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An inordinate fondness for inconspicuous brown frogs: integration of phylogenomics, archival DNA analysis, morphology, and bioacoustics yields 24 new taxa in the subgenus *Brygoomantis* (genus *Mantidactylus*) from Madagascar

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Abstract

Malagasy frogs of the subgenus *Brygoomantis* in the mantellid frog genus *Mantidactylus* currently comprise 14 described species of mostly brown, riparian frogs. Data from DNA barcoding suggested that the diversity of this subgenus is dramatically underestimated by current taxonomy. We here provide a comprehensive revision of this subgenus. We use hybrid-enrichment based DNA barcode fishing to obtain mitochondrial DNA fragments from the name-bearing type material of 16 of the 20 available names for members of this subgenus, and integrate these into a genetic dataset consisting of 1305 individuals sampled across Madagascar. By thus assigning the nomina to genetic lineages, we can confidently establish synonyms, revalidate old names, and describe the remaining diversity. We take an integrative approach to our descriptions, drawing together genetics, morphometrics and morphology, and bioacoustics for assignment. We also provide a robust phylogenomic hypothesis for the subgenus, based on 12,818 nuclear-encoded markers (almost 10 million base pairs) for 58 representative samples, sequenced using a hybrid-enrichment bait set for amphibians. Those data suggest a division of the subgenus into eight major clades and show that morphological species complexes are often paraphyletic or polyphyletic. Lectotypes are designated for *Rana betsileana* Boulenger, 1882; *Rana biporus* Boulenger, 1889; *Rana curta* Boulenger, 1882; *Mantidactylus ambohimitombi* Boulenger, 1918; *Mantidactylus tripunctatus* Angel, 1930; and *Rana inaudax* Peracca, 1893. For several other nomina, previous authors had considered a certain syntype as holotype; this has been seen as lectotype designation by implication, which, however, is ambiguous according to the provisions of the International Code of Zoological Nomenclature. Hence, we validate a previous lectotype designation by implication for *Limnodytes ulcerosus* Boettger, 1880 by explicitly designating the same individual as lectotype. In one other such case, that of *Mantidactylus brauni* Ahl, 1929, we deviate from previous authors and designate a different specimen as lectotype. We revalidate *Rana inaudax* Peracca, 1893 as *Mantidactylus inaudax* (Peracca, 1893) **bona species**, and *Mantidactylus tripunctatus* Angel, 1930 **bona species**. The identities of three further species (*M. ambohimitombi, M. biporus, M. tricinctus*) are largely redefined based on new genetic data. By designating the lectotype of *Rana aluta* (MZUT An725.1) as the neotype of *Mantidactylus laevis* Angel, 1929 we also stabilize the latter nomen (as junior synonym of *M. alutus*) whose original type material is lost. Based on DNA sequences of its lectotype, we consider *Mantidactylus brauni* Ahl, 1929 as junior synonym of *M. ulcerosus* (rather than *M. biporus*). We formally name 20 new species and four new subspecies: *M. ambohimitombi marefo* **ssp. nov.**, *M. ambohimitombi miloko* **ssp. nov.**, *M. mahery* **sp. nov.**, *M. steinfartzi* **sp. nov.**, *M. incognitus* **sp. nov.**, *M. jonasi* **sp. nov.**, *M. katae* **sp. nov.**, *M. kortei* **sp. nov.**, *M. riparius* **sp. nov.**, *M. fergusoni* **sp. nov.**, *M. georgei* **sp. nov.**, *M. jahnarum* **sp. nov.**, *M. marintsoai* **sp. nov.**, *M. grubenmanni* **sp. nov.**, *M. gudrunae* **sp. nov.**, *M. augustini* **sp. nov.**, *M. bletzae* **sp. nov.**, *M. brevirostris* **sp. nov.**, *M. eulenbergeri* **sp. nov.**, *M. glosi* **sp. nov.**, *M. stelliger* **sp. nov.**, *M. manerana* **sp. nov.**, *M. manerana fotaka* **ssp. nov.**, and *M. manerana antsanga* **ssp. nov.** This leaves *Mantidactylus* subgenus *Brygoomantis* with 35 described species and six subspecies (including nominate subspecies). Based on our taxonomic revision, we discuss (i) the importance of definitive assignment of historical names via archival DNA analysis; (ii) the relevance of the subspecies category to name geographic variation within species; (iii) the value of molecular characters in formal species diagnoses in taxa with substantial individual variation of morphology; (iv) the use of phylogenomic approaches for taxonomy, by confirming that some morphologically similar taxa are not each other's closest relatives, and in several cases belong to entirely different major subclades within *Brygoomantis*, thus facilitating lineage diagnosis; and (v) the need to interpret genetic distances in a probabilistic framework rather than using fixed thresholds, where higher distances confer a higher likelihood of genetic incompatibilities across the genome and thus completion of speciation.

Key words: Amphibia, Anura, Mantellidae, Madagascar, FrogCap, target enrichment, museomics, museum genomics, phylogenomics, integrative taxonomy

Introduction

In the face of large-scale habitat destruction and an increasing number of threatened species across the world's biodiversity hotspots (Ganzhorn *et al.* 2009; Myers *et al.* 2000), taxonomic work in these areas is being carried out with a sense of increasing urgency. At present, amphibians are thought to be amongst the most threatened animals globally, by virtue of their ecological sensitivity, extensive habitat loss, and the global anthropogenic transportation of fatal diseases (Brühl *et al.* 2013; Catenazzi 2015; Habel *et al.* 2019; Houlahan *et al.* 2000; Lötters *et al.* 2011; Price *et al.* 2014; Stuart *et al.* 2004). As such, taxonomic work on amphibians from global hotspots is a high priority. Few biodiversity hotspots outshine Madagascar, a tectonic island that comprises 0.4% of global land surface area but possesses 4% of all amphibian species known to date, almost all of them unique to this landmass (AmphibiaWeb 2022).

In the last three decades, taxonomic work on the amphibians of Madagascar (exclusively frogs) has been gaining momentum, especially since the completion of a DNA barcoding survey of Malagasy amphibians (Vieites *et al.* 2009), which revealed that Madagascar's then 244 scientifically named species were perhaps just over half of the actual amphibian diversity of the island (Vieites *et al.* 2009). Since 2009, around 130 new frog species have been formally named and added to the list of Madagascar's amphibians (AmphibiaWeb 2022). Yet, because many additional candidate new species have been discovered in the interim, the taxonomic gap in Madagascar's amphibians is closing more slowly than we might expect. To increase our chances of completing the taxonomic inventory of Malagasy frogs in the next 20 years, large, troublesome groups of unnamed species need to be addressed. Recently, we described 26 species of the

miniaturised microhylid frog genus *Stumpffia* Boettger, 1881 in a single monographic treatment (Rakotoarison *et al.* 2017); in the present work, we apply a similar approach to another, possibly even more challenging group.

The Madagascar-endemic mantellid genus *Mantidactylus* Boulenger, 1895 is divided into six subgenera: *Brygoomantis* Dubois, 1992, *Chonomantis* Glaw and Vences, 1994, *Hylobatrachus* Laurent, 1943, *Maitsomantis* Glaw and Vences, 2006, *Mantidactylus* Boulenger, 1895, and *Ochthomantis* Glaw and Vences, 1994. Of these, the subgenus *Brygoomantis* is currently the most diverse, with 14 recognised species (AmphibiaWeb 2022; Frost 2021). However, like other taxonomically complex frog clades (e.g. Rakotoarison *et al.* 2017), DNA barcoding revealed that these 14 named species represent only a small fraction of the extant diversity of this clade (Perl *et al.* 2014; Vieites *et al.* 2009). Vieites *et al.* (2009) identified 23 candidate new species of *Brygoomantis* and a further candidate was added by Rosa *et al.* (2012). Since 2009, only one of these candidate species has been described (Vences *et al.* 2018).

Why has so little recent taxonomic work been undertaken on *Brygoomantis*, when genetic evidence suggests there are so many accessible species ready to be described? Reasons include: (1) In addition to the 14 recognised species, there are six available synonyms: *Mantidactyus laevis* Angel, 1929, *Rana inaudax* Peracca, 1893, *Mantidactylus brauni* Ahl, 1929, *Rhacophorus fumigatus* Mocquard, 1895, *Mantidactylus brunneus* Ahl, 1929, *Mantidactylus tripunctatus* Angel, 1930. The identity of all 20 of these names must be clarified before new names are coined, to avoid further confusion of the already challenging taxonomic situation. (2) The whole genus is morphologically and chromatically cryptic, several species exhibit considerable variation in colour pattern, and these frogs have quiet, sometimes inconspicuous calls, making identification of species difficult, even when working with live specimens or fresh samples, but especially when examining old material. (3) Several genetic lineages were represented with only small sample sizes, meaning datasets are sometimes incomplete (e.g. no calling males known, so bioacoustic data cannot be used for identification). (4) Unlike other groups of Malagasy frogs, including *Stumpffia*, sequences of nuclear-encoded genes in *Brygoomantis* (as in other *Mantidactylus* groups; Scherz *et al.* 2019) are characterized by extensive allele sharing among some species, even for species that are unambiguously delimited by morphology or bioacoustics (Vences *et al.* 2018). The reasons for these differences in the amount of allele sharing among groups of Malagasy frogs are unstudied, but it is clear that they represent an important hurdle to species delimitation. Furthermore, mitochondrial introgression appears to occur in this genus (e.g. Scherz *et al.* 2019). This greatly impedes molecular species delimitation based on single or few markers. Finally, (5) because they are often abundant and rather easy to collect, most of the herpetofaunal species inventories carried out in Madagascar have reported species of *Brygoomantis*. Yet, only rarely did these studies include call recordings or even information on the sexual maturity of individuals of the encountered species. Subadults can be particularly hard to identify and to diagnose from small-sized species in the subgenus. As a result, the literature on *Brygoomantis* distribution and diversity is plagued with uncertainty and inaccuracy.

Tackling a case like *Brygoomantis*, where it is necessary to clarify numerous names while also sorting the many lineages into biologically meaningful units, is a daunting task, but can be broken down into a protocol of sequential steps. First, the assignment of names must be clarified. This can be done in a variety of ways, but two chief components that we use here are (i) logic- and plausibility-based argumentation based on all information contained in the original description and from the type specimens themselves, while maintaining a 'parsimony of taxonomic change' (Scherz *et al.* 2017b, 2021), and (ii) cutting-edge 'museomic' methods for sequencing 'archival' DNA from types, in our case using the 'barcode fishing' method pioneered in *Mantidactylus* by Rancilhac *et al.* (2020) and Scherz *et al.* (2020).

Second, lineages must be delimited into biologically meaningful units. These will generally be species, as conceived under the Unified Species Concept (de Queiroz 2007), which allows us to maintain conceptual consistency despite qualitatively and quantitatively different dataset composition. One approach for doing so is based on the congruence of semi-independent datasets, otherwise known as the integrative taxonomic approach (Dayrat 2005; Padial *et al.* 2009, 2010). In particular, the congruence of signals of mitochondrial and nuclear-encoded markers, coupled with a group-specific genetic distance threshold (often used in barcoding, e.g. Vieites *et al.* 2009) and other data such as bioacoustics or morphology, can yield support for clearly defined, independent lineages. Most of these may be species, but in some cases a lack of complete congruence may instead suggest incipient or incomplete speciation. These cases can be recognised as subspecies under a revised subspecies concept, as argued by de Queiroz (2020), and discussed by us below. Here, we also supplement this general congruence approach with a phylogenomic dataset based on thousands of genomic markers, which helps us to determine evolutionary relationships among lineages, confidently informing species delimitation in cases of morphological convergence.

Third, the task of re-defining the existing names according to the results of the name clarification and lineage delimitation, and describing the remaining lineages as new species remains. This can be accelerated and yet kept brief by adopting the formulaic approach at the heart of 'fast-track' taxonomy (Riedel *et al.* 2013), with abbreviated descriptions, deliberate omission of collected material that could not be reliably assigned based on genetic data, and an emphasis on diagnosis (Renner 2016). However, at the same time, data-rich descriptions remain of the greatest value for the longest time, and therefore detail should not be spared when it is readily available; a rapidly assembled taxonomic work need not—and indeed must not!—compromise on quality (Fernandez-Triana 2022; Zamani *et al.* 2021). There are

numerous available recent taxonomic monographs that illustrate that efficiency and detail can be balanced (e.g. Rakotoarison *et al.* 2017; Riedel *et al.* 2014; Riedel & Narakusumo 2019). For the current study, we followed Rakotoarison *et al.* (2017) in keeping description of colour pattern brief if it already is illustrated by photographs, and providing morphometric measurements of only a set of representative specimens identified by genetics, rather than trying to morphometrically assign to species the many hundreds of additional *Brygoomantis* specimens available in museum collections.

Here, we implement this protocol to revise the *Mantidactylus* subgenus *Brygoomantis*. We clarify the identity of all 20 existing names, revalidate two of them, and describe 20 new species and four new subspecies of *Brygoomantis*.

Materials and Methods

Fieldwork and sampling

This study is based on materials collected by numerous researchers over the past 30 years, on a large number of field campaigns. Detailed field methodology differed slightly over the years and among research teams, but in general, frogs were collected during opportunistic searches in a variety of habitats, usually along streams, by day and at night. During several expeditions we also specifically targeted tadpoles. We anesthetized specimens and then euthanized them with a lethal dose of MS222 or chlorobutanol. Tissue samples, usually from thigh muscle, were taken from freshly sacrificed specimens and preserved in separate vials in 95–100% ethanol or in ethylenediaminetetraacetic acid (EDTA). Vouchers were then fixed in 95% ethanol or 5% formalin, and thereafter deposited in 70–75% ethanol for long-term storage.

Voucher specimens analysed in this study were deposited in the Centre Universitaire Regional de la SAVA, Antalaha, Madagascar (CURSA), University of Kansas Biodiversity Institute and Natural History Museum, Lawrence KS (KU), Museo Regionale di Scienze Naturali, Torino (MRSN), Université d'Antananarivo, Mention Zoologie et Biodiversité Animale, Madagascar (UADBA), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Zoological Museum of Amsterdam (ZMA; collections now integrated in the Naturalis Museum in Leiden), Netherlands, Museum für Naturkunde, Berlin (ZMB), and Zoologische Staatssammlung München, Munich (ZSM). Additional voucher specimens were examined from the Natural History Museum, London (BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), and Senckenberg Museum Frankfurt (SMF). In addition, the following acronyms of herpetological museum collections were used: Museum of Comparative Zoology, Cambridge, USA (MCZ), University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ). ACZCV, APR, BOR, CRH, DRV, FAZC, FGMV, FGZC, JCR, MSZC, THC, and ZCMV refer to A. Crottini, A. P. Raselimanana, P. Bora, C.R. Hutter, D.R. Vieites, F. Andreone, F. Glaw and M. Vences, F. Glaw, J. Riemann, M.D. Scherz, T.R. Fulgence, and M. Vences field numbers, respectively. In some cases, specimens deposited in UADBA have not received final catalogue numbers yet; these are cited as UADBA followed by the respective field number in parentheses.

Morphology

Males and females of most species were distinguished based on the presence of large, well-developed femoral glands in males (rudimentary in females). In some species of the *M. curtus* clade, this distinction was not reliable; see discussion in the respective accounts. Furthermore, in many cases males could be identified already in the field, by direct observation of the emission of advertisement calls. In several preserved individuals, sex was also ascertained by gonad examination. Presence of vocal slits has not traditionally been studied in mantellids (e.g., Blommers-Schlösser 1979) and we refrain from using them to sex individuals until their presence and structure across species and sexes of mantellids have been comprehensively assessed in future research.

Morphological measurements (Fig. 1) of representative specimens were taken using different digital or analogue callipers to 0.1 mm by MV, as follows: snout–vent length (SVL), maximum head width (HW), head length from posterior maxillary commissure to snout tip (HL), horizontal eye diameter (ED), horizontal tympanum diameter (HTD), distance from eye to nostril (END), distance from nostril to snout tip (NSD), distance between nostrils (NND), foot length (FOL), foot length including tarsus (FOTL), tibia length (TIBL), hindlimb length from cloaca to tip of longest toe with the limb stretched (HIL), forelimb length from axilla to tip of longest finger with the limb stretched (FORL), hand length (HAL), and length and width of femoral gland (FGL, FGW). Webbing formulae follow Blommers-Schlösser (1979). For general terminology used in the study to refer to parts of the body, see Fig. 1.

Femoral glands are described using a terminology modified from Glaw *et al.* (2000) and Vences *et al.* (2007). Most *Mantidactylus* have a gland defined as 'type 3' by these authors, which is composed of two macrogland components: (1) A dense cluster of enlarged and circularly arranged gland granules whose secretion ducts (secretion pori) lead into a macroscopically recognisable central depression. This gland cluster was defined in Glaw *et al.* (2000) and Vences *et al.* (2007) as'A' structure', and is herein named 'distal ulcerous macrogland'. (2) A less distinct field of densely packed, smaller gland granules previously named 'B' structure', located in a more proximal position, i.e. between the ulcerous macrogland and the cloaca; this structure is here named 'proximal granular gland field' (Fig. 1). FGL was measured externally to comprise both gland structures, on the right thigh.

Visualisation of morphometric differentiation was conducted in R version 4.0.5 (R Core Team 2020) in R Studio version 1.2.5019 (RStudio Team 2019). Only adult

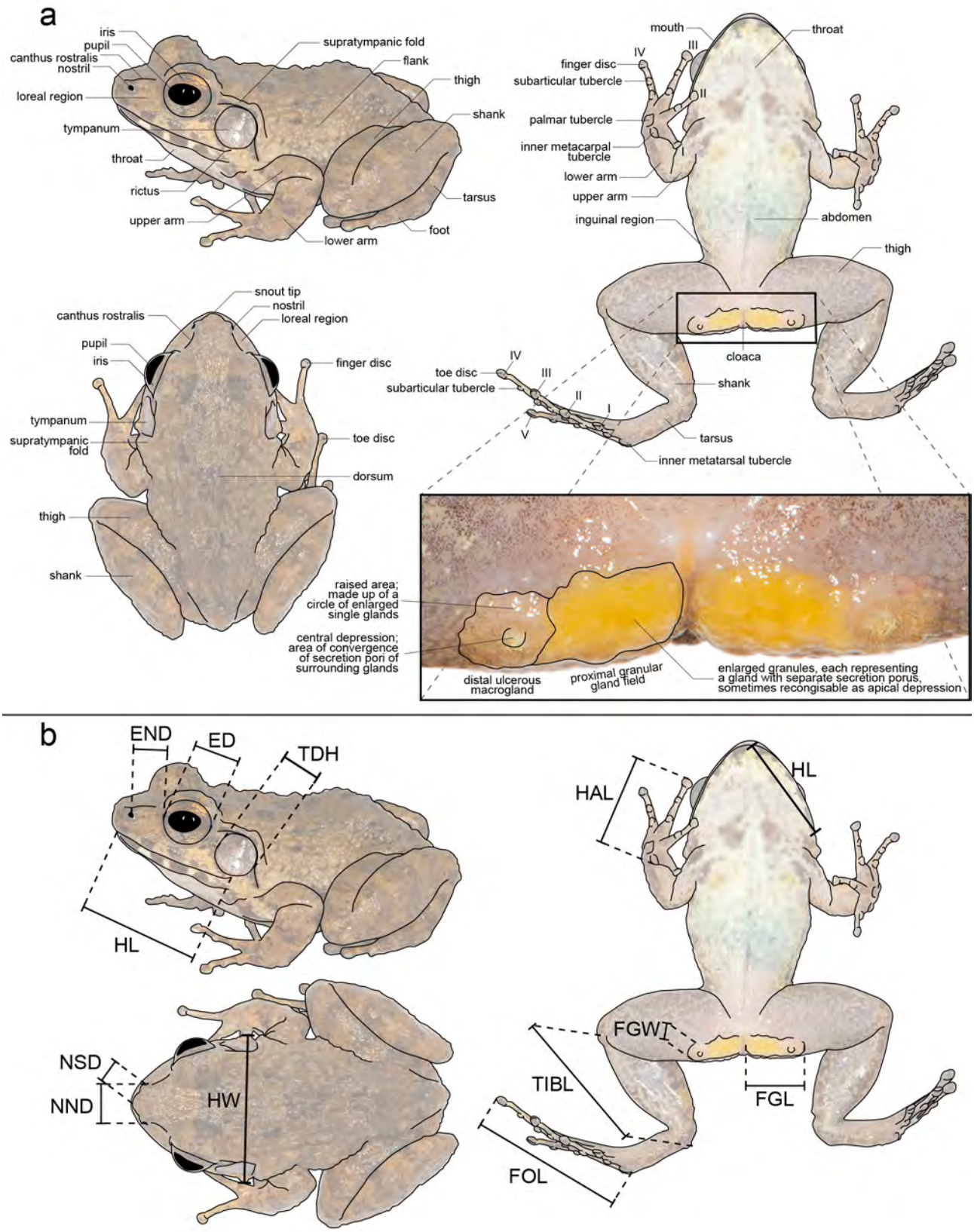

FIGURE 1. Graphic scheme indicating (a) regions of the body and (b) morphometrics measurements of *Mantidactylus* specimens of the subgenus *Brygoomantis* (exemplified by a specimen of *M. ulcerosus*), as referred to in the descriptions of morphology and tables throughout the manuscript. Labels in (a) refer to regions of the body and not necessarily to anatomical features. Femoral gland terminology as explained in the text. Measurement abbreviations in (b) are explained in the text; FORL (stretched forelimb length), HIL (stretched hindlimb length), and FOTL (foot length including tarsus) are not shown.

specimens were included in the visualisations, to avoid obscuring sexual size dimorphism.

Bioacoustics

We recorded anuran vocalization in the field using different digital or analogue devices such as Sony WM-D6C and Tensai RCR-3222 tape recorders with external microphones (Sennheiser Me-80, Vivanco EM 238), and Tascam DR07, DR05, Marantz PMD 661 MkII, or Roland EDIROL R-09 digital recorders, with built-in microphones (Tascam) or accessorized with semi-directional or supercardioid microphones (Marantz and Roland). We obtained digital recordings at a sampling rate of 44.1 kHz and 24-bit resolution and saved them as uncompressed files. Recordings were digitized or resampled at 22.05 kHz and 32-bit resolution and computer-analysed using the software CoolEdit Pro 2.0 (Syntrillium Software Corp.). Frequency information was obtained through Fast Fourier Transformation (FFT, width 1024 points) at Hanning window function; the audiospectrograms were obtained at Blackman window function with 256 bands resolution. For better direct comparison, as a compromise, figures of oscillograms and spectrograms were all produced at the same time scale (1000 ms), although in some cases this time scale was not optimal to display all details in the structure of calls (or call series). Temporal characters were measured from oscillograms and are given in milliseconds (ms) or seconds (s), as range followed by mean ± standard deviation in parentheses. Terminology of call descriptions and methods for call analyses follow those recommended by Köhler *et al.* (2017). In several cases, filtering was applied to recordings containing considerable background noise. In all instances of filtering, frequency sectors to be filtered were carefully chosen to avoid any effects on the bandwidth of the focal frog calls. Call recordings used for analysis were deposited in the Zenodo repository, DOI 10.5281/zenodo.6687413).

All advertisement calls described in this contribution were analysed using the same methodology and terminology. Even in cases where call parameters were formerly published from the same recordings, we reanalysed and redescribed these calls to ensure maximal comparability. Calls within the subgenus *Brygoomantis* are characterized by stereotyped sound units mostly arranged in more or less regular series, raising the question of which terminological scheme is best to be applied for their description. We here applied the call-centred terminological approach by Köhler *et al.* (2017) as we think, based on analyses of numerous recordings, it reflects best the actual calling behaviour in this subgenus, namely emission of calls in series of barely defined duration (with the duration of call series possibly depending on motivation and social context). Moreover, given our examination of all available call recordings of *Brygoomantis*, with this approach it seems more likely that we are comparing homologous call structures. As a consequence of this call-centred terminology, we here describe all *Brygoomantis* calls as single-note calls (most emitted in series). However, we are aware that this scheme, adopted for consistency and comparability, may not fully reflect the complexity of all *Brygoomantis* calls. Specifically, there are species that emit calls between long intervals in series that can go on for many minutes, or even hours, whereas other species, such as for example *M. alutus*, *M. tricinctus* or *M. ulcerosus*, emit calls separated by shorter, very regular intervals in series with a reasonably well-defined number of calls and duration. We use presence vs absence of such regular call series containing a limited number of calls as an additional diagnostic character.

Calls were obtained from almost all species, but were not recorded from *M. curtus*, *M. ambohimitombi marefo* **ssp. nov.**, *M. a. miloko* **ssp. nov.**, *M. madecassus*, *M. marintsoai* **sp. nov.**, *M. pauliani*, *M. gudrunae* **sp. nov.**, *M. bletzae* **sp. nov.**, *M. brevirostris* **sp. nov.**, *M. eulenbergeri* **sp. nov.**, *M. stelliger* **sp. nov.**, *M. manerana fotaka* **ssp. nov.**, and *M. m. antsanga* **ssp. nov.**

Molecular phylogenetics

We extracted total genomic DNA by standard salt extraction from tissue samples and amplified segments of mitochondrial and nuclear DNA by polymerase chain reactions (PCRs). DNA sequences of the mitochondrial 16S rRNA gene (16S) were amplified using previously established protocols described elsewhere with primers 16SA-L and 16SB-H (e.g. Vences *et al.* 2003). A fragment of the nuclear-encoded recombination-activating gene 1 (Rag-1) was obtained with primers Rag1-Manti-F1 (CGTGACAGAGTSAAAGGAGT) and Rag1-Manti-R1 (TCAATGATCTCTGGAACGTG) of Vences *et al.* (2018) with the following PCR protocol: 120 s at 94°C, followed by 35 cycles of (20 s at 94°C, 50 s at 53°C, 180 s at 72°C), and 600 s at 72°C. We resolved sequences directly with forward primers (forward and reverse primers for some samples for Rag-1) on automated capillary DNA sequencers. Sequences were error-checked with CodonCode Aligner (Codon Code Corp.). All newly obtained DNA sequences were submitted to GenBank (accession numbers OP179332–OP179611, OP189679–OP190409). 16S sequences were aligned with MAFFT v. 7.222 (Katoh & Standley 2013) and the best-fitting substitution model (General Time-Reversible, GTR+Γ) was determined based on the Bayesian Information Criterion implemented in MEGA7 (Kumar *et al.* 2016). We used this model for unpartitioned phylogenetic analysis of the 16S matrix under Maximum Likelihood (ML) in RAxML (Stamatakis 2014) using raxmlGUI v. 2.0 (Endler *et al.* 2020) and assessed node support with 100 ML fast bootstrap replicates. The alignment included a sample of *Mantidactylus opiparis,* a member of the subgenus *Chonomantis* which constitutes the sister group of *Brygoomantis* (Wollenberg *et al.* 2011), as the outgroup. Together with archival DNA sequences (see below), the total alignment consisted of 16S sequences of 1304 specimens of *Brygoomantis* plus the outgroup.

Rag-1 sequences were available from 265 *Brygoomantis* individuals representing all species and subspecies recognized herein. We analysed Rag-

1 sequences separately from the mitochondrial 16S sequences to obtain evidence from unlinked loci (mitochondrial vs nuclear) for genetic differentiation of lineages, where such differentiation would add further support as distinct species. Firstly, we used the presence of overlapping peaks (usually of approximately 50% intensity each, compared to non-overlapping peaks) in the electropherograms to identify putatively heterozygous sites in the Rag-1 sequences. We then inferred alleles using the PHASE algorithm (Stephens *et al.* 2001) as implemented in DnaSP v. 5.10.3 (Librado & Rozas 2009), and constructed an ML tree in MEGA7 (Kumar *et al.* 2016) from the phased and unpartitioned Rag-1 sequences using the Jukes-Cantor substitution model (the simplest available model, chosen to avoid overparameterization). This tree was analysed together with the phased alignment in the software Haploviewer, written by G. B. Ewing (http://www.cibiv.at/~greg/haploviewer) to build a network from the tree topology following the methodological approach of Salzburger *et al.* (2011).

Phylogenomics

Probe Design, Library Preparation, and Sequencing. Marker selection and probe design followed Hutter *et al.* (2021), using the Ranoidea-V2 probe-set. Probes were synthesized as biotinylated RNA oligos in a MYBAITS kit (Arbor Biosciences; Ann Arbor, MI) by matching publicly available frog transcriptomes to genomes to find orthologous markers. Matching sequences were clustered by their genomic coordinates to detect presence/absence across species and to achieve full locus coverage. To narrow the locus selection to coding regions, each cluster was matched to available coding region annotations from the *Nanorana parkeri* genome (Sun *et al.* 2015). Exons from all matching species were then aligned using MAFFT (Katoh & Standley 2013) and had various statistics calculated to aid in marker selection. Finally, the selected exons were separated into 120 bp-long bait sequences with 2x tiling (50% overlap among baits) using the MyBaits-2 kit (40,040 baits). The baits were then filtered, keeping those without sequence repeats, with a GC content of 30–50%, and only baits that did not match to their reverse complement or multiple genomic regions. Additionally, 86 commonly used sanger-sequencing-based legacy markers commonly used in phylogenetic analyses of frogs were included from Feng *et al.* (2017). These sequences were designed from consensus sequences across the multiple sequence alignments (Feng *et al.* 2017) and were then used for probe design. Finally, we included 2,166 successfully captured UCEs from Streicher *et al.* (2018). For these UCEs, we redesigned our probe sequences by creating consensus sequences across the multiple sequence alignments for each UCE from Streicher *et al.* (2018).

The genomic libraries for 58 *Brygoomantis* samples, including all but three species- and subspecies-level lineages of *Brygoomantis*, were prepared by Arbor BioScience's library preparation service. Prior to library preparation, the genomic DNA content of the samples was quantified and up to 4 µg were subjected to sonication with a QSonica Q800R instrument. After sonication and SPRI bead-based size-selection to modal lengths of roughly 300 bp, up to 500 ng of each sheared DNA sample were used in Illumina Truseq-style sticky-end library preparation. Following adapter ligation and fill-in, each library was amplified for six cycles using unique combinations of i7 and i5 indexing primers, and then quantified with fluorescence. 125 ng of 8 libraries were pooled for each capture reaction and subsequently enriched for targets using the MYbaits v 3.1 protocol. Following enrichment, library pools were amplified for 10 cycles using universal primers and subsequently pooled in equimolar amounts for sequencing. Samples were sequenced on an Illumina HiSeq X lane (shared with 38 samples from another project), with 150 bp paired-end reads.

SeqCap data processing pipeline. A bioinformatics pipeline for filtering adapter contamination, assembling loci, and exporting alignments in different formats and data types is available at (https://github.com/chutter/FrogCap-Sequence-Capture). The pipeline was scripted in R statistical software (R Core Team 2020). In a first step, adapter contamination, low complexity sequences, and other sequencing artifacts are removed using the program FASTP (default settings; Chen *et al.* 2017). Filtered reads are next matched to a database of publicly available genomes from bacteria, invertebrates, and other organisms to detect reads that represent contamination (see Hutter *et al.* 2021 for genomes used), using the program BBMap from BBTools (https://jgi.doe.gov/data-and-tools/bbtools/). Next, paired-end reads were merged using BBMerge (Bushnell *et al.* 2017). Finally, exact duplicates were removed using 'dedupe' from BBTools, removing read-pairs when both pairs were duplicated.

The merged singletons and paired-end reads were next *de novo* assembled using the program SPADES v.3.12 (Bankevich *et al.* 2012), which runs BAYESHAMMER (Nikolenko *et al.* 2013) error correction on the reads internally. Data were assembled using several different k-mer values (21, 33, 55, 77, 99, 127), where orthologous contigs resulting from the different k-mer assemblies were merged. We used the DIPSPADES (Sofanova *et al.* 2015) function from SPADES to better assemble polymorphic exons by generating a consensus sequence from both haplotypes from orthologous regions. The consensus haplotype contigs were then matched against reference loci sequences from the *N. parkeri* genome used to design the probes with BLAST (dc-megablast), keeping only those contigs that matched uniquely to the reference probe sequences. Contigs were discarded if they did not match at least 30% of the reference locus. Finally, we merged all discrete contigs that matched to the same reference locus, joining them together with Ns based on their match position within the locus.

The final set of matching loci was next aligned using MAFFT local pair alignment (max iterations = 1000; ep = 0.123; op = 3). Each locus was separately aligned with its corresponding reference used to design the probes. We screened each alignment for samples that were greater than 40% divergent from the reference sequence,

which are almost always incorrectly assigned contigs, and removed these. Alignments were kept if they had greater than three terminals and more than 100 bp. We next internally trimmed each alignment using TRIMAL (automatic1 function; Capella-Gutiérrez *et al.* 2009); and alignments were externally trimmed to ensure that at least 50% of the terminals had sequence data. This resulted in alignments of 12,951 loci.

Alignment decontamination and filtering. To assess the robustness of the phylogenetic inferences to spurious alignments (e.g. contaminations, in-paralogs, poorly aligned regions) and missing data, three consecutive filtering steps were applied, using custom scripts based on the ape package in R (Paradis & Schliep 2019): (1) All loci with fewer than 12 taxa were removed and gene trees were inferred with RAxML v 8.2.12 under a GTR+Γ substitution model and default settings. Taxa with very long terminal branches (in practice, longer than the 99% quantile of the terminal branch length distribution of a given gene tree) were identified as spurious, and the respective sequences removed from the alignment. After this step, 12,818 loci were retained, with an average alignment length of 736 bp, with a range between 68 and 12,014 bp (only two alignments <100 bp and 164 alignments <300 bp), an average of 57 taxa, and an average of 5% missing data per alignment (0–25%).

(2) Although the target loci were supposedly orthologs across Anura, this could not be verified in *Brygoomantis* due to the lack of genome resources. Therefore, in order to identify possible paralogs in the data set, a second decontamination step was carried out to identify excessively long internal branches (which are indicative of paralogs). For this purpose, gene trees were re-inferred from the reduced alignments, with the same settings as above. Long internal branches were detected in the gene trees (in practice, longer than the 99% quantile of the internal branch length distribution of a given gene tree) and gene trees were split in two on these branches. Subsequently, the subtree with the largest number of taxa was kept, and the sequences corresponding to the other subtree removed from the alignment.

(3) Gene trees were re-inferred from the reduced alignments, with the same settings as above, as well as a concatenation tree (methods as specified below). Filtering of both alignments and taxa was then performed based on topological distances (Robison-Foulds—RF—distances was used) between gene trees and the concatenation tree. First, loci yielding a topology very divergent from the concatenation tree (i.e. RF < 0.05 quantile of all RFs distribution) were removed. Secondly, terminals were removed on a per-alignment basis if this significantly improved the RF. All positions in the obtained matrix with >75% missing data were removed. After each of these steps, the filtered alignments were concatenated and used to perform phylogenetic inference, as described below.

Concatenated tree datasets. Four alternative variants of our FrogCap dataset were used for analysis, i.e., we produced concatenated matrices for the original set of loci, and the three progressively more filtered sets, and performed maximum likelihood (ML) phylogenetic analyses for all four of them. These phylogenetic inferences were run in IQ-Tree v 2.0 (Minh *et al.* 2020) using the best-fitting substitution models and alignment partitions, identified via ModelFinder (Kalyaanamoorthy *et al.* 2017) as implemented in IQ-Tree. We assessed support for the resulting topology using the SH-like approximate likelihood ratio test (aLRT) with 1000 pseudoreplicates. All four alignment subsets yielded identical and fully supported topologies. The tree obtained after the second filtering step was retained and used for the rest of the paper, given the congruence between all approaches, and because the third filtering step, besides stringently excluding misassembled sequences and cross-contaminations, may also introduce to some degree circular reasoning (by removing evidence in disagreement with the predominant phylogenetic signal in the data).

Additional phylogenomic and species network analyses. Besides the concatenation approach, we performed a series of additional analyses to verify the robustness of our phylogenomic topology. To perform species tree estimation to address potential incomplete lineage sorting (ILS), we used the software ASTRAL-III (Zhang *et al.* 2018), which conducts a summary-coalescent species tree analysis that is statistically consistent under the multi-species coalescent model. As input for ASTRAL-III, we performed maximum likelihood (ML) analyses on each alignment using IQ-Tree. To improve accuracy, we collapsed branches that were below 10% bootstrap support, as recommended by the authors.

To test for the impact of taxon sampling, we performed three rounds of taxon jackknifing with 1000 replicates on the concatenated data set, excluding per replicate one sample, to identify nodes that would be sensitive to 'rogue' samples possibly containing cross-contamination or being affected by hybridisation.

Because some of the performed analyses and topological instability among analyses suggest hybridization or introgression especially in the *M. curtus* clade (see Results below) we tested this formally by estimating species networks using the PhyloNetworks package (Solís-Lemus & Ané 2016; Solís-Lemus *et al.* 2017) in the programming language Julia (https://julialang.org). Gene trees from each alignment were used as input for this analysis and were filtered to reduce computational load. We filtered gene trees by including those with complete taxon sampling and excluding any gene trees with polytomies, which resulted in 5,916 out of ~12,000 gene trees being used. Additionally, gene trees were trimmed of taxa down to the *M. curtus* clade. First, we calculated the quartet concordance factors using the 'countquartetsintrees' function. The starting guide tree we used for the first iteration of the run (number of reticulations set to 0) was from the ML IQTree concatenation analysis and the filtered set of gene trees, which estimated a new tree under the multi-species coalescent (which was the same as the previous tree). We next performed five separate network analyses using SNaQ (Species Networks applying Quartets; 'snaq!' function) from one to five maximum reticulations allowed with 10 runs per analysis. To determine the best analysis and maximum number of

hybridizations, we calculated the network score (i.e., the pseudo deviant, a multiple of the negative log-likelihood up to a constant where the score 0 fits the data perfectly) and selected the best network from the lowest score. Due to the large amount of samples, a species network for the clade composed of the *M. betsileanus* clade, *M. fergusoni* clade, *M. ulcerosus* clade, and *M. stelliger* clade (the other group where topological incongruencies were observed; see below) could not be computed with the available computational resources.

Analysis of archival DNA

We employed the 'barcode fishing' strategy previously used by Rancilhac *et al.* (2020) and Scherz *et al.* (2020) to sequence fragments of three mitochondrial genes from 24 historical type specimens and one historical topotypical specimen: 16S, as well as a fragment of cytochrome oxidase, subunit I (cox1), and a fragment of cytochrome *b*. For this purpose, we used baits 70 nt in length designed by Arbor Biosciences from sequences of the majority of Malagasy frog species (including most of the nominal species, and several candidate species of *Brygoomantis*). 5962 baits were retained for target enrichment after filtering based on melting temperature and collapsing 99% identical baits. Tissue samples of thigh muscles were extracted from historical types using DNA-free scissors and stored in 100% ethanol in 1.5 ml tubes filled in a lab that was at this time naïve to *Mantidactylus* research. DNA extraction was performed in a clean lab dedicated to museum specimen and ancient DNA analyses. We washed samples with Qiagen PE Buffer, and extracted DNA following the protocol of Rohland *et al.* (2004), followed by purification using the protocol of Dabney *et al.* (2013). We then prepared libraries using a single-stranded (ss-DNA) approach optimised for ancient and archival DNA (Gansauge & Meyer 2013; Gansauge *et al.* 2017) using custom adapters from Gansauge and Meyer (2013). Next we amplified libraries with custom Illumina indexing primers described in Paijmans *et al.* (2017) after determining the optimal cycle number using qPCR (Basler *et al.* 2017; Gansauge & Meyer 2013).

We then captured ss-DNA libraries twice for the aforementioned target sequences using the Arbor Biosciences MyBaits kit, using 14.5 µL of each indexed library in a 24 h reaction at a hybridisation temperature of 65 °C and following the MyBaits target enrichment protocol except for reducing the bait volume to 2.75 µL and substituting the missing 2.75 µL in each reaction with nuclease-free water. After hybridization, the libraries were bound to streptavidin-coated magnetic beads, and the reactions washed and eluted according to the MyBaits kit protocol. We re-amplified the libraries via PCR in a reaction volume of 60 µL with the following PCR conditions: 120 s @ 95 °C, followed by a variable number of cycles, determined for each sample using qPCR, for 30 s@ 95 °C, 45 s @ 60 °C, 45 s @ 72 °C, with a final extension of 180 s @ 72 °C. We purified amplifications using a Min Elute PCR Purification Kit (Qiagen). Final elution was in a total volume of 30 µL of 10 nM Tris–CL, 0.05% TWEEN-20 solution (pH 8.0). We performed the procedure twice to increase target capture reactions success, as described in Li *et al.* (2015) and Paijmans *et al.* (2016). We determined the final library concentration and length distribution using Qubit 2.0 and 2200 TapeStation (Agilent Technologies) assays and sequenced the enriched library on an Illumina Next-Seq 500 sequencing platform using 500/550 High Output v2.5 kits (75 cycles SE, aimed at 3 million reads per sample) with custom sequencing primers (Paijmans *et al.* 2017).

After quality-trimming and adapter removal, we compared the reads automatically against reference sequences using the 'Museoscript' custom script described in Rancilhac *et al.* (2020) (https://github.com/rancilhac/Museoscript), using a similarity threshold to the references of 90%, in order to reduce the data set for further analysis. For this study, we focused on 16S because for this marker, DNA fragments of all known *Brygoomantis* lineages were available for comparison. Sequences of cytochrome *b* and cox1 were also assembled and submitted to Genbank. The reference library for read alignment included 16S sequences of *Mantidactylus alutus, M. betsileanus, M. bourgati, M. curtus, M. grubenmanni* **sp. nov.**, *M. inaudax, M. jonasi* **sp. nov.**, *M. katae* **sp. nov.**, *M. pauliani, M. tricinctus,* and *M. ulcerosus*, as well as *M. ambreensis* (subgenus *Ochthomantis*) and *M. guttulatus* (subgenus *Mantidactylus*). For types of species assigned to the subgenera *Hylobatrachus* and *Ochthomantis*, the library included *M. ambreensis, M. cowanii, M. femoralis, M. majori,* and *M. mocquardi* (all subgenus *Ochthomantis*), as well as *M. aerumnalis* and *M. albofrenatus* (subgenus *Chonomantis*), *M. betsileanus* (subgenus *Brygoomantis*), *M. argenteus* (subgenus *Maitsomantis*), *M. grandidieri* (subgenus *Mantidactylus*) and *M. lugubris* (subgenus *Hylobatrachus*).

Reads matching to the reference library were aligned to reference sequences of various *Brygoomatis* using CodonCode Aligner v 6.0.2 (CodonCode Corp.) with a majority-based alignment approach to align reads to reference sequences of various *Brygoomantis* for the three gene fragments. For the assembly, regions with a coverage of ≤5x were not considered, except in two cases where the overall coverage was very low (<100 reads matching the reference). The consensus sequences (of 16S, cytochrome *b* and cox1) obtained for the various type specimens were deposited in GenBank (accession numbers OP189679–OP189697).

Biogeography

Geographic regions were named according to Boumans *et al.* (2007) and Brown *et al.* (2016), i.e. the following regions (originally delimited primarily on the basis of major river basins, not on bioclimatic or biogeographical grounds) are distinguished: North, Sambirano, North East, North West, Northern Central East, West, Central, Southern Central East, South East, and South. These regions are consistently written in upper case and they are shown in Fig. 7. Some other general geographical descriptions such as 'central highlands' or 'east coast' do

not refer to well-defined regions and just indicate general geographical position; they are consistently written in lower case. We furthermore followed Brown *et al.* (2016) in defining 'northern Madagascar' as an area roughly delimited by a diagonal spanning from 15.5°S on the east coast to ca 15.0°S on the west coast. To circumscribe the distribution range of species, we used only locality records that were backed up by genetic evidence or, in a few cases of more easily recognisable species, by bioacoustic or morphological data. Maps were produced in QGIS 3.22 'Białowieża', using 1-second SRTM data made available by the US Geological Survey (USGS).

Rationale for species delimitation

The taxonomic procedure in this study followed the approach of Padial *et al.* (2010) using integration by congruence, similar to what we have done in previous comprehensive revisions (e.g. Crottini *et al.* 2015; Miralles *et al.* 2021; Rakotoarison *et al.* 2017). We sought for two or more independent lines of evidence supporting the distinctness of lineages, to serve as evidence for their evolutionary independence and thus species status in the framework of the general lineage or evolutionary species concept (de Queiroz 1998, 2007; Mayden 1997). The mitochondrial (16S) tree was used as initial evidence, by clustering 16S clades divergent from other such clades by sequence divergences >3%, a degree of divergence often corresponding to species-level units in anurans (Fouquet *et al.* 2007; Malone & Fontenot 2008; Vieites *et al.* 2009).

A second line of evidence was provided by divergence in the nuclear Rag-1 gene. As there is no recombination between mitochondrial and nuclear genes, both markers can be seen as largely independent from each other. Genealogical concordance between such markers has been long recognised as an important species criterion (Avise & Ball 1990), and can be highly informative even in the absence of monophyly (Weisrock *et al.* 2010), i.e. by strongly different allele frequencies or unique haplotypes not forming a clade. If nuclear DNA (nuDNA) and mitochondrial DNA (mtDNA) markers concordantly indicate a genetic separation of lineages, especially among geographically overlapping or co-occurring groups, it is of particular relevance to exclude mitochondrial introgression, which potentially can confound species delimitation based on mitochondrial markers alone. Additional lines of evidence used herein are morphological differentiation, in particular focusing on femoral gland size and shape, webbing, body size, skin texture (presence or absence of dorsolateral folds); and advertisement calls. Especially characters involved in mate recognition and sexual selection, such as anuran advertisement calls, are of high value for species delimitation as they are usually indicative of reproductive isolation (Padial *et al.* 2010).

Species delimitation in *Brygoomantis* proved particularly difficult in several cases due to the absence of sufficient reliably (genetically) identified voucher specimens, lack of sympatry among many closely related lineages (which could prove co-occurrence without genetic admixture), low or absent morphological differences among closely related lineages, nuclear haplotype sharing among many species-level lineages as already known from other *Mantidactylus* (e.g. Scherz *et al.* 2019), and secretive calling behaviour causing a general lack of bioacoustic data for some species complexes. However, it must be emphasized (cf. Miralles & Vences 2013; Padial *et al.* 2010) that negative results from any of these lines of evidence do not prove two lineages are conspecific. However, such negative evidence (i.e. the failure of a line of evidence to support species-level distinctness of two lineages) constitutes an additional challenge and elevates the bar for other lines of evidence to provide conclusive support for their evolutionary independence.

Our approach to species delimitation is classical, in the sense that we do not rely on statistical species delimitation, but rather base our delimitation on the congruence of multiple lines of evidence. In part, this decision is based on the rather fragmentary nature of our dataset—integrative algorithmic delimitation (iBPP; Solís-Lemus *et al.* 2015) is not able to cope well with such incomplete matrices of traits. Our integrative taxonomic approach, however, renders our species delimitation reasonably robust, as well as comprehensible and testable for future researchers.

As, in general, false negatives (failure to detect and describe a species) in taxonomy can be more easily corrected by future researchers than a false positive (wrongly describing an intraspecific lineage as a species) (Miralles & Vences 2013), we herein follow a conservative approach and refrain from describing some lineages as species when we deem evidence inconclusive or material insufficient. However, after Hillis (2020) and de Queiroz (2020), we consider the subspecies category (and nomenclatural rank) appropriate for such lineages that can be defined by genetic or phenotypic means but have not yet reached complete evolutionary independence (see also Hawlitschek *et al.* 2012; Vences *et al.* 2013). Consequently, we distinguish the following three categories within *Brygoomantis*: (i) species, i.e. evolutionarily independent lineages as in most cases ascertained by concordance of various lines of evidence (divergence in nuclear-encoded DNA, mitochondrial DNA, morphology, and bioacoustics). (ii) Subspecies, i.e. genetically divergent lineages for which our data suggest evolutionary independence has not yet been fully achieved; typically, these are allopatric lineages of substantial mitochondrial divergence but with widespread Rag-1 haplotype sharing and no noticeable differentiation in morphology or calls, often corresponding to what Vieites *et al.* (2009) named deep conspecific lineages; (iii) Unconfirmed candidate species, a rank assigned to samples of substantial mitochondrial divergence with insufficient other evidence; they might represent distinct species but could also be subspecies or represent population-level variation (see Vieites *et al.* 2009).

Procedure for lineage delimitation, genetic distances, and diagnosis

In practice, for an initial delimitation of genetic (mitochondrial) lineages, calculation of genetic distances, and identification of diagnostic nucleotide positions, we use various programs of the iTaxoTools project (Vences *et al.* 2021), namely the ASAPy tool implementing ASAP (Puillandre *et al.* 2021), MAFFTpy implementing MAFFT (Katoh & Standley 2013) for sequence alignment, TaxI2, and DNAdiagnoser.

These analyses were based on a subset of the 16S rRNA alignment, for which we attempted a balance among including (i) a maximum of DNA sequences and (ii) maximum of nucleotides, (iii) a minimum of missing data, and (iv) achieving an alignment length similar to that of Vieites *et al.* (2009) who provided reference 16S distance values among Malagasy frogs. Besides removing the archival DNA sequences and other sequences <300 bp (n=226; see Fig. 2), this required the exclusion of an additional 103 sequences, to obtain an alignment consisting of 976 sequences with complete or almost complete coverage of the 3'-terminal 16S fragment recommended for DNA barcoding by Vences *et al.* (2005) and used in Vieites *et al.* (2009). The alignment had a total length of 488 bp, with no more than 50 bp missing at the start and end of single sequences. We used MAFFTpy to perform a thorough alignment under the G-INS-i strategy. The 976-sequence 16S alignment was used as input in ASAPy to calculate initial hypotheses of species-level lineages, with a barcode gap prior of 3% based on Vieites *et al.* (2009). For each of the species-level subsets suggested by the preferred ASAP species partition, we then examined other lines of evidence (degree of Rag-1 haplotype sharing, amount of mitochondrial genetic distance, phylogenomic relationships, morphological and bioacoustic differentiation) in an integrative species delimitation approach.

We calculated uncorrected pairwise genetic distances (p-distances) from the same 16S alignment in TaxI2, obtaining minimum and maximum values of inter-lineage divergences for the previously defined lineages.

For diagnosing new species and subspecies named in this study, we build on the approach of Rakotoarison *et al.* (2017), providing a differential diagnosis using morphological, morphometric, chromatic, and bioacoustic characters in comparison to all nominal species described to date, and to any new species described previously in the text, while comparisons to other new species are then provided in the respective accounts in the subsequent text. Because a reliable morphological and bioacoustic diagnosis of all against all species of *Brygoomantis* is not possible (e.g. due to the lack of advertisement call data for many species), we follow the concept of 'lineage diagnosis' of Vijayakumar *et al.* (2014). Based on our phylogenomic tree we first determine in which major clade a species-level lineage is embedded; we then provide comparisons to the other species in this same clade, and in more detail to that species that constitutes the direct sister taxon of the new species. To species of other clades, we only performed some general comparisons, except in cases of extreme morphological similarity to the diagnosed species. In addition, we also follow Vijayakumar *et al.* (2014) in providing, in some cases, a 'field diagnosis', comparing the new species in more detail with other species occurring in syntopy or close sympatry. Lastly, in order to satisfy formal criteria, we refer to a list of diagnostic nucleotide sites, included as Supplementary Table 1, among all pairs of taxa, thereby providing in words a clear list of characters distinguishing the new species from all other *Brygoomantis*. For this purpose, the 16S data was once more subsetted to 882 sequences and trimmed to 448 bp, to obtain an alignment without any missing data at the start and end of the alignment, and re-aligned to the complete 16S sequence from the *Mantella madagascariensis* mitochondrial genome (Kurabayashi *et al.* 2006) as reference. We removed five nucleotide positions that required insertions (gaps) in the *M. madagascariensis* sequence, in order to provide unambiguous positional information of diagnostic sites relative to the reference. This trimmed alignment was then used in DNAdiagnoser to identify diagnostic nucleotide positions among lineages.

Suggestions for IUCN Red List assessments

We evaluated the conservation status of all *Brygoomantis* species against the appropriate IUCN Red List criteria (IUCN 2012), based on their distributions as estimated herein. In general, only criteria B and D2 can be applied to species where population size estimates are lacking. We calculated the Extent of Occurrence (EOO) of species in QGIS v 3.22 (QGIS Development Team 2022) by first calculating the minimum convex polygon around records using the Minimum Bounding Geometry tool of the Vector Geometry toolkit, and subsequently estimating the area in square kilometres of each polygon with the $area function of the field calculator. For species represented by just two records, or more than two records that occurred in an approximately straight line, a polygon was instead calculated by creating a rectangle 5 km wide by the distance between the furthest points long. Both tight minimum convex polygons and 5 km wide corridors will tend to give underestimated EOOs. Still, we deem this approach to be a closer match to our knowledge of species distribution than drawing the polygons around 'potentially suitable habitat' where the species has not yet been observed, particularly because most *Brygoomantis* species are found almost exclusively in association with bodies of water, flowing or still, and their distribution is therefore inherently patchy. One species known only from Nosy Boraha was estimated to have a distribution the size of that island, to be conservative.

TABLE 1. Sequencing and assembly metrics of target-capture sequencing of a segment of the 16S rRNA gene from liquid-preserved type specimens of historical nomina in the *Mantidactylus* subgenera *Brygoomantis*, *Ochthomantis*, and *Hylobatrachus*. Results for the latter two subgenera are here reported as the listed types were studied to exclude that they may refer to species of *Brygoomantis*. Assembly length is here reported not counting missing data in discontinuous assemblies. HT, holotype; LT, lectotype; PLT, paralectotype; ST, syntype. * according to lectotype designated herein. # only two separate short fragments recovered. ## probably all consisting of contamination, including human mtDNA. † MNHN 1894.001 is probably not a paralectotype of *Rana aluta*; see the relevant discussion, below.

Nomen	Specimen	Status	Year of collection	Reads (raw)	Reads (filtered)	Reference for assembly	Reads (assembly)	Length assembly
Subgenus *Brygoomantis*								
Rana aluta Peracca, 1893	MNHN 1894.001	topotypical specimen†	≤ 1893	3001331	29993	*M. alutus* (*M. betsileanus*)	2045 (2041)	157
Mantidactylus ambohimitombi Boulenger, 1918	BMNH 1947.2.26.25	LT *	1896	3302614	475894	*M. betsileanus*	221328	412
Mantidactylus bellyi Mocquard, 1895	MNHN 1983.240	HT	≤ 1893	3937013	97140	*M. bellyi* (*M. betsileanus*)	31627 (30700)	415
Rana betsileana Boulenger, 1882	BMNH 1947.2.26.44	PLT *	≤ 1882	3691121	321477	*M. betsileanus*	155396	411
Rana betsileana Boulenger, 1882	BMNH 1947.2.26.45	LT *	≤ 1882	3578636	310519	*M. betsileanus*	87650	411
Rana biporus Boulenger, 1889	BMNH 1947.2.26.47	LT *	≤ 1889	2299994	7578	*M. betsileanus*	6443	411
Mantidactylus bourgati Guibé, 1974	MNHN 1972.437	HT	1971	4044068	947438	*M. bourgati* (*M. betsileanus*)	186096 (174994)	409
Mantidactylus brauni Ahl, 1929	ZMB 53737	LT *	≤ 1929	1509708	96634	*M. betsileanus*	25925	414
Mantidactylus brunneus Ahl, 1929	ZMB 30514	HT	≤ 1929	3266458	240372	*M. betsileanus*	42034	411
Rana curta Boulenger, 1882	BMNH 1947.2.10.30	LT *	≤ 1882	2572258	200410	*M. betsileanus*	39260	406
Rhacophorus fumigatus Mocquard, 1895	MNHN 1895.258	HT	≤ 1895	3783324	313634	*M. betsileanus*	95158	411
Rana inaudax Peracca, 1893	MZUT An727.1	LT	≤ 1893	2678644	4772	*M. alutus*	4354	61 + 46 #
Mantidactylus madecassus Millot and Guibé, 1950	MNHN 1953.246	LT	1949	4592034	20642	*M. betsileanus*	12086	390
Mantidactylus multiplicatus Boettger, 1913	SMF 6733	HT	≤ 1905	3350467	262017	*M. betsileanus*	127565	411

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TABLE 1. (Continued)

Nomen	Specimen	Status	Year of collection	Reads (raw)	Reads (filtered)	Reference for assembly	Reads (assembly)	Length assembly
Gephyromantis tricinctus Guibé, 1947	MNHN 1931.0026	LT	1930	2675582	84	*M. betsileanus*	10	107 ##
Mantidactylus tripunctatus Angel, 1930	MNHN 1931.0024	LT *	1926	4238117	515476	*M. betsileanus*	220630	413
Limnodytes ulcerosus Boettger, 1880	SMF 6605	LT	≤ 1880	2424827	86456	*M. betsileanus*	14935	413
Subgenus *Ochthomantis*								
Mantidactylus catalai Angel, 1935	MNHN 1935.153	HT	≤ 1935	1451886	13	*M. femoralis*	0	0
Rana femoralis Boulenger, 1882	BMNH 1947.2.22.65	LT	≤ 1882	3622032	529123	*M. femoralis*	218031	267
Rana flavicrus Boulenger, 1889	BMNH 1947.2.26.53	HT	≤ 1885	2738970	107749	*M. femoralis*	65613	267
Mantidactylus majori Boulenger, 1896	BMNH 1947.2.10.26	PLT	≤ 1896	3706029	368200	*M. femoralis*	124909	264
Mantidactylus mocquardi Angel, 1929	MNHN 1929.207	HT	≤ 1929	4199370	451270	*M. femoralis*	184481	268
Mantidactylus poissoni Angel, 1937	MNHN 1937.001	HT	≤ 1937	3207653	114	*M. femoralis*	8	132
Subgenus *Hylobatrachus*								
Rana cowanii Boulenger, 1882	BMNH 1947.2.22.63	ST	≤ 1882	2936459	113638	*M. femoralis*	54749	267
Polypedates lugubris Duméril, 1853	MNHN 1994.1752	ST	≤ 1853	3762908	379894	*M. femoralis*	195992	269

Results

Archival DNA analyses

Our target-capture strategy successfully recovered partial or full contigs of the 16S rRNA fragment from 23 out of 25 historical specimens of *Mantidactylus* (which include 22 name-bearing types). Assembly statistics for all specimens are summarised in Table 1. We sampled 17 specimens of species assigned to the subgenus *Brygoomantis*, as well as eight specimens from the morphologically similar subgenera *Ochthomantis* and *Hylobatrachus*. We also obtained assemblies of cytochrome *b* and cox1 gene fragments for many of these samples, as these mitochondrial markers were also included in our bait set. As stated in the methods, due to the lack of complete reference libraries for these genes we did not use them for in-depth analysis. Furthermore, for most samples, we obtained much fewer reads for those two genes than for 16S. The respective sequence assemblies obtained have however been submitted to GenBank for future studies, and for those cases where references were available, the conclusions from cytochrome *b* and cox1 comparisons confirmed those obtained from the 16S sequences.

In two cases, 16S DNA barcode fishing was unsuccessful: the lectotype of *Gephyromantis tricinctus* yielded only 10 reads matching the reference sequence, including several contaminations with human mtDNA and other, unassignable reads, and the type of *Mantidactylus catalai* yielded no reads aligning to the reference. No usable cytochrome *b* or cox1 sequences were obtained from these two samples either. Our archival DNA analysis also does not include the holotype of *Mantidactyus laevis* Angel, 1929 (MNHN 1929.208; lost according to Guibé 1978), a species described from 'environs de Tananarive'; we rely on previous studies considering this *nomen* to represent a junior synonym of *Mantidactylus alutus* (e.g. Blommers-Schlösser & Blanc 1991; Glaw & Vences 1992a), the only species known to be present in and near Madagascar's capital Antananarivo (Tananarive in French).

Three samples yielded a low number of <5000 matching reads for 16S. From the sample of *Mantidactylus poissoni* (currently considered as a junior synonym of *M. femoralis* in the subgenus *Ochthomantis*), only eight reads aligning to the reference were obtained, but these did match other *Mantidactylus* in BLAST searches, and may enable clarificiation of the identity of this enigmatic taxon in the future. For the lectotype of *Rana inaudax* (subgenus *Brygoomantis*), we found 4354 matching reads, corresponding to three sections of the 16S gene. Of these, one low-coverage fragment was a mixture of reads from birds and human, thus representing contamination. The other two sections of 61 and 46 bp, respectively, had a coverage of 1057 and 3105 reads, and were almost complete matches with the sequence of specimen ZCMV 3259, previously considered to be *M. biporus* (one mismatch in the first fragment). In an exploratory phylogenetic analysis, representing the sample by these 107 nucleotides only, it clustered close to ZCMV 3259 and FGMV 2002.2252 from Fierenana. Finally, for a probable paralectotype of *Rana aluta*, only 2045 reads aligned to the reference, but the resulting contig of 157 bp reliably clustered with other sequences assigned to this species in the molecular tree.

The remaining 20 samples all yielded >5000 16S reads aligning to the respective reference, often many more: >50,000 reads in 13 samples, and >100,000 reads in nine samples (Table 1). As we illustrated in detail in a previous study on another *Mantidactylus* groups (Rancilhac *et al.* 2020), assembly coverage was highly variable over the entire 16S fragment of ca 415 bp, but usually amounted to several thousands of reads at multiple subsections with numerous diagnostic positions. The number of matching reads did not appear to depend on the age of the samples, which were collected from 1853 to 1971. One of the largest numbers of matching reads (195,992) was obtained from the oldest sample (a syntype of *Mantidactylus lugubris*) that had been liquid-preserved in the holdings of the Muséum National d'Histoire Naturelle, Paris since at least 1853. The two failed samples were from the same collections, dating from the 1930s. Overall, sample age (year of collection in Table 1) and number of reads in the assembly were not significantly correlated (Pearson correlation; $R = -0.104$; $P = 0.62$).

Except *Gephyromantis tricinctus*, which did not yield usable sequences, all sequences from samples of historical *Brygoomantis* specimens were included in phylogenetic analyses of the 16S marker and could thereby be reliably assigned to lineages. Samples of type specimens in the subgenera *Ochthomantis* and *Hylobatrachus* (Table 1) all clustered with lineages within their respective subgenera, confirming none of them represents an earlier available name for newly discovered species in *Brygoomantis*. All these sequences are made available in GenBank for further study; we here only briefly summarise that the new data confirm the identity of *M. femoralis, M. majori* and *M. mocquardi* as previously assessed (e.g. Poth *et al.* 2013; Randrianiaina *et al.* 2011). The data also appear to suggest that *Mantidactylus poissoni* might be the valid name to be applied to a species previously considered as *M.* sp. Ca47 (e.g. Perl *et al.* 2014; Poth *et al.* 2013; Randrianiaina *et al.* 2011; Vieites *et al.* 2009), and that *Rana flavicrus* (currently a synonym of *M. femoralis*) might belong to the subgenus *Hylobatrachus*. For the two type specimens of both nomina of this subgenus included (*Polypedates lugubris* and *Rana cowanii*), we recovered sequences clustering with those of a mitochondrial lineage named *M.* sp. Ca48 by Scherz *et al.* (2019), indicating that the taxonomy of this species complex (probably affected by mitochondrial introgression) requires further clarification.

TABLE 2. Uncorrected pairwise distances for a 488 bp fragment of the 16S rRNA gene between species and subspecies of *Mantidactylus* (*Brygoomantis*). Each cell shows the minimum and maximum value observed. Yellow highlighted cells are intraspecific distances. Blue-highlighted cells show distances between subspecies of the same species. Values above and below the diagonal are identical.

	***M.* Ca25**	***M. alutus***	***M. a. ambohimitombi***	***M. manerana antsanga***	***M. augustini***	***M. bellyi***	***M. betsileanus***	***M. biporus***	***M. bletzae***	***M. bourgati***	***M. brevirostris***	***M. curtus***	***M. eulenbergeri***	***M. fergusoni***	***M. manerana fotaka***	***M. georgei***	***M. glosi***	***M. grubenmanni***	***M. gudrunae***	***M. inaudax***	***M. incognitus***
***M.* Ca25**	0.0	8.7	10.5	10.3	10.3	8.7	6.4	10.9	10.5	10.3	10.3	10.7	9.6	2.6	9.9	9.3	8.8	11.8	12.4	9.0	7.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	0.2	10.1	11.6	10.3	11.1	9.8	7.9	11.6	11.2	10.7	10.7	12.1	10.1	3.7	10.1	10.5	9.3	12.6	14.2	10.5	8.2
M. alutus	8.7	0.0	6.2	5.2	6.0	7.8	7.2	6.4	5.9	5.6	7.6	6.8	6.2	7.4	4.9	6.6	4.3	10.3	9.9	3.9	7.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.1	1.9	8.0	6.2	7.4	10.3	9.2	8.0	7.9	6.5	8.7	8.9	7.0	9.6	5.8	8.9	6.0	11.6	12.3	6.4	9.2
M. ambohimitombi	10.5	6.2	0.0	7.0	7.4	10.3	8.8	6.8	6.6	5.6	8.6	6.8	7.2	10.0	5.7	8.8	6.1	10.5	10.1	5.1	10.1
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.6	8.0	0.8	7.5	8.4	12.5	11.3	8.0	8.3	6.5	9.4	9.5	7.7	11.7	6.6	11.8	6.9	12.8	13.2	7.4	11.4
M. manerana	10.3	5.2	7.0	0.0	7.0	9.7	9.1	7.4	6.8	7.6	8.6	7.0	7.0	9.3	3.9	7.4	6.0	10.9	11.1	3.7	9.9
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.3	6.2	7.5	0.0	7.8	10.7	10.5	8.2	7.9	8.1	8.8	8.3	7.4	9.9	3.9	9.3	6.5	11.3	12.6	5.6	10.1
M. augustini	10.3	6.0	7.4	7.0	0.0	9.2	10.1	4.9	6.6	7.4	9.4	8.2	6.8	9.9	6.6	8.6	4.7	11.6	12.0	4.7	9.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.1	7.4	8.4	7.8	3.7	12.1	11.4	5.8	8.5	8.3	10.3	9.8	7.6	11.2	7.2	11.2	5.3	14.3	13.6	8.2	11.1
M. bellyi	8.7	7.8	10.3	9.7	9.2	0.0	7.4	10.3	10.7	9.9	8.4	10.3	9.9	8.7	9.4	8.0	8.6	10.7	11.8	8.9	9.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.8	10.3	12.5	10.7	12.1	1.3	9.7	12.0	12.8	11.4	9.4	13.2	11.3	10.5	10.8	10.3	10.5	12.6	14.6	11.5	10.3
M. betsileanus	6.4	7.2	8.8	9.1	10.1	7.4	0.0	10.1	9.7	9.5	7.4	9.1	9.1	5.7	8.6	6.3	8.0	8.9	9.5	8.2	6.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.9	9.2	11.3	10.5	11.4	9.7	2.1	11.9	12.2	10.8	9.0	11.8	10.5	7.8	9.7	9.1	9.6	10.8	11.2	10.4	7.6
M. biporus	10.9	6.4	6.8	7.4	4.9	10.3	10.1	0.0	7.9	8.2	9.7	8.5	7.0	10.9	7.4	9.7	5.8	12.6	12.0	6.4	10.3
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.6	8.0	8.0	8.2	5.8	12.0	11.9	0.4	8.8	9.0	10.8	10.2	7.8	12.3	7.7	11.7	6.2	14.4	14.3	8.4	11.4
M. bletzae	10.5	5.9	6.6	6.8	6.6	10.7	9.7	7.9	0.0	8.1	8.6	8.8	8.1	10.3	6.4	8.7	6.1	12.2	12.4	5.7	10.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.2	7.9	8.3	7.9	8.5	12.8	12.2	8.8	4.1	9.2	11.0	11.2	9.2	11.5	7.2	10.8	7.4	13.5	14.7	7.6	12.1
M. bourgati	10.3	5.6	5.6	7.6	7.4	9.9	9.5	8.2	8.1	0.0	9.3	7.9	7.8	9.7	6.2	9.5	5.7	11.0	11.6	6.0	10.1
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.7	6.5	6.5	8.1	8.3	11.4	10.8	9.0	9.2	0.4	9.7	9.8	8.3	11.5	6.8	11.3	6.5	12.5	14.0	8.0	11.0
M. brevirostris	10.3	7.6	8.6	8.6	9.4	8.4	7.4	9.7	8.6	9.3	0.0	10.3	8.6	9.7	9.7	8.4	7.4	11.3	10.5	8.4	8.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.7	8.7	9.4	8.8	10.3	9.4	9.0	10.8	11.0	9.7	0.2	11.9	9.1	10.8	9.9	10.5	8.3	12.0	12.4	10.2	9.5

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TABLE 2. (Continued)

	M. Ca25	*M. alutus*	*M. a. ambo-himitombi*	*M. manerana antsanga*	*M. augus-tini*	*M. bellyi*	*M. betsile-anus*	*M. biporus*	*M. bletzae*	*M. bourgati*	*M. brevirostris*	*M. curtus*	*M. eulenbergeri*	*M. fergusoni*	*M. manerana fotaka*	*M. georgei*	*M. glosi*	*M. grubenmanni*	*M. gudrunae*	*M. inaudax*	*M. incognitus*
M. curtus	10.7	6.8	6.8	7.0	8.2	10.3	9.1	8.5	8.8	7.9	10.3	0.0	8.7	9.9	7.4	9.1	7.4	11.6	11.6	6.6	10.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.1	8.9	9.5	8.3	9.8	13.2	11.8	10.2	11.2	9.8	11.9	1.1	10.2	12.1	8.9	11.4	8.9	14.4	15.0	10.0	12.6
M. eulenbergeri	9.6	6.2	7.2	7.0	6.8	9.9	9.1	7.0	8.1	7.8	8.6	8.7	0.0	9.6	6.2	8.7	5.4	10.7	10.5	5.2	8.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.1	7.0	7.7	7.4	7.6	11.3	10.5	7.8	9.2	8.3	9.1	10.2	0.2	10.3	6.4	10.8	6.0	12.4	12.2	7.0	9.6
M. fergusoni	2.6	7.4	10.0	9.3	9.9	8.7	5.7	10.9	10.3	9.7	9.7	9.9	9.6	0.0	8.8	8.7	8.6	10.7	12.2	8.6	8.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3.7	9.6	11.7	9.9	11.2	10.5	7.8	12.3	11.5	11.5	10.8	12.1	10.3	2.5	9.7	10.3	9.3	12.3	14.5	11.1	9.1
M. manerana fotaka	9.9	4.9	5.7	3.9	6.6	9.4	8.6	7.4	6.4	6.2	9.7	7.4	6.2	8.8	0.0	7.8	5.9	10.7	11.2	3.5	8.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.1	5.8	6.6	3.9	7.2	10.8	9.7	7.7	7.2	6.8	9.9	8.9	6.4	9.7	0.0	9.2	6.3	11.6	12.8	5.3	9.3
M. georgei	9.3	6.6	8.8	7.4	8.6	8.0	6.3	9.7	8.7	9.5	8.4	9.1	8.7	8.7	7.8	0.0	7.6	9.9	9.9	7.2	7.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.5	8.9	11.8	9.3	11.2	10.3	9.1	11.7	10.8	11.3	10.5	11.4	10.8	10.3	9.2	4.3	9.8	12.2	13.0	9.4	10.2
M. glosi	8.8	4.3	6.1	6.0	4.7	8.6	8.0	5.8	6.1	5.7	7.4	7.4	5.4	8.6	5.9	7.6	0.0	10.4	11.2	4.8	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.3	6.0	6.9	6.5	5.3	10.5	9.6	6.2	7.4	6.5	8.3	8.9	6.0	9.3	6.3	9.8	0.0	12.1	13.9	6.7	9.4
M. grubenmanni	11.8	10.3	10.5	10.9	11.6	10.7	8.9	12.6	12.2	11.0	11.3	11.6	10.7	10.7	10.7	9.9	10.4	0.0	7.6	10.9	9.1
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.6	11.6	12.8	11.3	14.3	12.6	10.8	14.4	13.5	12.5	12.0	14.4	12.4	12.3	11.6	12.2	12.1	4.3	9.7	13.0	10.1
M. gudrunae	12.4	9.9	10.1	11.1	12.0	11.8	9.5	12.0	12.4	11.6	10.5	11.6	10.5	12.2	11.2	9.9	11.2	7.6	0.0	10.7	9.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	14.2	12.3	13.2	12.6	13.6	14.6	11.2	14.3	14.7	14.0	12.4	15.0	12.2	14.5	12.8	13.0	13.9	9.7	5.3	14.1	11.2
M. inaudax	9.0	3.9	5.1	3.7	4.7	8.9	8.2	6.4	5.7	6.0	8.4	6.6	5.2	8.6	3.5	7.2	4.8	10.9	10.7	0.0	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.5	6.4	7.4	5.6	8.2	11.5	10.4	8.4	7.6	8.0	10.2	10.0	7.0	11.1	5.3	9.4	6.7	13.0	14.1	3.7	10.3
M. incognitus	7.8	7.8	10.1	9.9	9.7	9.0	6.2	10.3	10.5	10.1	8.8	10.5	8.8	8.0	8.8	7.8	8.2	9.1	9.7	8.2	0.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.2	9.2	11.4	10.1	11.1	10.3	7.6	11.4	12.1	11.0	9.5	12.6	9.6	9.1	9.3	10.2	9.4	10.1	11.2	10.3	0.8
M. jahnarum	3.3	8.0	10.0	9.7	10.1	8.7	5.3	10.9	10.9	10.3	9.0	9.9	9.3	2.0	9.0	8.9	8.6	10.9	11.6	8.4	7.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3.7	9.2	11.2	9.9	11.5	9.8	6.9	11.6	12.1	10.7	9.4	11.3	9.9	3.1	9.2	10.1	9.1	11.8	13.4	10.5	8.0
M. jonasi	6.4	6.6	8.2	8.4	8.0	7.6	5.1	9.3	8.5	8.2	7.4	9.5	8.0	6.1	8.0	7.0	6.9	8.1	10.4	7.0	5.3
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.2	8.9	10.3	10.1	10.3	10.3	8.3	10.9	9.9	10.3	8.8	12.1	9.7	8.8	9.2	9.7	8.7	11.3	13.5	9.7	7.2

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TABLE 2. (Continued)

	***M.* Ca25**	***M. alutus***	***M. a. ambo-himitombi***	***M. manerana antsanga***	***M. augus-tini***	***M. bellyi***	***M. betsile-anus***	***M. biporus***	***M. bletzae***	***M. bourgati***	***M. brevirostris***	***M. curtus***	***M. eulenbergeri***	***M. fergusoni***	***M. manerana fotaka***	***M. georgei***	***M. glosi***	***M. grubenmanni***	***M. gudrunae***	***M. inaudax***	***M. incognitus***
M. katae	7.2	7.8	9.7	9.3	9.1	8.4	5.7	9.5	9.6	9.1	7.8	10.3	9.1	6.3	8.6	8.4	7.2	10.3	11.3	8.2	6.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.6	10.4	11.1	10.7	11.5	11.1	8.0	11.1	11.7	10.5	9.0	12.6	10.3	8.2	10.2	10.7	8.6	12.5	13.7	11.7	8.0
M. kortei	8.2	8.0	10.0	10.1	9.9	8.2	7.4	9.9	9.8	9.7	8.8	11.3	9.1	8.2	9.7	8.6	7.4	11.1	12.8	8.6	9.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.4	9.5	11.1	10.4	11.5	9.7	9.1	10.6	10.7	10.4	9.3	13.0	9.7	9.1	10.2	10.4	7.8	12.8	14.1	10.6	9.7
M. madecassus	10.5	6.0	2.9	6.4	6.4	9.4	9.0	6.9	5.7	6.0	8.4	6.6	7.0	9.9	5.3	8.2	5.5	9.9	10.5	5.7	9.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.7	7.0	3.3	6.4	7.2	10.5	10.7	7.1	7.2	6.2	8.6	7.8	7.4	10.9	5.3	9.4	5.8	11.1	12.2	7.2	10.1
M. mahery	10.9	5.1	7.4	7.4	7.6	10.3	10.0	8.2	8.4	7.6	9.4	8.6	7.0	10.7	7.0	7.8	6.6	12.2	12.0	5.7	10.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.1	6.4	8.9	8.6	8.4	12.0	12.0	9.6	9.9	9.0	10.5	11.0	7.9	12.2	8.1	9.9	8.1	14.7	14.4	8.2	11.2
M. amb. marefo	11.1	7.0	0.6	7.4	8.2	11.1	9.0	7.6	6.8	6.0	8.4	7.6	7.6	10.7	6.6	9.6	6.3	11.1	11.1	5.9	10.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.3	8.0	1.0	7.4	8.4	12.3	10.7	7.9	8.1	6.3	8.6	9.1	7.6	11.4	6.6	11.6	6.7	12.2	13.4	7.4	11.1
M. marintsoai	8.6	7.3	9.4	9.5	9.3	8.6	6.6	10.9	10.4	9.5	8.6	10.1	9.8	8.2	8.8	7.6	8.3	11.8	10.3	8.6	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.0	9.0	10.8	9.9	10.8	10.3	8.3	12.0	11.8	10.4	9.2	12.4	10.4	9.1	9.2	9.3	8.9	12.8	12.6	9.8	8.9
M. m. manerana	9.9	5.6	6.2	3.1	7.4	9.4	8.2	7.5	7.2	6.4	9.0	7.6	6.8	9.0	3.7	8.0	6.1	10.7	11.2	3.7	9.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.1	6.8	7.2	3.3	8.6	10.7	10.1	8.4	8.3	7.4	9.5	9.5	7.2	10.1	4.1	9.6	6.9	11.8	13.0	5.7	10.1
M. noralottae	7.6	7.4	9.2	9.7	9.1	8.7	6.2	9.5	9.8	9.1	8.0	10.5	8.9	7.4	9.1	8.4	7.6	10.3	11.4	8.2	6.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.9	8.8	10.5	9.9	10.3	10.1	7.3	10.1	10.8	9.7	8.4	12.2	9.5	8.4	9.5	9.4	8.0	11.7	13.0	10.1	7.5
M. pauliani	8.4	3.7	5.1	4.9	6.0	7.4	7.6	5.5	5.9	5.6	7.0	6.8	5.1	8.6	4.7	7.0	3.7	9.3	9.3	4.1	8.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.0	4.9	5.9	5.1	6.6	8.8	9.6	6.5	6.7	6.0	7.4	8.2	5.7	9.9	4.9	8.7	4.5	10.1	11.1	5.7	9.4
M. riparius	8.6	6.8	9.0	9.5	9.2	9.0	6.6	9.4	9.4	9.1	8.4	9.7	8.6	7.7	9.0	7.6	7.4	9.7	11.3	7.8	6.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.1	8.7	11.1	10.1	11.4	11.2	8.7	10.8	11.6	10.3	9.2	11.9	9.6	9.2	10.1	9.8	8.3	11.7	13.3	10.5	7.6
M. schulzi	7.2	7.4	10.1	8.9	9.5	7.2	6.9	9.8	10.0	9.1	7.2	10.6	8.5	7.9	10.0	7.0	8.1	8.3	9.1	8.3	7.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.3	9.7	12.0	9.8	11.4	8.9	8.7	11.1	11.1	10.3	8.2	12.1	9.5	9.1	10.7	8.4	8.7	9.3	10.9	10.2	8.4
M. steinfartzi	6.4	7.6	9.1	8.9	8.7	7.0	6.2	8.7	9.4	9.3	7.8	9.9	7.9	7.0	9.5	6.8	8.3	8.9	8.7	8.2	7.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.2	9.3	10.6	9.5	9.9	8.4	7.8	9.9	11.3	10.2	8.4	11.7	8.7	8.2	10.1	9.2	9.2	10.4	10.9	10.0	8.4

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TABLE 2. (Continued)

	M. Ca25	*M. alutus*	*M. a. ambo-himitombi*	*M. manerana antsanga*	*M. augus-tini*	*M. bellyi*	*M. betsile-anus*	*M. biporus*	*M. bletzae*	*M. bourgati*	*M. brevirostris*	*M. curtus*	*M. eulenbergeri*	*M. fergusoni*	*M. manerana fotaka*	*M. georgei*	*M. glosi*	*M. grubenmanni*	*M. gudrunae*	*M. inaudax*	*M. incognitus*
M. stelliger	9.4	6.8	8.8	8.2	9.1	7.6	7.4	9.3	9.6	9.3	8.4	9.3	9.3	8.0	8.6	7.4	7.2	10.1	8.9	7.2	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.7	8.0	10.1	8.2	10.1	8.6	8.8	10.1	10.1	9.5	8.4	10.6	9.6	9.1	8.6	8.5	7.8	11.0	10.3	8.9	8.6
M. tricinctus	12.1	9.9	9.9	12.1	10.9	11.3	10.3	11.6	11.8	11.1	11.3	11.4	9.9	12.1	10.3	9.5	10.6	7.0	5.3	9.5	9.1
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.8	11.4	11.9	12.4	13.4	13.5	12.1	13.0	13.2	12.3	11.9	13.9	10.9	13.3	11.6	12.4	12.1	9.6	7.0	12.2	10.3
M. tripunctatus	6.5	7.2	8.8	8.8	9.0	7.4	5.4	9.0	8.6	8.5	7.0	10.3	8.0	6.5	8.5	7.4	7.4	10.3	10.9	7.8	6.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.4	8.8	10.1	9.5	11.1	9.7	7.4	10.4	10.2	10.2	7.7	12.4	9.0	8.0	9.5	8.8	8.5	11.8	12.9	9.9	7.4
M. ulcerosus	10.7	8.8	11.3	10.7	9.9	3.1	8.4	11.3	11.3	10.1	9.2	11.3	11.1	9.4	10.7	8.4	8.8	9.9	11.6	10.3	9.4
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.3	10.8	13.0	11.5	11.9	4.5	10.3	12.5	13.0	11.3	10.1	14.2	11.9	10.9	11.4	10.3	10.0	11.7	13.9	12.2	10.7
M. amb. miloko	10.3	6.2	3.7	6.0	6.2	9.6	8.8	6.6	6.6	6.2	9.0	6.0	6.6	9.8	4.7	8.2	5.7	9.9	10.7	5.5	9.4
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.1	7.4	4.6	6.4	8.0	11.2	11.3	7.3	8.1	6.7	9.4	8.4	7.2	11.2	5.5	10.1	6.2	11.8	12.8	6.8	10.7

TABLE 2. (Continued)

	M. jahnarum	*M. jonasi*	*M. katae*	*M. kortei*	*M. madecassus*	*M. mahery*	*M. amb. marefo*	*M. marintsoai*	*M. m. manerana*	*M. noralottae*	*M. pauliani*	*M. riparius*	*M. schulzi*	*M. steinfartzi*	*M. stelliger*	*M. tricinctus*	*M. tripunctatus*	*M. ulcerosus*	*M. amb. miloko*
***M.* Ca25**	3.3	6.4	7.2	8.2	10.5	10.9	11.1	8.6	9.9	7.6	8.4	8.6	7.2	6.4	9.4	12.1	6.5	10.7	10.3
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3.7	9.2	8.6	8.4	10.7	12.1	11.3	9.0	10.1	7.9	9.0	9.1	8.3	7.2	9.7	12.8	7.4	11.3	11.1
M. alutus	8.0	6.6	7.8	8.0	6.0	5.1	7.0	7.3	5.6	7.4	3.7	6.8	7.4	7.6	6.8	9.9	7.2	8.8	6.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.2	8.9	10.4	9.5	7.0	6.4	8.0	9.0	6.8	8.8	4.9	8.7	9.7	9.3	8.0	11.4	8.8	10.8	7.4
M. ambohimitombi	10.0	8.2	9.7	10.0	2.9	7.4	0.6	9.4	6.2	9.2	5.1	9.0	10.1	9.1	8.8	9.9	8.8	11.3	3.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.2	10.3	11.1	11.1	3.3	8.9	1.0	10.8	7.2	10.5	5.9	11.1	12.0	10.6	10.1	11.9	10.1	13.0	4.6
M. man. antsanga	9.7	8.4	9.3	10.1	6.4	7.4	7.4	9.5	3.1	9.7	4.9	9.5	8.9	8.9	8.2	12.1	8.8	10.7	6.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.9	10.1	10.7	10.4	6.4	8.6	7.4	9.9	3.3	9.9	5.1	10.1	9.8	9.5	8.2	12.4	9.5	11.5	6.4
M. augustini	10.1	8.0	9.1	9.9	6.4	7.6	8.2	9.3	7.4	9.1	6.0	9.2	9.5	8.7	9.1	10.9	9.0	9.9	6.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.5	10.3	11.5	11.5	7.2	8.4	8.4	10.8	8.6	10.3	6.6	11.4	11.4	9.9	10.1	13.4	11.1	11.9	8.0

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TABLE 2. (Continued)

	M. jahnarum	*M. jonasi*	*M. katae*	*M. kortei*	*M. madecassus*	*M. mahery*	*M. amb. marefo*	*M. marintsoai*	*M. m. manerana*	*M. noralottae*	*M. pauliani*	*M. riparius*	*M. schulzi*	*M. steinfartzi*	*M. stelliger*	*M. tricinctus*	*M. tripunctatus*	*M. ulcerosus*	*M. amb. miloko*
M. bellyi	8.7	7.6	8.4	8.2	9.4	10.3	11.1	8.6	9.4	8.7	7.4	9.0	7.2	7.0	7.6	11.3	7.4	3.1	9.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.8	10.3	11.1	9.7	10.5	12.0	12.3	10.3	10.7	10.1	8.8	11.2	8.9	8.4	8.6	13.5	9.7	4.5	11.2
M. betsileanus	5.3	5.1	5.7	7.4	9.0	10.0	9.0	6.6	8.2	6.2	7.6	6.6	6.9	6.2	7.4	10.3	5.4	8.4	8.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	6.9	8.3	8.0	9.1	10.7	12.0	10.7	8.3	10.1	7.3	9.6	8.7	8.7	7.8	8.8	12.1	7.4	10.3	11.3
M. biporus	10.9	9.3	9.5	9.9	6.9	8.2	7.6	10.9	7.5	9.5	5.5	9.4	9.8	8.7	9.3	11.6	9.0	11.3	6.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.6	10.9	11.1	10.6	7.1	9.6	7.9	12.0	8.4	10.1	6.5	10.8	11.1	9.9	10.1	13.0	10.4	12.5	7.3
M. bletzae	10.9	8.5	9.6	9.8	5.7	8.4	6.8	10.4	7.2	9.8	5.9	9.4	10.0	9.4	9.6	11.8	8.6	11.3	6.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.1	9.9	11.7	10.7	7.2	9.9	8.1	11.8	8.3	10.8	6.7	11.6	11.1	11.3	10.1	13.2	10.2	13.0	8.1
M. bourgati	10.3	8.2	9.1	9.7	6.0	7.6	6.0	9.5	6.4	9.1	5.6	9.1	9.1	9.3	9.3	11.1	8.5	10.1	6.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.7	10.3	10.5	10.4	6.2	9.0	6.3	10.4	7.4	9.7	6.0	10.3	10.3	10.2	9.5	12.3	10.2	11.3	6.7
M. brevirostris	9.0	7.4	7.8	8.8	8.4	9.4	8.4	8.6	9.0	8.0	7.0	8.4	7.2	7.8	8.4	11.3	7.0	9.2	9.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.4	8.8	9.0	9.3	8.6	10.5	8.6	9.2	9.5	8.4	7.4	9.2	8.2	8.4	8.4	11.9	7.7	10.1	9.4
M. curtus	9.9	9.5	10.3	11.3	6.6	8.6	7.6	10.1	7.6	10.5	6.8	9.7	10.6	9.9	9.3	11.4	10.3	11.3	6.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.3	12.1	12.6	13.0	7.8	11.0	9.1	12.4	9.5	12.2	8.2	11.9	12.1	11.7	10.6	13.9	12.4	14.2	8.4
M. eulenbergeri	9.3	8.0	9.1	9.1	7.0	7.0	7.6	9.8	6.8	8.9	5.1	8.6	8.5	7.9	9.3	9.9	8.0	11.1	6.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.9	9.7	10.3	9.7	7.4	7.9	7.6	10.4	7.2	9.5	5.7	9.6	9.5	8.7	9.6	10.9	9.0	11.9	7.2
M. fergusoni	2.0	6.1	6.3	8.2	9.9	10.7	10.7	8.2	9.0	7.4	8.6	7.7	7.9	7.0	8.0	12.1	6.5	9.4	9.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3.1	8.8	8.2	9.1	10.9	12.2	11.4	9.1	10.1	8.4	9.9	9.2	9.1	8.2	9.1	13.3	8.0	10.9	11.2
M. man. fotaka	9.0	8.0	8.6	9.7	5.3	7.0	6.6	8.8	3.7	9.1	4.7	9.0	10.0	9.5	8.6	10.3	8.5	10.7	4.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.2	9.2	10.2	10.2	5.3	8.1	6.6	9.2	4.1	9.5	4.9	10.1	10.7	10.1	8.6	11.6	9.5	11.4	5.5
M. georgei	8.9	7.0	8.4	8.6	8.2	7.8	9.6	7.6	8.0	8.4	7.0	7.6	7.0	6.8	7.4	9.5	7.4	8.4	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.1	9.7	10.7	10.4	9.4	9.9	11.6	9.3	9.6	9.4	8.7	9.8	8.4	9.2	8.5	12.4	8.8	10.3	10.1
M. glosi	8.6	6.9	7.2	7.4	5.5	6.6	6.3	8.3	6.1	7.6	3.7	7.4	8.1	8.3	7.2	10.6	7.4	8.8	5.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.1	8.7	8.6	7.8	5.8	8.1	6.7	8.9	6.9	8.0	4.5	8.3	8.7	9.2	7.8	12.1	8.5	10.0	6.2

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TABLE 2. (Continued)

	M. jahnarum	*M. jonasi*	*M. katae*	*M. kortei*	*M. madecassus*	*M. mahery*	*M. amb. marefo*	*M. marintsoai*	*M. m. manerana*	*M. noralottae*	*M. pauliani*	*M. riparius*	*M. schulzi*	*M. steinfartzi*	*M. stelliger*	*M. tricinctus*	*M. tripunctatus*	*M. ulcerosus*	*M. amb. miloko*
M. grubenmanni	10.9	8.1	10.3	11.1	9.9	12.2	11.1	11.8	10.7	10.3	9.3	9.7	8.3	8.9	10.1	7.0	10.3	9.9	9.9
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.8	11.3	12.5	12.8	11.1	14.7	12.2	12.8	11.8	11.7	10.1	11.7	9.3	10.4	11.0	9.6	11.8	11.7	11.8
M. gudrunae	11.6	10.4	11.3	12.8	10.5	12.0	11.1	10.3	11.2	11.4	9.3	11.3	9.1	8.7	8.9	5.3	10.9	11.6	10.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	13.4	13.5	13.7	14.1	12.2	14.4	13.4	12.6	13.0	13.0	11.1	13.3	10.9	10.9	10.3	7.0	12.9	13.9	12.8
M. inaudax	8.4	7.0	8.2	8.6	5.7	5.7	5.9	8.6	3.7	8.2	4.1	7.8	8.3	8.2	7.2	9.5	7.8	10.3	5.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.5	9.7	11.7	10.6	7.2	8.2	7.4	9.8	5.7	10.1	5.7	10.5	10.2	10.0	8.9	12.2	9.9	12.2	6.8
M. incognitus	7.2	5.3	6.6	9.0	9.7	10.5	10.7	8.2	9.5	6.6	8.6	6.2	7.8	7.6	8.2	9.1	6.8	9.4	9.4
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.0	7.2	8.0	9.7	10.1	11.2	11.1	8.9	10.1	7.5	9.4	7.6	8.4	8.4	8.6	10.3	7.4	10.7	10.7
M. jahnarum	0.0	7.0	5.7	8.6	9.6	11.1	10.5	7.4	9.4	7.2	8.0	7.4	7.6	7.4	8.4	11.1	6.7	10.1	9.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	0.2	8.6	7.6	8.8	9.8	12.1	10.7	8.0	9.9	7.5	8.6	8.0	8.5	7.8	8.6	11.9	7.4	10.9	10.5
M. jonasi	7.0	0.0	5.3	6.4	8.6	9.2	8.4	7.0	7.8	5.3	7.0	5.4	5.2	5.6	7.0	9.7	4.1	7.2	8.8
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.6	5.5	7.8	8.4	10.7	11.2	9.7	8.5	10.3	6.7	8.2	7.1	6.9	8.1	8.3	12.4	6.9	9.6	10.7
M. katae	5.7	5.3	0.0	4.7	9.3	10.7	9.4	7.5	8.4	3.5	7.2	4.0	7.4	6.6	7.6	11.7	2.9	8.8	9.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.6	7.8	1.6	5.8	10.3	12.6	10.3	8.7	10.0	4.5	8.7	5.5	8.5	8.2	8.9	13.2	4.1	11.1	11.1
M. kortei	8.6	6.4	4.7	0.0	10.3	11.3	10.3	8.2	9.4	4.3	8.2	5.9	8.0	7.2	8.2	11.9	4.3	8.7	10.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.8	8.4	5.8	0.0	10.6	12.1	10.8	8.5	9.9	4.5	8.6	6.8	8.3	8.0	8.4	13.2	5.1	9.7	11.2
M. madecassus	9.6	8.6	9.3	10.3	0.0	7.6	3.3	9.2	5.7	9.2	4.9	9.4	9.7	8.8	8.4	9.7	9.2	10.9	2.5
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.8	10.7	10.3	10.6	0.0	8.5	3.3	9.8	6.4	9.4	5.1	10.3	10.2	9.5	8.4	10.7	9.9	11.6	3.3
M. mahery	11.1	9.2	10.7	11.3	7.6	0.0	8.2	10.0	7.6	9.9	5.5	10.3	10.4	9.9	9.7	11.1	9.6	11.3	7.4
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12.1	11.2	12.6	12.1	8.5	1.4	9.1	11.6	9.1	10.9	7.1	11.6	12.2	11.2	11.1	12.8	11.0	12.5	9.1
M. amb. marefo	10.5	8.4	9.4	10.3	3.3	8.2	0.0	10.0	6.6	9.4	5.5	9.4	10.8	9.7	9.4	10.9	8.6	11.9	4.1
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.7	9.7	10.3	10.8	3.3	9.1	0.0	10.5	7.2	9.9	5.7	10.5	11.6	10.1	9.4	11.7	9.4	12.7	4.5

...*Continued on the next page*

TABLE 2. (Continued)

	M. jahnarum	*M. jonasi*	*M. katae*	*M. kortei*	*M. madecassus*	*M. mahery*	*M. amb. marefo*	*M. marintsoai*	*M. m. manerana*	*M. noralottae*	*M. pauliani*	*M. riparius*	*M. schulzi*	*M. steinfartzi*	*M. stelliger*	*M. tricinctus*	*M. tripunctatus*	*M. ulcerosus*	*M. amb. miloko*
M. marintsoai	7.4	7.0	7.5	8.2	9.2	10.0	10.0	0.0	9.3	6.5	8.0	7.6	7.3	7.6	7.6	11.1	6.9	9.4	9.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.0	8.5	8.7	8.5	9.8	11.6	10.5	0.2	9.6	6.9	8.7	8.7	7.9	8.2	8.3	13.0	7.7	10.8	10.3
M. m. manerana	9.4	7.8	8.4	9.4	5.7	7.6	6.6	9.3	0.0	9.1	4.7	8.8	9.5	9.1	8.2	10.3	7.9	10.7	5.3
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9.9	10.3	10.0	9.9	6.4	9.1	7.2	9.6	0.6	9.5	5.5	9.6	10.5	9.9	8.4	11.3	8.8	11.6	6.2
M. noralottae	7.2	5.3	3.5	4.3	9.2	9.9	9.4	6.5	9.1	0.0	7.8	3.9	6.9	6.8	8.0	10.5	3.3	9.7	9.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.5	6.7	4.5	4.5	9.4	10.9	9.9	6.9	9.5	0.2	8.2	4.8	7.1	7.3	8.1	11.9	3.7	10.7	10.7
M. pauliani	8.0	7.0	7.2	8.2	4.9	5.5	5.5	8.0	4.7	7.8	0.0	7.2	7.0	7.2	7.0	9.3	6.8	8.4	4.9
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.6	8.2	8.7	8.6	5.1	7.1	5.7	8.7	5.5	8.2	0.2	8.2	7.9	8.0	7.2	10.3	7.6	9.2	5.3
M. riparius	7.4	5.4	4.0	5.9	9.4	10.3	9.4	7.6	8.8	3.9	7.2	0.0	7.1	7.4	7.6	10.1	3.7	9.4	9.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.0	7.1	5.5	6.8	10.3	11.6	10.5	8.7	9.6	4.8	8.2	0.2	7.8	8.5	8.2	11.7	4.3	11.1	10.5
M. schulzi	7.6	5.2	7.4	8.0	9.7	10.4	10.8	7.3	9.5	6.9	7.0	7.1	0.0	2.6	7.6	9.1	6.7	8.1	9.3
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.5	6.9	8.5	8.3	10.2	12.2	11.6	7.9	10.5	7.1	7.9	7.8	0.0	3.0	8.2	10.5	7.3	9.1	10.9
M. steinfartzi	7.4	5.6	6.6	7.2	8.8	9.9	9.7	7.6	9.1	6.8	7.2	7.4	2.6	0.0	7.4	9.2	5.6	8.4	8.6
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.8	8.1	8.2	8.0	9.5	11.2	10.1	8.2	9.9	7.3	8.0	8.5	3.0	1.2	7.8	10.7	6.8	9.3	9.7
M. stelliger	8.4	7.0	7.6	8.2	8.4	9.7	9.4	7.6	8.2	8.0	7.0	7.6	7.6	7.4	0.0	9.9	7.4	7.6	8.2
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8.6	8.3	8.9	8.4	8.4	11.1	9.4	8.3	8.4	8.1	7.2	8.2	8.2	7.8	0.0	10.7	7.9	8.0	8.4
M. tricinctus	11.1	9.7	11.7	11.9	9.7	11.1	10.9	11.1	10.3	10.5	9.3	10.1	9.1	9.2	9.9	0.0	10.1	11.7	9.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	11.9	12.4	13.2	13.2	10.7	12.8	11.7	13.0	11.3	11.9	10.3	11.7	10.5	10.7	10.7	3.9	11.5	13.1	11.5
M. tripunctatus	6.7	4.1	2.9	4.3	9.2	9.6	8.6	6.9	7.9	3.3	6.8	3.7	6.7	5.6	7.4	10.1	0.0	8.9	9.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	7.4	6.9	4.1	5.1	9.9	11.0	9.4	7.7	8.8	3.7	7.6	4.3	7.3	6.8	7.9	11.5	0.7	10.6	10.6
M. ulcerosus	10.1	7.2	8.8	8.7	10.9	11.3	11.9	9.4	10.7	9.7	8.4	9.4	8.1	8.4	7.6	11.7	8.9	0.0	10.7
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.9	9.6	11.1	9.7	11.6	12.5	12.7	10.8	11.6	10.7	9.2	11.1	9.1	9.3	8.0	13.1	10.6	0.8	12.1
M. amb. miloko	9.6	8.8	9.6	10.0	2.5	7.4	4.1	9.2	5.3	9.7	4.9	9.0	9.3	8.6	8.2	9.7	9.0	10.7	0.0
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10.5	10.7	11.1	11.2	3.3	9.1	4.5	10.3	6.2	10.7	5.3	10.5	10.9	9.7	8.4	11.5	10.6	12.1	2.7

TABLE 3. List of localities mentioned in the text, geographical coordinates, elevations, and species of *Mantidactylus* (*Brygoomantis*) occurring at the respective sites. Elevation (m above sea level [a.s.l.]) is partly based on references, own GPS readings, or has been inferred via GIS from the coordinates of records (marked with an asterisk). When elevation is given as NA (not applicable), it is because specimens were collected in that general area, but without precise coordinates from which to extract elevational range of its occurrence. Note that many additional (identified and unidentified) records of *Brygoomantis* species are available from published herpetological surveys (Rakotondravony & Goodman 2011) including numerous protected areas (e.g. Raselimanana *et al.* 2018), but since reliable species identification is almost impossible without examining specimens and/or genetic data, they are not considered in this table.

