–167 (155.4 ± 9.9); call repetition rate within call series ca. 580 calls/minute; dominant frequency 1614–2201 Hz (1813 ± 224 Hz), prevalent bandwidth 1300–4200 Hz.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from three localities (Fig. 24), (1) the type locality Ambolo near Ranomafana, (2) Mangevo in Ranomafana National Park, and (3) Ambohitsara. The known elevational range is 294–600 m a.s.l.

Mantidactylus (*Chonomantis*) *temachikus* sp. nov.

Figs 27, 29

Remark. Corresponds to *M.* sp. 3 (Vieites et al. 2009, in tables but not in tree) and *M.* sp. Ca3 (Perl et al. 2014), but not *M.* sp. 3 used by Carné & Vieites (2024), which used the confused sequence of *M. zipperi* discussed above as the reference for that candidate species.

Holotype: ZSM 324/2005 (field number FGZC 2161), adult male, collected on 18 January 2005 at Ambohitantely Special Reserve, Jardin Botanique (geographical coordinates ca. 18.1725° S, 47.2767° E, ca. 1580 m a.s.l.), Madagascar, by M. Vences, L. du Preez, P. Bora, L. Raharivololoniaina, R. D. Randrianiaina, T. Razafindraibe, and E. Randriamitso.

Paratype: One specimen: ZSM 381/2010 (FGZC 4388), adult male, collected on 9 April 2010 at Anjozorobe (18.4214° S, 47.9383° E, 1315 m a.s.l.), by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, K. Mebert, E. Rajeriarison, F. Randrianasolo, and S. Rasamison.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands, (c) sharp dorsolateral colour border between dorsal and lateral coloration along continuous dorsolateral folds, (d) smooth dorsal skin, (e) presence of a frenal stripe, (f) relatively small size (adult SVL 22.2–23.0 mm), and (h) molecular phylogenetic relationships.

Within *Chonomantis*, the species can be distinguished, besides other characters (see Table 8), from *M. brevipalmatus* and *M. delormei* by toe V < III (vs. V > III) and presence of distinct dorsolateral colour border (vs. absence); from *M. aerumnalis* by presence of distinct frenal stripe (vs. absence), largely uniform dorsum (vs. presence of dorsolateral light bands), toe V < III (vs. V = III) and throat irregularly marbled light with only poorly marked central line (vs. continuous line); from *M. melanopleura* and *M. opiparis* by toe V < III (vs. V > III), throat irregularly marbled light with only poorly marked central line (vs. continuous line); from *M. paidroa* by throat irregularly marbled light with only poorly marked central line (vs. usually continuous line), frenal stripe fading between eye and nostril (vs. running to nostril), and smaller tympanum (male TD/ED ratio ≤ 1.2 vs. > 1.4); from *M. zipperi* by presence of a distinct frenal stripe running to a point between eye and nostril (vs. faded anterior to eye), throat irregularly marbled light with only poorly marked central line (vs. continuous line), and smaller tympanum (male TD/ED ratio ≤ 1.2 vs. > 1.3); from *M. chonodus* by throat irregularly marbled light with only poorly marked central line (vs. continuous line) and presence of a distinct frenal stripe running to nostril (vs. absent or faded anterior to eye); from *M. maharira* by throat irregularly marbled light with only poorly marked central line (vs. continuous line) and toe V < III (vs. V = III); from *M. albofrenatus*, *M. malokila*, *M. charlotteianus*, *M. dichromus*, and *M. kitrinolaimus* by throat irregularly marbled light with only poorly marked central line (vs. dark with a central series of white spots, or relatively light with indistinct broad line in *M. kitrinolaimus*); from *M. malokila*, *M. charlotteianus*, *M. dichromus*, and *M. kitrinolaimus* by longer limbs (male ratio HIL/SVL 1.78–1.80 vs. ≤ 1.71); and from *M. albofrenatus* and *M. malokila* by frenal stripe fading at a point between eye and nostril (vs. running to nostril). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "A" at site 1119, "A" at site 1121, and "C" at site 1193 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult male in a good state of preservation (Fig. 27). Some muscle tissue removed from right thigh for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, as wide as body. Snout long and rounded to very weakly subacuminate in dorsal and lateral view. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, largely straight, loreal region concave. Tympanum distinct, larger than eye, oval, horizontal diameter of tympanum 120 % of horizontal eye diameter. Supratympanic fold basically absent or very weakly expressed, dorsal to the tympanum replaced by distinct dorsolateral fold running to the eye. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two small, rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle indistinct, not clearly visible. Fingers without webbing. Relative length of fingers: I < II < IV < III, fourth finger slightly longer than second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (93 %). Lateral metatarsalia largely separated by webbing. Inner and outer metatarsal tubercle distinct. Foot webbing formula: 1 (1), 2i (2), 2e (1), 3i (2.5), 3e (2), 4i (3.25), 4e (3.25), 5 (2). Relative length of toes: I < II < V < III < IV, third toe slightly longer than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth.

Mantidactylus aerumnalis

Mantidactylus ventrilineatus sp. nov.

Fig. 33. Photos of representative individuals of *Mantidactylus* (*Chonomantis*) *aerumnalis* and *M.* (*C.*) *ventrilineatus* sp. nov. (Ca1) in life, in dorsolateral and ventral views. All photos of *M. ventrilineatus* sp. nov. show specimens identified by mitochondrial DNA sequences. **A–B.** Male of *M. aerumnalis* from An'Ala (photos not reliably assignable to a voucher specimen). **C–D.** Male holotype ZSM 411/2006 (ZCMV 2964) of *M. ventrilineatus* sp. nov. from Ranomafana, photographed 2006. **E–F.** Specimen of *M. ventrilineatus* sp. nov. from Mangevo, Ranomafana, probably corresponding to UADBA-FGMV 2002.651, photographed 2003. **G–H.** Female paratype ZMA 20111 (ZCMV 647) of *M. ventrilineatus* sp. nov. from Vevembe, photographed 2004.

Femoral glands large and prominent, with clearly visible central depression.

Colour after 19 years in preservative dorsally uniformly brown with a very weakly contrasted pattern of darker markings, including a dark band between eyes. Dorsolateral folds constitute a marked colour border to the dark brown lateral colour that encompasses flanks, tympanic region and sides of the head ventral to the canthus rostralis. Especially on the posterior flanks the dark brown colour is washed with a poorly contrasted lighter marbling. A distinctly marked white frenal stripe runs from forelimb insertion to anterior part of the eye where it bends upwards and gets more diffuse. Here and in the supralabial area, some light colour with fine brown spotting is present. Limbs dorsally brownish with sharply delimited dark brown crossbands; approximately three such crossbands visible on thigh. Posterodorsal surface of thighs dark brown with light spots and markings. Ventral side with a whitish-cream ground colour, with a more yellowish tint on the limbs, and brown spots and speckles in different intensity: quite dense on throat, where the central area is only weakly spared, forming an interrupted and indistinct central white stripe; dark speckles become less intense towards the posterior belly; fine dark spotting on limbs.

Variation. Morphometric data of holotype and paratype, both males, are given in Table 6. Both specimens agree in the relevant morphological characters (e. g., body size, relative tympanum size), and share the typical throat coloration where relatively dense dark marbling leaves out a poorly defined, broad central light stripe, reminiscent of the pattern observed in *M. kitrinolaimus*. Females are unknown.

Etymology. The species epithet is a Latinized adjective derived from the ancient Greek word τεμάχιον (temáchion = "piece") meaning "fragmentary". It refers to the occurrence of the species in highly fragmented forest remnants (e. g., in Ambohitantely) but also to the fragmentary knowledge we currently have on this frog.

Natural history. Poorly known, especially because specimens have in the past (Vences & Glaw 2004) been confused with the sympatric *M. zipperi* and the DNA sequence accession number was confused in Vieites et al. (2009). Specimens were collected along streams in rainforests. Advertisement call and tadpole unknown.

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from four highland localities in the northern Central East and southern Central East of Madagascar (Fig. 24): (1) the type locality, Ambohitantely, (2) Anjozorobe, (3) an unspecified site in the Marolambo region, and (4) Ankazomivady. The reliably known elevational range is 1315–1580 m a. s. l.

Mantidactylus (*Chonomantis*) *ventrilineatus* sp. nov.

Figs 27, 33

Remark. Corresponds to *M.* sp. 1 (Vieites et al. 2009, Carné & Vieites 2024) and *M.* sp. Ca1 (Perl et al. 2014) and was subsumed under *M. aerumnalis* in previous publications (e. g., Glaw & Vences 2007).

Holotype: ZSM 411/2006 (field number ZCMV 2964), adult male, collected on 24 February 2006 at Imaloka, Ranomafana National Park, southern Central East of Madagascar (geographical coordinates 21.2421° S, 47.4652° E, 1020 m a. s. l.), by local collectors.

Paratypes: Six specimens: ZSM 378/2006 (ZCMV 3079), female, collected February 2006 at Ranomena, Ranomafana National Park (21.2123° S, 47.4350° E, ca. 1000 m a. s. l.) by M. Vences and collaborators. ZSM 179/2006 (BOR 1025), male, collected between 7–13 October 2005 at Kilimagnarivo, Befotaka-Midongy du Sud National Park (23.7975° S, 47.0096° E, 690–890 m a. s. l., by P. Bora. ZMA 20111 (ZCMV 647) and ZMA 20112 (ZCMV 679), two females, collected on 10 February 2004 at Vevembe (22.7948° S, 47.1871° E, 581 m a. s. l.) by M. Vences and E. Rajeriarison. ZMA 19404 (FGMV 2002.481) and ZMA 19405 (FGMV 2002.482), one female and one male, collected on 24 January 2003 at Mangevo, Ranomafana National Park (21.3872° S, 47.4550° E, ca. 590 m a. s. l.), by F. Rabemananjara, P. Bora, and E. Rajeriarison.

Additional material: Several additional specimens probably belong to this species (measurements in Zenodo repository) but are not included in the paratype series because no molecular data are available: MNHN 1930.415 (Vondrozo), MNHN 1975.382 (Ranomafana), MNHN 1975.373 (Ranomafana), ZFMK 47254 (Tolongoina). See Vences & Glaw (2004) for detailed collection data.

Diagnosis. Assigned to the subgenus *Chonomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands and of a rudimentary femoral gland in the female, (c) sharp dorsolateral colour border between dorsal and lateral coloration, less strongly expressed than in other *Chonomantis* but still distinct, and along continuous dorsolateral folds, (d) smooth dorsal skin, (e) relatively small size (adult SVL 22.8–32.0 mm), (g) specialized funnel-mouth tadpole, and (h) molecular phylogenetic relationships.

Within *Chonomantis*, the species differs from all species except *M. aerumnalis* and *M. chonodus* by the absence of a frenal stripe and rather uniform lateral head between tympanum and snout tip (vs. presence of at least an incomplete light frenal stripe in all other species), from all species except *M. aerumnalis* and *M. maharira* by toe length V = III (vs. V < III or V > III), and from all species except *M. aerumnalis* by light dorsolateral bands running next to the dorsolateral fold and separating the fold from the darker central area of the dorsum (vs. absence of such bands). For additional morphological differences to other *Chonomantis*, see Table 8. From its sister species *M. aerumnalis*, the new species differs by a generally smaller size of males (SVL 22.8–23.4 in four individuals; one specimen exceptionally 26.0 mm vs. 24.5–26.9 mm) and somewhat smaller femoral glands (FGL 3.4-3.6 vs. 4.2–4.4 mm). The species can also be distinguished from all other *Chonomantis* by diagnostic nucleotide positions: MolD identified a robust diagnostic nucleotide combination of "A" at site 966, "A" at site 1009, and "A" at site 1055 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of the holotype