Location	Lat.	Lon.	Elev.	Clade	Species
20 km north of Vatomandry	-19.1926	48.9128	15*	*fergusoni*	*M. georgei*
Alaotra region (swamp)	-17.774	48.083	933*	*betsileanus*	*M. betsileanus*
				curtus	*M. alutus*
Ambahavala	-24.1427	47.1057	346	*tricinctus*	*M. tricinctus*
Ambatobe	-15.25	50.43	14	*fergusoni*	*M. fergusoni*
				inaudax	*M. manerana antsanga*
				tricinctus	*M. grubenmanni*
Ambatomandondona	-18.9163	48.4196	932*	*betsileanus*	*M. katae*
Ambatovaky	-21.2826	47.3273	1201	*betsileanus*	*M. betsileanus*
Ambinanifaho	-14.6167	50.1333	27*	*fergusoni*	*M. fergusoni*
Ambodiriana	-16.6746	49.7028	158	*fergusoni*	*M. fergusoni*
Ambodisakoa	-17.312	48.6661	804	*betsileanus*	*M. betsileanus*
Ambodivohitra	-14.8409	49.9524	411*	*betsileanus*	*M. jonasi*
Ambohimitombo	-20.72	47.43	1150	*curtus*	*M. ambohimitombi ambohimitombi*
Ambohitantely	-18.172	47.302	1520	*betsileanus*	*M. betsileanus*
				curtus	*M. alutus*
				curtus	*M. ambohimitombi miloko*
				inaudax	*M. inaudax*
Ambohitantely: Jardin botanique	-18.1717	47.2817	1580	*betsileanus*	*M. betsileanus*
				curtus	*M. ambohimitombi miloko*
				inaudax	*M. inaudax*
Ambohitantely: Site 2	-18.1783	47.2904	1546	*betsileanus*	*M. betsileanus*
				inaudax	*M. inaudax*
Ambohitantely: Zone 3	-18.1995	47.2809	1574*	*betsileanus*	*M. betsileanus*
Ambohitsara	-21.3572	47.8157	294	*betsileanus*	*M. katae*
				stelliger	*M. stelliger*
				tricinctus	*M. grubenmanni*
Ambositra	-20.5167	47.25	1300	*curtus*	*M. curtus*
Ampasimazava	-16.9227	49.2493	445	*fergusoni*	*M. fergusoni*
Ampofoko (old camp)	-15.4229	49.1209	1034	*betsileanus*	*M. jonasi*
Ampotsidy	-14.4135	48.7173	1227–1380	*betsileanus*	*M. jonasi*
				inaudax	*M. inaudax*
An'Ala	-18.93	48.47	840	*betsileanus*	*M. katae*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
				biporus	*M. biporus*
				tricinctus	*M. grubenmanni*
Andapa	-14.6333	49.6167	580	*ulcerosus*	*M. bellyi*
Andasibe: orchid garden	-18.9327	48.4132	920	*betsileanus*	*M. betsileanus*
Andasibe: stream along road	-18.929	48.413	920	*betsileanus*	*M. katae*
Andasibe/Analamazaotra	-18.9333	48.4167	920	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				biporus	*M. eulenbergeri*
Andohahela: Camp 2005	-24.5440	46.7141	1548	*betsileanus*	*M. kortei*
Andohahela: Camp 1	-24.7586	46.8542	247	*betsileanus*	*M. katae*
				betsileanus	*M. tripunctatus*
				tricinctus	*M. gudrunae*
Andrakata	-14.6167	49.7167	460	*ulcerosus*	*M. bellyi*
Andramanolotra	-13.9969	50.0963	16*	*fergusoni*	*M. marintsoai*
Andrangoloaka	-19.00	47.95	1380	*curtus*	*M. alutus*
Andranofotsy	-15.4353	49.8439	85	*biporus*	*M. augustini*
				fergusoni	*M. fergusoni*
Andranonafindra Forest	-14.736	48.5483	1180	*betsileanus*	*M. jonasi*
Andringitra	-22.2	46.9	NA	*betsileanus*	*M. katae*
				curtus	*M. bourgati*
				curtus	*M. madecassus*
Andringitra: Andohariana Plateau	-22.1803	46.9003	2030	*curtus*	*M. bourgati*
Andringitra eastern slopes: Imaitso	-22.1403	46.9469	1509	*curtus*	*M. bourgati*
Andringitra western slopes: Siranandambo	-22.1303	46.8478	1590	*curtus*	*M. bourgati*
Andringitra western slopes: Iantaranomby	-22.1290	46.8467	1580	*curtus*	*M. bourgati*
Andringitra western slopes: Andramena	-22.1273	46.8533	1740	*curtus*	*M. bourgati*
Andringitra eastern slopes: Asaramanitra	-22.1358	46.8890	1590	*curtus*	*M. bourgati*
Andringitra eastern slopes: Riandahy	-22.1458	46.8915	1730	*curtus*	*M. bourgati*
Andringitra: Ambalamarovandana	-22.226	46.934	1530	*curtus*	*M. bourgati*
Andringitra: Cuvette Boby	-22.1947	46.8897	2488	*curtus*	*M. bourgati*
				curtus	*M. madecassus*
Andringitra: Pic Boby	-22.2	46.92	NA	*curtus*	*M. madecassus*
Angavokely	-18.9167	47.7333	1640	*curtus*	*M. ambohimitombi miloko*
Angorony: fragment near Maromandia	-14.2211	48.1421	115	*ulcerosus*	*M. ulcerosus*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Anivorano Est: Andrarihitra, Vohiposa	-18.7638	48.9468	60	*betsileanus*	*M. incognitus*
				biporus	*M. eulenbergeri*
				fergusoni	*M. georgei*
Anjozorobe	-18.4	47.8667	1250	*betsileanus*	*M. betsileanus*
				inaudax	*M. inaudax*
Ankarafantsika	-16.2839	46.7749	853*	*ulcerosus*	*M. ulcerosus*
Ankarafantsika: Ampondrabe Forest	-16.325	46.9233	250	*ulcerosus*	*M. ulcerosus*
Ankarafantsika: Andasiravina Forest	-16.3033	46.93	150	*ulcerosus*	*M. ulcerosus*
Ankarana	-12.9336	49.1269	90	*ulcerosus*	*M. bellyi*
Ankaratra	-19.3333	47.2667	NA	*curtus*	*M. alutus*
				curtus	*M. ambohimitombi ambohimitombi*
				curtus	*M. pauliani*
Ankaratra: Analafohy	-19.3442	47.275	2146	*curtus*	*M. ambohimitombi ambohimitombi*
Ankaratra: forest Ambohimiradrana road	-19.3325	47.2709	2000	*curtus*	*M. ambohimitombi ambohimitombi*
Ankaratra: Tavolotara	-19.3458	47.2791	2019	*curtus*	M. ambohimitombi ambohimitombi
Ankaratra: Tsiafajavona plateau	-19.3283	47.2617	2380	*curtus*	*M. ambohimitombi ambohimitombi*
Ankazomivady	-20.7722	47.1877	1735	*curtus*	*M. ambohimitombi miloko*
				curtus	*M. curtus*
Anosibe An'Ala	-19.4333	48.2167	636	*betsileanus*	*M. betsileanus*
Antambato: swamp ca 4 km from Antambato village (Antsaloana)	-14.4811	48.8999	1258	*betsileanus*	*M. jonasi*
Antambato: village stream	-14.493	48.8686	1188	*betsileanus*	*M. jonasi*
Antanambe	-16.4299	49.7846	263	*fergusoni*	*M. fergusoni*
Antara	-16.8875	49.1832	481*	*betsileanus*	*M. betsileanus*
Antoetra	-20.8013	47.3647	1680	*curtus*	*M. alutus*
				curtus	*M. ambohimitombi ambohimitombi*
				curtus	*M. curtus*
Antoetra: Farimazava Forest	-20.835	47.3325	1380–1420	*curtus*	*M. ambohimitombi ambohimitombi*
				curtus	*M. curtus*
Antokotelo	-18.4277	49.0096	308*	*fergusoni*	*M. georgei*
Antsahanoro	-14.845	50.1336	66*	*fergusoni*	*M. fergusoni*
Antsatramidola	-15.634	48.9675	404	*ulcerosus*	*M. ulcerosus*
Antsirakambiaty forest	-20.5949	46.5638	1601	*betsileanus*	*M. betsileanus*
				curtus	*M. curtus*
Bealanana-Antsohihy forest fragment	-14.7215	48.5627	1187	*betsileanus*	*M. jonasi*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Beanka	-18.0236	44.5022	254	*curtus*	*M. mahery*
Befanjana	-16.68	49.59	NA	*betsileanus*	*M. betsileanus*
				biporus	*M. augustini*
				fergusoni	*M. fergusoni*
				inaudax	*M. manerana antsanga*
				tricinctus	*M. grubenmanni*
Befotaka-Midongy: Rozabe Forest	-23.7368	47.0227	780–900	*tricinctus*	*M. tricinctus*
Belambo	-14.5487	49.7489	234*	*fergusoni*	*M. fergusoni*
				ulcerosus	*M. bellyi*
Bemandrevo/Samangorona/ Alaotra/Mangoro	-18.405	48.63	661*	*betsileanus*	*M. incognitus*
Bemanevika	-14.259	48.778	1130	*betsileanus*	*M. jonasi*
Bemanevika: Camp 1, Antsirakala	-14.4306	48.6018	1468	*betsileanus*	*M. jonasi*
Bemanevika: Camp 2	-14.3599	48.5902	1538	*betsileanus*	*M. jonasi*
Bemanevika: River	-14.4825	48.6272	1109	*betsileanus*	*M. jonasi*
Bemanevika/Antsirabe-Nord	-13.9864	49.9519	61*	*fergusoni*	*M. marintsoai*
Benavony	-13.7	48.4833	140	*ulcerosus*	*M. ulcerosus*
Berara	-14.3092	47.9153	170	*ulcerosus*	*M. ulcerosus*
Betampona	-17.8883	49.2277	190–517	*betsileanus*	*M. betsileanus*
				biporus	*M. biporus*
				biporus	*M. brevirostris*
				fergusoni	*M. georgei*
				tricinctus	*M. grubenmanni*
Betampona: Maintimbato	-17.8940	49.2283	NA	*betsileanus*	*M. georgei*
Betampona: Rendrirendry	-17.9186	49.2103	325	*betsileanus*	*M. betsileanus* *M. georgei*
Betampona: Sahabefoza	-17.9152	49.2090	349	*betsileanus*	*M. betsileanus*
				biporus	*M. brevirostris*
Betampona: Sahaindrana	-17.89383	49.19972	327	*betsileanus*	*M. betsileanus*
				biporus	*M. biporus*
Betampona: Sahambendrana	-17.8984	49.2154	458	*biporus*	*M. brevirostris*
Betampona: Vohitsivalana	-17.8846	49.2008	517	*biporus*	*M. biporus*
				fergusoni	*M. georgei*
Bevitagnono Forest	-14.7386	48.5172	1024–1041	*ulcerosus*	*M. ulcerosus*
Camp Ambatofotsy	-19.5431	48.3165	907	*betsileanus*	*M. katae*
Col des Tapias	-20.23	47.08	1503	*curtus*	*M. curtus*
Commune d'Andekaleka: Marovato	-18.686	48.6055	787	*betsileanus*	*M. incognitus*
Fanambana	-13.6138	50.0019	53	*ulcerosus*	*M. bellyi*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Fierenana (Camp)	-18.5433	48.4489	948	*betsileanus*	*M. betsileanus*
				inaudax	*M. inaudax*
Fivahona: Ambavala	-22.0447	46.9014	1508	*betsileanus*	*M. betsileanus*
				curtus	*M. bourgati*
Fivahona: Velotsoa	-22.0704	46.8759	1278	*betsileanus*	*M. betsileanus*
				curtus	*M. bourgati*
forest fragment, road from Lake Alaotra to Brieville (Andranogorika)	-17.7678	47.9842	1147	*betsileanus*	*M. betsileanus*
				inaudax	*M. inaudax*
Ibity	-20.1167	47.0167	2090	*curtus*	*M. alutus*
				curtus	*M. curtus*
Ifanadiana	-21.3	47.6333	530	*betsileanus*	*M. katae*
Irogno Forest	-14.75	48.492	958	*ulcerosus*	*M. ulcerosus*
Isalo	-22.42	45.27	NA	*betsileanus*	*M. noralottae*
				betsileanus	*M. riparius*
				curtus	*M. mahery*
Isalo: Ambovo	-22.2998	45.3526	996	*betsileanus*	*M. noralottae*
Isalo: Andriamanero	-22.35	45.4	640	*betsileanus*	M. noralottae
				betsileanus	*M. riparius*
Isalo: Anjofo	-22.3694	45.361	800	*betsileanus*	*M. noralottae*
Isalo: Canyon des rats	-22.4803	45.378	960	*curtus*	*M. mahery*
Isalo: Cascade des Nymphes	-22.5373	45.3759	870	*betsileanus*	*M. riparius*
				curtus	*M. mahery*
Isalo: Forêt d'Analalava	-22.5879	45.1308	719	*curtus*	*M. mahery*
Isalo: Hotel Isalo Ranch	-22.5926	45.3928	804	*curtus*	*M. mahery*
Isalo: Namazaha	-22.5367	45.3748	871	*betsileanus*	*M. riparius*
				curtus	*M. mahery*
Isalo: Oasis	-22.6269	45.3533	776	*curtus*	*M. mahery*
Isalo: Piscine naturelle	-22.5664	45.364	920	*betsileanus*	*M. riparius*
Isalo: Zahavola	-22.8037	45.2458	850	*curtus*	*M. mahery*
Itremo	-20.5091	46.4984	1648	*betsileanus*	*M. betsileanus*
				curtus	*M. ambohimitombi marefo*
				curtus	*M. curtus*
Ivohibe: Camp 3 (high elevation)	-22.4971	46.9576	1575	*biporus*	*M. bletzae*
Ivoloina	-18.0667	49.4	25	*fergusoni*	*M. georgei*
km 27 on RN Antsohihy-Mandritsara	-15.0532	48.2064	140	*ulcerosus*	*M. ulcerosus*
Lac Alaotra	-17.59	48.52	850	*betsileanus*	*M. betsileanus*
Lokobe National Park	-13.3988	48.3183	0–110	*ulcerosus*	*M. ulcerosus*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Mahanoro	-19.9062	48.8156	10	*betsileanus*	*M. incognitus*
Mahasoa campsite	-17.2977	48.702	1032	*betsileanus*	*M. betsileanus*
Mahatsara-Mantadia/Mantady	-18.8288	48.4327	995	*betsileanus*	*M. katae*
Makay	-21.6866	45.1700	174	*curtus*	*M. mahery*
Makira western slope: Camp 0, Sahaovy	-15.4889	49.0785	603	*betsileanus*	*M. jonasi*
				curtus	*M. mahery*
				ulcerosus	*M. ulcerosus*
Makira western slope: Camp 1, Angozongahy	-15.437	49.1186	1009	*betsileanus*	*M. jonasi*
Makira western slope: Hevirina (Pandanus swamp)	-15.449	49.1119	1093	*inaudax*	*M. inaudax*
				ulcerosus	*M. ulcerosus*
Makira western slope: Satellite Camp, source of Fotsialanana river	-15.4668	49.1289	1067	*betsileanus*	*M. jonasi*
Makira: Ambodivohangy	-15.2899	49.6203	83	*fergusoni*	*M. fergusoni*
Manantantely	-24.983	46.917	180	*betsileanus*	*M. tripunctatus*
				tricinctus	*M. gudrunae*
Mandena	-24.9522	47.0039	8	*betsileanus*	*M. tripunctatus*
Mandraka	-18.9289	47.8936	1210	*betsileanus*	*M. betsileanus*
Mangindrano: Camp 0 near Mangindrano (Ambinanitelo)	-14.2254	48.9634	1171	*betsileanus*	*M. jonasi*
Manombo	-23.01	47.7334	30	*tricinctus*	*M. tricinctus*
Manombo: Camp	-23.0283	47.7315	44	*tricinctus*	*M. tricinctus*
Manongarivo: Camp 0	-13.9756	48.4267	688	*ulcerosus*	*M. schulzi*
Manongarivo: Camp 1	-13.9769	48.4219	751	*ulcerosus*	*M. steinfartzi*
Mantasoa	-19.0167	47.8333	1430	*curtus*	*M. alutus*
Mariavaratra	-21.6245	47.4194	1144	*betsileanus*	*M. katae*
Maroantsetra	-15.427	49.7415	170	*fergusoni*	*M. georgei*
Marojejy	-14.4067	49.7671	NA	*fergusoni*	*M. fergusoni*
Marojejy: above Camp Simpona	-14.4408	49.7399	1576	*inaudax*	*M. manerana manerana*
Marojejy: between camps 2 and 3	-14.4344	49.7666	615*	*fergusoni*	*M. fergusoni*
				inaudax	*M. manerana manerana*
Marojejy: Camp 0	-14.4463	49.7852	310	*fergusoni*	*M. fergusoni*
Marojejy: Camp 1 (Mantella)	-14.4377	49.7756	481	*fergusoni*	*M. fergusoni*
Marojejy: Camp 3 (Simpona)	-14.4367	49.7434	1326	*betsileanus*	*M. jonasi*
				fergusoni	*M. fergusoni*
				inaudax	*M. manerana manerana*
Marojejy: close to Camp 1 (Mantella)	-14.4394	49.7771	465*	*fergusoni*	*M. fergusoni*
Marojejy: east of tourist trail	-14.446	49.8234	273*	*fergusoni*	*M. fergusoni*
				fergusoni	*M. marintsoai*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
				ulcerosus	*M. bellyi*
Marolambo	-20.05	48.1167	490	*betsileanus*	*M. katae*
Marolambo: Ambodisavoka	-20.0919	48.3222	287	*betsileanus*	*M. katae*
Maromizaha	-18.9762	48.4648	980–1100	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				biporus	*M. eulenbergeri*
Marotandrano-Riamalandy	-16.2833	48.8144	815–1015	*betsileanus*	*M. betsileanus*
Marovitsika	-22.525	46.9833	1000	*betsileanus*	*M. katae*
Masoala	-15.55	50.1167	NA	*betsileanus*	*M. jonasi*
				biporus	*M. augustini*
				fergusoni	*M. fergusoni*
Masoala: Ilampy Corridor	15.3920	50.0470	ca 550	*biporus*	*M. augustini*
Masoala: Ambatoledama Corridor	-15.267	49.983	ca 1000	*biporus*	*M. augustini*
Midongy du Sud	-23.5833	47.0167	600	*tricinctus*	*M. tricinctus*
Montagne d'Ambre: Gîte d'Etape	-12.5268	49.1721	1050	*betsileanus*	*M. jonasi*
				ulcerosus	*M. bellyi*
Montagne d'Ambre: Andrano créole	-12.495	49.1848	751–772	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Antomboko	-12.4907	49.1716	652–730	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Antsakomboiny	-12.4688	49.2207	467–480	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Betsikoboko	-12.4908	49.1787	623–743	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Cascade Antakarana	-12.5206	49.1724	997–1061	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Cascade sacrée	-12.5286	49.1708	1057–1192	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: high elevation around Grand Lac	-12.5963	49.1592	1372	*betsileanus*	*M. jonasi*
				ulcerosus	M. bellyi
Montagne d'Ambre: high elevation near Lac Maudit	-12.5839	49.1533	1225–1274	*betsileanus*	*M. jonasi*
				ulcerosus	*M. bellyi*
Montagne d'Ambre: low elevation	-12.5165	49.1713	484–737	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: mid-elevation	-12.5567	49.1623	1028–1105	*betsileanus*	*M. jonasi*
				ulcerosus	*M. bellyi*
Montagne d'Ambre: RE1	-12.5334	49.1877	1010–1057	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: RW1	-12.527	49.1676	1089–1125	*betsileanus*	*M. jonasi*
				ulcerosus	*M. bellyi*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Montagne d'Ambre: RW2	-12.5209	49.1666	1042–1093	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: West Slope	-12.5883	49.128	945–966	*ulcerosus*	*M. bellyi*
Montagne d'Ambre: Zanakatomboko	-12.487	49.1701	670–715	*ulcerosus*	*M. bellyi*
Montagne des Français: Andavakoera	-12.3333	49.35	80–200	*ulcerosus*	*M. bellyi*
Moramanga-Anosibe An'Ala/ Besariaka crossroad	-19.0994	48.2453	972*	*inaudax*	*M. inaudax*
Nahampoana	-24.9794	46.9839	16	*betsileanus*	*M. tripunctatus*
Namoly: Analabe	-22.1052	46.9446	1626*	*betsileanus*	*M. betsileanus*
				curtus	*M. bourgati*
Nosy Be	-13.3506	48.2759	19	*ulcerosus*	*M. ulcerosus*
Nosy Boraha	-16.8352	49.9271	NA	*fergusoni*	*M. jahnarum*
Nosy Boraha: Maromandia village	-16.9089	49.8678	20	*fergusoni*	*M. jahnarum*
Nosy Mangabe	-15.4893	49.764	50–115	*fergusoni*	*M. fergusoni*
Pic Saint-Louis	-25.008	46.962	365	*betsileanus*	*M. tripunctatus*
Ranomafana	-21.25	47.45	930	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				biporus	*M. glosi*
Ranomafana: Ambatolahidimy	-21.2471	47.4190	984	*betsileanus*	*M. katae*
Ranomafana: Ambatolahy	-21.2439	47.4262	950	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Ambatovory	-21.2380	47.4248	966	*betsileanus*	*M. katae*
				biporus	*M. glosi*
Ranomafana: Ambolo I	-21.2631	47.5070	650	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				tricinctus	*M. grubenmanni*
Ranomafana: Ambolo II	-21.2639	47.5086	675	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Andalangina	-21.2986	47.6022	486	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				biporus	*M. glosi*
Ranomafana: Beremby, Antaramanavana	-21.2310	47.5065	640	*betsileanus*	*M. katae*
				tricinctus	*M. grubenmanni*
Ranomafana: Beremby, Beremby	-21.2404	47.5250	618	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Beremby, Sahadikaina	-21.2461	47.5222	644	*betsileanus*	*M. katae*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Ranomafana: Beremby, Sahalavabe	-21.2075	47.5313	860	*betsileanus*	*M. katae*
				stelliger	*M. stelliger*
Ranomafana: Beremby, Sahalavakely	-21.2109	47.5304	780	*stelliger*	*M. stelliger*
Ranomafana: Bibiango (Old Bridge)	-21.2578	47.4183	1106	*betsileanus*	*M. katae*
Ranomafana: Fompohonina III	-21.2651	47.4225	1027*	*biporus*	*M. glosi*
				betsileanus	*M. katae*
Ranomafana: Imaloka	-21.2427	47.4651	1052	*tricinctus*	*M. grubenmanni*
Ranomafana: Kidonavo bridge	-21.2262	47.3696	1152	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Maharira	-21.3258	47.4025	1248	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
				biporus	*M. bletzae*
Ranomafana: near Park entrance	-21.2573	47.4211	936*	*betsileanus*	*M. betsileanus*
Ranomafana: Ranomafana National Park, Ampangadiamesa	-21.2423	47.4109	1147	*betsileanus*	*M. katae*
Ranomafana: Ranomafana National Park, Andranovoromainty	-21.2506	47.4178	1132	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Ranomafana, Ambodiriana	-21.2614	47.4413	710	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Ranomafana, Antenna	-21.2609	47.445	795	*betsileanus*	*M. betsileanus*
Ranomafana: Ranomafana, Imaloka	-21.2421	47.4652	1020	*betsileanus*	*M. katae*
				tricinctus	*M. grubenmanni*
Ranomafana: Ranomafanakely	-21.2487	47.3718	1134	*betsileanus*	*M. betsileanus*
				curtus	*M. alutus*
Ranomafana: Sahateza, Pond Donald	-21.2579	47.3597	1182	*betsileanus*	*M. katae*
Ranomafana: Sakaroa	-21.2648	47.4122	1046*	*betsileanus*	*M. katae*
Ranomafana: Talatakely, Piste E	-21.2628	47.4257	959	*betsileanus*	*M. katae*
				biporus	*M. glosi*
Ranomafana: Valohoaka	-21.2986	47.4386	1091*	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Ranomafana: Vatoharanana	-21.2890	47.4294	1000	*betsileanus*	*M. katae*
Ranomafana: Vohiparara, Sahamalaotra	-21.2352	47.3961	1170	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
road from Ranomafana to Tolongoina	-21.3536	47.6078	468	*betsileanus*	*M. betsileanus*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Sahafina-Brickaville	-18.8103	48.9800	64*	*betsileanus*	*M. incognitus*
				biporus	*M. eulenbergeri*
				fergusoni	*M. georgei*
Sahamalaza	-14.2488	47.9553	170	*ulcerosus*	*M. ulcerosus*
Sahambaky Forest (Lakato)	-19.065	48.34	980	*betsileanus*	*M. betsileanus*
Sahavontsira	-16.9057	49.2217	466	*biporus*	*M. brevirostris*
				inaudax	*M. manerana antsanga*
				tricinctus	*M. grubenmanni*
Sainte Luce	-24.7667	47.1833	30	*tricinctus*	*M. gudrunae*
Sainte Luce: forest at QMM climate station	-24.7798	47.1713	23	*tricinctus*	*M. gudrunae*
Sambava region	-14.2746	50.1664	12*	*fergusoni*	*M. fergusoni*
Sampanandrano (Anosy Mountains)	-24.1399	47.0742	539	*betsileanus*	*M. katae*
Site 1 near Ambodimandresy	-13.7133	49.4911	778	*ulcerosus*	*M. steinfartzi*
small stream next to Sofia, along road	-15.707	48.5807	252	*ulcerosus*	*M. ulcerosus*
Sorata: above campsite	-13.6831	49.441	1398–1417	*inaudax*	*M. manerana fotaka*
Sorata: above campsite, bamboo forest	-13.6746	49.4406	1516	*betsileanus*	*M. jonasi*
				inaudax	*M. manerana fotaka*
Sorata: above campsite, cloud forest	-13.6758	49.438	1599	*inaudax*	*M. manerana fotaka*
Sorata: Camp	-13.6851	49.4417	1279	*inaudax*	*M. manerana fotaka*
Sorata: gallery forest at creek near Andrafainkona, Ambararata	-13.7221	49.4385	776	*betsileanus*	*M. jonasi*
				ulcerosus	*M. bellyi*
Sorata (outside forest)	-13.7139	49.4966	844*	*ulcerosus*	*M. bellyi*
Tampolo forest (Analanjirofo)	-17.2887	49.4116	7	*fergusoni*	*M. georgei*
Toamasina	-18.1667	49.3833	20	*fergusoni*	*M. georgei*
Tolagnaro	-25.0333	46.95	60	*betsileanus*	*M. tripunctatus*
Torotorofotsy	-18.8747	48.3725	960	*betsileanus*	*M. betsileanus*
				betsileanus	*M. katae*
Torotorofotsy: Camp Prolemur	-18.7692	48.4266	956	*betsileanus*	*M. betsileanus*
Tsaranoro: Forêt Sacrée	-22.0812	46.7747	940	*betsileanus*	*M. betsileanus*
				curtus	*M. bourgati*
				curtus	*M. mahery*
Tsaratanàna	-13.98	48.84	NA	*betsileanus*	*M. jonasi*
				ulcerosus	*M. ulcerosus*
Tsaratanàna: Camp 0 (Ankijagna Lagnana)	-14.2399	48.9721	1162	*betsileanus*	*M. jonasi*

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TABLE 3. (Continued)

Location	Lat.	Lon.	Elev.	Clade	Species
Tsaratanàna: Manarikoba forest, Andampy	-14.0422	48.7617	730	*ulcerosus*	*M. schulzi*
Tsaratanàna: Manarikoba forest, Antsahamanara	-14.045	48.7853	1000	*ulcerosus*	*M. steinfartzi*
Tsingy de Bemaraha: Camp 1, Antranopasazy	-18.7086	44.7189	120	*curtus*	*M. mahery*
Tsingy de Bemaraha: Camp 2, Andafiabe on Beboka River	-18.7842	44.7794	177	*curtus*	*M. mahery*
Tsingy de Bemaraha: Camp 3, Bendrao Forest	-18.7844	44.8603	427	*curtus*	*M. mahery*
Tsingy de Bemaraha: Camp 4, Bendrao Forest	-18.7972	44.8814	420	*curtus*	*M. mahery*
Tsinjoarivo	-19.68	47.771	1610	*betsileanus*	*M. betsileanus*
				curtus	*M. alutus*
Tsinjoarivo: Camp 3, Vatateza	-19.7199	47.857	1319	*betsileanus*	*M. betsileanus*
Tsitongambarika: Andranomaizina	-24.5838	47.1474	42	*betsileanus*	*M. tripunctatus*
				tricinctus	*M. gudrunae*
Tsitongambarika: Ivohibe	-24.5612	47.1924	415	*betsileanus*	*M. tripunctatus*
				tricinctus	*M. gudrunae*
Vatolampy	-20.828	47.319	1580	*curtus*	*M. curtus*
Vohidrazana	-18.9661	48.5097	810	*betsileanus*	*M. incognitus*
				betsileanus	*M. katae*
				biporus	*M. eulenbergeri*
way to Sampanandrano	-24.1372	47.0949	411*	*betsileanus*	*M. katae*

Molecular lineage delimitation, phylogeny, and diagnoses

The Maximum Likelihood tree of the alignment of 1305 sequences of the 16S rRNA gene (alignment length 519 bp; Fig. 2) revealed a large number of deep mitochondrial lineages in the subgenus *Brygoomantis*, greatly exceeding the number of nominal species and available scientific names (including synonyms). The archival DNA sequences included in this analysis could each be unambiguously assigned to one of these deep mitochondrial lineages, allowing these lineages to be assigned to the corresponding names. An analysis with ASAP suggested a partition with 49 species-level lineages, based on an ASAP score of 1.5 (vs scores of 8.0–13.5 for other partitions). The genetic divergences between these lineages were high, with uncorrected pairwise 16S distances of >5% among the majority of them, including sister lineages (Fig. 3; Table 2).

For the nuclear-encoded Rag-1 gene, we obtained DNA sequences from 265 specimens of *Brygoomantis*. Because some of these sequences had poor-quality sections at the beginning and end, we trimmed the alignment to 351 bp, in order to be able to illustrate the variation among Rag-1 alleles of all 265 specimens in a haplotype network. The network (Fig. 4) revealed widespread allele sharing among many lineages, but placed several morphologically similar lineages clearly apart, without allele sharing. Thus, our data provide for these lineages evidence for concordant differentiation in the mitochondrial and nuclear genomes which is particularly relevant for species delimitation in conditions of sympatry (e.g. Miralles *et al.* 2021). We identified 13 ASAP-delimited lineages that do not share Rag-1 haplotypes: *M. ambohimitombi marefo* **ssp. nov.**, *M. biporus, M. bletzae* **sp. nov.**, *M. eulenbergeri* **sp. nov.**, *M. georgei* **sp. nov.**, *M. grubenmanni* **sp. nov.**, *M. gudrunae* **sp. nov.**, *M. kortei* **sp. nov.**, *M. marintsoai* **sp. nov.**, *M. pauliani, M. schulzi, M. steinfartzi* **sp. nov.**, and *M. tricinctus.* Haplotype sharing was detected in closely related, allopatric lineages such as *M. betsileanus* / *M. incognitus* **sp. nov.** / *M. jonasi* **sp. nov.**, or *M. fergusoni* **sp. nov.** / *M. jahnarum* **sp. nov.**, or *M. bellyi* / *M. ulcerosus*. On the other hand, in some cases, sympatric lineages that are not closely related and differ in morphology and/or bioacoustics sometimes do share Rag-1 haplotypes, such as *M. betsileanus* / *M. katae* **sp. nov.**, or *M. noralottae* /

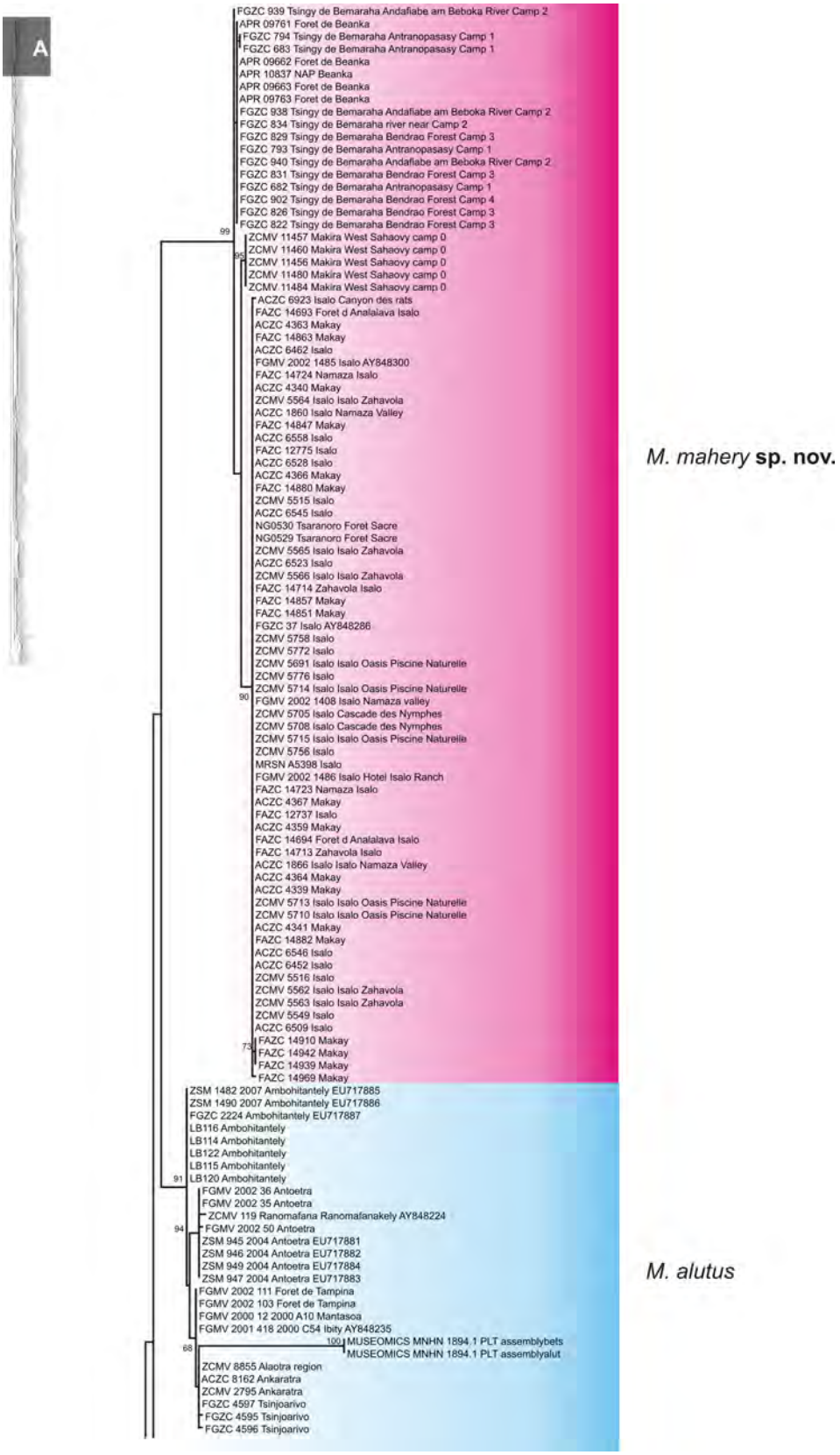


FIGURE 2. Maximum Likelihood tree of 1305 sequences of a fragment of the 16S rRNA gene (alignment length 519 bp) from a RAxML analysis. Numbers at nodes are bootstrap proportions in percent (100 ML fast bootstrap replicates); not shown if <50%. A sequence of *Mantidactylus melanopleura* was used as the outgroup (removed from the tree after analysis for better graphical representation). Note that some of the 'Museomics' sequences (obtained by targeted capture from historical type specimens) are represented twice, after assembly with different reference sequences. Some sequences in the analysis (several 'Museomics' sequences as well as others obtained from Illumina sequencing) only partially covered the fragment analysed (226 sequences < 300 bp). We emphasize that this tree is based on a single short mitochondrial marker and therefore is unlikely to represent the deep relationships among lineages correctly; for such relationships, refer to the phylogenomic tree (Fig. 5).

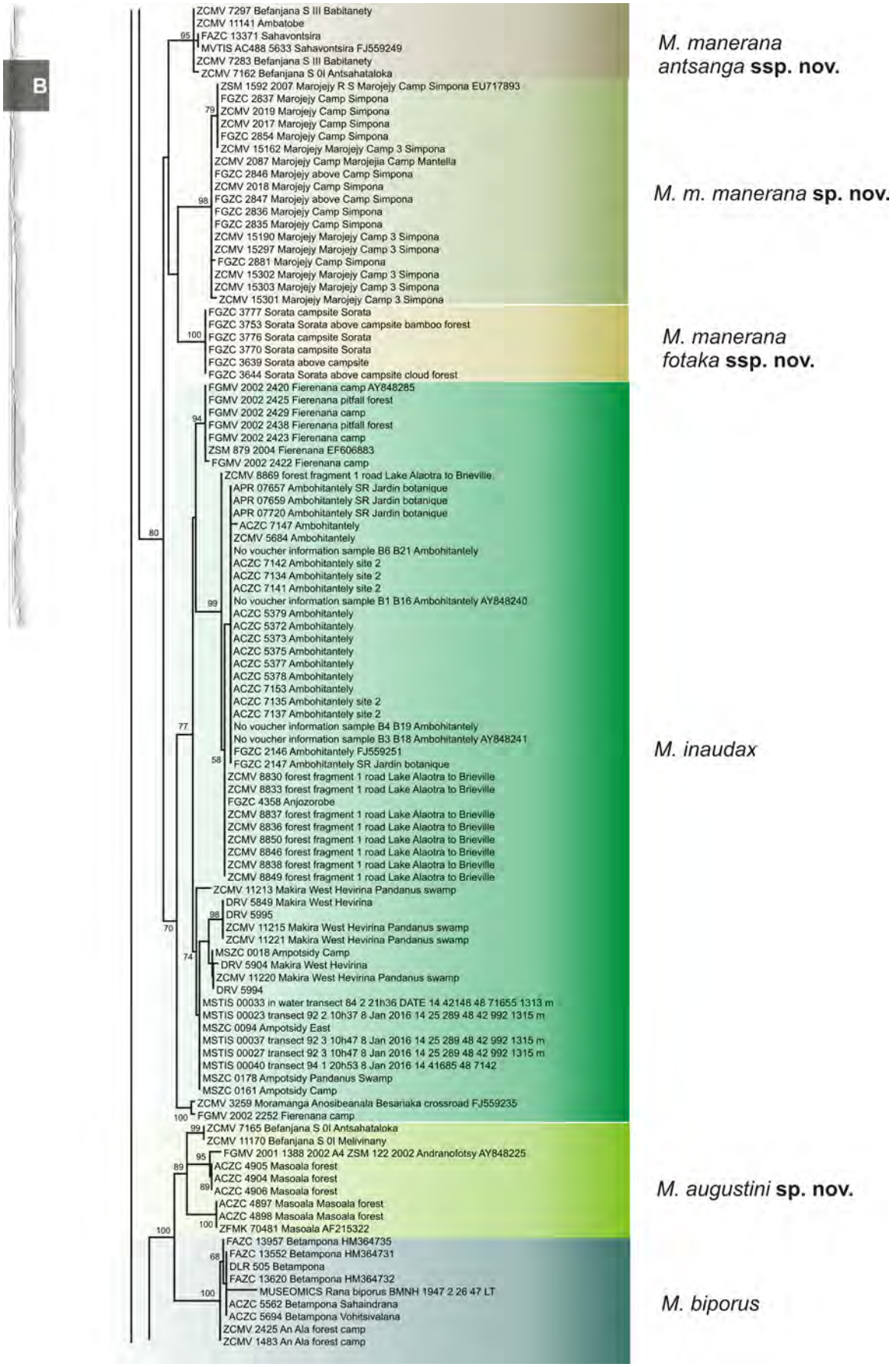
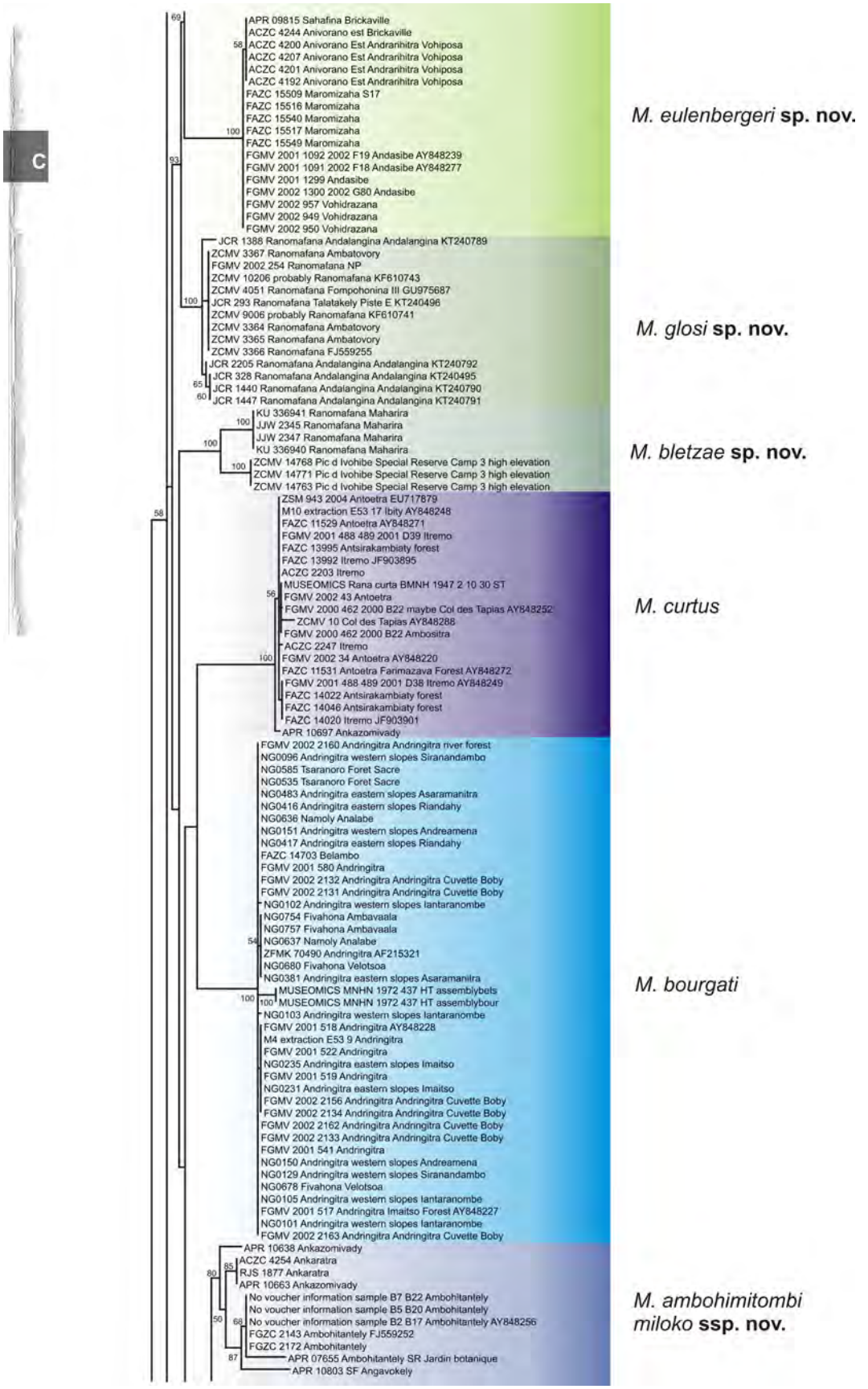


FIGURE 2. (Continued).



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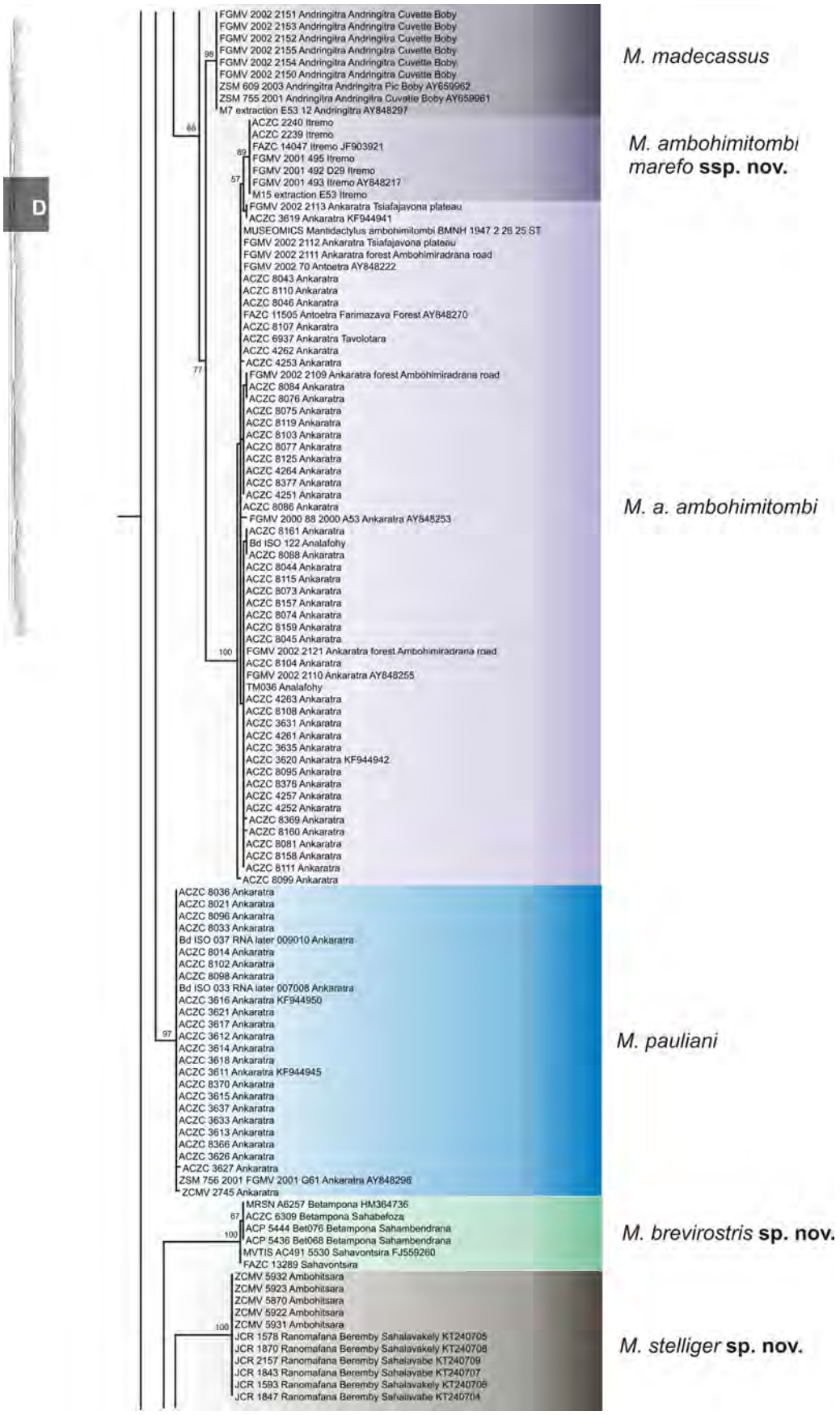
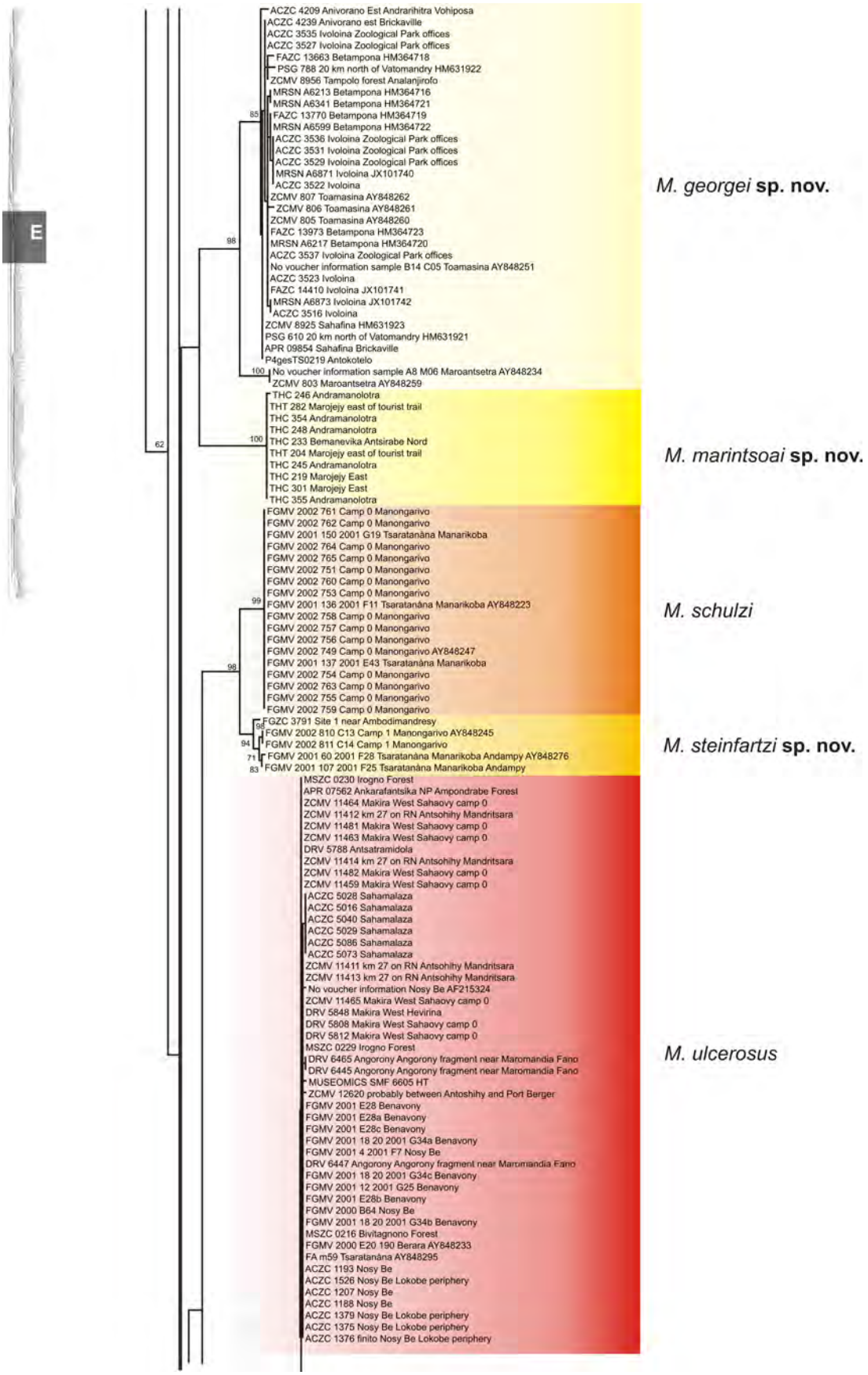


FIGURE 2. (Continued).



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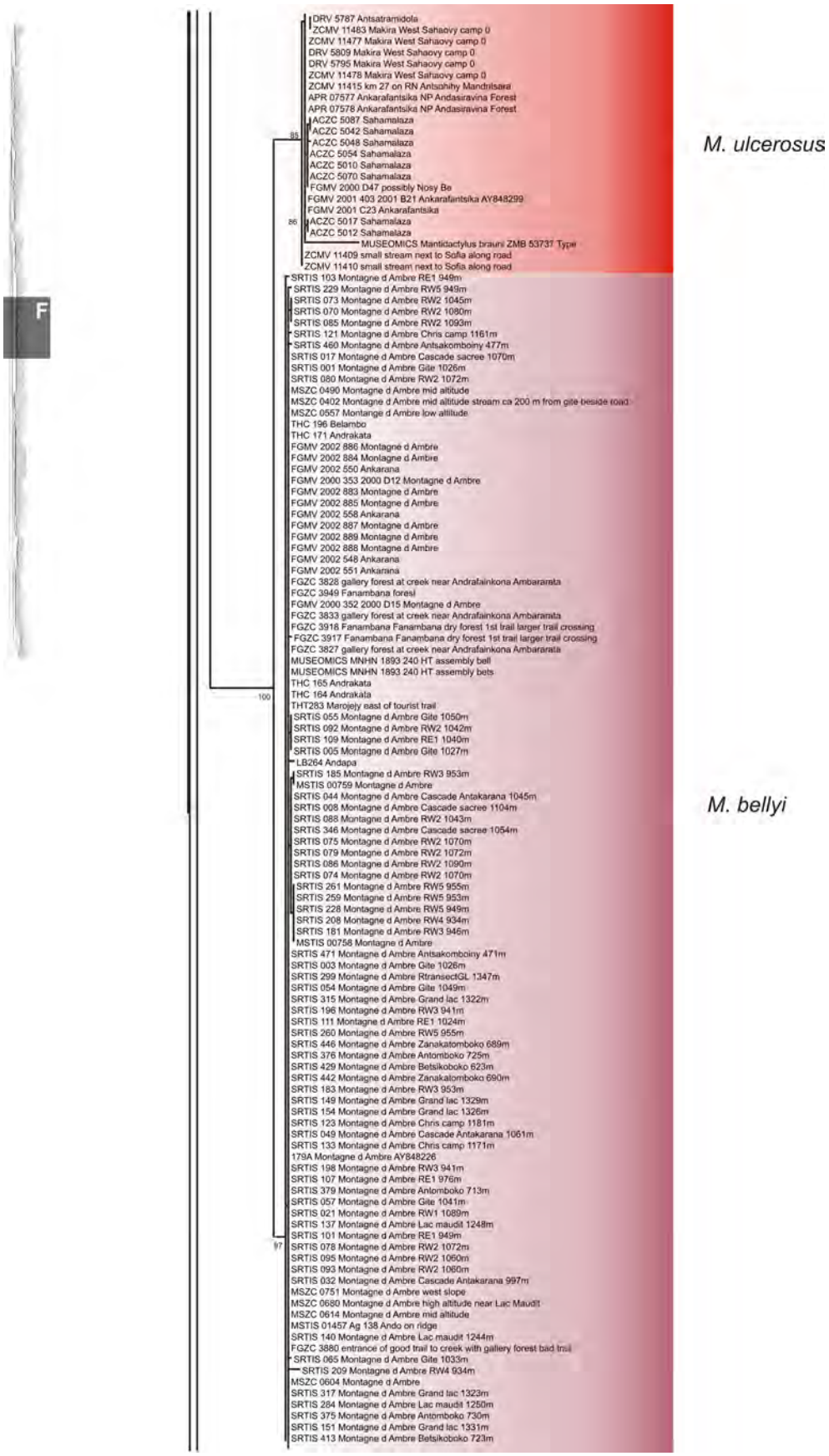

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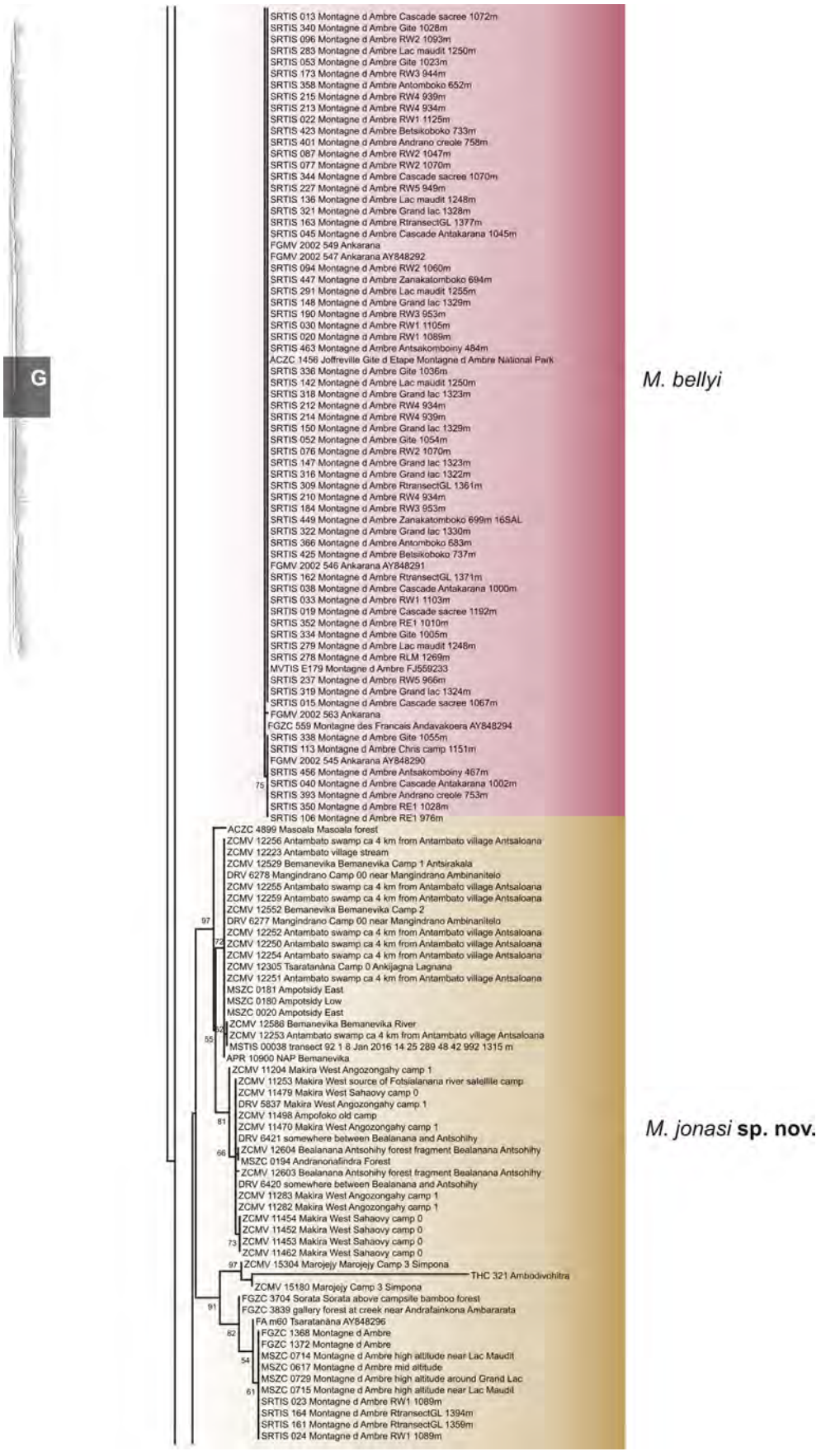

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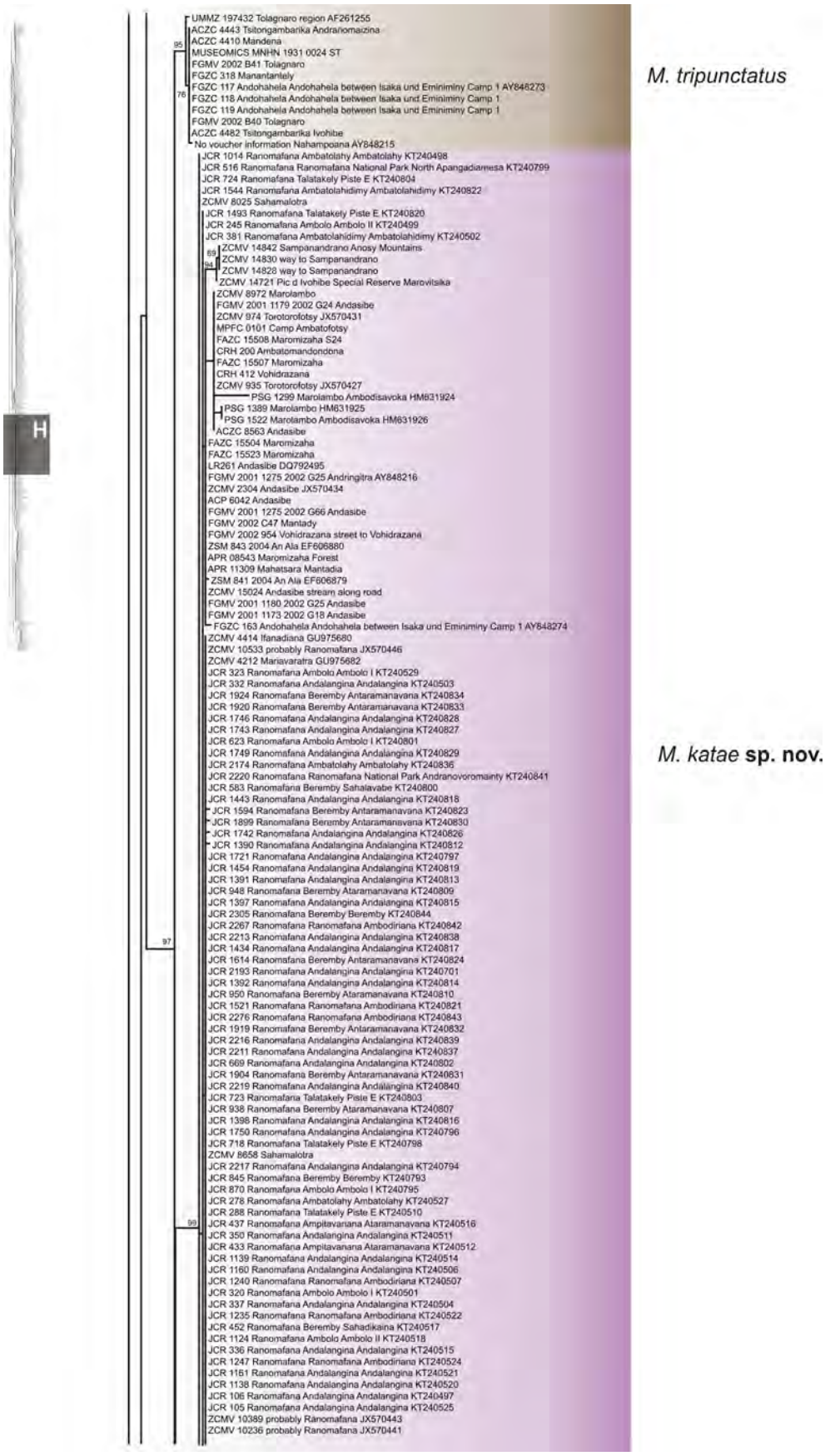

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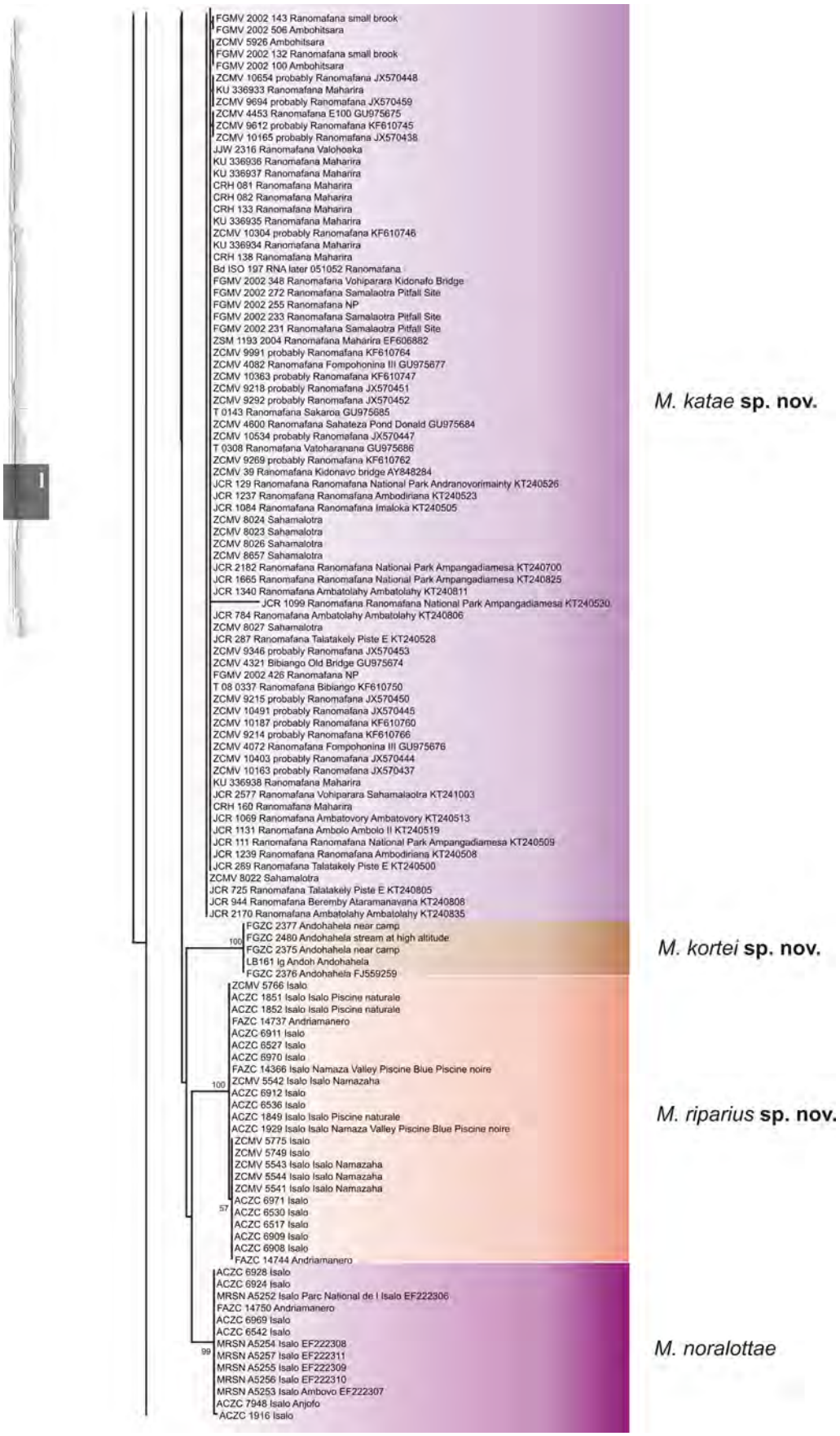


FIGURE 2. (Continued).

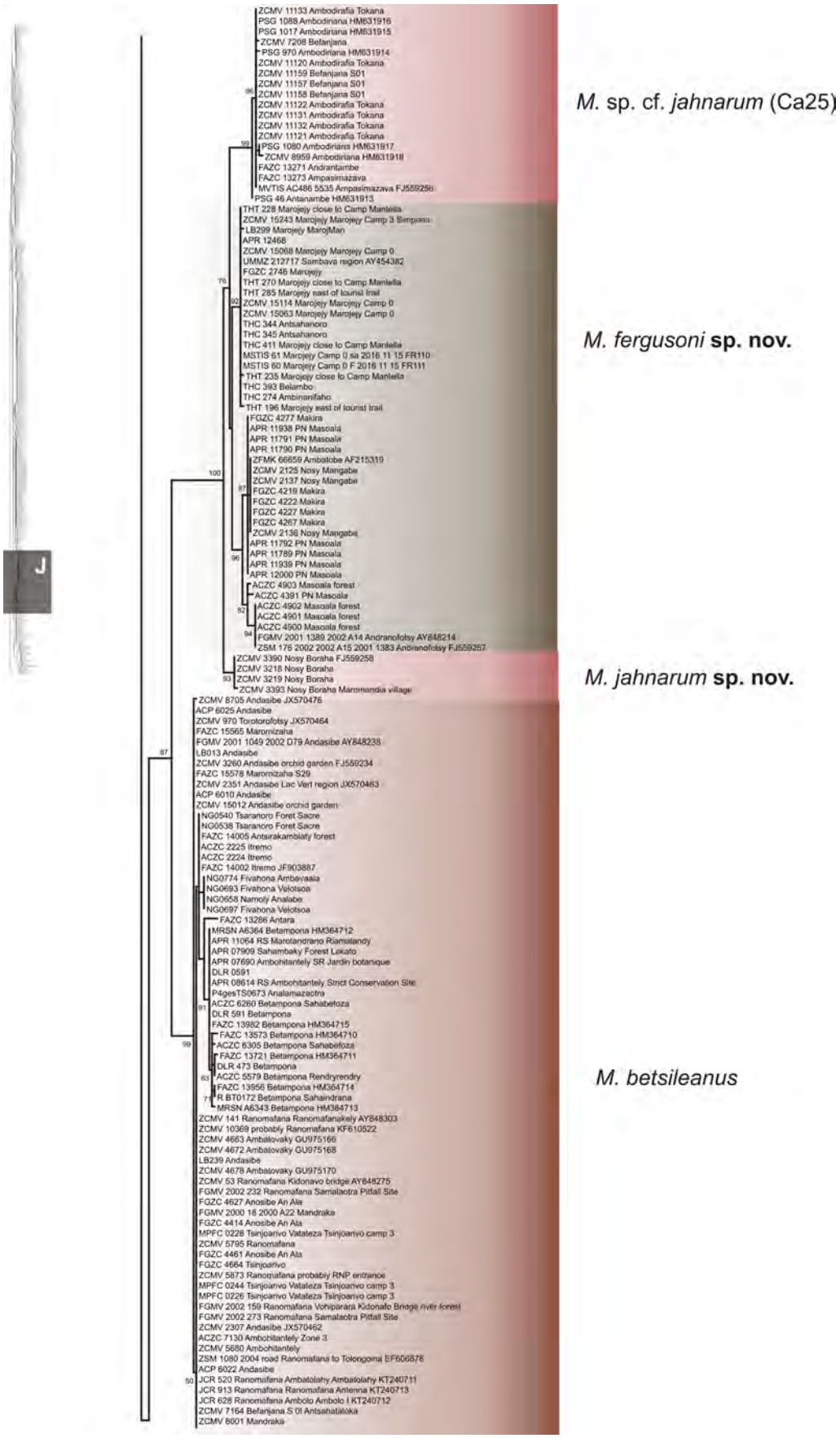
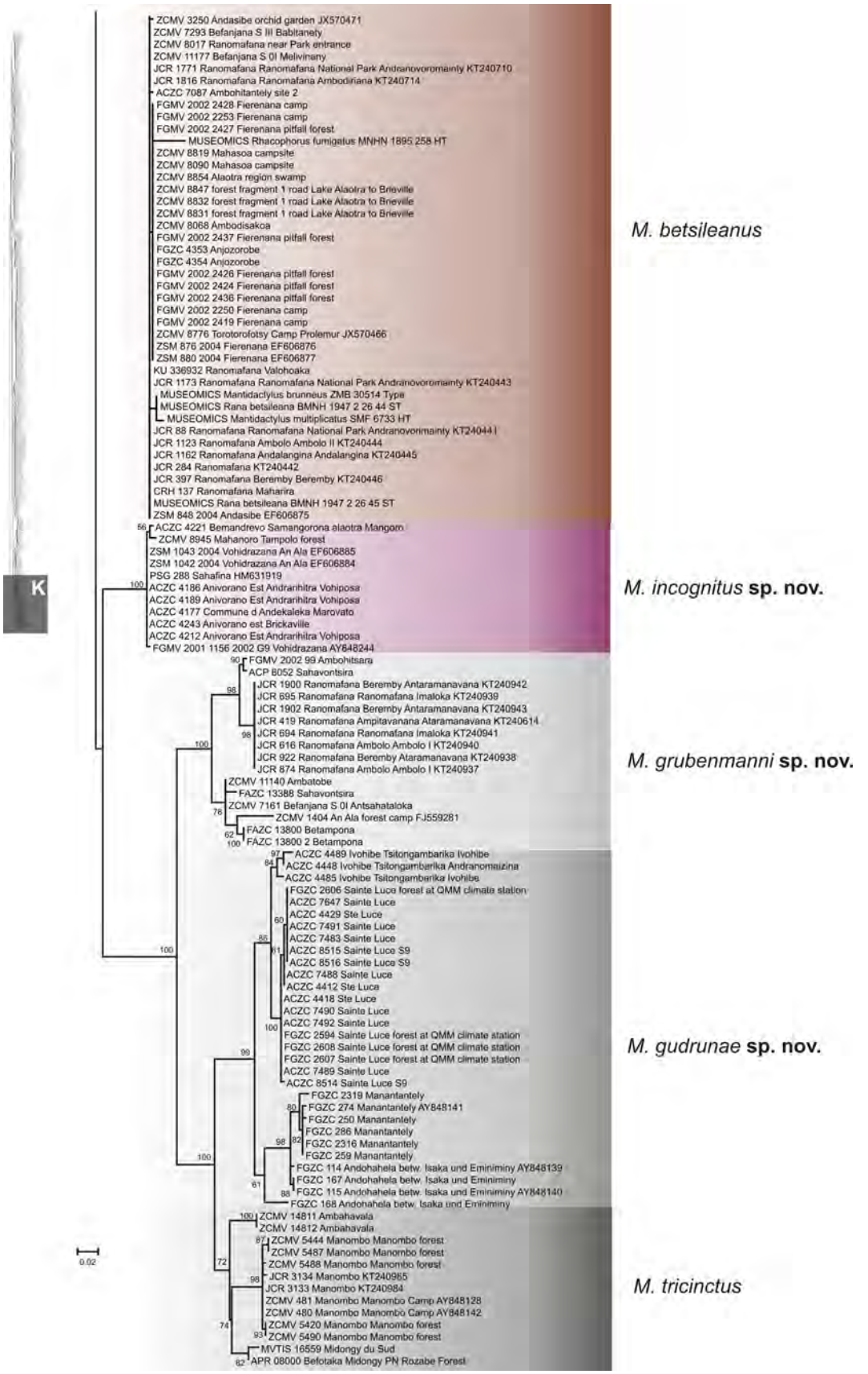


FIGURE 2. (Continued).



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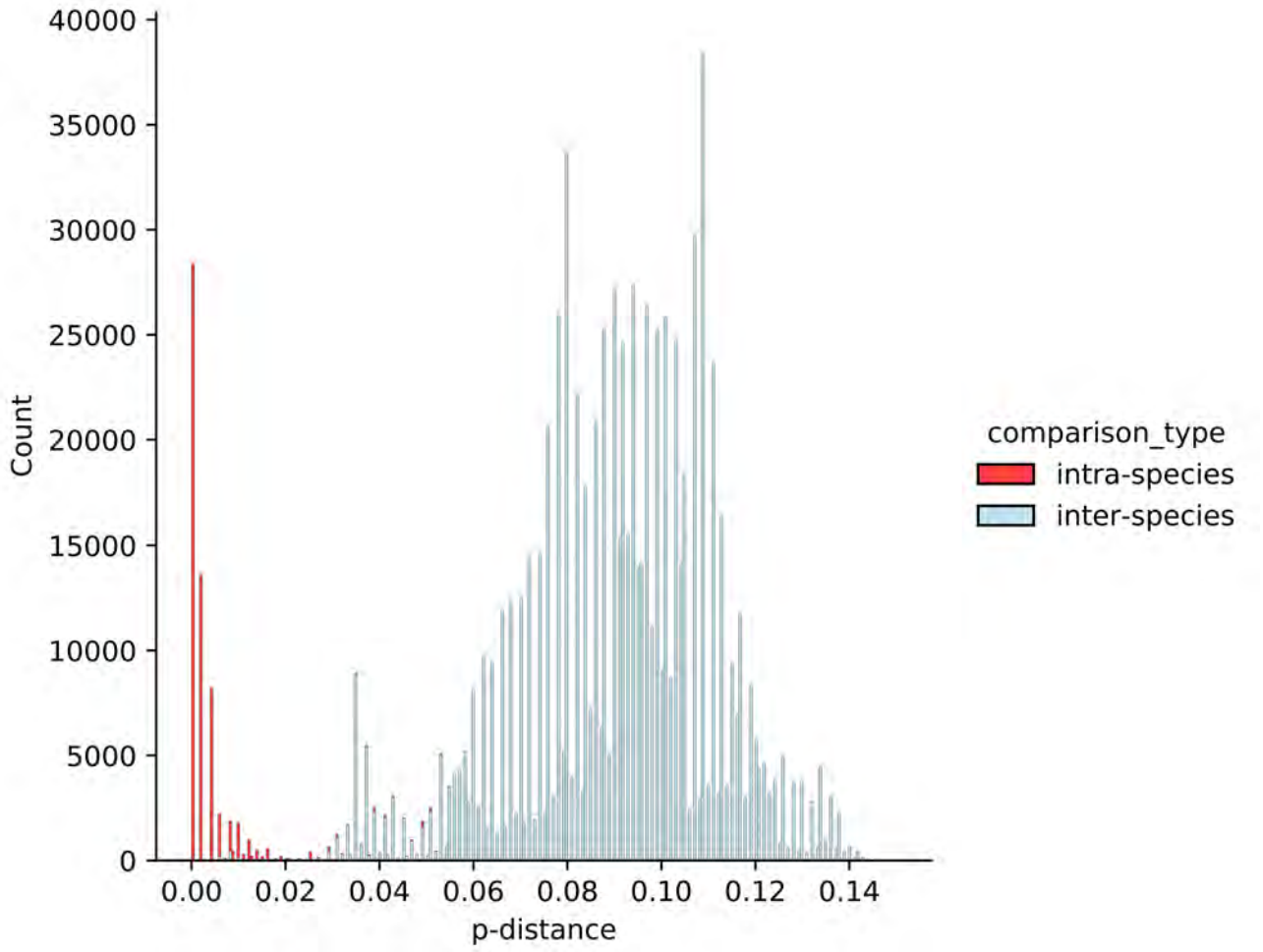

FIGURE 3. Distribution of uncorrected pairwise genetic distances for a fragment of the mitochondrial 16S rRNA gene, in an alignment of 976 sequences, complete or almost complete for 488 bp.

M. riparius **sp. nov.**, or *M. alutus / M. ambohimitombi.* These latter examples confirm that haplotype sharing in this relatively short fragment of nuclear-encoded DNA—caused either by incomplete lineage sorting or by occasional introgressive hybridization—also characterizes *Brygoomantis* lineages that undoubtedly represent valid species under multiple species criteria. For additional information on specific cases of haplotype sharing in this marker, see species accounts below.

For the following accounts of phylogeny, molecular diagnosis, and morphological, bioacoustic and biogeographical comparisons, we will partly anticipate our taxonomic conclusions and compare those lineages that we consider as distinct species or subspecies. A general rationale for our species hypotheses is provided in the section 'Taxonomic conclusions' below, and more detailed justifications in the 'Identity' paragraphs of each species account.

Using the FrogCap probe set, we successfully captured nuclear-encoded DNA sequences from 58 representative samples of all but three previously defined lineages (no samples could be included for the new species herein named *M. bletzae* **sp. nov.**, *M. marintsoai* **sp. nov.**, and *M. riparius* **sp. nov.**; see below). We retained alignments of 12,818 nuclear-encoded markers after filtering for phylogenetic analysis. A Maximum Likelihood analysis of the concatenated dataset (9,637,820 bp) revealed a phylogenetic tree (Fig. 5) with full aLRT support (100%) for all nodes without exception. Stringent and less stringent filtering strategies to exclude sequences representing possible contamination, misassembly or misalignments did not lead to changes in the tree topology or support, suggesting that the phylogenetic signal in the data was not influenced by senquencing and assembly artifacts.

Trees computed after taxon jacknifing were identical in topology to the ML tree, except for four cases: (i) removal of *M. alutus* which led to subtle changes within the *M. curtus* clade (*M. mahery* **sp. nov.** placed sister to all other taxa of the clade), and suggested the *M. inaudax* and *M. biporus* clades being sister to each other; (ii) similarly, also removal of *M. pauliani* led to the placement of *M. mahery* **sp. nov.** sister to all other taxa of the *M. curtus* clade; (iii) removal of *M. curtus* from Col des Tapias led to the placement of the second *M. curtus* individual, from Itremo, sister to specimens of *M. ambohimitombi marefo* **ssp. nov.** which were also collected in Itremo; and (iv) removal of *M. stelliger* **sp. nov.** led to the placement of the *M. fergusoni* clade and the *M. betsileanus* clade sister to each other.

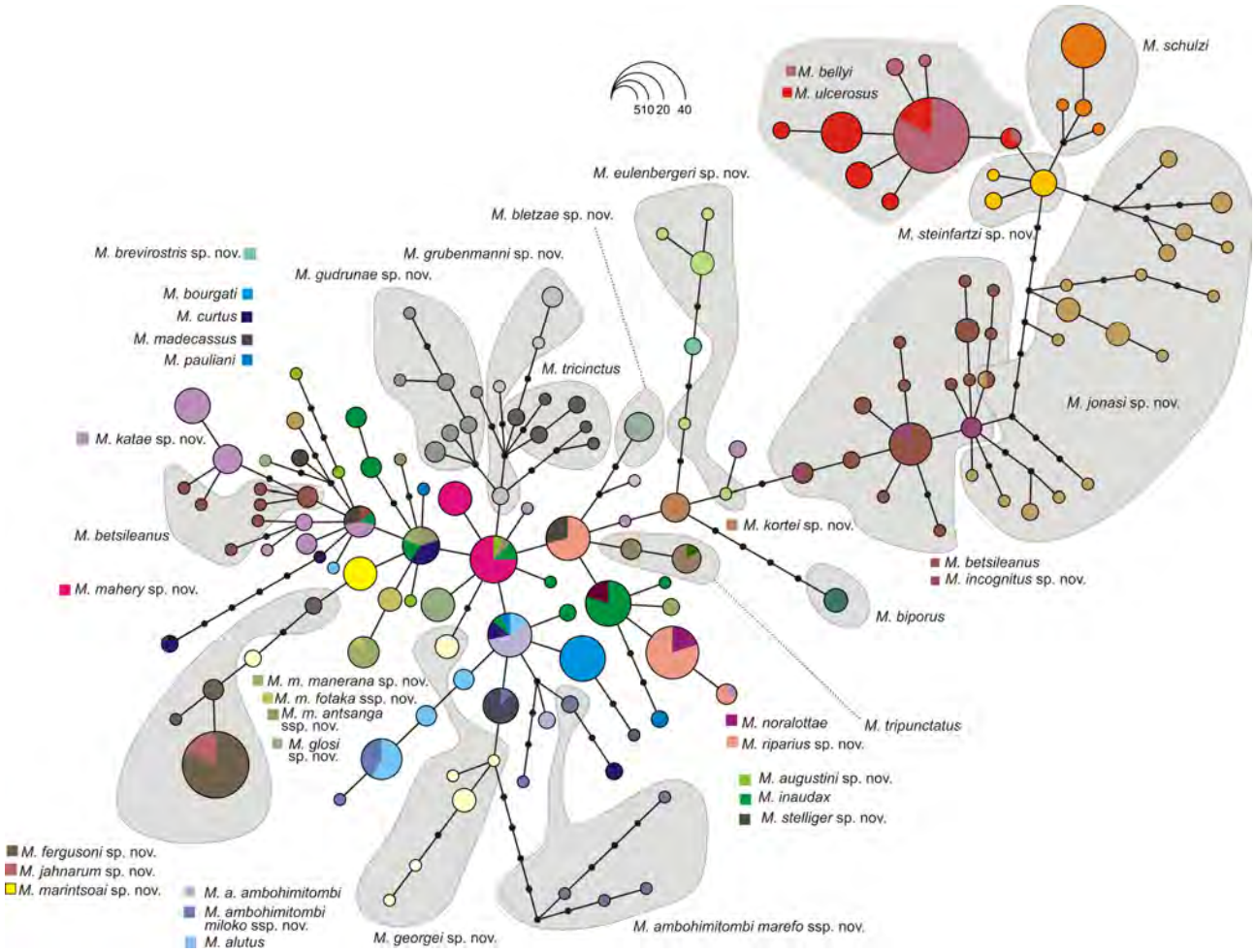

FIGURE 4. Network based on sequences of the nuclear-encoded Rag-1 gene (alignment length 351 bp) from 265 specimens of *Brygoomantis*. The network was built from phased alleles, i.e. each sample is represented twice. The size of circles is proportional to the number of sequences with the same allele. Small black dots represent hypothetical haplotypes (not sampled or extinct) separating sampled haplotypes, when they differ by more than one mutational step.

The species tree calculated with ASTRAL resulted in a near-identical tree topology (the only difference being in basal nodes of the *M. curtus* clade, where *M. mahery* **sp. nov.**, *M. alutus, M. pauliani,* and *M. bourgati,* split off successively; tree included in the Zenodo repository, DOI 10.5281/zenodo.6687413).

In the species network analysis of the *M. curtus* clade, the lowest scoring (lowest possible score of 0) and best model had *hmax* set to 3, and estimated two reticulations (included in Fig. 5). Notably, the higher *hmax* analyses still estimated two reticulation events at the same nodes. The best network has *M. ambohimitombi marefo* descending from *M*. a. *ambohimitombi* and *M*. *curtus* with inheritance values of 73% and 27%, respectively. In addition, the second hybridization in this network has *M. pauliani* as an ancestral hybrid 8% sister to the *M. curtus*, *M. a.* ambohimitombi, *M. ambohimitombi* miloko **ssp. nov.**, and *M. a. marefo* **ssp. nov.**, and *M. madecassus* clade and 92% sister to *M. mahery* **sp. nov.**

For those previously defined species-level lineages where two samples were included in the analysis, these always were resolved as monophyletic groups, except in the case of one individual of *M. tripunctatus* / *M. katae* **sp. nov.** that we hypothesize was affected by mitochondrial introgression (see discussion in the species accounts of these two species below).

The phylogenomic tree confirms several previous hypotheses on phylogenetic relationships among morphologically similar *Brygoomantis*, but also includes various surprises. Based on the phylogenomic data we here distinguish the following eight main clades within the subgenus (Fig. 5): (1) The *M. tricinctus* clade is composed of at least three genetically highly distinct, small-sized species, and is the sister group of all other *Brygoomantis*. (2) The *M. curtus* clade consists of predominantly large-sized species from the central highlands, but also including the relatively small-sized *M. alutus* and a species predominantly from western Madagascar (*M. mahery* **sp. nov.**, previously named *M.* sp. Ca14). (3–5) The *M. inaudax* clade, the *M. biporus* clade, and the *M. stelliger* clade include small to medium-sized species of rather stout appearance, with usually a short snout, broad head, short hindlimbs, and often small white spots on flanks, which were historically all assigned to a complex of species similar to *M. biporus*

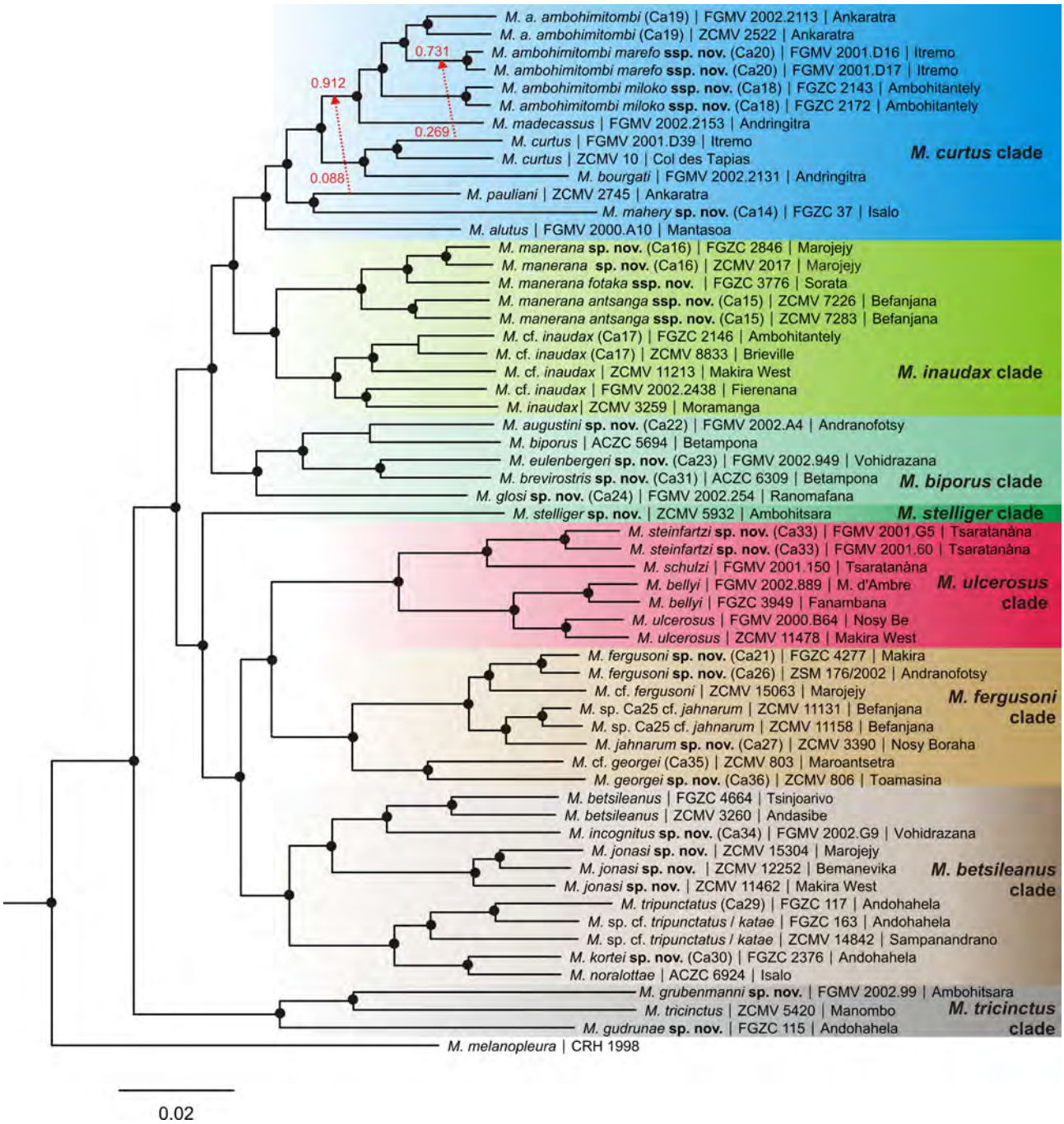

FIGURE 5. Maximum-Likelihood tree based on a partitioned analysis of 12,818 nuclear-encoded markers obtained via the FrogCap strategy, calculated with IQ-tree, for 58 representative individuals of species-level lineages in the subgenus *Mantidactylus* (*Brygoomantis*). Note that three species are missing from this analysis (*M. bletzae* **sp. nov.**, *M. marintsoai* **sp. nov.**, and *M. riparius* **sp. nov.**) and the identity of the two samples of *M. katae* **sp. nov.** in this tree is uncertain. For those lineages that previously (Perl *et al.* 2014; Vieites *et al.* 2009) had candidate species numbers assigned, these are reported in parenthesis after the name used in the classification proposed herein. All branches were fully supported by SH-like approximate likelihood ratio tests with 1000 pseudoreplicates (100% support, symbolized by black dots at nodes). The tree was rooted with *Mantidactylus grandidieri* (subgenus *Mantidactylus*) as outgroup (removed from graphical representation for better visualization of ingroup relationships), with the inclusion of *M. melanopleura* (subgenus *Chonomantis*) as hierarchical outgroup. Red arrows in the *M. curtus* clade indicate the two reticulation events detected by a Phylonetworks analysis performed separately for this clade (note that the topology recovered by this analysis in the Phylonetworks analysis differs in the position of *M. bourgati*; see original results of the Phylonetworks analysis in Zenodo repository, DOI 10.5281/zenodo.668741

(e.g. Glaw & Vences 2007) but which apparently do not form a monophyletic group; instead, the *M. inaudax* clade is sister to the *M. curtus* clade, and the *M. biporus* clade is sister to the group of these two clades; in contrast, the *M. stelliger* clade, composed of a single species only, is sister to the remaining taxa. (6) The *M. ulcerosus* clade is mostly distributed in the North, Sambirano and North West regions and contains the two closely related, large-sized species *M. bellyi* and *M. ulcerosus*, as well as two small-sized species. (7–8) Finally, the *M. betsileanus* clade and the *M. fergusoni* clade contain a series of morphologically relatively similar species, characterized by a slender body with long hindlimbs, pointed snout, and often a white marking on the snout tip. However, these frogs do not form a monophyletic group as the *M. fergusoni* clade is sister to the *M. ulcerosus* clade.

Morphology

We subsetted our complete morphological dataset to contain 11 morphometric measurements on 143 males and 155 females belonging to 39 lineages, excluding all individuals with any missing data. For direct comparison of measurements, we size-corrected by dividing by SVL, as this is a technique that can be applied in the field. There was consistent size dimorphism in almost all species of *Brygoomantis* (Fig. 6), with females being slightly to substantially larger than males. There were also tendencies toward sexual dimorphism in almost all other size-corrected traits, but in none was this more pronounced than in horizontal tympanum diameter; all species for which measurements of both sexes were available had moderate to strong tympanum size dimorphism, with males having larger tympana. Size dimorphism is also obvious when looking at the ratio HTD/ED (Fig. 6), which may facilitate sexing of species based on photographs without indication of scale or photographs of their venters, which has hitherto been necessary. The species in the *Mantidactylus curtus* clade have notably smaller relative tympanum size than all other species (though not relative to eye size), but still have pronounced tympanic size dimorphism between the sexes. *Mantidactylus mahery* **sp. nov.**, which is assigned to the *M. curtus* clade based on its genetic affinities, deviates from the rest of this clade in its larger eyes and tympanum and smaller foot length, compared to most other species.

Bioacoustics

Several species of *Brygoomantis* are locally common and it therefore is no surprise that their advertisement calls have been described early on, starting with the pioneering work of Blommers-Schlösser (1979). The formal call descriptions published to date, however, were rarely assigned to DNA barcoded individuals, and given the vast number of undescribed diversity in the genus, this left uncertainty surrounding many of these bioacoustic data. We confirm that earlier call descriptions for *M. alutus* and *M. betsileanus* (Blommers-Schlösser 1979), for *M. alutus, M. betsileanus*, and *M. ulcerosus* (Glaw & Vences 1994), for *M. noralottae* (Mercurio & Andreone 2007), and for *M. schulzi* (Vences *et al.* 2018) have been correctly assigned to species. The call CD of Vences *et al.* (2006) included recordings of 18 species and candidate species of *Brygoomantis*, largely corresponding to those analysed in more detail herein.

In this study, we provide information on the advertisement calls of 12 previously named species (including those herein revalidated) and 13 species newly named herein. For 16 species, recordings were available from DNA barcoded individuals (*M. alutus, M. augustini* **sp. nov.**, *M. bellyi, M. betsileanus, M. biporus, M. fergusoni* **sp. nov.**, *M. georgei* **sp. nov.**, *M. inaudax, M. jahnarum* **sp. nov.**, *M. jonasi* **sp. nov.**, *M. katae* **sp. nov.**, *M. manerana* **sp. nov.**, *M. riparius* **sp. nov.**, *M. schulzi, M. steinfartzi* **sp. nov.**, *M. tricinctus*). For one further species (*M. kortei* **sp. nov.**) assignment of the call to a voucher specimen is almost certain due to the collecting circumstances (specimen found in exactly the same place where a male was heard calling, with no other *Brygoomantis* in the collecting site). For five species, calls were assigned based on collecting locality and/or morphology of the calling individual (*M. ambohimitombi, M. mahery* **sp. nov.**, *M. ulcerosus, M. noralottae, M. grubenmanni* **sp. nov.**), and for a further three species, call recordings could only be tentatively attributed (*M. bourgati, M. glosi* **sp. nov.**, *M. tripunctatus*). Calls remain unknown for two species and two subspecies of the *M. curtus* clade (*M. ambohimitombi miloko* **ssp. nov.**, *M. ambohimitombi marefo* **ssp. nov.**, *M. madecassus, M. pauliani*), three species of the *M. biporus* clade (*M. bletzae* **sp. nov.**, *M. brevirostris* **sp. nov.**, *M. eulenbergeri* **sp. nov.**), one species each of the *M. betsileanus* clade (*M. incognitus* **sp. nov.**,), *M. fergusoni* clade (*M. marintsoai* **sp. nov.**), *M. tricinctus* clade (*M. gudrunae* **sp. nov.**), and *M. stelliger* clade (*M. stelliger* **sp. nov.**), as well as from two subspecies of the *M. inaudax* clade (*M. manerana antsanga* **ssp. nov.**, *M. manerana fotaka* **ssp. nov.**).

All *Brygoomantis* emit calls of relatively low intensity from the ground, typically very close to water, sometimes sitting in shallow water; for *M. ambohimitombi* we heard specimens calling from underwater, in a cold mountain brook. The advertisement calls can be emitted during the day, always from concealed positions, or at night from usually more exposed positions. The calls are usually distinctly pulsed, or, more rarely, pulsatile with more indistinct limits between energy peaks (Köhler *et al.* 2017), or a combination of both, repeated at relatively long and sometimes irregular intervals; or in other cases, repeated at relatively fast and regular succession resulting in regular call series. Although duration and number of calls per call series might depend on social context and motivation of the calling male, some of the described pattern in call series seem to be species-specific in *Brygoomantis* (e.g. fast vs slow repetition, regular vs irregular series).

Given the evolutionary relationships revealed from our phylogenomic perspective, several trends can be discerned regarding the evolution of advertisement call structure in the genus. Series of relatively short pulsed

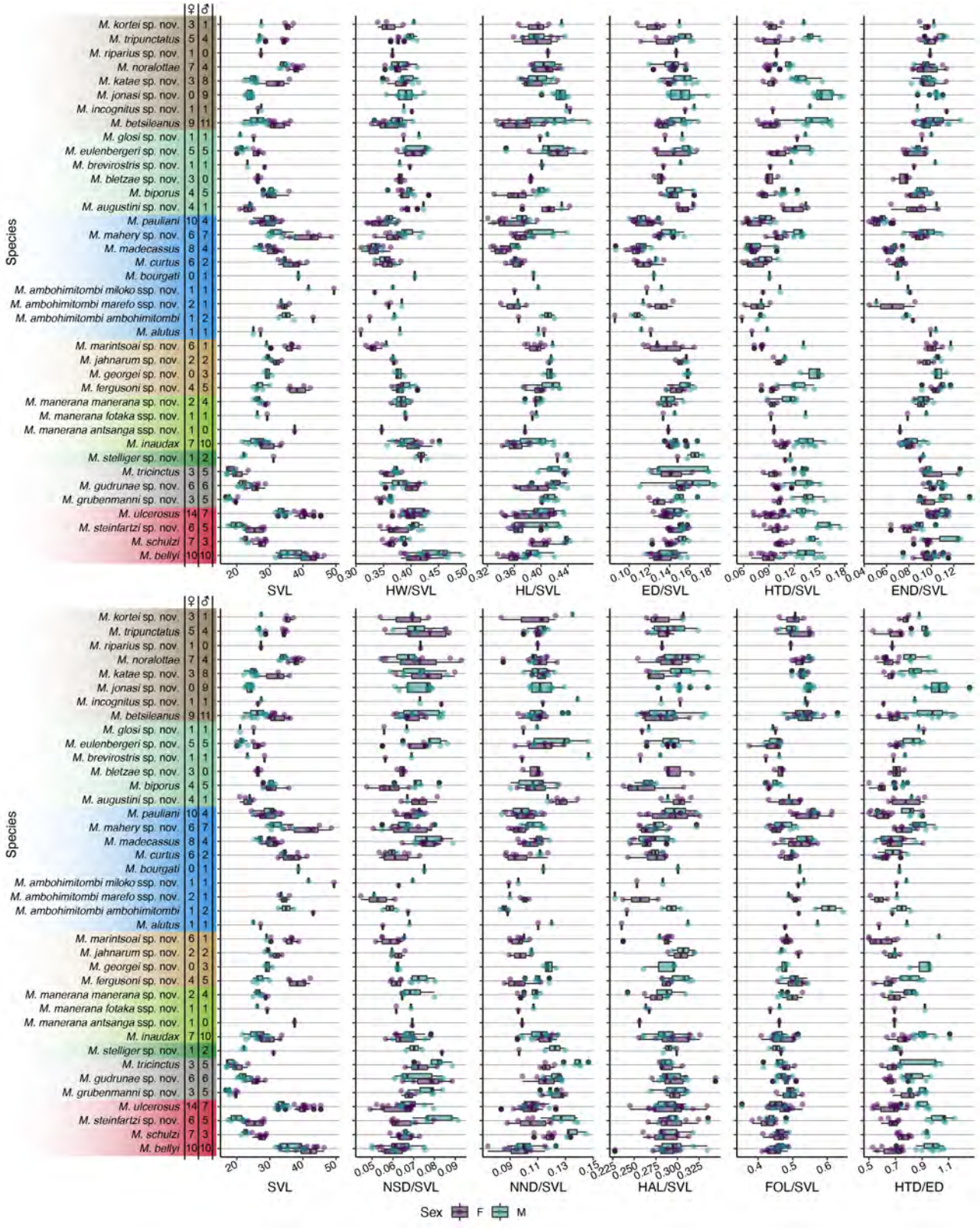

FIGURE 6. Overview of morphometrics of *Mantidactylus* (*Brygoomantis*) species. Points and boxplots are coloured by sex (purple = female, blue = male), with sample size per sex given beside the taxon names. Species are arranged according to the main clades to which they belong according to our phylogenomic analysis. SVL is repeated in the upper and lower panels to enable the reader to access relevant information quickly.

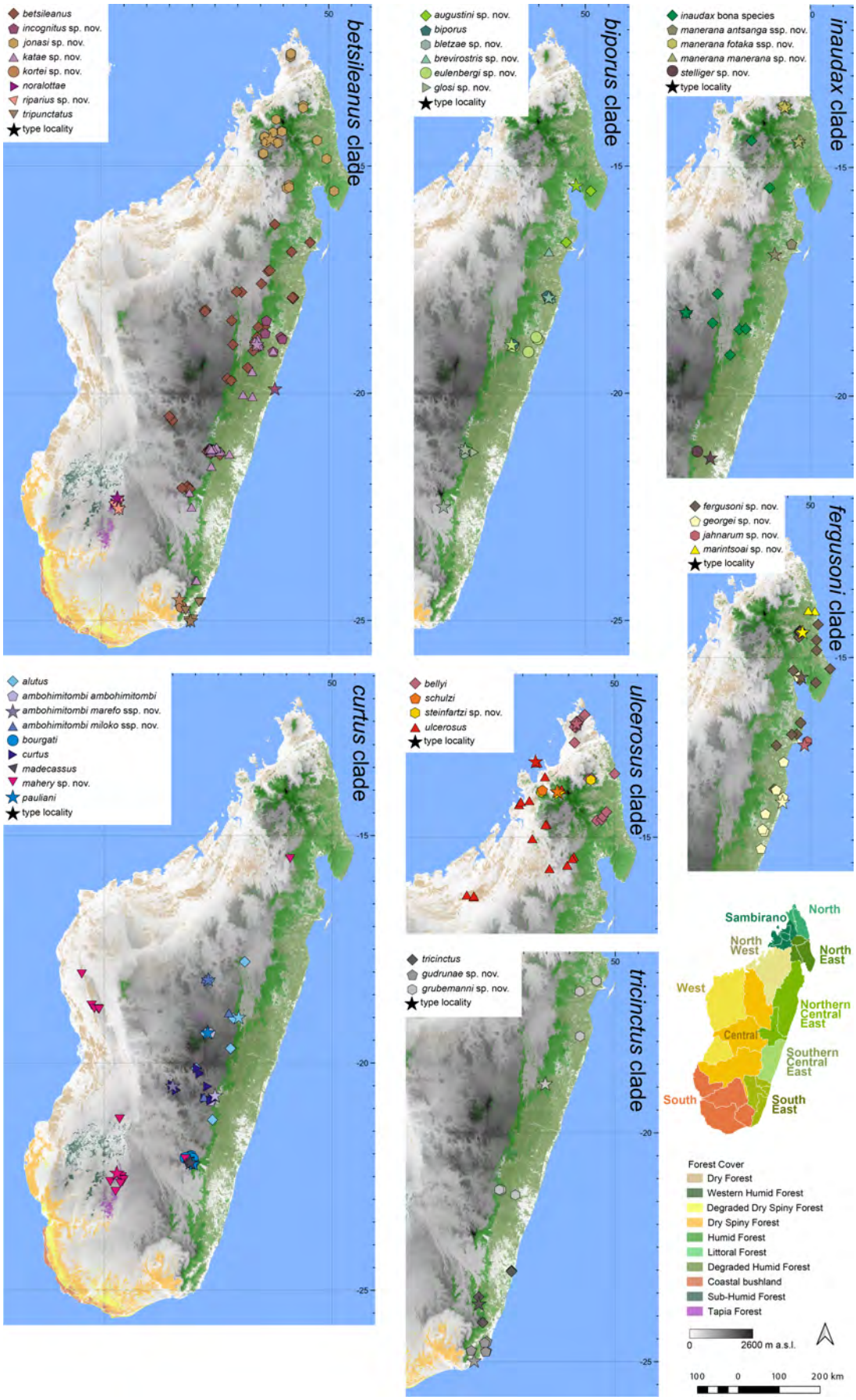

FIGURE 7. *Mantidactylus* subgenus *Brygoomantis* species distribution based on verified records, divided by clade (*Mantidactylus stelliger* **sp. nov.** is presented alongside the *inaudax* clade for practicality). Colours for species correspond to those in Figs 2 and 4. Inset map shows the geographic regions of Madagascar identified by Boumans *et al.* (2007), referred to throughout the text.

calls, sometimes repated at fast sucession, characterize species in the *M. tricinctus* clade, in the *M. biporus* clade, in the *M. inaudax* clade, and two species of the *M. curtus* clade that split from relatively basal nodes in that clade (*M. alutus, M. mahery* **sp. nov.**). Most species in the *M. betsileanus* clade and *M. fergusoni* clade emit long pulsed calls with even longer inter-call intervals within call series, which can be rather similar in general structure in different species, e.g. in the distantly related *M. georgei* **sp. nov.** (*M. fergusoni* clade) and *M. betsileanus* (*M. betsileanus* clade), despite measurable differences in various temporal variables. As an exception, calls of two species of these clades consist of a single pulse only and are of very short duration. These single-pulse calls are emitted in series of very variable duration and containing a variable number of calls; this is observed in *M. katae* **sp. nov.** (*M. betsileanus* clade) and *M. fergusoni* **sp. nov.** (*M. fergusoni* clade).

Taxonomically, it is interesting that several closely related species of *Brygoomantis* differ distinctly and consistently in their advertisement calls. For instance, the two sympatric sister species *M. schulzi* and *M. steinfartzi* **sp. nov.** both occur in the Tsaratanàna and Manongarivo Massifs (only slightly differing in elevation), and their calls differ in several temporal characteristics, despite similar overall structure, and differences are obvious to the human ear. Even more strongly expressed are the bioacoustic differences between the closely related *M. fergusoni* **sp. nov.** and *M. jahnarum* **sp. nov.** While the former emits very short single-pulse calls in irregular series, the latter emits short multi-pulse calls of very different general structure. We verified the bioacoustic characteristics of *M. fergusoni* **sp. nov.** in multiple individuals from two sites, and of *M. jahnarum* **sp. nov.** in different years at its type locality Nosy Boraha, confirming that these differences are a biological reality. Several other sister or closely related species (e.g. *M. augustini* **sp. nov.** vs *M. biporus*; *M. bellyi* vs *M. ulcerosus*; *M. betsileanus* vs *M. jonasi* **sp. nov.**; *M. grubenmanni* **sp. nov.** vs *M. tricinctus*) also show distinct differences in one or several temporal or spectral call variables.

In summary, the available bioacoustic data support the distinctness at the species level of numerous lineages identified by the molecular data. This is in particular the case if bioacoustics are interpreted in light of the phylogenomic results, which revealed that (i) sister species typically differ in advertisement calls, and (ii) lineages that have superficially similar calls often belong to different clades in the phylogeny.

Biogeography

Distribution maps of all species-level taxa recognised herein are shown in Fig. 7. Visualised as minimum convex polygons, it is evident that there are two areas with the greatest diversity of *Brygoomantis* species: the central east, and the central highlands (Fig. 8). There are only few species that occur on both east and west flanks of the eastern escarpment, highlighting the escarpment's role as a dispersal barrier for most species in this subgenus. The absence of any species polygon in the southern extent of Makira Natural Park (ca 16.00°S, 049.25°E) reflects both the lack of survey work in that area, as well as some degree of turnover in species composition between the North East, and Northern Central East.

Seldom do more than two species from a given clade occur sympatrically, but the total assemblage of *Brygoomantis* species can nevertheless be large at a given location (for example, with up to seven species in Ranomafana National Park), comprising members of up to five different clades (e.g. in Ranomafana and Betampona). Each clade has a different overall pattern that warrants brief comment:

The *inaudax* clade consists of three range-restricted species and the widespread *M. inaudax* **bona species**, which is found in remnant forests in the highlands.

The *betsileanus* clade is widespread, with local endemics in the South, while eastern species are rather widespread. In northern Madagascar, only *M. jonasi* **sp. nov.** is known to occur.

The *biporus* clade is distributed along the east coast of Madagascar (mainly in the South East, Southern Central East, Northern Central East, and North East regions) with localised range overlap among species. Only *M. glosi* **sp. nov**. is a rather localised endemic.

The *ulcerosus* clade is restricted to northern Madagascar plus the North West region. *Mantidactylus ulcerosus* itself does not seem to exceed the Sambirano region northwards; instead, it is replaced in those areas by the other three species of this clade. *Mantidactylus schulzi* is, according to current knowledge, a local endemic, but the other three species are more widespread.

The *fergusoni* clade is found at rather low elevation sites in the Northern Central East and the North East. *Mantidactylus jahnarum* is only known from Nosy Boraha, but the other species are more widespread.

The *tricinctus* clade is widespread in the South East, Southern Central East, and Northern Central East. So far, no sympatric populations of multiple species from within this clade are known.

Mantidactylus stelliger **sp. nov.** is restricted to a small area in the Southern Central East.

The *curtus* clade is restricted to the central highlands and the West and South of Madagascar. Several lineages are local endemics, and in several locations multiple species co-occur. *Mantidactylus mahery* **sp. nov.** occurs over a wide but extremely patchy range that includes three sites in the West and South, and extends into the North West (at the western slope of the Makira Massif.

Taxonomic conclusions and species accounts

Combining the molecular, morphological, bioacoustic and biogeographical evidence leaves no doubt that the diversity of *Brygoomantis* is dramatically underestimated by the current taxonomy. Numerous mitochondrial lineages in the subgenus differ by >5% 16S divergence, and by additional lines of evidence such as lack of Rag-1 allele sharing, advertisement call differences, and/or morphological differences. Importantly, in several cases a

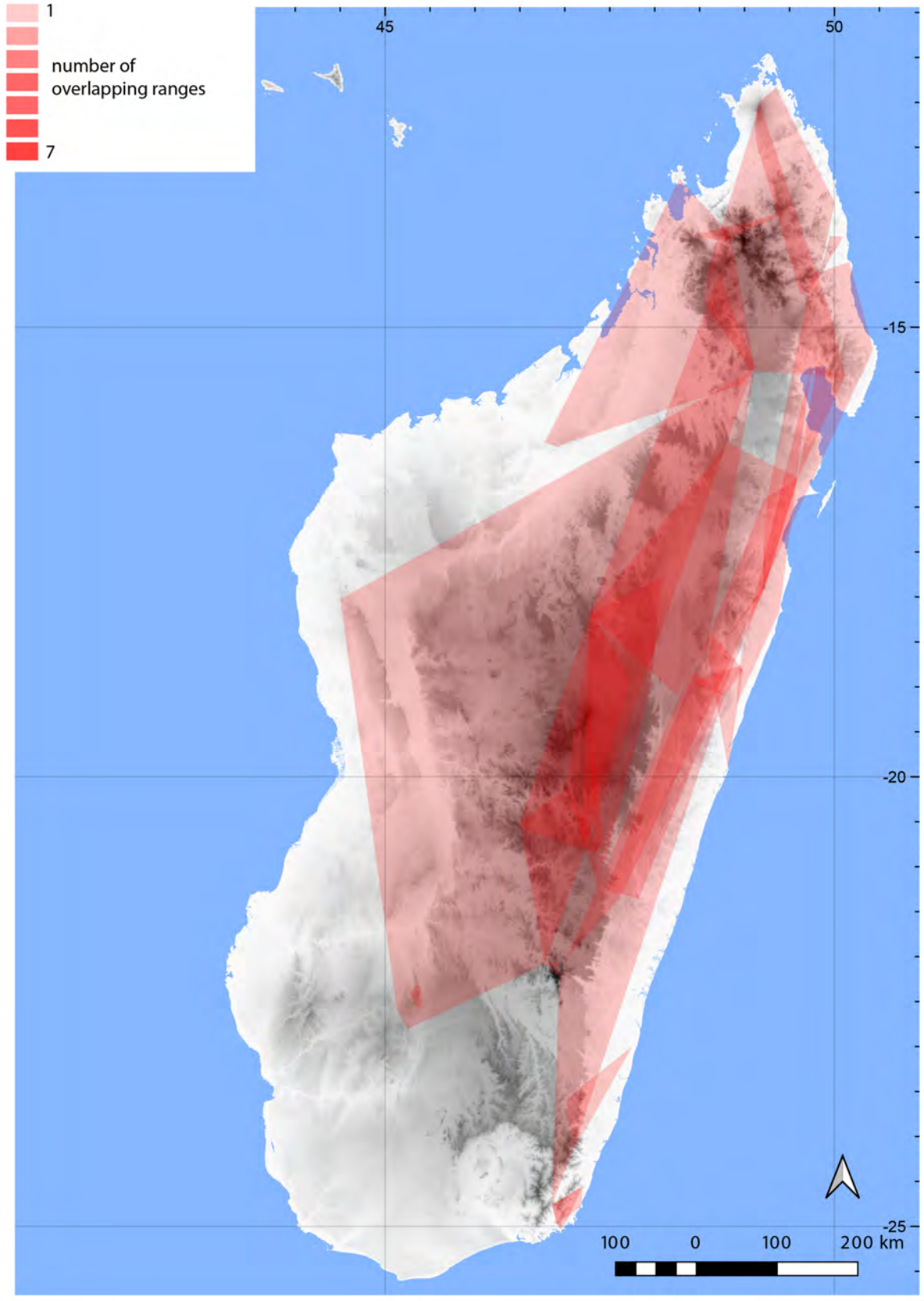

FIGURE 8. Heat map of *Brygoomantis* species distribution overlap (plotted as minimum convex polygons). This map is only based on species that are recorded from more than two localities (i.e. those for which a polygon could be plotted).

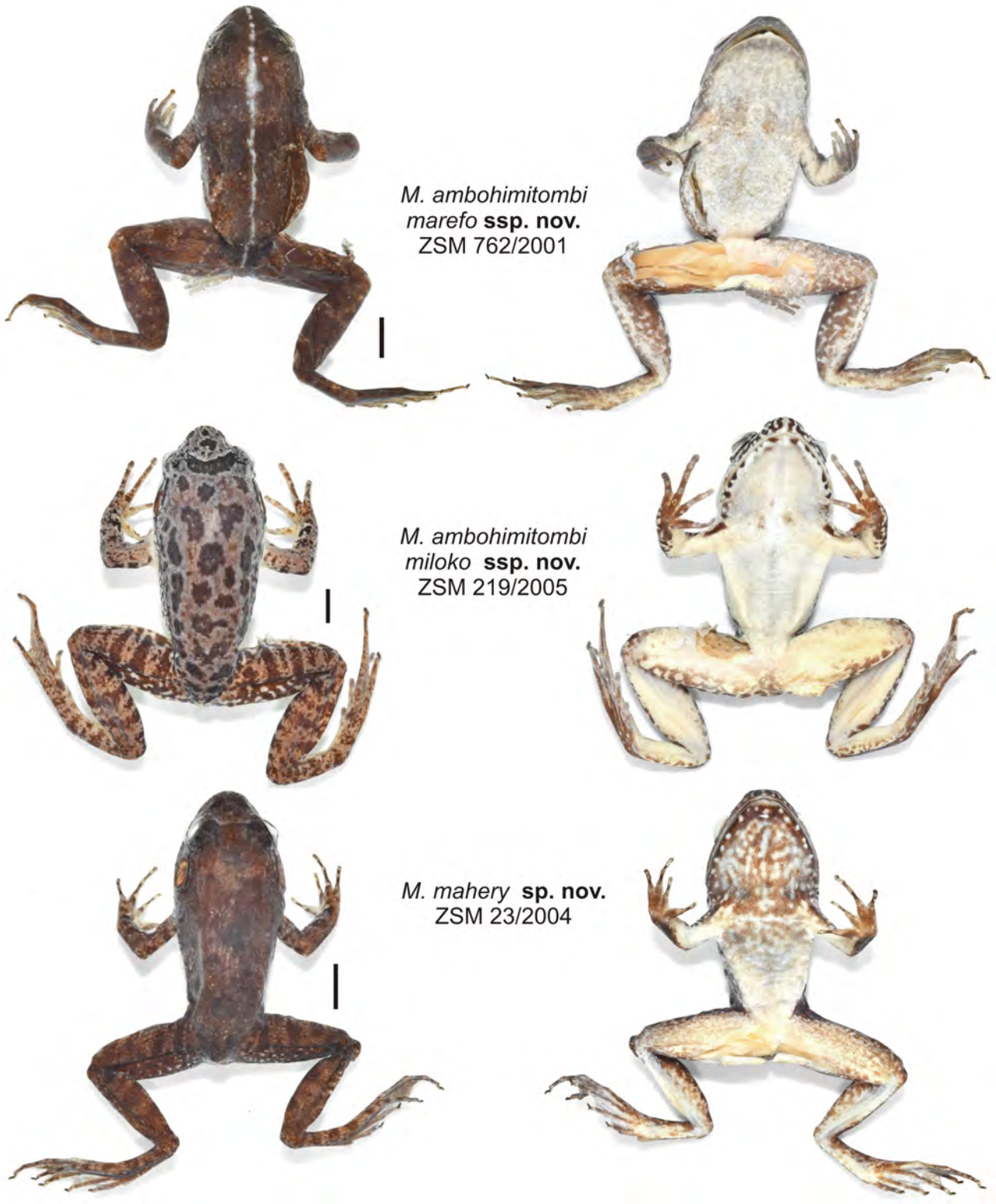

FIGURE 9. Preserved holotypes of newly named species and subspecies in the *M. curtus* clade. Scale bars equal 5 mm.

concordant differentiation is seen in fully sympatric sister species of relatively low genetic distance, such as in the case of *M. schulzi* vs *M. steinfartzi* **sp. nov.** (previously *M.* sp. Ca33) which differ only by 2.6–3.0% in the 16S fragment, yet are unambiguously distinct in Rag-1, bioacoustics, and morphology, suggesting full reproductive isolation. In several other cases, morphologically and bioacoustically similar species such as *M. betsileanus* and *M. georgei* **sp. nov.** (previously *M.* sp. Ca36) are placed in distant clades in the phylogenomic tree, providing clear evidence for their distinctness at the species level. In further cases, species are recovered as phylogenetically isolated, sister to a large group of species such as *M. stelliger* **sp. nov.** (a newly discovered species not included in previous studies), or are recovered as sister to morphologically and biogeographically rather distinct species, such as *M. mahery* **sp. nov.** (previously *M.* sp. Ca14)—a large-sized species from the West of Madagascar that turned out to be sister to the specialised montane endemic *M. pauliani*, which is not only smaller but also differs drastically in morphology (Fig. 5). Finally, some lineages, such as those in the *M. tricinctus* clade, differ by high 16S distances >7% which have not previously been observed at the intraspecific level in any Malagasy amphibians.

Our integrative species delimitation used the preferred 16S partition calculated by ASAP as a basis, accepting those mitochondrial lineages as species that were strongly supported by other lines of evidence as well. We considered several other lineages delimited by ASAP as subspecies, as only limited additional evidence was found for their distinctness. Furthermore, two lineages not supported by the preferred ASAP partition are regarded as separate taxa: the subspecies *M. ambohimitombi marefo* **ssp. nov.** and *M. a. miloko* **ssp. nov.** due to their morphological differences, and the species *M. jahnarum* **sp. nov.** due to its substantial bioacoustic differences to its closest relative, *M. fergusoni* **sp. nov.** (Fig. 5). Lastly, several species in our taxonomic scheme contain deep mitochondrial lineages that ASAP suggested to be distinct at the species-level, but where we have interpreted them as deep conspecific lineages; this is true especially for *M. tricinctus, M. grubenmanni* **sp. nov.**, *M. gudrunae* **sp. nov.**, *M. jonasi* **sp. nov.**, and to a lower degree to *M. augustini* **sp. nov.**, and *M. bletzae* **sp. nov.** Detailed justifications for the taxonomic status of each of these lineages is given in the 'Identity' section of each species or subspecies account below. In the species accounts, we provide formal differential diagnoses for all new species and subspecies described, and less detailed characterizations for all previously known nominal species.

A summary of character states and morphometric values of all species and subspecies of *Brygoomantis* is given in Table 4. As can be seen from the data, species and species groups show obvious morphological differences, but usually with at least some overlap in the majority of variables. This morphological variation leaves few or no unambiguous morphological differences between most species, and makes it necessary to refer to bioacoustic and molecular diagnostics. Analysis of molecular diagnostic sites in the 16S alignment revealed no unique diagnostic sites for any of the subspecies or species recognised herein. However, in all pairwise comparisons, diagnostic nucleotide positions were found (7–56 between species, and 3–23 between subspecies). A full list of the diagnostic positions numbered in relation to the complete *Mantella madagascariensis* 16S sequence is given in Supplementary Materials, thereby providing formal diagnostic characters validating all new taxa named below.

In the following, we arrange the large number of species and lineages in the subgenus *Brygoomantis* into the eight main clades revealed by the phylogenomic analysis (Fig. 5): the *Mantidactylus curtus* clade, *M. ulcerosus* clade, *M. betsileanus* clade, *M. fergusoni* clade, *M. tricinctus* clade, *M. biporus* clade, *M. inaudax* clade, and *M. stelliger* clade. For each of the clades, we first present the account of the historically first described species that gives the name to the clade, and subsequently the other species in alphabetical order.

Mantidactylus curtus clade

This clade comprises several small to large-sized species (23.4–65.0 mm adult SVL) typically characterized by a relatively short snout and short hindlimbs, sometimes a weakly developed frenal stripe (very rare in other *Brygoomantis*), and occurrences either in the Central Region or in the western regions of Madagascar (South, West and North-West), including several montane species: *Mantidactylus curtus, M. alutus, M. ambohimitombi, M. bourgati, M. madecassus, M. pauliani,* as well as one new species and two new subspecies named herein (holotypes are depicted in Fig. 9). The *M. curtus* clade was particularly difficult to revise because the calls of most species are—even by the standards of *Brygoomantis*—highly inconspicuous and rarely heard, and differences between males and females are not easy to recognise externally (males often have rather indistinct femoral glands, not too different from the gland rudiments of females). Two exceptions to this are *M. alutus,* a small-sized species with distinct femoral glands in males and distinct calls, and *M. mahery* **sp. nov.**, a widespread species in the West, reaching into the North West and into the South (Isalo). Furthermore, our analysis with the Phylonetworks package suggested two instances of reticulated evolution in this clade (see above), which further complicates taxonomic inference.

Mantidactylus curtus (Boulenger, 1882)

Type material.—*Rana curta* Boulenger, 1882 is based on seven syntypes, four of which are still available: BMNH 1947.2.10.28–31 from 'East Betsileo' and 'Ankafana, Betsileo'. We here designate the DNA-barcoded specimen BMNH 1947.2.10.30, probably an adult male (sex not unambiguously confirmed), as lectotype. In consequence, the type locality is now 'East Betsileo'. Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

TABLE 4. Summary of the most important diagnostic characters of species in the *Mantidactylus* subgenus *Brygoomantis*. SVL is given only based on reliably sexed specimens, summarised and rounded to the nearest mm from original measurements in Tables 5–11. Dorsolateral ridges are always weakly expressed in *Brygoomantis*, but clearly visible in some species while completely absent in others. Dorsal skin rugosity is estimated from pictures in life and can appear different in preservative: 0, smooth; 1, finely granular; 2, coarsely granular / tubercular. Webbing at toe 5 is given as 0, half or less than half of one phalanx free of web, not counting terminal phalanx (corresponding to numbers 0–0.5 in webbing formula); 1, about one phalanx free of web (0.75–1.25); 2, more than one phalanx free of web (1.5–2). (Yes) in parentheses indicates that the respective character state is found in some individuals of the respective species, and often only weakly expressed, while it is missing in others. Lat.met., state of the lateral metatarsalia, either separated (sep.) by webbing or connected (conn.) by tissue. NM, no measurements available. *For the advertisement calls of *M. katae* **sp. nov.** and *M. fergusoni* **sp. nov**., homology of call components remains unclear. Here, each unit is interpreted as single–pulse call (= single-pulse note) arranged in series (under this definition the provided pulse rate reflects call rate), but it would also be possible to consider the entire vocalization as single-note multi-pulsed call with very long duration, containing very widely spaced pulses. Values for pulse rate (pulses/second) are rounded. We here evaluate the presence versus absence of regular call series (last column), where regular series are considered as such, if calls are emitted at really regular intervals in series of similar duration containing a more or less defined number of calls. # In *M. ambohimitombi*, several unsexed individuals of the type series, probably females, reach sizes of up to 65 mm, being the largest of all *Brygoomantis* known. †One female of *M. biporus* of 19.3 mm SVL is probably a not fully mature specimen; other females of the species measure 31–36 mm SVL.

Species	SVL (M) [mm]	SVL (F) [mm]	(END + NSD) / SVL [%]	HTD/ SVL (males) [%]	FGW/SVL (males) [%]	SVL/ HIL [%]	Dorsolat. ridges	Dorsal skin	Lat. met.	Webbing toe 5	White spots on flanks	White marking on snout tip	Yellow inguinal marking	Pulses / call	Pulses / second	Regular call series
***M. curtus* clade**																
M. curtus	34	33–40	11–14	10	8	58–74	No	0	sep.	0	No	No	No	NM	NM	NM
M. alutus	25	27–31	13–17	9	6	60–67	Yes	1	sep.	1	(Yes)	No	No	20–27	67–130	Yes
M. amb. ambohimitombi	33–38	34–51 (65#)	13–16	8–11	8–10	52–69	(Yes)	1	sep.	0	(Yes)	No	(Yes)	9–14	56–69	No
M. amb. miloko **ssp. nov.**	42	49	13–16	10	7	54–66	No	1	sep.	1	(Yes)	No	No	NM	NM	NM
M. amb. marefo **ssp. nov.**	31–35	36	9–15	6–8	NM	59–70	No	0–1	sep.	0	No	No	No	NM	NM	NM
M. bourgati	33-39	32–40	11–18	NM	NM	59–65	(Yes)	1	sep.	0	No	No	No	36–50	46–54	No
M. madecassus	27–30	29–34	11–16	7–10	NM	59–72	No	0	sep.	0	No	No	No	NM	NM	NM
M. pauliani	30–31	31–33	9–14	8–9	NM	57–69	No	0–1	sep.	0	No	No	No	NM	NM	NM
M. mahery **sp. nov.**	29–37	34–49	14–18	11–13	7–9	66–75	(Yes)	1	sep.	0	No	No	No	21–26	108–667	Yes
***M. ulcerosus* clade**																
M. ulcerosus	29–36	33–45	15–19	11–14	6–12	66–71	(Yes)	2	sep.	0	No	No	No	45–65	50–220	Yes
M. bellyi	32–41	33–46	12–19	10–17	6–9	66–70	No	1–2	sep.	0	No	No	No	41–46	64–78	No
M. schulzi	21–24	25–29	14–19	14–15	11	61–72	(Yes)	1	sep.	0	No	Yes	No	6–73	55–130	(Yes)

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TABLE 4. (Continued)

Species	SVL (M) [mm]	SVL (F) [mm]	(END + NSD) / SVL [%]	HTD/ SVL (males) [%]	FGW/SVL (males) [%]	SVL/ HIL [%]	Dorsolat. ridges	Dorsal skin	Lat. met.	Webbing toe 5	White spots on flanks	White marking on snout tip	Yellow inguinal marking	Pulses / call	Pulses / second	Regular call series
M. steinfartzi **sp. nov.**	17–22	22–28	12–18	15–17	10–13	63–76	No	0–1	sep.	0	Yes	(Yes)	No	40–54	70–115	(Yes)
***M. betsileanus* clade**																
M. betsileanus	22–29	30–37	15–21	10–16	5–9	50–62	Yes	1	sep.	1	No	Yes	No	107–201	40–105	No
M. noralottae	33–36	37–40	15–19	10–12	5–7	59	Yes	0–1	sep.	0	(Yes)	No	No	92–108	37–41	No
M. tripunctatus	26–27	33–35	15–20	14–15	8–9	59–72	Yes	1	sep.	1	No	Yes	No	70–80	30–48	No
M. incognitus **sp. nov.**	27	26	13–16	14	10	54–61	Yes	1	sep.	1	No	Yes	No	NM	NM	NM
M. jonasi **sp. nov.**	22–25	NM	17–19	14–18	7–10	56–65	Yes	1–2	sep.	1	No	Yes	No	19–72	14–30	No
M. katae **sp. nov.**	22–27	26–36	15–20	12–15	9–13	55–62	Yes	1	sep.	0	No	Yes	No	(1)*	(10–16)*	(Yes)*
M. kortei **sp. nov.**	27	35–37	15–17	13	9	60–67	Yes	1	sep.	0	(Yes)	(Yes)	No	12–27	29–69	No
M. riparius **sp. nov.**	27	22-27	15–18	13	8	61–63	(Yes)	1	sep.	0	(Yes)	(Yes)	No	15–41	49–114	No
***M. fergusoni* clade**																
M. fergusoni **sp. nov.**	25–30	36–42	16–20	10–14	8–9	61–66	(Yes)	2	sep.	0	No	No	No	(1)*	(2–5)*	(Yes)*
M. georgei **sp. nov.**	28–31	NM	17–18	13–15	8–12	61–66	(Yes)	1–2	sep.	0	No	(Yes)	No	26–85	13–33	No
M. jahnarum **sp. nov.**	29–30	30–34	15–17	11	10–12	59–70	(Yes)	1–2	sep.	0	No	(Yes)	No	16–45	25–35	Yes
M. marintsoai **sp. nov.**	29	35–39	15–18	13	NM	61–65	(Yes)	1–2	sep.	1	No	No	No	NM	NM	NM
***M. tricinctus* clade**																
M. tricinctus	17–19	18–23	16–21	12–14	9–13	59–72	No	1	conn.	2	No	Yes	Yes	8–19	147–214	Yes
M. grubenmanni **sp. nov.**	17–18	19–20	15–20	12–16	10–11	61–64	No	1–2	conn.	2	(Yes)	Yes	Yes	3–7	48–182	Yes

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TABLE 4. (Continued)

Species	SVL (M) [mm]	SVL (F) [mm]	(END + NSD) / SVL [%]	HTD/ SVL (males) [%]	FGW/SVL (males) [%]	SVL/ HIL [%]	Dorsolat. ridges	Dorsal skin	Lat. met.	Webbing toe 5	White spots on flanks	White marking on snout tip	Yellow inguinal marking	Pulses / call	Pulses / second	Regular call series
M. gudrunae **sp. nov.**	20–25	23–29	17–20	11–15	8–13	62–68	No	1	(sep.)	1	No	Yes	Yes	NM	NM	NM
***M. biporus* clade**																
M. biporus	28–32	(19†)/31–36	13–22	10–12	6–9	66–74	No	0–1	sep.	1	Yes	No	No	15–21	130–211	Yes
M. augustini **sp. nov.**	24	21–25	13–18	13	8	60–65	(Yes)	0–1	sep.	1	Yes	No	No	9–15	44–71	Yes
M. bletzae **sp. nov.**	NM	26–27	13–15	NM	NM	65–67	Yes	1	sep.	0	Yes	No	No	NM	NM	NM
M. brevirostris **sp. nov.**	23	28	14–17	12	7	66–70	No	0–1	sep.	2	Yes	No	No	NM	NM	NM
M. eulenbergeri **sp. nov.**	20–23	25–28	14–17	12–14	7–11	67–75	(Yes)	0	sep.	1	(Yes)	No	No	NM	NM	NM
M. glosi **sp. nov.**	21	25	15–17	13	7	73–74	Yes	1	sep.	1	(Yes)	No	No	18–23	91–115	Yes
***M. stelliger* clade**																
M. stelliger **sp. nov.**	21–23	31	16–17	12	9–10	65–68	No	1	sep.	2	Yes	No	No	NM	NM	NM
***M. inaudax* clade**																
M. inaudax	22–30	27–33	13–16	12–16	6–10	67–76	No	0–1	sep.	1	(Yes)	No	No	17–28	61–143	Yes
M. m. manerana **sp. nov.**	25–28	28–29	15–17	9–12	7–9	65–69	Yes	1	sep.	1	Yes	(Yes)	No	26–31	63–116	(Yes)
M. m. fotaka **ssp. nov.**	26	29	14–16	13	9	71–74	Yes	1	sep.	1	Yes	(Yes)	No	NM	NM	NM
M. m. antsanga **ssp. nov.**	NM	38	14	NM	NM	71	Yes	NM	sep.	0	NM	NM	No	NM	NM	NM

Identity.—The name *Mantidactylus curtus* has been applied to a complex of genetically divergent lineages inhabiting various mountain ranges and areas of the central high plateau of Madagascar (e.g. Blommers-Schlösser & Blanc 1991; Glaw & Vences 1992a). Glaw and Vences (2006) revalidated *M. bourgati* to refer to the lineage of the Andringitra Massif, but the identity of *M. curtus* remained uncertain. We here provide a 16S sequence of the lectotype that clusters with a lineage from various localities not far from the type locality (e.g. Antoetra, Itremo, Col des Tapias), providing definitive evidence of the assignment of the nomen *curtus* to this lineage.

Evidence of introgression of genomic material from this species (*M. curtus*) into a syntopic lineage (*M. ambohimitombi marefo* ssp. nov., described below) was found in the Phylonetworks analysis (Fig. 5). Since the latter taxon appears to have a limited distribution range in the Itremo Massif, and the observed reticulation only concerned one *M. curtus* specimen from the same site, it is likely that this inter-species gene flow is localized and does not compromise the identity of *M. curtus* as independently evolving lineage.

Synonyms.—Boulenger (1895) considered *Rana inaudax* Peracca, 1893 to be a synonym of *M. curtus*, but that species name is revalidated below.

Diagnosis.—A member of the *M. curtus* clade and sister to *M. bourgati*. See Table 4 for a list of diagnostic morphological characters. The combination of relatively large body size of up to 39 mm, smooth skin, absence of dorsolateral ridges, strongly developed foot webbing with fully webbed fifth toe, and relatively short snout distinguishes this species from species of the other clades. Within the *M. curtus* clade, *M. alutus, M. madecassus* and *M. pauliani* have smaller body sizes (Table 4). *Mantidactylus curtus* has smooth dorsal skin, constituting a difference to many specimens of *M. ambohimitombi* and *M. bourgati* where the skin is somewhat granular. As far as known, *M. curtus* and its sister species *M. bourgati* occur allopatrically and therefore can be distinguished based on localities. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. curtus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 5. See Fig. 10 for colouration in life and its variation. Evidence for sexual size dimorphism is inconclusive (confirmed male SVL 33.7 mm [n = 1] vs confirmed female SVL 32.5–39.8 mm [n = 8]). In the male specimen MRSN A6757, FGL x FGW is 5.6 mm x 2.6 mm. In many other individuals, femoral glands are less distinct, and some of them cannot be reliably sexed by external examination.

Natural history.—Specimens were found in the vicinity of highland streams, usually quite close to the water.

Calls.—The call of this species has not been recorded.

Tadpoles.—A tadpole of *M. curtus* (ZSM 943/2004) was described by Schmidt *et al.* (2009). The tadpole description by Blommers-Schlösser (1979), based on material from Manjakatompo (Ankaratra) and Angavokely, probably refers to different species, as *M. curtus* is not among the species we have recorded from Ankaratra here. We have not re-sampled Angavokely, but *M. alutus* and *M. ambohimitombi miloko* **ssp. nov**. occur at sites nearby, the latter of which closely resembles *M. curtus*.

Distribution.—Endemic to a small area of the central highlands of Madagascar (Fig. 7). This species is known from Ambositra, Ankazomivady, Antoetra, Antsirakambiaty forest, Col des Tapias, Ibity, Itremo, and Vatolampy. Elevation range: 1300–2090 m a.s.l.

Etymology.—Latin adjective meaning 'shortened' or 'short', presumably in reference to the short snout of the species.

Mantidactylus alutus (Peracca, 1893)

Type material.—*Rana aluta* Peracca, 1893 is based on 25 syntypes according to the original description, 14 of the colour morph 'forma' A and 11 of the 'forma' B. According to Frost (2021), *Rana aluta* Peracca, 1893 includes the following syntypes: MZUT An725 and An729, MNHN 1894.1–2, and specimens in BMNH, all from 'dintorni di Andrangoloaka e dalla vicina valle dell'Umbi'. However, Gavetti and Andreone (1993) designated MZUT An725.1 as lectotype and redescribed this specimen including morphological measurements (summarised in Table 4). They listed 11 paralectotypes of colour morph A (MZUT An725.2–12) and 13 of colour morph B (MZUT An729), resulting in a total of 25 type specimens, although their numbers of individuals attributed to both colour morphs differ from the original description (Peracca 1893). However, since the total number of type specimens is in accordance with the number mentioned by Peracca (1893) the claim by Blommers-Schlösser and Blanc (1991) concerning the presence of two other syntypes at Paris (MNHN 1894.1 and 1894.2) does not seem to be correct (Gavetti & Andreone 1993: 106) and the same must be assumed for the specimens claimed by Boulenger (1895 '1894') to have been received by the BMNH from Peracca. An additional non-type specimen is MZUT An917 from Andrangoloaka (Gavetti & Andreone 1993), demonstrating that more than the 25 types were available in the MZUT collection. The MNHN and BMNH specimens are therefore not paralectotypes.

Identity.—In this study we obtained genetic data via barcode fishing from specimen MNHN 1894.1 from Andrangoloaka, marked as 'type' of *M. alutus* in the MNHN catalogue and provided by M.G. Peracca according to the MNHN catalogue, but, as discussed above, probably not representing one of the paralectotypes. The 16S sequence of this specimen clustered among specimens from the central highlands of Madagascar that are typically considered as *M. alutus* (Blommers-Schlösser 1979; Blommers-Schlösser & Blanc 1991; Glaw & Vences 1992a, 1994, 2007). Although this information does not refer to the lectotype of the species, little doubts thus remain that the nomen *M. alutus* has been correctly applied to this small-sized lineage from the central highlands.

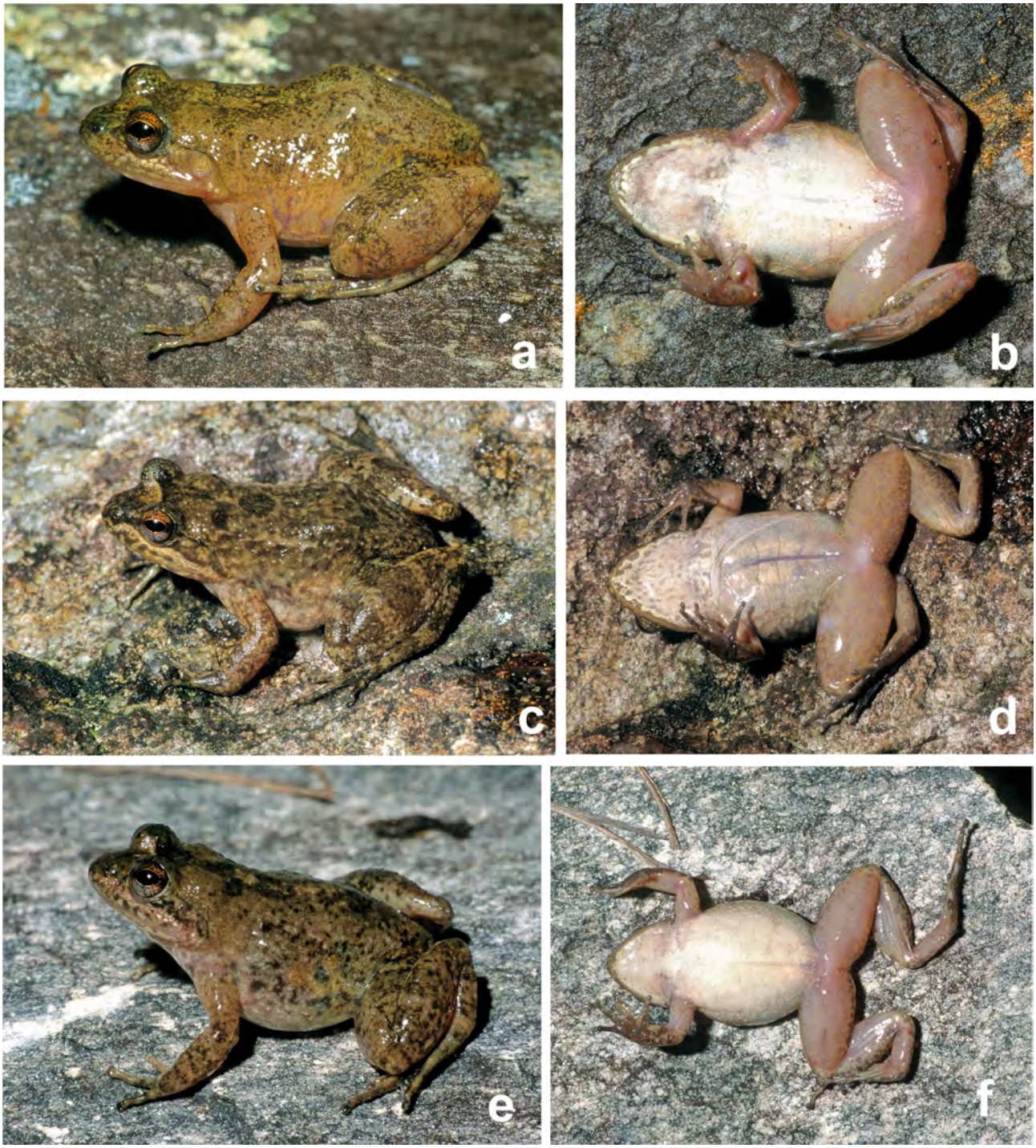

FIGURE 10. *Mantidactylus curtus* in life, in dorsolateral and ventral view. (a,b) Female specimen (ZSM 768/2001 = FGMV 2001.489) from Itremo, photographed in 2001 (note the almost complete absence of femoral glands). (c,d) Probable female (note small femoral glands) from Antoetra, photographed in 2003. (e,f), Probable female (ZSM 758/2001 = FGMV 2001.423; note rather small femoral glands) from Mount Ibity/Col des Tapias, photographed in 2001.

TABLE 5. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus curtus* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype. An asterisk (*) marks lectotypes designated in the current paper. For abbreviations of measurements, see Materials and Methods. All specimens are probable adults, but sex is difficult to ascertain externally in many species of this clade due to weak expression of femoral glands in male specimens, and is therefore only given for some specimens where gonad examination was possible. NM, not measured. # Measurements taken by Gavetti and Andreone (1993)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
M. alutus																	
MZUT An725.1 # [LT]	NA	M	Andrangoloaka	23.4	8.9	8.7	3.6	3.2	2.4	2.0	NM	NM	5.8	NM	18.6	NM	NM
MNHN 1894.2	NA	M	Andrangoloaka	27.2	8.4	11.0	3.3	1.9	2.7	1.5	3.0	14.8	6.4	40.9	18.9	13.0	11.9
MNHN 1894.1	NA	M	Andrangoloaka	25.0	9.5	9.9	2.8	2.2	2.6	1.7	3.0	15.0	7.8	41.7	20.8	14.3	11.6
ZSM 194/2021	ACZCV 341	F	Ankaratra	31.0	10.4	11.6	4.0	2.9	2.2	1.9	3.2	18.1	9.0	NM	NM	NM	13.0
M. ambohimitombi ambohimitombi (Ca19)																	
BMNH 1947.2.26.25 [LT*]	NA		Ambohimito-mbo forest	65.0	25.1	24.0	6.6	4.1	4.5	NA	5.8	36.6	17.4	110.3	52.5	35.2	NM
BMNH 1947.2.26.26 [PLT]	NA		Ambohimito-mbo forest	63.9	23.1	23.0	6.6	4.8	4.7	NA	5.6	35.5	17.1	99.2	48.2	35.1	NM
ZSM 191/2021	ACZCV 335	F	Analafohy	50.6	16.8	17.5	5.9	4.0	3.9	4.0	4.8	27.3	13.0	NM	NM	NM	23.7
ZSM 192/2021	ACZCV 336	F	Analafohy	38.9	12.9	15.0	5.0	2.7	2.6	2.4	4.9	23.0	11.6	NM	NM	NM	20.0
ZSM 193/2021	ACZCV 340	F	Ankaratra	33.5	11.4	12.7	4.4	3.0	2.7	2.6	4.0	19.7	11.0	NM	NM	NM	17.3
ZMA 6865 (1062)	NA	F	Manjakotompo	43.1	14.0	15.8	3.7	2.5	3.6	2.9	3.8	23.1	10.4	67.6	34.2	22.3	22.9
ZSM 190/2021	ACZCV 334	M	Analafohy	37.7	14.0	15.2	5.4	4.1	3.0	2.4	3.6	22.3	11.4	NM	NM	NM	18.0
ZSM 195/2021	ACZCV 342	M	Ankaratra	35.3	12.5	14.1	4.4	2.7	2.6	2.2	3.6	21.3	11.0	NM	NM	NM	17.3
ZSM 368/2000	FG/MV 2000.87	M	Manjakatompo	32.6	12.0	13.7	3.7	2.5	2.6	1.8	2.7	22.8	9.9	60.4	29.1	21.0	17.7
ZSM 369/2000	FG/MV 2000.88	M	Ankaratra	37.2	13.8	14.9	3.8	3.1	2.8	2.3	3.3	23.8	10.5	63.6	30.7	21.0	18.7
ZMA 6863 (671)	NA	?	Manjakotompo	34.3	12.4	13.9	3.9	2.6	2.3	2.2	3.6	19.7	9.2	58.0	27.7	19.2	17.4
ZMA 6863 (672)	NA	?	Manjakotompo	36.7	13.4	15.3	3.7	2.7	2.8	2.7	3.7	25.3	10.9	70.1	33.4	22.8	20.9
ZMA 6866 (1192)	NA	?	Manjakotompo	41.0	15.1	17.0	4.7	3.6	2.9	2.7	4.6	21.2	11.2	59.7	29.6	21.0	18.9
ZMA 6866 (1193)	NA	?	Manjakotompo	30.7	11.1	12.7	2.9	2.1	2.5	2.4	3.4	17.3	8.1	52.1	25.3	17.5	16.2
M. ambohimitombi miloko **ssp. nov.**																	
ZSM 219/2005 [HT]	FGZC 2143	M	Ambohitantely	41.7	15.3	16.5	5.5	4.3	3.3	2.9	4.0	23.9	11.8	67.0	32.1	22.2	19.6
ZSM 237/2005 [PT]	FGZC 2172	F	Ambohitantely	49.4	16.5	17.8	5.8	4.1	4.0	3.1	4.4	25.5	12.5	75.2	36.4	25.5	22.9

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TABLE 5. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
ZMA 6859 (675)	NA	?	Tampoketsa d'Ankazobe	32.9	10.9	12.6	3.1	2.2	2.2	2.1	3.3	20.8	9.1	52.8	25.9	27.4	16.5
ZMA 6859 (676)	NA	?	Tampoketsa d'Ankazobe	39.8	13.9	15.4	4.5	2.6	3.1	2.8	4.2	23.4	11.0	64.5	31.8	21.8	19.4
ZMA 6860 (910)	NA	?	Tampoketsa d'Ankazobe	39.0	13.7	14.7	4.1	2.1	3.0	3.1	4.0	23.8	11.1	69.4	33.1	23.4	21.2
ZMA 6860 (911)	NA	?	Tampoketsa d'Ankazobe	43.7	14.6	16.6	4.6	2.4	3.1	3.0	4.2	25.0	11.3	76.3	36.7	25.5	23.2
ZMA 6860 (912)	NA	?	Tampoketsa d'Ankazobe	43.8	15.4	16.6	4.9	2.5	3.0	2.7	4.3	23.9	11.6	70.9	34.2	23.7	21.1
ZMA 6860 (913)	NA	?	Tampoketsa d'Ankazobe	41.3	13.8	14.8	4.3	2.2	2.9	3.3	4.3	25.6	13.7	73.1	36.0	25.4	22.4
ZMA 6860 (914)	NA	?	Tampoketsa d'Ankazobe	35.9	14.5	15.0	3.9	2.6	3.1	2.3	3.4	24.2	11.2	65.9	31.5	22.9	19.7
ZMA 6860 (917)	NA	?	Tampoketsa d'Ankazobe	42.2	14.9	16.9	4.6	2.4	3.4	3.1	4.2	25.9	11.5	73.4	35.8	24.9	21.6
ZMA 6861 (732)	NA	?	Angavokely Carion	36.5	12.5	14.8	3.4	3.0	3.2	2.3	3.7	21.1	10.4	64.4	30.8	20.7	18.7
ZMA 6862 (1100)	NA	?	Angavokely Carion	41.5	13.9	15.8	4.3	2.7	2.9	2.6	4.2	22.9	10.3	64.9	30.0	20.8	19.6
ZMA 6862 (1101)	NA	?	Angavokely Carion	43.5	14.4	16.4	4.1	3.1	3.4	2.7	4.2	24.1	11.3	66.1	33.2	23.4	20.2
ZMA 6862 (1103)	NA	?	Angavokely Carion	43.1	14.3	15.8	3.8	2.3	3.3	3.1	3.9	23.9	11.9	67.4	32.6	23.0	20.4
ZMA 6862 (1105)	NA	?	Angavokely Carion	44.0	15.2	16.7	4.8	2.9	3.2	2.6	4.4	24.0	12.3	68.5	33.4	23.5	21.1
M. ambohimitombi marefo **ssp. nov.** (Ca20)																	
ZSM 762/2001 [HT]	FGMV 2001.493	M	Itremo	33.4	12.8	12.2	3.8	2.7	1.7	1.7	3.0	20.3	7.6	48.9	22.0	16.3	14.3
ZSM 761/2001 [PT]	FGMV 2001.492	F	Itremo	35.9	12.8	12.2	4.3	2.2	1.6	1.6	3.5	20.7	8.5	51.5	24.2	17.8	15.7

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TABLE 5. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
MRSN A6747 [PT]	FAZC 14047	F?	Antsirakambiaty forest	32.8	11.9	12.4	4.7	3.0	2.8	2.0	3.4	17.3	9.1	50.5	23.9	17.0	15.2
ZSM 759/2001 [PT]	FGMV 2001.476	M	Itremo	34.1	12.3	12.6	3.4	2.4	2.0	1.9	3.6	19.4	8.6	51.7	23.8	17.0	15.0
ZSM 760/2001 [PT]	FGMV 2001.478	M	Itremo	30.9	12.2	11.6	3.4	1.8	1.9	1.5	3.4	20.5	8.3	52.5	24.4	16.7	15.6
ZSM 763/2001 [PT]	FGMV 2001.495	M	Itremo	34.6	13.7	13.5	3.7	2.8	1.8	1.8	3.0	19.2	8.6	52.2	23.2	16.3	14.9
M. bourgati																	
MNHN 1972.437 [HT]	NA	M?		38.6	15.7	15.0	4.8	3.5	2.7	2.9	4.4	23.4	11.6	64.4	29.4	20.1	19.6
ZSM 769/2001	FGMV 2001.517	F	Andringitra, Andohariana	32.3	12.5	12.6	3.4	2.3	2.9	2.7	3.6	20.0	9.0	54.0	25.6	17.5	17.2
ZSM 770/2001	FGMV 2001.520	M	Andringitra, Andohariana	33.0	13.2	NM	3.3	2.8	2.6	1.9	3.4	21.4	9.4	55.5	26.5	18.3	17.8
ZSM 771/2001	FGMV 2001.521	F	Andringitra, Andohariana	34.0	11.9	12.7	3.6	2.7	2.5	1.8	3.2	21.5	9.6	55.5	25.7	18.1	17.2
ZSM 772/2001	FGMV 2001.522	F	Andringitra, Andohariana	39.3	14.7	15.1	4.0	2.7	3.7	3.2	4.3	23.1	11.1	65.4	28.7	20.3	19.8
ZSM 773/2001	FGMV 2001.523	F	Andringitra, Andohariana	40.0	14.8	15.1	4.2	3.0	2.5	2.0	4.0	23.4	10.5	63.8	29.0	20.5	19.6
ZSM 774/2001	FGMV 2001.580	M	Andringitra, Imaitso	38.9	14.9	15.4	4.1	3.4	3.5	2.8	3.5	22.7	10.0	60.1	26.4	19.0	18.4
ZSM 775/2001	FGMV 2001.581	F	Andringitra, Imaitso	35.7	13.9	13.6	3.9	2.3	3.1	2.5	3.4	21.5	10.2	60.6	27.3	19.3	19.2
M. curtus																	
BMNH 1947.2.10.30 [LT*]	NA	M?		35.3	11.8	12.6	4.4	2.5	2.7	2.0	3.9	20.8	9.4	56.1	25.8	17.4	NM
BMNH 1947.2.10.28 [PLT]	NA	F		38.4	14.1	14.2	4.6	3.4	2.7	2.8	4.5	20.5	11.0	55.5	26.0	17.8	NM
ZSM 757/2001	FGMV 2001.422	F	Ibity	36.0	13.0	13.1	3.9	2.3	2.4	2.0	3.4	20.4	10.2	55.3	25.3	18.0	16.9
ZSM 758/2001	FGMV 2001.423	F	Ibity	32.5	12.4	12.2	3.5	1.9	2.5	2.2	3.4	20.3	9.3	53.0	23.5	16.6	15.4

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TABLE 5. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
ZSM 766/2001	FGMV 2001.473	F	Itremo	39.0	13.5	13.9	4.1	2.6	2.4	2.2	3.4	22.6	10.3	60.1	28.0	19.4	18.7
MRSN A6748	FAZC 14046	F?	Antsirakambiaty	41.2	13.8	14.3	5.0	3.1	2.9	2.2	3.8	20.2	10.0	58.6	27.4	19.4	17.4
MRSN A6760	FAZC 13995	F?	Antsirakambiaty	33.5	11.9	12.4	4.5	2.9	2.5	2.2	2.9	18.5	9.0	51.4	23.0	16.4	15.6
MRSN A6757	FAZC 13993	M	Antsirakambiaty forest	33.7	12.5	12.3	4.3	3.4	2.4	2.1	3.8	18.3	9.5	45.4	19.3	16.9	15.2
ZSM 764/2001	FGMV 2001.462	F	Itremo	37.8	14.4	14.1	4.1	2.0	2.5	2.3	3.7	21.6	9.7	57.9	26.2	17.7	16.9
ZSM 765/2001	FGMV 2001.463	F	Itremo	34.3	13.1	12.6	3.6	1.9	2.4	1.9	3.1	21.1	9.0	59.3	27.4	19.0	17.5
ZSM 767/2001	FGMV 2001.488	F	Itremo	39.8	13.7	13.6	3.6	2.0	2.5	2.0	3.6	22.2	9.7	61.3	28.5	18.9	18.2
ZSM 768/2001	FGMV 2001.489	F	Itremo	37.9	14.0	13.9	3.6	2.5	2.2	1.8	3.3	22.1	8.8	52.9	25.7	17.9	16.5
M. madecassus																	
MNHN 1953.246 [LT]	NA	F?	Andringitra	27.5	9.6	9.7	3.1	1.9	1.8	2.2	3.0	16.6	7.9	47.0	22.4	15.3	NM
MNHN 1989.3592 [PLT]	NA	F?	Andringitra	31.0	9.6	10.2	3.0	2.3	1.8	2.0	3.0	16.7	7.6	43.1	21.0	14.5	NM
MNHN 1989.3594 [PLT]	NA	F?	Andringitra	29.2	10.6	10.3	3.2	2.9	2.0	2.2	3.3	16.3	7.7	43.7	17.2	14.7	NM
MNHN 1989.3591 [PLT]	NA	M?	Andringitra	25.4	8.0	8.6	2.2	1.6	1.7	1.8	3.0	12.7	6.2	36.1	21.3	12.0	NM
MNHN 1972.1182	NA	F	Andringitra	32.0	10.8	11.1	3.5	2.3	1.9	2.6	3.2	17.2	8.5	51.0	24.8	18.3	NM
MNHN 1972.1185	NA	F	Andringitra	32.4	10.9	11.0	3.3	2.2	2.1	2.7	3.1	17.1	8.7	50.5	25.2	17.7	NM
MNHN 1972.1192	NA	F	Andringitra	33.7	10.9	11.2	3.5	2.6	2.0	2.5	3.4	18.0	8.4	49.6	25.1	16.7	NM
MNHN 1972.1204	NA	F	Andringitra	29.3	9.5	10.0	3.1	2.0	1.8	2.2	3.3	16.2	7.7	44.7	25.3	13.1	NM
MNHN 1972.1206	NA	F	Andringitra	31.4	10.5	10.2	3.5	2.1	2.1	2.3	3.4	19.0	8.5	51.4	21.4	17.2	NM
MNHN 1972.1198	NA	M	Andringitra	27.0	9.4	9.9	3.3	2.0	1.7	2.4	3.0	15.5	7.8	45.4	20.1	15.0	NM
MNHN 1972.1199	NA	M	Andringitra	29.8	9.9	10.7	3.4	2.9	2.0	2.1	3.3	17.6	8.8	48.6	23.7	16.8	NM
MNHN 1972.1190	NA	M?	Andringitra	27.0	9.2	9.9	3.1	1.7	2.0	2.2	2.8	15.3	7.0	42.4	21.1	14.2	NM
ZSM 755/2001	FGMV 2001.538	?	Andringitra, Cuvette Boby	29.7	10.0	9.8	3.4	2.2	1.8	1.4	2.6	16.7	7.7	48.1	23.0	16.1	14.4

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TABLE 5. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
M. pauliani																	
MNHN 1972.1508 [HT]	NA	M	Ankaratra	31.0	11.0	11.0	3.1	2.5	1.8	2.3	2.6	18.0	8.9	50.4	25.7	17.2	NM
MNHN 1972.1510 [PT]	NA	F	Ankaratra	33.7	11.5	10.8	4.0	2.2	1.6	2.2	3.1	18.7	8.9	48.7	24.2	17.0	NM
MNHN 1972.1511 [PT]	NA	F	Ankaratra	31.1	10.7	10.8	3.3	2.0	1.5	2.1	2.7	17.6	8.3	47.1	23.8	16.0	NM
MNHN 1972.1515 [PT]	NA	F	Ankaratra	32.9	10.6	11.1	3.4	2.2	1.6	2.0	3.1	18.2	9.6	49.1	23.8	16.7	NM
MNHN 1972.1509 [PT]	NA	F?	Ankaratra	29.7	11.2	11.7	3.1	2.8	1.9	2.1	3.1	17.4	9.0	47.5	24.4	17.0	NM
MNHN 1972.1512 [PT]	NA	F?	Ankaratra	27.7	10.0	10.5	3.4	2.2	1.5	2.1	3.0	17.5	8.7	42.1	24.2	17.0	NM
MNHN 1972.1513 [PT]	NA	F?	Ankaratra	25.8	9.6	9.7	3.4	2.1	1.7	1.9	2.7	16.6	8.4	44.9	23.1	15.8	NM
MNHN 1972.1514 [PT]	NA	M	Ankaratra	29.5	11.0	11.3	3.3	2.7	1.6	2.1	3.0	17.7	9.0	47.4	24.5	16.7	NM
MNHN 1972.1516 [PT]	NA	M?	Ankaratra	31.6	11.5	11.9	3.5	3.1	1.7	2.3	3.0	18.9	8.9	50.1	25.5	17.3	NM
ZMA 6803 (1184)	NA	F	Ankaratra	31.6	10.1	10.4	3.4	2.0	1.4	2.3	3.0	16.5	8.1	45.5	22.1	15.6	NM
ZMA 6803 (1185)	NA	F?	Ankaratra	27.5	9.2	9.3	3.4	2.3	1.4	1.7	3.1	15.7	7.8	42.8	21.8	15.2	NM
ZMA 6803 (1186)	NA	F?	Ankaratra	26.9	8.8	9.2	3.2	1.6	1.4	1.8	2.7	16.0	8.6	44.8	21.4	14.7	NM
ZMA 6803 (1187)	NA	F?	Ankaratra	24.4	8.6	9.1	3.1	1.6	1.3	1.7	2.8	15.0	7.4	41.6	20.2	14.0	NM
ZMA 6803 (1188)	NA	M?	Ankaratra	24.8	8.8	9.1	3.2	1.8	1.5	1.8	2.7	15.4	8.0	41.1	20.5	14.0	NM
ZMA 6803 (1184)	NA	?	Ankaratra, 2200 m	31.2	10.2	10.5	3.5	1.8	1.4	1.5	2.8	16.0	7.9	45.6	21.8	14.9	13.6
ZMA 6803 (1185)	NA	?	Ankaratra, 2200 m	27.8	9.1	9.2	3.4	1.8	1.4	1.7	3.1	15.5	7.9	42.0	21.1	15.4	12.9
ZMA 6803 (1186)	NA	?	Ankaratra, 2200 m	26.8	8.9	9.0	3.4	1.6	1.7	1.6	3.0	16.1	7.4	43.8	21.4	15.3	13.2
ZMA 6803 (1187)	NA	?	Ankaratra, 2200 m	24.4	8.5	9.2	3.3	1.6	1.7	1.8	2.7	15.0	7.9	41.3	20.4	14.5	13.1
ZMA 6803 (1188)	NA	?	Ankaratra, 2200 m	24.5	8.7	9.1	3.3	1.5	1.3	1.7	2.7	15.1	7.7	40.8	20.7	14.2	13.5
ZSM 756/2001	NA	?	Ankaratra	25.7	8.6	9.4	3.0	1.5	1.4	1.4	2.2	15.4	7.5	44.1	20.7	14.7	13.8
M. mahery **sp. nov.** (Ca14)																	
ZSM 23/2004 [HT]	FGZC 37	M	Isalo	30.4	11.7	12.7	4.3	4.0	3.2	1.8	3.5	17.8	8.3	45.1	21.1	15.0	13.2
ZSM 136/2006 [PT]	FGZC 940	F	Bemaraha	45.0	17.0	16.3	5.8	4.9	3.7	3.5	4.6	23.0	12.4	59.9	27.6	19.7	17.9

...Continued on thte next page

TABLE 5. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
ZSM 26/2004 # [PT]	FGZC 42	F	Ranohira,creek nearby	36.0	13.8	13.0	4.7	3.5	3.3	2.6	3.3	11.2	9.5	NM	NM	16.4	15.6
ZSM 567/2009 [PT]	ZCMV 11457	F	Makira (Sahaovy)	41.6	13.9	14.8	5.2	3.6	4.0	2.1	3.7	22.8	12.1	60.9	21.9	19.5	17.5
ZSM 569/2009 [PT]	ZCMV 11484	F	Makira (Sahaovy)	43.2	15.3	16.2	6.2	4.3	3.7	2.7	4.2	23.1	11.1	60.4	27.6	19.3	17.4
ZSM 61/2006 [PT]	FGZC 793	F	Bemaraha	48.6	17.6	18.4	6.4	4.8	4.2	2.9	4.6	24.5	12.4	64.5	30.0	21.1	18.9
ZSM 942/2003 [PT]	FGMV 2002-1486	F	Isalo	34.2	12.8	13.3	4.4	3.8	3.2	2.7	3.5	17.9	9.0	49.0	22.5	16.1	14.6
ZSM 134/2006 [PT]	FGZC 938	M	Bemaraha	33.7	13.1	14.1	5.2	4.3	3.0	2.7	3.3	18.0	9.7	48.1	22.1	15.8	14.7
ZSM 135/2006 [PT]	FGZC 939	M	Bemaraha	33.2	12.4	12.8	4.9	4.3	3.2	2.2	3.4	17.4	8.8	44.7	20.9	15.0	13.2
ZSM 25/2004 # [PT]	FGZC 39	M	near Ranohira	31.0	12.1	11.2	4.0	3.7	2.8	1.7	3.5	9.6	8.5	NM	NM	13.8	13.4
ZSM 9/2006 [PT]	FGZC 682	M	Bemaraha	37.2	14.2	14.1	5.0	4.0	2.8	2.5	3.8	19.7	10.1	49.9	23.2	15.8	15.9
ZSM 941/2003 [PT]	FGMV 2002-1485	M	Isalo	30.1	12.5	13.2	3.9	3.9	3.0	2.0	3.2	16.8	8.4	45.4	21.1	15.1	13.3
ZSM 927/2003 # [PT]	FGMV 2002.1421	M	Isalo	29.2	12.3	11.2	4.2	3.5	3.2	2.0	3.3	8.5	9.4	NM	NM	15.0	14.6

Synonyms.—The taxon *Mantidactylus laevis* Angel, 1929 was listed as a dubious species by Guibé (1978) and considered a synonym of *M. alutus* by Glaw and Vences (1992a). The holotype MNHN 1929.208, collected by G. Petit from the vicinity of Antananarivo (type locality 'environs de Tananarive'; SVL 32 mm according to the original description) was reported to be lost according to Guibé (1978), and this has been confirmed by S. Grosjean (pers. comm. to A. Ohler, 22 January 2022). Because *M. alutus* is the only species of *Brygoomantis* occurring in the Antananarivo area, little doubts remain that this synonymy is correct. In order to stabilize synonymies and as the holotype has been lost for more than 40 years, we here designate the lectotype of *Rana aluta*, MZUT An725.1 as the neotype of *Mantidactylus laevis* Angel, 1929.

Diagnosis.—A member of the *M. curtus* clade and sister to a monophyletic group of all other species of the clade. See Table 4 for a list of diagnostic morphological characters. The combination of relatively small body size of up to 31 mm, slightly granular skin with (weakly expressed) dorsolateral ridges, small tympanum diameter of ca 9% of SVL in males, absence of small white spots on flanks, presence of a light frenal stripe in most specimens, and advertisement calls as a regular series of short pulsed notes distinguishes *M. alutus* from species of the other clades. Within the *M. curtus* clade, *M. ambohimitombi, M. bourgati* and *M. curtus* have larger body sizes, and *M. madecassus* and *M. pauliani* are high-elevation endemics with usually a shorter snout and absence of dorsolateral ridges (Table 4). For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. alutus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 5. See Fig. 11 for colouration in life and its variation. Some individuals have a light vertebral stripe. There is moderate sexual size dimorphism (confirmed male SVL 23.4–27.2 mm [n = 2] vs confirmed female SVL 31.0 mm [n = 2]). Males with large and distinct femoral glands (e.g. Fig. 11b); in MNHN 1894.1 and 1894.2, FGL and FGW are 2.4 mm x 1.4 mm and 1.7 mm x 1.4 mm, respectively. The glands can be of orange/yellow colour in some individuals in life (e.g. Fig. 11b), which may be related to the reproductive state.

Natural history.—Typically found in slow-flowing parts of streams or associated swamps in Madagascar's highlands. Often at the edge of forest or in streams devoid of forest, with some gallery vegetation only. Males call from the edge or very shallow parts of water, from concealed positions during the day or from more open positions at night. See Vences *et al.* (2002) for observations from Ankaratra. This species is also abundant in parks of Antananarivo, e.g. in the Tsimbazaza garden (Glaw & Vences 2007).

Calls.—The advertisement call of *M. alutus*, recorded on 21 January 2003, 17:30 h, near Antoetra, 20.5–21.0°C air temperature (Vences *et al.* 2006: CD 2, track 61, cut 1), consists of a short, regularly pulsed note, emitted in series at regular intervals (Fig. 12). Notes exhibit distinct amplitude modulation, with amplitude continuously increasing from the beginning, reaching maximum call energy at the middle of the note, before continuously decreasing towards the note's end. Numerical parameters of eight analysed calls are as follows: call duration (= note duration) 149–290 ms (234.3 ± 53.5 ms); 20–27 pulses per note (24.1 ± 2.7); pulse duration 5–8 ms (6.3 ± 1.0 ms); pulse repetition rate within notes 83.3–130.4 pulses/s (108.2 ± 17.3); dominant frequency 1040–1116 Hz (1081 ± 26 Hz); prevalent bandwidth 600–4800 Hz; call repetition rate (= note repetition rate) within regular series ca 110 calls/min.

Calls recorded on 1 January 1994, 18:20 h, at Manjakatompo, 18°C air temperature (Vences *et al.* 2006: CD 2, track 61, cut 2) generally agree in character with the calls described above. Calls of a series containing nine calls have the following parameters: call duration (= note duration) 254–310 ms (278.5 ± 16.8 ms); 21–27 pulses per note (23.7 ± 2.2); pulse duration 3–6 ms (4.9 ± 0.7 ms); pulse repetition rate within notes 66.7–120.0 pulses/s (83.2 ± 19.0); dominant frequency 1270–1378 Hz (1326 ± 45 Hz); prevalent bandwidth 800–5600 Hz; call repetition rate (= note repetition rate) within series ca 115 calls/min.

Tadpoles.—The tadpoles of *M. alutus* were described by Blommers-Schlösser (1979) and Schmidt *et al.* (2009).

Distribution.—Endemic to the central highlands of Madagascar (Fig. 7). This species is known from Antananarivo, Ankaratra, Ibity, Ambohitantely, Ranomafanakely, Antoetra, a swamp in the Alaotra region, Mantasoa, Forêt de Tampina, and Tsinjoarivo. Elevation range: 933–2090 m a.s.l.

Etymology.—Probably derived from the Greek adjective ἄλουτος, meaning 'unwashed' or 'speckled', presumably in reference to the dorsal colour pattern.

Mantidactylus ambohimitombi ambohimitombi Boulenger, 1919

Type material.—*Mantidactylus ambohimitombi* Boulenger, 1919 is based on a series of syntypes that include BMNH 1947.2.26.25–32 from 'Ambohimitombo Forest'. Blommers-Schlösser and Blanc (1991) noted that syntypes BMNH 1947.2.26.31–32 may be referable to *Mantidactylus curtus*, without justification. We here designate the DNA-barcoded specimen BMNH 1947.2.26.25, a large-sized individual of 65.0 mm SVL, as lectotype. Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

Identity.—*Mantidactylus ambohimitombi* Boulenger, 1919 is typically considered a valid species (Blommers-Schlösser & Blanc 1991; Frost 2021; Glaw & Vences 1992a, 1994), although it was considered of uncertain status by Glaw and Vences (2007). It is morphologically close to *M. curtus* but distinguished by its distinctly larger body size. It was not assigned to a genetic lineage by Vieites *et al.* (2009).

FIGURE 11. *Mantidactylus alutus* in life, in dorsolateral and ventral view. (a,b) Adult male from near Lake Mantasoa (ZSM 355/2000), photographed in 2000. (c,d) Adult male from near Antoetra (probably ZMA 19550 = FGMV 2002.50), photographed in 2003. (e) Adult male from Manjakatompo, photographed in 1991. (f) Specimen from Antakasina (this specimen has not been sequenced and its identification is therefore tentative; the locality is thus not included in the species account).

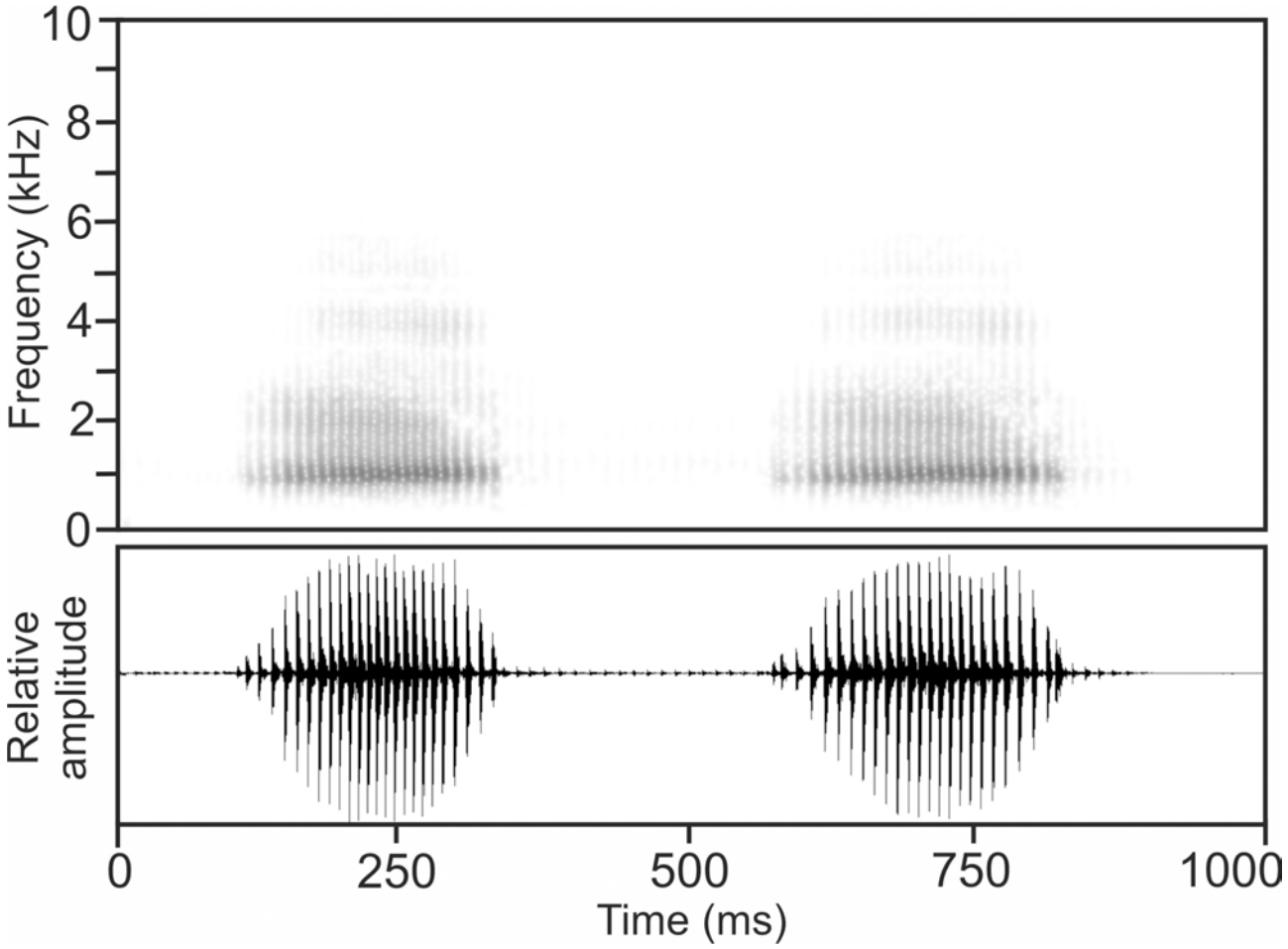

FIGURE 12. Audiospectrogram and corresponding oscillogram of two advertisement calls from a regular call series of *Mantidactylus alutus*, recorded on 21 January 2003 near Antoetra (20.5–21.0°C air temperature). Recording highpass-filtered at 375 Hz.