Adult male in a good state of preservation (Fig. 27). Some muscle tissue removed from left thigh and shank for molecular analysis. Measurements are given in Table 6. Body slender. Head longer than wide, wider than body. Snout long and subacuminate to rounded in dorsal and lateral view. Nostrils directed laterally, slightly protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, straight, loreal region concave. Tympanum distinct, slightly smaller than eye, oval, horizontal diameter of tympanum 88 % of horizontal eye diameter. Supratympanic fold distinct, running straight from eye to posterior tympanum and then bending towards forelimb insertion. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I < II < IV < III, fourth finger slightly longer than second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (94 %). Lateral metatarsalia largely separated by webbing. Inner and outer metatarsal tubercle distinct. Foot webbing formula: 1 (1), 2i (1.5), 2e (1), 3i (2), 3e (1.5), 4i (2.5), 4e (2.5), 5 (1). Relative length of toes: I < II < III < V < IV, third toe slightly shorter than fifth. Skin on the upper surface smooth, with distinct dorsolateral folds. Ventral side smooth. Femoral glands large and prominent, with clearly visible central depression.

Colour after 18 years in preservative dorsally light brown with a weakly contrasted thin light vertebral line bordered by very weakly contrasted darker longitudinal pattern. Dorsolateral folds dark brown and constituting a sharp dorsolateral colour border between the light dorsal and darker lateral colour. Supratympanic fold and canthus rostralis also lined with dark brown, and tympanic region and sides of the head underneath these folds uniformly brown, without frenal stripe. Limbs dorsally brownish with sharply delimited dark brown crossbands visible especially on thighs where three crossbands are visible. Posterodorsal surface of thighs with a pattern of contrasted dark brown and lighter elements. Throat and chest dark brown with a distinct central longitudinal light stripe. Abdomen beige with brown marbling in its anterior part. Ventral surface of limbs beige with brown spotting.

Variation. For measurements of the type series, see Table 6; all measurements of specimens assigned to this species are available from https://doi.org/10.5281/zenodo.15161297. All specimens examined agree closely in colour and pattern with the holotype. Four males (holotype, one paratype and two additional specimens) are homogeneous in body size (22.8–23.4 mm) whereas one paratype (ZMA 19405) is larger (26.0 mm). Overall, males are smaller than females (SVL 22.8–26.0 mm vs. 25.9–32.0 mm) and have a slightly larger tympanum, with overlapping values (TD/ED 0.67–0.88 vs. 0.52–0.74).

Etymology. The species epithet is a Latin adjective derived from "venter" and "lineatus", meaning striped venter, and referring to the typical continuous ventral stripe, often extending onto the belly, characteristic of this species.

Natural history. Poorly known. Specimens were collected along streams in rainforests. Advertisement call not recorded. The tadpole, with the funnel-shaped morphology of the oral disc typical for *Chonomantis*, was described by Grosjean et al. (2011) under the name *M. aerumnalis* (Ranomafana).

Distribution. According to the collection data of the type series and additional samples included in the genetic analysis (Fig. 1), the species is currently known from four localities in the southern Central East and South East of Madagascar (Fig. 23): (1) the type locality, Ranomafana, (2) Antoetra, (3) Vevembe, and (4) Befotaka-Midongy. In addition, voucher specimens assigned to this species originate from (5) Vondrozo (a village close to Vevembe), and (6) Tolongoina (not far from Ranomafana) (localities not included in the map). The reliably known elevational range is 590–1020 m a.s.l.

Fig. 34. Photos of representative individuals of *Mantidactylus* (*Ochthomantis*) *rabibisoai* sp. nov. (Ca64) in life, in dorsolateral and ventral views. **A–B.** Male holotype ZMA 20143 (ZCMV 644) from Vevembe, photographed 2004. **C–D.** Male paratype ZMA 20222 (ZCMV 9) from Ranomafana, photographed 2004.

Mantidactylus (*Ochthomantis*) *rabibisoai* sp. nov.

Figs 34–35

Remark. Corresponds to *M.* sp. 64 of Randrianiaina et al. (2011), Poth et al. (2013), and Carné & Vieites (2024); not included in the accounts of Vieites et al. (2009) and Perl et al. (2014).

Holotype: ZMA 20143 (field number ZCMV 644), adult male, collected on 10 February 2004 at Vevembe (geographical coordinates 22.7948° S, 47.1871° E, 581 m a. s. l.), South East of Madagascar, by M. Vences and E. Rajeriarison.

Paratype: Two specimens: ZMB 81952 (NSH 1571), female, collected on 21 February 2011 at Beremby, Ranomafana National Park (21.2404° S, 47.5260°E, 628 m a. s. l.) by J. C. Riemann and S. H. Ndriantsoa. ZMA 20222 (ZCMV 9), male (call voucher), collected on 19 January 2004 in Ranomafana village next to Manja hotel (21.2617° S, 47.4595° E, 619 m a. s. l.) by M. Vences.

Diagnosis. Assigned to the subgenus *Ochthomantis* in the genus *Mantidactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (verified by external observation), (b) presence of a central depression in male femoral glands, (c) specialized tadpole with reduced keratodonts on oral disc, and (d) molecular phylogenetic relationships.

Within *Ochthomantis*, the species differs from all species by combination of (a) presence of yellowish colour in the inguinal region, (b) yellowish colour on venter, (c) absent or poorly expressed dark pattern on ventral side,

Fig. 35. Photographs of the preserved holotype *Mantidactylus* (*Ochthomantis*) *rabibisoai* sp. nov. in dorsal and ventral views.

(d) relatively uniform dorsal colour without distinct pattern, (e) distinctly expressed frenal stripe, (f) sharp and continuous colour border on the flanks between yellowish ventral and brownish dorsal colour, (g) weakly granular to smooth dorsal skin, (h) male SVL 43.4–47.3 mm, (i) relative tympanum diameter (ratio TD/ED) in males 0.84–0.86 mm.