A 16S sequence of the lectotype surprisingly clusters with a lineage predominantly known from the Ankaratra Massif. We therefore redefine this lineage provisionally as corresponding to *M. ambohimitombi.* In previous studies the populations from the Ankaratra Massif have been considered as confirmed candidate species *M.* sp. 19 by Vieites *et al.* (2009), and *M.* sp. Ca19 by Perl *et al.* (2014). They were referred to as '*M.* sp. aff. *curtus* "Ankaratra"' by Schmidt *et al.* (2009). We emphasize that this attribution is preliminary; since only mtDNA data (no genomic information) are available from the lectotype, and no fresh samples are available from Ambohimitombo forest where the original syntype series was collected, we cannot exclude that mitochondrial introgression has taken place, potentially blurring a hypothetical differentiation between the Ankaratra and Ambohimitombo populations. Our Phylonetworks analysis provided evidence for gene flow of syntopic *M. curtus* into *M. ambohimitombi marefo* **ssp. nov.** from Itremo (Fig. 5), providing a first hint that reticulated evolution may have played a role in the origin of the various morphologically divergent frogs that we here subsume in the species *M. ambohimitombi.* A more in-depth analysis of ranges, and of gene flow among various lineages of the *M. curtus* clade (*M. curtus, M. bourgati, M. ambohimitombi*) is necessary to understand their evolutionary history and verify their taxonomy.

In our phylogenomic tree, two other lineages form a monophyletic group with specimens of *M. ambohimitombi* from Ankaratra, and these are in subsequent accounts described as subspecies of *M. ambohimitombi*; see the rationale in the respective accounts below.

Diagnosis.—Mantidactylus ambohimitombi is a member of the *M. curtus* clade; it is here defined as containing three deep genetic lineages considered as subspecies, and is sister to the morphologically very distinct *M. madecassus*. See Table 4 for a list of diagnostic morphological characters. The following account only diagnoses the nominal subspecies *M. a. ambohimitombi* from other species in *Brygoomantis*; see below for diagnoses and comparisons of the two other subspecies. The combination of relatively large body size of up to 51 mm at Ankaratra (up to 65 mm in the type series from Ambohimitombo forest), slightly granular skin without dorsolateral ridges in most specimens, strongly developed foot webbing with fully webbed fifth toe, small tympanum diameter with a maximum of 11% of SVL in males, distinguishes *M. a. ambohimitombi* from species

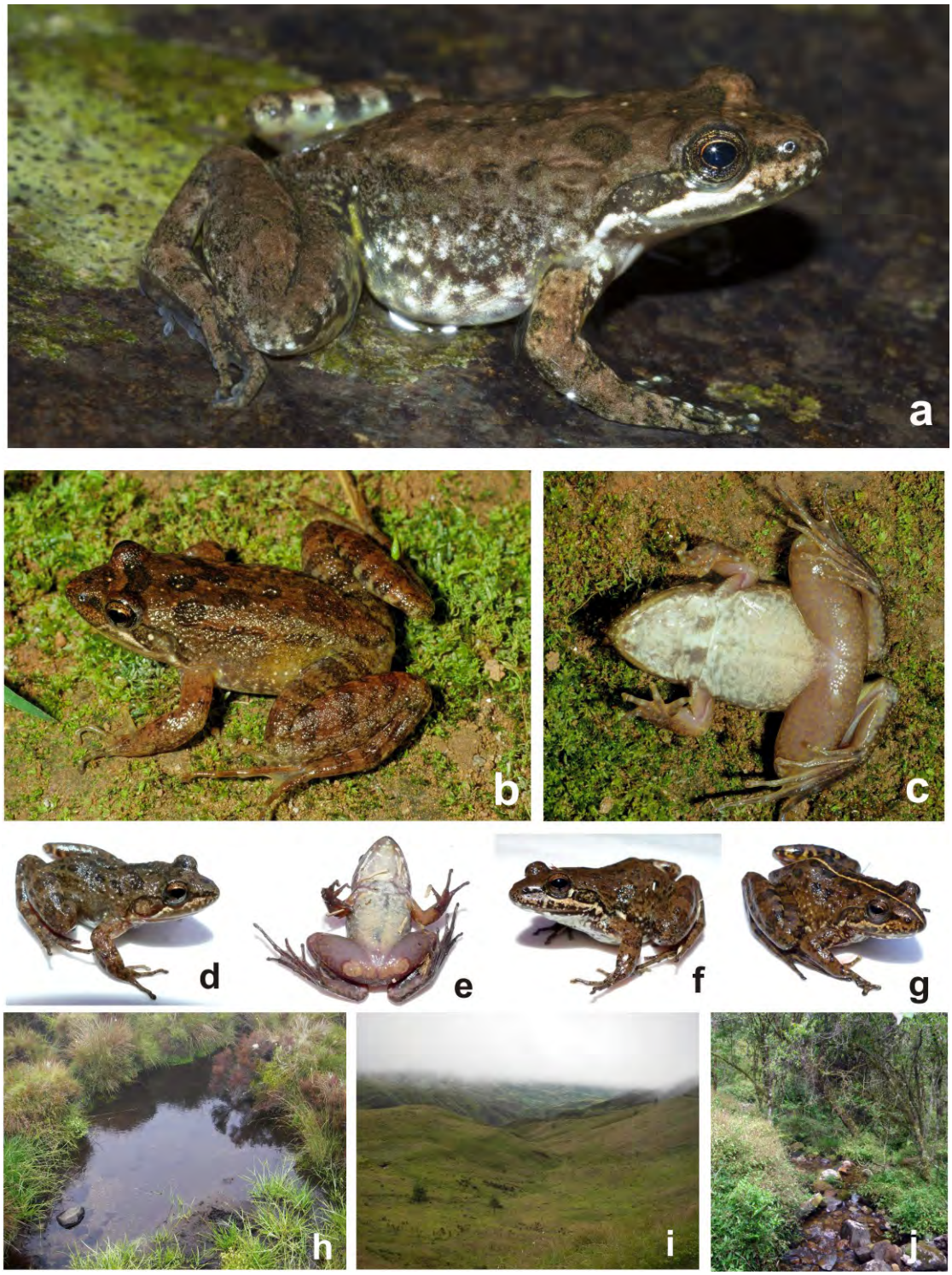

FIGURE 13. *Mantidactylus a. ambohimitombi* in life, in dorsolateral and ventral view, and their habitat. (a) Adult specimen (ACZC 6937; unsexed) from Ankaratra. (b,c) Adult specimen, possibly an adult male due to relatively distinct femoral glands, photographed in 1992. (d,e) Adult male (ACZC 8376; note the well-developed, prominent femoral glands and relatively large tympanum) from Ankaratra. (f) Adult specimen (ACZC 8377; unsexed) from Ankaratra. (g) Adult specimen (ACZC 8109; unsexed) with dorsal stripe from Ankaratra. (h) Pond at high-elevation on the Ankaratra Massif. (i) Landscape at high elevation in the Ankaratra Massif; streams in the valleys are habitat of *M. ambohimitombi,* and in area of rapids, of *M. pauliani*. (j) Stream in Manjakatompo forest, Ankaratra Massif, habitat of *M. ambohimitombi*.

of the other clades. Within the *M. curtus* clade, *M. alutus, M. madecassus* and *M. pauliani* have smaller body sizes and are distinguished by either a usually shorter snout (*M. madecassus, M. pauliani*), or advertisement calls emitted in regular series (in *M. alutus*, vs single notes) (Table 4); *M. curtus* usually has a smoother skin and a somewhat shorter snout; *M. bourgati* is morphologically very similar but appears to occur only on the Andringitra Massif. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. a. ambohimitombi* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 5. See Fig. 13 for colouration in life and its variation. A light vertebral stripe occurs in few individuals. There is pronounced sexual size dimorphism (at Ankaratra, largest confirmed male SVL 37.7 vs female SVL 50.6 mm). As discussed above, the type series is comprised of particularly large-sized animals reaching 65.0 mm in SVL. Femoral glands are only distinct in some male specimens, possibly due to seasonal effects; in two specimens, ZSM 190/2021 (ACZCV 334) and ZSM 195/2021 (ACZCV 342), FGL and FGW are 4.7 mm x 3.8 mm and 4.0 mm x 3.0 mm, respectively.

Natural history.—A common species on the Ankaratra Massif, especially above the tree line along streams and swamp in montane savanna and heatland, but also in rainforest (reported by Vences *et al.* 2002 under the name *M. curtus*). Males were found calling during the day underwater.

Calls.—The advertisement call of *M. a. ambohimitombi*, recorded on 16 February 2006, 14:50 h, at Ankaratra, consists of a short, pulsed note (Fig. 14), emitted in series at slow succession and somewhat irregular intervals. The calls were emitted from several shy animals at the border of a mountain stream, partly underwater, and identification of the calling specimen was therefore impossible. Notes exhibit slight amplitude modulation, with maximum call energy occurring either at first third of the note's length or at the centre of the note, and the terminal pulse of the note always being of lowest energy. The initial pulse is sometimes separated from the second pulse by a slightly longer inter-pulse interval. Numerical parameters of 20 analysed calls are as follows: call duration (= note duration) 136–218 ms (180.2 ± 18.7 ms); 9–14 pulses per note (10.9 ± 1.5); pulse duration 5–8 ms (6.3 ± 1.0 ms); pulse repetition rate within notes 56.1–69.3 pulses/s (62.3 ± 5.1); dominant frequency 925–1012 Hz (959 ± 30 Hz); prevalent bandwidth 500–3100 Hz; call repetition rate (= note repetition rate) in regular series ca 11–20 calls/min.

Tadpoles.—A tadpole of *M. a. ambohimitombi* was described under the name '*M.* sp. aff. *curtus* "Ankaratra"' by Schmidt *et al.* (2009).

Distribution.—Apparently endemic to a small area of the central highlands of Madagascar (Fig. 7). The nominal form is known from Ankaratra. Mitochondrial sequences assignable to this lineage have also been recorded from Analafohy and Antoetra; however, confirmation is needed, especially at Antoetra, as to whether this is evidence of true co-occurrence, or is a result of introgression with *M. curtus,* which is common in this locality. The type locality Ambohimitombo forest is close to Antoetra. Elevation range: 1150–2380 m a.s.l.

Etymology.—Formulated from the type locality, 'Ambohimitombo Forest'.

Mantidactylus ambohimitombi marefo **ssp. nov.**

Identity and justification.—This lineage has been considered as confirmed candidate species *M.* sp. 20 by Vieites *et al.* (2009) and *M.* sp. Ca20 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *pauliani* "Itremo"' by Glaw and Vences (2007). It has been collected only at its type locality, Itremo. It is characterized by rather aquatic habits and a morphology reminiscent of *M. pauliani*, with a short and rounded snout as in that species. Its mitochondrial DNA is near-identical to that of the nominal lineage, *M. a. ambohimitombi* (0.6–1.0 % p-distance) which, however, is morphologically distinct and also differs in Rag-1 haplotypes. Our phylogenomic tree confirms close relationships between this lineage and the one from Ankaratra, and for now we therefore consider a status of subspecies as adequate for the Itremo lineage, especially given that very little is known about its biology, since both its tadpoles and calls are unknown.

Diagnosis.—*Mantidactylus ambohimitombi marefo* is a member of the *M. curtus* clade, and direct sister group of *M. a. ambohimitombi.* See Table 4 for a list of diagnostic morphological characters. The combination of smooth skin, strongly expressed foot webbing with a fully webbed fifth toe, small tympanum diameter of a maximum of 8% of SVL in males, short snout, and body size of 31–36 mm distinguishes *M. a. marefo* from the species of the other clades in *Brygoomantis* (Table 4). Within the *M. curtus* clade, distinguished from *M. alutus* by absence of dorsolateral ridges, absence of frenal stripe, and a shorter snout; from *M. madecassus* by somewhat smaller body size, less contrasted dorsal pattern and single (vs bilobed) subarticular tubercles; from *M. pauliani* by somewhat larger body size of males; from *M. a. ambohimitombi* and *M. bourgati* by smoother skin. Morphological distinction is most difficult from the sympatric *M. curtus* which appears to have a slightly lighter dorsal colour, less aquatic habits, a more pointed snout and narrower head in most specimens; these differences are obvious when comparing several individuals in the field, but not immediately apparent from the measurements taken from preserved specimens. A further difference between *M. ambohimitombi marefo* and *M. curtus* and probably all other *Brygoomantis* is the presence, in many individuals of this subspecies, of a bluish ring along the eye, particularly distinct posteriorly; this unique colour pattern is recognisable in life, and is not on the iris itself but on the skin surrounding the eye (Fig. 15). For detailed distinction from other new species or subspecies described herein, see the respective accounts. A full list of molecular diagnostic sites in the 16S gene of *M. a. marefo* in pairwise comparisons to all

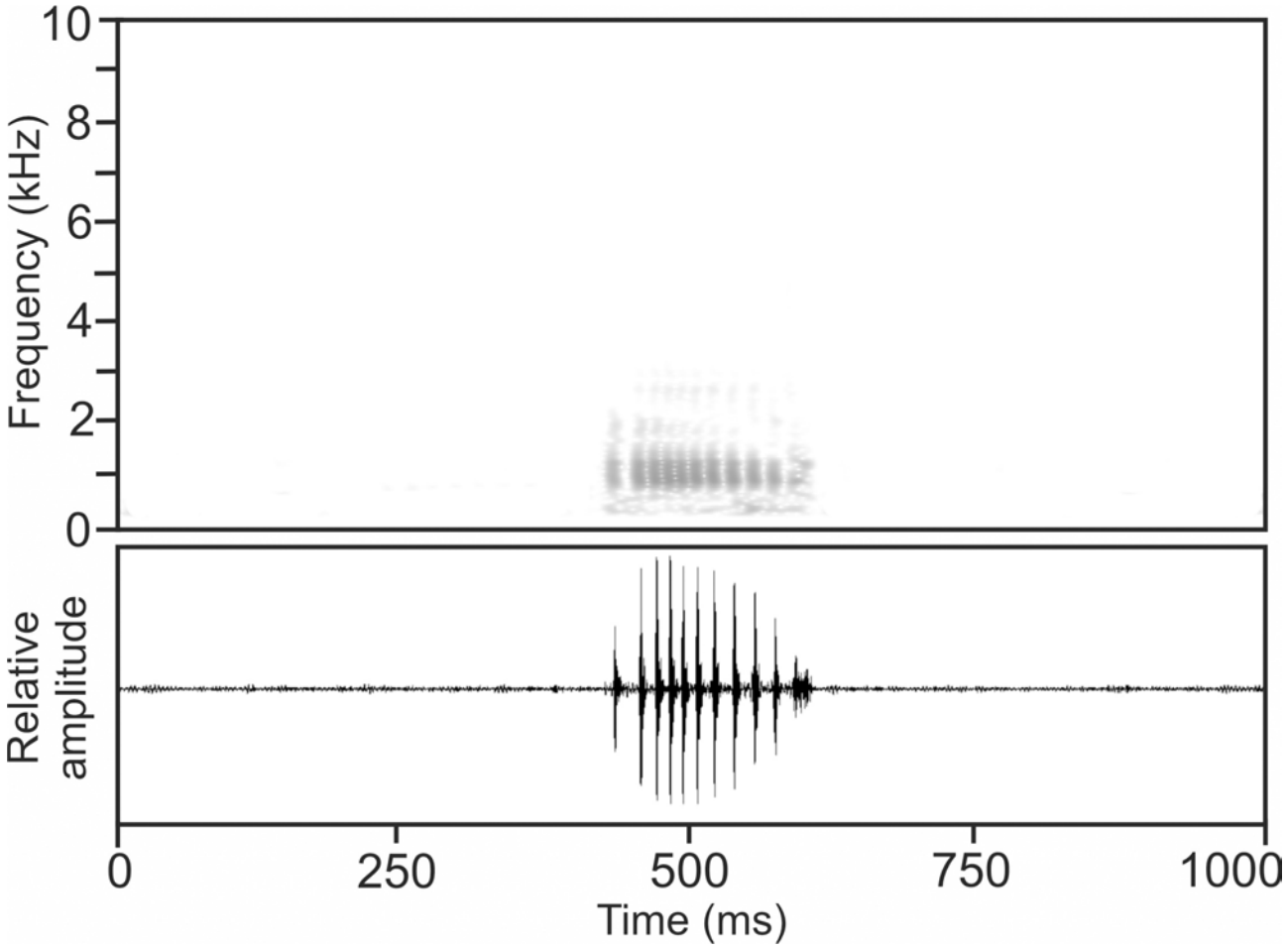

FIGURE 14. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus a. ambohimitombi*, recorded on 16 February 2006 at Ankaratra. Recording bandpass-filtered at 220–6000 Hz.

other *Brygoomantis* species (and subspecies) is provided as Supplementary appendix.

Holotype.—ZSM 762/2001 (FGMV 2001.493), adult male, collected by M. Vences, D.R. Vieites, L. Raharivololoniaina, and D. Rakotomalala on 10 March 2001 in a small stream outside a forest patch at Itremo (20.6022°S, 046.5711°E, 1648 m a.s.l.), Amoron'i Mania Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession AY848217).

Paratypes.—A total of five paratypes: ZSM 761/2001 (FGMV 2001.492), adult female, and ZSM 759/2001 (FGMV 2001.476), ZSM 760/2001 (FGMV 2001.478), ZSM 763/2001 (FGMV 2001.495), three specimens of unknown sex and maturity, with the same collection data as the holotype; MRSN A6747 (FAZC 14047), putative female, collectd by F. Andreone and J.E. Randrianirina on 29 November 2008 in Antsirakambiaty forest, Itremo.

Description of the holotype.—Adult specimen, probably a male, in mediocre state of preservation (Fig. 9). Part of right thigh muscle removed as tissue sample, and a longitudinal cut made on venter for gonad examination. Body rather slender. Head as wide as body. Snout rounded in dorsal view; snout and head overall very short. Nostrils directed laterally, not protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis not clearly recognisable. Loreal region weakly concave. Tympanum recognisable, rounded, its horizontal diameter about 71% of eye diameter. Supratympanic fold present, beginning straight, and gently bending midway towards forelimb insertion. Tongue ovoid and bifid. Maxillary teeth present. Vomerine teeth not recognisable; maybe traces of vomerine teeth partly covered by tissue lateral to choanae. Choanae rounded. Subarticular tubercles single.

Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II=IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot distinctly longer than tibia (114%). Lateral metatarsalia separated. Inner metatarsal tubercle present, outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(0.25), 2i(1), 2e(0.25), 3i(1), 3e(0.5), 4i(1.5), 4e(1.5), 5(0.5). Relative length of toes: I<II<V=III<IV. Skin on the upper surface smooth in preservative with some scattered larger granules; in life similar. No dorsolateral folds. Ventral side smooth. Femoral glands present only as rather distinct proximal granular gland field whereas an obvious distal ulcerous macrogland appears to be missing.

Colour in preservative: dorsally uniformly brown with a light vertebral line. Weakly recognisable slightly darker crossbands on limbs. Ventrally dirty beige-brownish without clear pattern. Himdlimbs dorsally

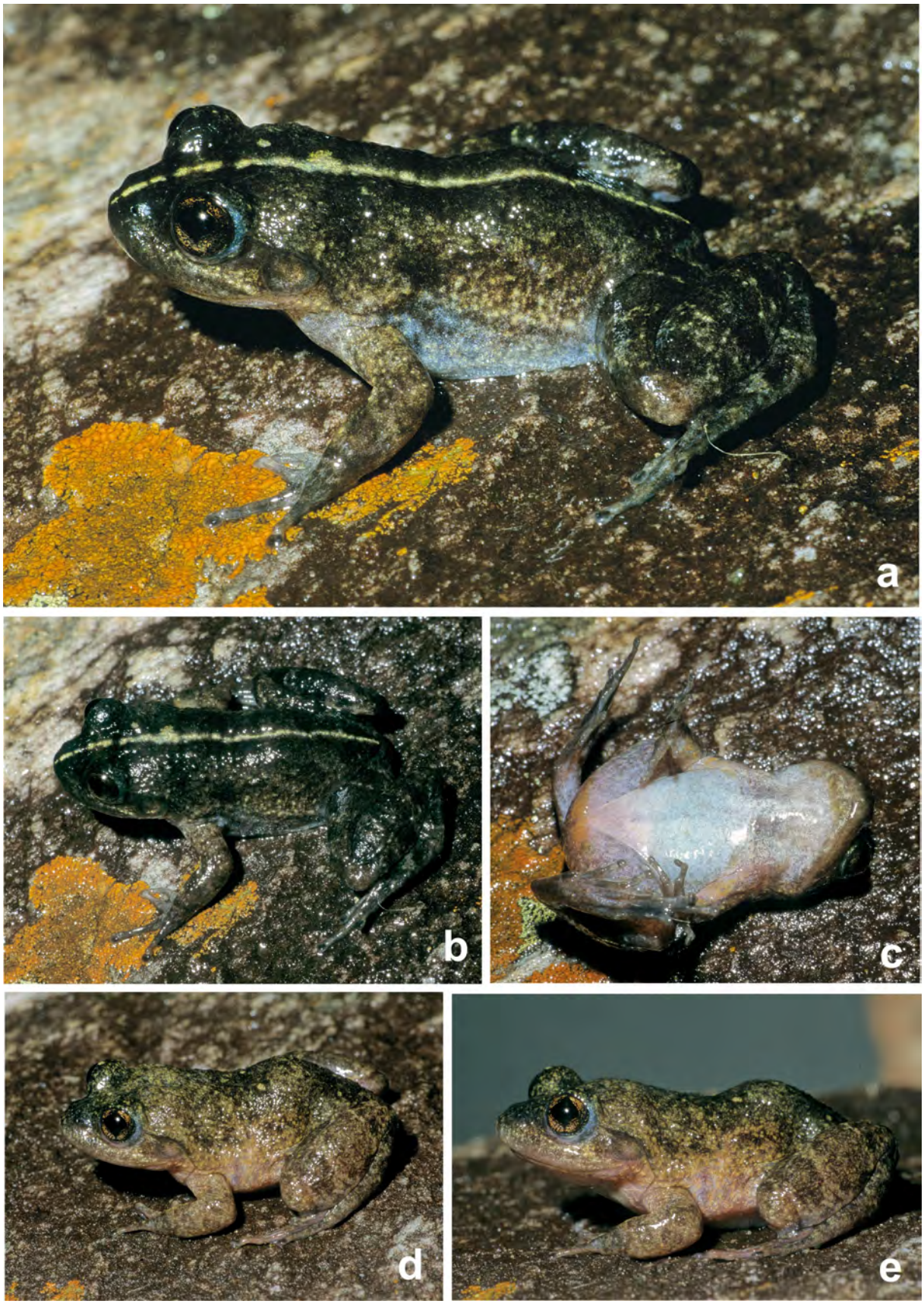

FIGURE 15. *Mantidactylus ambohimitombi marefo* **ssp. nov.** from Itremo in life, in dorsolateral, ventral, and/or lateral view. (a,b,c) Probably adult male (holotype ZSM 762/2001 = FGMV 2001.493; note rather distinct, orange-coloured femoral glands), photographed in 2001. (d,e) Second specimen (probably corresponding to a voucher specimen preserved in UADBA), photographed in 2001. Note bluish partial ring around the eye in both individuals.

brown with light mottling. Colour in life similar to that in preservative. Dorsal side dark greyish-brown. Femoral glands light orange.

Variation.—Variation in measurements is given in Table 5. See Fig. 15 for colouration in life and its variation. The apparent absence of vomerine teeth in this subspecies could be of taxonomic value but is here (Table 4) not included in the table of diagnostic characters as it may be variable; small aggregations of vomerine teeth recognisable in ZSM 759/2001 (in general, vomerine teeth in the *M. curtus* clade are present in all species except *M. madecassus* and *M. pauliani*, which *Mantidactylus ambohimitombi marefo* most closely resembles). In general, specimens have a characteristic appearance with a rounded and short snout, differing from most individuals of the nominal subspecies *M. a. ambohimitombi*, but this character is poorly reflected in the available measurements (e.g. Table 4), probably due to an idiosyncratic variation of various landmarks and proportions in each individual. Possibly a slight size dimorphism, with males (30.9–34.6 mm SVL, n=4) slightly smaller than the single available female (35.9 mm SVL, n=1). Femoral glands in probable male specimens (e.g. the holotype) were rather distinctly recognisable by their light orange colour in life (Fig. 15) but not very prominent or distinct, and preserved specimens are therefore difficult to sex as seems to be typical in several taxa of the *M. curtus* clade.

Natural history.—Specimens were collected at Itremo in syntopy with *M. curtus*, a species that is morphologically similar based on standard morphometric measurements taken herein (Table 5), but were immediately recognised in the field due to their distinctive habitus and aquatic habits. While *M. curtus* were typically found at the edge of small streams in an area of low-canopy gallery forest, and also in streams within fragments of closed forest, *M. a. marefo* was always found fully submerged in relatively deep pools of the stream (approximately 30–50 cm of depth), outside of dense forest.

Calls.—The call of this subspecies has not been recorded.

Tadpoles.—The tadpole of this subspecies has not been described.

Distribution.—Apparently microendemic to the Itremo massif (Fig. 7). Elevation range: ~1648 m a.s.l.

Etymology.—The subspecies name is derived from the Malagasy adjective marefo, meaning 'weak', and refers to the surprisingly weak mitochondrial genetic divergence from its sister lineage *M. a. ambohimitombi* despite substantial morphological and ecological differences. The subspecies name is used as a noun in apposition.

Mantidactylus ambohimitombi miloko **ssp. nov.**

Identity and justification.—This lineage of the *M. curtus* clade was considered as confirmed candidate species *M.* sp. 18 by Vieites *et al.* (2009) due to its mitochondrial divergence in concert with slight but distinct differences in colour pattern, and as *M.* sp. Ca18 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *curtus* "Ambohitantely"' by Glaw and Vences (2007). We here consider this lineage provisionally as a subspecies of *M. ambohimitombi* based on the following rationale: (i) it belongs to the same general mitochondrial lineage as the nominal subspecies in the 16S tree, and the two are also closely related in the phylogenomic tree; (ii) morphologically, the two lineages are similar to each other, except for a somewhat more distinct dorsal pattern in *M. a. miloko* **ssp. nov.**; (iii) based on two samples in our mitochondrial tree, RJS 1877 and ACZC 4254, a very similar mitochondrial haplotype to the one from Ambohitantely also occurs at Ankaratra, suggesting the possibility of past or ongoing gene flow between localities or mitochondrial introgression; and (iv) based on sequences of specimens APR 10803, APR 10638, and APR 10663, the lineage also occurs in Angavokely and Ankazomivady, thus rather close to Ankaratra, suggesting the two lineages may be parapatric and could hypothetically have a hybrid zone. Since the status of the Ambohitantely population as a fully isolated evolutionary lineage is thus not fully verifiable with the data at hand, we consider the status as a subspecies of *M. ambohimitombi* to be adequate.

Holotype.—ZSM 219/2005 (FGZC 2143), adult male, collected by M. Vences, L. du Preez, P. Bora, L. Raharivololoniaina, R.D. Randrianiaina, T. Razafindraibe, E. Randriamitso on 18 January 2005 at Ambohitantely Special Reserve, 'Jardin Botanique', at a site about 500 m from the geographical coordinates 18.1725°S, 047.2768°E, 1580 m a.s.l., Analamanga Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratype.—A single paratype: ZSM 237/2005 (FGZC 2172), adult female, with the same collection data as holotype.

Additional material.—The following specimens probably belong to this taxon but are only assigned tentatively and not designated as paratypes because no molecular data is available: ZMA 6859 (two specimens with field numbers 675 and 676) and ZMA 6860 (six specimens with field numbers 910–914, 917), collected by R.M.A. Blommers-Schlösser in 1972 at 1500 m (ZMA 6859) and 2200 m a.s.l. (ZMA 6860) at Tampoketsa d'Ankazobe.

Diagnosis.—Mantidactylus ambohimitombi miloko is a member of the *M. curtus* clade, and the sister group of *M. a. ambohimitombi* + *M. a. marefo.* Morphologically, it is very similar to *M. a. ambohimitombi*. See Table 4 for a list of diagnostic morphological characters. The combination of relatively large body size of up to 49 mm, slightly granular skin without clearly defined dorsolateral ridges, and small tympanum diameter of a maximum of 10% of SVL in males, distinguishes *M. a. miloko* **ssp. nov.** from species of the other clades. Within the *M. curtus* clade, *M. alutus, M. madecassus* and *M. pauliani* have smaller body sizes and are distinguished by either a usually shorter snout (*M. madecassus, M. pauliani, M. a. marefo*), or presence of rather distinct dorsolateral ridges (*M. alutus*) (Table 4); *M. curtus* usually has a smoother skin and a somewhat shorter snout; *M. bourgati* is morphologically very similar but appears to occur only on the Andringitra Massif. Compared to other subspecies

of *M. ambohimitombi*, the new subspecies differs from *M. a. marefo* by its distinct dorsal pattern, lack of bluish colour around the eye, and more pointed snout; and from *M. a. ambohimitombi* by the usually more distinct dorsal pattern. For detailed distinction from other new species and subspecies described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. a. miloko* in pairwise comparisons to all other *Brygoomantis* species and subspecies is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 9). Tissue sample taken ventrally from right thigh. Femoral gland partly detached to examine their structure internally. Body rather slender. Head slightly wider than body. Snout rounded in dorsal and lateral view. Nostrils directed dorsolaterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis almost not recognisable, slightly concave. Loreal region slightly concave. Tympanum distinct, elliptical, wider than high, its diameter 78% of eye diameter. Supratympanic fold distinct, beginning straight, with a distinct, angular 90° bend at the posterior edge of tympanum towards insertion of forelimb. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth distinct in rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle present, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I=II<IV<III. Finger discs minimally enlarged. Nuptial pads absent. Foot longer than tibia (113%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but recognisable. Webbing formula: 1(0.25), 2i(1), 2e(0.5), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(0.75). Relative length of toes: I<II<V=III<IV. Skin on the upper surface smooth, with some granules on flanks, and some longitudinal tubercles forming interrupted and weakly expressed dorsolateral folds. Ventral side smooth. Femoral glands distinct but relatively small, with a distal ulcerous macrogland consisting of at least eight large granules and an external central depression, and a weakly expressed proximal granular gland field visible in internal view.

Colour in preservative: light brown dorsally with large and contrasted dark brown patches all over the dorsal surface, distinct dark crossbands on limbs, and a light frenal stripe with some dark markings on the upper lip. Ventrally uniformly light grey with alternating dark-light pattern ventrally on the lower lip. Colour in life similar to that in preservative, but more contrasted (Fig. 16).

Variation.—Variation in measurements is given in Table 5. Too few specimens have been sexed to assess the degree of sexual size dimorphism. Femoral glands distinct and large (but not differing in colour from surrounding ventral skin of thigh) in the male holotype (Fig. 16). In contrast, specimens from the ZMA collection are difficult to sex externally as femoral glands are often indistinct, as seems to be typical for several taxa in the *M. curtus* clade, possibly due to seasonal effects.

Natural history.—Specimens were collected around clean highland streams running in open areas between forest fragments. Specimens at Angavokely and Ankazomivady that appear to belong to this taxon based on mitochondrial DNA were found on wet rocks along slow-moving parts of streams.

Calls.—The call of this subspecies has not been recorded.

Tadpoles.—Probably reported from Angavokely by Blommers-Schlösser (1979)..

Distribution.—Endemic to the central highlands of Madagascar, north of the distribution of the nominal subspecies (Fig. 7). This subspecies is currently known from Ambohitantely, and probably also from Angavokely, and Ankazomivady. A mitochondrial haplotype corresponding to this subspecies has also been detected at Ankaratra, but due to the limited information on the sampling event and the absence of specimens (only tissue sampels were collected) this record (which might also represent mitochondrial introgression) requires confirmation. Elevation range: 1520–1735 m a.s.l.

Etymology.—The subspecies name is derived from Malagasy word miloko, meaning ‘painted’, referring to the rather distinct dorsal pattern of well-delimited dark blotches characterizing this subspecies. The subspecies name is used as a noun in apposition.

Mantidactylus bourgati Guibé, 1974

Type material.—*Mantidactylus bourgati* Guibé, 1974 is based on the holotype MNHN 1972.437 (given in error as 1972.427 in the original publication but correct in the handwritten catalogue) by original designation from ‘Ambalamarovandana’, a site in the Andringitra Mountains, and seven paratypes (MNHN 1972.440, 1972.449, 1972.464, 1972.472, 1972.476, 1972.479, and 1972.491)

Identity.—*Mantidactylus bourgati* has long been considered a synonym of *M. curtus* but was resurrected as a separate species by Glaw and Vences (2006) based primarily on strong genetic divergences. We here provide a 16S sequence obtained by barcode fishing from the holotype MNHN 1972.437 confirming the attribution of the lineage containing all samples of *curtus*-like stream frogs from the Andringitra Massif to this nomen.

Diagnosis.—A member of the *M. curtus* clade and sister to *M. curtus*. See Table 4 for a list of diagnostic morphological characters. The combination of relatively large body size of at least up to 41 mm (Table 5; larger specimens observed in the field), slightly granular skin, strongly expressed foot webbing with almost fully webbed fifth toe distinguishes this species from species of the other clades. Within the *M. curtus* clade, *M. alutus, M. madecassus* and *M. pauliani* have smaller body sizes (Table 4). *M. curtus* has a very smooth dorsal skin while in *M. bourgati* the skin is usually somewhat granular. Morphological distinction from *M. a. ambohimitombi* and *M. a. miloko* is most difficult, but as far as known, the distributions of these taxa do not overlap with that of *M. bourgati. M. bourgati* differs further from *M. alutus* by longer advertisement calls emitted at irregular intervals (vs regular series in *M. alutus*). For detailed distinction from

FIGURE 16. *Mantidactylus ambohimitombi miloko* **ssp. nov.** in life, in dorsolateral and ventral view. (a,b,c) Adult male (holotype ZSM 219/2005 = FGZC 2143; note distinct and large femoral glands), from Ambohitantely Special Reserve.

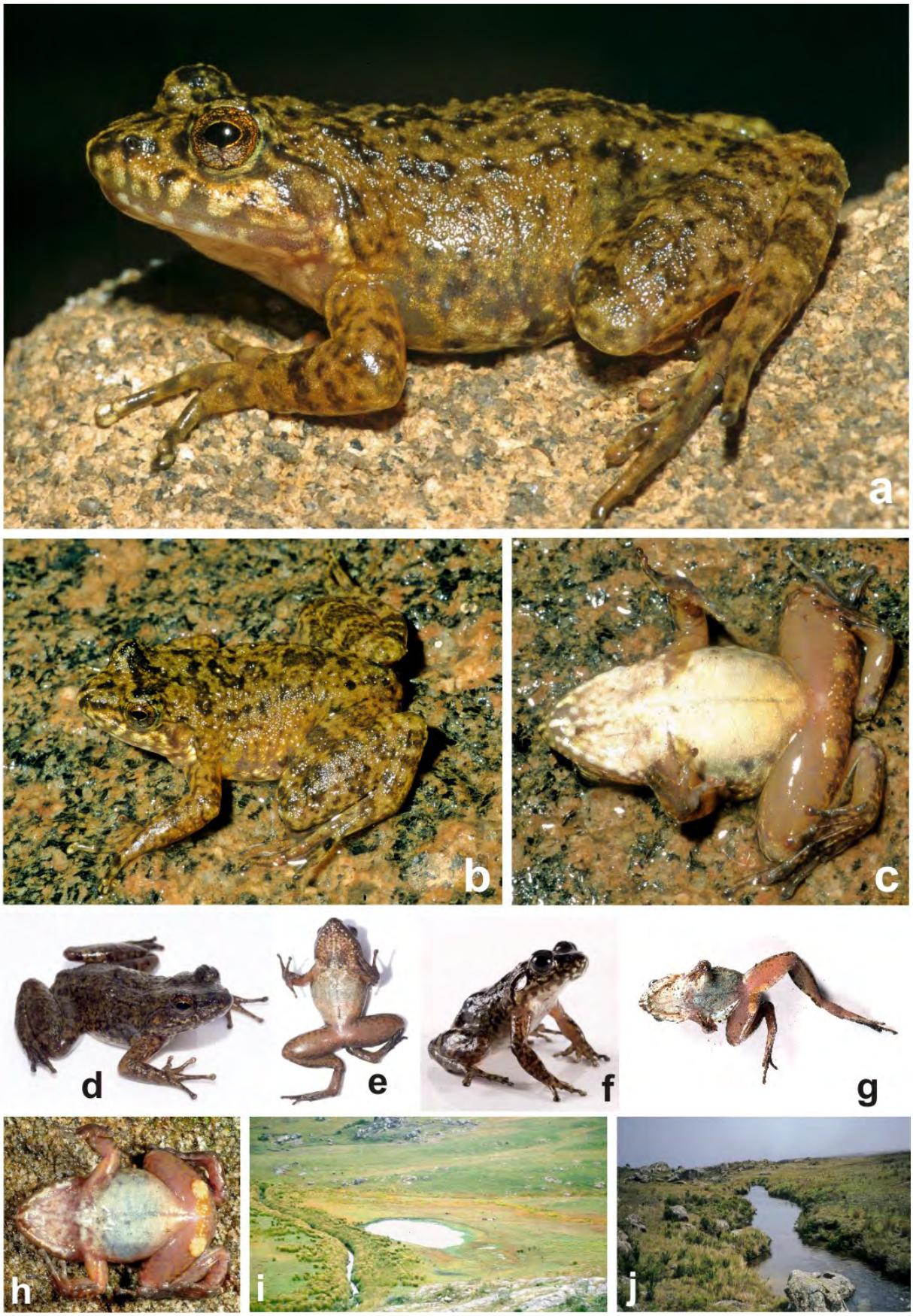

FIGURE 17. *Mantidactylus bourgati* in life, in lateral, dorsolateral, and/or ventral view, and their habitat. (a,b,c) Adult specimen (ZSM 770/2001 = FGMV 2001.520; possibly an adult male due to relatively distinct femoral glands) from Andringitra, photographed in 2001. (d,e) Adult female (ACZC 10819) from Riandahy, Andringitra. (f,g) Adult male (ACZC 10698) from Imaitso, Andringitra. (h) Adult male from Andringitra, photographed in 1994. (i) View of the Andohariana Plateau (Andringitra Massif) with stream inhabited by *M. bourgati.* (j) Stream at the Andohariana Plateau (Andringitra), habitat of *M. bourgati.*

new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. bourgati* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 5. See Fig. 17 for colouration in life and its variation. From our sample, it is unclear whether sexual size dimorphism exists in this species; in the specimens measured, male SVl is 33.0–38.9 mm (n=2) and female SVL is 32.3–40.0 mm (n=13). Femoral glands in adult males in life are often clearly visible and prominent (Fig. 17) but in preserved specimens, a clear distinction between males and females (which probably also have visible gland rudiments) is often not possible without examination of gonads.

Natural history.—Specimens of *M. bourgati* are common in and around small slow-flowing montane streams at high elevations in the Andringitra Massif, e.g. on the Andohariana Plateau at 2000 m a.s.l. where they can be found at the edge of the water. They do not seem to occur higher up the massif, e.g. at Cuvette Boby we found only *M. madecassus*. However, at somewhat lower elevations (e.g. Imaitso forest at ca 1500 m a.s.l.), *M. bourgati* is also common along large streams running through rainforest. Our call recordings were made from a swamp area next to such a stream where specimens were observed during the day in the shallow water.

Calls.—The advertisement call of *M. bourgati*, has been recorded on 16 January 1994, 10:00 h, at Andringitra National Park, in a forest swamp area close to Ambalamarina, 19°C air temperature, but the calling specimens could not be seen, and the attribution to *M. bourgati* is tentative (Vences *et al.* 2006: CD 2, track 77). The call consists of a regularly pulsed note (Fig. 18), emitted in series at somewhat irregular intervals. Notes exhibit some amplitude modulation, with amplitude continuously increasing from the beginning, reaching maximum call energy at the middle of the note, before continuously decreasing towards the note's end. Numerical parameters of four analysed calls are as follows: call duration (= note duration) 756–1020 ms (872.8 ± 112.6 ms); 36–50 pulses per note (43.8 ± 5.9); pulse duration 8–10 ms (8.7 ± 0.8 ms); pulse repetition rate within notes 45.8–54.1 pulses/s (50.8 ± 4.1); dominant frequency 1063–1106 Hz (1087 ± 18 Hz); prevalent bandwidth 880–1740 Hz; call repetition rate (= note repetition rate) within series ca 19–29 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently microendemic to Andringitra and nearby areas (Fig. 7). This species is known from Andringitra (various sites, type locality), Belambo, Fivahona, and Tsaranoro. Elevation range: 940–2488 m a.s.l.

Etymology.—Eponym for 'Professor [Robert M.] Bourgat of the University of Lomé (Togo), who collected several frogs during his voyages in Madagascar' (translated from Guibé 1973a).

Mantidactylus madecassus (Millot & Guibé, 1950)

Type material.—The taxon *Racophorus* [misspelling of *Rhacophorus* in the original description] (*Philautus*) *madecassus* Millot and Guibé, 1950 is based on the lectotype MNHN 1953.246 from 'Andringitra: Cirque Boby (altitude: 2.520 métres)', designated by Vences and Glaw (1999). The eight paralectotypes, all from the same locality, are numbered MNHN 1989.3590–3597.

Identity.—*Mantidactylus madecassus* is a morphologically distinct and apparently microendemic species restricted to high elevations on the Andringitra Massif. Its identity has been unambiguously assessed by Vences and Glaw (1999) based on morphology, and is here confirmed by a 16S sequence obtained from the lectotype, MNHN 1953.246.

Diagnosis.—A member of the *M. curtus* clade and sister to *M. ambohimitombi* from which it strongly differs morphologically. See Table 4 for a list of diagnostic morphological characters. The combination of a body size of 27–34 mm (Table 5), smooth dorsal skin without dorsolateral ridges, strongly expressed foot webbing with almost fully webbed fifth toe, small tympanum size in males (7–10% of SVL), vomerine teeth absent, and especially, the bilobed subarticular tubercles (unique in *Mantidactylus madecassus* and illustrated by Vences & Glaw 1999) distinguishes this species from species of the other clades in *Brygoomantis*. Within the *M. curtus* clade, this high-elevation endemic differs from all species by its double or rather bilobed subarticular tubercles, and from all species exept *M. curtus, M. pauliani,* and *M. ambohimitombi marefo*, by a conspicuously short snout in many specimens. The species is an endemic to high elevations on the Andringitra Massif, where at slightly lower elevations, also *M. bourgati* occurs; a distinction from that species can readily be achieved by the combination of bilobed subarticular tubercles, shorter snout, usually smaller size and smoother skin, as well as more uniform silvery-whitish ventral colour in *M. madecassus*. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. madecassus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 5. See Fig. 19 for colouration in life and its variation. There is weak sexual size dimorphism (confirmed male SVL 27.0–29.8 mm [n = 2] vs confirmed female SVL 29.3–33.7 mm [n = 5]). For a more detailed discussion of this species' morphology and a morphometric comparison to *M. pauliani*, see Vences and Glaw (1999). Relative tympanum size is larger in males than in females (Vences & Glaw 1999). Femoral glands in males include a distal ulcerous macrogland only, and rudimentary glands are also present in females.

Natural history.—Specimens were found in small, cold, clear mountain streams at high elevations of the Andringitra Massif. They were sitting in the water, especially in shallow side puddles next to the canal-like streams, at night.

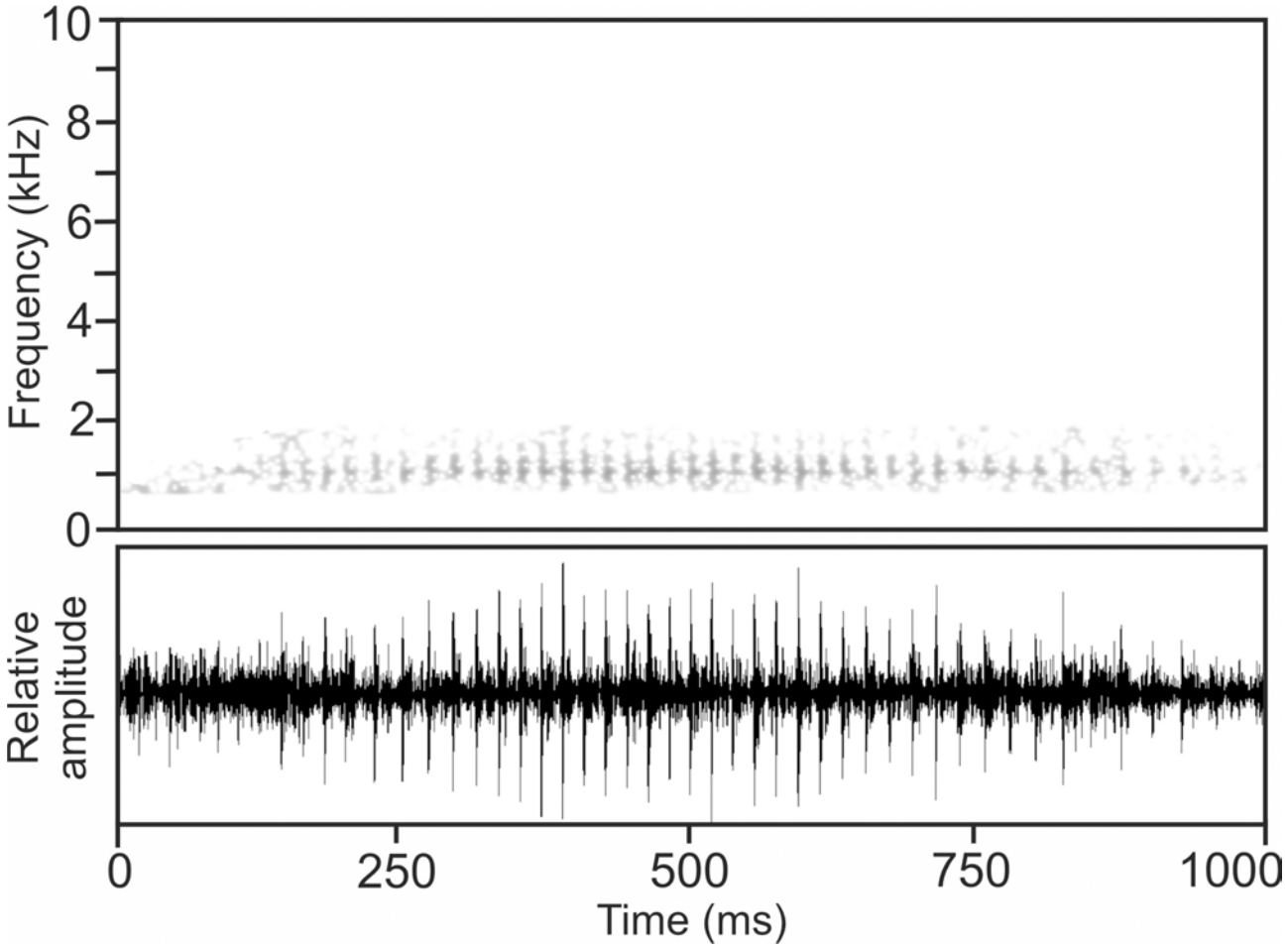

FIGURE 18. Audiospectrogram and corresponding oscillogram of one advertisement call tentatively assigned to *Mantidactylus bourgati*, recorded on 16 January 1994 at Andringitra National Park, close to Ambalamarina (19°C air temperature). Recording bandpass-filtered at 700–2000 Hz.

Calls.—The call of this species has not been recorded.

Tadpoles.—The tadpole of *M. madecassus* was described by Thomas *et al.* (2005).

Distribution.—Apparently microendemic to high elevations on the Andringitra Massif (Fig. 7). Elevation range: ~2488 m a.s.l.

Etymology.—Latin adjective referring to the occurrence of the species in Madagascar.

Mantidactylus pauliani Guibé, 1974

Type material.—*Mantidactylus pauliani* Guibé, 1974 is based on the holotype (by original designation) MNHN 1972.1508 from 'Nosiarivo (massif d' l'Ankaratra)'. There are eight paratypes (Vences & Glaw 1999): MNHN 1972.1509–1516.

Identity.—*Mantidactylus pauliani* is a morphologically distinct and apparently microendemic species restricted to high elevations on the Ankaratra Massif. Its identity has been assessed by Vences and Glaw (1999) and is unambiguous due to its microendemic distribution and typical short-snouted appearance. Therefore, no genetic data from the name-bearing type were collected.

Diagnosis.—A member of the *M. curtus* clade and sister to *M. mahery* **sp. nov.** (described below), from which it strongly differs morphologically. See Table 4 for a list of diagnostic morphological characters. The combination of a body size of 25–34 mm (Table 5), small tympanum size in males (8–9% of SVL), smooth dorsal skin without dorsolateral ridges, absence of vomerine teeth, and strongly expressed foot webbing with fully webbed fifth toe distinguishes *M. pauliani* from species of the other clades in *Brygoomantis*. Within the *M. curtus* clade, this high-elevation endemic differs from all species exept *M. curtus, M. madecassus,* and *M. ambohimitombi marefo*, by a conspicuously short snout in most specimens, from *M. madecassus* by the single (vs bilobed) subarticular tubercles, and from *M. a. marefo* by absence of a bluish ring around the eye. *Mantidactylus pauliani* is endemic to high elevations at the Ankaratra Massif, where it is sympatric with *M. a. ambohimitombi*, which differs by larger body size, more pointed snout, and more contrasted dorsal pattern. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. madecassus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

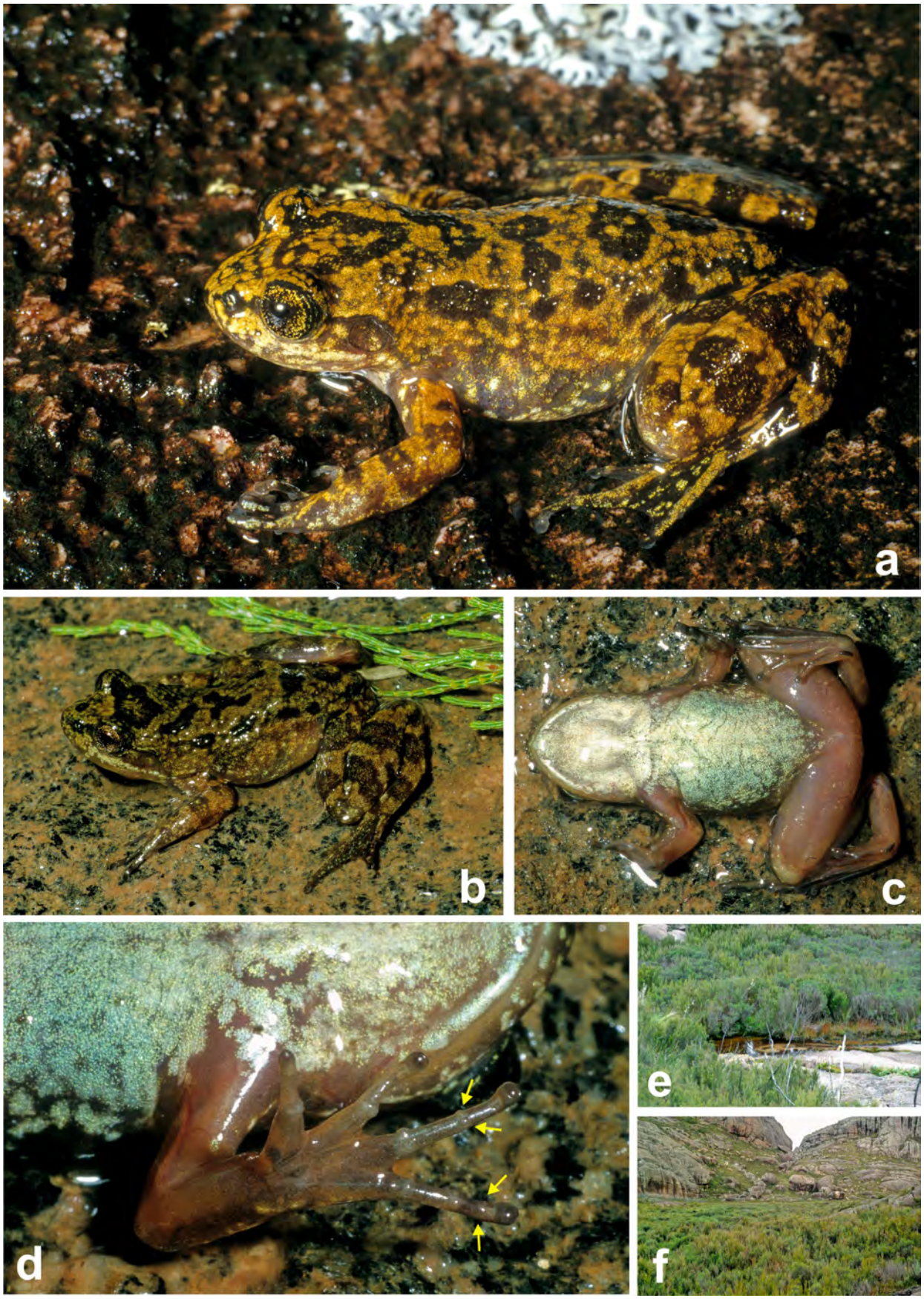

FIGURE 19. *Mantidactylus madecassus* in life, in dorsolateral and ventral view, and their habitat. (a) Adult specimen (unsexed) from Cuvette Boby, Andringitra Massif, photographed in 1994. (b,c) Adult specimen (ZSM 755/2001 = FGMV 2001.538; unsexed) from Cuvette Boby, Andringitra Massif, photographed in 2001, and (d) closeup of ventral surface of its hand showing the bilobed subarticular tubercles (yellow arrows). (e) Pond at Cuvette Boby, habitat of *M. madecassus*. (f) Landscape at Cuvette Boby.

Variation.—Variation in measurements is given in Table 5. See Fig. 20 for colouration in life and its variation. There is weak sexual size dimorphism (confirmed male SVL 29.5–31.0 mm [n = 2] vs confirmed female SVL 31.1–33.7 mm [n = 4]), and males have a slightly larger tympanum diameter than females (Vences & Glaw 1999). This is consistent with weak sexual size dimorphism reported by Andreone *et al.* (2014). Based on formalin-fixed and well-preserved voucher specimens of the MNHN collection, Vences and Glaw (1999) illustrate femoral glands in internal view, and document that females have weakly developed glands that are reminiscent in structure of those of males but with overall smaller gland granules. This same phenomenon of relatively well-developed gland rudiments in females, may also apply to several other species in the *M. curtus* clade and could make it difficult to sex preserved individuals. Future studies should assess whether femoral gland prominence in these frogs might also be influenced by seasonal effects.

Natural history.—Specimens were found sitting in the water or on exposed rocks in montane streams both inside and outside of forest (see Vences *et al.* 2002 for more information). *Mantidactylus pauliani* is rarely encountered and considered highly threatened (Andreone *et al.* 2005). Age structure, population estimate, and status of infection with *Batrachochytrium dendrobatidis* were studied by Andreone *et al.* (2014). They found adult specimens ranging 3–8 years old, with no significant difference in age between males and females. Specimens reach sexual maturity in the second year in males and third year in females. Chytrid was not identified in these frogs.

Calls.—The call of this species has not been recorded.

Tadpoles.—The tadpole of this species has not yet been described in detail.

Distribution.—Apparently microendemic to high elevations on the Ankaratra massif (Fig. 7). Elevation range: all verified sites are from >2000 m a.s.l. (up to

FIGURE 20. *Mantidactylus pauliani* from Ankaratra in life, in various views. (a) Unsexed adult specimen (not collected). (b,c) Adult specimen (ZSM 756/2001; unsexed), photographed in 2001. (d,e) Adult female (not collected; yellowish oocytes visible through the abdominal skin). (f) Unsexed adult specimen (not collected).

at least 2200 m a.s.l.) (see Vences *et al.* 2002 for more information).

Etymology.—Eponym for R. Paulian, who initiated and directed the CNRS programme 'Study of montane ecosystems in the Malagasy region' (RCP 225) (loosely translated from Guibé 1973b).

Mantidactylus mahery **sp. nov.**

Identity and justification.—This lineage has been considered as confirmed candidate species *M.* sp. 14 by Vieites *et al.* (2009) and *M.* sp. Ca14 by Perl *et al.* (2014). This is a relatively large-sized species of *Brygoomantis* from western Madagascar with a morphology superficially similar to *M. ulcerosus* which, however, is not its closest relative and concordantly differs in mitochondrial and nuclear genes and in advertisement call structure. Both species occur syntopically at least at one site (Makira). Although *M. mahery* **sp. nov.** mainly occurs in western Madagascar unlike the other species of the *M. curtus* clade which live in the central highlands, the phylogenomic data unambiguously support its inclusion in the group. Even more surprising, the phylogenomic tree places the species sister to *M. pauliani*, which is a montane endemic from the Ankaratra Massif that differs in numerous morphological characters. The status of *M. mahery* **sp. nov.** as a separate species is well supported by multiple lines of evidence.

Holotype.—ZSM 23/2004 (field number FGZC 37), adult male collected by F. Glaw, M. Puente, R. Randrianiaina, and M. Teschke (née Thomas) on 21 January 2004 in Isalo at a creek near Ranohira (22.5856°S, 045.3997°E, 813 m a.s.l.), Ihorombe Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession AY848286).

Paratypes.—A total of 12 paratypes: ZSM 25/2004 (FGZC 39), adult male, and ZSM 26/2004 (FGZC 42), adult female, with the same collection data as the holotype; ZSM 567/2009 (ZCMV 11457) and ZSM 569/2009 (ZCMV 11484), two adult females, collected by M. Vences, D.R. Vieites, F.M. Ratsoavina, R.D. Randrianiaina, E. Rajeriarison, T. Rajofiarison, and J. Patton on 20 June 2009 in Sahaovy ('Camp 0'), Makira (15.4889°S, 049.0785°E, 607 m a.s.l.); ZSM 9/2006 (FGZC 682), adult male, and ZSM 61/2006 (FGZC 793), adult female, collected by F. Glaw, J. Köhler, P. Bora, and H. Enting on 18 and 23 March 2006, respectively, at Antranopasazy ('Camp 1'), Tsingy de Bemaraha National Park (18.7086°S, 044.7189°E, 146 m a.s.l.); ZSM 134/2006 (FGZC 938), ZSM 135/2006 (FGZC 939), two adult males, and ZSM 136/2006 (FGZC 940), adult female, collected by F. Glaw, J. Köhler, P. Bora, and H. Enting on 31 March 2006 at Andafiabe on the Beboka River ('Camp 2'), Tsingy de Bemaraha National Park (18.7842°S, 044.7794°E, 177 m a.s.l.); ZSM 927/2003 (FG/MV 2002.1421), putative male, ZSM 941/2003 (FG/MV 2002-1485), adult male, and ZSM 942/2003 (FG/MV 2002-1486), adult female, collected by G. Aprea, M. Puente, L. Raharivololoniaina, M. Teschke (née Thomas), and D.R. Vieites between 29 January and 1 February 2003 at Hotel Isalo Ranch (22.5929°S, 045.3928°E, ca 800 m a.s.l.).

Diagnosis.—*Mantidactylus mahery* **sp. nov.** is a member of the *M. curtus* clade as revealed by the phylogenomic analysis, and sister to the morphologically strongly different *M. pauliani.* While all other species in the *M. curtus* clade occur on the central plateau of Madagascar, *M. mahery* is distributed in western Madagascar, including some rather arid areas where it appears to be the only *Brygoomantis* present, and it is also present in one locality in the North West (western slope of Makira). See Table 4 for a list of diagnostic morphological characters. The combination of a large body size of up to 49 mm, slightly granular skin with (weakly expressed) dorsolateral ridges, absence of white spots on flanks and of white marking on snout tip, and short pulsed advertisement calls emitted in regular series distinguishes the new species from species of the other clades. In the North West it can occur syntopically with the similarly sized *M. ulcerosus* which however has a distinctly more tubercular dorsal skin, and more pulses per note in advertisement calls. Within the *M. curtus* clade, the new species differs by its larger tympanum diameter in males (11–13% of SVL) from all other species (Table 4). *Mantidactylus alutus, M. madecassus* and *M. pauliani* furthermore are smaller and have a shorter snout (Table 4). For detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. alutus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 9). Tongue excised as tissue sample (tongue no longer present); femoral glands partly detached for examination in internal view. Body rather slender (in this, differing from many other specimens of this species which are stouter). Head as wide as body. Snout rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, elliptical, diameter about 93%
of eye diameter. Supratympanic fold present, beginning straight, with a rather distinct bend midway towards forelimb insertion. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticalur tubercles single. Outer metacarpal tubercle present, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I=II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (115%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not present. Webbing formula: 1(0.25), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(2), 4e(1), 5(0.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface quite smooth with very few scattered granules on flanks. Ventral side smooth. Femoral glands present, in external view with a distal ulcerous macrogland and a large proximal granular gland field.

Colour in preservative: dorsum dark brown. Forelimbs

FIGURE 21. *Mantidactylus mahery* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male from Ranohira (near Isalo), photographed in 2004. (c,d) Adult male from Isalo, photographed in 1994. (e,f) Adult female from Makira Reserve (western slope), Sahaovy campsite, photographed in 2009. (g,h) Adult male from Tsingy de Bemaraha National Park, photographed in 2006. (i,j) Subadult specimen, probably a female, from Tsingy de Bemaraha National Park, photographed in 2006. (k) Adult specimen (unsexed) from Tsingy de Bemaraha National Park, photographed in 2006.

brown with poorly defined darker markings. Hindlimbs brown with poorly defined darker crossbands. Inguinal region without whitish spots. Snout tip without a light dot. Venter beige with brown mottling, throat darker than belly. Lower lip with alternating light and brown spots. Toe discs dark. Colour in life of holotype unknown.

Variation.—Variation in measurements is given in Table 5. See Fig. 21 for colouration in life and its variation. In life, dorsum is brown with distinct darker markings. Dark band between eyes is present. Forelimbs brown with very indistinct darker markings; hindlimbs with indistinct darker crossbands. Belly beige; throat with distinct white and brown mottling. A longitudinal white line on abdomen and throat is present. Femoral glands distinctly orange.

There is moderate sexual size dimorphism (confirmed male SVL 29.2–37.2 mm [n = 7] vs confirmed female SVL 34.2–48.6 mm [n = 6]). Horizontal tympanum diameter is 80–100% of eye diameter in males and 69–86% of eye diameter in females. Skin on the back with very few indistinct tubercles on the flanks. Colour on the back varies from light brown with distinct darker markings (e.g. ZSM 927/2003) to uniformly dark brown. Two dark spots on the back at the level of forelimb insertion always more or less distinctly present, except in the holotype (ZSM 23/2004), whose colour is too dark to see any markings. A dark brown more or less triangular band between eyes is always present. A light vertebral band or line is not present. An indistinct light dot on the snout tip is never present except in ZSM 25/2004. Lower lip with more (e.g. ZSM 23/2004) or less (e.g. ZSM 25/2004) distinct alternating light and brown spots. Venter and throat from uniformly beige with faint markings (e.g. ZSM 26/2004) to dark brown mottled (e.g. ZSM 23/2004). A longitudinal light median line on abdomen and throat is present in ZSM 25/2004. Hindlimbs always distinctly striped (e.g. ZSM 941/2003) except in ZSM 23/2004 where hindlimbs are striped indistinctly dark-brown. Forelimbs brown with irregular darker markings and stripes. Femoral glands of males large and prominent with a clear proximal granular gland field in ZSM 25/2004 and ZSM 941/2003, in ZSM 23/2004 and ZSM 927/2003 less prominent with indistinct proximal granular gland field. In external view a central depression in the middle of the femoral gland can be seen, thus indicating a distal ulcerous macrogland. In females femoral glands are always small but distinctly present (e.g. ZSM 942/2003), but a proximal granular gland field is never present. In life, males in reproductive state have femoral glands orange coloured (Fig. 21b, h), and sometimes (Fig. 21b) the proximal granular gland field is larger and more prominent than the distal ulcerous macrogland, which is uncommon among mantellines; the granular gland fields on the two opposite thighs contact each other medially.

Natural history.—The species is known from various sites in the West and North West of Madagascar, reaching into the South at Isalo. It has been found along running water (including very slowly running streams) in and outside of forest. At the western slope of the Makira Reserve it was found with *M. ulcerosus* and *M. jonasi* **sp. nov.** (see below) along a relatively large stream in degraded remnants of rainforest.

Calls.—The advertisement call of *M. mahery*, recorded on 28 January 1994 at Isalo National Park, near Ranohira, 23.4°C air temperature (Vences *et al.* 2006: CD 2, track 76), consists of a short, pulsed note, emitted in regular series at fast succession (Fig. 22). Pulse repetition rate is distinctly higher at the beginning of calls and significantly reduces after approximately one quarter of the call's duration. Amplitude modulation is present, with highest call energy occurring at the beginning of the call and continuously decreasing towards its end. Numerical parameters of eight analysed calls are as follows: call duration (= note duration) 120–144 ms (131.8 ± 8.7 ms); 21–26 pulses per note (24.1 ± 2.3); pulse duration 1–2 ms (1.6 ± 0.5); pulse repetition rate within notes 107.8–667.0 pulses/s (331.4 ± 205.3); dominant frequency 1004–1270 Hz (1151 ± 95 Hz); prevalent bandwidth 800–4500 Hz; call repetition rate (= note repetition rate) within regular series ca 211–218 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to an eclectic collection of disparate localities, mostly in the West of Madagascar, but reaching the eastern rainforest escarpment at Makira in the North West, and Tsaranoro in the Central region (Fig. 7). This species is known from Isalo (various localities), Forêt de Beanka, Makay, Makira West (Sahaovy, Camp 0), Tsaranoro, and Tsingy de Bemaraha (various localities). Elevation range: 120–960 m a.s.l.

Etymology.—The species name is derived from the Malagasy adjective mahery, meaning 'big' or 'strong', and refers to the rather stout body shape of this species. The name is used as a noun in apposition.

<u>*Mantidactylus ulcerosus* clade</u>

This clade contains two species characterized by a rather stout morphology and medium to large body sizes (28.5–46.4 mm adult SVL), occurring in the North, Sambirano, and North West regions, and from some sites in the North East (*M. ulcerosus, M. bellyi*) as well as two small-sized species (17.3–28.9 mm adult SVL) apparently restricted to the Tsaratanàna and Manongarivo Massifs in the Sambirano Region (*M. schulzi,* and one new species named herein as *M. steinfartzi* **sp. nov.**, based on the holotype depicted in Fig. 23).

Mantidactylus ulcerosus (Boettger, 1880)

Type material.—The taxon *Limnodytes ulcerosus* Boettger, 1880 is based on a syntype series from 'insula Nossi-Bé' that according to Frost (2021) included SMF 1068.1a–b, MCZ 9331–9334 and 2164 (on exchange from SMF; Barbour & Loveridge 1929), and UMMZ 60296 (on exchange from MCZ). The name-bearing type has been considered to be SMF 6605, lectotype designated by implication as it was considered the holotype by Mertens (1967), Guibé (1978) and Blommers-Schlösser (1979). However, in the original description, Boettger (1880) mentioned explicitely a male and a female specimen, and provided morphometric data for these

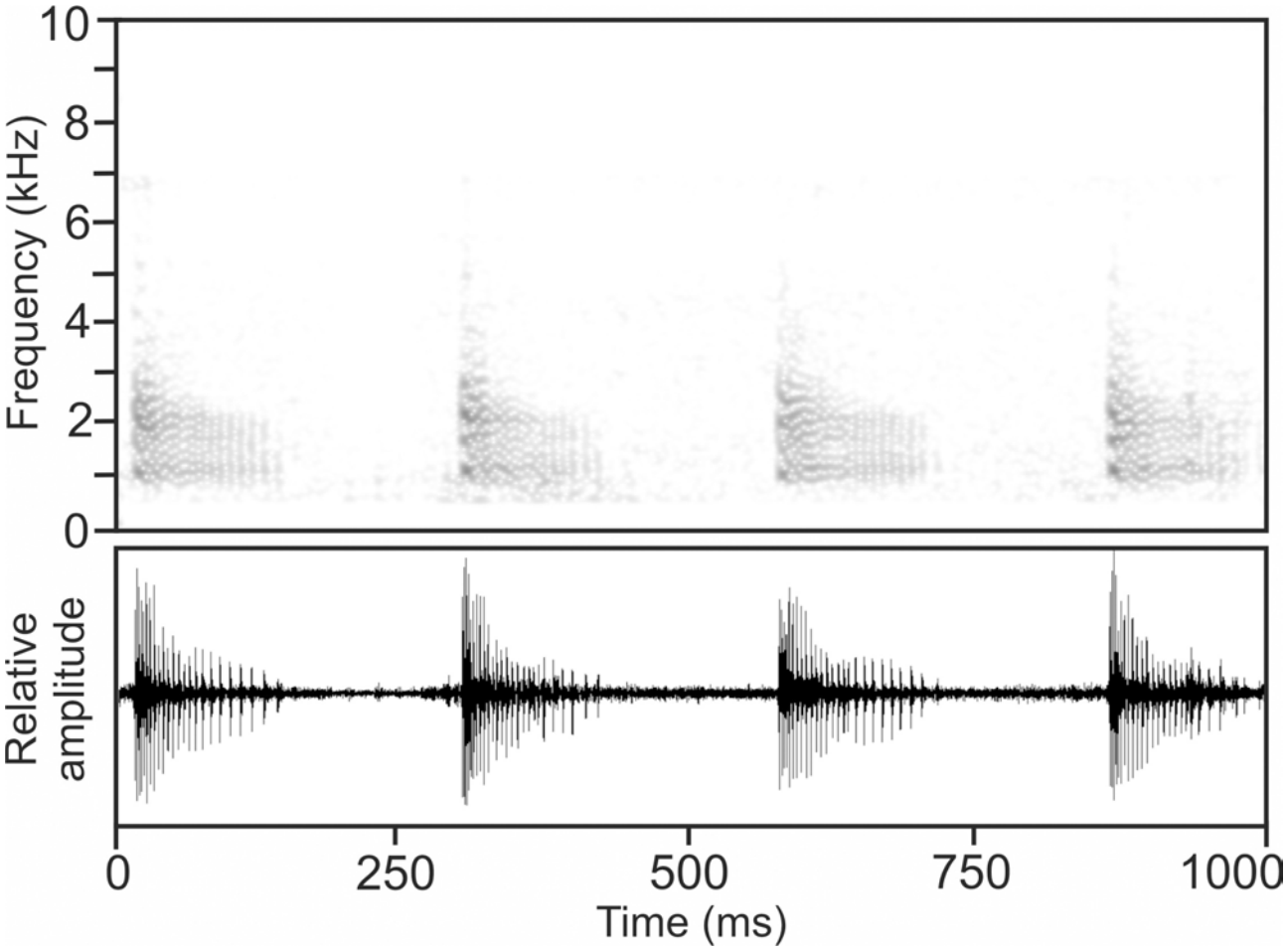

FIGURE 22. Audiospectrogram and corresponding oscillogram of four advertisement calls from a regular call series (comprising eight calls) of *Mantidactylus mahery*, recorded on 28 January 1994 at Isalo National Park, near Ranohira (23.4°C air temperature). Recording bandpass-filtered at 500–7000 Hz.

FIGURE 23. Preserved holotype specimens of *M. steinfartzi* **sp. nov.**, the single newly named species in the *M. ulcerosus* clade. Scale bars equal 5 mm.

two specimens. Also, he stated 'multa spec.' after the locality information indicating that his description was based on more than one specimen. Mertens (1967) and subsequent authors therefore must have been aware of the fact that *Limnodytes ulcerosus* was based on syntypes. Furthermore, Article 74.5 of the Code (ICZN 1999) states unambiguously for lectotype designations before 2000, that 'When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term "holotype" does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type.' Since the lectotype designation by the authors listed above was not explicit in terms of the Code, we here stabilize it by expressly designating SMF 6605 (from which we obtained a 16S sequence) as lectotype of *Limnodytes ulcerosus* out of the available series of syntypes, in agreement with the choice of this specimen by previous authors.

Identity.—Only one lineage of *Brygoomantis* has so far been reliably recorded from Nosy Be (Andreone *et al.* 2003; and the present study), and the nomen *ulcerosus* has been correctly assigned to this lineage in the recent literature (e.g. Glaw & Vences 1992a, 1994, 2007; Penny *et al.* 2017; Perl *et al.* 2014; Vieites *et al.* 2009). This assignment was confirmed by the 16S sequence of the lectotype, obtained by barcode fishing and included in our molecular analysis. Genetic results confirmed that this species occurs in the Sambirano region, and at Sahamalaza in the North West (Penny *et al.* 2017), across the northern mountain escarpment from Tsaratanàna to Makira. However, all records from eastern Madagascar (e.g. Blommers-Schlösser & Blanc 1991) belong to other, unrelated species of *Brygoomantis*.

Synonyms.—The nomen *Mantidactylus brauni* Ahl, 1929 is usually considered a junior synonym of *Mantidactylus biporus* (e.g. Frost 2021; Guibé 1978) but has been considered doubtfully distinct from that species by Blommers-Schlösser and Blanc (1991), and as a *nomen dubium* by Glaw and Vences (1992a). It is based on two unnumbered syntypes from 'Akkoraka (Central-Madagascar)' according to the original description, and on a 'holotype' ZMB 31617 (a supposed lectotype designation 'by implication') by Guibé (1978). However, Blommers-Schlösser & Blanc (1991) doubted whether the syntypes of this species have been correctly identified, and furthermore, as discussed above, a lectotype designation by implication is not a valid nomenclatural act according to article 74.5 of the Code. We located the specimen ZMB 53737 (locality according to catalogue: 'Akkorotha, Madagaskar'; collector / donor: [S.G.] Braun) at the Museum für Naturkunde (Berlin) labelled as type of *M. brauni* and succeeded to obtain a 16S sequence by barcode fishing from this specimen. Consequently, we here deviate from Guibé (1978) and designate specimen ZMB 53737 as lectotype of *Mantidactylus brauni* Ahl, 1929, which is justified in order to clarify the identity of this nomen. According to the respective 16S sequence, the lectotype firmly cluster among sequences of *M. ulcerosus*, and based on this genetic information we include *Mantidactylus brauni* as junior synonym *of M. ulcerosus.*

Diagnosis.—A member of the *M. ulcerosus* clade as revealed by the phylogenomic analysis, and sister to the morphologically very similar *M. bellyi.* See Table 4 for a list of diagnostic morphological characters. The combination of a large body size of up to 45 mm, strongly tubercular dorsal skin usually without well-defined dorsolateral ridges, large tympanum size in males (11–14% of SVL), absence of white spots on flanks and of white marking on snout tip, and pulsed advertisement calls emitted in regular series distinguishes *M. ulcerosus* from species of the other clades. Some species in the *M. fergusoni* clade can be morphologically similar, but they occur in eastern Madagascar (vs Sambirano and North West regions), and have highly different advertisement calls (Table 4). Within the *M. ulcerosus* clade, the new species differs by its large body size and tubercular dorsal skin from *M. schulzi*, and by its advertisement call emitted in regular call series from *M. bellyi* (single calls). *M. ulcerosus* can occur sympatrically with *M. mahery* in the North West of Madagascar, but that species differs by a smoother skin and fewer pulses per note in advertisement calls. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. ulcerosus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Re-description of the lectotype (SMF 6605). Adult female in good state of preservation. Body stout. Head as wide as body. Snout rounded. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, rounded, diameter about 68% of eye diameter. Supratympanic fold distinct, beginning straight, with a rather distinct bend midway towards insertion of forelimb. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present.Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded.

Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Subarticular tubercles single. Outer metacarpal tubercle not recognisable, inner metacarpal tubercle present. Foot almost as long as tibia (96%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle present. Webbing formula: 1(0.5), 2i(1), 2e(0.5), 3i(2), 3e(1), 4i(2), 4e(1.5), 5(0). Relative length of toes: I<II<V<III<IV. Skin on the upper surface with few scattered granules and tubercles on flanks. Ventral side smooth. Femoral glands small but present. Proximal granular gland field present.

Colour in preservative: dorsum red-brown, with indistinct irregular darker markings. Forelimbs light brown with poorly defined darker markings. Hindlimbs light brown with indistinct darker crossbands. Inguinal region without few scattered whitish spots. Snout tip without a whitish spot. Venter beige, throat darker than belly. Lower lip with distinct

FIGURE 24. *Mantidactylus ulcerosus* in life, in various views, and a clutch of its eggs. (a,b,c) Adult male (FGZC 5590; note rather distinct, orange-coloured femoral glands) from Nosy Be. (d,e) Adult male from Nosy Be, photographed in 2000. (f,g) Adult male from Manongarivo, photographed in 2003. (h) Adult female (MSZC 0229, voucher deposited in UADBA) from Bevitagnono, photographed in 2016. (i) Adult male (ZSM 101/2016 = MSZC 0230) from Bevitagnono, photographed in 2016. (j,k) Adult male from Angorony, photographed in 2010. (l) Adult specimen (unsexed) from Ankarafantsika, photographed in 2001. (m) Adult specimen (unsexed) from Ambilobe, photographed in 1991. (n) Clutch with developing embryos, probably assignable to *M. ulcerosus*, photographed at Nosy Be in 2000. (o,p,q) Adult female (ZSM 568/2009 = ZCMV 11459; note rudimentary femoral glands) from Makira Reserve (western slope), Sahaovy campsite, photographed in 2009. (r,s) Adult male from Makira Reserve (western slope), Sahaovy campsite, photographed in 2009.

irregular brown spots. Toe discs light brown to grey. Inner side of tibia brown mottled with beige.

Variation.—Variation in measurements is given in Table 6. See Fig. 24 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 28.5–35.9 mm [n = 8] vs confirmed female SVL 32.5–45.4 [n = 14]). Males have a larger tympanum than females (HTD/ED ratio is 53–79% in females, 74–95% in males). Specimens with a light vertebral stripe, or with a broad light vertebral band, occur regularly. Dorsolateral ridges are absent in many individuals, but can be recognised in others (Fig. 24). Femoral glands in males are distinct, often orange-coloured in life, and with distinct distal ulcerous macrogland and proximal granular gland field; the granular gland fields on the two opposite thighs contact each other medially.

Natural history.—Common along small streams with shallow water and associated swamps, where males emit their advertisement calls at night from the ground next to the water or sitting in shallow water. Males often begin calling in the late afternoon. Found in primary rainforest or transitional/dry forest and also in degraded areas and secondary forest, as long as some vegetation cover is present around the streams. Previous descriptions of eggs and embryos (Blommers-Schlösser 1979) refer to other species of *Brygoomantis*. Figure 24n shows a clutch of eggs probably assignable to this species.

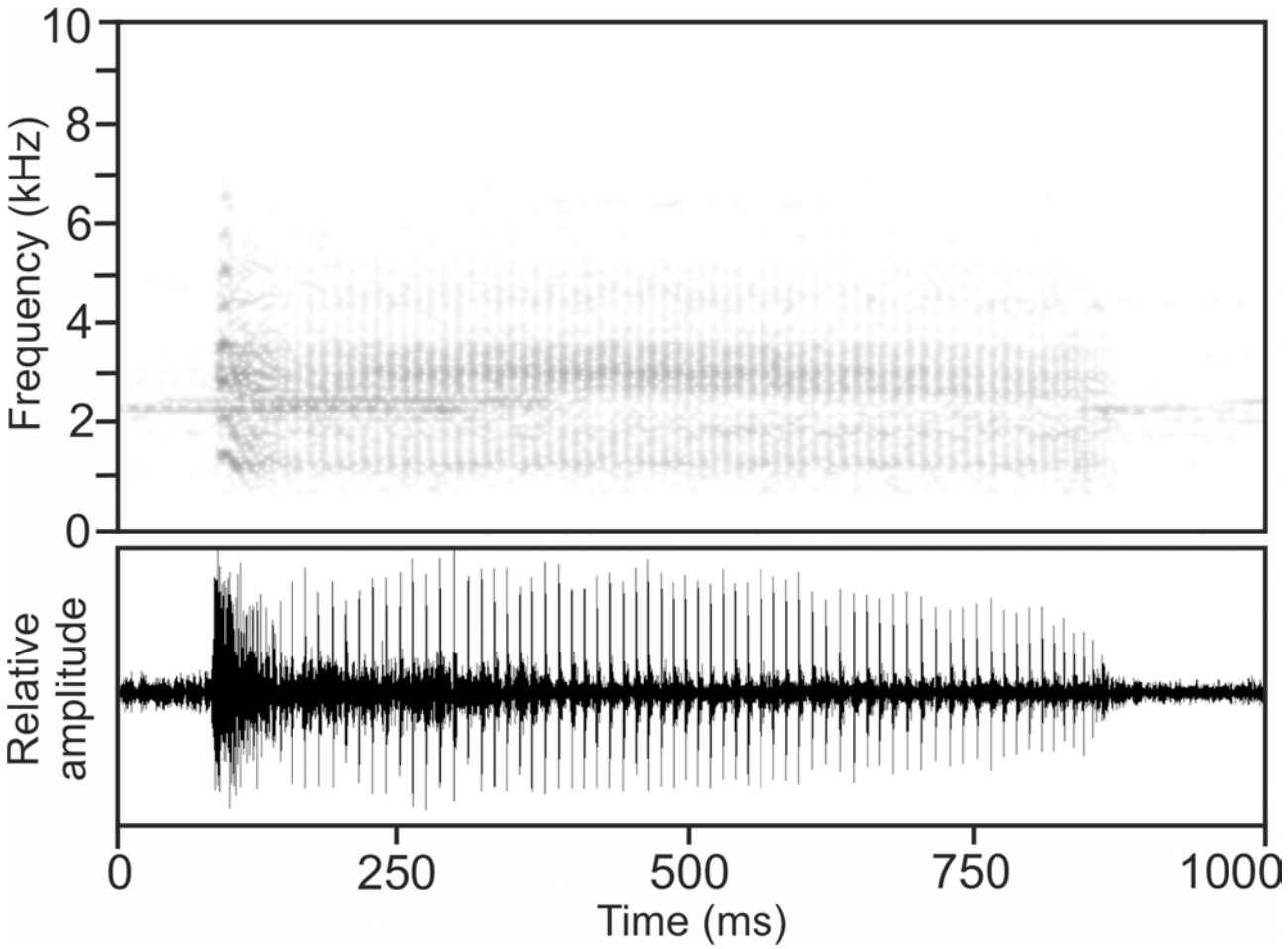

FIGURE 25. Audiospectrogram and corresponding oscillogram of one advertisement call from a call series of *Mantidactylus ulcerosus* (first call of a call series containing four calls), recorded on 10 February 1992 at the type locality Nosy Be. Recording bandpass-filtered at 700–7000 Hz.