Besides other characters, the new species can be distinguished from *M. ambony*, *M. ambreensis* and *M. majori* by presence of yellow patch in the inguinal region (vs. absence) and by a more irregularly shaped border between ventral and dorsal colour; from *M. femoralis* by often larger body size (SVL 43.4–47.3 mm vs. 28.9–37.5 mm in four genetically identified males measured by us: ZSM 366/2010, ZSM 370/2010, ZSM 1781/2010; the smallest being call voucher ZSM 1795/2010), much longer duration of advertisement calls (see Fig. 36), and by a smoother dorsal skin (vs. usually strongly granular); from *M. danieli*, *M. olgae*, and *M. tavaratra* by continuous colour border between yellowish ventral and brown dorsal colour on the flanks (vs. absence), and probably from *M. danieli* and *M. olgae* by a less granular dorsal skin texture (vs. moderately to strongly granular); from *M. macrotympanum* by presence of yellow patch in the inguinal region and a continuous colour border between yellowish ventral and brown dorsal colour on the flanks (vs. absence) and a smaller tympanum (ratio TD/ED in males 0.84–0.86 vs. 0.94 according to Rabibisoa et al. 2023); and from *M. mocquardi* by presence of a continuous colour border between yellowish ventral and brown dorsal colour on the flanks (vs. absence in most individuals) and rather uniform whitish or yellowish ventral side (vs. silvery white, often with distinct black pattern), and a rather rounded snout (vs. pointed). Phylogenetically (Fig. 14) the species forms a clade with *M. catalai* and *M. poissoni*. However, it differs from both species by a continuous colour border between yellowish ventral and brown dorsal colour on the flanks (vs. absence), a rather smooth skin (vs. granular), and from *M. catalai* by presence of a continuous frenal stripe (vs. frenal stripe absent or interrupted by dark markings). The species also differs from all other *Ochthomantis* by diagnostic DNA positions: MolD identified a robust diagnostic nucleotide combination of “T” at site 1114, and “A” at site 1175 (positions relative to the full 16S rRNA gene of *Mantella baroni*).

Description of holotype

Adult male in a good state of preservation (Fig. 35). Some tissue on left thigh removed as tissue sample for molecular analysis. Measurements are given in Table 6. Body moderately slender. Head longer than wide, wider than body. Snout rather short, pointed in lateral and dorsal views. Nostrils directed laterally, protuberant, much nearer to the tip of the snout than to the eye. Canthus rostralis distinct, straight, loreal region concave. Tympanum distinct, smaller than eye, oval, wider than its height, horizontal diameter of tympanum 84 % of horizontal eye diameter. Supratympanic fold rather distinct, straight above tympanum, behind tympanum bending towards forelimb insertion. Tongue ovoid, posteriorly bifid. Maxillary teeth present. Vomerine teeth form two large, rounded aggregations, positioned postero-

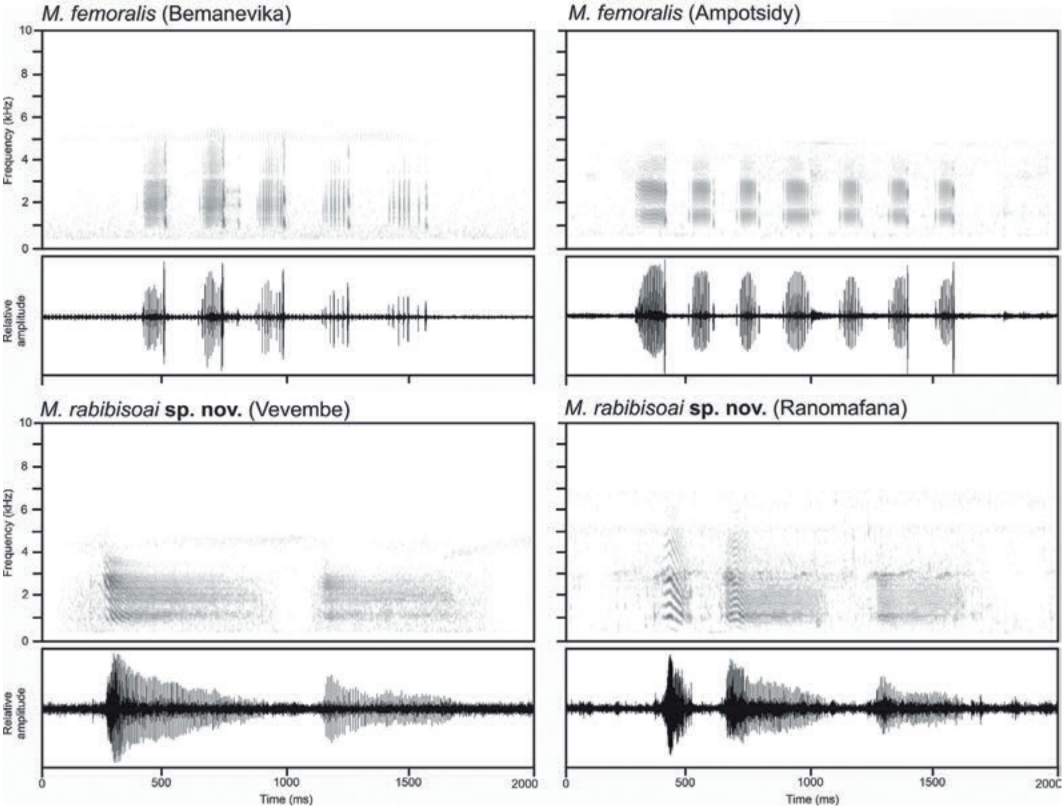

Fig. 36. Audiospectrograms and corresponding oscillograms of advertisement calls of *Mantidactylus* (*Ochthomantis*) *femoralis* from Bemanevika (recorded on 28 June 2010 from specimen ZSM 1795/2010) and from Ampotsidy (recorded on 9 January 2016 at from specimen ZSM 92/2016); and of *M. rabibisoai* sp. nov. from the type locality Vevembe (from the holotype ZMA 20143, recorded on 10 February 2004) and from Ranomafana (from paratype from paratype ZMA 20222, recorded on 19 January 2004), all displayed at the same time scale (2000 ms).