TABLE 6. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus ulcerosus* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype. An asterisk (*) marks lectotypes designated in the current paper. A hash (#) marks measurements taken by AH and thus not fully comparable with other measurements, all taken by MV. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
M. ulcerosus																			
SMF 6605 [LT*]	NA	F	Nosy Be	45.4	17.8	18.7	6.9	4.9	4.4	2.5	4.2	26.2	12.1	65.8	30.3	21.7	20.6	NA	NA
ZMB 53737 [LT *brauni**]	NA	M	Uncertain (Akkoraka)	28.5	11.4	11.7	3.9	3.1	3.7	1.4	2.5	17.9	8.2	NM	NM	NM	14.8	NM	NM
ZFMK 52659 #	NA	F	Nosy Be	32.5	12.5	11.3	4.7	3.7	3.2	2.2	3.7	11.5	9.4	NM	NM	16.0	15.9	2.5	2.2
ZFMK 52666 #	NA	F	Nosy Be	38.7	15.7	13.2	5.3	2.8	4.1	1.9	4.0	13.5	11.5	NM	NM	17.8	19.2	NA	NA
ZFMK 52667 #	NA	F	Nosy Be	40.7	17.4	14.8	5.7	3.2	4.7	2.8	4.3	16.2	12.1	NM	NM	21.5	18.8	2.1	1.5
ZFMK 52668 #	NA	F	Nosy Be	40.6	16.3	14.6	5.6	3.7	4.1	2.7	4.3	11.6	11.1	NM	NM	19.3	18.7	NA	NA
ZFMK 53668 #	NA	F	Nosy Be	40.3	15.8	14.7	5.4	3.6	4.2	2.8	4.4	15.0	12.1	NM	NM	19.3	19.4	1.8	1.4
ZSM 407/2000 #	FGMV 2000.437	F	Benavony	37.4	15.6	15.7	5.4	3.9	3.7	2.5	4.6	14.4	12.5	NM	NM	18.7	19.1	1.3	1.1
ZSM 408/2000 #	FGMV 2000.438	F	Benavony	40.0	16.6	15.6	5.4	3.7	4.5	2.2	4.4	15.4	12.2	NM	NM	19.5	20.2	1.1	1.1
ZSM 563/2009	ZCMV 11465	F	Makira (Sahaovy)	42.1	16.0	17.7	5.6	4.4	4.1	2.2	4.5	22.4	11.5	61.8	27.5	19.9	16.9	NA	NA
ZSM 566/2009	ZCMV 11481	F	Makira (Sahaovy)	40.5	15.9	16.7	5.3	3.8	3.9	2.8	4.0	24.2	12.3	61.5	27.9	19.9	18.7	NA	NA
ZSM 568/2009	ZCMV 11459	F	Makira (Sahaovy)	43.3	17.5	17.3	5.8	3.1	4.2	2.5	4.4	24.3	13.2	61.0	27.7	19.5	18.1	NA	NA
ZSM 599/2001 #	FGMV 2001.20	F	Benavony	40.3	16.4	15.1	6.0	3.4	4.6	2.5	3.9	13.9	12.8	NM	NM	19.3	19.5	NA	NA
ZSM 707/2001	FGMV 2001.270	F	Ankarafantsika	40.7	14.9	16.9	5.6	3.9	4.2	2.8	3.4	23.1	10.9	57.3	25.5	17.4	17.6	NA	NA
ZSM 989/2001 #	NA	F	Ankarafantsika	34.7	13.6	12.0	4.3	3.0	3.6	2.3	3.7	12.1	8.5	NM	NM	15.2	16.6	1.3	1.1
ZFMK 53669 #	NA	M	Nosy Be	32.2	13.7	12.4	4.4	4.1	3.5	2.0	3.5	10.7	9.2	NM	NM	14.2	16.5	3.4	2.5
ZFMK 53670 #	NA	M	Nosy Be	33.8	13.6	12.5	4.6	4.0	3.8	2.2	4.0	12.0	9.3	NM	NM	14.4	15.5	3.5	2.9
ZSM 565/2009	ZCMV 11478	M	Makira (Sahaovy)	34.6	13.3	14.0	5.0	3.7	3.4	2.6	3.4	19.4	9.5	51.2	23.0	16.6	14.6	5.7	3.0

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TABLE 6. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 590/2001	FGMV 2001.4	M	Nosy Be	35.9	13.8	15.6	5.5	5.2	3.8	2.3	3.6	19.5	10.6	51.0	22.9	16.5	15.9	7.0	4.4
ZSM 598/2001 #	FGMV 2001.19	M	Benavony	32.9	13.9	13.0	5.2	4.5	3.8	2.1	3.3	12.7	10.2	NM	NM	14.8	15.1	3.1	2.1
ZSM 708/2001	FGMV 2001.400	M	Ankarafant-sika	33.9	14.3	14.7	5.1	4.4	3.9	2.7	3.7	19.4	9.5	50.1	22.3	16.2	14.2	6.7	2.9
ZSM 709/2001 #	FGMV 2001.401	M	Ankarafant-sika (Ampi-joroa)	31.7	13.7	12.5	4.3	4.1	3.6	2.1	3.2	12.1	9.5	NM	NM	11.2	14.6	4.2	2.6
M. bellyi																			
MNHN 1983.240 [HT]	NA	F	Montagne d'Ambre	36.7	15.4	15.9	5.2	3.9	NM	NM	NM	21.2	11.5	56.0	26.4	18.2	16.3	1.3	1.3
ZFMK 52660 #	NA	F	Andrakata	39.1	16.9	13.9	5.7	3.8	3.9	2.6	4.1	13.8	8.9	NM	NM	16.1	18.3	4.0	3.3
ZFMK 52661 #	NA	F	Andrakata	40.6	15.5	13.6	5.3	2.8	3.4	2.5	4.1	13.5	11.5	NM	NM	18.9	21.0	NA	NA
ZFMK H14140 #	NA	F	'Diego-island' (near Antsiranana)	37.9	15.1	13.3	5.5	3.1	3.5	2.0	2.8	14.0	10.6	NM	NM	17.0	18.0	NA	NA
ZFMK H14142 #	NA	F	'Diego-island' (near Antsiranana)	37.0	15.4	13.9	4.8	3.7	4.3	1.6	3.9	NM	11.7	NM	NM	17.5	19.4	NA	NA
ZFMK H14143 #	NA	F	'Diego-island' (near Antsiranana)	33.0	13.5	12.6	4.9	3.6	3.8	1.9	3.8	10.1	9.4	NM	NM	15.6	17.1	NA	NA
ZSM 197/2004 #	FGZC 370	F	Montagne d'Ambre ANGAP House	46.4	18.0	16.9	5.9	4.1	4.3	3.0	4.7	17.0	12.6	NM	NM	20.1	22.2	NA	NA
ZSM 292/2004 #	FGZC 560	F	Montagne des Francais, Andavakoera	41.3	19.0	14.2	5.1	3.8	3.9	2.5	3.7	14.1	12.3	NM	NM	20.1	20.5	NA	NA

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TABLE 6. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 293/2004 #	FGZC 563	F	Montagne des Francais, Andavakoera	44.2	19.0	15.9	5.4	4.1	4.5	2.4	3.8	14.1	12.6	NM	NM	18.8	19.4	2.2	1.6
ZSM 358/2004 #	FGZC 411	F	Montagne dÀmbre	44.4	18.9	15.9	5.3	3.8	4.2	2.9	4.2	15.1	13.2	NM	NM	20.4	20.3	NA	NA
ZSM 755/2003 #	FGMV 2002.549	F	Ankarana	43.6	18.7	15.9	5.7	3.4	4.7	2.8	4.5	13.9	12.6	NM	NM	18.6	19.7	NA	NA
ZSM 756/2003 #	FGMV 2002.551	F	Ankarana	43.3	16.9	16.5	5.6	4.2	4.2	2.4	4.4	14.8	13.1	NM	NM	19.6	19.9	NA	NA
ZFMK 62201 #	NA	M	Ankarana	33.3	15.1	13.0	4.9	5.0	3.4	2.5	4.1	12.0	9.1	NM	NM	14.4	15.4	2.8	2.2
ZFMK H14141 #	NA	M	'Diego-island' (near Antsiranana)	31.7	14.8	12.0	5.0	4.5	3.5	2.4	3.7	10.8	10.6	NM	NM	14.0	16.2	4.4	2.4
ZSM 208/2004	FGZC 408	M	Montagne d'Ambre	40.1	15.8	15.9	5.6	5.5	3.0	2.0	3.8	21.7	11.4	57.3	25.4	18.3	17.0	3.4	2.4
ZSM 209/2004	FGZC 409	M	Montagne d'Ambre	40.5	16.8	16.1	4.7	5.0	3.9	2.5	4.2	23.0	11.4	59.3	27.0	19.2	17.8	3.9	2.7
ZSM 231/2004 #	FGZC 452	M	Montagne d'Ambre	40.7	20.0	15.4	5.2	5.1	4.5	2.7	3.8	14.6	12.4	NM	NM	18.5	20.1	3.5	2.5
ZSM 291/2004 #	FGZC 559	M	Montagne des Francais, Andavakoera	35.5	16.4	13.3	4.8	4.1	3.7	2.1	3.4	12.1	11.3	NM	NM	16.7	16.7	3.1	2.1
ZSM 294/2004 #	FGZC 564	M	Montagne des Francais, Andavakoera	33.1	15.5	12.5	4.2	4.3	3.4	2.0	3.2	12.1	9.9	NM	NM	15.3	16.2	3.0	2.3
ZSM 295/2004 #	FGZC 566	M	Montagne des Francais, Andavakoera	33.1	14.8	13.0	5.0	4.8	3.4	2.0	2.9	12.9	9.6	NM	NM	15.8	16.1	4.3	2.9
ZSM 323/2005 #	FGZC 2715	M	Andapa	35.2	14.9	13.1	5.1	3.6	3.6	2.4	3.7	12.9	10.6	NM	NM	17.2	18.3	3.0	2.4
ZSM 753/2003	FGMV 2002.545	M	Ankarana	38.1	16.0	16.0	5.6	5.9	3.9	1.9	3.9	19.7	10.7	55.0	25.0	17.8	16.9	4.4	3.3

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TABLE 6. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 754/2003	FGMV 2002.596	M	Ankarana	41.0	17.6	17.9	6.0	6.8	3.3	2.6	4.2	22.7	11.6	59.8	26.9	NM	17.5	4.6	3.3
Mantidactylus schulzi																			
ZSM 653/2001 [HT]	MV 2001.150 (HT)	M	Tsaratanàna, Manarikoba	23.5	9.0	10.2	3.4	3.2	2.9	1.6	3.1	19.3	6.6	35.9	15.5	10.5	10.9	5.2	2.7
ZSM 821/2003 [PT]	FGMV 2002.751	M	Manongarivo	22.9	8.7	10.0	3.5	3.2	2.1	1.5	3.0	14.0	6.4	34.9	14.8	10.5	10.8	5.0	2.6
ZSM 822/2003 [PT]	FGMV 2002.752	M	Manongarivo	21.4	8.5	9.5	3.4	3.2	2.7	1.4	3.1	13.9	6.8	34.8	15.2	10.5	10.2	4.9	2.4
ZSM 651/2001 [PT]	MV 2001.136	F	Tsaratanàna, Manarikoba	28.7	10.5	11.6	4.1	3.0	2.7	1.8	3.5	17.9	8.6	44.8	20.4	13.8	14.0	NA	NA
ZSM 652/2001 [PT]	MV 2001.137	F	Tsaratanàna, Manarikoba	26.2	9.5	10.7	3.6	2.7	2.6	1.8	3.0	16.3	8.2	41.1	18.4	12.2	12.7	NA	NA
ZSM 654/2001 [PT]	MV 2001.15	F	Tsaratanàna, Manarikoba	27.3	9.5	10.5	3.8	2.7	2.3	1.6	3.3	15.7	7.1	38.9	16.8	11.3	11.9	NA	NA
ZSM 823/2003 [PT]	FGMV 2002.753	F	Manongarivo	28.9	10.3	11.9	3.9	3.2	2.8	2.0	3.1	17.4	8.2	43.6	19.4	13.4	13.1	NA	NA
ZSM 824/2003 [PT]	FGMV 2002.755	F	Manongarivo	27.1	10.1	10.5	4.0	3.2	2.6	1.7	3.2	16.3	7.6	42.1	18.4	12.3	13.3	NA	NA
ZSM 825/2003 [PT]	FGMV 2002.757	F	Manongarivo	24.7	9.6	10.8	3.5	2.5	2.4	1.8	3.3	15.5	7.4	39.6	17.6	11.9	12.7	NA	NA
ZSM 826/2003 [PT]	FGMV 2002.759	F	Manongarivo	28.5	10.3	11.0	3.5	2.8	2.8	1.8	3.4	15.2	7.6	39.7	18.5	12.5	12.6	NA	NA
Mantidactylus steinfartzi **sp. nov.** (Ca33)																			
ZSM 658/2001 [HT]	FGMV 2001.107	M	Manarikoba	21.5	8.9	9.2	3.3	3.5	1.8	1.9	2.6	13.9	6.4	30.9	13.6	9.3	9.6	3.9	2.6

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TABLE 6. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZMA 19567 # [PT]	FGMV 2002.2315	M	Manongarivo Camp 1	17.3	7.3	6.2	2.6	2.8	1.6	1.2	2.4	7.3	5.8	NM	NM	7.7	9.3	2.1	1.9
ZSM 659/2001 # [PT]	FGMV 2001.110	M	Manarikoba forest, Camp1	19.7	7.9	7.1	3.1	2.9	1.7	1.8	2.5	7.3	5.9	NM	NM	8.3	10.0	2.9	2.0
ZSM 663/2001 [PT]	FGMV 2001.118	M	Manarikoba	22.3	8.8	9.1	3.4	3.3	2.0	1.7	2.5	14.4	6.2	33.5	13.9	9.9	10.1	4.1	2.9
ZSM 843/2003 [PT]	FGMV 2002.810	M	Manongarivo	18.3	7.4	7.8	2.8	3.2	1.9	1.4	2.5	11.9	5.3	28.9	12.6	8.8	9.1	3.3	2.2
ZMA 19568 # [PT]	FGMV 2002.2317	F	Manon-garivo, Camp 1	22.6	9.1	8.1	3.6	2.5	2.0	1.8	2.7	8.7	7.0	NM	NM	9.6	11.2	1.5	0.8
ZSM 655/2001 # [PT]	FGMV 2001.68	F	Manarikoba forest, Camp1	21.9	8.8	7.7	3.4	2.2	1.8	1.3	2.6	8.4	7.1	NM	NM	9.4	11.0	1.2	0.9
ZSM 657/2001 [PT]	FGMV 2001.98	F	Manarikoba	28.2	10.2	10.2	3.9	2.8	2.1	2.0	2.9	15.5	7.5	37.0	16.6	10.8	11.2	1.8	1.4
ZSM 660/2001 [PT]	FGMV 2001.113	F	Manarikoba	28.2	9.7	10.4	3.9	2.6	1.8	1.7	2.7	16.6	7.9	39.7	17.2	11.4	11.7	1.6	1.4
ZSM 661/2001 [PT]	FGMV 2001.116	F	Manarikoba	27.3	9,8	10.2	3.9	2.3	2.2	1.7	2.4	16.0	7.9	38.0	16.9	12.3	11.0	1.3	1.2
ZSM 844/2003 [PT]	FGMV 2002.811	F	Manongarivo	23.5	8.8	9.4	3.3	2.4	1.8	1.4	2.5	15.0	6.7	37.2	16.1	10.6	11.5	1.2	1.0

Calls.—The advertisement call of *M. ulcerosus*, recorded on 10 February 1992, 19:00 h, at Nosy Be (Vences *et al.* 2006: CD 2, track 74, cut 1), consists of a pulsed note (Fig. 25), emitted in series at regular intervals and very fast succession (short inter-call intervals). Notes exhibit some complexity in pulse structure, with the initial pulse of each note being distinctly longer in duration and containing highest call energy compared to subsequent pulses. This initial pulse seems to contain some substructure and amplitude modulation and sounds more distorted than subsequent pulses. Relative amplitude of pulses slightly decreases towards the end of the note. Within the recorded short call series of four calls, these become successively shorter from the beginning to the end of the series. Numerical parameters of four analysed calls were as follows: call duration (= note duration) 453–779 ms (593.0 ± 143.2 ms); 45–65 pulses per note (54.8 ± 9.0); pulse duration 1–3 ms (2.3 ± 0.6 ms); pulse duration of initial pulses 27–37 ms (31.8 ± 4.1 ms); pulse repetition rate within notes (excluding initial pulse) 83.9–104.5 pulses/s (92.4 ± 7.6); dominant frequency 3101–3605 Hz (3308 ± 196 Hz); prevalent bandwidth 880–5500 Hz; call repetition rate (= note repetition rate) within regular call series ca 68 calls/min.

Calls recorded from a chorus on 30 June 2009 from a site at km 27 of the road from Antsohihy to Mandritsara, 24°C air temperature, generally agreed in character with calls described from Nosy Be. They also exhibit the complex pulse structure described above, with initial pulses being very narrowly spaced and sometimes fused. Calls were emitted in series, containing 4–9 calls. The recording was difficult to analyse due to many overlapping calls, but the following call parameters could be measured (10 calls analysed): call duration (= note duration) 355–565 ms (447.4 ± 63.0 ms); pulse duration 1–4 ms (1.8 ± 0.9 ms); pulse repetition rate within notes varied from ca 50–220 pulses/s; dominant frequency 2798–2885 Hz (2847 ± 37 Hz); prevalent bandwidth 1000–3800 Hz; call repetition rate (= note repetition rate) within regular call series ca 70–88 calls/min.

Calls recorded on 24 February 2001 at Ankarafantsika, 28°C air temperature, also agreed with the calls described above, with very narrowly spaced initial pulses, partly fused. Calls were emitted in series containing 3–5 calls. Recordings were of poor quality, containing overlapping calls and background noise. However, the following parameters could be measured (8 calls analysed): call duration (= note duration) 551–1047 ms (667.3 ± 160.0 ms); pulse repetition rate within notes varied from ca 50–400 pulses/s (maximum values from initial pulses); prevalent bandwidth 900–3400 Hz; call repetition rate (= note repetition rate) within regular call series ca 66–87 calls/min.

Distress calls of a female from Nosy Be were described by Glaw and Vences (1992b).

Tadpoles.—Tadpoles assignable to this species (from the type locality Nosy Be) were briefly mentioned and their tooth formula described by Glaw & Vences (1994). The tadpole description by (Blommers-Schlösser 1979) was based on east coast specimens not identified by genetics that almost certainly belong to other species of *Brygoomantis*.

Distribution.—Widespread in the North West (including the western slopes of the Makira Reserve) and Sambirano regions of Madagascar, over a wide range of elevations and habitat types (Fig. 7). This species is known from Angorony, Ankarafantsika, Antsatramidola, Benavony, Berara, the border of the Bealanana district (Bevitagnono and Irogno forest), between Antsohihy and Mandritsara, between Antoshihy and Port Berger, Makira West (Sahaovy, Camp 0), Nosy Be (type locality) including Lokobe National Park, Sahamalaza, and Tsaratanàna. It was also recorded from Nosy Komba (Hyde Roberts & Daly 2014). Records from the forests of Belambo and Anjiamangirana and in the Namoroka National Park (Raselimanana 2008) require genetic confirmation. Elevation range: 0–1093 m a.s.l.

Etymology.—Latin adjective meaning 'full of sores' or 'ulcerated', presumably in reference to the granular dorsal skin or maybe to the femoral glands.

Mantidactylus bellyi Mocquard, 1895

Type material.—*Mantidactylus bellyi* Mocquard, 1895 is based on the holotype MNHN 1893.240 (by monotypy) from 'Montagne d'Ambre' (according to Guibé 1978), and this number had been given incorrectly as 1893.420 by Guibé (1950). According to the original description, there are no paratypes.

Identity.—This species was previously considered a junior synonym of *M. curtus* (e.g. Blommers-Schlösser & Blanc 1991) and was resurrected as separate species by Glaw and Vences (2006). It is the sister species of *M. ulcerosus*. A very extensive *Brygoomantis* sampling at its type locality Montagne d'Ambre, reflected by 150 sequences in our 16S data set, found only two lineages at this Massif in northernmost Madagascar: one corresponding to a lineage morphologically similar to *M. betsileanus* and described below as *M. jonasi* **sp. nov.**, and one corresponding to specimens of a lineage typically (Glaw & Vences 2006, 2007) assigned to *M. bellyi.* We obtained barcode fishing 16S data of the holotype MNHN 1893.240 and confirm this nomen has been correctly assigned.

Diagnosis.—A member of the *M. ulcerosus* clade as revealed by the phylogenomic analysis, and sister to the morphologically very similar *M. ulcerosus.* See Table 4 for a list of diagnostic morphological characters. The combination of a large body size of up to 46 mm, strongly tubercular dorsal skin in most individuals, absence of dorsolateral ridges, large tympanum size in males (10–17% of SVL) and absence of white spots on flanks and of white marking on snout tip distinguishes *M. bellyi* from species of the other clades. Some species in the *M. fergusoni* clade can be morphologically similar, but they occur in eastern Madagascar (vs Sambirano and North West regions), and have strongly different advertisement calls (Table 4). Within the *M. ulcerosus* clade, the species differs by its large body size and tubercular dorsal skin from *M. schulzi*, and by its advertisement call consisting

of single calls (vs note series) from *M. schulzi* and *M. ulcerosus*. For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. bellyi* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Re-description of the holotype. Adult male in poor state of preservation. Skin on various places lacerated and completely discoloured. Body rather stout. Head wider than body. Snout rounded. Nostrils directed laterally, slightly protuberant. Position of nostrils not recognisable due to the bad state of preservation. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, rounded, diameter about 75 % of eye diameter. Supratympanic fold distinct, beginning straight, with a rather distinct bend midway towards jaw. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle present, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot as long as tibia (101%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle present. Webbing formula: 1(0.5), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(1.5), 5(0). Relative length of toes: I<II<V<III<IV. Skin on the upper surface with a few ridges on flanks. Ventral side smooth. Femoral glands present, in external view not consisting of single, sharply delimited granules but distal ulcerous macrogland having a rather irregular tubercular surface with a median depression. Proximal granular gland field present.

Colour in preservative: dorsum beige-brown, with distinct irregular darker markings. Forelimbs light brown with very poorly defined darker markings. Hindlimbs light brown with very indistinct darker crossbands. Inguinal region without whitish spots. Snout tip seems to be without a whitish spot. Venter uniformly beige. Lower lip uniformly beige. Toe discs brown to grey, darker than feet.

Variation.—Variation in measurements is given in Table 6. See Figs 26–27 for colouration in life and its variation. Specimens with a light vertebral stripe occur. There is moderate sexual size dimorphism (confirmed male SVL 31.7–41.0 mm [n = 11] vs confirmed female SVL 36.7–46.4 mm [n = 12]). Males have a larger tympanum than females (HTD/ED ratio is 53–77% in females, 71–113% in males). Femoral glands in males large and distinct, orange coloured in life, with the proximal granular gland field sometimes occupying a larger surface than the distal ulcerous macrogland (Fig. 26o) which is relatively unusual in mantellines; the proximal granular gland field on the two opposite thighs contact each other medially. Rasolonjatovo *et al.* (2022) describe the genetic diversity and phylogeographic structure of *M. bellyi* on Montagne d'Ambre.

Natural history.—Similar to *M. ulcerosus, M. bellyi* is found in and along small shallow streams in primary as well as degraded rainforest and dry forest. Males were heard calling at night from the water or at the edge of the water. Rasolonjatovo *et al.* (2018) report on the attempted predation of a *Boophis* tadpole by an adult *M. bellyi* and reported an adult female *M. bellyi* repeatedly emitting a series of rapid scratch-like vocalisations from a hidden place on the rough magmatic rock forming the edge of the pool. Rasolonjatovo *et al.* (2020) report on thermal ecology of *M. bellyi* on Montagne d'Ambre across its elevational range (467–1394 m a.s.l.), and Rasolonjatovo *et al.* (2022) described its genetic diversity and phylogeographic structure on Montagne d'Ambre.

Calls.—The advertisement call of *M. bellyi*, recorded on 17 March 2000 at the entrance of Montagne d'Ambre National Park, 21.6°C air temperature (Vences *et al.* 2006: CD 2, track 75), consists of a regularly pulsed note (Fig. 28), emitted at irregular intervals, but not regular call series. Notes exhibited distinct amplitude modulation, with call energy being highest at the beginning of the note, followed by continuous decrease of energy towards the note's end. Pulses were very narrowly spaced. Numerical parameters of three analysed calls were as follows: call duration (= note duration) 594–682 ms (630.0 ± 46.1 ms); 41–46 pulses per note (43.7 ± 2.5); pulse duration 7–11 ms (8.3 ± 1.2 ms); pulse repetition rate within notes 63.8–77.8 pulses/s (69.9 ± 4.9); dominant frequency 2497–2583 Hz (2532 ± 32 Hz), with a second peak of almost identical energy at around 880–920 Hz; prevalent bandwidth 660–3200 Hz; call repetition rate (= note repetition rate) not identifiable with available recordings.

Variation in the advertisement call over populations of *M. bellyi* on Montagne d'Ambre was investigated by Rasolonjatovo *et al.* (2022) for 23 male specimens. In all cases, the calls typically consisted of a single note, with minor variation of call duration between individuals, and without significant differences in call parameters between sites. Dominant frequency was negatively correlated with body size.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Distributed in the North and North East of Madagascar; apparently allopatrically distributed with respect to its sister species, *M. ulcerosus* (Fig. 7). In Montagne d'Ambre National Park (the type locality) it is well documented from across the whole elevational range of the mountain. Additionally, our genetic results confirm its presence in Ankarana, Fanambana forest, Andrakata, Marojejy, Montagne des Français, Belambo, Andapa, and Andrafainkona/Ambarata. Elevation range: 53–1372 m a.s.l.

Etymology.—Eponym for a 'Mr Belly' according to the original description, who collected the type specimens. This probably refers to Édouard Belly, to whom Charles A. Alluaud referred as 'adjoint à ma mission par le Muséum de Paris' for his travels in northern Madagascar (Alluaud 1893).

Mantidactylus schulzi Vences, Hildenbrand, Warmuth, Andreone & Glaw, 2018

Type material.—Based on holotype (by original designation) ZSM 653/2001 from 'Tsaratanàna Massif, Manarikoba Forest, Andampy, "Camp 0" (14.0422°S,

FIGURE 26. *Mantidactylus bellyi* in life, in dorsolateral and ventral view. (a,b) Adult male from Montagne d'Ambre, photographed in 2000. (c,d) Adult male from Montagne d'Ambre, photographed in 2004. (e,f) Adult male from Montagne d'Ambre, photographed in 2003. (g,h) Adult female from Montagne d'Ambre, photographed in 2003. (i,j) Adult female from Montagne d'Ambre. (k) Adult specimen (unsexed) from Andapa. (l,m,n,o) Two adult males from Montagne des Français, photographed in 2004. (p,q,r,s). Two adult males from Ankarana, photographed in 2003.

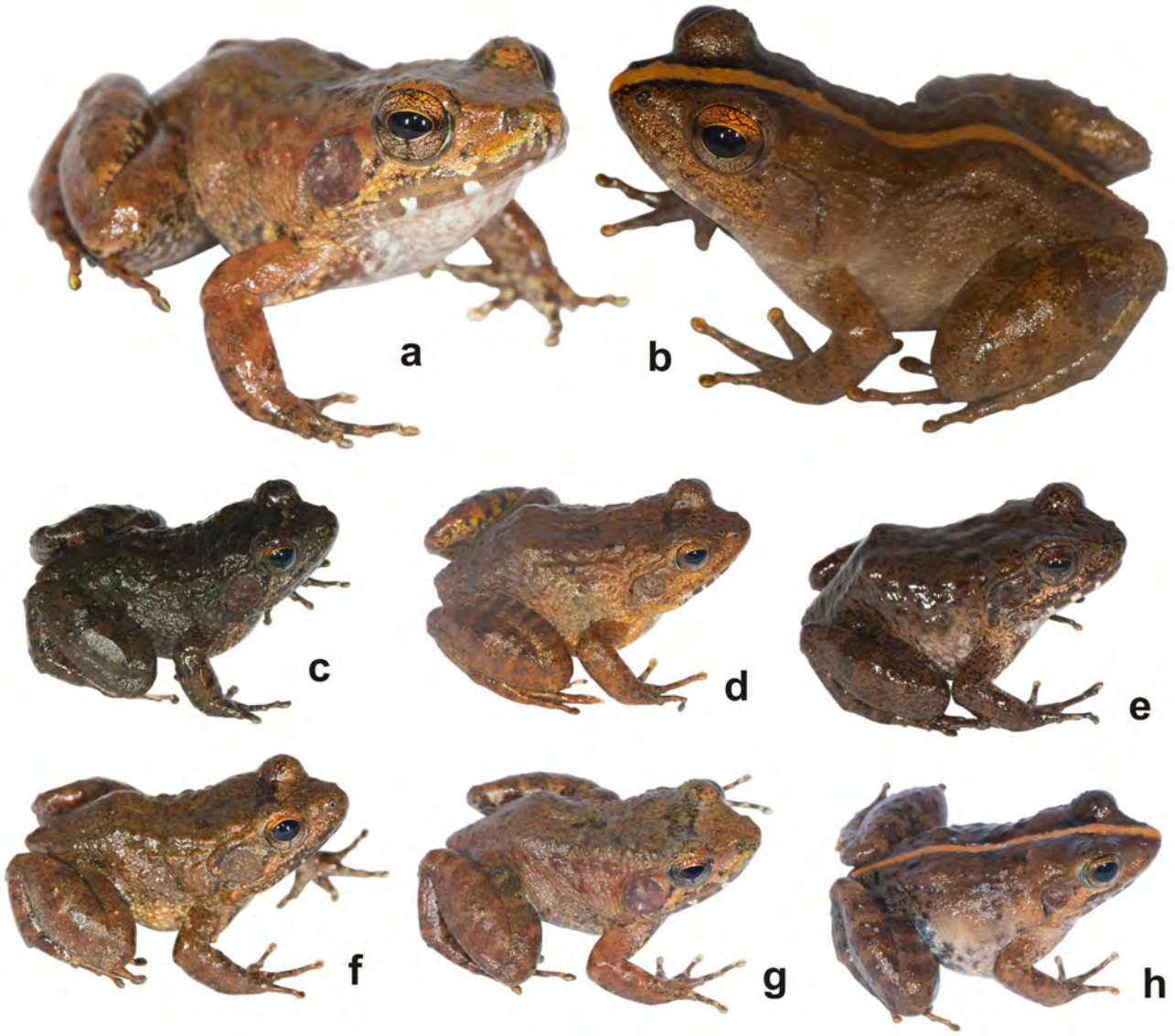

FIGURE 27. *Mantidactylus bellyi* from Montagne d'Ambre in life, all photographed in 2017–2018. (a,g) Adult male specimens tissue-sampled and included in molecular analysis (SRTIS numbers). (b) Unsexed adult (MSZC 0557, voucher deposited in UADBA). (c) Adult male (ZSM 39/2018 = MSZC 0751). (d) Adult female (MSZC 0616, voucher deposited in UADBA). (e) Adult female (ZSM 37/2018 = MSZC 0490). (f) Adult male (not collected). (h) Adult female (MSZC 0402, voucher deposited in UADBA).

048.7617°E, ca 730 m above sea level), former Antsiranana province, northern Madagascar'. A total of 19 paratypes: ZMA 19374 (FGMV 2002.754), ZMA 19375, ZSM 821–826/2003 from Manongarivo, Camp 0 (13.9756°S, 048.4267°E, 688 m a.s.l.); ZSM 651–652/2001 and 654/2001 from the type locality; and the following uncatalogued paratypes from the UADBA collection: FGMV 2002.749, FGMV 2002.756, FGMV 2002.758, FGMV 2002.760, FGMV 2002.761, FGMV 2002.763, FGMV 2002.764, and FGMV 2002.765.

Identity.—This species has been previously referred to as *M.* sp. 33 'Tsaratanàna' (in Vences *et al.* (2018) mistakenly stated to be Ca32). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Tsaratanàna Andampy"' by Glaw and Vences (2007). The identity of this small-sized species is well established by genetic data from the holotype and several paratypes provided in the original description. It was previously thought (e.g. Glaw & Vences 2007) to be related to *M. biporus*, but our phylogenomic tree firmly places it in the *M. ulcerosus* clade.

Diagnosis.—A member of the *M. ulcerosus* clade as revealed by the phylogenomic analysis, and sister to the sympatric *M. steinfartzi* **sp. nov.** described below. See Table 4 for a list of diagnostic morphological characters. The combination of a small body size of up to 29 mm, slightly tubercular dorsal skin, absence of clearly defined, continuous dorsolateral ridges, large tympanum size in males (14–15% of SVL), absence of white spots on flanks, and presence of a white marking on snout tip, distinguishes *M. schulzi* from species of most other clades exept for the *M. betsileanus* clade and *M. fergusoni* clade. It differs from members of the *M.*

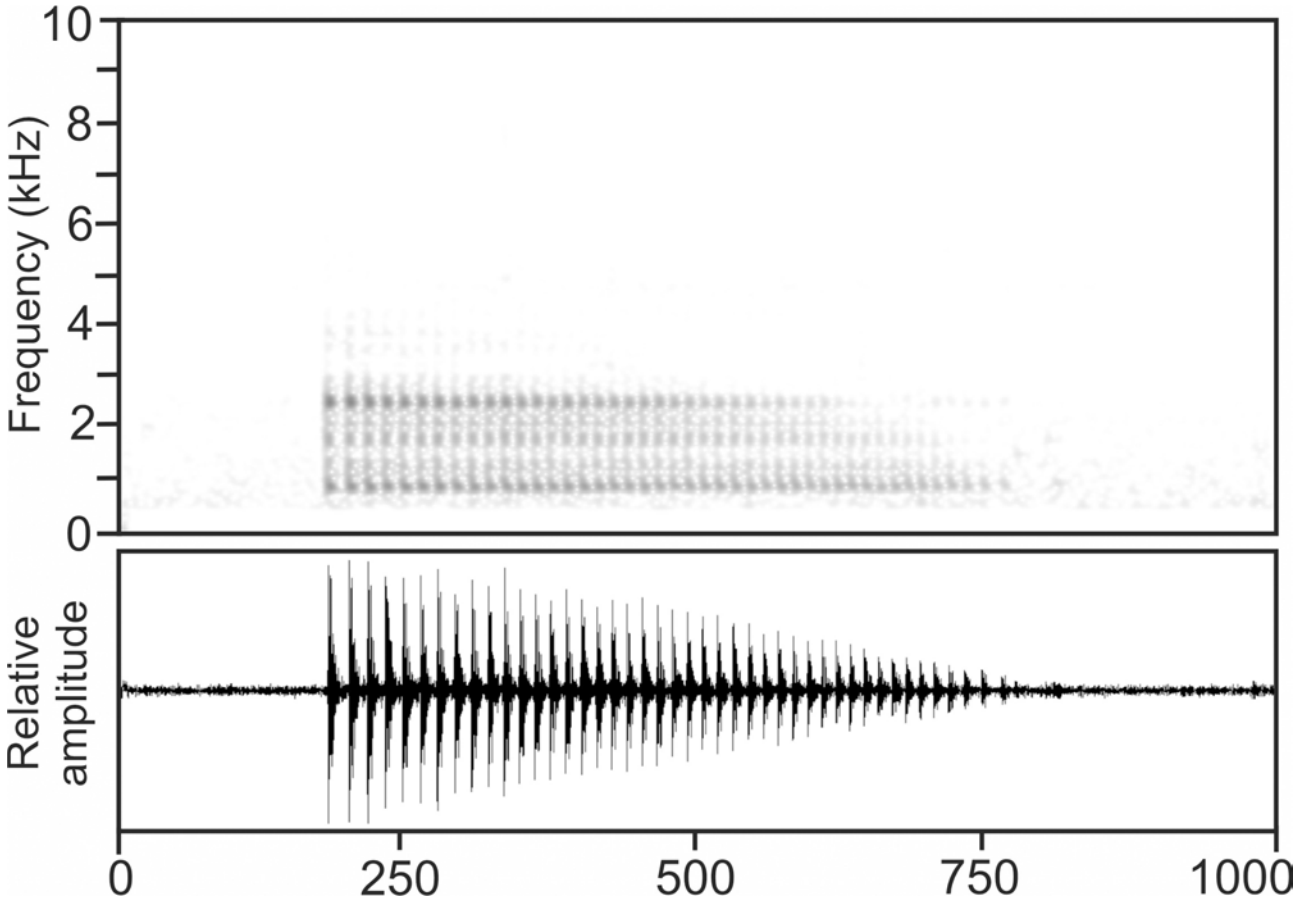

FIGURE 28. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus bellyi*, recorded on 17 March 2000 at the entrance of the Montagne d'Ambre National Park (21.6°C air temperature). Recording bandpass-filtered at 460–8000 Hz.

fergusoni clade by smaller body size of both sexes, and from members of the *M. betsileanus* clade by smaller body size of females, and by a combination of more expressed webbing and larger femoral glands (Table 4), and from all other *Brygoomantis* with known advertisement calls by details of temporal call variables. Within the *M. ulcerosus* clade, *M. schulzi* differs by a distinctly smaller body size and several other characters from *M. bellyi* and *M. ulcerosus*. For a detailed comparison with its sister species *M. steinfartzi* **sp. nov.**, see description of that species below; for detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. schulzi* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 6. See Fig. 29 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 21.4–23.5 mm [n = 3] vs confirmed female SVL 24.7–28.9 mm [n = 7]). Males have a somewhat larger tympanum than females (HTD/ED ratio is 71–82% in females, 91–94% in males). Femoral glands are very prominent in males, with a particularly large distal ulcerous macrogland, and a relatively small proximal granular gland field; the granular gland fields on the two opposite thights contact each other medially. The glands have a light brown to yellowish tone in life, but are not distinctly orange as in the large-sized species *M. bellyi* and *M. ulcerosus*.

Natural history.—All specimens were observed in small streams and rivulets in primary rainforest. Calling males were observed directly next to the water. Both in Tsaratanàna and Manongarivo, this species occurred at slightly lower elevation than its sister species, *M. steinfartzi* **sp. nov.**, but the sites are in close proximity to one another (i.e. <500 m linear distance at Manongarivo, <2600 m at Tsaratanàna).

Calls.—The advertisement call of *M. schulzi* recorded on 10–11 February 2001 at Andampy campsite, Manarikoba forest, Tsaratanàna Strict Nature reserve, 25–26°C air temperature (Vences *et al.* 2006: CD2, track 70), has been adequately described by Vences *et al.* (2018). It consists of a pulsed note of very variable duration (Fig. 30), sometimes emitted in short series of 2–3 calls. Numerical parameters of 30 analysed calls are as follows: call duration (= note duration) 11–996 ms (301 ± 306 ms); 6–73 pulses per note (27 ± 21); pulse duration 1–3 ms (2 ± 1 ms); pulse repetition rate within notes approximately 55–130 pulses/s; dominant frequency is difficult to

FIGURE 29. *Mantidactylus schulzi* in life, in dorsolateral and ventral view. (a,b) Adult male (holotype ZSM 653/2001 = MV 2001.150), from Andampy Campsite, Manarikoba Forest, Tsaratanàna Massif. (c,d) Adult male (paratype, ZMA 19375), from Camp 0, Manongarivo Massif.

determine, but roughly ranges between 2900–3400 Hz; prevalent bandwidth 1500–3900 Hz; call repetition rate (= note repetition rate) within regular series ca 30–50 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the Sambirano Region in northern Madagascar (Fig. 7). This species is known from Tsaratanàna (Manarikoba, type locality) and Manongarivo. Elevation range: 688–730 m a.s.l.

Etymology.—Eponym for Stefan Schulz, professor of organic chemistry at Braunschweig University of Technology, in recognition of his contributions to the study of volatile pheromones in *Brygoomantis* and other mantellines.

Mantidactylus steinfartzi **sp. nov.**

Identity and justification.—This lineage was considered as *M*. sp. 33 by Vieites *et al.* (2009) and *M*. sp. Ca33 by Perl *et al.* (2014) and Vences *et al.* (2018). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Tsaratanàna Antsahamanara"' by Glaw and Vences (2007). It occurs in sympatry (although not strict syntopy) with its sister species *M. schulzi* but is distinguished from it by advertisement calls, morphology, and concordant differentiation of 16S and Rag-1. It was previously thought (e.g. Glaw & Vences 2007) to be related to *M. biporus*, but our phylogenomic tree firmly places it in the *M. ulcerosus clade*.

Holotype.—ZSM 658/2001 (FGMV 2001.107), adult male (seen calling), collected by F. Andreone, F. Mattioli, J.E. Randrianirina, and M. Vences between 4–9 February 2001 at Antsahamanara 'Camp 1' (14.0450°S, 048.7844°E, ca 1000 m a.s.l.), Manarikoba forest, Tsaratanàna Massif, Diana Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of 11 paratypes: ZSM 659/2001 (FG/MV 2001.110) and ZSM 663/2001 (FG/MV 2001.118), two adult males, and ZSM 655/2001 (FG/MV 2001.68), ZSM 657/2001 (FG/MV 2001.98), ZSM 660/2001 (FG/MV 2001.113), ZSM 661/2001 (FG/MV 2001.116), four adult females, with the same collection data as the holotype; ZSM 843/2003 (FG/MV 2002.0810), and ZMA 19567 (FG/MV 2002.2315), two adult males, and ZSM 844/2003 (FG/MV 2002.0811) and ZMA 19568 (FG/MV 2002.2317), two adult females, collected by F. Glaw, R.D. Randrianiaina, and M. Vences on 3 February 2003 at 'Camp 1' on the Manongarivo Massif (13.9770°S, 048.4220°E, 751 m a.s.l.); UADBA-A uncatalogued (FGZC 3791), specimen of unknown age and sex, collected by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F.M. Ratsoavina, and A. Razafimanantsoa

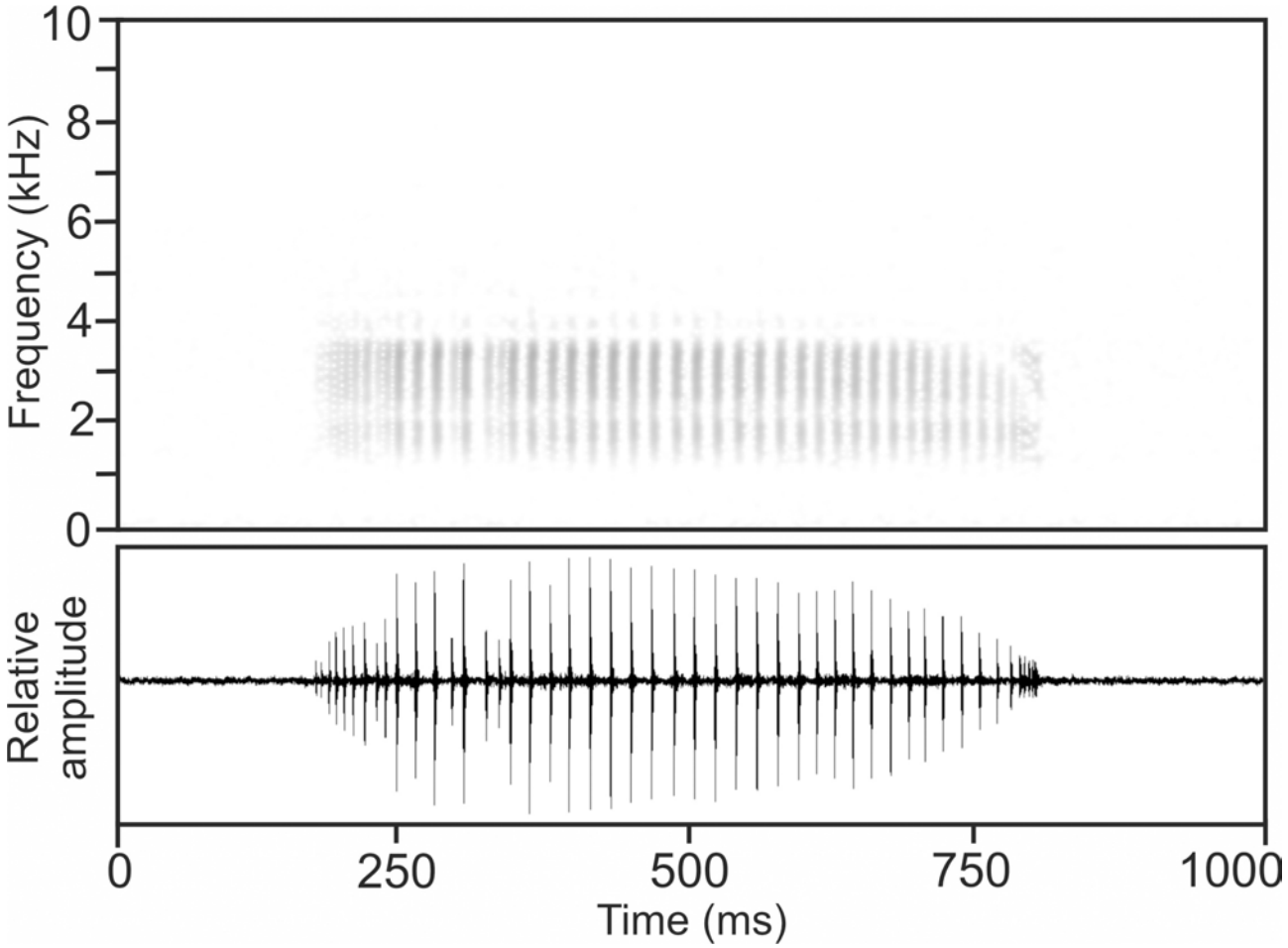

FIGURE 30. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus schulzi*, recorded in 2001 at Andampy Campsite, Manarikoba forest, Tsaratanàna Strict Nature Reserve (25–26°C air temperature).

on 3 December 2012 near Ambodimandresy (13.7133°S, 049.4911°E, 778 m a.s.l.).

Diagnosis.—*Mantidactylus steinfartzi* **sp. nov.** is a member of the *M. ulcerosus* clade as revealed by the phylogenomic analysis, and sister to the sympatric *M. schulzi.* See Table 4 for a list of diagnostic morphological characters. The combination of a small body size of up to 28 mm, smooth to slightly tubercular dorsal skin, absence of dorsolateral ridges, large tympanum size in males (15–17% of SVL), presence of white spots on flanks, and absence or weak expression of a white marking on snout tip, distinguishes *M. steinfartzi* **sp. nov.** from most other species of *Brygoomantis* from other clades: members of the *M. betsileanus* clade typically have a distinct white marking on the snout tip and no white spots on the flanks, and (except for *M. betsileanus* and *M. riparius* **sp. nov.** which differ in the number of pulses per note; Table 4) a lower pulse rate in advertisement calls; members of the *M. fergusoni* clade are larger, have a more granular dorsal skin, no white spots on the flanks, and lower pulse rate in advertisement calls; and members of the *M. biporus* and *M. inaudax* clades have, as far as known, fewer pulses per note in advertisement calls (Table 4). Within the *M. ulcerosus* clade, the new species differs by a distinctly smaller body size and several other characters from *M. bellyi* and *M. ulcerosus*. It is morphologically rather similar to its sister species *M. schulzi* which, however, usually has no white dots on the flanks and a more distinctly expressed white marking on the snout, more granular dorsal skin, a smaller tympanum in males, a slightly larger male body size, and also differs in details of advertisement calls: a rather irregularly emitted note of quite variable number of pulses in *M. schulzi* vs less variability in pulse number and emission of short series of usually two calls in *M. steinfartzi* **sp. nov.** For detailed distinction from new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. steinfartzi* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in a mediocre state of preservation (softly fixed, similar to all other available specimens of this species; Fig. 23); muscle tissue from left thigh removed, femoral glands partly detached for examination in internal view. Body rather stout. Head as wide as body. Snout rather pointed. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, large, wider than high, horizontal diameter of tympanum 106% of horizontal eye

diameter. Supratympanic fold distinct, beginning straight above, with a rather distinct 45° bend midway towards insertion of forelimb, following the outline of the large tympanum. Tongue ovoid, distinctly bifid posteriorly. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (97%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle very small but recognisable. Webbing formula: 1(0.5), 2i(1), 2e(0.5), 3i(2), 3e(1), 4i(2), 4e(2), 5(0.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth (in life slightly granular), slightly glandular dorsolaterally. No dorsolateral ridges or folds. Ventral side smooth. Femoral glands large and very distinct in external view.

Colour in preservative: dorsally almost uniformly brown, with a few indistinct and irregular large markings. A somewhat darker patch is present between the eyes. Limbs with poorly contrasted dark crossbands. Flanks and sides of head with scattered whitish spots. Snout tip with a poorly contrasted light spot. Venter beige, throat and chest with brown pigment and a light medial line on the throat. Lower lip ventrally with distinct alternating light and brown spots. Colouration in life not recorded for holotype specimen.

Variation.—Variation in measurements is given in Table 6. See Fig. 31 for colouration in life. There is moderate sexual size dimorphism (confirmed male SVL 17.3–22.3 mm [n = 5] vs confirmed female SVL 21.9–28.2 mm [n = 6]). Males have a distinctly larger tympanum than females (HTD/ED ratio is 59–73% in females, 94–114% in males). Compared to the holotype, in other male specimens the femoral glands were smaller (Fig. 31), and smaller than in the sister species *M. schulzi*. In life the glands have a slightly yellowish tone (Fig. 31).

Natural history.—All specimens were observed in small streams and brooks in primary rainforest. Calling males were observed from one headwater pool, calling from positions directly next to the water during the day.

Calls.—The advertisement call recorded on 4 February 2001 at Antsahamanara Campsite, Manarikoba forest, Tsaratanàna Strict Nature Reserve, 20°C air temperature (Vences *et al.* 2006: CD2, track 73), consists of a pulsed note (Fig. 32), emitted in groups containing two calls. Notes exhibit slight amplitude modulation, with maximum call energy occurring at approximately the middle of the note's duration. Pulse repetition rate within notes is higher at the beginning of the note and slightly decreases after approximately the first quarter of the note's duration. Numerical parameters of six analysed calls were as follows: call duration (= note duration) 516–721 ms (615.3 ± 87.8 ms); 40–54 pulses per note (47.2 ± 5.1); pulse duration 2–5 ms (2.9 ± 1.0 ms); pulse repetition rate within notes 69.8–115.4 pulses/s (87.2 ± 17.5); dominant frequency 3193–3716 Hz (3416 ± 184 Hz); prevalent bandwidth 2700–4300 Hz; call repetition rate (= note repetition rate) within call groups ca 24–36 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the Sambirano Region in northern Madagascar (Fig. 7). This species is known from Tsaratanàna (Manarikoba, type locality), Manongarivo, and Ambodimandresy. Elevation range: 751–1000 m a.s.l.

Etymology.—We dedicate this species with an apparent ecological (elevational) component in species formation to our colleague Sebastian Steinfartz, in recognition of his contributions to the field of ecology-driven population differentiation and speciation.

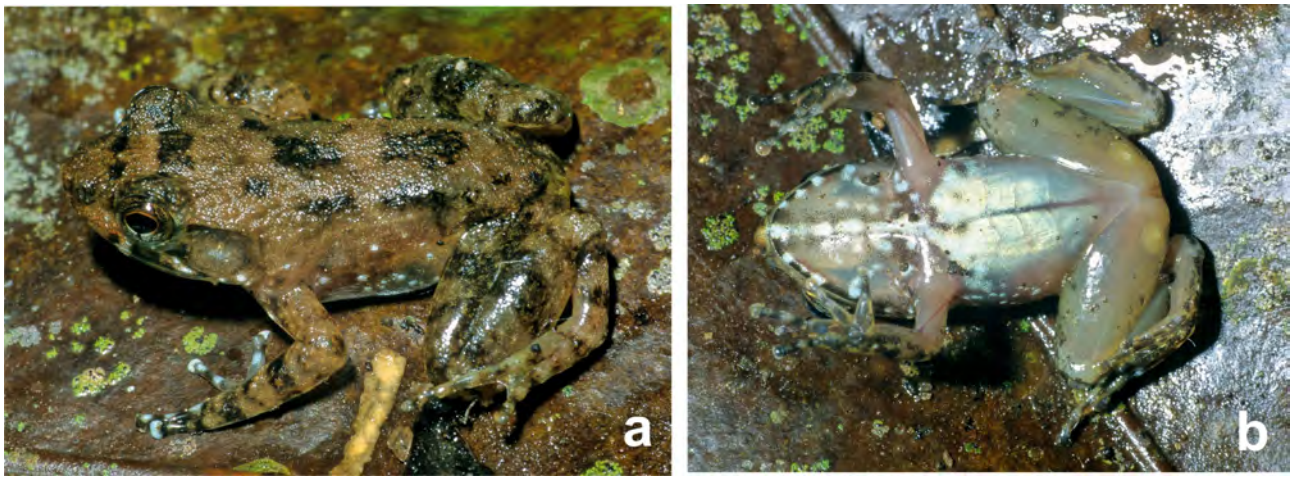

FIGURE 31. *Mantidactylus steinfartzi* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male (photos not corresponding to a voucher in ZSM; possibly deposited in UADBA or MRSN) from Antsahamanara Campsite, Manarikoba Forest, Tsaratanàna Massif, photographed in 2001. Note the relatively small-sized femoral glands, and lower amount of dark pigmentation on throat, compared to its sympatric sister species, *M. schulzi* (compare Fig. 29; small size possibly due to age effects, given that the holotype of *M. steinfartzi* **sp. nov.** has relatively large femoral glands).

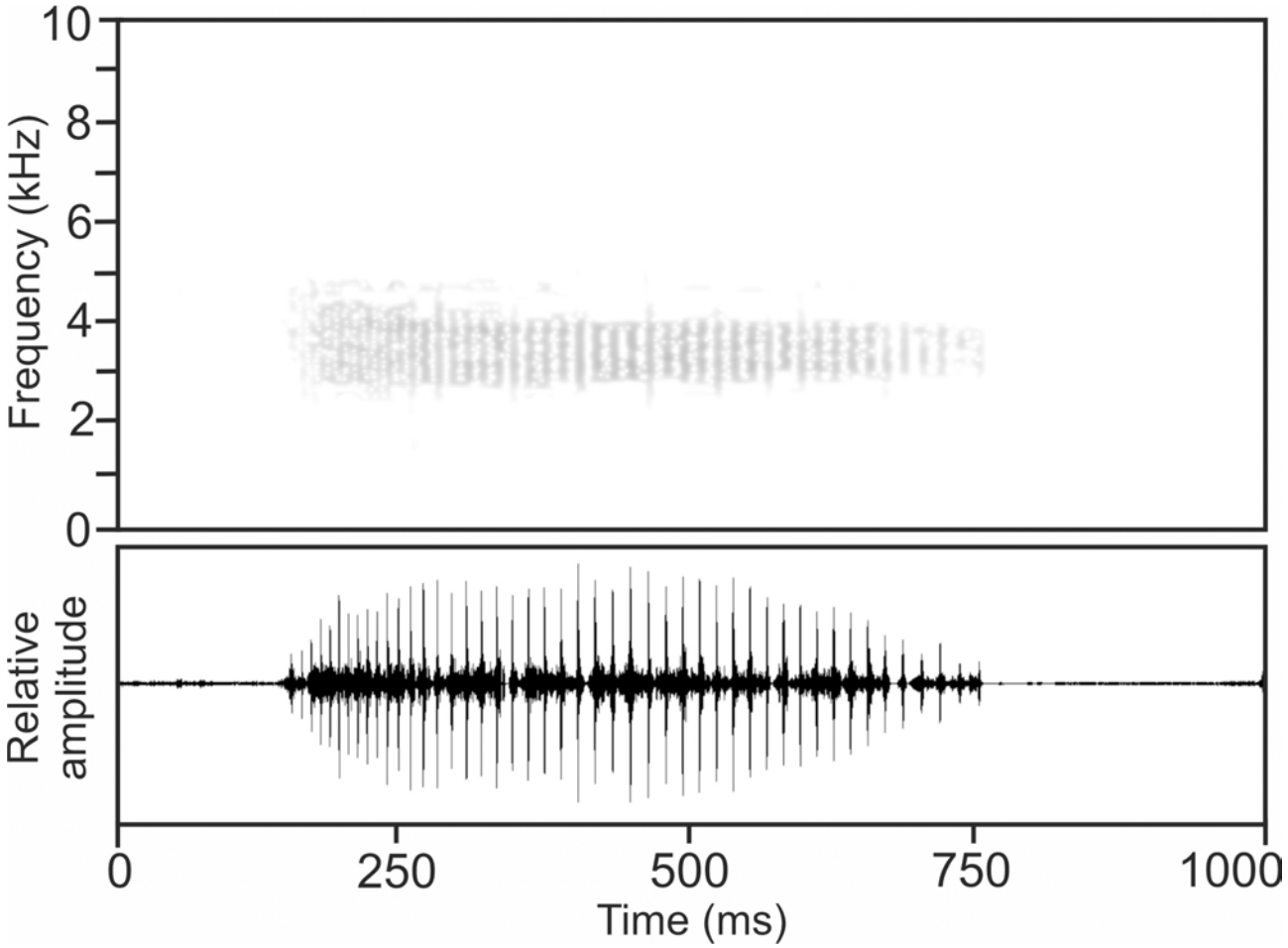

FIGURE 32. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus steinfartzi* **sp. nov.** (second call from a call group containing two calls), recorded on 4 February 2001 at Antsahamanara Campsite, Manarikoba forest, Tsaratanàna Strict Nature Reserve (20°C air temperature). Recording bandpass-filtered at 1500–5000 Hz.

Mantidactylus betsileanus clade

A rather species-rich clade of small to medium sized species (21.1–40.0 mm adult SVL), most of which are characterized by comparatively slender body shape with comparatively long limbs, relative to most other *Brygoomantis* species, and a more or less strongly expressed white tip on the snout. Contains: *M. betsileanus, M. noralottae, M. tripunctatus* (revalidated herein) and five new species (named based on holotypes depicted in Fig. 33). Note that several morphologically or bioacoustically similar species previously considered to be related to *M. betsileanus* (e.g. Glaw & Vences 2007) are here placed in a different clade (*M. fergusoni* clade, see below).

Mantidactylus betsileanus (Boulenger, 1882)

Type material.—*Rana betsileana* Boulenger, 1882 is based on an uncertain number of syntypes (Boulenger 1882 mentioned seven containers, lettered a–g, but several of these contained more than one specimen), which include BMNH 1947.2.26.33–45 (according to Blommers-Schlösser & Blanc 1991) and MCZ 15362 (on exchange from BMNH; Barbour & Loveridge 1946), from 'East Betsileo' and 'Ankafana, Betsileo'. We here designate BMNH 1947.2.26.45, an adult male, as lectotype of this species. Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

Identity.—This nomen has been assigned by Blommers-Schlösser (1979) to specimens she collected in the Northern Central East with relatively small femoral glands in males, a typical white tip on the snout, and a single-note, long, pulsed call. This definition of *Mantidactylus betsileanus* was followed in subsequent accounts (e.g. Glaw & Vences 1992a, 1994, 2007; Vences *et al.* 2006). Morphology of the lectotype (designated here) and of several paralectotypes examined agrees with this definition. Here we furthermore sequenced by barcode fishing the lectotype BMNH 1947.2.26.45 and paralectotype BMNH 1947.2.26.44, and thus provide genetic confirmation for this assignment.

Synonyms.—Several junior synonyms have been assigned to *M. betsileanus* (Blommers-Schlösser &

Blanc 1991; Frost 2021), and the identity of these nomina has remained enigmatic due to the small amount of information on their name-bearing types which are often in a poor state of preservation. By barcode fishing we here robustly assign the following names as junior synonyms to this species:

Rhacophorus fumigatus Mocquard, 1895, according to Guibé (1950), Blommers-Schlösser and Blanc (1991), and Frost (2021) based on holotype MNHN 1895.258 (by monotypy), from 'Madagascar . . . . côte ouest'. The sequence obtained from the holotype specimen clusters firmly among sequences of *M. betsileanus*. It should be noted that the type locality is probably in error as *M. betsileanus* has so far not been found on Madagascar's western coast.

Mantidactylus multiplicatus Boettger, 1913 is based on the holotype (by monotypy) SMF 6733 (formerly 1068.5a) from 'Alaotra-See, Ost-Madagascar'. The 16S sequence obtained from the holotype firmly clusters with sequences of *M. betsileanus,* confirming this nomen as a junior synonym of *M. betsileanus*, in agreement with previous assertions (e.g. Blommers-Schlösser & Blanc 1991). *Mantidactylus multiplicatus* has recently been used as a valid species name (e.g. Poth *et al.* 2012, 2013) and this view was followed by Frost (2021); however, our new data provide clear evidence that the nomen *multiplicatus* does not apply to the lineage initially studied by Poth *et al.* (2012), which instead represents a new species, described below as *M. katae* **sp. nov.**

Mantidactylus brunneus Ahl, 1929, based on an unnumbered holotype in the ZMB collection from 'Nord-West-Madagascar' that has been reported lost (Frost 2021; Guibé 1978). We rediscovered the holotype of this nomen in the ZMB collection, corresponding to ZMB 30514. The 16S sequence obtained from this specimen firmly clusters with sequences of *M. betsileanus*. As with other species named by E. Ahl, the locality is probably wrong as *M. betsileanus* is not known to occur in north-western Madagascar.

Another nomen previously considered a synonym of *M. betsileanus* (*Mantidactylus tripunctatus* Angel, 1930) (Frost 2021) is herein resurrected as the name for a genetically divergent lineage of *Brygoomantis* from southern Madagascar (see species account below).

Diagnosis.—A member of the *M. betsileanus* clade as revealed by the phylogenomic analysis, and sister to the poorly known *M. incognitus* **sp. nov.** described below. See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size in males (SVL 22–29 mm) and distinctly larger size in females (SVL 30–37 mm), slightly tubercular dorsal skin with distinct continuous dorsolateral ridges, reduced webbing (one phalanx of fifth toe free of web), absence of white spots on flanks, presence of a white marking on snout tip, and advertisement call consisting of a single, long note composed of more than 100 pulses distinguishes *M. betsileanus* from species of all other clades. Within the *M. betsileanus* clade, the species

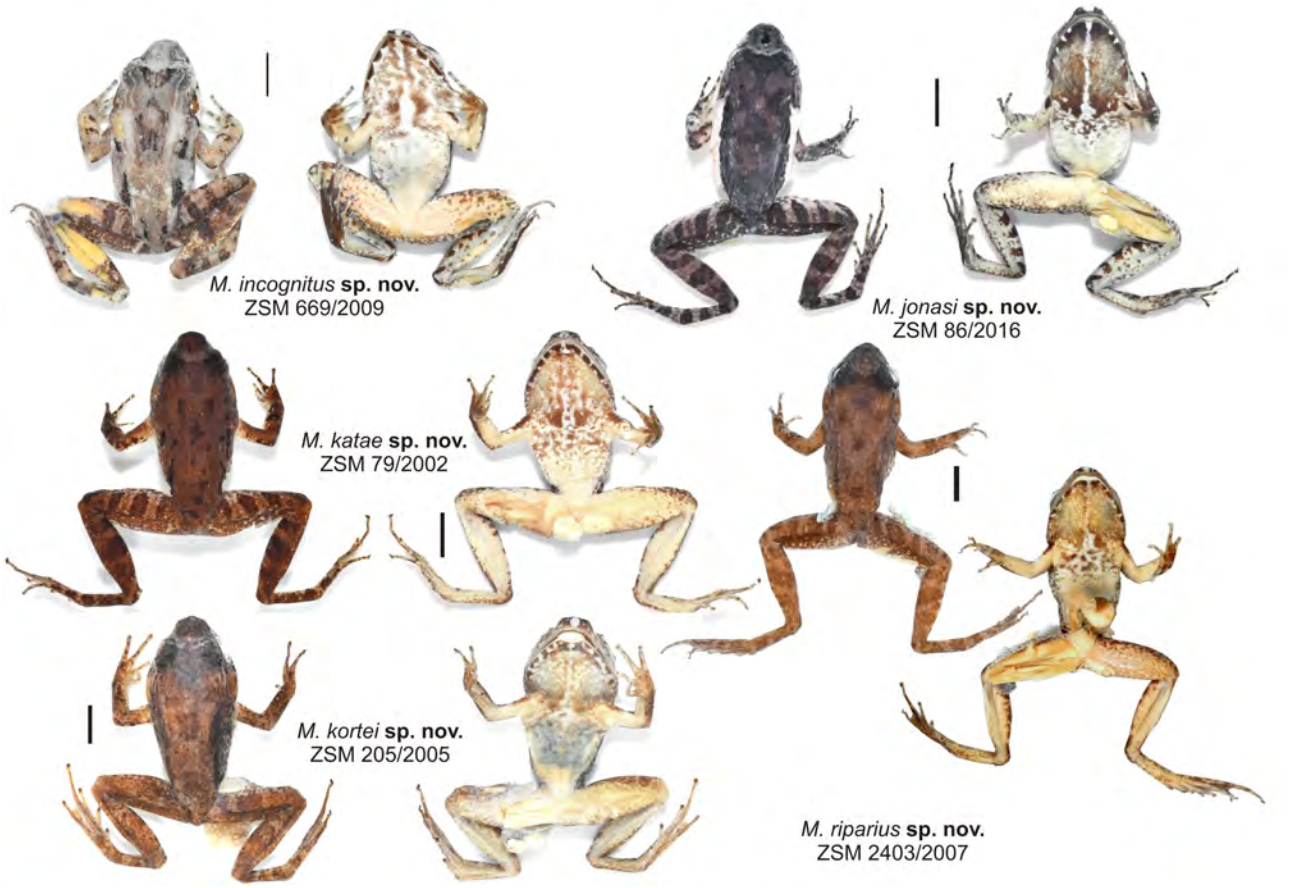

FIGURE 33. Preserved holotype specimens of newly named species in the *M. betsileanus* clade. Scale bars equal 5 mm.

FIGURE 34. *Mantidactylus betsileanus* in life, in anterior, dorsolateral, and ventral view. (a,b,c) Adult male from Andasibe, photographed in 1991. (d) Adult male from Andasibe, photographed in situ in a small cavity next to a swamp where it was emitting its call, photographed in 1991. (e,f) Adult male from Mahasoa, photographed in 2008. (g,h) Adult male from Andasibe, photographed in 1995. Note in the ventral views the relatively small femoral glands, with the distal ulcerous macroglands placed at considerable distances from each other, which constitutes a typical character state of this species; and in the frontal view (a), the white dot on the snout tip which is typical for this and several allied species.

differs from all species except possibly *M. incognitus* **sp. nov.** (for which calls are unknown) by a higher number of pulses in its advertisement calls (Table 4); it also differs from *M. noralottae* by smaller size of males, and from the sympatric *M. katae* **sp. nov.** by smaller size of femoral glands (see account of that species below). For a detailed distinction from its sister species *M. incognitus* **sp. nov.**, and from all other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. betsileanus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 7. See Fig. 34 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 21.9–29.0 mm [n = 11] vs confirmed female SVL 29.5–36.2 mm [n = 10]). Males also have distinctly larger tympanum sizes

than females (HTD/ED ratio is 57–78% in females, 72–115% in males). Femoral glands are relatively small, indistinct, and relatively widely spaced, i.e. the distal ulcerous macrogland on opposite thighs are rather widely separated and the proximal granular gland fields are indistinct, although probably present. The proximal granular gland fields on opposite thighs probably are contacting each other medially (compare with the syntopic *M. katae* **sp. nov.** which has much larger femoral glands).

Natural history.—A common species whose typical calls are often heard from small running water bodies in rainforest but also in forest fragments and degraded areas or plantations nearby. Calls are emitted during day and night, especially during the day often from concealed positions directly at the edge of water. Very common in swamp areas, also ricefields next to rainforest, as long as the water is shallow and is at least very slightly flowing. Usually sitting in shallow water or along the stream bank, hiding in the leaf litter nearby water bodies or sometimes found sitting on low vegetation about 0.3 m hight. In Ranomafana and surrounds found at an elevational range between 550–1132 m a.s.l. *M. betsileanus* was successfully bred in captivity in the Mitsinjo amphibian husbandry research and captive breeding facility at Andasibe (Edmonds *et al.* 2012). The size and structure of a population from near Andasibe was studied by Edmonds *et al.* (2019).

Calls.—The advertisement call of *M. betsileanus*, recorded on 29 January 1994 at Mandraka, 23–24°C air temperature (Vences *et al.* 2006: CD2, track 62, cut 1), consisted of a long, regularly pulsed note (Fig. 35), emitted at more or less regular intervals, but always in slow succession. Notes exhibited some amplitude modulation, with call energy increasing rapidly to the maximum at the beginning of the note, followed by continuous decrease of energy towards the note's end. Pulse repetition rate was higher in the centre of the note and slightly lower at its beginning and end. Call energy was distributed across a wide frequency range. Numerical parameters of four analysed calls were as follows: call duration (= note duration) 2907–3103 ms (3046.5 ± 93.3 ms); 165–178 pulses per note (173.0 ± 7.7); pulse duration 4–7 ms (5.5 ± 1.0 ms); pulse repetition rate within notes 46.3–64.5 pulses/s (57.0 ± 5.1); dominant frequency 1399–1421 Hz (1410 ± 12 Hz), with a second peak of almost identical energy at around 2650 Hz; prevalent bandwidth 1100–6000 Hz; call repetition rate (= note repetition rate) ca 3.7 calls/min.

Calls recorded on 12 February 2008 at a forest fragment northeast of Lake Alaotra, at an estimated

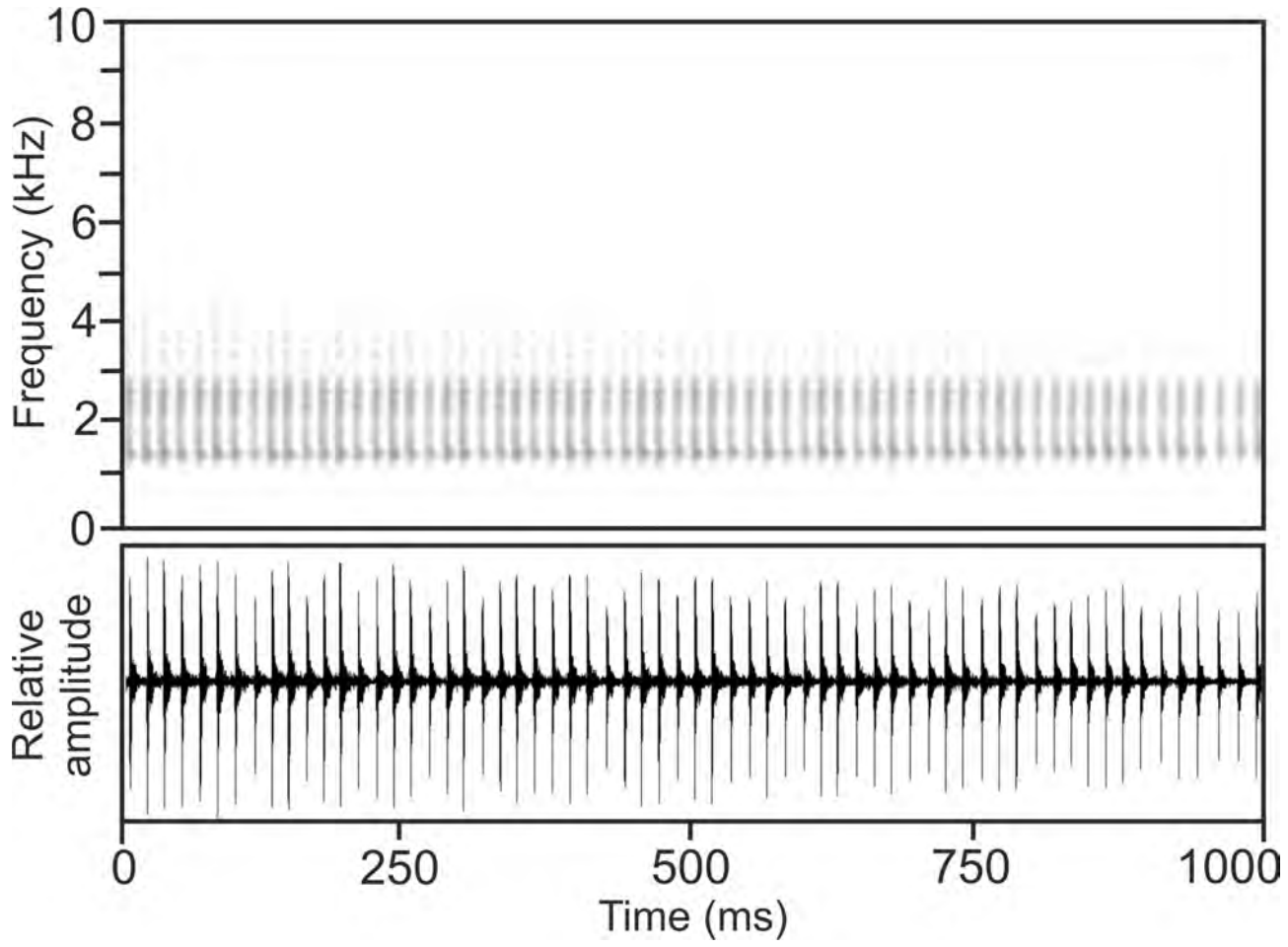

FIGURE 35. Audiospectrogram and corresponding oscillogram of a 1000 ms section of one advertisement call (call duration 3109 ms) of *Mantidactylus betsileanus*, recorded on 29 January 1994 at Mandraka (23–24°C air temperature). Recording bandpass-filtered at 550–8000 Hz.

20–25°C air temperature, perfectly agreed with the call described above from Mandraka. Numerical parameters of five analysed calls were as follows: call duration (= note duration) 2464–3650 ms (3235.0 ± 438.3 ms); 181–199 pulses per note (192.3 ± 9.9); pulse duration 4–7 ms (5.3 ± 0.9 ms); pulse repetition rate within notes 39.5–71.4 pulses/s (56.8 ± 12.1); dominant frequency 1356–1464 Hz (1404 ± 42 Hz), with a second peak of almost identical energy at around 2800–2900 Hz; prevalent bandwidth 1100–6000 Hz; call repetition rate (= note repetition rate) ca 3.1 calls/min.

Calls recorded on 25 March 2006, 18:00 h, at the crossing of the Moramanga-Anosibe An'Ala and Besariaka roads, estimated 20–25°C air temperature, also agreed with the calls described from Mandraka. Although difficult to analyse in detail due to many overlapping calls (including those of syntopic *M. inaudax*), following numerical parameters could be measured (10 calls originating from at least three individuals analysed): call duration (= note duration) 1560–2279 ms (2010.9 ± 278.6 ms); 107–173 pulses per note (136.0 ± 33.7); pulse duration 2–5 ms (3.6 ± 0.8 ms); pulse repetition rate within notes 63.5–81.6 pulses/s (74.0 ± 6.5); dominant frequency 1261–1574 Hz (1414 ± 148 Hz), with a second peak of almost identical energy at around 2700–3150 Hz; prevalent bandwidth 1000–4200 Hz

Calls recorded on 25 March 2006, at night, at the orchid garden in Andasibe, estimated 20–25°C air temperature, agreed with the calls described above as well. Numerical parameters of six analysed calls, originating from two individuals are as follows: call duration (= note duration) 1887–2868 ms (2439.0 ± 351.9 ms); 173–201 pulses per note (184.3 ± 14.7); pulse duration 4–7 ms (5.5 ± 0.9 ms); pulse repetition rate within notes 56.0–105.3 pulses/s (70.1 ± 17.1); dominant frequency 1238–1340 Hz (1289 ± 38 Hz), with a second peak of almost identical energy at around 2700–2900 Hz; prevalent bandwidth 1000–4600 Hz; call repetition rate (= note repetition rate) ca 4–5 calls/min.

A divergent call has been recorded from specimen MRSN A6343 (FAZC 13875; accession number of 16S sequence HM364713), at Betampona. The calls of this individual were recorded at 19:00 on 14 November 2007, at 20°C air temperature. They consisted of a very long, regularly pulsed note, with very short pulses. Numerical parameters of five analysed calls were as follows: call duration (= note duration) 3490–7507 ms (6148.8 ± 1552.6 ms); 78–164 pulses per note (134.8 ± 33.6); pulse duration 2 ms (2.0 ± 0.0 ms); pulse repetition rate within notes 19.2–24.6 pulses/s (21.9 ± 1.7); dominant frequency 1670–1826 Hz (1719 ± 61 Hz); prevalent bandwidth 1000–4800 Hz. Especially the pulse repetition rate in these calls differed strongly from all other available recordings and we have therefore not included it in the characterization of this diagnostic feature in Table 4. More data on the advertisement calls and genetics of *M. betsileanus* at Betampona are necessary to understand the identity of this population and exclude the possibility of mitochondrial introgression into another *Brygoomantis* species at this site.

Tadpoles.—The tadpole of *M. betsileanus* was described by Blommers-Schlösser (1979), Knoll *et al.* (2007), and Scheld *et al.* (2013). The effect of diet on their development was reported by Soamiarimampionona *et al.* (2015).

Distribution.—Widespread over a large area of central Madagascar, from sea level on the east coast to the central highlands (Fig. 7). This species is known from the vicinity of Lac Alaotra (type locality of *M. multiplicatus*), Ambatovaky, Ambodisakoa, Ambohitantely, Andasibe, Anjozorobe, Anosibe An'Ala, Antara, Antsirakambiaty forest, Befanjana, Betampona, Fierenana, Fivahona, Itremo, Mahasoa, Mandraka, Maromizaha, Marotandrano-Riamalandy, Namoly, Ranomafana and surrounds, Sahambaky Forest (Lakato), Torotorofotsy, Tsaranoro, and Tsinjoarivo. Elevation range: 190–1648 m a.s.l.

Etymology.—Latin adjective meaning 'of or from Betsileo', derived from the region Betsileo and the suffix -ânus meaning 'of or pertaining to'.

Mantidactylus noralottae Mercurio & Andreone, 2007

Type material.—The species is based on holotype (by original designation) MRSN A5317 from 'Ambovo, Parc National de l'Isalo, Fianarantsoa Faritany, Ranohira Fivondronana, 22°30.48′S, 45°21.15′E, 996 m a.s.l.'. A total of 12 paratypes were defined in the original description: MRSN A5036 (FAZC 13021), MRSN A5035 (FAZC 13020), MRSN A5254 (FAZC 13008), MRSN A5318 (FAZC 13024), SMF 85861 (ex MRSN A5253 / FAZC 13007), SMF 85862–85864 (ex MRSN A5255–5257 / FAZC 13011–13013), MRSN A5252 (FAZC 13005), PBZT-FAZC 12996, PBZT-FAZC 12998, and ZSM 49/2011 (ex MRSN A5319 / FAZC 13022), all with the same locality, date and collector as the holotype.

Identity.—This species is genetically defined by the sequences of various paratypes published in the original description (MRSN A5252 and A5254; SMF 85861–SMF 85864 corresponding to previous MRSN A5253 and A5255–A5257; Mercurio & Andreone 2007). Unfortunately, no genetic data are available for the holotype or the call voucher paratype, MRSN A5317. However, both the holotype and the call voucher are comparatively large-sized individuals of 34.8 and 33.4 mm SVL, respectively, and thus distinctly larger than the second species of the *M. betsileanus* clade occurring at Isalo (described below as *M. riparius* **sp. nov.**). Furthermore, according to measurements in Mercurio & Andreone (2007) and here reproduced in Table 7, the male holotype of *M. noralottae* has a smaller relative tympanum size and smaller femoral glands than the third species of *Brygoomantis* at Isalo, *M. mahery* (see above and Tables 4–5), confirming the holotype of *M. noralottae* is conspecific with the paratypes and other individuals usually assigned to this taxon.

Diagnosis.—A member of the *M. betsileanus* clade as revealed by the phylogenomic analysis, sister to *M. kortei* **sp. nov.** described below. See Table 4 for a list of diagnostic morphological characters. The combination

of a moderate body size in males (SVL 33–36 mm) and distinctly larger size in females (SVL 36–40 mm), rather smooth to slightly tubercular dorsal skin with distinct continuous dorsolateral ridges, relatively large tympanum (10–12% of SVL), absence of white spots on flanks, absence of a white marking on snout tip, and advertisement call consisting of a single, long note composed of ≥90 pulses distinguishes *M. noralottae* from species of all other clades (Table 4); *M. noralottae* may appear superficially similar to some species of the *M. curtus* clade but these have a smaller tympanum and less pulses in advertisement calls. Within the *M. betsileanus* clade, the species differs from all species except *M. betsileanus* (for *M. incognitus* **sp. nov.** calls are unknown) by a higher number of pulses in advertisement calls (Table 4); it differs from these two species by larger body size of males, and from *M. betsileanus* also by fewer pulses in advertisement calls (Table 4). For a detailed distinction from its sister species *M. kortei* **sp. nov.**, from the sympatric *M. riparius* **sp. nov.**, and from all other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. noralottae* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 7. See Fig. 36 for colouration in life and its variation. A light vertebral line can be present. There is moderate sexual size dimorphism (confirmed male SVL 32.8–35.5 mm [n = 4] vs confirmed female SVL 35.5–40.0 mm [n = 7]). Tympanum size is somewhat larger in males compared to females (HTD/ED ratio is 56–63% in females, 63–95% in males). Femoral glands in males are not very prominent and not conspicuously coloured.

Natural history.—According to Mercurio and Andreone (2007) the species inhabits canyons in the Isalo limestone massif, and can be found from the initial openings all the way to their deep end (eg. Anjofo waterfall). Individuals can climb on rocks and cling at 150–200 cm height above the water or the ground. Mercurio and Andreone (2007) also provide some information on stomach content, according to which the species feeds on different groups of insects. Although the species co-occurs with *M. noralottae* at Isalo, the two species have so far not been found in the same streams or at exactly the same sites in this massif.

Calls.—The advertisement call of *M. noralottae*, recorded on 18 December 2004, 20:00 h, at Ambovo, Isalo National Park, 20°C air temperature (from paratype MRSN A5319), consisted of a very long, regularly pulsed note (Fig. 37), emitted in irregular series. Each note showed some significant amplitude modulation with call energy slowly increasing to approximately the middle of the note's duration and then slowly decreasing towards its end. Numerical parameters of five analysed calls were as follows: call duration (= note duration) 2054–2705 ms (2411.4 ± 273.9 ms); ca 92–108 pulses per note (100.6 ± 7.1); pulse duration 9–15 ms (10.9 ± 1.6 ms); pulse repetition rate within notes 37.4–41.2 pulses/s (39.7 ± 1.3); dominant frequency 1345–1405 Hz (1370 ± 26 Hz); prevalent bandwidth 1200–2100 Hz; call repetition rate (= note repetition rate) ca 12 calls/min.

Tadpoles.—The tadpole of this species has not been described.

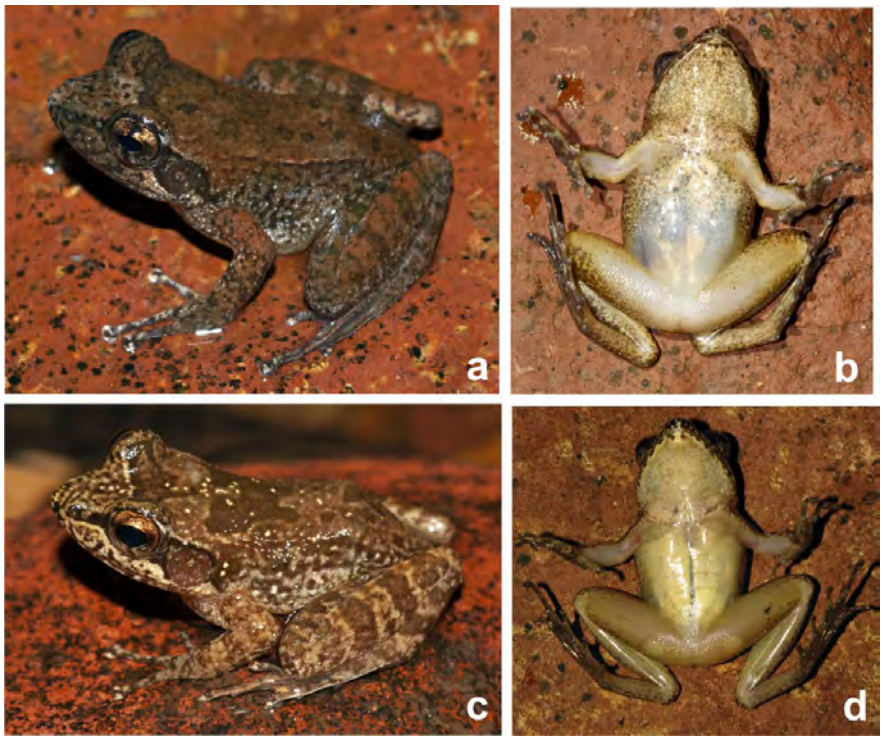

FIGURE 36. *Mantidactylus noralottae* from the Isalo massif in life, in dorsolateral and ventral view. (a,b) Adult female (tissue ACZC 7948; FAZC 14340). (c,d) Adult male (tissue ACZC 7947; FAZC 14339).

TABLE 7. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus betsileanus* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype. An asterisk (*) marks lectotypes designated in the current paper. A hash (#) marks measurements taken by AH, an asterisk (*) specimens measured by V. Mercurio and F. Andreone, and thus not fully comparable with other measurements, all taken by MV. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
M. betsileanus																			
BMNH 1947.2.26.45 [LT*]	NA	M	Betsileo and Ankafana	22.8	7.6	8.9	3.2	2.3	2.4	1.5	2.5	13.5	6.0	40.1	17.8	12.8	NM	2	1.6
BMNH 1947.2.26.33 # [PLT]	NA	F	Betsileo and Ankafana	31.5	11.8	10.5	4.4	2.5	2.9	2.1	3.3	11.3	9.3	NM	NM	17.5	18.8	NA	NA
BMNH 1947.2.26.34 # [PLT]	NA	F	Betsileo and Ankafana	30.3	11.5	10.4	4.2	3.0	3.0	2.3	3.4	11.5	9.5	NM	NM	16.3	17.5	1.1	1.0
BMNH 1947.2.26.41 # [PLT]	NA	F	Betsileo and Ankafana	30.7	11.9	10.5	4.4	2.9	2.9	1.9	3.5	10.3	8.6	NM	NM	14.9	16.9	0.8	0.7
BMNH 1947.2.26.42 # [PLT]	NA	F	Betsileo and Ankafana	29.5	11.1	10.4	3.8	2.7	3.2	2.2	3.3	10.2	8.8	NM	NM	16.5	17.7	1.3	0.9
BMNH 1947.2.26.44 [PLT]	NA	F	Betsileo and Ankafana	30.0	10.2	10.9	4.0	2.3	2.8	2.0	3.3	17.5	8.6	57.4	26.6	17.7	NM	NA	NA
ZMB 30514 [HT *brunneus*]	NA	F	Probably eastern or central Madagascar	31.4	10.8	11.8	4.0	2.7	2.9	1.9	3.5	17.0	8.2	53.5	24.5	16.2	16.6	NA	NA
SMF 6733 [HT *multiplicatus*]	NA	F	Lac Alaotra	36.2	12.8	14.6	4.6	3.0	3.8	2.4	3.6	19.5	9.5	59.9	27.9	19.6	19.9	NA	NA
MNHN 1895.258 [HT *fumigatus*]	NA	F	West coast of Madagascar	33.2	11.8	13.6	3.5	2.4	3.2	2.5	3.1	NM	NM	NM	NM	NM	NM	NA	NA
MRSN A7042	FAZC 15565	F	Maromizaha	35.5	12.4	13.6	4.6	3.6	3.0	2.4	3.4	21.4	9.4	62.0	28.5	19.3	18.9	NA	NA
ZSM 200/2021	FAZC 15578	F	Maromizaha	34.4	11.3	14.0	4.7	3.4	2.9	2.5	4.0	20.0	8.9	59.4	21.3	17.4	17.8	NA	NA
ZMA 20206	ZCMV 53	M	Ranomafana	24.3	9.8	8.9	3.5	3.3	2.6	2.0	2.6	8.7	6.6	NM	NM	12.2	13.3	3.0	2.1
ZMA 20210	ZCMV 141	M	Ranomafana	24.1	9.2	8.1	3.3	3.7	2.1	1.6	2.6	7.7	6.1	NM	NM	11.4	12.2	2.7	2.0
ZSM 1772/2008	ZCMV 8017	M	Ranomafana	21.9	8.2	9.6	3.4	3.0	2.0	1.8	2.8	13.9	7.2	39.9	17.7	12.5	12.2	2.5	1.9
ZSM 1773/2008	ZCMV 8068	M	Ambodisakoa	25.0	9.0	10.5	3.8	4.1	2.9	2.1	3.3	15.7	7.4	41.1	19.0	13.3	12.8	3.0	2.0
ZSM 1774/2008	ZCMV 8776	M	Mantadia (Camp Prolemur)	28.5	11.1	12.0	4.0	4.6	2.9	1.8	3.0	16.4	7.8	47.5	22.4	15.2	14.1	3.0	1.5
ZSM 1775/2008	ZCMV 8778	M	Mantadia (Camp Prolemur)	29.0	10.7	12.6	4.5	4.6	2.8	2.0	3.0	15.5	7.6	46.5	21.7	15.2	13.5	2.7	2.3

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TABLE 7. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 391/2006	ZCMV 3260	M	Andasibe	26.2	10.1	11.7	4.4	4.3	3.3	2.2	3.0	17.1	8.7	51.9	23.8	16.5	15.5	3.0	1.8
ZSM 738/2009	ZCMV 7164	M	Befanjana	28.9	10.4	11.8	4.5	3.8	3.3	1.8	3.0	18.3	8.6	48.2	22.0	14.1	15.6	3.2	2.0
ZSM 739/2009	ZCMV 7293	M	Befanjana	27.4	10.5	12.9	4.4	3.4	2.7	1.9	2.8	17.0	7.9	48.5	22.2	15.0	14.9	3.7	2.3
ZSM 82/2002	FGMV 2001.1049	M	Andasibe	27.8	10.5	10.2	3.8	3.9	2.6	1.8	3.1	10.0	8.0	NM	NM	14.3	14.6	2.6	1.7
M. noralottae																			
MRSN A5317 * [HT]	NA	M	Isalo	34.8	13.5	15.0	4.9	4.0	3.3	2.5	3.7	17.8	10.0	NM	25.9	18.7	NM	2.2	2.5
MRSN A5036 * [PT]	NA	M	Isalo	35.5	12.9	14.8	5.2	4.2	3.0	2.3	3.7	19.8	11.5	NM	29.8	19.3	NM	2.0	1.7
MRSN A5319 * [PT]	NA	M	Isalo	33.4	12.2	13.0	4.0	3.8	3.2	1.8	3.6	18.3	11.0	NM	28.3	18.3	NM	2.5	2.0
SMF 85861 * [PT]	NA	M	Isalo	32.8	13.5	12.8	5.1	3.2	3.4	2.3	3.7	14.9	9.1	NM	28.6	18.3	NM	2.0	2.0
MRSN A5252 * [PT]	NA	F	Isalo	38.8	14.5	16.6	5.5	3.4	4.4	2.2	4.5	18.8	11.0	NM	27.8	19.9	NM	NA	NA
MRSN A5254 * [PT]	NA	F	Isalo	37.7	13.3	14.5	5.5	3.4	3.4	3.3	4.4	18.8	11.1	NM	26.7	19.9	NM	NA	NA
MRSN A5318 * [PT]	NA	F	Isalo	38.5	15.2	16.3	5.6	3.6	3.2	2.8	4.3	19.8	11.5	NM	30.5	20.5	NM	NA	NA
SMF 85862 * [PT]	NA	F	Isalo	37.8	14.1	14.7	5.9	3.3	3.2	2.8	3.9	17.5	9.6	NM	29.1	18.8	NM	NA	NA
SMF 85863 * [PT]	NA	F	Isalo	35.5	13.3	14.5	4.4	3.2	3.3	3.3	4.4	18.8	11.1	NM	27.0	19.6	NM	NA	NA
SMF 85864 * [PT]	NA	F	Isalo	40.0	15.5	15.5	5.6	3.4	4.4	2.2	3.4	20.0	11.1	NM	31.1	21.1	NM	NA	NA
ZSM 49/2011 [PT]	FAZC 13020 / MRSN A5035	F	Isalo	36.9	13.6	15.2	5.3	3.8	3.7	2.6	4.1	23.1	11.5	62.6	28.4	18.7	19.7	NA	NA
ZSM 188/2021	ACZCV 295	J?	Isalo, Canyon des rats	26.2	9.6	10.9	3.8	2.8	2.5	2.0	3.0	16.2	9.0	44.7	19.6	12.9	13.7	NA	NA
M. tripunctatus (Ca29)																			
MNHN 1931 23 # [PLT]	NA	J?	St.Louis (Fort Dauphin), Befotaka (Farafangana)	21.1	8.7	8.5	3.3	2.7	2.5	1.3	2.6	6.0	6.1	NM	NM	10.4	11.9	NA	NA
MNHN 1931.24 [LT*]	NA	J?	St.Louis (Fort Dauphin), Befotaka (Farafangana)	23.0	8.5	10.2	3.4	2.0	2.7	1.7	2.6	18.4	6.6	37.2	17.2	12.5	12.0	NA	NA
MNHN 1931.21 [PLT]	NA	F?	St.Louis (Fort Dauphin), Befotaka (Farafangana)	28.7	10.8	12.2	3.2	2.4	3.0	2.5	3.2	17.5	8.3	NM	22.6	15.8	15.6	NA	NA
ZSM 71/2004	FGZC 119	M	Andohahela	26.4	10.3	11.5	4.3	4.0	3.0	1.9	3.1	17.5	8.0	45.6	20.0	13.5	14.3	3.9	2.0
ZFMK 52665 #	NA	M?	Tolagnaro (Fort Dauphin)	27.4	10.8	10.8	4.4	3.6	3.0	1.9	2.8	9.3	7.4	NM	NM	12.7	13.8	2.1	1.8

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TABLE 7. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZFMK 52663 #	NA	M	Tolagnaro (Fort Dauphin)	26.6	10.7	9.9	4.0	3.7	2.5	1.6	3.0	9.5	8.6	NM	NM	13.0	14.2	3.4	2.0
ZFMK 53666 #	NA	M	Tolagnaro (Fort Dauphin)	27.0	11.1	10.4	3.9	3.7	3.0	2.3	3.1	9.5	7.4	NM	NM	13.7	13.8	3.8	2.4
ZFMK 52664 #	NA	F	Tolagnaro (Fort Dauphin)	35.1	13.6	12.6	4.9	3.6	3.4	3.0	3.5	12.5	9.3	NM	NM	15.9	19.2	NA	NA
ZFMK 53667 #	NA	F	Tolagnaro (Fort Dauphin)	32.9	12.0	12.3	4.8	3.2	3.6	2.4	3.3	NM	NM	NM	NM	15.3	16.8	NA	NA
ZFMK 56185 #	NA	F	Nahampoana	34.1	12.9	12.7	4.9	2.6	3.2	2.3	3.7	11.7	10.1	NM	NM	16.8	17.9	NA	NA
ZSM 172/2004	FGZC 318	F	Manantantely	33.8	12.7	13.3	5.0	3.3	3.5	1.9	3.7	20.8	9.4	59.0	25.4	18.5	18.0	NA	NA
ZSM 70/2004	FGZC 117	F	Andohahela	34.7	12.6	14.4	4.4	4.1	3.1	2.7	3.9	22.6	10.0	62.5	28.4	19.3	19.3	NA	NA
M. incognitus **sp. nov.** (Ca34)																			
ZSM 669/2009 [HT]	ZCMV 8945	F	Mahanoro	26.4	10.6	11.7	4.1	2.5	3.0	2.2	3.0	15.3	8.0	48.8	20.9	14.3	15.0	NA	NA
MRSN A6694 [PT]	RJS 1801 (ACZC 4189)	M	Anivorano Est	27.4	10.6	12.0	4.5	3.8	2.4	2.0	3.8	16.2	7.7	44.9	21.4	14.7	14.4	4.1	2.8
M. jonasi **sp. nov.**																			
ZSM 86/2016 [HT]	MSZC 0180	M	Ampotsidy	24.2	8.6	9.7	4.3	4.0	2.5	1.9	2.9	14.4	7.2	39.7	18.9	13.0	11.6	2.5	1.7
ZSM 133/2018 [PT]	MSZC 0714	M	Montagne d'Ambre	24.8	10.5	10.8	3.5	4.4	2.6	1.9	3.2	15.6	7.8	42.9	19.6	13.9	13.1	3.0	1.9
ZSM 134/2018 [PT]	MSZC 0715	M	Montagne d'Ambre	24.9	10.0	10.4	3.6	3.6	2.6	1.7	3.0	15.8	7.5	41.6	19.3	13.3	12.8	3.0	2.1
ZSM 1773/2010 [PT]	ZCMV 12603	M	Bealanana-Antsohihy	23.8	9.3	10.4	3.8	3.5	2.5	1.5	2.5	14.2	7.2	40.7	19.0	12.9	11.9	3.0	2.0
ZSM 1774/2010 [PT]	ZCMV 12604	M	Bealanana-Antsohihy	22.8	8.6	9.9	3.5	3.4	2.0	1.8	2.5	14.0	6.9	39.9	18.0	12.6	11.9	2.7	1.7
ZSM 2220/2007 [PT]	FGZC 1368	M	Montagne d'Ambre	23.1	9.2	9.8	3.5	3.8	2.4	1.8	2.4	14.7	7.0	40.9	18.1	12.7	12.6	3.5	2.0
ZSM 2222/2007 [PT]	FGZC 1372	M	Montagne d'Ambre	24.5	10.0	10.8	3.4	3.5	2.7	1.9	2.9	15.0	6.8	42.4	19.8	13.4	13.0	4.0	2.5
ZSM 551/2009 [PT]	ZCMV 11462	M	Makira West	22.4	8.4	9.6	3.1	3.4	2.2	1.5	2.5	13.6	7.5	34.7	17.6	12.1	11.8	3.4	2.2
ZSM 89/2016 [PT]	MSZC 0194	M	Andranonafindra	24.6	9.6	10.4	4.0	4.3	2.6	1.5	2.6	15.1	7.4	41.2	20.1	13.8	12.7	3.9	2.2
M. katae **sp. nov.** (Ca28)																			
ZSM 79/2002 [HT]	FGMV 2001.1179 (2002.G24)	M	Andasibe	24.6	9.9	10.3	4.0	2.9	2.5	1.6	2.6	15.7	7.3	43.7	19.4	13.0	13.4	4.1	2.6

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TABLE 7. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 637/2003 [PT] #	FGMV 2002.132	M	Ranomafana	23.2	9.6	8.7	3.3	2.7	2.3	1.8	2.7	8.2	7.8	NM	NM	12.1	13.6	3.5	2.4
ZSM 668/2003 [PT] #	FGMV 2002.255	M	Ranomafana	24.5	9.4	9.0	4.1	3.1	2.3	1.8	2.6	8.7	7.7	NM	NM	13.0	14.0	4.3	3.3
ZSM 708/2003 [PT] #	FGMV 2002.348	M	Ranomafana	22.1	9.0	8.5	3.2	2.7	2.0	1.3	2.7	7.5	6.6	NM	NM	11.0	12.6	3.8	2.4
ZSM 81/2002 [PT]	FGMV 2001.1275 (2002.G66)	M	Andasibe	26.1	9.1	10.6	3.4	3.2	2.4	1.9	2.6	14.9	7.1	43.5	20.5	14.1	13.5	4.7	2.8
ZSM 91/2004	FGZC 163	M	Andohahela	27.2	9.9	11.5	4.0	3.7	2.8	1.9	3.4	17.3	8.2	46.0	21.6	NM	13.6	4.5	2.7
ZSM 196/2021 [PT]	FAZC 15504	M	Maromizaha	25.6	9.8	10.6	4.0	3.5	2.5	2.2	2.9	15.5	7.1	41.4	18.8	13.6	12.7	4.3	2.9
ZSM 197/2021 [PT]	FAZC 15507	M	Maromizaha	25.5	9.7	10.3	4.1	3.4	2.1	1.9	3.0	15.0	7.9	45.3	20.1	13.7	13.8	4.0	2.9
ZSM 80/2002 [PT] #	FGMV 2001.1180	F	Andasibe	25.6	10.1	9.5	3.7	2.5	2.9	2.3	3.0	10.0	7.7	NM	NM	13.4	15.5	1.4	1.4
ZSM 83/2002 [PT]	FGMV 2001.1173 (2002.G18)	F	Andasibe	35.9	12.8	13.6	5.0	3.4	3.3	2.2	3.8	20.7	9.5	61.8	27.7	18.8	18.5	1.1	1.1
MRSN A7043 [PT]	FAZC 15523	F	Maromizaha	32.5	12.6	13.8	4.4	2.7	3.0	2.5	3.7	20.6	8.7	59.6	27.0	17.7	18.6	NA	NA
M. kortei **sp. nov.**																			
ZSM 205/2005 [HT]	FGZC 2376	M	Andohahela	27.4	11.1	11.8	4.1	3.6	2.8	1.9	3.7	16.7	8.4	43.1	20.2	13.9	12.7	5.8	2.6
ZSM 195/2005 [PT]	FGZC 2480	F	Andohahela	34.6	12.3	13.7	4.4	3.2	3.1	2.4	3.9	19.1	9.5	55.6	25.5	17.5	16.9	NA	NA
ZSM 203/2005 [PT]	FGZC 2377	F	Andohahela	37.1	12.6	13.6	4.0	3.2	3.6	2.0	3.1	20.8	9.8	55.0	24.6	17.1	16.7	NA	NA
ZSM 204/2005 [PT]	FGZC 2375	F	Andohahela	35.0	13.5	14.4	4.7	3.7	3.4	2.7	4.3	21.7	10.7	58.3	27.0	18.6	17.6	1.7	1.3
M. riparius **sp. nov.**																			
ZSM 2403/2007 [HT]	ZCMV 5766	M	Isalo	27.3	10.5	11.4	4.4	3.6	2.6	2.2	3.0	16.0	8.1	45.1	20.7	14.3	13.7	5.0	2.1
ZSM 186/2021 [PT]	ACZCV 281	F	Isalo: Andremanero	27.3	10.0	11.2	4.0	2.7	2.7	2.0	3.0	16.8	7.7	43.5	19.4	13.5	13.4	NA	NA
ZSM 187/2021 [PT]	ACZCV 283	F	Isalo: Andremanero	21.5	7.3	9.0	3.3	2.0	1.9	1.4	2.6	12.0	5.7	34.2	14.7	10.0	10.5	NA	NA

Distribution.—Apparently microendemic to the Isalo massif (Fig. 7). Elevation range: 640–996 m a.s.l.