lateral to choanae. Choanae small, rounded. Subarticular tubercles single. Outer and inner metacarpal tubercle not clearly recognizable due to state of fixation but probably present. Fingers without webbing. Relative length of fingers: I < II < IV < III, fourth finger distinctly longer than second. Terminal discs of fingers and toes slightly enlarged. Nuptial pads absent. Foot and tibia almost of same length. Lateral metatarsalia fully separated by webbing. Inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable. Foot webbing formula: 1 (1), 2i (1.5), 2e (0.75), 3i (1.75), 3e (1), 4i (2.25), 4e (2.25), 5 (0.75). Relative length of toes: I < II < III < V < IV, third toe slightly shorter than fifth. Skin on the upper surface smooth. Ventral side smooth. Femoral glands distinct, with distinct cetntral depression.

After 21 years in preservative, dorsally rather uniformly brownish. The forelimbs are dorsally of a lighter brown with few small dark brown spots; hindlimbs also have some lighter brown areas but several indistinct darker crossbands (about three to four crossbands recognizable on thigh). Flanks of same light brown colour as dorsum, but rather sharply delimited at mid-flanks from the whitish ventral colour; the two colours are separated by an irregular but sharply delimited dark stripe. This stripe continues from the forelimb insertion underneath the tympanum and eye to the nostril. The area below this dark stripe, up to the snout tip, is made up of light colour forming an extensive frenal stripe. Ventrally, whitish on throat, chest, and abdomen, indistinctly washed with some brown pigment. On the posterior throat and chest there are two thin symmetrical dark lines. Limbs ventrally cream, largely without darker pattern.

Variation. The two paratypes agree with the holotype in morphometric variables (Table 6). Paratype ZMA 20222 also agrees strikingly with the holotype in colour pattern (Fig. 31) with a more expressed broad dark band running dorsally from eye to eye; paratype ZMB 81952 has this band expanded to a larger dark brown triangular patch pointing posteriorly, and also has poorly expressed irregular dark spots on chest and anterior belly. A description of ZMB 81952 with photos of the preserved specimen is available from https://doi.org/10.5281/zenodo.15161297.

Etymology. The species epithet is a patronym for Nirhy H. C. Rabibisoa, Malagasy herpetologist and specialist for the taxonomy of *Ochthomantis* frogs.

Natural history. Rather poorly known. Specimens were collected along streams in rainforest. Paratype ZMA 20222 was calling at night from the ground, near the bank of Namorona River. Tadpole morphology described by Randrianiaina et al. (2011).

Advertisement call. Advertisement calls of *M. rabibisoai* recorded from the holotype on 10 February 2004 at Vevembe (Fig. 36, Table 9) consist of a long, pulsed note, repeated in series of two consecutive calls, with the first call being longer in duration and exhibiting a greater number of pulses emitted at a higher rate. In addition to distinctly separated pulses, amplitude modulation is evident within calls, with maximum call energy present at the beginning of each call, constantly decreasing towards its end. Numerical call parameters of 6 analyzed calls are as follows: call duration (= note duration) 527–696 ms (610.0 ± 71.9 ms); inter-call interval within regular call series 206–231 ms (218.0 ± 12.5 ms); pulses/call 58–114 (83.3 ± 22.3); pulses/second within calls 86–294 (170.0 ± 88.4); dominant frequency 1108–1345 Hz (1172 ± 80 Hz); prevalent bandwidth 700–3200 Hz.

Advertisement calls recorded from paratype ZMA 20222 on 19 January 2004 at Ranomafana generally agree in character with those from Vevembe. However, call series can be composed of more than two calls (2–4). In these cases (n = 2), initial notes of a series are distinctly shorter in duration (128–130 ms) and exhibit a distinctly higher pulse rate (545–583 pulses/second), overall resulting in greater variation of numerical call parameters. Numerical call parameters of 9 analyzed calls are as follows: call duration (= note duration) 128–487 ms (326.8 ± 150.8 ms); inter-call interval within regular call series 121–246 ms (165.3 ± 43.8 ms); pulses/call 48–113 (65.2 ± 21.8); pulses/second within calls 153–583 (290.4 ± 169.2); dominant frequency 1128–1318 Hz (1199 ± 67 Hz); prevalent bandwidth 700–5000 Hz.

Distribution. According to the collection data of the type series, the species is currently known from three sites in the southern Central East and South East of Madagascar (Fig. 25): (1) the type locality Vevembe, (2) Beremby in Ranomafana National Park, and (3) Ranomafana village. The reliably known elevational range is 581–628 m a. s. l.

Future direction in *Chonomantis* and *Ochthomantis* systematics

The current study, combining previously published and new DNA sequences, revealed a great number of previously unnamed genetic lineages in *Chonomantis* and *Ochthomantis*, leading to the description of nine new species. Some of these new species are delimited with high reliability, for instance *M. rabibisoai* within *Ochthomantis* which is characterized by high mitochondrial divergence and morphological characters of adults and tadpoles, as well as bioacoustics. Also in *Chonomantis*, species like *M. ventrilineatus* and

Table 9. Comparative numerical parameters of advertisement calls of *Mantidactylus femoralis* and *M. rabibisoai* sp. nov. Inter-call intervals measured within call series; pulse rate calculated within calls.

	M. femoralis Bemanevika	*M. femoralis* Ampotsidy	*M. rabibisoai* sp. nov. Vevembe	*M. rabibisoai* sp. nov. Ranomafana
call duration (= note duration) [ms]	70–170 (106.4 ± 23.4)	74–125 (99.9 ± 17.9)	527–696 (610.0 ± 71.9)	128–487 (326.8 ± 150.8)
inter-call interval [ms]	101–168 (136.9 ± 18.8)	74–146 (100.2 ± 19.3)	206–231 (218.0 ± 12.5)	121–246 (165.3 ± 43.8)
pulses/call	4–20 (12.1 ± 4.4)	7–23 (12.7 ± 5.4)	58–114 (83.3 ± 22.3)	48–113 (65.2 ± 21.8)
pulses/second	84–236 (138.0 ± 51.0)	88–214 (156.8 ± 49.8)	86–294 (170.0 ± 88.4)	153–583 (290.4 ± 169.2)
dominant frequency [Hz]	1330–1927 (1526 ± 235)	1285–1446 (1367 ± 57)	1108–1345 (1172 ± 80)	1128–1318 (1199 ± 67)

to a lesser degree, *M. flaviventris* are differentiated genetically and can be recognized by morphology. In several other cases of new *Chonomantis* species, however, we only had a limited amount of voucher specimens for examination, which only differed by subtle morphological differences from their closest relatives. The justification for recognizing these species relies on the combination of evidence from high genetic divergences at levels not known to occur intraspecifically in amphibians, subtle morphological differences to sister taxa, isolated phylogenetic position, as well as absence of obvious admixture in nuclear genes with related species occurring in sympatry. One reason to formally name all these species, even in cases where voucher specimens are scarce, was the need to include them in conservation assessments. We are convinced that our approach was conservative, i. e., that all taxa described here in are well-differentiated species but that several genetic lineages currently lumped under the same species name may be split as additional separate species in the future. After all, it is important to keep in mind that species are hypotheses (Pante et al. 2015) that may be challenged when new data become available; however, the classification herein certainly provides a more realistic picture of *Chonomantis* and *Ochthomantis* diversity than the previous taxonomy.

One challenge in species delimitation of *Chonomantis* and *Ochthomantis* in the current study was the limited resolution provided by analysis of nuclear-encoded DNA. Fragments of nuclear-encoded, single-copy, protein-coding genes have been extensively used to understand patterns of species divergence in Malagasy anurans. In particular, fragments of RAG1, but also POMC, SACS, and KIAA1239 have proven to be highly informative of lineage divergence in mantellid groups such as *Boophis*, *Gephyromantis*, and *Spinomantis* (Sabino-Pinto et al. 2019, Vences et al. 2012, 2022a), as well as microhylids such as *Anilany*, *Cophyla*, or *Stumpffia* (Rakotoarison et al. 2015, 2017, Petzold et al. 2025), and in many of these examples, closely related sibling species could be concordantly delimited by mitochondrial phylogenies and a lack of allele sharing in these nuclear markers. The same is true for several groups of reptiles, perhaps most strikingly in dwarf geckos (Vences et al. 2022b, 2024a) and miniaturized chameleons (Glaw et al. 2012, Rakotoarison et al. 2024), where numerous morphologically cryptic and partly co-occurring species have completely separated phylogroups recognizable even by networks and trees of short nuclear-encoded gene fragments. In contrast, *Mantidactylus* has proven a much more difficult group of frogs for assessing nuclear genetic variation based on single, short markers. In basically all subgenera studied to date, haplotype sharing has been detected between at least some well-established species, and some species had a large diversity of nuclear alleles that did not form discrete haplogroups (subgenus *Mantidactylus*: Rancilhac et al. 2020, *Brygoomantis*: Scherz et al. 2022a, *Hylobatrachus*: Scherz et al. 2019, *Chonomantis* and *Ochthomantis*: data herein, see Figs 2, 13). Still, some of the species reported by these studies to share nuclear alleles are unequivocally separated at species level, with different morphologies and advertisement calls, and sometimes occurring in syntopy. The processes behind these differences in nuclear DNA differentiation among larger groups of tropical frogs are unstudied. While the encountered high proportion of allele sharing may be exaggerated due to the short length of some of the used fragments, e. g. for RAG1 (compare haplotype networks for short and long RAG1 fragments in *Chonomantis*: Fig. 2 vs. 4 and 6), this does not explain why in other groups such as cophylines, distinct inter-species phylogroups are observed for equally short fragments of the same genes. Comparative population genomics, ideally involving the sequencing of long stretches of DNA, e. g. via target enrichment approaches such as FrogCap (e. g. Hutter et al. 2022) will help to shed light on the genome-wide patterns of inter-species differentiation in these different groups of frogs, and ultimately help decipher possible underlying processes of genome evolution, demography, and/or hybridization and introgression.

While short nuclear DNA fragments have proven to carry less taxonomic signal in *Mantidactylus* than in other groups of amphibians, and in the absence of sufficiently comprehensive bioacoustic datasets, the integration of morphology with genetics have allowed to characterize many of the new species in the subgenera *Chonomantis* and *Ochthomantis* (Rabibisoa et al. 2023 and data herein). In anurans, rich sets of morphological characters can be extracted from both the larval and postmetamorphic stages (e. g., Haas 2003, Roelants et al. 2011, Sherratt et al. 2017, Wollenberg Valero et al. 2017), with relatively different patterns of interspecific variation encountered in the two subgenera analyzed here. In *Ochthomantis*, tadpole morphology especially in the specialized mouthparts is highly variable between species (Randrianiaina et al. 2011, dos Santos Dias et al. 2024), and substantial differences are also obvious among the adults of several species (Rabibisoa et al. 2023). Based on our phylogenetic results, in some cases, the taxonomic signal in the adult and larval morphologies are decoupled: for instance, adults of the newly described *M. rabibisoai* are morphologically rather similar to *M. femoralis*, but its tadpoles are reminiscent of *M. mocquardi* (Randrianiaina et al. 2011). In *Chonomantis*, some species such as *M. brevipalmatus* and *M. delormei*, or *M. aerumnalis* and *M. ventrilineatus*, are morphologically distinct from other species in the subgenus, but on average, species of *Chonomantis* are perhaps morphologically more similar to each other and easier to confuse with each other than species of *Ochthomantis*. This trend is, however, extreme in tadpole morphology which turned out to be extremely uniform among the 10 species of *Chonomantis* studied by Grosjean et al. (2011). Accordingly, in the character tracing analysis of Wollenberg Valero et al. (2017), distinctly more evolutionary change was detected in *Ochthomantis* vs. *Chonomantis* tadpoles, whereas some evolutionary change in adult morphology was observed in both subgenera. The interplay of natural selection acting upon larval vs. adult morphologies in frogs (Sherratt et al. 2017, Wollenberg Valero et al. 2017) remains a rewarding topic fur future research, and will benefit from an improved understanding of species diversity in *Mantidactylus* frogs, to which we have contributed herein.