Etymology.—Eponym for Nora Lotta Mercurio née Fröhder, wife of V. Mercurio, one of the authors of the original description.

Mantidactylus tripunctatus Angel, 1930 **bona species**

Type material.—*Mantidactylus tripunctatus* Angel, 1930 is based on syntypes: MNHN 1931.21, 1931.23–25 and MCZ 14280 [formerly MNHN 1931.22] (Barbour & Loveridge 1946; Guibé 1978), from 'Pic St. Louis, province de Fort-Dauphin' and 'Befotaka, province de Farafangana ... à l'altitude de 700 mètres, au bord d'un torrent, en forêt'. We here designate MNHN 1931.24, probably a subadult/juvenile specimen from Pic St. Louis, as lectotype because we could obtain genetic data from this specimen. Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

Identity.—This nomen has been considered a *nomen dubium* by Guibé (1978), Blommers-Schlösser and Blanc (1991) and Glaw and Vences (1992a), and as a junior synonym of *M. betsileanus* by Frost (2021). Using barcode fishing we obtained a 16S sequence of the lectotype which firmly clusters among sequences of a lineage morphologically similar to *M. betsileanus* that is widespread and common in the Tolagnaro (= Fort Dauphin) area, including the environments of the Pic St. Louis, and considered as *M.* sp. 29 or *M.* sp. Ca29 by Vieites *et al.* (2009) and Perl *et al.* (2014), and depicted as '*Mantidactylus* sp. aff. *betsileanus* "Tolagnaro"' by Glaw and Vences (2007). In the phylogenomic tree, a specimen of *M. tripunctatus* is placed in a subclade with *M. noralottae* and two other new species described below as *M. katae* **sp. nov.** and *M. kortei* **sp. nov.**, and relationships between these species are also supported by the 16S tree; all of the species differ from each other in their advertisement calls, and *M. noralottae* also is characterized by larger body size (Table 4), confirming their species-level distinctness and justifying elevation of *M. tricinctus* to species status.

Diagnosis.—A member of the *M. betsileanus* clade as revealed by the phylogenomic analysis, probably sister

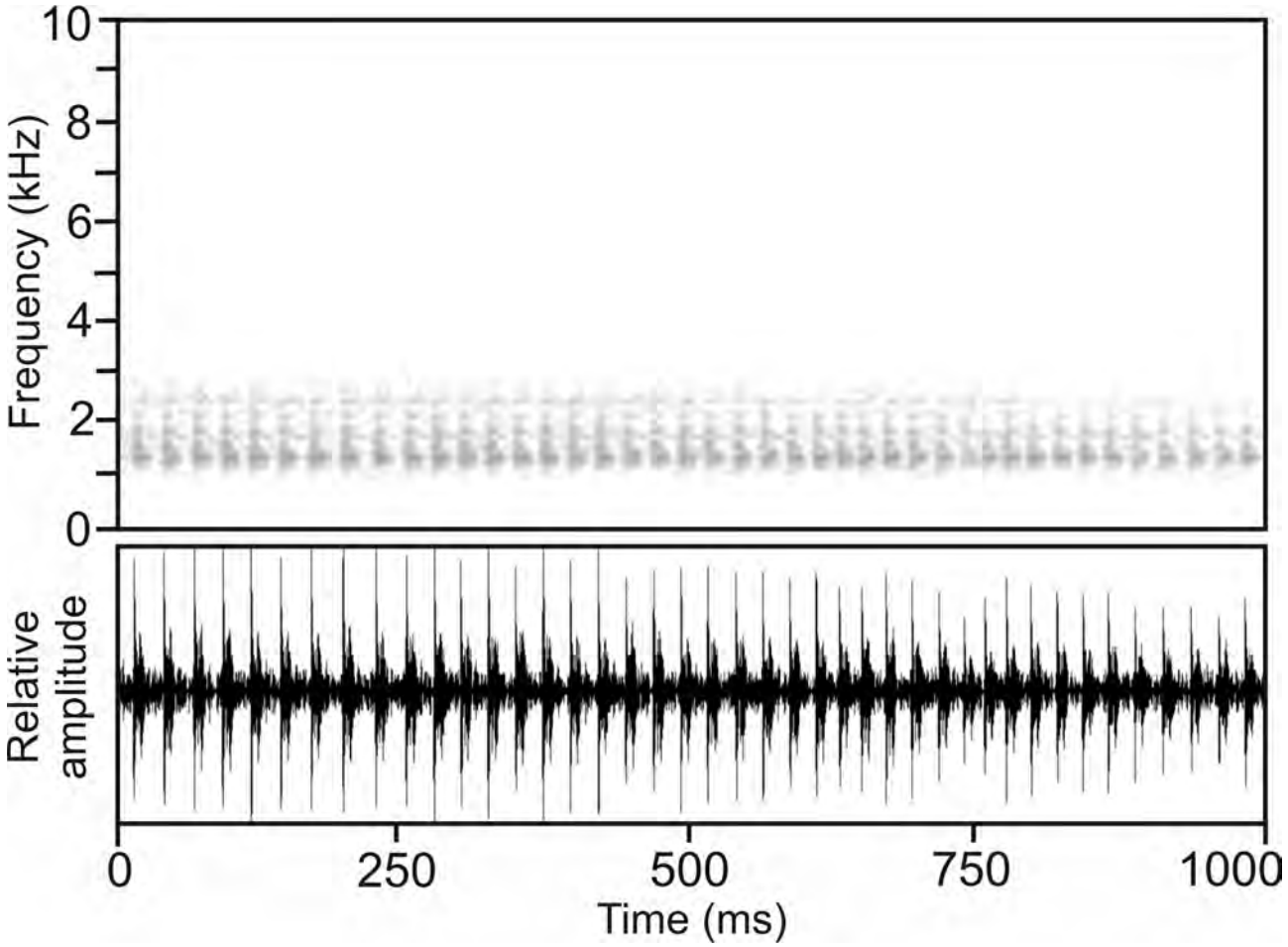

FIGURE 37. Audiospectrogram and corresponding oscillogram of a 1000 ms section of one advertisement call (call duration 2704 ms) of *Mantidactylus noralottae*, recorded 18 December 2004 at Ambovo, Isalo National Park (20°C air temperature). Recording bandpass-filtered at 1000–3500 Hz.

to *M. katae* **sp. nov.** described below (but see below for uncertainties regarding the samples of *M. katae* included in the phylogenomic analysis). See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size in males (SVL 26–27 mm) and distinctly larger size in females (SVL 33–35 mm), slightly tubercular dorsal skin with distinct continuous dorsolateral ridges, reduced webbing (one phalanx of fifth toe free of web), absence of white spots on flanks, presence of a white marking on snout tip, and advertisement call consisting of a single, long note composed of ≥70 pulses distinguishes *M. tripunctatus* from species of all other clades (Table 4). Within the *M. betsileanus* clade, the species differs from *M. betsileanus* by a lower number of pulses in advertisement calls and a lower pulse repetition rate; and from *M. noralottae* by smaller body size and presence of a distinct white marking on snout tip (Table 4). For a distinction from the new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. tripunctatus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 7. See Fig. 38 for colouration in life and its variation. A light vertebral line can be present. There is pronounced sexual size dimorphism (confirmed male SVL 26.4–27.0 mm [n = 3] vs confirmed female SVL 32.9–34.7 mm [n = 5]). Tympanum size is quite variable but does not seem to differ consistently and strongly between sexes (HTD/ED ratio is 53–93% in females, 93–95% in males).

Natural history.—At the base of Pic St. Louis (Tolagnaro) we observed calling males at night, sitting at the edge of shallow puddles in a small, very slowly running stream surrounded by remains of rainforest.

Calls.—Advertisement calls of individuals probably belonging to *M. tripunctatus* (but not DNA barcoded), recorded in February 1991 at a site near Tolagnaro, air temperature unknown (Vences *et al.* 2006: CD2, track 68, cut 1), consists of a long, regularly pulsed note (Fig. 39), emitted in series. The available recording was of relatively poor quality and partly suffered from the overlap of calls of different individuals, making it difficult to assess and measure all parameters precisely. Numerical parameters of five analysed calls were as follows: call duration (= note duration) 1380–1870 ms (1612.8 ± 197.8 ms); ca 70–80 pulses per note (estimate according to overlap of calls); pulse duration 11–19 ms (14.2 ± 2.6 ms); pulse repetition rate within notes 41.7–47.6 pulses/s (45.6 ± 2.3); dominant frequency 1383–1556 Hz (1460 ± 75 Hz); prevalent bandwidth 1200–3400 Hz; call repetition rate (= note repetition rate) ca 8–9 calls/min.

Calls recorded on 1 January 1992 at Pic St. Louis near Tolagnaro, 23°C air temperature (Vences *et al.* 2006: CD2, track 68, cuts 2 & 3), generally agree in character with the other calls from Tolagnaro described above. Although difficult to evaluate due to overlapping calls of multiple individuals, call duration seems to be longer, roughly ranging from 2100–2600 ms. Pulse repetition rate in these calls is slightly lower and ranges from ca 30–39 pulses/s.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently microendemic to a small area in far South East of Madagascar (Fig. 7). This species is known from Andohahela, Manantantely, Mandena, Nahampoana, Pic St. Louis, and Tsitongambarika. Elevation range: 8–415 m a.s.l.

Etymology.—Latin adjective meaning 'having three spots', presumably in reference to some feature of the colouration.

Mantidactylus incognitus **sp. nov.**

Identity and justification.—This enigmatic lineage is

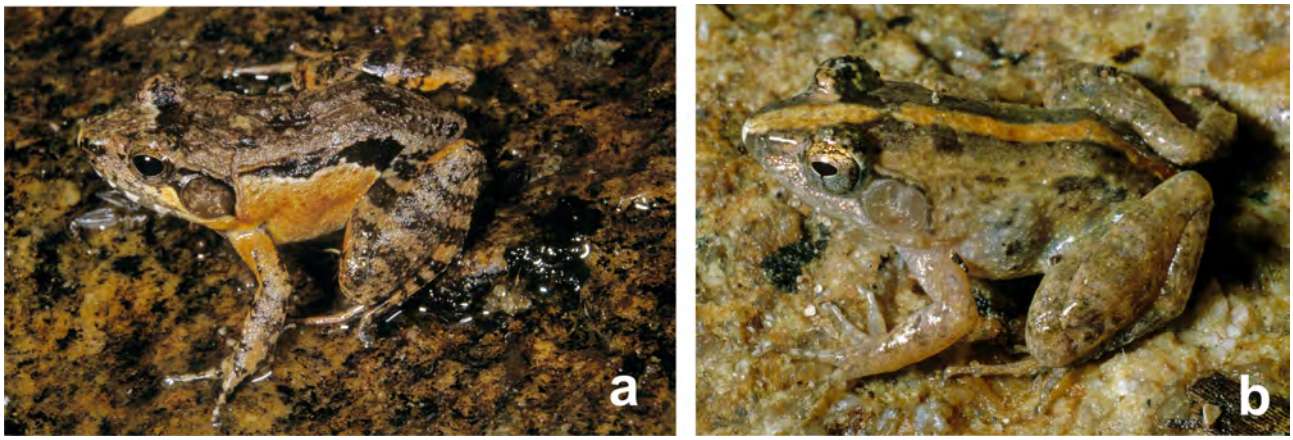

FIGURE 38. Specimens assigned to *Mantidactylus tripunctatus* in life, in dorsolateral view. (a) Probably adult male (based on large tympanum size) from Pic St Louis near Tolagnaro, photographed in 1991. (b) Probably adult male (based on large tympanum size) from Nahampoana, photographed in 1991.

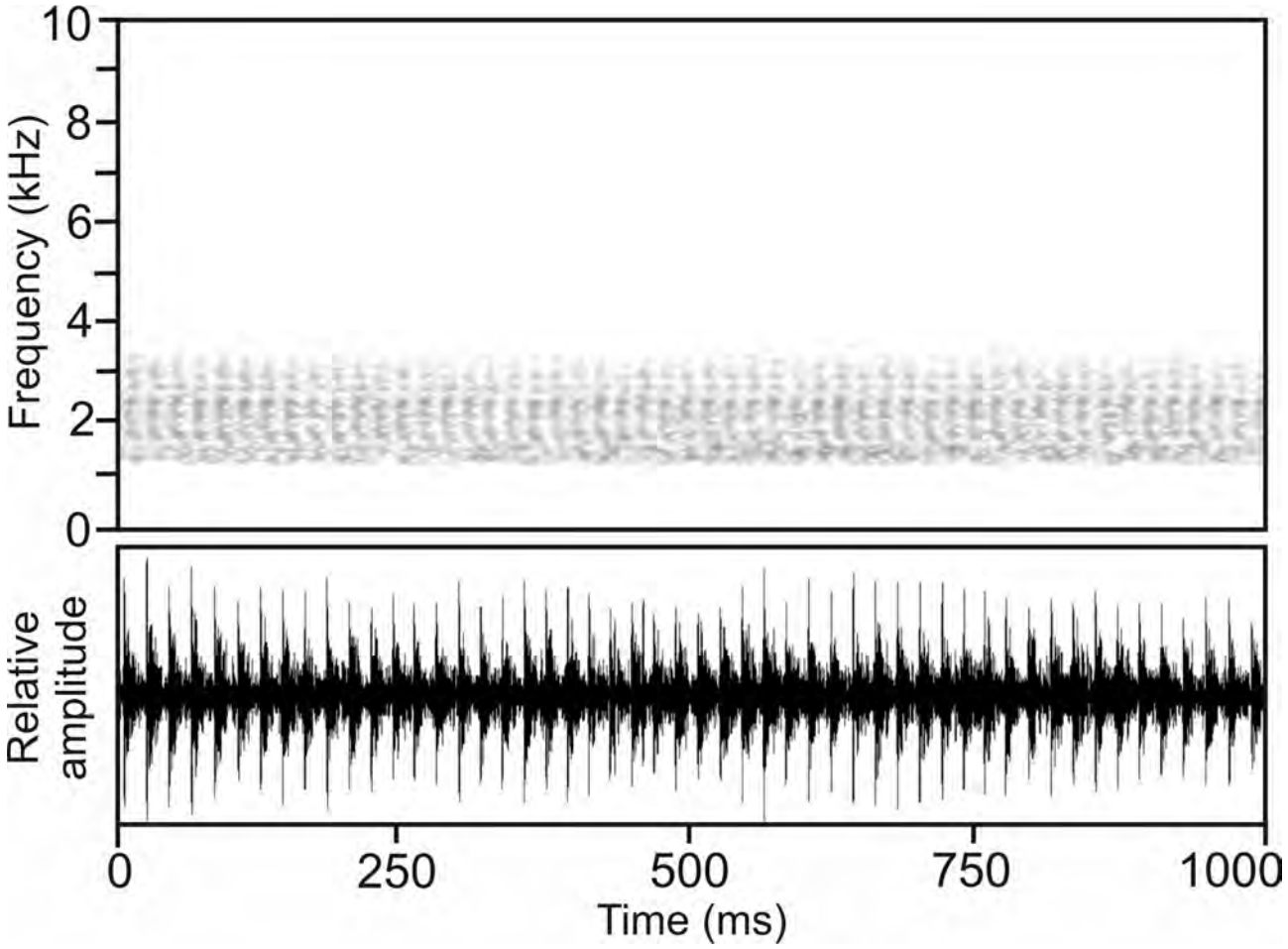

FIGURE 39. Audiospectrogram and corresponding oscillogram of a 1000 ms section of one advertisement call (call duration 1545 ms) of *Mantidactylus tripunctatus*, recorded February 1991 near Tolagnaro. Recording bandpass-filtered at 1200–4100 Hz.

phenotypically assigned to the *M. betsileanus* clade and has been considered as unconfirmed candidate species *M*. sp. 34 by Vieites *et al.* (2009), and *M.* sp. Ca34 by Perl *et al.* (2014). Only a minimal amount of information on this lineage is available. It is phylogenetically sister to *M. betsileanus* in our FrogCap analysis (Fig. 5) with which it also shares Rag-1 haplotypes, and it occurs parapatrically but in close geographic proximity with this species. We here consider it as distinct species due to its highly divergent mitochondrial DNA sequences (6.2–7.6% 16S divergence to *M. betsileanus*), and the distinct dorsal ridges, and tubercles above the eye seen in the holotype (absent or more weakly expressed in *M. betsileanus*). Furthermore, also the FrogCap analysis supports a substantial genomic divergence, given the long branch length separating this lineage from *M. betsileanus*. *Mantidactylus incognitus* **sp. nov.** is the only species of *Brygoomantis* for which no photos in life are available (same applies also to one subspecies, *M. manerana antsanga* **ssp. nov.**; see below).

Holotype.—ZSM 669/2009 (ZCMV 8945), probably a subadult female, collected by P.-S. Gehring, F.M. Ratsoavina, and E. Rajeriarison on 22 April 2009 at Mahanoro (19.6536°S, 048.7780°E), Antsinanana Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of two paratypes: UADBA uncatalogued (MV 2001.1156 = 2002.G9), specimen of unknown sex and maturity, collected by M. Vences on 26–27 November 2001 in Vohidrazana (precise coordinates unavailable); MRSN A6694 (RJS 1801 = ACZC 4189), adult male, collected by J.E. Randrianirina at Anivorano Est (18.7638°S, 048.9468°E, 60 m a.s.l.).

Additional material.—Two series of tadpoles, ZSM 1042/2004 and ZSM 1043/2004, from Vohidrazana.

Diagnosis.—*Mantidactylus incognitus* **sp. nov.** is a member of the *M. betsileanus* clade as revealed by the phylogenomic analysis, representing the sister species of *M. betsileanus*. See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size in males (SVL 27 mm), dorsal skin with several distinct dorsolateral ridges and supraocular tubercles, reduced webbing (one phalanx of fifth toe free of web), absence of white spots on flanks, and presence of a white marking on snout tip, distinguishes *M. incognitus* **sp. nov.** from species of all other clades (Table 4). Within the *M. betsileanus* clade, the new species differs from *M. noralottae* by smaller body size and presence of a distinct white marking on snout tip; and from *M. betsileanus,*

M. noralottae, and *M. tripunctatus* by distinct dorsal ridges (in addition to the dorsolateral ridges) and strongly expressed supraocular tubercles. For a distinction from the other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. incognitus* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Specimen in moderate state of preservation (soft fixation); probably a subadult female with rudimentary ovary based on gonad examination. Some muscle tissue removed from left thigh (Fig. 33), and a longitudinal lateroventral cut made for gonad examination. Some skin missing from left thigh and shank dorsally. Body relatively slender. Head as wide as body. Snout rather truncate in dorsal and lateral views which might be a preservation artefact. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, rather small, rounded, horizontal diameter of tympanum 61% of horizontal eye diameter. Supratympanic fold distinct, beginning straight behind eye, with gentle ca 45° bending midway towards forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth form two small rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (95%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but clearly recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1.5), 3i(2), 3e(1), 4i(2), 4e(2.5), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface with numerous discontinuous but distinct longitudinal ridges, one of these extending into supraocular region. A series of distinct supraocular tubercles. Ventral side smooth. Small rudimentary femoral glands visible.

Colour in preservative: dorsally light brown to beige, with a slightly darker shade medially on dorsum. Several of the dorsal ridges are lined with dark brown. Distinct dark crossbands on limbs. A dark band between eyes and a relatively small white patch on snout tip. Ventrally light beige with distinct and contrasted brown pattern on throat and chest. Throat with disctinct, interrupted median light stripe. Lower lips ventrally with alternating light-dark pattern. Colour of holotype in life not documented.

Variation.—Variation in measurements is given in Table 7. Colouration in life unknown. Insufficient number of reliably sexed, adult specimens available to assess sexual dimorphism.

Natural history.—Very little is known on the habits of this species. Tadpoles at Vohidrazana were collected from a stream in degraded rainforest.

Calls.—The call of this species is unknown.

Tadpoles.—The tadpole of *M. incognitus* was described under the name '*Mantidactylus* sp. aff. *betsileanus* "Vohidrazana"' by Knoll *et al.* (2007).

Distribution.—Distributed in a rather small area of the Northern Central East (Fig. 7). This species is known from Anivorano Est, Bemandrevo, Andekaleka, Mahanoro, Sahafina, and Vohidrazana. Elevation range: 10–810 m a.s.l.

Etymology.—The Latin adjective incognitus, meaning 'unknown', referring to the extremely poor knowledge we have on this genetically distinct species.

Mantidactylus jonasi **sp. nov.**

Identity and justification.—This lineage previously was considered to represent a northern deeply divergent conspecific lineage of *M. betsileanus*, due to its superficial similarity in advertisement calls, and very similar morphology. However, closer investigation revealed that (i) the mitochondrial divergence is very high (5.1–8.3%), (ii) there is almost no haplotype sharing with *M. betsileanus* in the nuclear gene Rag-1, (iii) the calls from various sites have a consistently lower pulse repetition rate and lower number of pulses per call, and (iv) the northern specimens are very slightly but consistently smaller than *M. betsileanus.* Taken together, this is reliable evidence for a distinctness at species level.

Holotype.—ZSM 86/2016 (MSZC 0180), adult male, collected by M.D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D.H. Nomenjanahary, and J. Rabearivony on 9 January 2016 in Ampotsidy (14.42832°S, 048.72129°E, 1227 m a.s.l.), Sofia Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of eleven paratypes: ZSM 133/2018 (MSZC 0714) and ZSM 134/2018 (MSZC 0715), two adult males, collected by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison on 30 November 2017 at high elevation on Montagne d'Ambre (12.58516°S, 049.14875°E, 1225 m a.s.l.); UADBA uncatalogued (MSZC 0617), adult male, collected by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison on 16 November 2017 at intermediate elevation on Montagne d'Ambre (12.52660°S, 049.16806°E, 1071 m a.s.l.); UADBA uncatalogued (MSZC 0729), unsexed individual, collected by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison between 2–4 December 2017 at high elevation on Montagne d'Ambre (12.59247°S, 049.15302°E, 1372 m a.s.l.); ZSM 2220/2007 (FGZC 1368) and ZSM 2222/2007 (FGZC 1372), two adult males, collected by F. Glaw, P. Bora, H. Enting, J. Köhler, and A. Knoll on 11–12 March 2007 near the Gîte d'Étape on Montagne d'Ambre (ca 12.527°S, ca 049.172°E, ca 1040 m a.s.l.); ZSM 1773/2010 (ZCMV 12603) and ZSM 1774/2010 (ZCMV 12604), two adult males, collected by M. Vences, D. Vieites, R.D. Randrianiaina, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison on 29 June 2010 in a forest fragment between Bealanana and Antsohihy

(14.72145°S, 048.56272°E, 1187 m a.s.l.); ZSM 89/2016 (MSZC 0194), adult male, collected by M.D. Scherz and M. Rakotondratisma on 14 January 2016 in a forest called Andranonafindra between Bealanana and Antsohihy (14.73600°S, 048.54831°E, 1180 m a.s.l.); ZSM 551/2009 (ZCMV 11462), adult male, collected by M. Vences, D.R. Vieites, F.M. Ratsoavina, R.D. Randrianiaina, E. Rajeriarison, T. Rajofiarison, and J. Patton on 20 June 2009 at Sahaovy ('Camp 0'), Makira (15.4889°S, 049.0785°E, 607 m a.s.l.); ZSM 484/2016 (ZCMV 15180), adult male, collected by M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences, and J. Razafindraibe on 17 November 2016 at Camp 3 'Simpona' on the Marojejy Massif (ca 14.4366°S, ca 049.7434°E, ca 1325 m a.s.l.).

Diagnosis.—*Mantidactylus jonasi* **sp. nov.** is a member of the *M. betsileanus* clade as revealed by the phylogenomic analysis, and sister to the monophyletic group containing *M. betsileanus* and *M. incognitus*. See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size in males (SVL 22–25 mm), slightly to moderately tubercular dorsal skin with distinct continuous dorsolateral ridges, reduced webbing (one phalanx of fifth toe free of web), absence of white spots on flanks, presence of a white marking on snout tip, and advertisement call consisting of a single, long pulsed note distinguishes *M. jonasi* **sp. nov.** from species of all other clades. Within the *M. betsileanus* clade, the new species has long been confused with *M. betsileanus* from which it cannot be reliably distinguished based on morphology, although it may have a tendency towards a somewhat more tubercular dorsal skin than *M. betsileanus* (Figs 40 vs 34), and a slightly smaller body size. It can be distinguished from *M. betsileanus* by fewer pulses per note, and lower pulse repetition rate, in advertisement calls (Table 4). *Mantidactylus jonasi* **sp. nov.** is distinguished from *M. noralottae* by smaller size of males and presence of a distinct white marking on snout; from *M. tripunctatus* by a smaller size, and by fewer pulses per note and a lower pulse repetition rate, in advertisement calls; and from *M. incognitus* by absence of distinct dorsal ridges and less strongly expressed supraocular tubercles. For a detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. jonasi* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 33). Some muscle tissue removed from left thigh. Body relatively slender. Head as wide as body. Snout rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, large, wider than high, horizontal diameter of tympanum 93% of horizontal eye diameter. Supratympanic fold poorly recognisable, basically identical with outer edge of tympanum and tightly following it. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (112%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(traces), 2i(traces), 2e(1.5), 3i(2), 3e(2), 4i(2.25), 4e(2.5), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth with weakly recognisable dorsolateral folds and some granules on flanks (in life, dorsolateral folds distinct and more granular on dorsum). Ventral side smooth. Femoral glands small and at substantial distance from cloaca, with a distinct distal ulcerous macrogland; no clearly recognisable proximal granular gland field.

Colour in preservative: dorsally dark brown with some variation in tone on central dorsum. Ventrally of dorsolateral folds, with slightly darker brown which then sharply borders on a light beige flank colour with some remains of reddish colour. Frenal area light with some dark markings. Anterior dorsal surface of head lighter than dorsum. A distinct and contrasting white patch on tip of snout. Limbs with dark crossbands. Ventrally light beige, throat and chest dirty brown with some light-dark pattern on chest and a white median line on throat. Upper lip ventrally dark brown with white spots. Colour in life similar to preservative but more contrasting colours; the light colouration on flanks and sides of head was orange.

Variation.—Variation in measurements is given in Table 7. See Fig. 40 for colouration in life and its variation. No females were available to us to assess sexual dimorphism. Femoral glands in life often more distinct than in *M. betsileanus,* with clearly recognisable proximal granular gland field, not conspicuously coloured.

Natural history.—Regularly observed along different kinds of running waters, in primary and degraded rainforest. Males were heard calling from the edges of rainforest streams at night. Despite a superficial similarity with *M. betsileanus*, this species appears to occur less often in swamps and water bodies such as rice fields.

The holotype was collected beside a spring or seep in disturbed forest with little understory, only a few metres from a larger river. Nearby, a nest containing a cluster of eggs and a frog (presumed to be a guarding parent) was observed ~1 m above the water line, along the bank of the spring (MDS, pers. obs.).

Calls.—Calls recorded on 9 January 2016, 23:37 h, at Ampotsidy in the Bealanana District from the holotype, air temperature not measured but likely below 20°C, were moderately motivated and consisted of a pulsed note, with pulse repetition rate increasing within the note from its beginning to its end. Numerical call parameters of six analysed calls were as follows: call duration (= note duration) 1589–2120 ms (1899.6 ± 192.9 ms); 44–50 pulses per note (46.3 ± 2.6); pulse duration 4–6 ms (5.1 ± 0.5 ms); pulse repetition rate within notes 13.8–30.2 pulses/s (23.1 ± 6.8); dominant frequency 1464–1550 Hz (1498 ± 33 Hz); prevalent bandwidth 800–4800 Hz.

Calls recorded on 20 June 2009, 20:00 h, at the western slope of the Makira Massif, air temperature estimated

FIGURE 40. *Mantidactylus jonasi* **sp. nov.** in life, in dorsolateral and ventral view. (a) Adult male (MSZC 0617, voucher deposited in UADBA) from Montagne d'Ambre, photographed in 2017. (b) Adult male (ZSM 133/2018 = MSZC 0714) from Montagne d'Ambre, photographed in 2017. (c) Adult male from Montagne d'Ambre, photographed in 2007. (d,e) Adult male from Tsaratanàna, photographed in 2010. (f,g,h,i,j) Two adult males from Makira (western slope, probably Sahaovy), photographed in 2009. (k) Adult male (ZSM 89/2016 = MSZC 0194) from Bealanana. (l) Adult male (holotype ZSM 86/2016 = MSZC 0180) from Ampotsidy. (m) Adult male (ZSM 87/2016 = MSZC 0147) from Ampotsidy. (n) Adult female (MSZC 0181, voucher deposited in UADBA) from Ampotsidy. (o,p) Adult male (ZSM 484/2016 = ZCMV 15180) from Marojejy, Camp 3 'Simpona', photographed in 2016. (q,r) Male, possibly subadult due to its small femoral glands (ZSM 84/2016 = MSZC 0020) from Ampotsidy. Note in the ventral views that the distal ulcerous macrogland components of the femoral glands are placed at considerable distances from each other, which constitutes a typical character state of this species.

at 20–25°C, seemed to be reasonably motivated and generally agreed with calls from Ampotsidy, Bealanana district, described above. The call consisted of a regularly pulsed note (Fig. 41) of rather variable duration. Numerical call parameters of 14 analysed calls were as follows: call duration (= note duration) 1060–2773 ms (1919.9 ± 446.1 ms); 19–45 pulses per note (32.9 ± 7.6); pulse duration 6–12 ms (9.1 ± 1.6 ms); pulse repetition rate within notes 16.6–18.9 pulses/s (17.9 ± 1.0); dominant frequency 1644–1755 Hz (1681 ± 45 Hz); prevalent bandwidth 900–5500 Hz; call repetition rate (= note repetition rate) ca 3–5 calls/min.

Calls recorded on 7 June 2010 at Ambatoria, Tsaratanàna, air temperature estimated 20–25°C, also showed a rather low pulse repetition rate, comparable to calls from Makira West and Ampotsidy. Numerical call parameters of six analysed calls were as follows: call duration (= note duration) 2152–2895 ms (2466.3 ± 255.6 ms); 53–72 pulses per note (61.7 ± 7.5); pulse duration 4–6 ms (4.2 ± 0.5 ms); pulse repetition rate within notes 14.7–29.9 pulses/s (25.3 ± 5.4); dominant frequency 1217–1415 Hz (1280 ± 68 Hz), with a second frequency peak of almost identical call energy at ca 2700–2800 Hz; prevalent bandwidth 800–4800 Hz; call repetition rate (= note repetition rate) ca 4–5 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Widespread in northern Madagascar (Fig. 7). This species is known from Ampotsidy, Ambodivohitra, Ampofoko, Andranonafindra, Antambato, Bemanevika, Makira, Mangindrano, Marojejy, Masoala, Montagne d'Ambre, Sorata, and Tsaratanàna. Elevation range: 411–1538 m a.s.l.

Etymology.—L. Rancilhac wishes to dedicate this species to his brother, Jonas Rancilhac, in recognition of his personal support.

Mantidactylus katae **sp. nov.**

Identity and justification.—This lineage has been considered as confirmed candidate species *M.* sp. 28 by Vieites *et al.* (2009) and *M.* sp. Ca28 by Perl *et al.* (2014). It was reported as '*Mantidactylus* sp. aff. *betsileanus* "slow calls"' by Glaw and Vences (2007), and has previously been considered as *M. multiplicatus* (e.g. Poth *et al.* 2012, 2013); however, DNA barcodes obtained

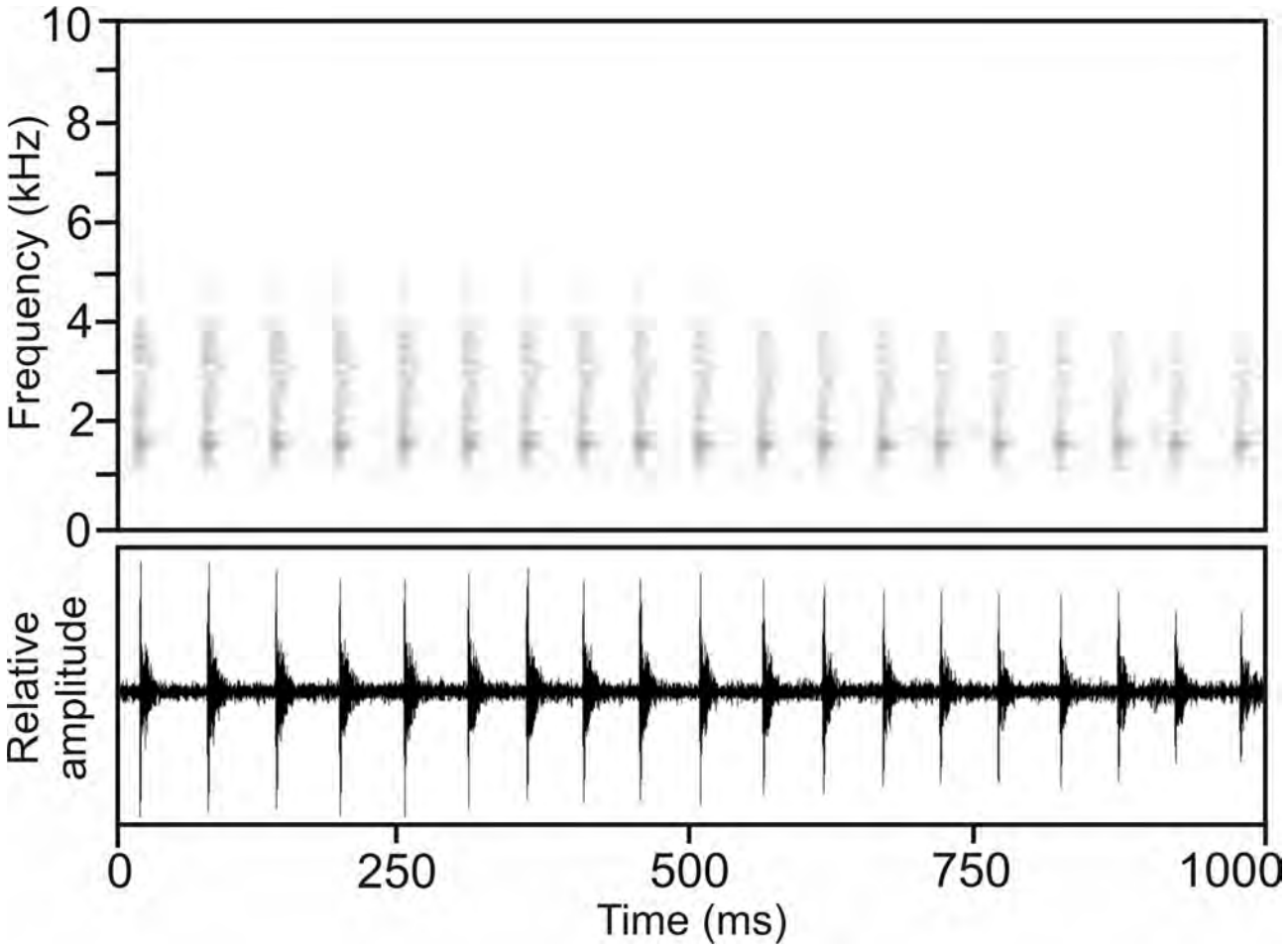

FIGURE 41. Audiospectrogram and corresponding oscillogram of a 1000 ms section of one advertisement call (call curation 1530 ms) of *Mantidactylus jonasi* **sp. nov.**, recorded on 20 June 2009 at the western slope of the Makira Massif (air temperature estimated at 20–25°C). Recording bandpass-filtered at 900–6000 Hz.

in the present study have shown that this assignment was wrong and that the holotype of *M. multiplicatus* is conspecific with *M. betsileanus,* and the nomen therefore a junior synonym of *M. betsileanus* (see account of that species). *Mantidactylus katae* is a widespread species with a unique call, characterized by a very low pulse repetition rate (or rather, consisting of a single-pulse note repeated regularly). It also is genetically distinct in mitochondrial DNA and does not appear to share Rag-1 haplotypes with other similar species, including the sympatric (and syntopic) *M. betsileanus.*

Unfortunately, due to failure of other samples, *M. katae* **sp. nov.** is only represented by two individuals from the South East of Madagascar in our phylogenomic tree, from where no reliable call recordings are available. The samples (FGZC 163 and ZCMV 14842) cluster closely with *M. tripunctatus.* However, these samples correspond to those alleles that also in the Rag-1 haplotype network cluster close to *M. tripunctatus*, and we cannot exclude that they represent individuals of *M. tripunctatus* with an introgressed *M. katae* mitochondrial genome. The exact phylogenetic position of *M. katae* therefore remains in need of confirmation; the phylogenetic tree of Wollenberg *et al.* (2011), based on multiple mitochondrial genes, placed it (as *M.* sp. 28) in a clade with *M. noralottae* and *M. tripunctatus* (as *M.* sp. 29), which would agree with the affinities suggested by our phylogenomic tree. Typical *M. katae* from the Southern Central East and Northern Central East of Madagascar differ from both *M. noralottae* and *M. tripunctatus* very strongly in advertisement call structure, by femoral gland morphology, and do not share Rag-1 haplotypes with these two species, thus leaving no doubt about the species status of this lineage.

Holotype.—ZSM 79/2002 (FGMV 2001.1179), an adult male, collected by M. Vences on 1 December 2001 at Andasibe (ca 18.9333°S, ca 048.4167°E, 920 m a.s.l.), Alaotra-Mangoro Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of 17 paratypes: ZSM 79–81; 83/2002 (FGMV 2001.1197 = 2002.G24; FGMV 2001.1180 = 2002.G25; FGMV 2001.1275 = 2002.G66; FGMV 2001.1173 = 2002.G18), two adult females and two adult males, collected by M. Vences on 1–5 December 2001 at Andasibe (ca 18.9333°S, 048.4167°E, 920 m a.s.l.); ZSM 637/2003 (FG/MV 2002.132), adult male, collected by F. Glaw, M. Puente, L. Rahariviololoniaina, M. Teschke (née Thomas), and D.R. Vieites on 15 January 2003 beside a small brook in Ranomafana National Park (21.250°S, 047.450°E, 932 m a.s.l.); ZSM 668/2003 (FG/MV 2002.255), adult male, collected by F. Glaw, M. Puente, L. Rahariviololoniaina, M. Teschke (née Thomas), and D.R. Vieites on 16 January 2003 in Ranomafana National Park (21.250°S, 047.450°E, 932 m a.s.l.); ZSM 708/2003 (FG/MV 2002.348), adult male, collected by F. Glaw, M. Puente, L. Rahariviololoniaina, M. Teschke (née Thomas), and D.R. Vieites on 20 January 2003 at Kidonafo Bridge, Ranomafana (21.2262°S, 047.3696°E, 1152 m a.s.l.); ZSM 196/2021 (FAZC 15504, extraction ACP 3659, tissue ACZC 8591), ZSM 197/2021 (FAZC 15507, ACP 3662, ACZC 8594), and MRSN A7043 (FAZC 15523, ACP 3662, ACZC 8594), two males and one female collected at Maromizaha (18.9771°S, 048.4682°E, ca 1000 m a.s.l.), in January 2017 by E. Coppola; ZMB 81918 (JCR 105), adult male collected on 16 March 2010 by J.C. Riemann, and S.H. Ndriantsoa at Andalangina, Ranomafana area (21.29844°S, 047.60343°E, 480 m a.s.l.); ZMB 81920 (field NSH 1069; GenBank JCR 1069), adult female, collected on 12 May 2010 by J.C. Riemann, and S.H. Ndriantsoa at Ambatovory, Ranomafana area (21.23966°S, 047.42581°E, 953 m a.s.l.); ZMB 81922 (field NSH 2577; GenBank JCR 2577), adult male, collected on 26 March 2012 by J.C. Riemann, and S.H. Ndriantsoa at Sahamalaotra, Ranomafana area (21.23688°S, 047.39887°E); UADBA-A 43149 (JCR 106), adult male collected on 16 March 2010 by J.C. Riemann, and S.H. Ndriantsoa at Andalangina, Ranomafana area (21.29844°S, 047.60343°E, 480 m a.s.l.); UADBA-A 62106 (JCR 245), subadult collected on 21 April 2010 by J.C. Riemann, and S.H. Ndriantsoa at Ambolo, Ranomafana area (21.26386°S, 047.50862°E, 643 m a.s.l.); UADBA-A 62104 (JCR 320), adult female collected on 21 May 2010 by J.C. Riemann, and S.H. Ndriantsoa at Ambolo, Ranomafana area (21.26307°S, 047.50696°E, 660 m a.s.l.); UADBA-A 62105 (JCR 323), adult female collected on 21 May 2010 by J.C. Riemann, and S.H. Ndriantsoa at Ambolo, Ranomafana area (21.26307°S, 047.50696°E, 660 m a.s.l.).

Additional material.—The following specimens are assigned to *M. katae* **sp. nov.** based on morphology, but have not been DNA barcoded: ZMA 20232 (ZCMV 236), adult male, collected by M. Vences and I. de la Riva on 24 January 2004 at Ranomafana National Park, Maharira base camp (21.3258°S, 047.4024°E, 1248 m a.s.l.); ZFMK 62212, adult female, collected by F. Glaw, D. Rakotomalala, and F. Ranaivojaona on 10 March 1996 at Andasibe; ZMA 6828-863; 6828-864, adult male and female, collected on 23 September 1972, and ZMA 6886-641–643, three adult males, collected by R.M.A. Blommers-Schlösser on 4 April 1972 at Andasibe; ZMA 6833-149 and 6833-156–158, two adult females and two adult males, collected by R.M.A. Blommers-Schlösser on 1 July 1971 at Ranomafana. Furthermore, the following specimen (included in our phylogenomic analysis) from the South of Madagascar agrees with *M. katae* **sp. nov.** in mitochondrial DNA but due to the absence of bioacoustic data from this population, its identity is in need of confirmation: ZSM 91/2004 (FGZC 163), adult male, collected by F. Glaw, M. Puente, M. Thomas and R. Randrianiaina on 31 January 2004 at 'Camp 1' between Isaka and Eminiminy, Andohahela (24.7586°S, 046.8542°E, 247 m a.s.l.).

Diagnosis.—*Mantidactylus katae* **sp. nov.** is a member of the *M. betsileanus* clade, related to *M. noralottae* and *M. tripunctatus*. See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size (male SVL 22–27 mm), slightly tubercular dorsal skin with distinct continuous dorsolateral ridges, absence of white spots on flanks, presence of a white marking on snout tip, large femoral glands (FGW up to 13% of SVL) that contact each other

medially, and advertisement call consisting of a single pulse repeated at a slow rate of 10–16 calls per second distinguishes *M. katae* **sp. nov.** from species of all other clades. The only other species with a similar advertisement call structure is *M. fergusoni* **sp. nov.** which has a larger size and more tubercular dorsal skin (see account of that species below). Within the *M. betsileanus* clade, the new species can be distinguished from all other species by its unique call structure and larger femoral glands (Table 4); furthermore from *M. noralottae* by smaller size of males and presence of a distinct white marking on snout. For a field diagnosis from the syntopic species *M. betsileanus,* according to our measurements, *M. katae* differs by a smaller dot on the snout tip (dot on the snout tip is 9–14% of head width vs 13–24%), a smaller distance between the femoral glands (distance between the femoral glands is 0–14% of SVL vs 13–22%), larger femoral glands (femoral gland length is 19–31% of SVL vs 13–22%), and a higher number of granules per femoral gland (5–8 vs 1–5). For a detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. katae* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 33). Some muscle tissue removed from right thigh. Femoral glands partly detached for examination in internal view. Body relatively slender. Head slightly wider than body. Snout rounded in dorsal view, slightly truncate in lateral view. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, slightly wider than high, horizontal diameter of tympanum 73% of horizontal eye diameter. Supratympanic fold rather distinct, running rather straight from behind eye and bending about 45° about midway towards forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (97%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1), 4i(2.25), 4e(2), 5(0.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth with numerous longitudinal folds and ridges, granular on flanks. Ventral side smooth. Femoral glands large and distinct, very close to cloaca, with a distinct distal ulcerous macrogland; no clearly recognisable proximal granular gland field.

Colour in preservative: dorsally dark brown with some poorly contrasting, slightly darker markings and a slightly lighter band between eyes. Dark crossbands on limbs. Ventrally light beige with dark pattern on chest and throat, also extending on anterior belly. Throat with light colour medially, forming a very irregular and discontinuous broad medial stripe. Upper lip ventrally dark brown with white spots. Colouration of holotype in life not documented.

Variation.—Variation in measurements is given in Table 7. See Fig. 42 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 22.1–27.2 mm [n = 7] vs confirmed female SVL 25.6–35.9 mm [n = 3]). Males have a larger tympanum than females (HTD/ED ratio is 61–68% in females, 73–100% in males). Femoral glands in males are large and very distinct, of a quite characteristic shape. They consist of a large-sized distal ulcerous macrogland located rather close to the insertion of the thighs and thus almost in contact with each other. Consequently, the proximal granular gland field (by definition located proximally from the ulcerous macrogland) is basically absent in these frogs. Glands are typically coloured yellowish in life.

Natural history.—Occurs along running water bodies in rainforest, where specimens can often be seen calling at night from muddy banks of somewhat larger, slow-moving streams. It often occurs in syntopy with *M. betsileanus* in rainforest, including forest fragments (Riemann *et al.* 2015), and along streams with at least a narrow gallery forest band surrounded by degraded or unforested areas. However, in contrast to *M. betsileanus* it is not found in rice fields or other plantations (Ndriantsoa *et al.* 2017). Usually sitting in shallow water or along the shore, hiding in the leaf litter or perched on low vegetation up to 0.5 m hight in the vicinity of a stream. Found at an elevational range between 450–1142 m a.s.l. in Ranomafana and surrounds. Females with visible eggs (transparent abdominal wall) were observed in May 2010 and from January to June in 2011 in the Ranomafana area.

Calls.—The advertisement call of *M. katae*, recorded on 17 December 1994 at Andasibe, ca 20°C air temperature (Vences *et al.* 2006: CD2, track 64, cut 2), consists of a simple, very short, single pulse 'click' note, emitted in long series at regular intervals and fast succession (Fig. 43). The duration of the call series analysed from Andasibe was 7568 ms. Numerical parameters of 47 analysed calls were as follows: call duration (= note duration) 2–5 ms (3.6 ± 0.8 ms); 1 pulse per note (1.0 ± 0.0); pulse duration = note duration = call duration; dominant frequency 3036–3165 Hz (3108 ± 46 Hz); prevalent bandwidth 1250–3540 Hz; call repetition rate (= note repetition rate = pulse repetition rate) within regular series 696–971 calls/min (840 ± 106 calls/min).

Calls recorded on 24 January 2004 at Maharira forest, Ranomafana National Park, 18.4°C air temperature (Vences *et al.* 2006: CD2, track 64, cut 1) are in agreement with the calls from Andasibe in all spectral and temporal parameters, except for slightly lower dominant frequency ranging from 2713–2993 Hz (2833 ± 123 Hz), and slightly lower call repetition rate, ranging from 515–731 calls/min (626 ± 109 calls/min). Both slight differences can be explained by potentially larger body size of the calling male and lower temperature during recording and leave no doubt about the conspecificity of the calls from the two localities.

Another call recording from Andasibe, obtained on 20

FIGURE 42. *Mantidactylus katae* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male from Andasibe, photographed in 1995. (c,d) Adult male from An'Ala, photographed in 1996. (e,f) Adult male from Ranomafana, photographed in 2003. Note the large femoral glands, with distal ulcerous macroglands of opposite thighs almost contacting each other medially, which constitutes the main morphological diagnostic character compared to the often syntopic *M. betsileanus*.

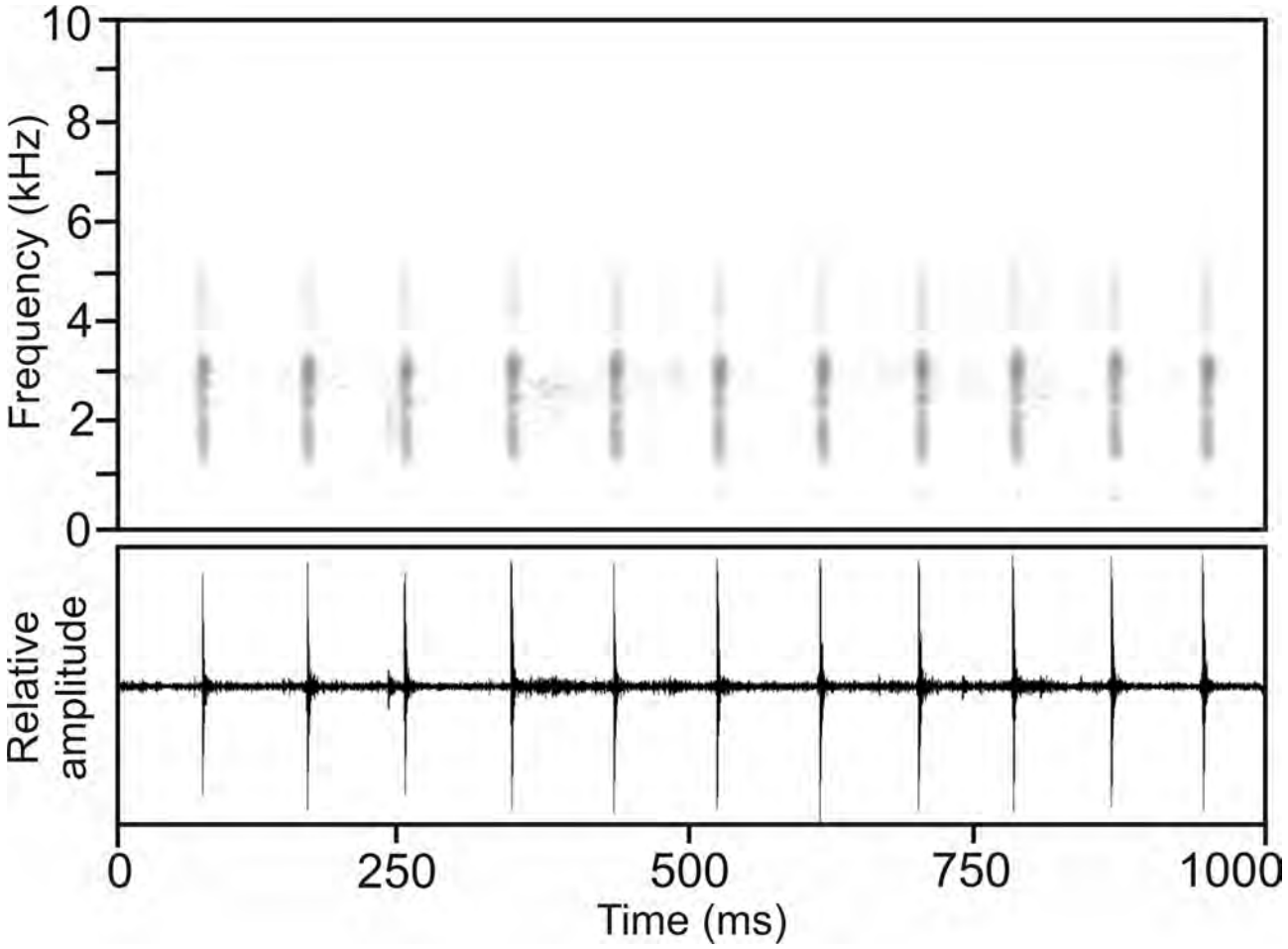

FIGURE 43. Audiospectrogram and corresponding oscillogram of a 1000 ms section of a series of advertisement calls (11 calls displayed) of *Mantidactylus katae*, recorded on 17 December 1994 at Andasibe (ca 20°C air temperature). Recording bandpass-filtered at 500–6000 Hz.

March 1995, 23.4°C air temperature (Vences *et al.* 2006: CD2, track 63) is similar to the calls described above, but differs by shorter call series (2226–2520 ms), slightly longer call duration (= note duration = pulse duration) of 8–10 ms, and lower dominant frequency of 1323–1433 Hz (1365 ± 52 Hz). However, the latter might be due to recording equipment and/or recording conditions, as the calls described above have a second frequency peak that roughly corresponds to the lower dominant frequency range described here. Call repetition rate (= note repetition rate = pulse repetition rate) is in the same range compared to the calls described above, ranging from 630–857 calls/min (741 ± 90 calls/min).

Tadpoles.—The tadpole of *M. katae* was described by Knoll *et al.* (2007) under the name '*M.* sp. aff. *betsileanus* "very slow calls"'.

Distribution.—Widespread in eastern Madagascar (Fig. 7). This species is known from Ambatomandondona, Ambohitsara, An'Ala, Andasibe, Andohahela, Andringitra, Bibiango, Ambatofotsy, Ifandiana, Mahatsara-Mantadia, Mariavatra, Mantady, Marolambo, Maromizaha, Pic d'Ivohibe, Ranomafana (various sites, including Valohoaka, Ambatolahidimy, Ambatolahy, Ambolo, Ampitavanana, Andalangina, Beremby, Bibiango, Kidonavo, Maharira, Ampangadiamesa, Andranovorimainty, Ambodiriana, Imaloka, Sahamalaotra, Talatakely, and Vohiparara), Sahamalotra, Sahateza, Torotorofotsy, and Vohidrazana. Elevation range: 247–1248 m a.s.l.

Etymology.—We dedicate this species to Katharina ('Kat') Wollenberg Valero, in recognition of her numerous contributions to the research on little brown frogs of Madagascar, and specifically on the behaviour of this species (under the name *M. multiplicatus*) in the framework of studies of their femoral gland compounds (Poth *et al.* 2012).

Mantidactylus kortei **sp. nov.**

Identity and justification.—This lineage has only been found at high elevations of the Andohahela Massif, in a swamp and along streams. In previous DNA barcoding assessments, it has been considered as *M.* sp. 30 by Vieites *et al.* (2009) and *M.* sp. Ca30 by Perl *et al.* (2014). It is sister to *M. noralottae* from Isalo in the phylogenomic analysis (but according to 16S data may also be closely related to *M. riparius* **sp. nov.** which is not represented in the phylogenomic analysis; see below). However, it differs from *M. noralottae* in advertisement call and morphology (e.g. smaller body size; Table 4), and from its two siblings by a high genetic divergence (≥4.3% from *M. noralottae*,

and ≥5.9% from *M. riparius* **sp. nov.**), supporting its species status. Some individuals of *M. kortei* sp. nov. are characterized by a relatively short snout, but this is apparently not the case in all individuals.

Holotype.—ZSM 205/2005 (FGZC 2376), adult male, collected by P. Bora, F. Glaw, and M. Vences on 26 January 2005 near camp, Andohahela (24.5440°S, 046.7141°E, 1548 m a.s.l.), Anosy Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of three paratypes: ZSM 203/2005 (FGZC 2377) and ZSM 204/2005 (FGZC 2375), two adult females with the same collection data as the holotype; ZSM 195/2005 (FGZC 2480), an adult female, collected by F. Glaw, M. Vences, and P. Bora on 28 January 2005 in a stream at high elevation, Andohahela (ca 24.544°S, ca 046.714°E, ca 1650 m a.s.l.).

Diagnosis.—*Mantidactylus kortei* **sp. nov.** is a member of the *M. betsileanus* clade and related to *M. noralottae* in the phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size (male SVL 27 mm), slightly tubercular dorsal skin with distinct continuous dorsolateral ridges, relatively large tympanum (13% of SVL in males), presence of a white marking on the snout tip in most specimens, and advertisement call consisting of a single pulsed note not repeated in regular series distinguishes *M. kortei* **sp. nov.** from species of all other clades. Species of the *M. fergusoni* clade are larger and have typically a more tubercular dorsum, while species of the *M. curtus* clade are often larger and most have a smaller tympanum. Some specimens of the new species have whitish dots on the flanks and only an indistinct white marking on the snout tip, which impedes their distinction from some species of the *M. biporus, M. stelliger* and *M. inaudax* clades where advertisement calls are unknown. However, the usually more pointed snout, larger tympanum, longer limbs, and overall different appearance of *M. kortei* **sp. nov.** should make a distinction straightforward (Table 4). Within the *M. betsileanus* clade, the new species can be distinguished from *M. betsileanus, M. noralottae* and *M. tripunctatus* by having fewer pulses per note in advertisement calls; furthermore from *M. noralottae* by smaller body size. *Mantidactylus katae* has a different advertisement call structure and larger femoral glands; *M. jonasi* has typically more pulses per note in advertisement calls, a slower pulse repetition rate, and a more tubercular dorsum; and *M. incognitus* has more expressed dorsal and dorsolateral ridges and supraocular tubercles (Table 4). For a detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. kortei* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 33). Tissue sample taken ventrally from right thigh. Femoral gland partly detached to examine their structure internally. Body rather slender. Head wider than body. Snout rounded in dorsal view, truncate in lateral view. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region slightly concave. Tympanum distinct, large, elliptical, wider than high, its diameter 88% of eye diameter. Supratympanic fold distinct, beginning straight, with a distinct, angular 90° bend midway towards insertion of forelimb. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth distinct in elliptical aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle present, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I≤II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (110%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but recognisable. Webbing formula: 1(0.25), 2i(1.5), 2e(0.5), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(0.5). Relative length of toes: I<II<V=III<IV. Skin on the upper surface smooth, granular on flanks, with relatively well recognisable dorsolateral folds (distinct in life). Ventral side smooth. Femoral glands present, and distinct, the distal ulcerous macrogland consisting of five large granules with an external central depression, and with a moderately expressed proximal granular gland field, particularly visible in internal view.

Colour in preservative: dorsum brown, with indistinct irregular darker markings and some white spotting on flanks and with poorly contrasted crossbands on limbs. Loreal region light brown with dark markings. Snout tip with a distinct light dot. Venter beige, throat and chest with brown mottling. Lower lip ventrally with alternating light and brown spots. Colour in life similar to that in preservative, but more contrasted.

Variation.—Variation in measurements is given in Table 7. See Fig. 44 for colouration in life and its variation. There may be pronounced sexual size dimorphism, but sample sizes are low (confirmed male SVL 27.4 mm [n = 1] vs confirmed female SVL 34.6–37.1 mm [n = 3]).

Males may have a slightly larger tympanum than females (HTD/ED ratio is 73–80% in females, 88% in the male). Femoral glands in males are relatively prominent, but not prominently coloured in life, at least not in the only male available for examination.

Natural history.—Calls of a large number of males were heard during the day, after heavy cyclonic rainfall from a sun-exposed swamp area in grassland directly next to primary rainforest. Several specimens were also found next to small streams in rainforest.

Calls.—The advertisement call of *M. kortei*, recorded on 27 January 2005 at Andohahela National Park (specimens not seen calling, therefore attribution of calls not completely certain, but very likely), 17.6°C air temperature (Vences *et al.* 2006: CD2, track 78), consists of a pulsed note (Fig. 45), emitted in series at irregular intervals and slow succession. Notes exhibited slight amplitude modulation, with maximum call energy occurring either during the first third of the note's length or at the centre of the note, and the terminal pulse of the note always containing the lowest energy. In some calls, initial pulses were separated by longer inter-pulse intervals, whereas the 3-5 terminal pulses

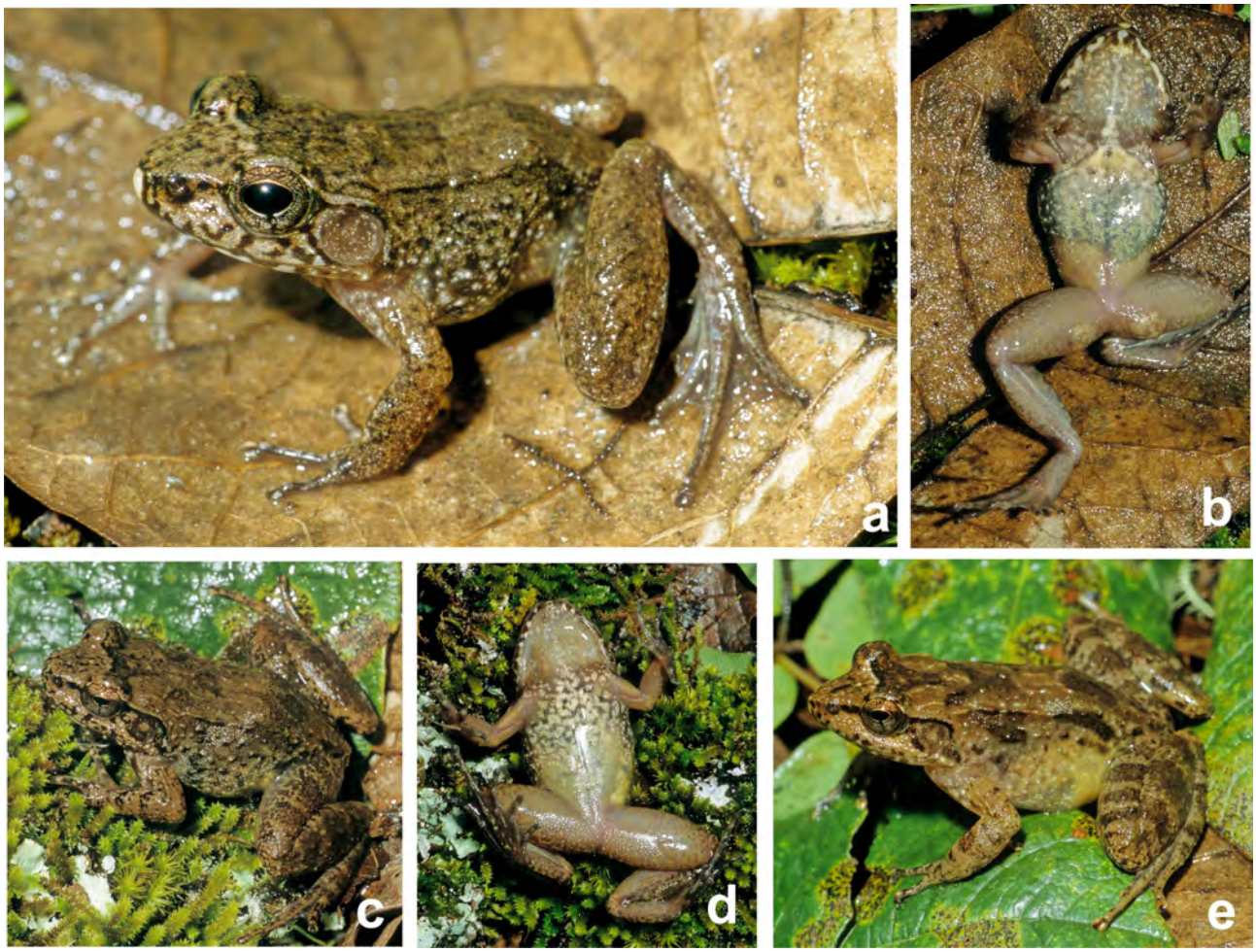

FIGURE 44. *Mantidactylus kortei* **sp. nov.** from Andohahela in life, in dorsolateral and ventral view. All photographs taken in 2005. (a,b) Adult male (holotype ZSM 205/2005 = FGZC 2376). (c,d) Adult female (ZSM 204/2005 = FGZC 2375). (e) Female specimen (probably preserved in UADBA). Note the relatively broad and short head of the first two specimens and the more pointed head of the third specimen in (e) which however showed no difference to the other two specimens in the molecular markers analysed.

of all calls are narrowly spaced and have very short inter-pulse intervals. Numerical parameters of nine analysed calls, corresponding to at least two different individuals, are as follows: call duration (= note duration) 254–511 ms (356.9 ± 94.5 ms); 12–27 pulses per note (18.9 ± 4.6); pulse duration 3–6 ms (4.4 ± 0.8 ms); pulse repetition rate within notes (excluding narrowly spaced terminal pulses) 29.0–69.0 pulses/s (47.9 ± 10.1); dominant frequency 1123–1399 Hz (1224 ± 124 Hz); prevalent bandwidth 750–3200 Hz; call repetition rate (= note repetition rate) ca 4–11 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently microendemic to high elevations in Andohahela National Park (Fig. 7). Elevation range: ~1548 m a.s.l.

Etymology.—We dedicate this species to Martin Korte, cellular neurobiologist of Braunschweig University of Technology, in recognition of his continued support of our research activities over the past 15 years.

Mantidactylus riparius **sp. nov.**

Identity and justification.—This lineage of the *M. betsileanus* clade was first discovered by Cocca *et al.* (2018) and named '*Mantidactylus* sp. aff. *multiplicatus* Ca65 "Isalo"'. It was not included in earlier DNA barcoding assessments of Madagascar's anuran diversity. It represents the third *Brygoomantis* species occurring in the Isalo massif, besides *M. mahery* and *M. noralottae.* Both this lineage and *M. noralottae* have so far only been recorded from Isalo and belong to the *M. betsileanus* clade according to the 16S tree. *Mantidactylus kortei* appears also to belong to this clade, and is morphologically and bioacoustically similar to this lineage. However, we here consider the Isalo lineage as a separate species from *M. kortei* due to its high genetic divergence of 5.9–6.8% in the 16S gene, absence of Rag-1 haplotype sharing and ecological divergence (found in canyons in the dry Isalo sandstone massif, vs *M. kortei* occurring only on high elevations in humid rainforest of Andohahela).

Holotype.—ZSM 2403/2007 (ZCMV 5766), adult

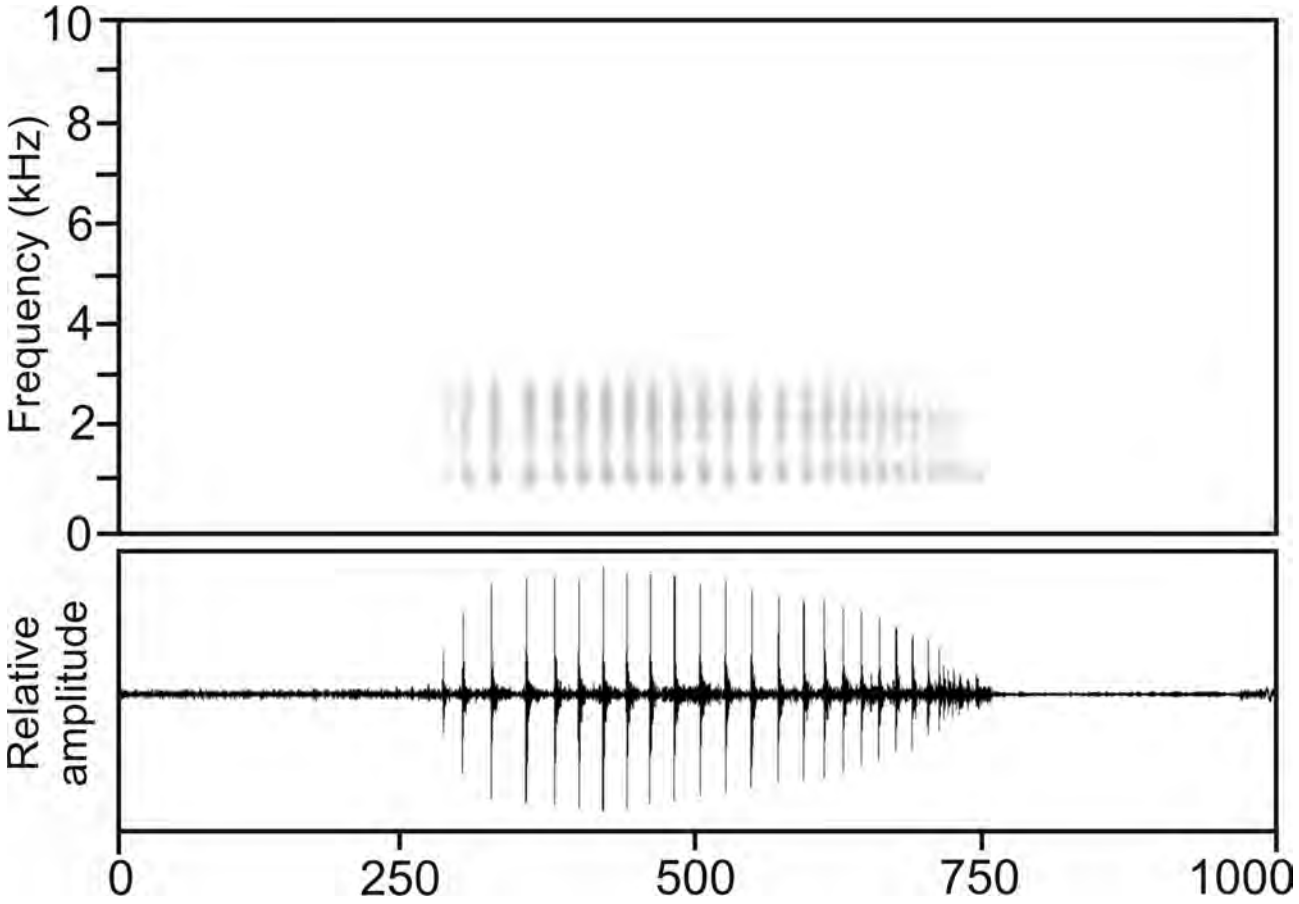

FIGURE 45. Audiospectrogram and corresponding oscillogram of one advertisement call tentatively assigned to *Mantidactylus kortei*, recorded on 27 January 2006 at Andohahela National Park (17.6°C air temperature). Recording bandpass-filtered at 500–4000 Hz.

male, collected by L. du Preez, C. Weldon, O. Verneau, and L. Raharivololoniaina on 16 February 2007 at Isalo (Cascade des Nymphes), Ihorombe Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of eight paratypes: ZSM 186/2021 (ACZCV 281, extraction ACP 2294, tissue ACZC 6908) and ZSM 187/2021 (ACZCV 283, ACP 2296, ACZC 6911), two probable females, collected on 25 November 2014 by A. Crottini, G.M. Rosa and F. Andreone at the Isalo Massif (Andriamanero: Antsifotra canyon); UADBA uncatalogued (ZCMV 5541–5544, ZCMV 5749, ZCMV 5775), six specimens of unkonwn sex and maturity, collected by L. du Preez, C. Weldon, O. Verneau, and L. Raharivololoniaina in February 2007 in the Isalo Massif.

Diagnosis.—*Mantidactylus riparius* **sp. nov.** is a member of the *M. betsileanus* clade and related to *M. noralottae* and *M. kortei* based on the 16S tree (not included in the phylogenomic analysis). See Table 4 for a list of diagnostic morphological characters. The combination of a relatively small body size (male SVL 27 mm), slightly tubercular dorsal skin, relatively large tympanum (13% of SVL in males), and advertisement call consisting of a single pulsed note not repeated in regular series distinguishes *M. riparius* **sp. nov.** from species of all other clades. Species of the *M. fergusoni* clade are larger and have typically a more tubercular dorsum, while species of the *M. curtus* clade are often larger and most have a smaller tympanum. Some specimens of the new species have whitish dots on the flanks and most have only an indistinct white marking on the snout tip, which impedes their distinction from some species of the *M. biporus, M. stelliger* and *M. inaudax* clades where advertisement calls are unknown. However, the usually more pointed snout, larger tympanum, longer limbs, and overall different appearance of *M. riparius* **sp. nov.** should make a distinction straightforward (Table 4). Within the *M. betsileanus* clade, the new species can be distinguished from *M. betsileanus, M. noralottae* and *M. tripunctatus* by having fewer pulses per note in advertisement calls; furthermore from *M. noralottae* by smaller body size. *Mantidactylus katae* has a different advertisement call structure and larger femoral glands; *M. jonasi* has typically more pulses per note in advertisement calls, a lower pulse repetition rate, and a more tubercular dorsum; *M. incognitus* has more expressed dorsal and dorsolateral ridges and supraocular tubercles (Table 4). The new species is most similar to the allopatric *M. kortei* from which it cannot be reliably distinguished by morphology or calls, despite a tendency of a faster pulse rate in advertisement calls which however might be influenced by temperature (Table 4). For a detailed

distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. riparius* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male, in good state of preservation except for a large part of the right thigh excised for tissue sampling, and belly cut open (with some inner organs including bladder removed for parasite sampling) (Fig. 33). Body slender. Head slightly wider than body. Snout rounded in lateral view, slightly pointed in dorsal view. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis straight; loreal region concave. Tympanum distinct and rather large, wider than high, horizontal diameter of tympanum 82% of horizontal eye diameter. Supratympanic fold distinct, following the outer edge of the tympanum, regularly curved. Tongue ovoid, bifid. Maxillary teeth present. Vomerine teeth form two small rounded aggregations, positioned posterolateral to choanae. Choanae small and rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly longer than tibia (104%). Lateral metatarsalia separated. Inner metatarsal tubercle present, small. Outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(1), 2i(1.5), 2e(0.75), 3i(1.75), 3e(1), 4i(1.5), 4e(1), 5(0.5). Relative length of toes: I<II<V=III<IV. Skin on the upper surface smooth. Ventral side smooth. Femoral gland distinct.

Variation.—Variation in measurements is given in Table 7. See Fig. 46 for colouration in life and its variation. Given the small sample sizes of measured individuals, an assessment of sexual dimorphism is not possible. Femoral glands in males are relatively weakly expressed and not conspicuously coloured in life.

Natural history.—Found along semi-permanent streams and in natural pools of oasis at Isalo sandstone massif. It is a relatively shy species that hides in the crevices of the rocks. The species is found in syntopy with both *Mantidactylus mahery* and *M. noralottae*.

Calls.—The advertisement call of *M. riparius* (FAZC 14746; ACP4528), recorded on 12 February 2011, at Isalo (Andriamanero), unknown air temperature, consisted of a pulsed note (Fig. 47) of variable duration, emitted in somewhat irregular series. Notes exhibited amplitude modulation, with call energy rapidly increasing from the beginning of the note, reaching its maximum after approximately one tenth of the note's duration, continuously decreasing afterwards. Pulse repetition rate within notes was highest at the beginning and decreases towards the note's end. Call energy was distributed in a wide frequency band. Numerical parameters of 12 analysed calls were as follows: call duration (= note duration) 249–697 ms (348.4 ± 139.2 ms); 15–41 pulses per note (21.0 ± 8.1); pulse duration 2–5 ms (3.8 ± 1.3 ms); pulse repetition rate within notes 49.2–114.3 pulses/s (74.0 ± 27.5); dominant frequency 1518–1574 Hz (1549 ± 28 Hz); prevalent bandwidth 950–7400 Hz; call repetition rate (= note repetition rate) within series ca 5–9 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently microendemic to the Isalo massif (Fig. 7). Elevation range: 640–920 m a.s.l.

Etymology.—The Latin adjective riparius, meaning 'inhabiting the banks of rivers', making reference to the preferred microhabitat of this (and other) *Brygoomantis* species.

Mantidactylus fergusoni clade

This clade contains a series of medium-sized species (27.8–42.2 mm adult SVL) that have usually been thought to be related to or similar to *M. betsileanus* in previous studies (e.g. Glaw & Vences 2007; Vieites *et al.* 2009). Our phylogenomic tree, however, places them in a clade sister to the *M. ulcerosus* clade, which agrees with some of their morphological features, such as a stouter body and a less distinctly expressed or absent white dot on the tip of the snout in many specimens. According to our classification, this clade contains four new species, named after the holotypes depicted in Fig. 48, and we name the clade after the alphabetically first of the new species, *M. fergusoni* **sp. nov.**, described in the following.

Mantidactylus fergusoni **sp. nov.**

Identity and justification.—This lineage has been previously considered as confirmed candidate species *M.* sp. 26 by Vieites *et al.* (2009) and *M.* sp. Ca26 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *betsileanus* "Andranofotsy"' by Glaw and Vences (2007). Our phylogenomic analysis confirms that this lineage is in a major clade (here named the *M. fergusoni* clade) containing only scientifically unnamed lineages, and its status as distinct species is therefore out of question. However, deciding how many species exist in this clade is complicated. *Mantidactylus* sp. Ca26 forms a clade with several other divergent mitochondrial lineages of uncertain status; here we consider the lineage previously named *M.* sp. 21 (Vieites *et al.* 2009) or *M.* sp. Ca21 (Perl *et al.* 2014) from Nosy Mangabe, Makira, Masoala, and Cap Est/Ambato as conspecific with *M. fergusoni* (note that *M.* sp. 21 was wrongly placed in the tree of Vieites *et al.* [2009], probably due to a sequence confusion in the alignment used for phylogenetic analysis). As a further deep conspecific lineage we consider samples from Marojejy and additional sites in the North East. Samples from Nosy Boraha (*M.* sp. Ca27) according to our phylogenomic analysis (Fig. 5) form a clade with the lineage *M.* sp. Ca25 (see Vieites *et al.* 2009) from different sites on the mainland adjacent to Nosy Boraha, and together are sister to *M. fergusoni* **sp. nov.**; the Nosy Boraha population is described below as *M. jahnarum* **sp. nov.** based on its bioacoustic differentiation.

Holotype.—ZSM 126/2002 (MV 2001.1389), adult male, collected by M. Vences on 17 December 2001 at

FIGURE 46. *Mantidactylus riparius* **sp. nov.** from the Isalo massif in life, in dorsolateral and ventral view. (a,b) Adult male (ACZC 1849 = FAZC 14351). (c) Adult female (ACZC 1852 = FAZC 14353). (d) Adult female (ACZC 1929; yellowish oocytes visible through the skin on the flank). (e,f) Adult female (ACZC 1923 = FAZC 14366).

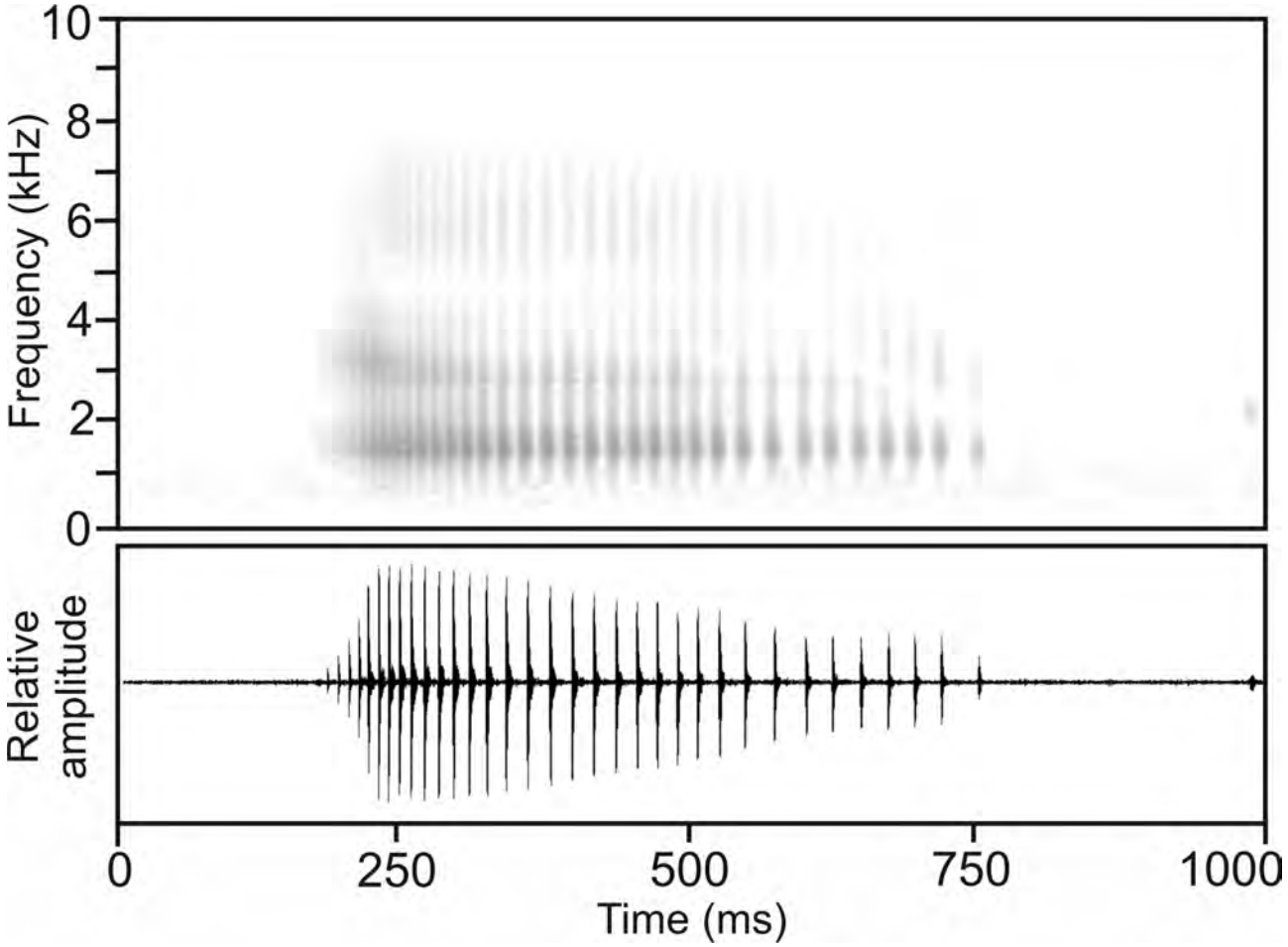

FIGURE 47. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus riparius*, recorded on 12 February 2011 at Isalo (air temperature unkown). Recording bandpass-filtered at 500–8000 Hz.

Andranofotsy (15.4353°S, 049.8439°E, 85 m a.s.l.), Analanjirofo Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession AY848214).

Paratypes.—A total of six paratypes: ZSM 124/2002 (MV2001.1433), female, ZSM 125/2002 (MV2001.1434), adult male, and ZSM 176/2002 (FGMV 2001.1383), specimen of unknown sex and maturity, all with the same collection data as the holotype; ZSM 5050/2005 (ZCMV 2125), adult female, and ZSM 5051/2005 (ZCMV 2136), adult male, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 22 February 2005 on Nosy Mangabe (ca 15.50°S, 049.77°E, 50–100 m a.s.l.); ZSM 355/2010 (FGZC 4277), adult female, collected by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, F.M. Ratsoavina on 3 April 2010 at Ambodivoahangy (15.2899°S, 049.6203°E, ca 100 m a.s.l.).

Additional material.—The following three specimens are assigned to *M. fergusoni* **sp. nov.** but come from a genetically divergent population and have in part (ZFMK specimens) not been sequenced, and therefore they are not included in the paratype series: ZSM 201/2005 (FGZC 2746), adult male, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 14 February 2005 at Marojejy, Camp 1 'Mantella' (14.4377°S, 049.7756°E, 481 m a.s.l.); ZFMK 59938, adult male, and ZFMK 59939, adult female, collected by F. Glaw and O. Ramilison on 22 February 1995 at Marojejy (near Camp Mantella).

Diagnosis.—A member of the *M. fergusoni* clade as revealed by the phylogenomic analysis, and sister to *M. jahnarum* **sp. nov.** described below. See Table 4 for a list of diagnostic morphological characters. The combination of a small to moderate body size in males (SVL up to 25–30 mm) and distinctly larger body size in females (36–42 mm), tubercular dorsal skin, large tympanum size in males (10–14% of SVL), absence of white spots on flanks and of white marking on snout tip, and advertisement call consisting of a single-pulse note distinguishes *M. fergusoni* **sp. nov.** from most species of the other clades. Two species from the *M. ulcerosus* clade (*M. ulcerosus* and *M. bellyi*) can be morphologically similar, but they occur in the Sambirano and North West regions, and have strongly differing advertisement calls (Table 4). One species of the *M. betsileanus* clade (*M. katae*) has an advertisement call of similar general structure, but has a faster and more regular call repetition rate, less tubercular dorsum, larger femoral glands, and a distinct white marking on snout tip (Table 4). *M. fergusoni* **sp. nov.** may also show superficial similarities to other species of the *M. betsileanus* clade but does not appear to occur sympatrically with any of them; in general it has a more tubercular dorsum and differs from all of these by

advertisement call structure (Table 4). The *M. fergusoni* clade contains only species newly named herein; for a distinction from these other species, see below. A full list of molecular diagnostic sites in the 16S gene of *M. fergusoni* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 48). Part of left shank muscle removed as tissue sample, femoral glands partly detached for examination in internal view. Body slender. Head wider than body. Snout rounded. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis very weak, slightly concave. Loreal region concave. Tympanum distinct, large, slightly wider than high, its horizontal diameter about 91% of eye diameter. Supratympanic fold present, beginning straight, with a rather distinct bend midway towards jaw / forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth present in two rounded to ovoid aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I≤II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly longer than tibia (104%). Lateral metatarsalia separated. Inner and outer metatarsal tubercles present. Webbing formula: 1(0.5), 2i(1.5), 2e(0.5), 3i(2), 3e(1), 4i(2.5), 4e(2), 5(0.5). Relative length of toes: I<II<V=III<IV. Skin on the upper surface quite smooth in preservative (but rather tubercular in life). Ventral side smooth. Femoral glands present, with a distinct and large distal ulcerous macrogland internally consisting of six large granules. Proximal granular gland field relatively indistinct, only recognisable in internal view.

Colour in preservative: dorsum brown with a minimal reddish shade. Forelimbs and hindlimbs with distinct brown crossbands. Venter beige, chest and throat rather dark brown with distinct light markings and a central median line on throat. Colour in life was similar to preservative, but with a distinct reddish-brown colour dorsally.

Variation.—Variation in measurements is given in Table 8. See Fig. 49 for colouration in life and its variation. There is pronounced sexual size dimorphism (confirmed male SVL 24.9–29.9 mm [n = 5] vs confirmed female SVL 35.7–42.2 mm [n = 4]). Males have a somewhat larger tympanum than females (HTD/ED ratio is 69–67% in females, 67–96% in males). Femoral glands are distinct but not particularly prominent in males, and only with a slight yellowish tone in life; very small, rudimentary glands recognisable in females.

Natural history.—Habitat and habits of this species are poorly known, but so far it has been found in primary or somewhat degraded rainforest. At Andranofotsy, calling males were observed at night from the shore of a shallow puddle next to a small spring in rainforest.

Calls.—The advertisement call of *M. fergusoni*, recorded on 16 December 2001 near Andranofotsy, 25.4°C air temperature (Vences *et al.* 2006, CD 2, track 69), consists of a simple, short, single pulse 'click' note, emitted in series (Fig. 50). Inter-call intervals were irregular with some calls (= notes) occurring in pairs with lower inter-call interval in-between. Call energy was distributed in a wide frequency band. Numerical parameters of 13 analysed calls were as follows: call duration (= note duration) 9–12 ms (10.5 ± 0.8 ms); 1 pulse per note (1.0 ± 0.0); pulse duration = note duration = call duration; dominant frequency 1626–1690 Hz (1669 ± 26 Hz); prevalent bandwidth 700–5700 Hz;

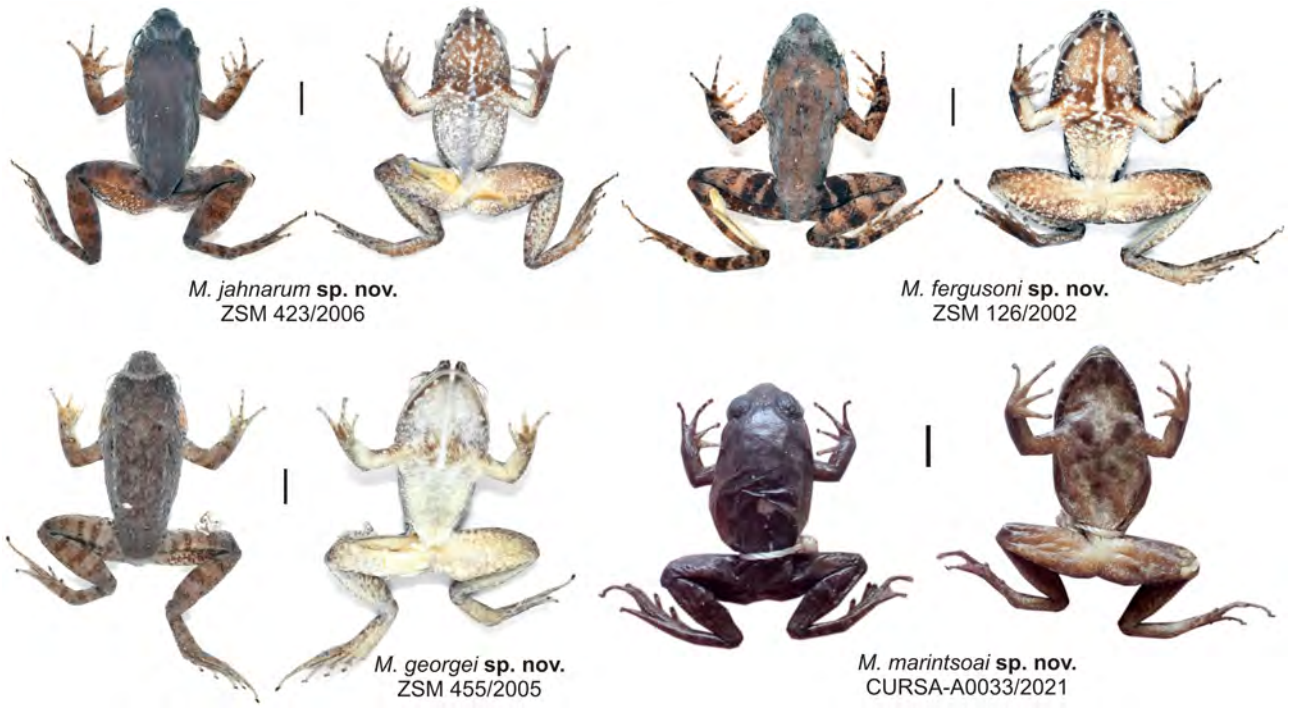

FIGURE 48. Preserved holotype specimens of newly named species in the *Mantidactylus fergusoni* clade. Scale bars equal 5 mm.