Most, if not all, of the frog specimens of the subgenera *Chonomantis* and *Ochthomantis* included in this study were opportunistically collected in the field and catalogued with only a preliminary field identification, i. e., the new species described herein were not identified as such upon collection. Without doubt and similar to the situation in other *Mantidactylus* subgenera (Scherz et al. 2019, 2022, Rancilhac et al. 2020) this was caused by a sometimes puzzling, high amount of morphological variation within species, especially in *Ochthomantis*, in combination with a high morphological similarity between species. Furthermore, and different from the equally hyperdiverse subgenus *Brygoomantis* (see Scherz et al. 2022a), calling specimens of *Chonomantis* and, especially, *Ochthomantis* are not always easy to find, and the advertisement calls of many species remain unknown and thus cannot be used as a character for taxonomy (Köhler et al. 2017) or field identification (Vences et al. 2008). Consequently, given the absence of targeted sampling, the representation of species in the collections available to us can be seen as representative of their rarity and/or findability in the wild, and these data can be compared with the transect-based information on rarity of their tadpoles (Strauß et al. 2013). In this context, it is striking that, especially in *Chonomantis*, some intriguingly different patterns are apparent. Some species, such as *M. melanopleura* among *Chonomantis* and *M. femoralis* among *Ochthomantis*, are widely represented in both, the sampling of adult specimens and tadpoles, and widespread across Madagascar (Strauß et al. 2013 and Fig. 1 herein). Other species, such as *M. opiparis* appear to be at least locally very common (e. g., in streams of Ranomafana National Park according to tadpole sampling: Strauß et al. 2013 and Fig. 1 herein), but much less represented in the available adult collections, perhaps also because the adults usually escape by fast and long jumps when approached (Fig. 1; the vast majority of samples included therein are from tadpoles). Furthermore, several populations from northern Madagascar originally assigned to *M. opiparis* turned out to be *M. zipperi* instead. Other species are rare in both tadpole and adult collections; in the Ranomafana area, the source of the largest and most systematic tadpole collections, this applies to *M. rabibisoai* among *Ochthomantis* and *M. chonodus*, *M. maharira*, and *M. malokila* among *Chonomantis*, all of which are known from few samples only. As with other amphibians in Madagascar, future studies should systematically assess whether they may be locally restricted to certain habitats, genuinely rare (i. e., occurring in low densities), or more seasonal or secretive in their habits and therefore rarely encountered. The example of *M. opiparis*, which in Ranomafana is very common in tadpole transects but far less represented in adult collections, indicates that indeed some species of these *Mantidactylus* subgenera may simply be more secretive than others.

Such information will also add to the reliability of conservation assessments, which, for most Malagasy frogs at present, can only be grounded on the species' distribution pattern (e. g., Andreone et al. 2005, 2008). Providing a full, detailed threat assessment of all species of *Chonomantis* and *Ochthomantis* is beyond the scope of the present paper, but we here provide some preliminary suggestions.

For *Ochthomantis*, the work of Rabibisoa et al. (2023) has led to a substantial improvement of our knowledge on taxonomy and distribution. Currently (IUCN 2024), *M. ambreensis*, *M. femoralis*, *M. mocquardi* and *M. majori* are categorized as Least Concern (LC), and *M. zolitschka* as Critically Endangered. Furthermore, Scherz et al. (2020) suggested a status of Near Threatened for *M. ambony*. The new taxonomic and distributional data from Rabibisoa et al. (2023) and herein do not require a modification of the assessments for the LC species, but the much expanded range of *M. zolitschka* suggests a less dramatic threat status for this species which may be best classified as Near Threatened or even Least Concern. The remaining *Ochthomantis* species are still unassessed. Two of these, *M. danieli* and *M. tavaratra*, are rather widespread in northern Madagascar, including several protected areas, and a status of Least Concern will probably turn out to be most appropriate for them. The same is probably true for *M. catalai*, which occurs at multiple sites and over a wide range in the southern Central East and South East, including at least one protected area (Ranomafana National Park). The four other species, *M. macrotympanum* and *M. olgae* in northern Madagascar, *M. poissoni* in the northern Central East and *M. rabibisoai* in the southern Central East and South East, appear to be less widely distributed and based on the frequency of collection, perhaps relatively rare. Given the widespread deforestation affecting their distribution ranges, it is likely that they all qualify into one of the threatened categories, probably Vulnerable or Endangered; a specific assessment would require the review of all locality records in Rabibisoa et al. (2023), not only the genetically confirmed ones herein.