FIGURE 49. *Mantidactylus fergusoni* **sp. nov.** in life, in dorsolateral, dorsal, and ventral view. (a,b) Adult male (holotype ZSM 126/2002 = FGMV 2001.1389) from Andranofotsy. (c,d) Adult female (ZSM 124/2002 = FGMV 2001.1434) from Andranofotsy. (e,f,g) Female specimen (ZCMV 15063) from a large stream near Camp 1 'Mantella', Marojejy, photographed in 2016.

call repetition rate (= note repetition rate) within series ca 210–290 calls/min.

Calls recorded on 31 March 2010 at Ambodivohangy, Makira area (from specimen ZSM 361/2010 = FGZC 4219), 24°C estimated air temperature, agree with those described above from Andranofotsy, apart from somewhat lower call repetition rate within series. Calls consisted of a simple short 'click' note emitted isolated or more often in series at irregular intervals. Numerical parameters of 28 analysed calls were as follows: call duration (= note duration) 7–13 ms (8.9 ± 1.4 ms); 1 pulse per note (1.0 ± 0.0); pulse duration = note duration = call duration; dominant frequency 1571–1722 Hz (1638 ± 54 Hz); prevalent bandwidth 700–5500 Hz; call repetition rate (= note repetition rate) within series ca 100–170 calls/min.

Tadpoles.—The tadpole of this species has not been described.

TABLE 8. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus fergusoni* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype. A hash (#) marks measurements taken by AH, an asterisk (*) specimens measured by FTR and AR, and thus not fully comparable with other measurements, all taken by MV. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
M. fergusoni **sp. nov.** (Ca26)																			
ZSM 126/2002 [HT]	FGMV 2001.1389	M	Andranofotsy	27.8	10.3	11.6	4.4	4.0	3.0	1.9	2.8	17.5	8.7	48.7	22.5	15.1	14.5	3.6	2.6
ZFMK 59938 #	NA	M	Marojejy, Camp Mantella	26.0	10.6	9.7	3.9	2.6	2.9	1.8	2.9	8.9	8.0	NM	NM	13.4	14.5	2.8	2.2
ZSM 125/2002 [PT]	FGMV 2001.1434	M	Andranofotsy	26.2	10.1	11.2	4.2	3.1	2.4	2.0	3.1	15.8	7.7	41.8	19.1	13.3	13.4	3.9	2.4
ZSM 201/2005 #	FGZC 2746	M	Marojejy, Camp Mantella	24.9	9.9	10.0	4.1	3.3	2.7	1.8	2.7	10.2	7.9	NM	NM	12.3	14.0	3.4	2.3
ZSM 5051/2005 [PT]	ZCMV 2136	M	Nosy Mangabe	29.9	11.4	12.8	4.1	3.6	3.5	2.4	3.3	17.6	8.5	45.6	21.0	14.0	14.8	3.7	2.5
ZFMK 59939 #	NA	F	Marojejy, Camp Mantella	35.7	14.7	13.4	5.4	2.9	3.8	2.1	4.0	12.7	10.4	NM	NM	16.3	19.6	NA	NA
ZSM 124/2002 [PT]	FGMV 2001.1433	F	Andranofotsy	36.1	13.6	14.5	5.6	3.6	3.9	2.3	3.1	22.5	10.2	60.2	28.3	19.4	18.9	NA	NA
ZSM 355/2010 [PT]	FGZC 4277	F	Makira	40.3	15.2	16.3	5.5	3.8	4.1	2.4	3.9	24.6	11.8	66.5	30.0	21.2	21.2	NA	NA
ZSM 5050/2005 [PT]	ZCMV 2125	F	Nosy Mangabe	42.2	15.4	16.7	6.0	4.0	4.2	2.7	3.8	24.4	11.9	69.4	30.6	21.0	21.7	NA	NA
M. georgei **sp. nov.** (Ca35/Ca36)																			
ZSM 455/2005 [HT]	ZCMV 806	M	Toamasina	30.7	11.9	12.4	4.9	4.7	3.2	1.9	3.5	17.4	8.0	46.2	20.6	14.1	13.7	4.0	3.3
ZSM 454/2005	ZCMV 803	M	Maroantsetra	29.0	10.9	12.0	4.6	3.7	3.3	1.8	3.4	17.4	8.6	46.9	20.3	13.9	13.8	4.0	2.4
ZSM 456/2005 [PT]	ZCMV 807	M	Toamasina	28.4	10.5	11.9	4.4	4.2	2.9	1.8	3.5	16.3	8.4	46.3	20.4	13.8	13.5	4.6	3.3
M. jahnarum **sp. nov.** (Ca27)																			
ZSM 423/2006 [HT]	ZCMV 3390	M	Nosy Boraha	30.3	11.1	12.6	4.7	3.3	3.1	1.8	3.2	17.2	8.9	46.1	21.1	14.0	14.4	4.8	3.0

... *Continued on the next page*

TABLE 8. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 424/2006 [PT]	ZCMV 3393	M	Nosy Boraha	28.5	10.5	11.8	4.5	3.1	3.1	1.7	3.0	17.5	9.1	40.8	20.0	13.5	14.1	4.6	3.4
ZSM 520/2006 [PT]	ZCMV 3218	F	Nosy Boraha	33.6	12.5	13.8	4.9	3.6	3.0	2.0	3.0	21.5	9.7	57.2	26.3	17.5	17.1	NA	NA
ZSM 521/2006 [PT]	ZCMV 3219	F	Nosy Boraha	30.4	11.1	12.6	4.7	2.9	3.1	2.0	3.2	19.4	9.7	50.7	23.2	15.6	15.4	NA	NA
M. marintsoai **sp. nov.**																			
CURSA-A033/2021 [HT] *	THC301	M	Bangoabe, Marojejy	29.0	10.3	12.1	3.7	3.8	3.4	1.9	2.9	16.4	8.1	44.7	20.2	14.0	14.2	NM	NM
CURSA-A036/2021 [PT] *	THC354	F	Andramanolotra	36.7	12.4	14.6	4.7	3.0	3.5	1.9	3.3	20.6	8.7	60.6	24.6	17.7	17.6	NM	NM
CURSA-A035/2021 [PT] *	THC233	F	Antsirabe-Nord (Bemanevika)	36.8	11.7	14.0	4.2	3.0	3.8	2.3	3.6	21.8	10.8	59.8	25.6	18.2	18.5	NM	NM
CURSA-A034/2021 [PT] *	THC248	F	Andramanolotra	34.6	11.4	13.0	4.1	2.8	3.8	1.9	3.1	20.0	10.0	52.9	23.7	16.4	16.4	NM	NM
ZSM uncatalogued [PT] *	THC246	F	Andramanolotra	36.5	12.7	14.6	6.0	3.0	3.8	2.0	3.8	21.0	10.6	56.9	25.7	17.6	17.8	NM	NM
ZSM uncatalogued [PT] *	THC245	F	Andramanolotra	38.7	12.6	15.1	5.9	3.2	3.7	2.5	3.7	22.3	11.0	59.6	25.9	18.2	18.9	NM	NM
ZSM uncatalogued [PT] *	THC355	F?	Andramanolotra	30.3	10.0	12.3	4.4	2.2	3.0	1.9	3.0	18.0	8.7	49.4	22.0	14.9	15.2	NM	NM

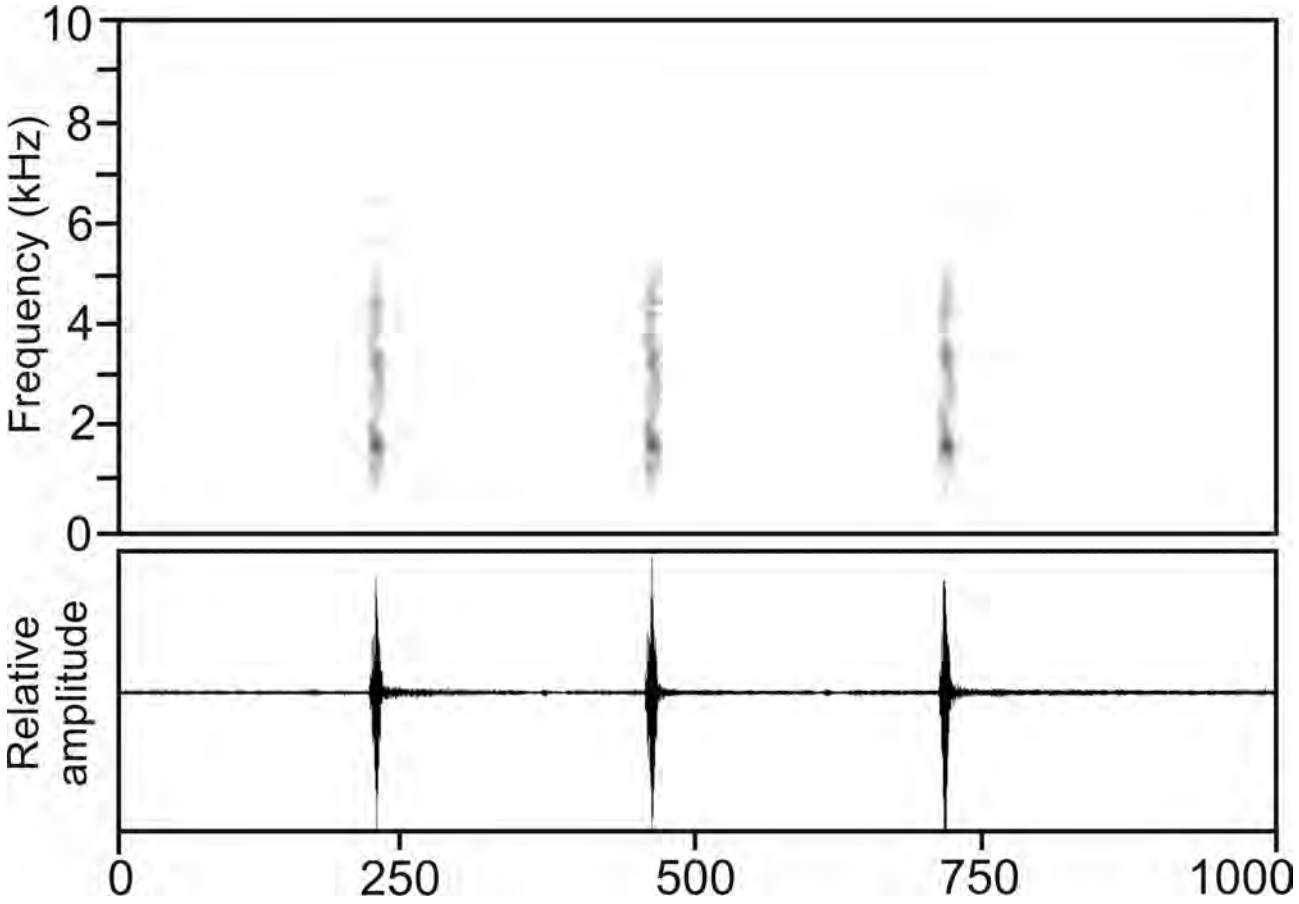

FIGURE 50. Audiospectrogram and corresponding oscillogram of three advertisement calls of *Mantidactylus fergusoni*, recorded on 21 December 2001 at Andranofotsy (25.4°C air temperature). Recording bandpass-filtered at 500–8000 Hz.

Distribution.—Endemic to low-elevations of Northern Central East and North East (Fig. 7). This species is known from Ambato, Ambinanifaho, Ambodirafia Tokana, Ambodiriana, Ambodivohangy (Makira), Ampasimazava, Andranofotsy (type locality), Andrantambe, Antanambe, Antsahanoro, Befanjana, Belambo, various sites within Marojejy National Park, Masoala, Nosy Mangabe, and the Sambava region. Elevation range: 12–1326 m a.s.l.

Etymology.—We dedicate this species to Barry Ferguson, an outspoken worker on environmental justice for Madagascar, in acknowledgement of his support of the first author's work on Madagascar's herpetofauna.

Mantidactylus georgei **sp. nov.**

Identity and justification.—This lineage of the *M. fergusoni* clade has previously been considered as confirmed candidate species *M.* sp. 36 by Vieites *et al.* (2009) and *M.* sp. Ca36 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *betsileanus* "Toamasina"' by Glaw and Vences (2007). It was additionally referred to as *Mantidactylus* sp. aff. *betsileanus* [Ca AY848260] by Rosa *et al.* (2011, 2012). It consists of frogs that are bioacoustically somewhat similar to *M. betsileanus*, but strongly differ in genetics and in various aspects of morphology and advertisement calls (Table 4). *Mantidactylus georgei* **sp. nov.** forms a clade with another lineage from Maroantsetra considered as confirmed candidate species *M.* sp. 35 by Vieites *et al.* (2009) and *M.* sp. Ca35 by Perl *et al.* (2014), which we here consider to be a deep conspecific lineage. Due to the high genetic divergence and distinct bioacoustic differentiation of *M. georgei* **sp. nov.** to other species in the *M. fergusoni* clade, its status as distinct species is out of question.

Holotype.—ZSM 455/2005 (ZCMV 806), adult male, collected on 23 February 2004 by M. Vences ca 10 km north of Toamasina (coordinates not taken; coordinates of Toamasina city: 18.167°S, 049.383°E, 22 m a.s.l.), Antsinanana Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession AY848261).

Paratypes.—A total of six paratypes: ZSM 456/2005 (ZCMV 807), an adult male with similar collection data to the holotype; MRSN A6213, adult male, and MRSN A6223, adult female, both from Betampona, Maintimbato (17.8940°S, 49.2283°E), collected on 21 February 2007 by G.M. Rosa and J. Noël; MRSN A6341, adult male, with same locality and collectors as previous specimens but collected on 17 November 2007; MRSN A6217 and MRSN A6599, adult males, both collected at Betampona, Rendrirendry (17.9186°S, 49.2103°E), by G.M. Rosa

FIGURE 51. *Mantidactylus georgei* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male (holotype ZSM 455/2005 = ZCMV 806), from near Toamasina, photographed in 2004. (c,d) Adult female (probably corresponding to ZMA 19496 = FGMV 2002.2259, not DNA barcoded), from near Toamasina, photographed in 2003. (e,f) Adult male (paratype ZSM 456/2005 = ZCMV 807), from near Toamasina, photographed in 2004. (g,h) Adult male (FAZC 13917) from Betampona. (i,j) Adult female (FAZC 13973) from Betampona. (k,l) Adult male from Maroantsetra, photographed in 2003. (m,n) Adult female from Maroantsetra, photographed in 2003.

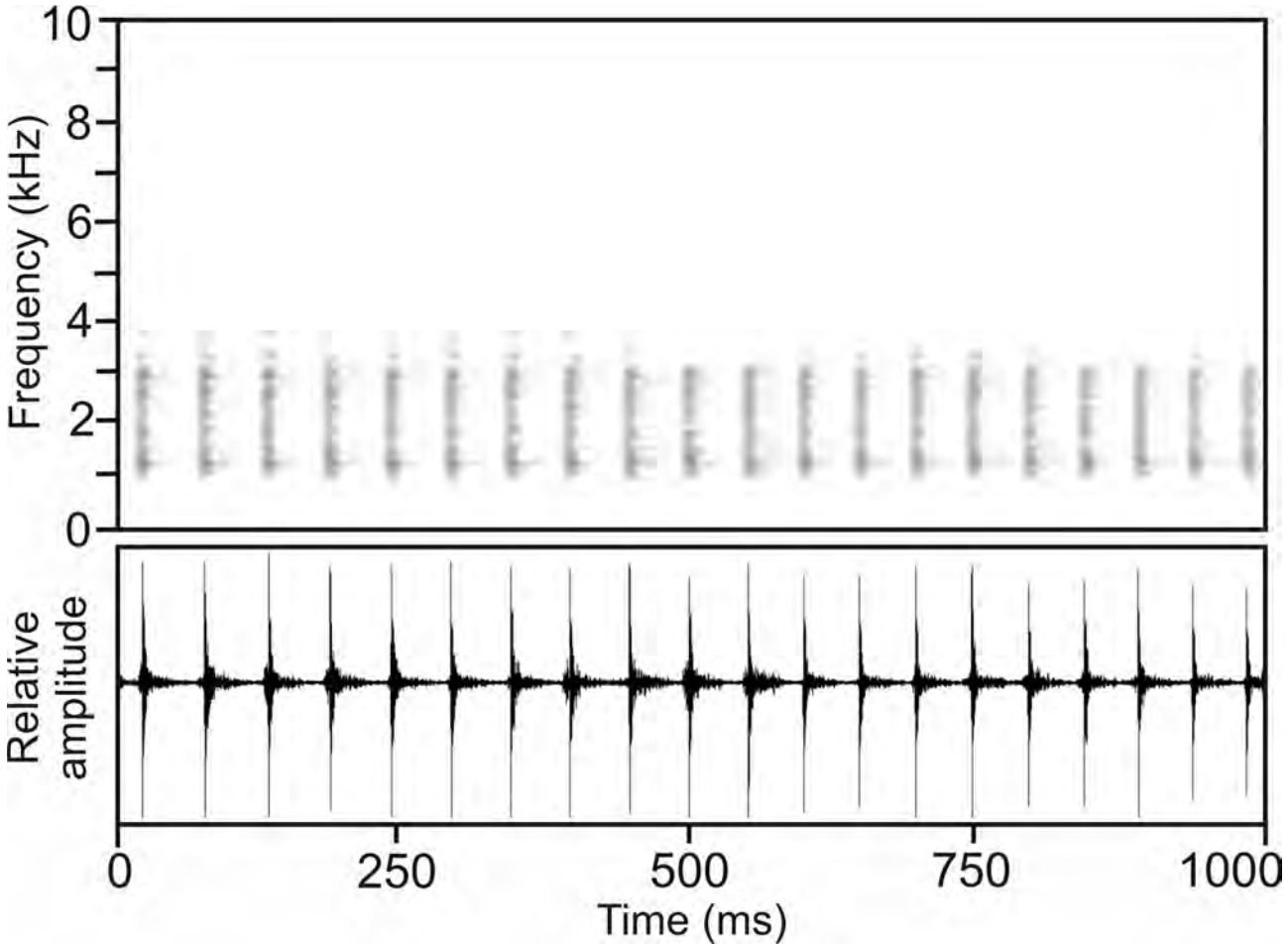

FIGURE 52. Audiospectrogram and corresponding oscillogram of a 1000 ms section of the advertisement call (call duration 2195 ms) of *Mantidactylus georgei*, recorded from the holotype on 29 February 2004 north of Toamasina (25.2°C air temperature). Recording bandpass-filtered at 500–4100 Hz.

and J. Noël, on 23 March 2007 and 30 November 2007, respectively.

Additional material.—ZSM 454/2005 (ZCMV 803) an adult male from a genetically divergent population, collected by M. Vences on 24 February 2004 at Maroantsetra (15.4456°S, 049.7375°E, 10 m a.s.l.). ZMA 19496 (FGMV 2002.2259, adult female, collected near Tomasina by M. Vences on 10 February 2003 (specimen not DNA barcoded).

Diagnosis.—*Mantidacytlus georgei* **sp. nov.** is a member of the *M. fergusoni* clade as revealed by the phylogenomic analysis, and splits from a basal node of this clade. See Table 4 for a list of diagnostic morphological characters. The combination of small to moderate body size in males (SVL up to 28–31 mm), moderately tubercular dorsal skin, large tympanum size in males (13–15% of SVL), absence of white spots on flanks, presence of a white marking on the snout tip of many individuals (especially males), and advertisement call consisting of a single, relatively long and pulsed note distinguishes *M. georgei* **sp. nov.** from most species of the other clades (Table 4). Two species from the *M. ulcerosus* clade (*M. ulcerosus* and *M. bellyi*) can be morphologically similar, but they occur in the Sambirano and North West regions, and exhibit higher pulse repetition rates in advertisement calls (Table 4). *M. georgei* **sp. nov.** shows similarities to species of the *M. betsileanus* clade but in general it has a more tubercular dorsum and differs from most of these by advertisement call structure (Table 4); furthermore, sympatry with species of the *M. betsileanus* clade is rare, and is only known from Betampona where the new species co-occurs with *M. betsileanus.* Within the *M. fergusoni* clade, it strongly differs from *M. fergusoni* in advertisement call structure, and by the more common presence of a white marking on the snout tip. For a distinction from other new species in the *M. fergusoni* clade, see below. A full list of molecular diagnostic sites in the 16S gene of *M. georgei* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 48). Tissue sample taken ventrally from right thigh. Remaining (left) femoral gland partly detached to examine its structure internally. Second and third finger of left hand mutilated. Body rather slender. Head as wide as body. Snout rounded.

Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, elliptical, wider than high, its diameter 96% of eye diameter. Supratympanic fold distinct, beginning straight, with a rather distinct, angular bend midway towards insertion of forelimb. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle present, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I=II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (103%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but recognisable. Webbing formula: 1(1), 2i(1), 2e(1), 3i(2), 3e(1), 4i(2), 4e(2), 5(0.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface with granules, many of which form irregular longitudinal ridges. Ventral side smooth. Femoral glands present, with a distinct distal ulcerous macrogland and a moderately expressed proximal granular gland field.

Colour in preservative: dorsum brown, with indistinct irregular darker markings. A dark brown band between eyes is attached to a grey band on the head surface. Forelimbs brown with poorly defined darker markings. Hindlimbs brown with darker crossbands. Inguinal region without scattered whitish spots. Snout tip with a distinct light dot. Venter beige, throat and belly with very little brown mottling on thorax. Lower lip ventrally with alternating light and brown spots on the one side, on the other side uniformly beige-brown. Toe discs dark.

Variation.—Variation in measurements is given in Table 8. See Fig. 51 for colouration in life and its variation. No females available to assess sexual dimorphism. Femoral glands in life are rather distinct and prominent in males, consisting mostly of a large distal ulcerous macrogland and with only weakly recognisable proximal granular gland field, often with a somewhat yellowish colour; small, rudimentary glands recognisable in females.

Natural history.—Both near Toamasina and Maroantsetra, calling males were found at night from the shores of small streams and swampy areas next to ricefields, in heavily degraded secondary forest habitat. In Betampona and Ivoloina this species is commonly found along stream banks. In Ivoloina *M. georgei* is the only *Brygoomantis* species that can be found in the area, while in Betampona it occurs (often syntopically) with four *Brygoomantis* species. In Betampona it has been recorded in all campsites except Sahabefoza and Sahembendrana (which correspond to the campsites presenting the most pristine conditions).

Calls.—The advertisement call of the holotype of *M. georgei* recorded on 29 February 2004 a few km north of Toamasina, 25.2°C air temperature (Vences *et al.* 2006: CD2, track 66), consisted of a long to very long, regularly pulsed note (Fig. 52). Notes exhibited slight amplitude modulation, with call energy decreasing towards the note's end. Numerical parameters of 11 analysed calls were as follows: call duration (= note duration) 1425–3206 ms (2532.7 ± 527.4 ms); 26–64 pulses per note (46.9 ± 11.3); pulse duration 5–12 ms (7.9 ± 2.1 ms); pulse repetition rate within notes 12.7–24.4 pulses/s (18.1 ± 3.3); dominant frequency 1227–1722 Hz (1483 ± 184 Hz), with a second peak of almost identical energy at around 2970–3040 Hz; prevalent bandwidth 900–3400 Hz; call repetition rate not possible to identify with the available recordings.

Calls recorded on 24 February 2004, 21:00 h, at Maroantsetra, 24.1°C air temperature (Vences *et al.* 2006: CD2, track 65), very likely correspond to *M. georgei* and generally agreed with the calls described above, apart from somewhat higher pulse repetition rate and slightly higher number of pulses per note. Numerical parameters of six analysed calls were as follows: call duration (= note duration) 2470–3149 ms (2826.8 ± 278.7 ms); 51–85 pulses per note (71.7 ± 14.9); pulse duration 5–10 ms (7.9 ± 0.9 ms); pulse repetition rate within note 17.8–32.6 pulses/s (25.0 ± 4.9); dominant frequency 1260–1345 Hz (1287 ± 34 Hz); prevalent bandwidth 900–3800 Hz; call repetition rate not possible to identify with the available recording.

Additional calls have been recorded at Betampona and present an overall similar structure to the previous descriptions for the species (Rosa *et al.* 2011: track 35).

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to low-elevation areas of the Northern Central East of Madagascar (Fig. 7). This species is known from Anivorano Est, Antokotelo, Betampona, Ivoloina, Maroantsetra, Sahafina, Tampolo forest (Analanjirofo), Toamasina, and the vicinity of Vatomandry. Elevation range: 7–517 m a.s.l.

Etymology.—We dedicate this species, which occurs, among other sites along Madagascar's east coast, in Betampona Strict Nature Reserve, to Georges, our guide on numerous field expeditions in Betampona, in recognition of his dedication to the study of the herpetofauna of Betampona. The species epithet *georgei* is derived from the English translation of our guide's name (George) as it thereby becomes easier to pronounce.

Mantidactylus jahnarum **sp. nov.**

Identity and justification.—This lineage of the *M. fergusoni* clade has previously considered as confirmed candidate species *M.* sp. 27 by Vieites *et al.* (2009), and *M.* sp. Ca27 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *betsileanus* "Nosy Boraha"' by Glaw and Vences (2007). The phylogenomic data place it sister to *M. fergusoni*, and its mitochondrial divergence from *M. fergusoni* (2.0–3.1%) is comparatively low, compared with other divergences observed among species of *Brygoomantis*. However, it distinctly differs by its advertisement calls (heard in multiple years from many individuals at the type locality, the islet Nosy Boraha) that consists of several short, pulsed notes, somewhat reminiscent of the call of species of the *M. ulcerosus* clade. We therefore here consider this lineage as the separate species *M. jahnarum* **sp. nov.** which, according to genomic data, may also include populations

FIGURE 53. *Mantidactylus jahnarum* **sp. nov.** in life, in dorsolateral and ventral view. (a,b,c) Adult male (holotype ZSM 423/2006) from Nosy Boraha, photographed in 2006. (d) Unsexed specimen from Nosy Boraha, photographed in 1991. (e,f) Adult male from Nosy Boraha, photographed in 1991.

from the mainland adjacent to Nosy Boraha which were named *M.* sp. Ca25 by Vieites *et al.* (2009) and which we here provisionally include in *M. jahnarum* **sp. nov.** as deep conspecific lineage.

Holotype.—ZSM 423/2006 (ZCMV 3390), adult male (call voucher), collected by M. Vences and J.E. Randrianirina on 7–8 March 2006 at Maromandia village on Nosy Boraha (16.9089°S, 049.8678°E, 20 m a.s.l.), Analanjirofo Region, Madagascar. 16S and cox1 barcode sequences of the holotype are available from GenBank (accessions FJ559258 and JN133220).

Paratypes.—A total of three paratypes: ZSM 424/2006 (ZCMV 3393), adult male, with same collection data as holotype; ZSM 520/2006 (ZCMV 3218) and ZSM 521/2006 (ZCMV 3219), two adult females, collected by M. Vences and J.E. Randrianirina on 7–8 March 2006 in a forest several km from Maromandia village (coordinates not taken), Nosy Boraha (= Île Sainte Marie).

Diagnosis.—*Mantidactylus jahnarum* **sp. nov.** is a member of the *M. fergusoni* clade as revealed by the phylogenomic analysis, and is the sister species of *M. fergusoni*. See Table 4 for a list of diagnostic morphological characters. The combination of a moderate body size (male SVL 29–30 mm, female SVL 30–34 mm), moderately tubercular dorsal skin, moderate tympanum size in males (11% of SVL), absence of white spots on flanks, presence of a white marking on the snout tip of many individuals (especially males), and regularly pulsed advertisement call emitted in regular series distinguishes *M. jahnarum* **sp. nov.** from most species of the other clades (Table 4). Two species from the *M. ulcerosus* clade (*M. ulcerosus* and *M. bellyi*) can be morphologically similar, but they occur in the Sambirano and North West regions, and have higher pulse repetition rates in advertisement calls (Table 4). *Mantidactylus jahnarum* **sp. nov.** shows similarities to species of the *M. betsileanus* clade but does not appear to occur sympatrically with any of them; in general, it has a more tubercular dorsum and differs from most of these by advertisement call structure (Table 4). Within the *M. fergusoni* clade, it differs from *M. fergusoni* and *M. georgei* in advertisement call structure: *M. fergusoni* has single-pulse calls repeated 2–5 times per second, whereas *M. georgei* does not arrange calls in regular series. For a distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. jahnarum* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

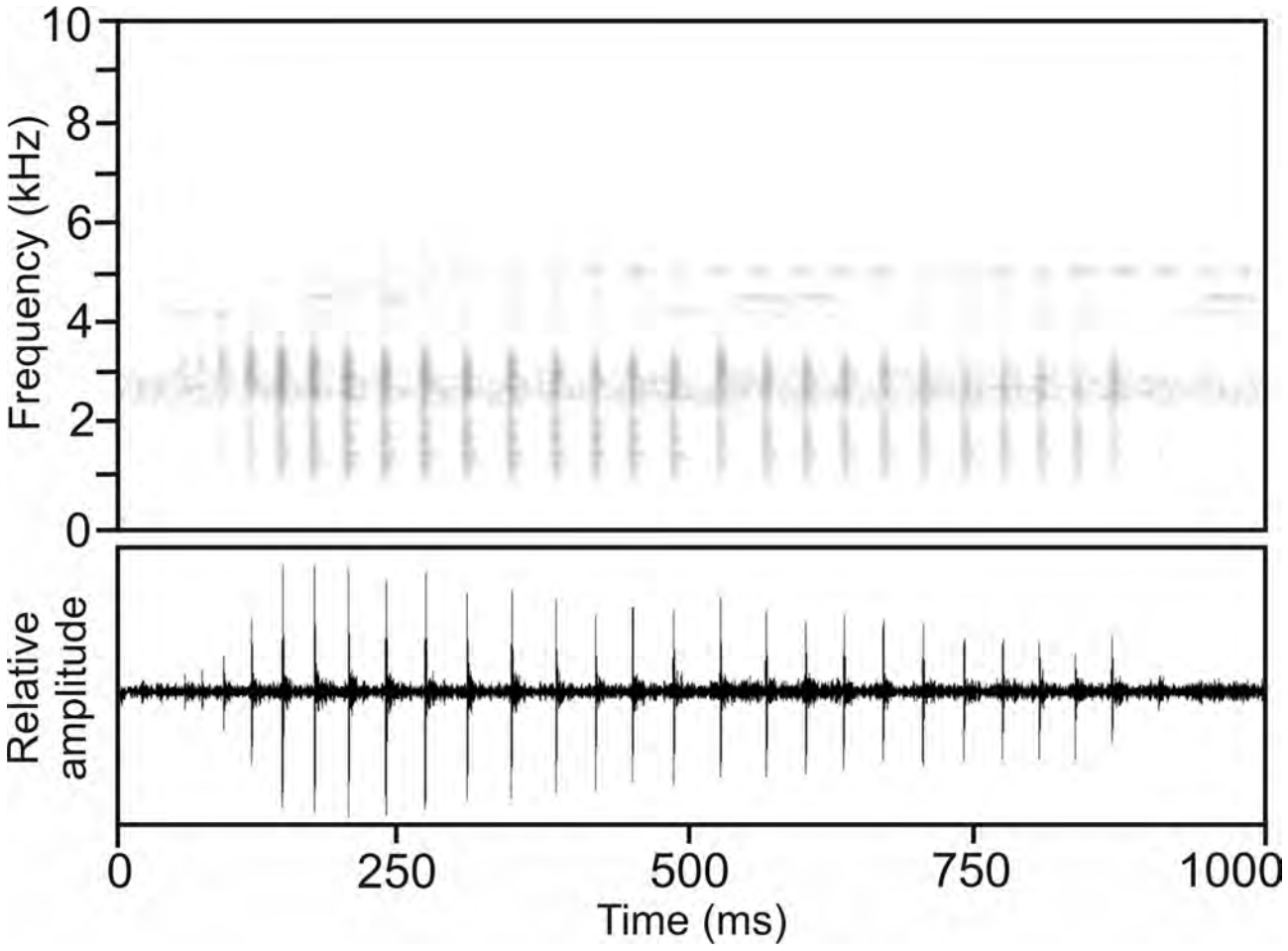

FIGURE 54. Audiospectrogram and corresponding oscillogram of one advertisement call of the holotype of *Mantidactylus jahnarum*, recorded on 7 March 2006 at Maromandia village, Nosy Boraha. Recording bandpass-filtered at 500–6500 Hz.

Description of the holotype.—Adult male in good state of preservation (Fig. 48). Part of right thigh muscle removed as tissue sample; femoral glands partly detached for examination in internal view. Body relatively slender. Head as wide as body. Snout rounded. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, rather straight. Loreal region concave. Tympanum distinct, large, slightly wider than high, its horizontal diameter about 75% of eye diameter. Supratympanic fold present, beginning straight, with a rather distinct bend midway towards jaw / forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I≤II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (97%). Lateral metatarsalia separated. Inner and outer metatarsal tubercles present. Webbing formula: 1(0.5), 2i(1.5), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(0.5). Relative length of toes: I<II<V=III<IV. Skin on the upper surface quite smooth in preservative with some granules on the lower flanks (but rather tubercular in life). Ventral side smooth. Femoral glands present, with a distinct and large distal ulcerous macrogland, internally consisting of four large granules. Proximal granular gland field not recognisable.

Colour in preservative: dorsum uniformly dark brown. Very weak signs of crossbands on fore- and hindlimbs. Venter dark grey, chest and throat rather dark brown with distinct light spots which form an interrupted and indistinctly marked central median line on throat. In life, colour of the holotype was similar to preservative, with a somewhat lighter tone of brown dorsally and a more whitish venter.

Variation.—Variation in measurements is given in Table 8. See Fig. 53 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 28.5–30.3 mm [n = 2] vs confirmed female SVL 30.4–33.6 mm [n = 2]). Also, sexual dimorphism in relative tympanum size seems to be absent (HTD/ED ratio is 62–73% in females, 69–70% in males). Femoral glands in life are rather distinct and prominent in males, with a large distal ulcerous macrogland, often with a somewhat yellowish colour but still with some of the dark pigmentation found elsewhere on the ventral side of the thigh.

Natural history.—Similar to *M. georgei*, this species appears to tolerate heavy habitat degradation. At Nosy Boraha, it can be found next to streams in rainforest, but calling males can also be heard at night from slowly running, shallow water bodies in highly degraded forest, including plantations and swamps next to villages shaded by some larger trees.

Calls.—The advertisement call of *M. jahnarum*, recorded on 7 March 2006 at Maromandia village, Nosy Boraha, from the holotype, at an at 25°C, consisted of a regularly pulsed note of variable duration (Fig. 54), emitted in series at regular intervals. Pulses were very short in duration. Regular call series seemed to consist of 4–6 calls, with the first call of the series being of longest duration. Notes exhibited slight amplitude modulation, with maximum call energy occurring shortly after the beginning of the note, continuously decreasing towards the note's end. Numerical parameters of 20 analysed calls were as follows: call duration (= note duration) 568–1558 ms (976.9 ± 277.9 ms); 16–45 pulses per note (29.1 ± 7.9); pulse duration 1–2 ms (1.1 ± 0.3 ms); pulse repetition rate within notes 25.0–35.4 pulses/s (29.3 ± 3.9); dominant frequency 2971–3120 Hz (2999 ± 60 Hz); prevalent bandwidth 1000–3400 Hz; call repetition rate (= note repetition rate) within regular series ca 36-47 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently microendemic to the islet of Nosy Boraha (Fig. 7), although a related lineage provisionally assigned to this species occurs on the adjacent mainland. Elevation range: ~20 m a.s.l.

Etymology.—We dedicate this species to our microbiologist colleagues Martina and Dieter Jahn, in recognition of their support of biodiversity research at the University of Technology in Braunschweig. We intentionally deviate from Article 31.1.2 of the Code and form the name using the feminine plural ending -arum, and not the masculine plural ending, -orum, with the intention of drawing attention to the already overly male-dominated taxonomic nomenclature, and the desire for a more egalitarian declension. To stabilise the nomen as coined here, we define it as a noun in apposition.

Mantidactylus marintsoai **sp. nov.**

Identity and justification.—This lineage was newly identified in this study. It consists of frogs from the North East of Madagascar that form a mitochondrially homogeneous lineage that probably is the sister group of *M. georgei* (Fig. 2; *M. marintsoai* **sp. nov.** is not included in the phylogenomic tree), with which it shares a unique Rag-1 haplotype (Fig. 4). Despite the lack of unambiguous morphological differences to *M. georgei* and the absence of bioacoustic data for *M. marintsoai* **sp. nov.**, we here name this lineage as new species, given its enormous genetic divergence (7.6–9.3% uncorrected 16S distance to *M. georgei*).

Holotype.—CURSA-A0033/2021 (field number THC301), adult male, collected by T.R. Fulgence, D.A. Martin, R. Randriamanantena, R. Botra, E. Befidimanana, A. Wurz, K. Osen, H. Kreft, A. Andrianarimisa, and F. M. Ratsoavina on 30 August 2018 in the eastern part of Marojejy National Park 'Bangoabe' (14.4467°S, 049.8251°E, ca 225 m a.s.l.), Sava Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of six paratypes: CURSA-A0034/2021 (THC248, THC245, THC246), three adult females, collected by T.R. Fulgence, D.A. Martin, R. Randriamanantena, R. Botra, E. Befidimanana, A. Wurz, K. Osen, H. Kreft, A. Andrianarimisa, and F. M. Ratsoavina on 18 January 2018 in a stream of Fokontany Andramanolotra/Sambava (13.9953°S, 050.0711°E, ca 54 m a.s.l.); CURSA-A0036/2021 (THC354), adult

FIGURE 55. *Mantidactylus marintsoai* **sp. nov.** in life, in dorsolateral, dorsal and ventral view. (a) Unsexed adult (tissue THT 204, not collected). (b,c) Adult female (THT282, not collected). (d,e) Adult female (CURSA-A036/2021 = THC354). (f,g) Adult male (holotype CURSA-A033/2021 = THC301).

female, and THC355, juvenile, collected by the same team on 22 November 2018 in the same location; CURSA–A0035/2021(THC233) adult female, collected by T.R. Fulgence, D.A. Martin, R. Randriamanantena, R. Botra, E. Befidimanana, A. Wurz, K. Osen, H. Kreft, A. Andrianarimisa, and F. M. Ratsoavina on 3 February 2018 in a stream in the Antsirabe-Nord/Vohemar, Fokontany of Bemanevika (13.9864°S, 049.9519°E, ca 61 m a.s.l.).

Diagnosis.—*Mantidactylus marintsoai* **sp. nov.** is a member of the *M. fergusoni* clade, and is probably the sister lineage of *M. georgei*, according to the 16S tree (it is not included in the phylogenomic analysis). See Table 4 for a list of diagnostic morphological characters. The combination of a moderate to large body size (male SVL 29 mm, female SVL 35–39 mm), moderately tubercular dorsal skin, relatively large tympanum size in males (13% of SVL), absence of white spots on flanks, and absence of a white marking on the snout tip, distinguishes *M. marintsoai* **sp. nov.** from most species of the other clades (Table 4). Two species from the *M. ulcerosus* clade (*M. ulcerosus* and *M. bellyi*) can be morphologically similar; these two species occur in the Sambirano and North West regions, and the distribution area especially of *M. bellyi* may overlap with that of *M. marintsoai* **sp. nov.** which is known from the North East; a distinction may be possible by the apparently more strongly developed foot webbing in *M. bellyi* and *M. ulcerosus* (Table 4). *Mantidactylus marintsoai* **sp. nov.** shows similarities to species of the *M. betsileanus* clade but does not appear to occur sympatrically with any of them; in general, it has a more tubercular dorsum and seems to lack a distinct white marking on the snout tip which characterizes many species of the *M. betsileanus* clade (Table 4). Within the *M. fergusoni* clade, a bioacoustic comparison is not possible due to the lack of call data for *M. marintsoai* **sp. nov.**; the species might be distinguished from *M. fergusoni, M. georgei* and *M. jahnarum* by less developed foot webbing (Table 4), and seems to differ from many specimens of *M. georgei* and *M. jahnarum* by the lack of a clear white marking on snout tip. For a distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. marintsoai* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 48). For measurements, see Table 8. Body rather stout. Head longer than wide. Snout rather pointed. Nostrils directed laterally, slightly protuberant,

nearer to tip of snout than to eye. Canthus rostralis distinct, loreal region slightly concave. Tympanum distinct, large, round, horizontal diameter of tympanum 97% of horizontal eye diameter. Supratympanic fold distinct, beginning straight above, with rather distinct bend midway towards insertion of forelimb. Tongue ovoid, distinctly bifid posteriorly. Vomerine teeth form two elongate aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle not recognisable, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (98%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not recognisable. Webbing formula: 1(1), 2i(1), 2e(0.5), 3i(2), 3e(1), 4i(2), 4e(2), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, dorsolaterally smooth. Ventral side smooth. Femoral glands small and distinct in external view.

Colour in preservative: dorsally brown, with two distinct light spots. Forelimbs light brown with 2–3 dark brown crossbands on hand and arm. Hindlimbs light brown with distinct dark brown crossbands. Inguinal region with few scattered whitish spots. Snout tip with a light spot (width 1.1 mm, height 1.2 mm), tympanum region slightly lighter than remaining head sides. Venter beige with light brown mottling, throat darker than belly with brown mottling. Lower lip with distinct alternating light and brown spots. Toe discs dark brown.

Variation.—Variation in measurements is given in Table 8. See Fig. 55 for colouration in life and its variation. Some individuals have mid-dorsal stripes (Fig. 55b). There may be pronounced sexual size dimorphism, but sample sizes are small (confirmed male SVL 29.0

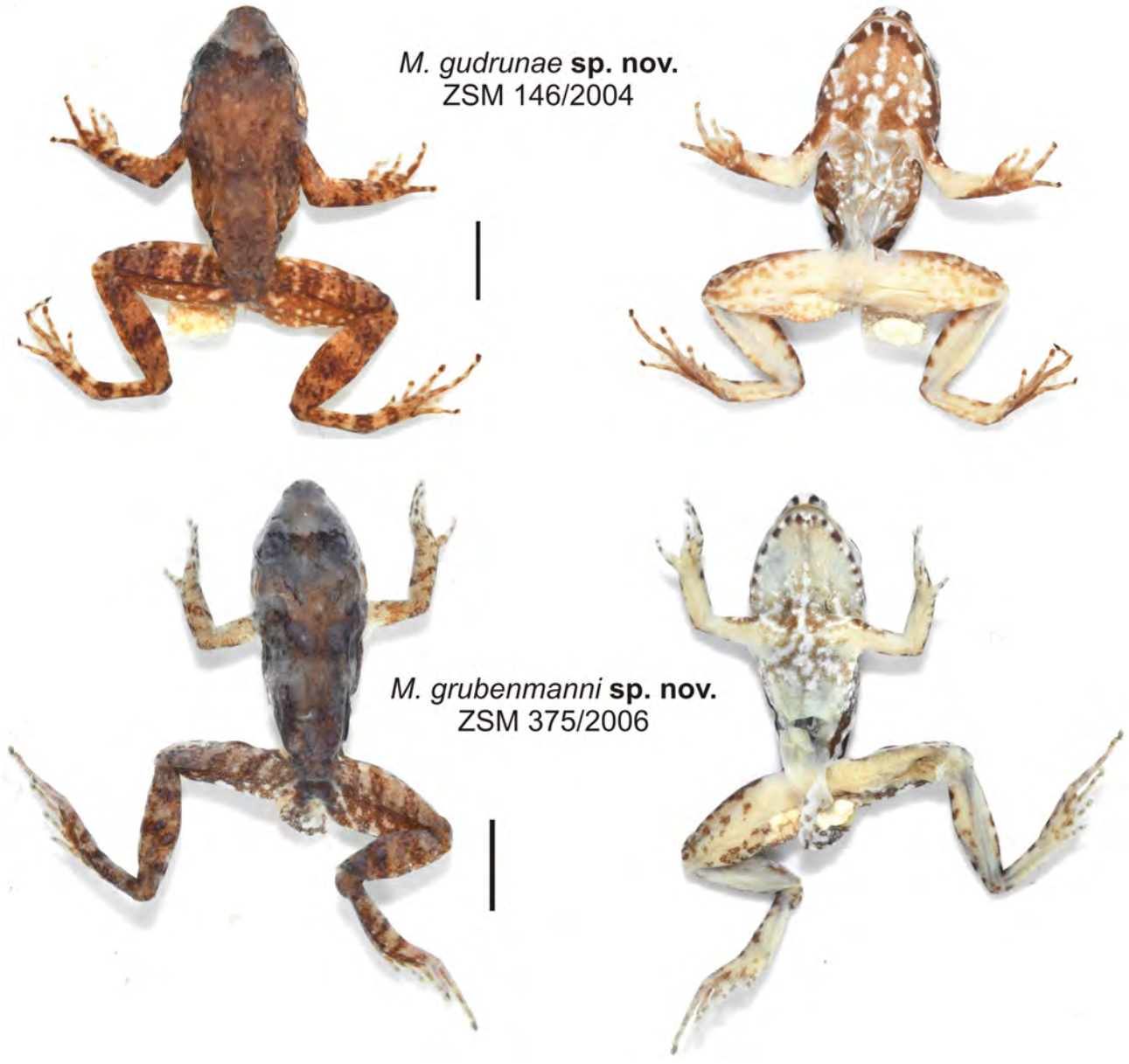

FIGURE 56. Preserved holotype specimens of newly named species in the *Mantidactylus tricinctus* clade. Scale bars equal 5 mm.

mm [n = 1] vs confirmed female SVL 34.6–38.7 mm [n = 5]). Males seem to have a larger tympanum than females (HTD/ED ratio is 103% in the only known male, 50–71% in females). Femoral glands in life, in the only known male, are relatively small and indistinct, and not conspicuously coloured; tiny rudimentary glands are recognisable in females.

Natural history.—Found in rainforest patches of the North East of Madagascar. All individuals were found in or near streams in rainforest, including degraded primary forest, secondary forest, and narrow riparian forest fragments. In 2019, the riparian forest beside the village of Bemanevika was felled.

Call.—The call of this species has not been recorded.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Apparently endemic to a rather small area of the North East of Madagascar (Fig. 7). This species is known from Marojejy, Andramanolotra, and Bemanevika village (a Fokontany of Antsirabe-Nord, in the Vohemar district). Elevation range: 16–273 m a.s.l.

Etymology.—T.R. Fulgence wishes to dedicate this species to his father, the late Marintsoa, in recognition of his support of his son's scientific career and pursuit of a PhD degree. The name is used as a noun in apposition.

Mantidactylus tricinctus clade

A clade of one previously named and two new species, characterized by small body size (17.1–28.6 mm adult SVL), reduced webbing, and similarity in general body shape with especially the smaller species in the *M. betsileanus* clade. Contains: *M. tricinctus* and two new species, which are named based on holotypes depicted in Fig. 56.

Mantidactylus tricinctus (Guibé, 1947)

Type material.—*Gephyromantis tricinctus* Guibé, 1947 was originally described based on two syntypes: MNHNP 1931.26–27. As discussed by Glaw and Vences (1999), Guibé (1947) considered the female MNHN 1931.26 as 'gynétype' and the male MNHN 1931.27 as 'androtype' (see Frizzell 1933) whereas the other four specimens of the original series of *G. tricinctus*, containing the following specimens: MNHN 1931.26A (relabelled MNHN 1994.611), and MNHN 1931.26B (relabelled MNHN 1994.612) from Befotaka; and MNHN 1931.27A (relabelled MNHN 1994.613), and MNHN 1931.27B (relabelled MNHN 1994.614) from Vondrozo, all collected by R. Decary, were expressly indicated as 'paratypes' and thus are not name-bearing specimens. Guibé (1950) considered the 'gynétype' and the 'androtype' each as holotype, but as the nomen then was based on two specimens, these have to be considered syntypes. The nomen is currently based on lectotype MNHN 1931.26 designated by Blommers-Schlösser and Blanc (1991).

Identity.—Glaw and Vences (1999) resurrected *M. tricinctus* which was previously considered a synonym of *M. biporus* (see Blommers-Schlösser & Blanc 1991) based on new material from An'Ala. The genetic data presented herein suggest three morphologically similar deeply divergent mitochondrial lineages that conform with the lectotype (and paralectotypes) of *tricinctus* in their morphological characters (e.g. small body size, reduced webbing). Our attempts of barcode fishing from the lectotype was unsuccessful and the few 16S reads obtained were inconclusive, probably contaminated with *Homo sapiens* reads. However, we succeeded in PCR-amplifying and sequencing 16S from a specimen (ZSM 176/2006 = MVTIS 16559) from the Midongy du Sud National Park (Bora *et al.* 2007) (also known as Befotaka-Midongy), and thus presumably from very close to the type locality. Based on the phylogenetic position of this sample, we circumscribe *M. tricinctus* to a lineage

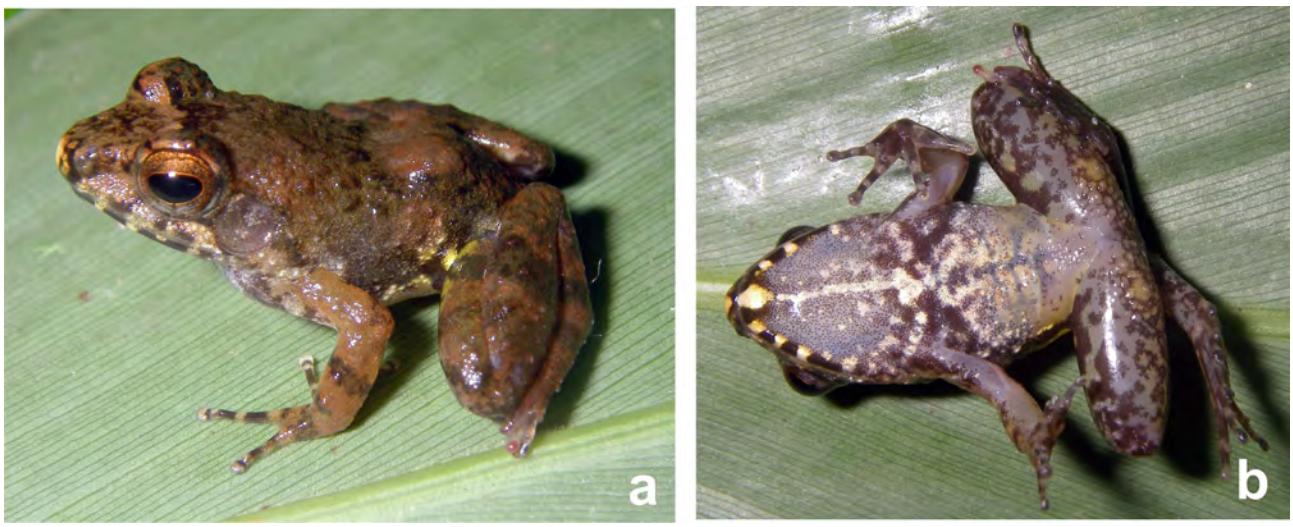

FIGURE 57. *Mantidactylus tricinctus* in life, in dorsolateral and ventral view. (a,b) Adult male (not assignable to a voucher number; voucher probably deposited in UADBA) from Manombo Special Reserve, photographed in 2007.

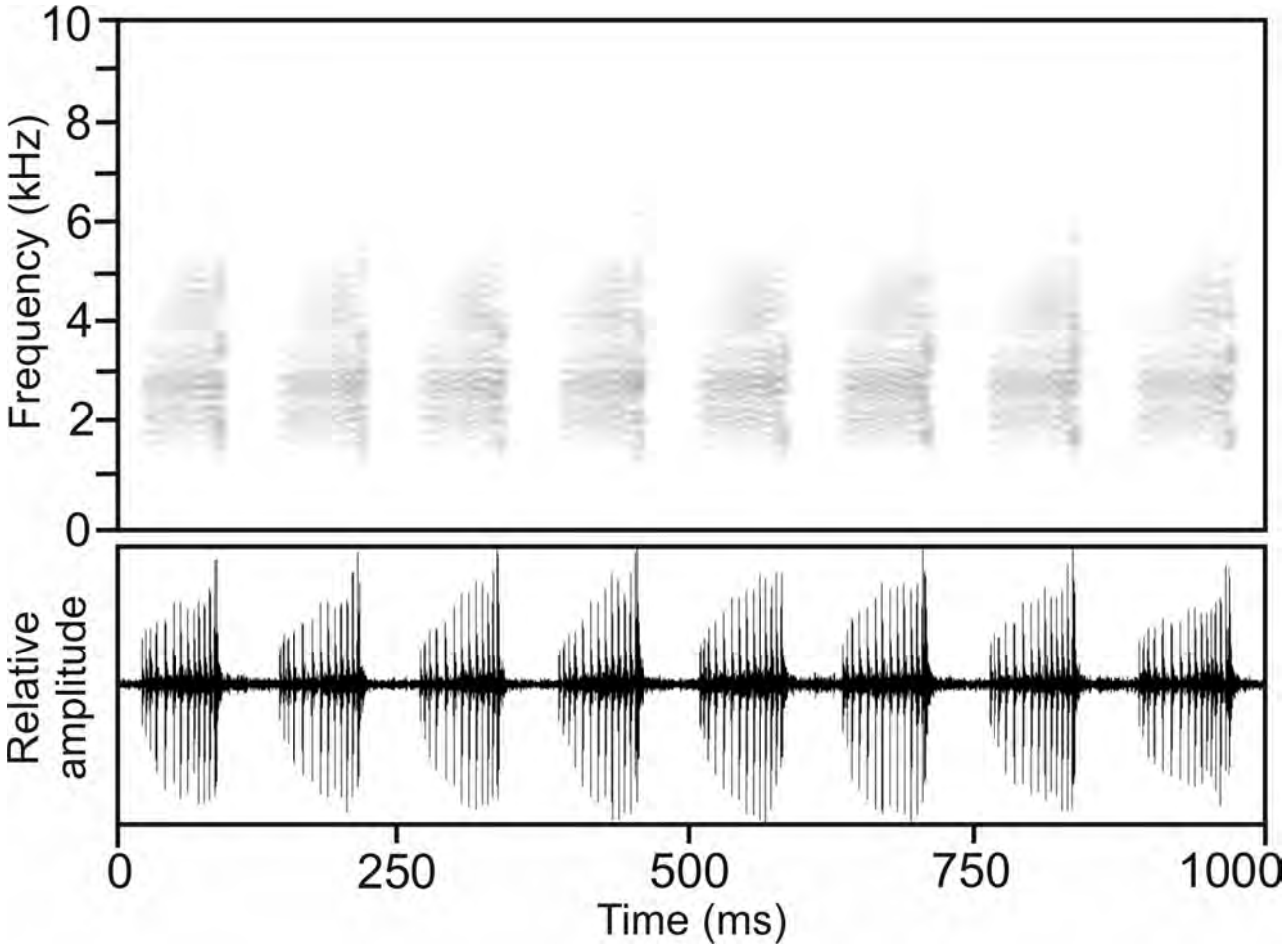

FIGURE 58. Audiospectrogram and corresponding oscillogram of a 1000 ms section of a series of advertisement calls (8 calls figured) of *Mantidactylus tricinctus*, recorded on 23 February 2007 at Manombo (air temperature estimated at 25°C). Recording bandpass-filtered at 1200–7600 Hz.

known from Midongy, Manombo Special Reserve, and Ambahavala in the Anosy Mountains, and consider the lineages from the southernmost Southern Central East, and from the Northern Central East, as two new species named below.

Additional material.—ZSM 176/2006 (BOR 1066), adult male, and ZSM 177/2006, adult female, collected by P. Bora between September and October 2005 in Befotaka-Midongy National Park (precise coordinates unavailable); ZSM 2377/2007 (ZCMV 5444), adult female, and ZSM 2415/2007 (ZCMV 5420), adult male, collected by M. Vences, G. Safarek, E. Rajeriarison, and T. Rajeriarison on 23 February 2007 1 km south of 'site 2', Manombo Special Reserve (precise coordinates not taken).

Diagnosis.—A member of the *M. tricinctus* clade as revealed by the phylogenomic analysis, and sister to *M. grubenmanni* **sp. nov.** described below. See Table 4 for a list of diagnostic morphological characters. The combination of very small body size (below 20 mm male SVL), connected lateral metatarsalia, reduced webbing, presence of a light (often yellowish) marking on snout tip, a yellow inguinal marking, and a short, pulsed advertisement call emitted in rapid succession in regular series, readily distinguishes *M. tricinctus* from all other nominal species of *Brygoomantis*. Most similar to its sister species *M. grubenmanni* **sp. nov.** and to a lesser degree, to *M. gudrunae* **sp. nov.**; for comparisons, see the diagnoses of these species below. For detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. tricinctus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 9. See Fig. 57 for colouration in life. There is weak sexual size dimorphism (confirmed male SVL 16.8–19.2 mm [n = 6] vs confirmed female SVL 18.0–23.4 mm [n = 3]). Males have a larger tympanum than females (HTD/ED ratio is 59–73% in females, 73–105% in males). Femoral glands in males not very prominent, with a yellowish tone in life.

Natural history.—At Manombo, males were heard emitting their advertisement calls from the shore of slow-moving streams in degraded rainforest.

Calls.—The advertisement call of *M. tricinctus*, recorded on 23 February 2007 at Manombo, at an estimated air temperature of 25°C, consisted of a short, pulsed note, emitted in regular series at very fast succession (Fig. 58).

Amplitude modulation was present, with relative amplitude increasing from the beginning of the call, reaching its maximum with the terminal pulse. Numerical parameters of 64 analysed calls were as follows: call duration (= note duration) 45–113 ms (83.4 ± 19.0 ms); 8–19 pulses per note (15.5 ± 3.6); pulse duration 2–5 ms (2.8 ± 1.1); pulse repetition rate within notes 147.1–214.3 pulses/s (177.2 ± 27.7); dominant frequency 2787–2906 Hz (2851 ± 59 Hz), with a second peak of almost equal energy at ca 2100–2200 Hz; prevalent bandwidth 1400–5300 Hz; call repetition rate (= note repetition rate) within regular series ca 470–580 calls/min. Call series consist of 35–42 calls (n = 3), but calls were also emitted isolated (possibly territorial function) or in short groups containing 2–3 calls.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the South East (Fig. 7). This species is known from Ambahavala, Midongy du Sud/Befotaka-Midongy National Park (type locality), and Manombo. Elevation range: 30–900 m a.s.l.

Etymology.—Latin adjective formed from the stems 'tri' meaning 'three' and 'cinctus' meaning 'crowned' or 'girded', presumably in reference to the colour pattern.

Mantidactylus grubenmanni **sp. nov.**

Identity and justification.—This lineage is one of three species in the *M. tricinctus* clade. It corresponds to specimens from An'Ala used by Glaw and Vences (1999) for a redescription of *M. tricinctus*; however, it is very strongly divergent in mitochondrial DNA and concordantly, also in Rag-1 sequences, and differs in advertisement calls, suggesting it represents a distinct species. It was depicted as '*Mantidactylus* sp. aff. *tricinctus* "An'Ala"' by Glaw and Vences (2007).

Holotype.—ZSM 375/2006 (ZCMV 1404), adult male with distinct femoral glands, collected by D.R. Vieites, M. Vences, F. Rabemananjara, P. Bora, C. Weldon, and J. Patton on 7–8 February 2006 at An'Ala (forest camp; 18.91926°S, 048.48796°E, 889 m a.s.l.), Alaotra-Mangoro Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession FJ559281).

Paratypes.—A total of eight paratypes: ZSM 376/2006 (ZCMV 1425), unsexed adult without externally visible femoral glands (probably a female), with the same collecting data as the holotype. Furthermore, we also designate as paratypes ZFMK 62252–62254, three adult females, and ZFMK 62251, 62255–62257, four adult males, collected by F. Glaw and D.M. Rakotondramanana on 3 February 1996 in An'Ala; although the identity of these topotypical specimens was not confirmed by genetic data, their morphological identity is unambiguous.

Additional material.—The following specimens belong to genetically divergent populations and therefore are not included in the paratype series: ZMB 81959 (JCR 616), adult female, collected on 1 March 2011 by J.C. Riemann, and S.H. Ndriantsoa at Ambolo, Ranomafana area (21.26307°S, 047.50696°E, 660 m a.s.l.); ZMB 81960 (JCR 694), adult male, collected on 14 March 2011 by J.C. Riemann, and S.H. Ndriantsoa at Imaloka, Ranomafana area (21.24274°S, 047.46507°E, 1052 m a.s.l.); ZMB 81958 (JCR 419), adult female, collected on 2 June 2010 by J.C. Riemann, and S.H. Ndriantsoa at Antaramanavana, Ranomafana area (21.23997°S, 047.50647°E, 641 m a.s.l.); ZMB 81961 (field NSH 1900, GenBank JCR 1900), collected on 26 March 2011 by J.C. Riemann, and S.H. Ndriantsoa at Antaramanavana, Ranomafana area (21.23997°S, 047.50647°E, 641 m a.s.l.); ZMB 81962 (JCR 874), adult male, collected on 23 May 2011 by J.C. Riemann, and S.H. Ndriantsoa at Ambolo, Ranomafana area (21.26307°S, 047.50696°E, 660 m a.s.l.); ZMB 81963–81964 (JCR 922–923), adult male and female, collected on 9 June 2011 by J.C. Riemann, and S.H. Ndriantsoa at Antaramanavana, Ranomafana area (21.23997°S, 047.50647°E, 641 m a.s.l.); ZSM 2416/2007 (ZCMV 5925) and ZSM 2417/2007 (ZCMV 5930), female and male from Ambohitsara (21.3571°S, 047.8156°E), collected on 3 March 2007 by M. Vences, K.C. Wollenberg, and E. Rajeriarison.

Diagnosis.—*Mantidactylus grubenmanni* **sp. nov.** is a member of the *M. tricinctus* clade as revealed by the phylogenomic analysis, and sister to *M. tricinctus*. See Table 4 for a list of diagnostic morphological characters. The combination of very small body size (below 20 mm male SVL), connected lateral metatarsalia, reduced webbing, presence of a light (often yellowish) marking on snout tip, a yellow inguinal marking, and a short, pulsed advertisement call emitted in rapid succession in regular series, readily distinguishes *M. grubenmanni* **sp. nov.** from all other nominal species of *Brygoomantis* except its sister species *M. tricinctus* from which it is morphologically indistinguishable. It differs from *M. tricinctus* by fewer pulses per note in advertisement calls, and a generally lower pulse repetition rate. For detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. grubenmanni* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in mediocre state of preservation (Fig. 56). Tissue removed from left thigh. Belly cut open for parasitological examination. Left femoral glands partly detached for examination in internal view. Body slender. Head slightly wider than body. Snout rounded in dorsal view, slightly truncate in lateral view. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region concave. Tympanum distinct and large, rounded, horizontal diameter of tympanum 93% of horizontal eye diameter. Supratympanic fold in its first part almost identical to tympanum edge, thereafter distinct, running rather straight from behind eye and bending about 45° close to posterior edge of tympanum towards forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth form two small, rounded patches, positioned posteromedial from choanae. Choanae rounded. Subarticular tubercles

FIGURE 59. *Mantidactylus grubenmanni* **sp. nov.** in life, in dorsolateral and ventral view. (a) Adult male (ZFMK 62251) from An'Ala, photographed in 1996. (b) Ventral side of another male (not reliably attributable to a voucher specimen) from An'Ala, photographed in 1996. (c,d) Adult female from An'Ala, photographed in 1996. (e,f) Adult male (ZSM 2417/2007) from Ambohitsara, photographed in 2007.

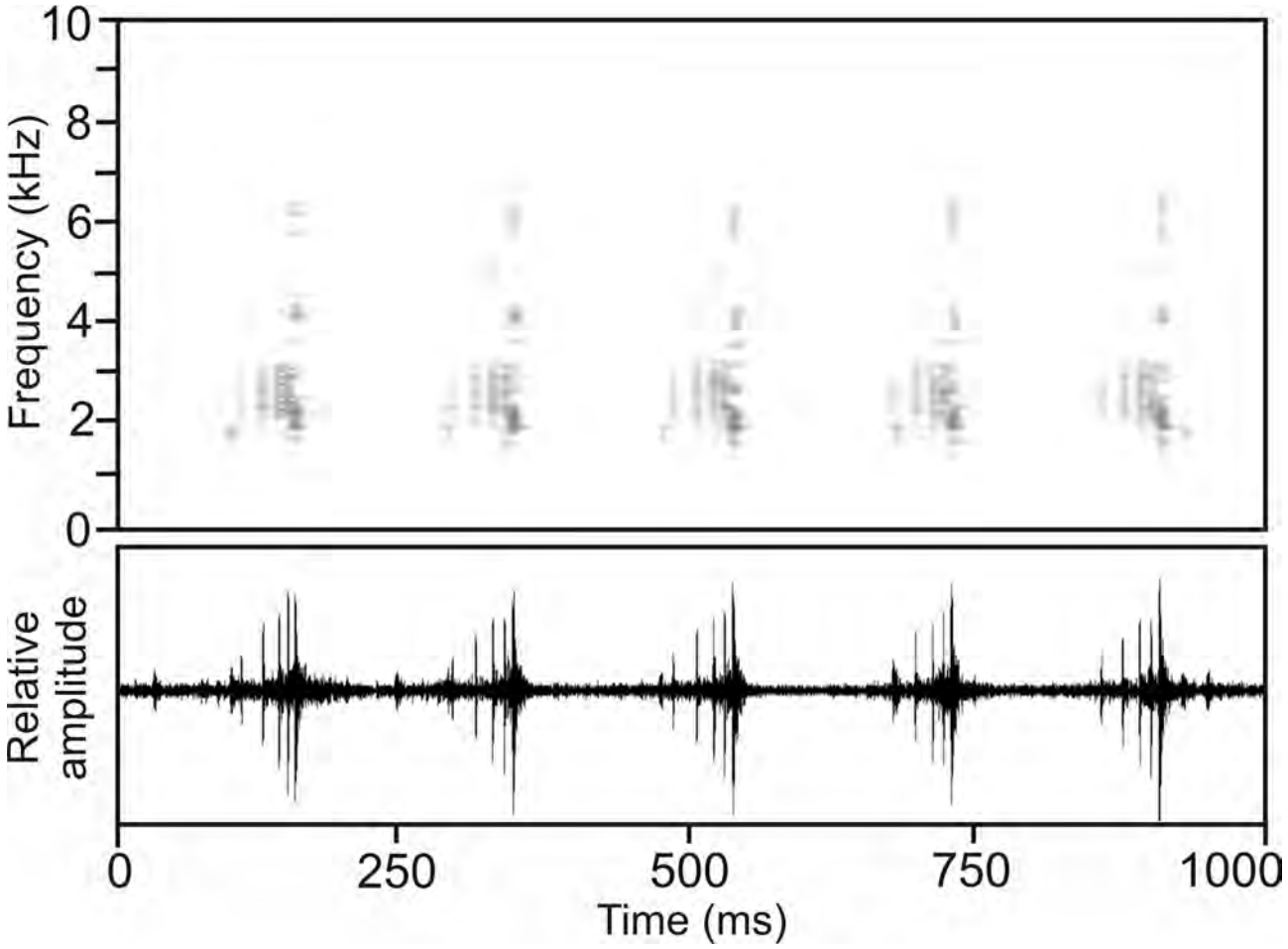

FIGURE 60. Audiospectrogram and corresponding oscillogram of a series of advertisement calls (five calls figured) of *Mantidactylus grubenmanni*, recorded on 3 February 1996 at An'Ala (29.6°C air temperature). Recording bandpass-filtered at 1000–6700 Hz.

single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot almost of exact same length as tibia (101%). Lateral metatarsalia connected. Inner and small outer metatarsal tubercle present. Feet with very poorly expressed webbing, absent or only traces among some toes. Webbing formula: 1(no web), 2i(no web), 2e(1.5), 3i(2.5), 3e(2), 4i(3), 4e(traces), 5(traces). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth with some scattered granules. Ventral side smooth. Femoral glands with a large and distinct distal ulcerous macrogland; no clearly recognisable proximal granular gland field.

Colour in preservative: dorsally almost uniformly brown, with a lighter anterior surface of head and some indistinct lighter markings laterally on head. Limbs with dark crossbands. Ventrally light beige with a small amount of brown marking on chest, anterior belly and posterior part of throat. No clear median light line recognisable on throat. Lower lip ventrally with alternating white / dark brown pattern. Colour of holotype in life not documented.

Variation.—Variation in measurements is given in Table 9. See Fig. 59 for colouration in life and its variation. There is moderate sexual size dimorphism (confirmed male SVL 16.7–17.9 mm [n = 5] vs confirmed female SVL 19.2–20.3 mm [n = 3]). Males have an only slightly larger tympanum than females (HTD/ED ratio is 68–87% in females, 81–93% in males). Femoral glands of males in life quite distinct and coloured with a conspicuous yellowish shade; a large and distinct distal ulcerous macrogland is clearly visible.

Natural history.—As reported by Glaw and Vences (1999), males in An'Ala have been observed calling at daytime in a shallow, partly sun-exposed swamp with dense vegetation in primary forest, near or on perches directly above the water. They were sitting on leaves, fallen branches and similar structures, generally only 0–2 cm above the water level. Calling behaviour of one individual male was observed for several minutes. This specimen moved forward during its vocalisations, in a conspicuously jerky, disrupted way. In the Ranomafana area, found along streams in rainforest inside Ranomafana National Park and forest fragments in Ambolo and Ampitavanana, but not found outside forest. Specimens were observed sitting in areas of shallow water and along the banks or hiding in leaf litter in the vicinity of a stream. At Ranomafana and surrounds found at an elevational range between 641–1052 m a.s.l. A female with visible

eggs was found in June 2010 at Ampitavanana, another in March 2011 at Ambolo. ZMB 81960 (JCR 694) was observed calling at a stream bank at Imaloka inside Ranomafana National Park at late afternoon (17:00 h) on 14 March 2011.

Calls.—The advertisement call of *M. grubenmanni*, recorded on 3 February 1996 at An'Ala, 29.6°C air temperature (Vences *et al.* 2006: CD2, track 71), consisted of a very short, pulsed note, emitted singly or in long regular series at very fast succession (Fig. 60). Amplitude modulation was present, with relative amplitude increasing from the beginning of the call, reaching its maximum with the terminal pulse. Pulse structure within notes was somewhat complex, with terminal pulses having longer duration and being more narrowly spaced. Numerical parameters of 52 analysed calls were as follows: call duration (= note duration) 26–87 ms (68.1 ± 17.5 ms); 3–7 pulses per note (5.5 ± 0.9); pulse duration 2–12 ms (4.5 ± 2.8); pulse repetition rate within notes 47.6–181.8 pulses/s (89.2 ± 40.3); dominant frequency 2015–2338 Hz (2286 ± 104 Hz); prevalent bandwidth 1500–3400 Hz; call repetition rate (= note repetition rate) within regular series ca 310 calls/min. The longest call series recorded had a duration of 8.52 s and contained 43 calls. Calls recorded on 14 March 2011 at Ranomafana from specimen ZMB 81960 (JCR 694) agree in structure and parameters with those described above from An'Ala. The longest regular call series from this recording had a duration of 7.15 seconds and contained 33 calls, repeated at a rate of 272 calls/minute.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Widespread in Northern Central East and Southern Central East (Fig. 7). This species is known from Ambatobe, Ambohitsara, An'Ala, Befanjana, Betampona, several localities in Ranomafana (Ambolo, Ampitavanana, Beremby, Imaloka), and Sahavontsira. Elevation range: 14–1052 m a.s.l.

Etymology.—We dedicate this species to Moritz Grubenmann, dedicated microbiologist and naturalist from Zürich with an enormous knowledge on the Malagasy flora and fauna, in acknowledgement of his constant support of our research with numerous important observations and excellent photographs of Malagasy amphibians and reptiles.

Mantidactylus gudrunae **sp. nov.**

Identity and justification.—This lineage has been considered as confirmed candidate species *M.* sp. 7 by Vieites *et al.* (2009) and *M.* sp. Ca7 by Perl *et al.* (2014). It is a member of the *M. tricinctus* clade, and strongly differs from the two other lineages in the clade (*M. tricinctus* and *M. grubenmanni*) by concordant strong divergence in 16S and Rag-1 sequences. Furthermore, it also differs in various morphological features (see Diagnosis below). We are therefore confident that this lineage represents a distinct, evolutionarily isolated separate species.

Holotype.—ZSM 146/2004 (field number FGZC 274), adult male, collected by F. Glaw, M. Puente, R.D. Randrianiaina, and M. Teschke (née Thomas) on 7 February 2004 at Manantantely (24.983°S, 046.917°E, 20–150 m a.s.l.), Anosy Region, Madagascar. 16S and cox1 barcode sequences of the holotype are available from GenBank (accessions AY848141 and JN133257).

Paratypes.—A total of six paratypes: ZSM 136/2004 (FGZC 250), ZSM 138/2004 (FGZC 259), two adult males, and ZSM 154/2004 (FGZC 286), adult female, with the same collection data as the holotype (7–8 February 2004); ZSM 68/2004 (FGZC 115), adult female, collected by F. Glaw, M. Puente, M. Teschke (née Thomas), and R. Randrianiaina on 29–31 January 2004 at 'Camp 1', between Isaka and Eminiminy, Andohahela National Park (24.7586°S, 046.8542°E, 247 m a.s.l.); ZSM 95/2004 (FGZC 167), adult male, and ZSM 96/2004 (FGZC 168), adult female, collected by F. Glaw, M. Puente, M. Teschke (née Thomas), and R. Randrianiaina on 31 January 2004 above 'Camp 1', between Isaka and Eminiminy, Andohahela National Park (ca 24.750°S, ca 046.850°E, ca 350 m a.s.l.).

Additional material.—The following specimens belong to genetically divergent populations and therefore are not included in the paratype series: ZSM 196/2005 (FGZC 2594), adult female, collected by F. Glaw, and P. Bora on 4 February 2005 in the forest at the QMM Climate Station, Sainte Luce (24.7798°S, 047.1713°E, 23 m a.s.l.); ZSM 181/2021 (ACZCV 375, extraction ACP 3589, tissue ACZC 8514), ZSM 182/2021 (ACZCV 376, ACP 3590, ACZC 8515), ZSM 183/2021 (ACZCV 377, ACP 3591, ACZC 8516), collected by S. Hyde Roberts at Sainte Luce (S9) on 10 October 2016; MRSN A7044 (FAZC 15282, ACP0997, ACZC4429), collected by F. Andreone and G.M. Rosa on 21 February 2012 at Sainte Luce; MRSN A7045 (FAZC 15419, ACP 1053, ACZC 4485) and MRSN A7046 (FAZC 15427, ACP 1057, ACZC 4489), one male and one female, collected by F. Andreone and G.M. Rosa on 29 February 2012 at Tsitongambarika, Ivohibe.

Diagnosis.—*Mantidactylus gudrunae* **sp. nov.** is a member of the *M. tricinctus* clade as revealed by the phylogenomic analysis, and sister to a monophyletic group comprising *M. tricinctus* and *M. grubenmanni*. See Table 4 for a list of diagnostic morphological characters. The combination of small body size (male SVL 20–25 mm, female SVL 23–29 mm), presence of a whitish marking on snout tip and of a yellow inguinal marking, and absence of white spots on flanks, distinguishes *M. gudrunae* **sp. nov.** from members of other *Brygoomantis* clades (Table 4).

Within the *M. tricinctus* clade, it differs from both *M. tricinctus* and *M. grubenmanni* by a slightly larger body size (male SVL 20–25 mm vs <20 mm), more strongly expressed webbing on foot, and lateral metatarsalia only partly connected or separated by webbing (vs connected). For detailed distinction from other new species described herein, see the respective species accounts. A full list of molecular diagnostic sites in the 16S gene of *M. gudrunae* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

TABLE 9. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus tricinctus* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
M. tricinctus																			
MNHN 1931.26 [LT]	NA	F	Befotaka	18.0	6.9	7.8	2.2	1.5	1.7	1.3	2.2	12.6	5.5	30.3	NM	9.1	NM	NA	NA
MNHN 1931.27 [PLT]	NA	M	Vondrozo	17.1	6.3	7.3	2.2	2.3	1.7	1.2	2.4	9.6	4.8	26.6	NM	8.2	NM	2.1	1.6
MNHN 1994.611 [PLT]	NA	M	Befotaka	17.1	6.4	7.1	2.2	2.2	1.6	1.4	2.2	10.0	5.0	26.1	NM	7.1	NM	2.3	1.5
MNHN 1994.612 [PLT]	NA	M	Befotaka	19.2	7.2	7.6	2.3	2.3	1.9	1.7	2.7	10.5	5.4	26.7	NM	8.7	NM	2.7	1.8
MNHN 1994.613 [PLT]	NA	M	Vondrozo	18.1	6.7	7.6	2.7	2.5	2.0	1.7	2.5	11.4	4.8	NM	NM	NM	NM	2.2	1.8
ZSM 177/2006	NA	F	Befotaka-Midongy	19.7	7.0	8.6	3.2	1.9	1.8	1.3	2.2	11.7	5.5	30.5	14.4	9.4	9.4	NA	NA
ZSM 2377/2007	ZCMV 5444	F	Manombo	23.4	8.1	10.2	3.3	2.4	2.9	1.9	2.7	14.4	6.6	38.8	17.8	10.9	11.9	NA	NA
ZSM 2415/2007	ZCMV 5420	M	Manombo	19.1	7.2	8.4	3.4	2.5	2.4	1.5	2.8	12.6	5.6	29.4	14.0	9.0	9.6	2.8	2.0
ZSM 176/2006	BOR 1066	M	Befotaka-Midongy	16.8	6.2	6.9	3.0	2.2	1.6	1.4	2.3	9.9	4.8	25.3	11.7	7.7	7.7	2.9	2.2
M. grubenmanni **sp. nov.**																			
ZSM 375/2006 [HT]	ZCMV 1404	M	An'Ala	17.9	6.5	7.6	3.0	2.8	2.4	1.2	2.0	11.4	4.8	28.3	13.3	8.8	8.7	3.0	1.9
ZFMK 62252 [PT]	NA	F	An'Ala	20.3	7.0	8.2	2.6	2.1	1.8	1.3	2.3	13.5	6.0	32.7	NM	10.0	NM	NA	NA
ZFMK 62253 [PT]	NA	F	An'Ala	19.2	6.5	7.7	2.3	2.0	1.8	1.3	2.5	12.7	5.5	30.8	NM	8.7	NM	NA	NA

...Continued on the next page

TABLE 9. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZFMK 62254 [PT]	NA	F	An'Ala	19.7	6.9	7.9	2.8	1.9	2.2	1.4	2.5	13.1	6.1	32.0	NM	10.4	NM	NA	NA
ZFMK 62251 [PT]	NA	M	An'Ala	16.7	6.0	6.7	2.5	2.2	1.8	1.4	2.0	11.1	4.8	27.4	NM	8.4	NM	2.5	1.8
ZFMK 62255 [PT]	NA	M	An'Ala	17.6	6.3	7.4	2.7	2.5	1.9	1.4	2.1	11.5	5.5	27.5	NM	9.0	NM	2.9	1.7
ZFMK 62256 [PT]	NA	M	An'Ala	17.8	6.5	7.3	2.6	2.4	1.6	1.3	2.1	11.7	5.5	29.4	NM	8.6	NM	2.6	1.7
ZFMK 62257 [PT]	NA	M	An'Ala	17.8	6.5	7.2	2.6	2.1	2.1	1.4	2.2	11.6	5.3	28.0	NM	8.6	NM	2.5	1.8
M. gudrunae **sp. nov.**																			
ZSM 146/2004 [HT]	FGZC 274	M	Manantantely	21.1	NM	8.8	3.2	2.8	2.5	1.7	2.6	13.0	5.6	32.9	14.4	9.7	10.0	4.4	2.5
ZSM 183/2021	ACZC 8516	F	Sainte Luce (S9)	28.6	11.1	11.7	4.4	2.9	2.8	2.0	3.3	17.8	8.2	44.9	20.2	13.6	13.4	NA	NA
ZSM 154/2004 [PT]	FGZC 286	F	Manantantely	24.4	10.1	8.9	3.8	2.5	2.5	1.9	3.1	8.5	6.6	NM	NM	10.8	12.5	1.4	1.1
ZSM 196/2005	FGZC 2594	F	Ste. Luce	26.3	10.4	9.5	4.2	2.6	2.7	1.7	2.6	10.6	7.5	NM	NM	12.6	13.7	NA	NA
ZSM 68/2004 [PT]	FGZC 115	F	Andohahela	25.3	10.5	10.4	3.8	2.4	2.5	2.0	2.9	9.8	8.7	NM	NM	12.9	14.3	1.5	1.1
ZSM 96/2004 [PT]	FGZC 168	F	Andohahela	26.5	10.8	10.1	3.9	3.1	2.9	2.2	2.9	10.7	8.2	NM	NM	12.9	14.0	1.5	1.0
MRSN A7046	FAZC 15427	F	Tsitongambarika	22.6	8.0	9.6	3.2	2.2	2.1	2.0	2.8	13.4	6.7	36.3	16.5	11.0	10.7	NA	NA
ZSM 182/2021	ACZC 8515	M	Sainte Luce (S9)	24.4	9.0	10.1	2.7	2.6	2.7	1.6	2.9	14.4	6.8	36.3	16.3	11.1	11.3	3.2	2.5
ZSM 136/2004 [PT]	FGZC 250	M	Manantantely	21.8	8.6	9.4	4.0	3.3	2.4	1.4	2.7	14.6	6.8	34.9	16.4	10.9	10.8	3.7	2.8
ZSM 138/2004 [PT]	FGZC 259	M	Manantantely	20.5	7.9	9.0	3.8	2.9	2.0	1.4	2.6	13.7	5.8	31.8	14.2	9.8	9.3	4.2	2.5
ZSM 95/2004 [PT]	FGZC 167	M	Andohahela	20.2	8.6	7.8	2.9	2.7	2.1	1.7	2.3	8.5	6.2	NM	NM	9.7	10.5	2.3	1.6
MRSN A7044	FAZC 15282	M	Sainte Luce	23.0	8.0	9.6	3.6	2.7	2.6	1.4	2.9	13.6	6.5	33.7	15.2	10.4	11.0	3.2	2.1
MRSN A7045	FAZC 15419	M	Tsitongambarika	21.9	8.0	9.2	3.7	3.0	2.4	1.8	2.8	12.6	6.4	34.5	15.4	10.0	10.2	2.5	2.3

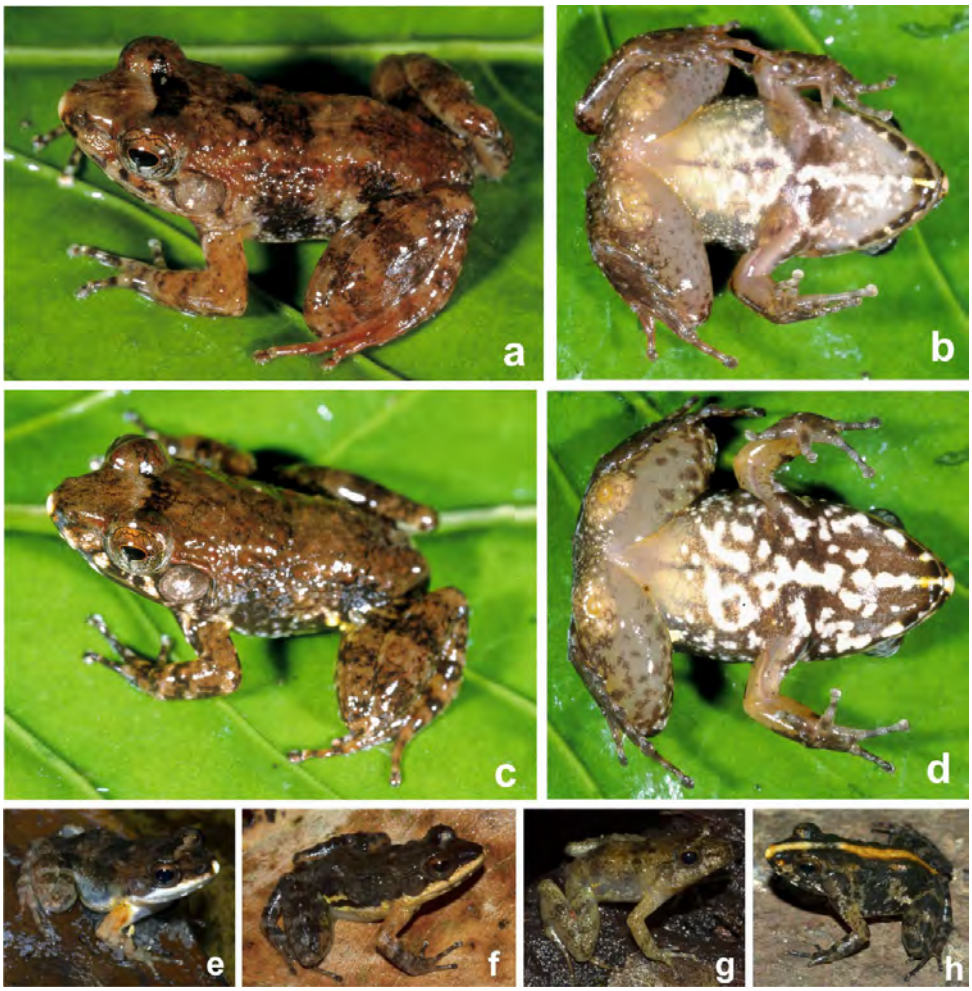

FIGURE 61. *Mantidactylus gudrunae* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male from Manantantely, photographed in 2004. (c,d) Adult male (holotype ZSM 146/2004 = FGZC 274) from Manantantely, photographed in 2004. (e) Unsexed specimen (ACZC 9918 = FAZC 15246) from Sainte Luce. (f) Unsexed specimen (ACZC 4418 = FAZC 15257) from Sainte Luce. (g) Unsexed specimen (ACZC 4447 = FAZC 15324) from Tsitongambarika. (h) Unsexed specimen (ACZC 4489 = FAZC 15427) from Tsitongambarika.

Description of the holotype.—Adult male in good to moderate state of preservation (Fig. 56). Tongue removed as tissue sample; femoral glands partly detached for examination in internal view. Body relatively slender. Head as wide as body. Snout rounded in dorsal view, truncate in lateral view. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct and large, rounded, horizontal diameter of tympanum 88% of horizontal eye diameter. Supratympanic fold in its first part almost identical to tympanum edge, thereafter distinct, running rather straight from behind eye and bending about 70° close to posterior edge of tympanum towards forelimb insertion. Maxillary teeth present. Vomerine teeth form two elongated aggregations, directed posteromedially from choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly shorter than tibia (97%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle indistinct but recognisable. Webbing formula: 1(no web), 2i(no web), 2e(traces), 3i(2), 3e(1), 4i(2.5), 4e(2.25), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, some granules on flanks (in life, also tubercular on dorsum, without dorsolateral folds or longitudinal ridges). Ventral side smooth. Femoral glands with a large and distinct distal ulcerous macrogland; and a small proximal granular gland field apparently made up of only a few gland granules.

Colour in preservative: dorsally almost uniformly brown, with a dark band between the eyes bordering on a lighter colour on the anterior head surface. Some white spots and markings laterally on head. Limbs with dark crossbands. Ventrally, beige on limbs, brown with distinct white pattern on throat, chest and anterior belly. Larger white spots arranged to form a median intrreupted white line on throat. Lower lip ventrally with alternating white/dark brown pattern. In life, colourarion was similar but more contrasted. A small yellowish marking was present

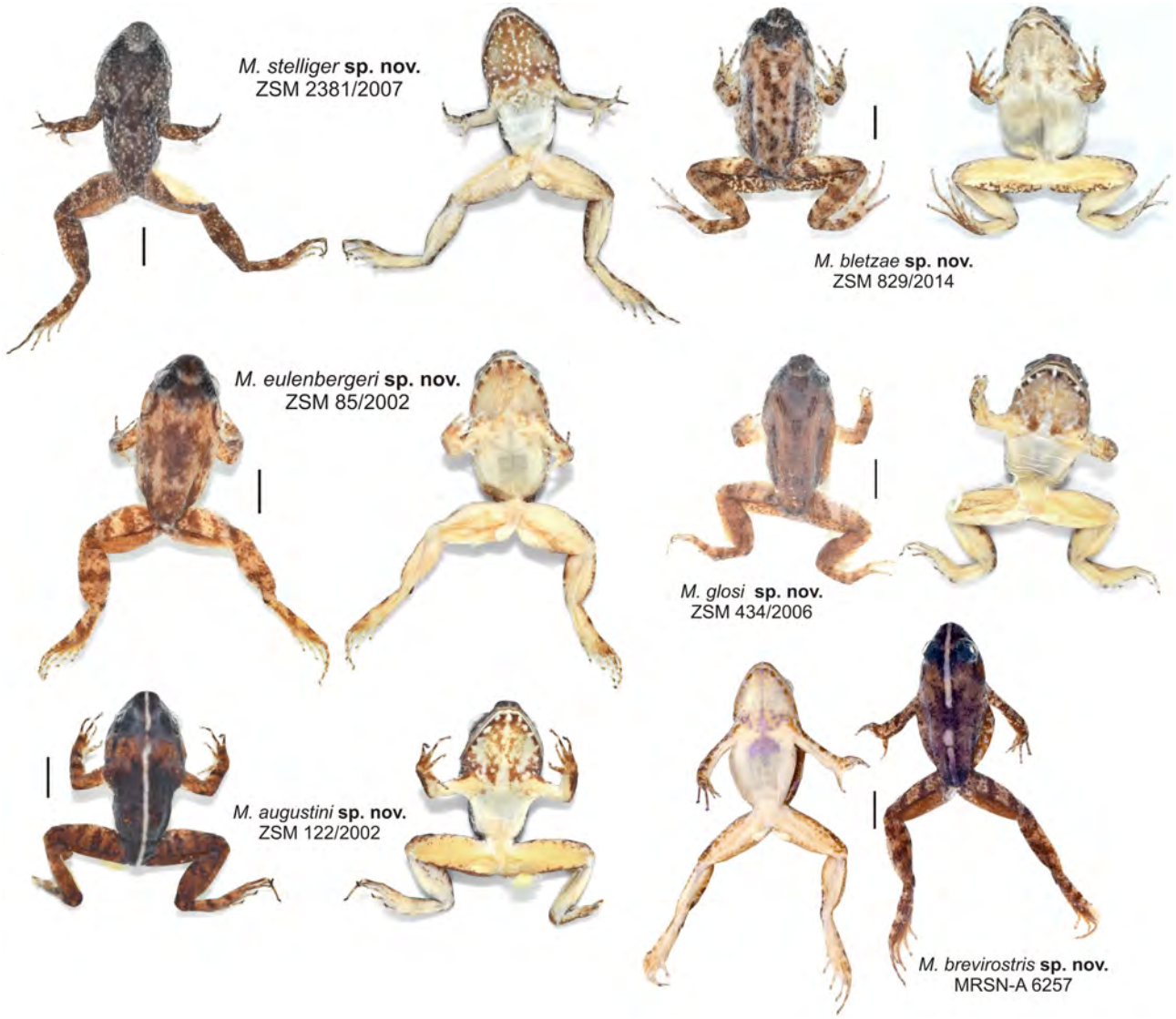

FIGURE 62. Preserved holotype specimens of newly named species in the *Mantidactylus biporus* clade and of the *M. stelliger* clade. Scale bars equal 5 mm.

in the inguinal region. The light ventral pattern was bright silvery white.