In *Chonomantis*, the Red List (IUCN 2024) currently lists six species as Least Concern: *M. aerumnalis*, *M. brevipalmatus*, *M. charlotteae*, *M. melanopleura*, *M. opiparis*, *M. zipperi*; and three other species as Endangered: *M. albofrenatus*, *M. delormei*, *M. paidroa*. The data presented herein suggests that *M. opiparis* may be less widespread than previously thought because most of the northern populations previously attributed to this species (Vences & Glaw 2004, Glaw & Vences 2007) may in fact be *M. zipperi*. However, this is unlikely to change the conservation assessment for *M. opiparis* which still occurs in a rather wide area of the northern Central East and southern Central East, including multiple protected areas. We furthermore have synonymized *M. charlotteae* with *M. albofrenatus*, and identified numerous populations previously considered as *M. charlotteae* as new species; still, our taxonomic rearrangement leads to a much expanded range for *M. albofrenatus*, which therefore should be reclassified as Least Concern. In contrast, most of the species of *Chonomantis* newly described here occupy only limited ranges, and often are only known from low-elevation sites (e. g., *M. chonodus*, *M. dichromus*, *M. kitrinolaimus*) or from the central highlands (*M. temachikus*) where the remaining forests are heavily fragmented and under particularly high anthropogenic pressure (e. g., Vallan 2000, Gehring et al. 2010). Most of them will therefore turn out to fall in one of the threatened categories. As discussed by Scherz et al. (2019), the increased exploration of natural habitats in Madagascar on one hand leads to the the realization that some species are more widely distributed – and thus less threatened with extinction – than previously thought. At the same time, it has also led to the discovery of new, often range-restricted species, which overall increases the number and proportion of threatened species in Madagascar's batrachofauna. Finally, it is important to highlight that several of the widespread Least Concern species of *Mantidactylus* in the subgenera *Chonomantis* and *Ochthomantis*, in particular *M. albofrenatus*, *M. danieli*, *M. femoralis*, *M. majori*, *M. mocquardi*, *M. tavaratra*, and *M. zipperi* as currently defined, each contain several deep mitochondrial lineages of uncertain taxonomic status, several of which may in the future be recognized as distinct species with rather restricted ranges and thus higher threat level.

Acknowledgements

We are indebted to numerous colleagues, students, and guides for their help during field expeditions in Madagascar, in particular F. Andreone, L. Ball, M. C. Bletz, P. Bora, J. Borrell, J. L. Brown, A. Crottini, I. de la Riva, H. Enting, J. Forster, P.-S. Gehring, K. Glaw, T. Glaw, J. Glos, F. Mattioli, K. Mebert, S. H. Ndriantsoa, D. H. Nomenjanahary, M. Pabijan, D. Parker, C. Patton, J. L. Patton, L. du Preez, D. Prötzel, F. Rabemananjara, N. H. C. Rabibisoa, J. M. Rafanoharana, L. Raharivololoniaina, H. Raherinjatovo, E. Rajeriarison, T. Rajoafiarison, M. Rakotondratsima, R. D. Randriniaina, J. E. Randrianirina, S. Rasamison, F. M. Ratsoavina, A. Razafimanantsoa, E. Razafimandimby, J. Razafindraibe, A. Sarovy, T. Starnes, M. Teschke (née Thomas), D. Vallan, D. R. Vieites, and C. Weldon. M. Hofreiter (Potsdam) facilitated archival DNA analysis in his laboratory. W. Böhme (Bonn), D. Marques and U. Wüest (Basel), and E. Doondorp (Leiden) allowed sampling of historical type material kept under their care. Research was carried out in the framework of cooperation accords among the Département de Biologie Animale, Université d'Antananarivo, Madagascar National Parks, the Technische Universität Braunschweig, and the Zoologische Staatssammlung München. Permits for collection and export of specimens were kindly issued by the Ministère de l'Environnement et du Développement Durable of Madagascar.

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Managing editor of this article: Roland R. Melzer

Appendix 1. Call descriptions of species of the subgenera *Chonomantis* and *Ochthomantis*

Mantidactylus (*Chonomantis*) *zipperi*

The advertisement call of *M. zipperi* recorded on 2 January 2016 at Ampotsidy from specimen ZSM 99/2016 (MSZC 0127) consists of a short pulsatile note emitted in call series consisting of 23–28 calls (n = 3) and lasting for 8303–9083 ms. Numerical call parameters are as follows: call duration (= note duration) 36–56 ms (50.6 ± 5.2 ms); inter-call interval within regular call series 157–391 ms (224.0 ± 68.4 ms); and dominant frequency 1626–1665 Hz (1645 ± 14 Hz).

Thus, the call from Ampotsidy in northern Madagascar is in general agreement with those reported from An'Ala, the *M. zipperi* type locality, by Vences & Glaw (2004) but it has slightly longer call duration. The An'Ala calls (newly analyzed herein) have the following call parameters: call duration (= note duration) 28–45 ms (32.8 ± 5.8 ms); inter-call interval within regular call series 185–275 ms (214.0 ± 39.3 ms); and dominant frequency 1477–1913 Hz (1725 ± 225 Hz).

Mantidactylus (*Ochthomantis*) *femoralis*

Advertisement calls of *M. femoralis* recorded on 28 June 2010 at Bemanevika from specimen ZSM 1795/2010 (ZCMV 12547) consist of a distinctly pulsed note repeated in series containing 2–14 calls. Remarkably, duration, number of pulses per call, and pulse rate is highly variable among calls, with initial calls of a series usually containing more pulses emitted at a higher rate compared to following calls that usually exhibit decreasing pulse rates towards the end of a call series. Frequency is distributed within a broad band, with only a barely evident energy peak. Numerical call parameters of 23 analyzed calls of 3 males are as follows: call duration (= note duration) 70–170 ms (106.4 ± 23.4 ms); inter-call interval within regular call series 101–168 ms (136.9 ± 18.8 ms); pulses/call 4–20 (12.1 ± 4.4); pulses/second within calls 84–236 (138.0 ± 51.0); dominant frequency 1330–1927 Hz (1526 ± 235 Hz); prevalent bandwidth 800–6000 Hz.

Advertisement calls of *M. femoralis* recorded on 9 January 2016 at Ampotsidy from specimen ZSM 92/2016 (MSCZ 0179) generally agree in character with those described from Bemanevika. Calls were emitted in series containing 2–7 calls. Numerical call parameters of 15 analyzed calls are as follows: call duration (= note duration) 74–125 ms (99.9 ± 17.9 ms); inter-call interval within regular call series 74–146 ms (100.2 ± 19.3 ms); pulses/call 7–23 (12.7 ± 5.4); pulses/second within calls 88–214 (156.8 ± 49.8); dominant frequency 1285–1446 Hz (1367 ± 57 Hz); prevalent bandwidth 900–6000 Hz.