Variation.—Variation in measurements is given in Table 9. See Fig. 61 for colouration in life and its variation. There is weak sexual size dimorphism (confirmed male SVL 20.2–24.4 mm [n = 7] vs confirmed female SVL 22.6–28.6 mm [n = 6]). Males have a larger tympanum than females (HTD/ED ratio is 62–79% in females, 75–96% in males). Femoral glands of males in life distinct and coloured with a conspicuous yellowish shade; a large and distinct distal ulcerous macrogland is clearly visible, as is a smaller proximal granular gland field.

Natural history.—Specimens have been found along slow running water bodies in coastal rainforest. They are active during the night and call from water. Their call is rarely heard. The colouration of this species is quite variable, with some specimens showing an orangish colouration on the arms or on the dorsal stripe. Sometimes reminiscent of the colouration of species in the subgenus *Ochthomantis* (e.g. Fig. 61f).

Calls.—The calls of this species have not yet been recorded.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the South East of Madagascar (Fig. 7). This species is known from Andohahela, Manantantely, Sainte Luce, and Tsitongambarika. Elevation range: 23–415 m a.s.l.

Etymology.—We dedicate this species to Gudrun Grubenmann from Zürich. Together with her husband Moritz, she has been travelling in Madagascar for many decades and has supported our research with important observations of Malagasy amphibians and reptiles.

Mantidactylus biporus clade

A species-rich, diverse and probably not monophyletic group, containing species characterized by a mostly rather small body size (20.5–35.8 mm adult SVL), short and rounded snout, and typically stout body shape

with short hindlimbs. Species in this group often have scattered white spots, especially on flanks and laterally on the head. Contains: *M. biporus* and five new species, described based on holotypes depicted in Fig. 62. Note that several other species previously thought to be related to *M. biporus* (or reported to be morphologically similar), are assigned to the *M. ulcerosus* clade (*M. schulzi* and *M. steinfartzi*; see above), and to the *M. inaudax* and *M. stelliger* clades (see respective accounts below). One of the new species named in the following (*M. bletzae* **sp. nov.**) is not included in the phylogenomic tree, and its relationships are not reliably resolved in the 16S tree. We here assign it tentatively to the *M. biporus* clade, but it might also be related to the *M. inaudax* clade.

Mantidactylus biporus (Boulenger, 1889)

Type material.—According to Blommers-Schlösser and Blanc (1991), *Rana biporus* Boulenger, 1889 is based on syntypes BMNH 1947.2.26.46–52 from 'Madagascar'. We here designate BMNH 1947.2.26.47, an adult female from which we could obtain a DNA sequence, as lectotype. Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

Identity.—Considering the large number of genetically highly divergent lineages conforming at least roughly to the morphology of *M. biporus*, and the lack of a precise type locality, the identity of this nomen has long remained obscure. Using barcode fishing we obtained a sequence of the lectotype which clusters with specimens of a previously (Perl *et al.* 2014; Vieites *et al.* 2009) unreported lineage found in Betampona as well as in An'Ala, allowing us herein to newly ascribe this name to that lineage. The lineage previously (Vieites *et al.* 2009) assigned to *M. biporus* is reassigned to *M. inaudax* below.

It is worth mentioning that in the original description (Boulenger 1889), the species was described as '*Rana biporus*', and the species epithet may have been meant as a noun in apposition, making the emendation '*Rana bipora*' (e.g. Blommers-Schlösser & Blanc 1991; Guibé 1978) unjustified (see also Frost 2021). However, given the species is now in the genus *Mantidactylus* (of masculine gender) this has no bearing on the name *Mantidactylus biporus* as currently used.

The species has been previously referred to as *Mantidactylus* sp. aff. *biporus* [Ca HM364733] (sp. Ca76) by Rosa *et al.* (2011, 2012).

Synonyms.—Previously *Mantidactylus brauni* Ahl, 1929 was considered a synonym, but we have shown here that that nomen is a junior synonym of *M. ulcerosus*.

Reference specimens.—ZSM 1982/2006 (ZCMV 2425), adult male, and ZSM 396/2006 (ZCMV 1483), adult female, collected by D.R. Vieites, M. Vences, F. Rabemananjara, P. Bora, C. Weldon, and J. Patton on 07–19 February 2006 at An'Ala (forest camp) (18.91926°S, 048.48796°E, 889 m a.s.l.); MRSN A6180 (FAZC 13480), adult male, collected by G.M. Rosa on 4 February 2007 at Sahabefoza in Betampona (17.9142°S, 049.2077°E, 349 m a.s.l.); MRSN A6266 (FAZC 13675), adult male, collected by G.M. Rosa on 27 February 2007 at Vohitsivalana in Betampona (17.8862°S, 049.2025°E, 517 m a.s.l.); MRSN A6374 (FAZC 13835), adult male, collected by G.M. Rosa on 29 October 2007 at Sahabefoza in Betampona (at geographical coordinates 17.91438°S, 49.20778°E, 325 m a.s.l); ZSM 184/2021 (ACZCV 201 = ACZC 5694), putative female, collected on 14 November 2013 at Vohitsivalana, Betampona (17.8862°S, 049.2026°E), by A. Crottini, D. Salvi, E. Scanarini, Georges, and Jean Noël.

Diagnosis.—A member of the *M. biporus* clade, sister to the new species *M. augustini* **sp. nov.** (described below) according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of a moderate body size (male SVL 28-32 mm, female SVL 31–36 mm [one probably immature female 19.3 mm]), rather smooth dorsal skin without dorsolateral ridges, moderate to relatively large tympanum size in males (10–12% of SVL), presence of white spots on flanks, absence of a white marking on the snout tip, and a short, pulsed advertisement call emitted in rapid succession in regular series, distinguishes *M. biporus* from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *Mantidactylus inaudax* (*M. inaudax* clade) is morphologically similar but appears to have a larger tympanum in males, and a lower pulse repetition rate in advertisement calls. *Mantidactylus biporus* is distinguished from its sister species *M. augustini* **sp. nov.** by larger body size, smaller tympanum, shorter hindlimbs, less pulses per note and higher pulse rate in advertisement calls. For a distinction from the other (all new) species in the *M. biporus, M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. biporus* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Variation.—Variation in measurements is given in Table 10. See Fig. 63 for colouration in life and its variation. A light vertebral line can be present. There is weak sexual size dimorphism (confirmed male SVL 28.0–31.6 mm [n = 5] vs confirmed female SVL 30.5–35.8 mm [n = 2]; one further female, ZSM 184/2021, measures only 19.3 mm but we hypothesize it is an immature specimen). Males have a slightly larger tympanum than females (HTD/ED ratio is 60–70% in females, 69–79% in males). Femoral glands of males in life are not documented. Females, both in preservative as in life (Fig. 63c) have a distinct pattern of two distinct gland rudiments next to each other which almost certainly explains the species name.

Natural history.—Males call during the day and night from flooding zones of small forest streams.

Calls.—The advertisement call of *M. biporus* recorded at Betampona on 31 October 2007 at 20:00 h, 19°C air temperature (Rosa *et al.* 2011: track 34), consisted of a short, regularly pulsed note (Fig. 64), emitted in regular series at very fast succession. Slight amplitude modulation was present, with relative amplitude increasing from the beginning of the call, reaching its maximum approximately

FIGURE 63. *Mantidactylus biporus* from Betampona in life, in dorsolateral and ventral view. (a) Adult male, MRSN A6374 (FAZC 13835). (b,c) Adult female (FAZC 13957). (d) Unsexed specimen (ACZC 5694). (e) Adult female (FAZC 13552). (f) Adult male (FAZC 13620). Note the eponymous pair of small pores visible on the ventral thigh in (c).

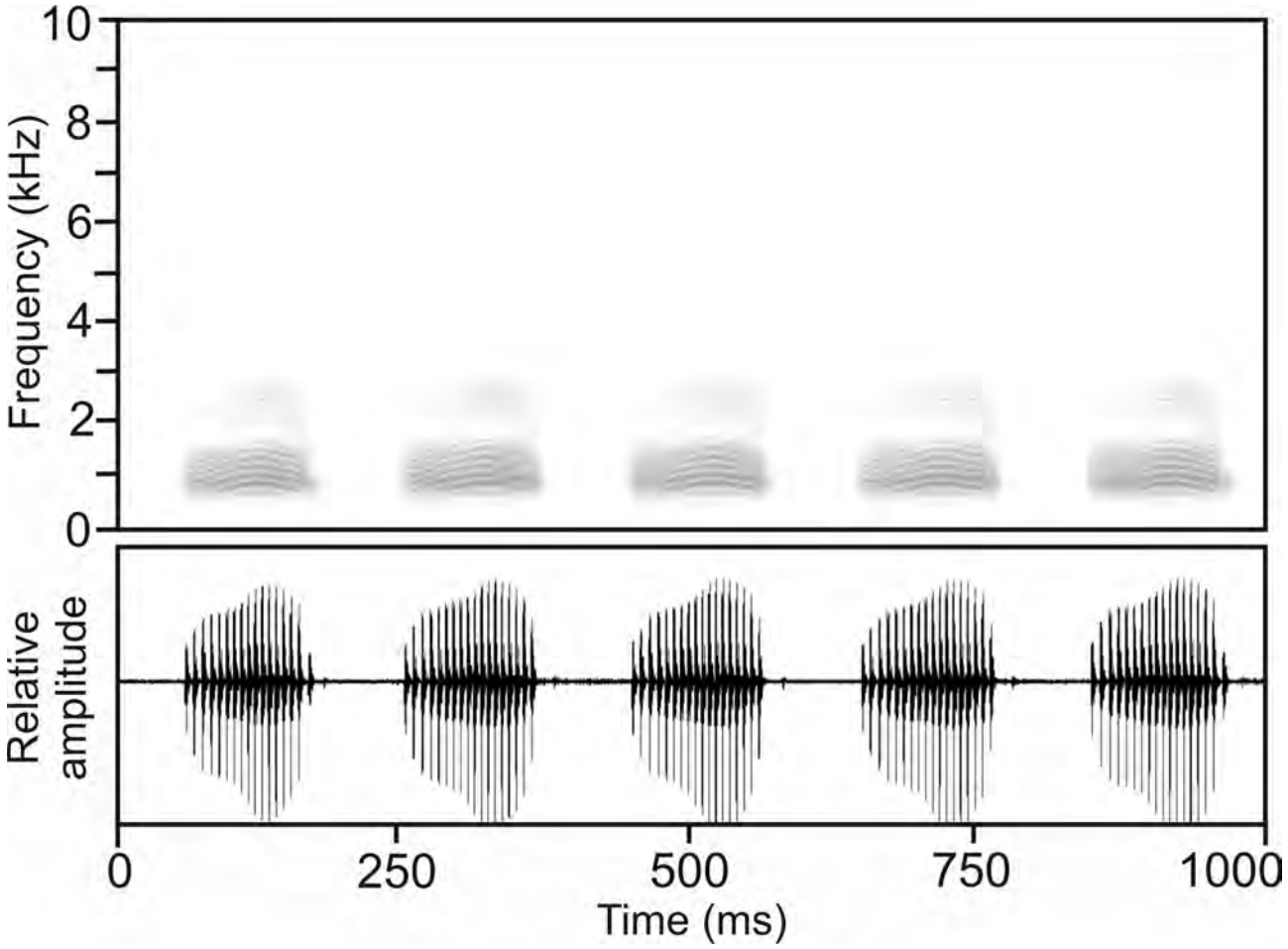

FIGURE 64. Audiospectrogram and corresponding oscillogram of a 1000 ms section of a series of advertisement calls (five calls figured) of *Mantidactylus biporus* recorded on 31 October 2007 at Betampona (19°C air temperature).

at the last third of the note's duration. Calls in call series tended to become louder and longer from the beginning to the end of a series. Numerical parameters of 45 analysed calls of two individuals were as follows: call duration (= note duration) 93–132 ms (109.7 ± 11.2 ms); 15–21 pulses per note (17.4 ± 1.8); pulse duration 4–5 ms (4.7 ± 0.5); pulse repetition rate within notes 130.4–210.5 pulses/s (165.8 ± 27.9); dominant frequency 832–997 Hz (884 ± 61 Hz); prevalent bandwidth 400–3000 Hz; call repetition rate (= note repetition rate) within regular series ca 300–360 calls/min. Call series (n = 4) had a duration of 2290–5875 ms.

Tadpoles.—The tadpole of this species has not been described. The tadpole described under this name by Knoll *et al.* (2007) refers to *M. inaudax* **bona species**, see below.

Distribution.—Endemic to low-elevation rainforest in the Northern Central East (Fig. 7). This species is known from An'Ala and Betampona. The type locality cannot currently be narrowed down. Elevation range: 190–840 m a.s.l.

Etymology.—Latin noun in apposition meaning 'double pores', presumably in reference to the femoral glands of this species where especially in females, two separate gland rudiments are visible.

Mantidactylus augustini **sp. nov.**

Identity and justification.—This lineage is a member of the *M. biporus* clade from the lowlands of the North East of Madagascar and has previously been considered as confirmed candidate species *M.* sp. 22 by Vieites *et al.* (2009) and *M.* sp. Ca22 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Andranofotsy"' by Glaw and Vences (2007). This lineage is sister to the true *M. biporus* according to our phylogenomic analysis, but is characterized by a high uncorrected pairwise-distance in the 16S rRNA marker (4.9–5.8%). It also is concordantly differentiated in the nuclear Rag-1 gene, not sharing its haplotype with *M. biporus* (Fig. 4). Moreover, the two lineages differ distinctly in male advertisement call. Based on the concordance of high mitochondrial divergence with nuclear and bioacoustic differentiation, we are convinced it represents a distinct species. A deep conspecific lineage of *M. augustini* **sp. nov.** co-occurs with the main lineage in Masoala. As we have only limited data on this lineage, we tentatively include it in our circumscription of this species, but note that it may later transpire to represent another distinct species.

Holotype.—ZSM 122/2002 (MV 2001.1388), adult male, collected by M. Vences on 17 December 2001 at Andranofotsy (wood nearby, 15.4353°S, 049.8439°E, 85

m a.s.l.), Analanjirofo Region, Madagascar. 16S and cox1 barcode sequences of the holotype are available from GenBank (accessions AY848225 and JN133225).

Paratypes.—A total of six paratypes: ZSM 740/2009 (ZCMV 11170), possibly female, collected by J.E. Randrianirina on 15 May 2009 at Melivinany 'S 0I', Manompana, Forêt de Befanjana (precise coordinates unavailable); MRSN A3600 (FN 7678 = ACZC 4904), adult female, collected by F. Andreone, and J.E. Randrianirina on 1 December 1998 in Beanjada 'Corridor 1', Ambatoledama Corridor, Masoala (ca 15.267°S, ca 049.983°E, ca 1000 m a.s.l.); MRSN A2905 (FN 7238 = ACZC 4897), possibly female, collected by J.E. Randrainirina on 6 November 1998 at Andranobe, Masoala National Park (coordinates unavailable); MRSN A3540 (ACZC 4898), possibly female, collected by R. Nincheri on 24 July 1993 in Masomihenija forest, Ambodilalono, Masoala peninsula (coordinates unavailable); MRSN A6740 (FAZC 14292 = ACZC 4906), presumed subadult female, collected by J.E. Randrianirina on 27 April 2008 at Farankaraina (coordinates unavailable); MRSN A3737 (FAZC 10009 = ACZC 4905), juvenile, collected by F. Andreone and J.E. Randrianirina on 1 December 1999 at 'Camp 4', Antsarahan'Ambarato in the Ilampy Corridor, Masoala peninsula (15.3920°S, 050.0470°E, ca 550 m a.s.l.).

Additional material.—ZFMK 70481 from Masoala probably belongs to this species but is not included in the paratype series due to the lack of genetic data.

Diagnosis.—*M. augustini* **sp. nov.** is a member of the *M. biporus* clade, sister to *M. biporus* according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of a small body size (male SVL 24 mm, female SVL 21–25 mm), rather smooth dorsal skin with weakly expressed dorsolateral ridges in some individuals, large tympanum size in males (13% of SVL), presence of white spots on flanks, absence of a white marking on the snout tip, and a short, pulsed advertisement call emitted in regular series, distinguishes *M. augustini* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *Mantidactylus inaudax* (*M. inaudax* clade) is morphologically similar but appears to have shorter hindlimbs, less pulses per note, and higher pulse repetition rate in advertisement calls. *M. augustini* **sp. nov.** is distinguished from its sister species, *M. biporus*, by smaller body size, larger tympanum, longer hindlimbs, more pulses per note and a lower pulse rate in advertisement calls (Table 4), as well as a higher dominant frequency (1263–1356 Hz vs 832–997 Hz), and a lower call repetition rate (200–230 vs 300–360 calls/min). For a distinction from the other (all new) species in the *M. biporus, M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. augustini* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype. Adult male in moderate state of preservation (Fig. 62). Left foot missing (taken as tissue sample), femoral glands partly detached for examination in internal view. Body rather stout. Head wider than body. Snout rounded. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, rounded, diameter 82% of eye diameter. Supratympanic fold closely following outer edge of tympanum, not clearly recognisable as separate structure in preserved specimen. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle recognisable, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (111%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4i(3), 4e(3), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth. Ventral side smooth. Femoral glands present, relatively small, consisting of a distal ulcerous macrogland; no proximal granular gland field recognisable.

Colour in preservative: dorsum brown, with indistinct irregular darker and lighter markings and a light vertebral band. Forelimbs brown with darker markings. Hindlimbs brown with indistinct darker crossbands. Inguinal region with few whitish spots. Snout tip without a light dot. Venter uniformly beige, throat darker than belly with brown mottling. Lower lip with distinct alternating light and brown spots. Toe discs dark. Toes light and dark striped.

Colour in life: dorsum dark brown with indistinct darker markings. Similar to colour in preservative. Forelimbs brown with indistinct darker markings; hindlimbs with dark crossbands. Venter uniformly beige, throat with distinct brown mottling. A beige vertebral band is present. On the flanks few white spots present. Skin on the back smooth.

Variation.—Variation in measurements is given in Table 10. See Fig. 65 for colouration in life and its variation. Data on sexual size dimorphism is inconclusive, and our sample size is small (confirmed male SVL 23.9 mm [n = 1] vs confirmed female SVL 20.9–25.0 mm [n = 3]). There does not seem to be a clear size dimorphism in tympanum diameter (HTD/ED ratio is 68–92% in females, 82% in the male). Femoral glands of the male in life were not very strongly expressed; small gland rudiments are recognisable also in a female (Fig. 65c).

Natural history.—At the type locality, calling males were observed at night from the shore of a very shallow running water of a spring in rainforest.

TABLE 10. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus biporus* clade and the *M. stelliger* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype. An asterisk (*) marks lectotypes designated in the current paper. A hash (#) marks measurements taken by AH and thus not fully comparable with other measurements, all taken by MV. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
Mantidactylus biporus																			
BMNH 1947.2.26.47 [LT*]	NA	F	Madagascar	35.8	13.7	13.9	4.7	2.8	2.8	1.7	3.7	18.1	8.5	51.2	22.3	15.3	NM	NA	NA
BMNH 1947.2.26.48 # [PLT]	NA	F?	Madagascar	28.0	12.1	10.0	4.6	2.3	2.8	1.9	3.5	9.4	8.6	NM	NM	12.2	12.8	1.5	1.2
BMNH 1947.2.26.50 # [PLT]	NA	F?	Madagascar	29.4	11.3	9.7	4.2	2.5	2.4	1.8	3.3	10.0	7.2	NM	NM	12.6	12.0	1.4	1.2
BMNH 1947.2.26.49 [PLT]	NA	M	Madagascar	29.9	10.7	11.9	4.1	3.1	2.7	2.2	2.7	15.9	7.8	41.7	19.5	13.6	NM	3.9	2.5
MRSN A6180	FAZC 13480	M	Betampona	31.6	12.6	12.5	4.8	3.3	2.7	2.6	3.6	17.4	8.7	43.3	20.1	14.0	12.8	3.0	2.2
MRSN A6266	FAZC 13675	M	Betampona	29.9	12.0	12.1	4.9	3.7	2.9	2.1	3.7	16.6	8.0	41.5	19.4	14.0	11.5	3.3	2.1
MRSN A6374	FAZC 13835	M	Betampona	31.0	12.6	12.7	4.5	3.4	2.7	2.2	3.3	17.6	8.4	42.0	19.6	14.1	12.5	3.4	2.7
ZSM 1982/2006	ZCMV 2425	M	An'Ala	28.0	11.0	11.0	3.8	3.0	2.7	1.7	2.7	15.1	7.0	38.2	17.3	11.8	11.2	2.3	1.8
ZSM 396/2006	ZCMV 1483	F	An'Ala	30.5	11.5	11.4	4.3	3.0	2.8	1.7	2.9	16.0	8.0	42.9	18.7	13.2	12.1	1.4	1.2
ZSM 184/2021	ACZCV 201	F?	Betampona: Vohitsivalana	19.3	8.0	8.6	2.8	1.8	2.4	1.8	2.7	11.0	5.7	29.2	13.2	8.7	8.6	NA	NA
Mantidactylus augustini **sp. nov.** (Ca22)																			
ZSM 122/2002 [HT]	FGMV 2001.1388 (2002. A4)	M	Andranofotsy	23.9	10.1	10.3	3.9	3.2	2.5	1.6	2.8	15.9	6.9	36.7	16.9	11.7	10.5	3.3	2.0
MRSN A3600 [PT]	FN 7678 (ACZC 4904)	F	Masoala forest	25.0	9.6	10.3	3.7	3.4	1.6	1.6	3.0	14.8	7.5	38.3	17.0	11.8	10.6	NA	NA
ZFMK 70481 #	NA	F	Masoala	24.2	9.5	9.0	3.8	2.6	2.0	1.8	3.0	9.7	6.8	NM	NM	10.4	11.4	1.4	1.3

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TABLE 10. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
MRSN A2905 [PT]	FN 7238 (ACZC 4897)	F?	Masoala forest	24.4	10.3	10.8	4.0	2.9	2.7	1.7	3.0	NM	7.4	NM	17.4	12.6	11.1	NA	NA
MRSN A3540 [PT]	ACZC 4898	F?	Masoala forest	22.6	9.3	10.0	3.7	2.4	2.4	1.6	2.9	14.8	6.9	37.8	17.4	11.8	11.1	NA	NA
ZSM 740/2009 [PT]	ZCMV 11170	F	Melivinany, Manompana	20.9	8.2	8.6	3.1	2.7	1.9	1.7	2.9	13.9	6.6	33.0	15.3	10.9	9.8	1.7	1.3
MRSN A6740 [PT]	FAZC 14292 (ACZC 4906)	FJ?	Farankaraina	16.4	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NA	NA
MRSN A3737 [PT]	FAZC 10009 (ACZC 4905)	J	Masoala forest	16.4	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NA	NA
Mantidactylus bletzae **sp. nov.**																			
ZSM 829/2014 [HT]	ZCMV 14771	F	Ivohibe	27.3	10.6	10.5	3.4	2.4	1.8	1.8	3.0	16.1	7.9	41.0	18.6	12.2	12.4	NA	NA
ZSM 827/2014 [PT]	ZCMV 14763	F	Ivohibe	25.8	9.8	9.9	3.4	2.6	2.0	1.6	2.9	15.5	7.4	39.3	18.1	12.2	11.8	NA	NA
ZSM 828/2014 [PT]	ZCMV 14768	F	Ivohibe	26.2	9.8	10.1	3.5	2.3	2.1	1.7	2.6	15.6	8.3	40.5	18.6	12.3	12.0	NA	NA
Mantidactylus brevirostris **sp. nov.**																			
MRSN A6257 [HT]	FAZC 13581	M	Betampona: Sahambendrana	23.2	8.8	9.3	3.5	2.7	2.4	1.6	3.4	14.7	6.5	34.9	15.6	10.7	10.4	2.7	1.6
ZSM 185/2021 [PT]	ACZCV 265	F	Betampona: Sahabefoza	28.4	11.3	11.4	3.8	2.6	2.4	1.6	2.8	16.3	7.3	40.6	17.9	12.0	12.0	NA	NA
Mantidactylus eulenbergeri **sp. nov.** (Ca23)																			
ZSM 85/2002 [HT]	FGMV 2001.1092	M	Andasibe	21.6	9.2	8.7	3.3	3.0	1.8	1.4	2.3	12.5	5.7	29.7	13.2	9.0	7.9	3.4	2.3
ZFMK 62214 #	NA	M	Andasibe	23.3	9.1	8.1	3.7	2.7	2.1	1.8	2.5	9.2	6.6	NM	NM	10.1	10.1	2.2	2.2

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TABLE 10. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
MRSN A7047 [PT]	FAZC 15517	M	Maromizaha	21.9	9.5	9.5	3.5	3.1	2.1	1.7	2.9	13.9	6.4	32.4	14.8	10.0	9.6	2.5	1.5
MRSN A7048 [PT]	FAZC 15549	M	Maromizaha	20.9	8.1	8.6	3.0	2.5	1.8	1.8	2.7	12.0	6.3	31.2	13.9	9.7	9.4	2.0	1.4
ZSM 199/2021 [PT]	FAZC 15516	M	Maromizaha	20.5	8.8	9.2	3.3	2.5	1.8	1.7	3.0	12.6	6.5	30.3	13.7	9.5	9.4	2.7	1.6
MRSN A6700 [PT]	RJS 1820 (ACZC 4200)	F	Anivorano Est forest	26.4	11.1	12.3	4.4	2.9	2.5	2.0	3.4	16.2	7.6	39.3	17.8	12.0	12.0	NA	NA
ZSM 84/2002 [PT]	FGMV 2001.1090	F	Andasibe	28.0	10.5	10.7	3.5	2.6	2.1	1.9	2.9	15.6	7.4	39.0	17.1	11.9	11.4	2.3	1.0
ZSM 198/2021 [PT]	FAZC 15509	F	Maromizaha	26.7	10.4	11.0	3.4	2.4	2.1	2.0	2.5	16.0	7.9	35.6	16.0	10.0	10.4	NA	NA
MRSN A7049 [PT]	FAZC 15540	F	Maromizaha	25.0	10.1	11.0	3.6	2.5	1.9	1.9	3.0	14.1	7.2	37.4	16.8	11.6	11.0	NA	NA
ZSM 919/2003 [PT]	FGMV 2002.949	F	Vohidrazana	20.0	8.5	8.5	3.2	2.3	1.9	1.1	2.3	12.6	5.8	29.4	13.9	9.3	9.0	1.4	1.2
Mantidactylus glosi **sp. nov.**																			
ZSM 434/2006 [HT]	ZCMV 3366	M	Ranomafana	21.0	8.7	8.6	3.2	2.8	2.1	1.4	2.3	11.9	5.6	28.9	13.5	9.3	9.1	2.5	1.5
ZSM 433/2006 [PT]	ZCMV 3364	F	Ranomafana	25.1	9.7	10.0	3.4	3.1	2.3	1.4	2.5	13.8	6.5	34.1	16.0	11.3	10.1	1.2	1.0
Mantidactylus stelliger **sp. nov.**																			
ZSM 2381/2007 [HT]	ZCMV 5932	M	Ambohitsara	22.6	9.7	10.0	3.9	2.6	2.1	1.5	2.6	13.8	6.4	33.1	15.0	9.8	9.9	2.8	2.2
ZSM 2380/2007 [PT]	ZCMV 5922	M	Ambohitsara	21.6	8.8	9.4	3.4	2.5	2.0	1.6	2.8	13.8	6.4	33.3	14.9	10.2	10.1	2.6	1.9
ZSM 2379/2007 [PT]	ZCMV 5870	F	Ambohitsara	31.1	13.0	13.2	4.6	3.4	2.8	2.6	3.0	19.1	9.3	46.2	20.8	14.5	13.6	1.1	0.8

FIGURE 65. *Mantidactylus augustini* **sp. nov.** from Andranofotsy in life, in dorsolateral and ventral view. (a,b,c) Adult female (FGMV 2001.1431, voucher deposited in UADBA), photographed in 2001. (d,e) Adult male (holotype ZSM 122/2002 = FGMV 2001.1388 = 2002.A4), photographed in 2001.

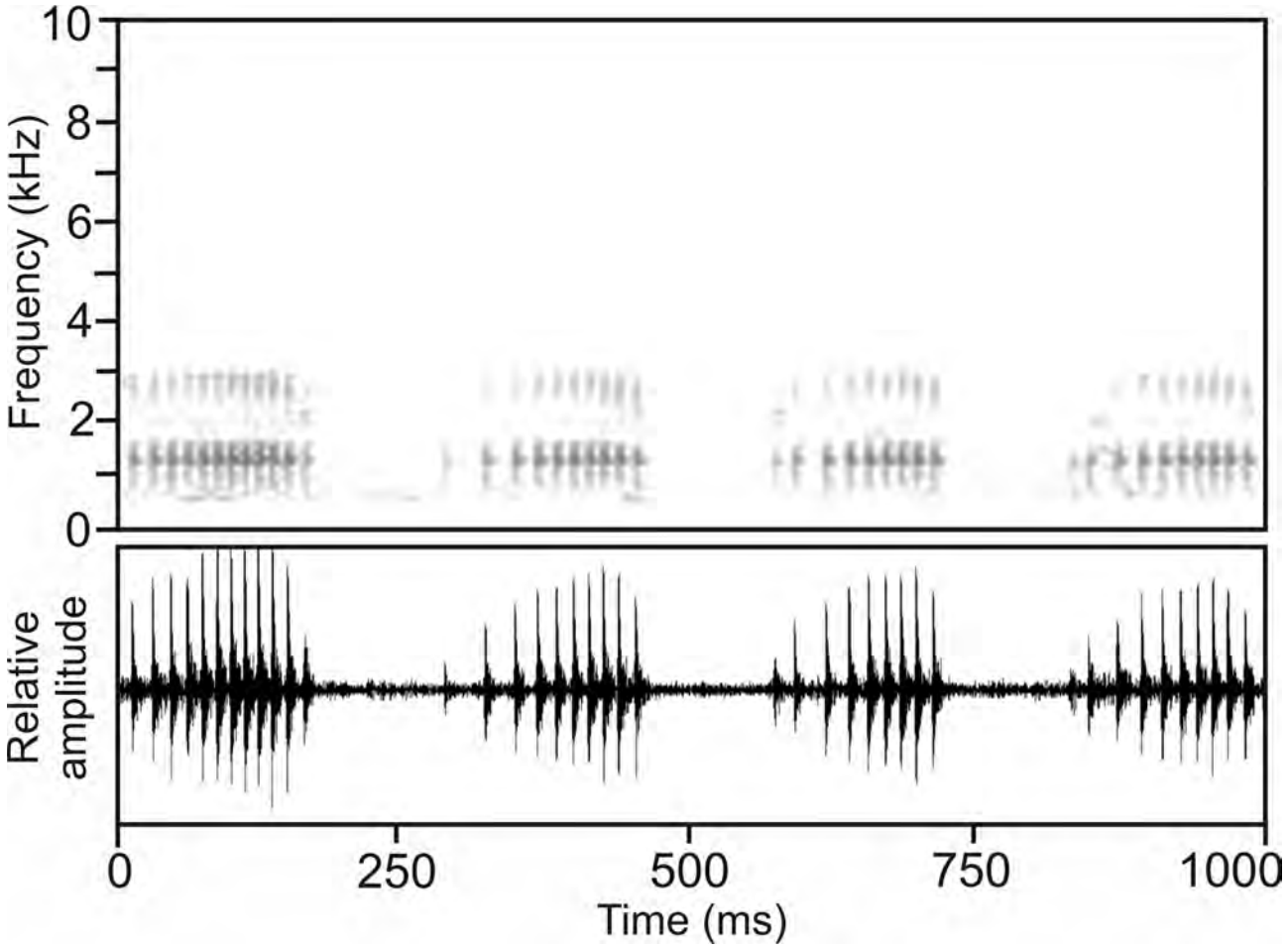

FIGURE 66. Audiospectrogram and corresponding oscillogram of a 1000 ms section of a series of advertisement calls (four calls figured) of *Mantidactylus augustini* **sp. nov.**, recorded on 16 December 2001 at Andranofotsy (25.4°C air temperature). Recording bandpass-filtered at 500–3500 Hz.

Calls.—The advertisement call of *M. augustini*, recorded on 16 December 2001 near Andranofotsy, 25.4°C air temperature (Vences *et al.* 2006: CD2, track 72), consisted of a short, pulsed note, emitted in regular series at fast succession (Fig. 66). Pulse repetition rate was distinctly lower at the beginning of calls and increased after approximately one half of the call's duration. Amplitude modulation was present, with relative amplitude increasing from the beginning of the call, reaching its maximum at the last quarter of the call's duration. Numerical parameters of seven analysed calls were as follows: call duration (= note duration) 154–236 ms (178.8 ± 26.6 ms); 9–15 pulses per note (10.4 ± 2.1); pulse duration 7–12 ms (9.1 ± 1.6); pulse repetition rate within notes 44.4–71.4 pulses/s (59.0 ± 10.3); dominant frequency 1263–1356 Hz (1304 ± 39 Hz); prevalent bandwidth 700–3150 Hz; call repetition rate (= note repetition rate) within regular series ca 200–230 calls/min.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the North East of Madagascar (Fig. 7). This species is known from Masoala, Manompana (Befanjana), Antsahataloka, and Andranofotsy. Elevation range: Ranging from near sea level (85 m a.s.l.) to ~1000 m a.s.l.

Etymology.—We dedicate this species to Augustin Sarovy, an excellent musician, guide, and ecologist from Maroantsetra, whose help was crucial to collect the holotype of this new species and to record its call.

Mantidactylus bletzae **sp. nov.**

Identity and justification.—This lineage, known from two high-elevation sites in the Southern Central East and South East of Madagascar, was newly identified in this study. It resembles species of the *M. biporus* and *M. inaudax* clades phenotypically. By the presence of dorsolateral ridges, it resembles some species of the *M. inaudax* clade, but in the 16S tree, it is placed more closely to species of the *M. biporus* clade, although its relationships are not reliably resolved. We here consider it tentatively as a member of the *M. biporus* clade, pending its inclusion in a future phylogenomic analysis. The new species is characterized by a high mitochondrial divergence (≥5.7% from all other species; closest species *M. inaudax* **bona species** and *M. madecassus*), and an isolated position in the mitochondrial tree, without obvious close relationships

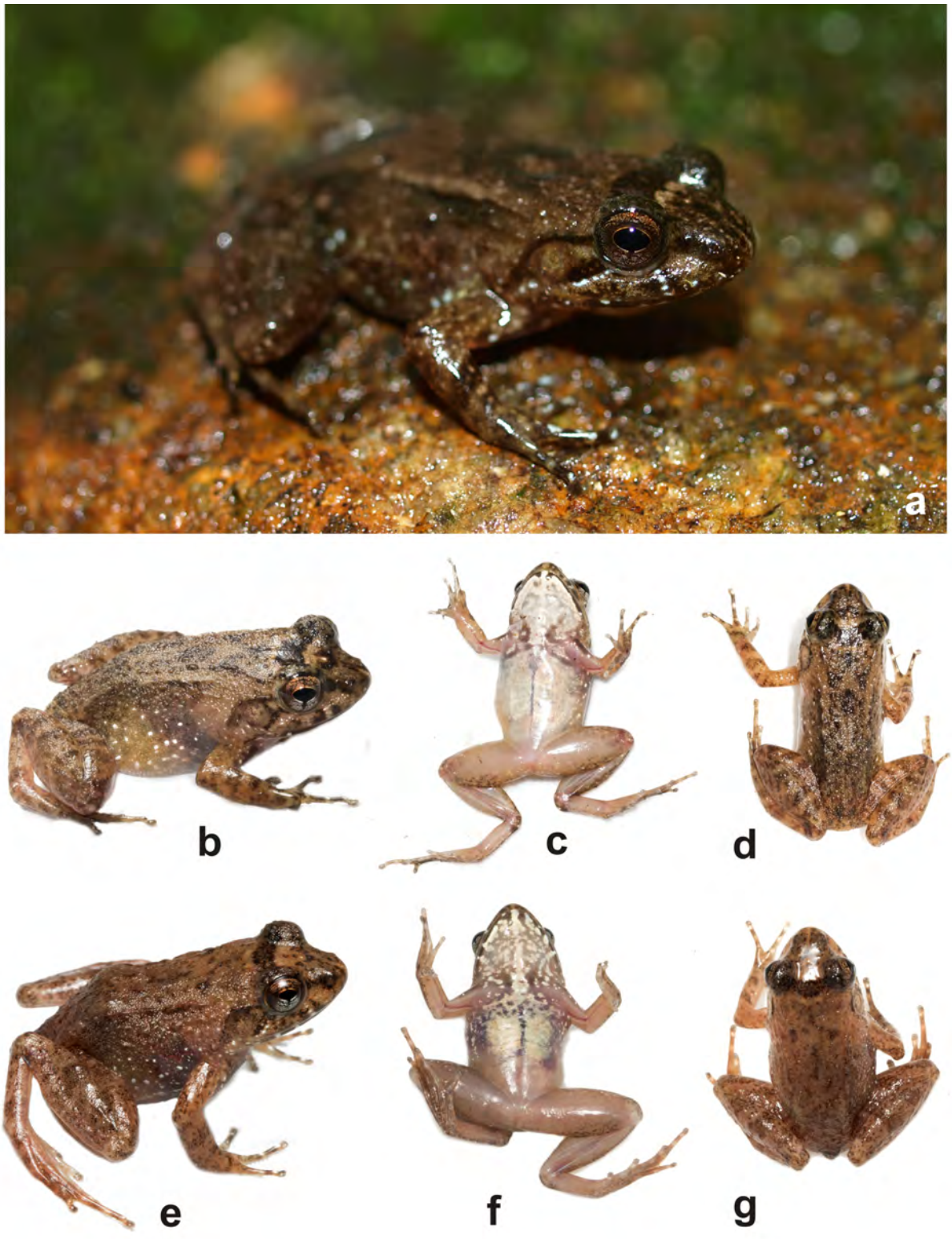

FIGURE 67. *Mantidactylus bletzae* **sp. nov.** in life, in dorsolateral, ventral, and dorsal view. (a) Adult female (ZSM 827/2014 = ZCMV 14763) from Campsite 3, Pic d'Ivohibe Special Reserve, photographed in 2014. (b,c,d) Adult female (KU336940 = CRH 125) from Ranomafana. (e,f,g) Adult female (KU336941 = CRH 146) from Ranomafana.

to any other species. It also is concordantly differentiated in the nuclear Rag-1 gene with a unique haplotype (Fig. 4). Based on the concordance of high mitochondrial divergence with nuclear differentiation, we are convinced it represents a distinct species.

Holotype.—ZSM 829/2014 (ZCMV 14771), adult female, collected by A. Rakotoarison, M. Bletz, D. Edmonds, and F. Randrianasolo on 11 November 2014 at Pic d'Ivohibe Special Reserve, Camp 3 (22.49710°S, 046.95758°E, 1566 m a.s.l.), Ihorombe Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of two paratypes: ZSM 827/2014 (ZCMV 14763) and ZSM 828/2014 (ZCMV 14768), two adult females, with the same collection data as the holotype. Specimens from Ranomafana are not included in the paratype series as they were not examined morphologically and are genetically divergent.

Diagnosis.—*Mantidactylus bletzae* **sp. nov.** is considered to be a member of the *M. biporus* clade based on affinities in the 16S tree. Its precise relationships remain unclarified, as it was missing from our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of a small body size (female SVL 26–27 mm), slightly granular dorsal skin with weakly expressed but distinctly recognisable dorsolateral ridges, presence of white spots on flanks, and absence of a white marking on the snout tip distinguishes *M. bletzae* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *Mantidactylus inaudax* (*M. inaudax* clade) is morphologically similar but appears to have a somewhat larger body size, no dorsolateral ridges, shorter hindlimbs, and less developed foot webbing; *M. biporus* has a larger body size, lacks dorsolateral ridges, and has less developed foot webbing; *M. augustini* has somewhat longer hindlimbs, somewhat less granular dorsal skin and less clearly expressed dorsolateral ridges, and less developed foot webbing (Table 4). For a distinction from the other new species in the *M. biporus, M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. bletzae* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult female in excellent state of preservation (Fig. 62). Tongue has been excised as tissue sample. Head as wide as body. Snout rounded in dorsal view. Nostrils directed laterally, not protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weakly expressed, slightly concave. Loreal region concave. Tympanum distinct, small, rounded, its horizontal diameter about 71% of eye diameter. Supratympanic fold present, beginning straight, bending abruptly midway towards jaw / forelimb insertion. Maxillary teeth present. Vomerine teeth present in two small rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot of similar length as tibia (98%). Lateral metatarsalia separated. Inner metatarsal tubercle present, outer metatarsal tubercle poorly recognisable. Webbing formula: 1(0.5), 2i(1.25), 2e(1), 3i(2), 3e(1), 4i(2), 4e(1.5), 5(0.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface quite smooth in preservative with poorly recognisable dorsolateral folds which in life probably were more clearly visible as in other photographed specimens, along with scattered small granules. Ventral side smooth. Femoral glands absent.

Colour in preservative: dorsum light brown with a quite distinct dark brown pattern, including dark longitudinal stripes running ventral of the dorsolateral folds, some dark patches in the vertebral region, and a broad dark band between the eyes. Fore- and hindlimbs with distinct dark brown crossbands. Ventrally whitish on belly and beige on limbs, with weak dark mottling on throat and chest, and lower jaw ventrally bordered by an interrupted dark line. The colour in life was not recorded.

Variation.—Variation in measurements is given in Table 10. See Fig. 67 for colouration in life and its variation. No male specimens available to assess sexual dimorphism.

Natural history.—Poorly known. Specimens were found in a swampy area near a small pool.

Calls.—The call of this species has not been recorded.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to Southern Central East (Fig. 7). This species is known from Pic d'Ivohibe Special Reserve (Camp 3, at high elevation), and Maharira in Ranomafana National Park. Elevation range: 1248–1575 m a.s.l.

Etymology.—We dedicate this species to Molly C. Bletz, who contributed to collecting the type specimens from Pic d'Ivohibe, in recognition of her substantial contributions to amphibian conservation and research in Madagascar.

Mantidactylus brevirostris **sp. nov.**

Identity and justification.—A deep genetic lineage of the *M. biporus* clade known from Betampona, and Sahavontsira. This lineage has been considered as unconfirmed candidate species *M.* sp. 31 by Vieites *et al.* (2009) and *M.* sp. Ca31 by Perl *et al.* (2014). It was referred to as '*M.* sp. aff. *biporus* [Ca FJ559260]' by Rosa *et al.* (2012). According to the phylogenomic analysis, it represents the sister taxon of another lineage named below (*M. eulenbergeri* **sp. nov.**) but differs from that lineage by a 16S distance of 8.6–9.1%, and possibly by at least one morphological difference in foot webbing, suggesting a status as distinct species.

Diagnosis.—*Mantidactylus brevirostris* **sp. nov.** is a member of the *M. biporus* clade, sister to the new species *M. eulenbergeri* **sp. nov.** (described below) according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of a small body size (male SVL 23 mm,

FIGURE 68. *Mantidactylus brevirostris* **sp. nov.** from Betampona in life, in dorsolateral view. (a) Unsexed individual (ACP5444 = Bet76). (b) Unsexed individual (ACP5463 = Bet101). (c) Unsexed individual (ACP5463 = Bet68). (d) Unsexed individual (ACP5467 = Bet91).

FIGURE 69. *Mantidactylus eulenbergeri* **sp. nov.** in life, in dorsolateral and ventral view. (a,b) Adult male (holotype ZSM 85/2002 = FGMV 2001.1092) from Andasibe.

female SVL 28 mm), rather smooth dorsal skin without dorsolateral ridges, large tympanum size in males (12% of SVL), presence of white spots on flanks, and absence of a white marking on the snout tip, distinguishes *M. brevirostris* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. The distantly related *M. inaudax* (*M. inaudax* clade) is morphologically very similar but appears to reach larger body sizes, has more developed foot webbing, and has in many individuals a pattern where the colour of flanks differs from that on the dorsum; *M. biporus* occurs syntopically with *M. brevirostris* **sp. nov.** but has a larger body size and a more developed foot webbing; *M. augustini* has longer hindlimbs and a more developed foot webbing; *M. bletzae* has a more granular dorsal skin with dorsolateral ridges and a more developed foot webbing (Table 4). For a distinction from the other new species in the *M. biporus, M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. brevirostris* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Holotype.—MRSN A6257 (FAZC 13581), adult male, collected by G.M. Rosa, and F. Andreone on 9 February 2007 at Sahambendrana, Réserve Naturelle Intégrale de Betampona (17.8984°S, 049.2154°E, 458 m a.s.l.), Antsinanana Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession HM364736).

Paratypes.—A single paratype: ZSM 185/2021 (ACZCV 265, extraction ACP 2211; tissue ACZC 6309), adult female, collected by A. Crottini, D. Salvi, E. Scanarini, George, J. Nöel, and F. Andreone on 22 November 2013 at Betampona (Sahabefoza).

Description of the holotype.—Adult male in good state of preservation (Fig. 62). Fourth and fifth finger from right foot missing (taken as tissue sample). Body rather stout. Head as wide as body. Snout rounded in dorsal view, somewhat truncate in lateral view. Nostrils directed laterally, not protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, large, as wide as high, horizontal diameter of tympanum 89% of horizontal eye diameter. Supratympanic fold not clearly recognisable, basically corresponding to outer edge of tympanum. Tongue ovoid, bifid posteriorly. Maxillary teeth present. Vomerine teeth form two somewhat elongate aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot very slightly longer than tibia (103%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2.25), 3e(2), 4i(2.5), 4e(2.5), 5(1.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, without recognisable dorsolateral ridges. Ventral side smooth. Femoral glands small but distinct in external view.

Colour in preservative: dorsally brown, with small dark brown speckles arranged irregularly to give an appearance of three large broad patches of darker colour interrupted by lighter areas. A broad beige vertebral stripe is present and is interrupted in the middle of the dorsum, probably representing a colouration anomaly. Some white spots on the upper jaw and underneath the eye. Two to three relatively distinct dark crossbands on hindlimbs. Ventrally beige, with sparse dark pigmentation on throat, and an alternating light-dark pattern ventrally on lower lip. Colour in life unknown.

Variation.—Variation in measurements is given in Table 10. See Fig. 68 for colouration in life and its variation. Too few specimens have been sexed to assess the degree of sexual size dimorphism. Femoral glands in life are not documented (no photographs of the ventral side available).

Natural history.—Species usually observed in slow-running parts of streams and other small courses. Active both day and night. Quite shy and able to hide under the mud or actively swimming when disturbed.

Calls.—The call of this species has not been recorded.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to low-elevation (< 500 m a.s.l.) rainforest in the Northern Central East (Fig. 7). It is currently known from Betampona and Sahavontsira. Elevation range: 190–517 m a.s.l.

Etymology.—The species epithet is a Latin third-declension two-termination adjective, derived from the adjective 'brevis', meaning short, and 'rostrum', meaning snout, in the genitive singular, and refers to the short snout observed in several individuals of this species.

Mantidactylus eulenbergeri **sp. nov.**

Identity and justification.—This lineage is a member of the *M. biporus* clade and has been considered as confirmed candidate species *M.* sp. 23 by Vieites *et al.* (2009), and *M.* sp. Ca23 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Andasibe"' by Glaw and Vences (2007). It shows a rather distinctive morphology with a very short snout in at least some specimens, and differs from other lineages of the *M. biporus* clade by concordant divergence in 16S and Rag-1. According to the phylogenomic analysis, it represents the sister taxon of *M. brevirostris* but differs from that lineage by a 16S distance of 8.6–9.1%, and possibly by a difference in foot webbing (Table 4). We consider the available evidence sufficient to assign a status of separate species to this lineage.

Holotype.—ZSM 85/2002 (field number MV 2001.1092), adult male, collected by M. Vences on 23–25 November 2001 at Andasibe (18.9333°S, 048.4167°E, 915 m a.s.l.), Alaotra-Mangoro Region, Madagascar. 16S and cox1 barcode sequences of the holotype are available from GenBank (accessions AY848239 and JN133224).

Paratypes.—A total of seven paratypes: ZSM 84/2002

(MV 2001.1090), adult female, with same collection data as the holotype; ZSM 919/2003 (FGMV 2002.949), putative female, collected by G. Aprea and collaborators on 20 February 2003 in Vohidrazana; ZSM 198/2021 (FAZC 15509, extraction ACP 3664, tissue ACZC 8596), ZSM 199/2021 (FAZC 15516, ACP 3671, ACZC 8603), MRSN A7047 (FAZC 15517, ACP3672, ACZC8604), MRSN A7048 (FAZC 15549, ACP3702, ACZC8636), MRSN A7049 (FAZC 15540, ACP3693, ACZC8627), all collected in January 2017 at Maromizaha (18.9713°S, 048.4642°E) by E. Coppola.

Additional material.—The following specimens (without genetic data) are tentatively assigned to this species: ZFMK 52674–52675, collected by F. Glaw and M. Vences in February 1991 and ZFMK 62214 collected by F. Glaw on 1 February 1996 (all from Andasibe).

Diagnosis.—*Mantidactylus eulenbergeri* **sp. nov.** is a member of the *M. biporus* clade, sister to *M. brevirostris* according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of small body size (male SVL 20–23 mm, female SVL 25–28 mm), smooth dorsal skin with weakly expressed dorsolateral ridges sometimes recognisable, large tympanum size in males (12–14% of SVL), presence of (sometimes only few) white spots on flanks, and absence of a white marking on the snout tip, distinguishes *M. eulenbergeri* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *M. inaudax* (*M. inaudax* clade) is morphologically similar but differs by larger body size; *M. biporus* has a larger body size; *M. augustini* has longer hindlimbs; *M. bletzae* has a more granular dorsal skin with dorsolateral ridges; *M. brevirostris* has a less developed foot webbing (Table 4). For a distinction from other new species in the *M. biporus, M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. eulenbergeri* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in moderate state of preservation (Fig. 62). Tissue sample removed from right thigh. Body stout. Head as wide as body. Snout very short and rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, rounded, diameter 91% of eye diameter. Supratympanic fold indistinct, following exactly the outline of the large tympanum. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer metacarpal tubercle recognisable, inner metacarpal tubercle present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (114%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not present. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1), 4i(2.5), 4e(2.5), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth. Ventral side smooth. Femoral glands distinct, consisting mainly of a distal ulcerous macrogland recognisable in external view, while only a very small proximal granular gland field is recognisable in external view. Skin on the back is smooth.

Colour in preservative: dorsum brown, with distinct irregular darker markings. A dark brown band between eyes present. Forelimbs brown with distinct darker markings. Hindlimbs brown with distinct darker crossbands. Inguinal region without whitish spots. Snout tip without a light dot. Venter beige, throat darker than belly. Lower lip with distinct alternating light and brown spots. Toe discs dark. Toes light and dark striped. Colour in life as in preservative but more vibrant (Fig. 69).

Variation.—Variation in measurements is given in Table 10. There is pronounced sexual size dimorphism (confirmed male SVL 20.0–23.3 mm [n = 6] vs confirmed female SVL 25.0–28.0 mm [n = 4]). Horizontal tympanum diameter is 73–86% of eye diameter in males and 60–78% of eye diameter in females. Skin on the back is smooth. Colour on the back brown with few indistinct markings (e.g. ZSM 84/2002). Few white spots on the flanks are always present. Two dark spots on the back at level of forelimb insertion are present only in ZSM 84/2002. A light interrupted vertebral line is present in ZFMK 62214, ending on the snout tip with a distinct white dot. A light vertebral band is never present. A dark brown and more or less triangular band between eyes is always present. Lower lip with more (e.g. ZSM 85/2002) or less (e.g. ZSM 84/2002) distinct alternating light and brown spots. Venter and throat uniformly beige, in ZFMK 62214 with little white spots. A longitudinal white median line on thorax and throat is present in ZFMK 62214 and very faintly in ZSM 84/2002. Forelimbs brown with irregular darker markings and stripes. Femoral glands of adult males are large and prominent with one indistinct spot on the femoral gland as a small side structure proximal to the cloaca in ZSM 85/2002, with two distinct spots in ZFMK 62214. In females femoral glands are small but can be recognised (e.g. ZSM 84/2002), with two gland rudiments of the same size on each shank.

Natural history.—A species found along small and shallow running water bodies in rainforest.

Calls.—The call of this species has not been recorded

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the Northern Central East (Fig. 7). This species is known from Anivorano Est, Sahafina, Andasibe, Maromizaha, and Vohidrazana. Elevation range: 60–1100 m a.s.l.

Etymology.—We dedicate this species to Klaus Eulenberger, former chief veterinary of Leipzig Zoo, in recognition of his contributions to knowledge on husbandry and veterinary care of captive amphibians and reptiles.

Mantidactylus glosi **sp. nov.**

Identity and justification.—This species has been considered as confirmed candidate species *M.* sp. 24

by Vieites *et al.* (2009), and *M.* sp. Ca24 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Ranomafana"' by Glaw and Vences (2007) and Schmidt *et al.* (2009) [tadpoles]. A lineage of the *M. biporus* clade with strong divergence in 16S and not immediately closely related to another lineage in the phylogenomic tree (i.e. sister to a subclade with four other species). Also characterized by differentiation in Rag-1 from other species in the *M. biporus* clade, and therefore here seen as distinct species.

Holotype.—ZSM 434/2006 (ZCMV 3366), adult male, collected by M. Vences, Y. Chiari, T. Rajofiarison, E. Rajeriarison, P. Bora, and T. Razafindrabe on 26 February 2006 at Ambatovory (upstream river from Ambatolahy), Ranomafana National Park (21.23798°S, 047.42478°E, 966 m a.s.l.), Vatovavy-Fitovinany Region, Madagascar. A 16S barcode sequence of the holotype is available from GenBank (accession FJ559255).

Paratypes.—A total of four paratypes: ZSM 433/2006 (ZCMV 3364), adult female, with same collection data as holotype; UADBA uncatalogued (ZCMV 3365, ZCMV 3367), two specimens of unknown sex and maturity, with same collection data as the holotype; UADBA 20667 (FGMV 2002.254), unknown sex and maturity, collected by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas, and D.R. Vieites on 16 January 2003 in Ranomafana National Park.

Diagnosis.—*Mantidactylus glosi* **sp. nov.** is a member of the *M. biporus* clade and is sister to the assemblage of all other species in the clade according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of small body size (male SVL 21 mm, female SVL 25 mm), slightly granular dorsal skin with weakly expressed and sometimes discontinuous but clearly recognisable dorsolateral ridges, large tympanum size in males (13% of SVL), presence of white spots on flanks in at least some individuals, and absence of a white marking on the

FIGURE 70. *Mantidactylus glosi* **sp. nov.** (a) Adult female (possibly corresponding to ZSM 433/2006 = ZCMV 3364), from Ambatovory, Ranomafana, in dorsolateral view, photographed in 2003. (b). Specimen from Ambatovory, Ranomafana, in dorsolateral view, photographed in 2003 and only tentatively attributed to this species. (c, d) Female JCR328 from Andalangina, Ranomafana, in dorsolateral and ventral views.

snout tip, distinguishes *M. glosi* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *M. inaudax* (*M. inaudax* clade) differs by larger body size, smoother dorsal skin and longer hindlimbs; *M. biporus* differs by larger body size and smoother dorsal skin; *M. augustini* differs by longer hindlimbs; *M. bletzae* differs by more developed foot webbing and longer hindlimbs; *M. brevirostris* has a less developed foot webbing, smoother dorsal skin, and longer hindlimbs; *M. eulenbergeri* has a smoother dorsal skin (Table 4). For a distinction from other new species in the *M. stelliger* and *M. inaudax* clades, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. glosi* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 62). Part of right thigh muscle removed as tissue sample. Body rather stout. Head slightly wider than body. Snout rounded to weakly pointed in dorsal view. Nostrils directed laterally, not protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis not recognisable. Loreal region concave. Tympanum distinct, large, rounded, its horizontal diameter about 88% of eye diameter. Supratympanic fold present, beginning straight, with a distinct almost 90° bend midway towards jaw / forelimb insertion. Tongue ovoid, distinctly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs very slightly enlarged. Nuptial pads absent. Foot of similar length as tibia (102%). Lateral metatarsalia separated. Inner and outer metatarsal tubercles present. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(2), 4i(2.5), 4e(2), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface quite smooth in preservative with a few granules on the lower flank; in life, as in photographed specimens of this species, likely with small scattered granules and one pair of poorly developed continuous dorsolateral folds—these are weakly recognisable in preservative. Ventral side smooth. Femoral glands present, made up by a distinct but relatively small distal ulcerous macrogland internally consisting of five large granules. Proximal granular gland field not recognisable.

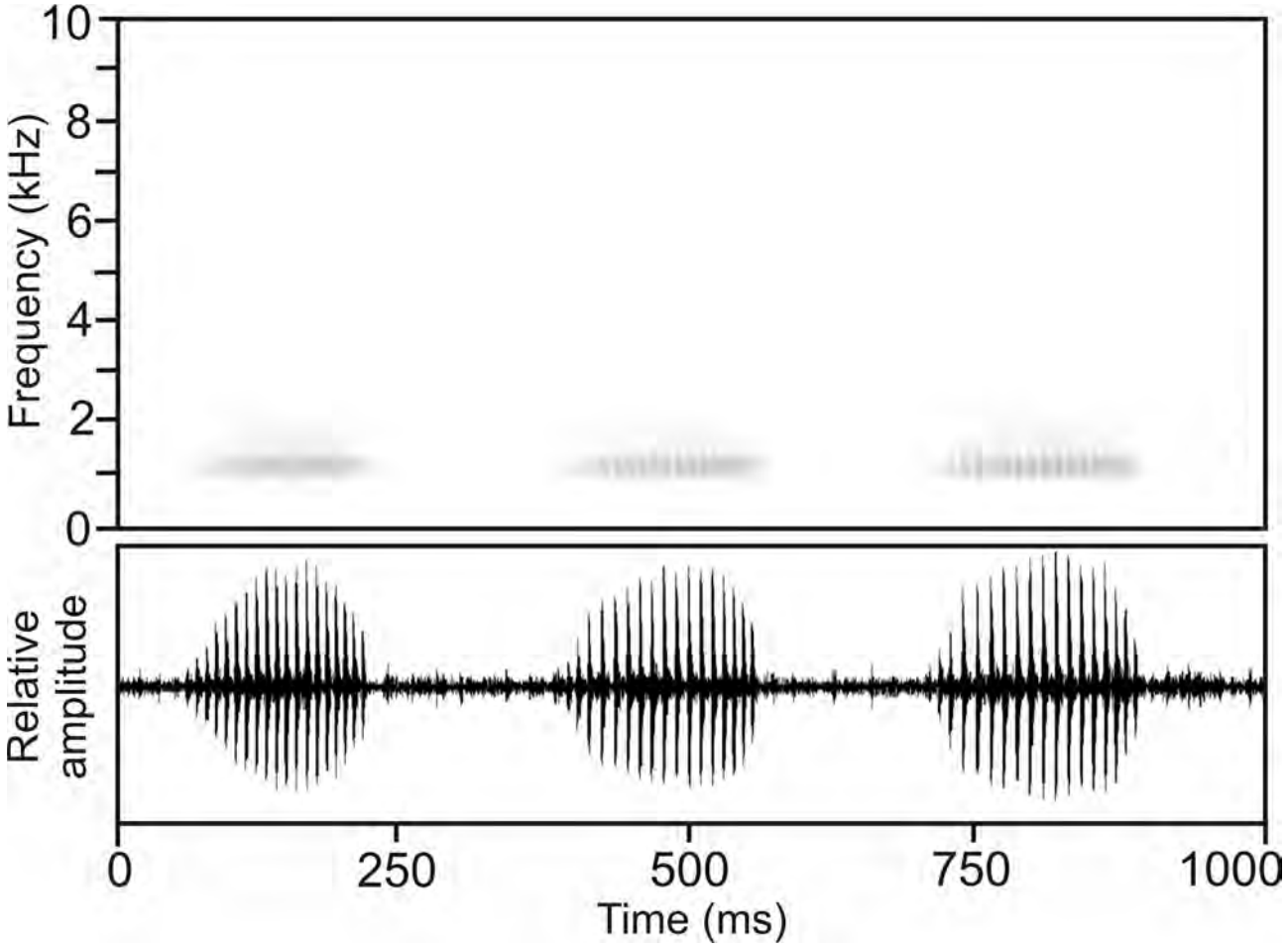

FIGURE 71. Audiospectrogram and corresponding oscillogram of a 1000 ms section of a series of advertisement calls (three calls figured) tentatively allocated to *Mantidactylus glosi*, recorded on 26 February 2006 at Ambatovory (air temperature not measured). Recording bandpass-filtered at 640–2300 Hz.

Colour in preservative: dorsum light brown with poorly defined darker brown patches forming a characteristic pattern: one patch between the eyes, others in dorsolateral position. Weakly developed crossbands on fore- and hindlimbs. A few small white spots scattered on the flanks and on the upper jaw where two rows of 2–3 spots are recognisable, one along the tympanum and directed posteroventrally, the other at mid-eye, directed anteroventrally. Venter beige, throat and chest with brownish pigment forming a rather irregular mottling. The lower jaw is ventrally marked by an alternating series of contrasting dark and light markings. Colour in life not recorded.

Variation.—Variation in measurements is given in Table 10. See Fig. 70 for colouration in life and its variation. A light vertebral line can be present. There may be weak sexual size dimorphism, but our sample size is small (confirmed male SVL 21.0 mm [n = 1] vs confirmed female SVL 25.1 mm [n = 1]). This is confirmed by additional measurements taken in the field from two males (both 23.5 mm) and three females (27.0–29.3 mm). Male and female relative tympanum size seems to be similar (HTD/ED ratio is 91% in the female, 88% in the male). Femoral glands of males in life not documented; in one female, rudimentary glands are visible (Fig. 70d).

Natural history.—Can be observed during day and night. At Ambatovory, specimens were found in a primary rainforest area characterized by a slow-moving stream and extended forested swamp areas next to the running water; calls were emitted from near-stagnant areas in this swamp. Often sitting in shallow parts of slow-moving streams or on the shore. Occurs in syntopy with *M. katae* at Talatakely, Ranomafana National Park, and at a stream with some riparian vegetation in a degraded part close to a forest fragment and banana plantation at Andalangina. Found at an elevational range between 450–971 m a.s.l. in Andalangina and Talatakely. A female with visible eggs was detected on the bank of a slow-moving stream with shallow parts at Talatakely on 6 May 2010, two females with visible eggs were found at Andalangina, one on 25 May 2010 , and one on 25 May 2011.

Calls.—A single call series containing six calls recorded on 26 February 2006 at Ambatovory, air temperature not taken, is here assigned to *M. glosi*, although this assignment is somewhat uncertain given that the calling male has not been observed. The advertisement call consisted of a short, regularly pulsed note repeated at regular intervals and fast succession (Fig. 71). Notes exhibit some amplitude modulation with a fast increase of call energy at the beginning of the note, reaching its maximum approximately at half of the note's duration. Call energy was distributed in a relatively narrow frequency band. Numerical parameters of six analysed calls were as follows: call duration (= note duration) 159–214 ms (190.8 ± 20.7 ms); 18–23 pulses per note (20.3 ± 2.3); pulse duration 4–6 ms (4.9 ± 0.5); pulse repetition rate within notes 90.9–115.4 pulses/s (104.1 ± 10.4); dominant frequency 1070–1201 Hz (1124 ± 47 Hz); prevalent bandwidth 800–2100 Hz; call repetition rate (= note repetition rate) within regular series ca 180 calls/min.

Tadpoles.—The tadpole of *M. glosi* was described under the name '*M.* sp. aff. *biporus* "Ranomafana"' by Schmidt *et al.* (2009).

Distribution.—Apparently microendemic to the Ranomafana area (Fig. 7). This species is known from various sites within Ranomafana National Park, and from Andalangina (ca 20 km from Ranomafana). Elevation range: 486–1027 m a.s.l.

Etymology.—We dedicate this species to Julian Glos, in recognition of his contributions to research on conservation of Madagascar's amphibians.

<u>*Mantidactylus stelliger* clade</u>

This clade contains a single, newly discovered species (described based on the holotype depicted in Fig. 62), and according to our phylogenomic analysis occupies an isolated phylogenetic position (sister to the monophyletic group containing *M. betsileanus, M. fergusoni* and *M. ulcerosus* clades).

Mantidactylus stelliger **sp. nov.**

Identity and justification.—This lineage, phenotypically similar to species in the *M. biporus* clade, occupies an isolated position in the phylogenomic tree and in the 16S tree. It was newly discovered in this study and therefore has not been included in previous DNA barcoding assessments of Madagascar's amphibians. We here consider it as distinct species due to its isolated phylogenetic position, high mitochondrial divergences of at least 6.8% uncorrected pairwise 16S distance to all other *Brygoomantis* species, and morphological differences (see Diagnosis below).

Holotype.—ZSM 2381/2007 (ZCMV 5932), adult male, collected by M. Vences, K.C. Wollenberg, and E. Rajeriarison on 3 March 2007 at Ambohitsara (21.3572°S, 047.8157°E), Vatovavy-Fitovinany Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of four paratypes: ZSM 2379/2007 (ZCMV 5870), adult female, and ZSM 2380/2007 (ZCMV 5922), adult male, with the same collection data as the holotype; UADBA uncatalogued (ZCMV 5923, ZCMV 5931), two specimes of unknown sex and maturity, with the same collection data as the holotype.

Diagnosis.—*Mantidactylus stelliger* **sp. nov.** is the sole member of the *M. stelliger* clade according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of small body size (male SVL 21–23 mm, female SVL 31 mm), slightly granular dorsal skin without dorsolateral ridges, large tympanum size in males (12% of SVL), presence of white spots on flanks in at least some individuals, and absence of a white marking on the snout tip, distinguishes *M. stelliger* **sp. nov.** from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *M. inaudax* (*M. inaudax* clade) differs by larger body size and

FIGURE 72. *Mantidactylus stelliger* **sp. nov.** from Ambohitsara in life, in dorsolateral, ventral, and anterior view. (a,b) Adult male (holotype ZSM 2381/2007 = ZCMV 5932), photographed in 2007. (c,d) Adult male (ZSM 2380/2007 = ZCMV 5922), photographed in 2007. (e,f) Adult female (ZSM 2379/2007 = ZCMV 5870), photographed in 2007.

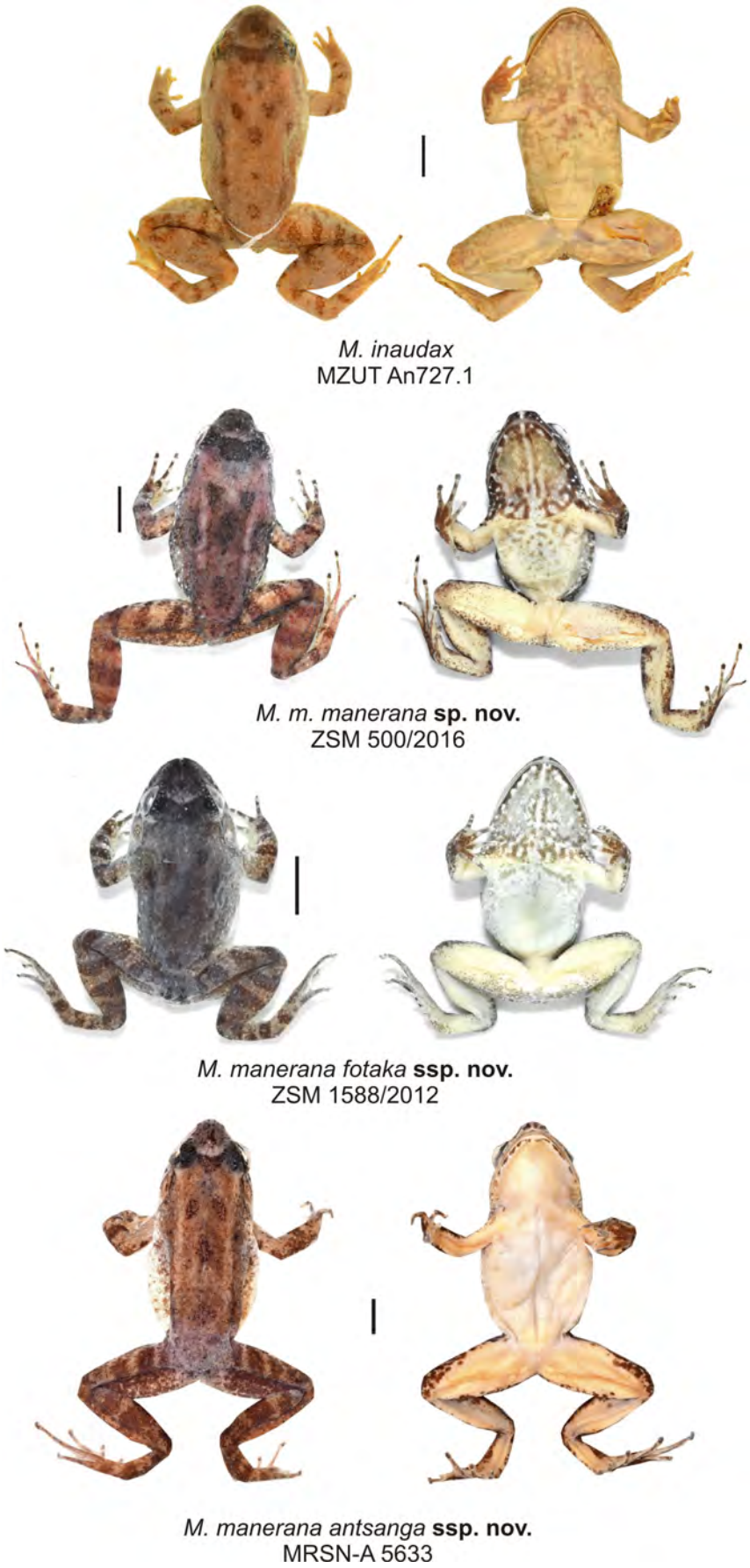

FIGURE 73. Preserved lectotype of *Mantidactylus inaudax*, and holotype specimens of newly named species and subspecies in the *M. inaudax* clade. Scale bars equal 5 mm.

more developed foot webbing. Species of the *M. biporus* clade differ as follows: *M. biporus* by larger body size and and more developed foot webbing; *M. augustini* by longer hindlimbs and more developed foot webbing; *M. bletzae* by more developed foot webbing and presence of dorsolateral ridges; *M. brevirostris* possibly by somewhat smoother dorsal skin and smaller femoral glands; *M. eulenbergeri* by more developed foot webbing and smoother dorsal skin; *M. glosi* by shorter hindlimbs and more developed foot webbing (Table 4). For a distinction from new species in the *M. inaudax* clade, see the diagnoses in the respective species accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. stelliger* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Description of the holotype.—Adult male in good state of preservation (Fig. 62). Part of right thigh muscle removed as tissue sample. Femoral glands partly detached for examination in internal view. Body rather stout. Head wider than body. Snout rounded in dorsal view. Nostrils directed laterally, not protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis not clearly recognisable. Loreal region very weakly concave. Tympanum distinct, rounded, its horizontal diameter about 67% of eye diameter. Supratympanic fold present, beginning straight, and gently curving midway towards jaw/forelimb insertion, following the rounded form of the tympanum. Tongue ovoid and bifid. Maxillary teeth present. Vomerine teeth present in two small rounded aggregations, positioned posterolateral to choanae. Choanae more or less rounded, somewhat elliptical/slit-like. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs minimally enlarged. Nuptial pads absent. Foot of similar length as tibia (99%). Lateral metatarsalia separated. Inner metatarsal tubercle present, outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4i(2.5), 4e(3), 5(1.5). Relative length of toes: I<II<V<III<IV. Skin on the upper surface slightly granular in preservative, especially on flanks; in life similar. No dorsolateral folds are recognisable. Ventral side smooth. Femoral glands present, with a distinct and relatively large distal ulcerous macrogland internally consisting of 4–5 large granules. Proximal granular gland field not recognisable.

Colour in preservative: upper surfaces brown with a larger darker brown marking covering much of the anterior dorsum, and areas of lighter grey-brown on the anterior head and posterior dorsum, flanks and limbs. The whole dorsal surface is covered with numerous poorly defined lighter spots. Dark crossbands on limbs. On the flanks, several more clearly defined light spots are present, and small white spots also form on the upper jaw a posteroventrally directed row running along the border of the tympanum, and an anteroventrally directed row underneath the eye. Venter light beige, throat and chest brown with light markings and a discontinuous central white line. Colour in life was similar to colour in preservative, with overall more vivid and contrasted pattern. Ventral skin was somewhat translucent, spots on throat and chest silvery white.

Variation.—Variation in measurements is given in Table 10. See Fig. 72 for colouration in life and its variation. There may be pronounced sexual size dimorphism, but our sample size is small (confirmed male SVL 21.6–22.6 mm [n = 2] vs confirmed female SVL 31.1 mm [n = 1]). Male and female relative tympanum sizes do not seem to differ (HTD/ED ratio is 74% in the female, 67–74% in the males). Femoral glands of males in life relatively distinct, with a yellowish tone, and mostly consisting of a distinct distal ulcerous macrogland, with only small remnants of a proximal granular gland field.

Natural history.—Poorly known. Specimens were collected from near a stream in a remnant of primary rainforest. At Ranomafana National Park specimens were found during day and night at two streams in primary forest (elevational range between 777–835 m a.s.l.) sitting in shallow parts of the streams. Two females with visible eggs were detected at Sahalavakely on 22 February 2011, another female with visible eggs was found at Sahalavabe on 23 March 2011.

Calls.—The call of this species has not been recorded.

Tadpoles.—The tadpole of this species has not been described.

Distribution.—Endemic to the Southern Central East (Fig. 7). This species is known from Ambohitsara and Ranomafana National Park (Sahalavabe and Sahalavakely near Beremby). Elevation range: 294–860 m a.s.l.

Etymology.—The Latin adjective in the masculine nominative singular stelliger, meaning ‘starry’, in reference to the white spots that are often present on the flanks of this species.

Mantidactylus inaudax clade

A clade with several lineages of rather small size (21.7–37.5 mm adult SVL) bearing morphological similarities to species in the *M. biporus* clade, but phylogenetically sister to the *M. curtus* clade. Unlike most species in the *M. biporus* clade, many individuals in the *M. inaudax* clade have dorsolateral folds (which can be weakly expressed). The clade contains one widespread and genetically variable species for which we here revalidate the historical name *M. inaudax*. The clade further contains one new species for which we name, in addition, two deep lineages as subspecies (see justification in the respective accounts), based on holotypes depicted in Fig. 73.

Mantidactylus inaudax (Peracca, 1893) **bona species**

Type material.—The nomen is based on a series of three syntypes, originally under the single number MZUT An727, but now divided into An727.1–An727.3, from ‘dintorni di Andrangoloaka e dalla vicina valle dell’Umbi’ (Gavetti & Andreone 1993; Peracca 1893). Andrangoloaka is at ca 19.00°S, ca 047.95°E. These specimens were thought lost by Guibé (1978) and Blommers-Schlösser and Blanc (1991) but were rediscovered by Gavetti and

FIGURE 74. *Mantidactylus inaudax* in life, in dorsolateral and ventral view. (a,b) Adult male from a forest fragment west of Lake Alaotra, photographed in 2008. (c,d,e) Adult female from a forest fragment west of Lake Alaotra, photographed in 2008, and femoral gland closeup (e). (f,g) Adult male from a forest fragment west of Lake Alaotra, photographed in 2008. (h,i) Adult male from a forest fragment west of Lake Alaotra, photographed in 2008. (j,k,l) Adult female from Fierenana, photographed in 2003, and femoral gland closeup (l). (m,n,o) Adult male from Fierenana, photographed in 2003, and femoral gland closeup (o). All of these specimens correspond to collected voucher specimens but cannot be reliably assigned to specific voucher numbers.

Andreone (1993). We here designate as lectotype MZUT An727.1, an adult female individual of 32.1 mm SVL (Fig. 73). Lectotype designation is justified by the need to stabilize this and other nomina in *Brygoomantis*, given the uncertain identity and morphological similarity of many taxa in the subgenus.

Identity.—The name *Rana inaudax* Peracca, 1893 was placed in the synonymy of *M. curtus* by Blommers-Schlösser and Blanc (1991) although this synonymy was doubted by Gavetti and Andreone (1993) because it was not based on specimen examination (see also Frost 2021). We here provide a 16S sequence of the lectotype that clusters with a lineage from various localities not far from the type locality of Andrangoloaka (e.g. Fierenana and the road between Moramanga and Anosibe An'Ala). We thereby provide genetic evidence of the assignment of the nomen *inaudax* to this lineage, which was previously considered as the true *M. biporus* (Vieites *et al.* 2009), and we therefore revalidate the name *M. inaudax* for this lineage. The lineage to which the lectotype belongs is closely related to another from Ambohitantely and other nearby sites that has been assigned to candidate species *M.* sp. 17 by Vieites *et al.* (2009), and *M.* sp. Ca17 by Perl *et al.* (2014). It was depicted as '*M.* sp. aff. *biporus* "Ambohitantely"' by Glaw and Vences (2007). In the course of this study, we discovered several other deep lineages from the western slope of the Makira reserve, from Ampotsidy, and from Fierenana and the road Moramanga to Anosibe An'Ala (previously considered as the true *M. biporus*) that all form a mitochondrial clade with Ca17 and partly share Rag-1 haplotypes with it. Our phylogenomic analysis of this clade recovers these different lineages as a monophyletic group, but with a different topology of relationships among them than recovered in our mitochondrial tree. We conservatively treat all of these deep lineages as conspecific.

Additional material.—The following specimens are all tentatively assigned to *M. inaudax*, despite substantial genetic variation among several populations (visualized in Fig. 2): ZSM 180/2005 (FGZC 2146), adult male, and ZSM 181/2005 (FGZC 2147), adult female, collected by M. Vences, L. du Preez, P. Bora, L. Raharivololoniaina, R.D. Randrianiaina, T. Razafindraibe, and E. Randriamitso on 18 January 2005 at Ambohitantely Jardin Botanique (ca 18.17°S, ca 047.27°E, ca 1580 m a.s.l.); ZFMK 60141–60142, adult male and female, collected by F. Glaw and D. Vallan on 6 April 1995 at Ambohitantely (ca 18.17°S, ca 047.27°E, ca 1580 m a.s.l.); ZMA 19310 (FGMV 2002.2435), ZMA 19311 (FGMV 2002.2439), ZMA 19314 (FGMV 2002.2429), ZMA 19331 (FGMV 2002.2441), four adult females, ZMA 19341 (FGMV 2002.2252), putative female, and ZMA 19343 (FGMV 2002.2423) and ZMA 19345 (FGMV 2002.2251), two adult males, collected by M. Vences, D.R. Vieites, and collaborators on 19 February 2003 in Fierenana (18.5299°S, 048.5901°E); ZSM 1768/2008 (ZCMV 8869), adult male, collected by D.R. Vieites, J. Patton, P. Bora, and M. Vences on 22 February 2008 in the Andranogorika forest fragment, near the road to Brieville (17.76781°S, 047.98415°E); ZSM 363/2010 (FGZC 4358), adult male, collected by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, K. Mebert, E. Rajeriarison, F. Randrianasolo, and S. Rasamison on 8 April 2010 in Fanamby forest (18.4214°S, 047.9383°E, 1315 m a.s.l.); ZSM 398/2006 (ZCMV 3259), adult male, collected by M. Vences, R.D. Randrianiaina, and E. Edwards on 25 March 2006 at the crossroad between Moramanga–Anosibe An'Ala and Besariaka (19.0959°S, 048.2402°E); ZSM 548/2009 (ZCMV 11213), adult male, collected by M. Vences, D.R. Vieites, F.M. Ratsoavina, R.D. Randrianiaina, E. Rajeriarison, T. Rajofiarison, and J. Patton on 23 June 2009 at Hevirina (pandanus swamp), Makira (15.4490°S, 049.1119°E, 1093 m a.s.l.); ZSM 85/2016 (MSZC 0161), adult male, collected by M.D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D.H. Nomenjanahary, and J. Rabearivony on 8 January 2016 beside a muddy spring in Ampotsidy, Bealanana District (14.4194°S, 048.7194°E, 1340 m a.s.l.); ZSM 88/2016 (MSZC 0178), adult male, collected by M.D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D.H. Nomenjanahary, and J. Rabearivony on 8 January 2016 in a pandanus swamp in Ampotsidy, Bealanana District (14.4169°S, 048.7144°E, 1371 m a.s.l.).

Diagnosis.—*Mantidactylus inaudax* belongs to the *M. inaudax* clade according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of small to moderate body size (male SVL 22–30 mm, female SVL 27–33 mm), rather smooth dorsal skin without dorsolateral ridges, large tympanum size in males (12–16% of SVL), presence of white spots on flanks in at least some individuals, and absence of a white marking on the snout tip, distinguishes *M. inaudax* from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *M. stelliger* (*M. stelliger* clade) differs by smaller body size and less developed foot webbing. Species of the *M. biporus* clade differ as follows: *M. biporus* by smaller tympanum in males, and a higher pulse repetition rate in advertisement calls; *M. augustini* by longer hindlimbs, fewer pulses per note, and lower pulse repetition rate in advertisement calls; *M. bletzae* by a somewhat smaller body size, presence of dorsolateral ridges, longer hindlimbs, and more developed foot webbing; *M. brevirostris* by less developed foot webbing, possibly smaller body size, and differences in colour pattern; *M. eulenbergeri* by smaller body size; *M. glosi* by smaller body size, more granular dorsal skin and shorter hindlimbs (Table 4). For a distinction from new species and subspecies in the *M. inaudax* clade, see the diagnoses in the respective taxa accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. inaudax* in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Translation of original description.—To facilitate a revised treatment of this nomen, we here provide a translation of Peracca's detailed description of *Rana inaudax* from the original Italian:

Vomerine teeth in two oblique groups behind the posterior margin of the choanae.
Cordiform tongue, rather small, bifurcated in two posteriorly short rounded appendages.

Moderate head, subacute snout protruding about 1 mm over the lower jaw; rounded canthus rostralis; slightly concave loreal region; inter-orbital space equal in width to the upper eyelid, equaling the distance between the antero-internal eye and nostril. Tympanum clearly visible, about ¾ of the eye diameter, equal in diameter to the distance between the antero-internal corner of the eye and the nostril, surmounted by a small skin fold starting from the posterior-external corner of the eye and disappearing at the origin of the arm.

Digits of the feet terminated by discs almost twice as large as those of the hands. Internal metatarsal tubercle oval, protruding, very large. A small external metatarsal tubercle, conical. Almost entirely webbed toes. By pulling the posterior extremities forward along the body, the tibio-tarsal joint barely reaches the posterior corner of the eye.

The skin of the head, the back, the hips, the upper surface of the posterior extremities, and the posterior surface of the thighs is finely granular; in other regions it is smooth. On the lower surface of the thighs a small circular glandular relief can be observed on each side, presenting a median depression in which 5 or 6 point-like pores (femoral pores) are visible.

Colouration—Basic colour of the upper parts grey-brown or slate grey, more or less light. A black spot connects the eyes, preceded by a lighter band. On the back there is an irregular dark spot, sometimes shaped like a V. The posterior extremities have narrow black bands. The lips and cheeks are dotted with white. Lower face of a dirty yellowish white, turning to flesh-grey on the throat, irregularly speckled with white.

Dimensions:

			♀	♀	♂
Length	*from snout to vent*	*mm*	*33*	*29.5*	*22*
	of the arm		*18.5*	*15.5*	*13.5*
	of the leg		*47.5*	*38*	*32*
	of the shank		*14.5*	*12*	*10*
	of the foot		*15*	*13*	*10.5*
Head width			*13*	*11*	*9*
Inner metatarsal tubercle			*2*	*2*	*1.5*

Three specimens.

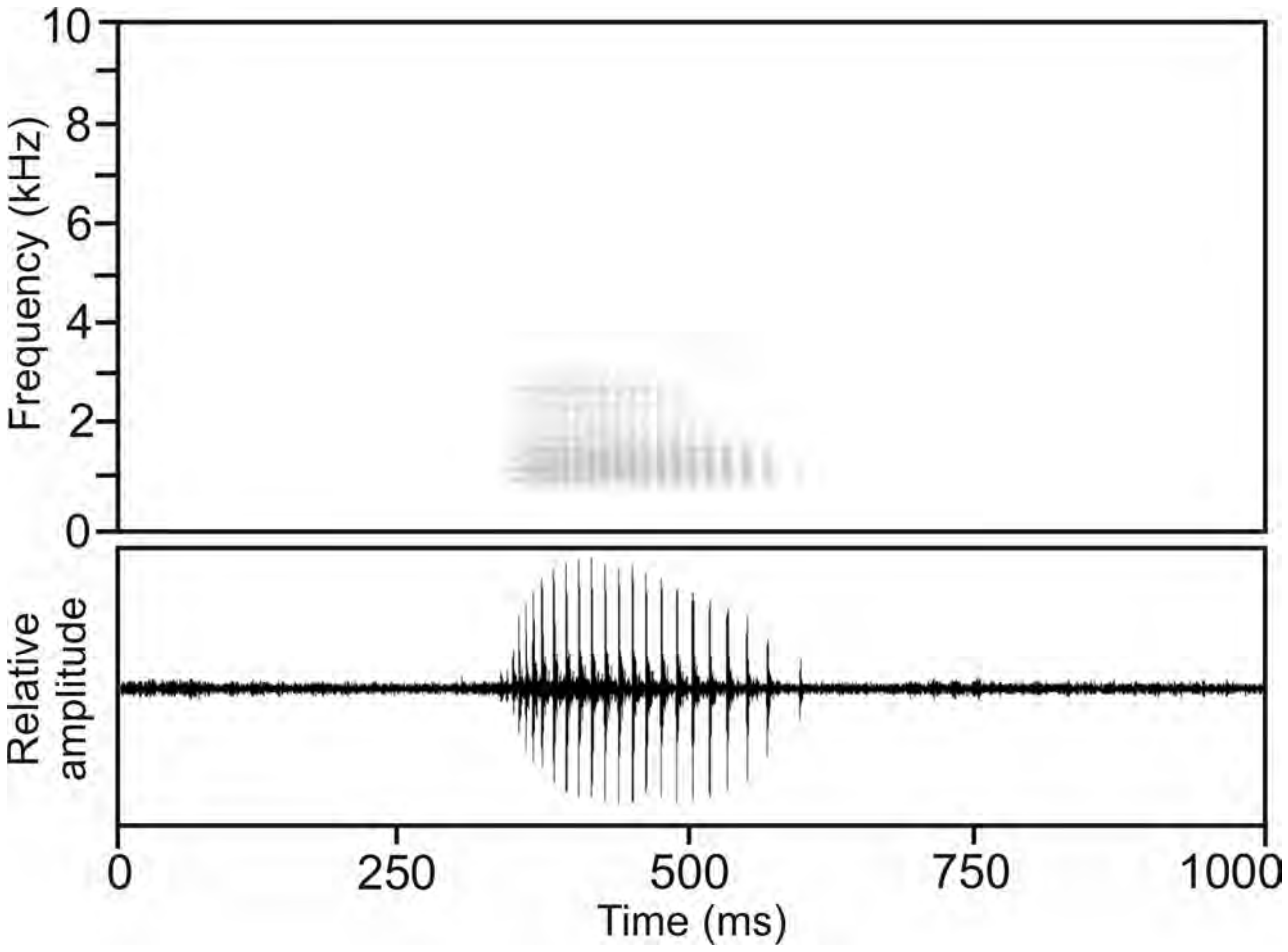

FIGURE 75. Audiospectrogram and corresponding oscillogram of one advertisement call of *Mantidactylus inaudax*, recorded on 23 June 2009 at Makira West (air temperature estimated at 20–25°C). Recording bandpass-filtered at 640–6500 Hz.

Description of referred specimen ZSM 180/2005 (FGZC 2146).—Adult male in good state of preservation. Tissue removed from right thigh; femoral glands partly detached for examination in internal view. Body rather stout. Head as wide as body. Snout rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant. Nostrils nearer to tip of the snout than to eye. Canthus rostralis weak, slightly concave. Loreal region weakly concave. Tympanum distinct, large, elliptical, diameter 78% of eye diameter. Supratympanic fold distinct, beginning straight, with a rather distinct bend midway towards insertion of forelimb, following the outer edge of the tympanum. Tongue ovoid, distinctly posteriorly bifid. Maxillary teeth present. Vomerine teeth present in two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Outer and inner metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (113%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle not clearly recognisable. Webbing formula: 1(1), 2i(1), 2e(0.5), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth. Ventral side smooth. Femoral glands present, in external view consisting of a well-recognisable distal ulcerous macrogland and a distinct proximal granular gland field.

Colour in preservative: dorsum brown, with indistinct irregular darker markings. Dark brown band between eyes present. Forelimbs brown with poorly defined darker markings. Hindlimbs light brown with indistinct darker crossbands. Inguinal region with few scattered whitish dots. Snout tip with an indistinct light dot. Venter beige, throat darker than belly. Lower lip with indistinct alternating light and brown spots. Toe discs dark. Fourth toe quite short in relation to third and fifth toe.

Variation.—Variation in measurements is given in Table 11. See Fig. 74 for colouration in life and its variation. There is pronounced sexual size dimorphism (confirmed male SVL 21.7–25.1 mm [n = 10] vs confirmed female SVL 26.9–32.1 mm [n = 7]). Males have larger tympanum sizes than females (HTD/ED ratio is 63–82% in females, 84–111% in males). Skin on the back is smooth (ZSM 180/2005) or granular (ZFMK 60141, ZFMK 60142). Colour on the back is light brown with few indistinct markings in ZFMK 60141 and ZFMK 60142, darker brown with few indistinct markings in ZSM 180/2005. A dark brown more or less triangular band between eyes is always present. Two dark spots on the back at the level of the forelimb insertion are always present (not visible for ZFMK 60141 and ZFMK 60142 because their skin is in pieces). A light vertebral line or a light vertebral band are never present. A small but distinct light dot on the snout tip is present in the two males. Lower lip with more (e.g. ZFMK 60141) or less (e.g. ZFMK 60142) distinct alternating light and brown spots. Venter and throat from uniformly beige in ZFMK 60141 and ZFMK 60142 or brown with distinct mottling in ZSM 180/2005. A longitudinal white median line on abdomen and throat is never present. Hindlimbs more or less distinctly striped. Forelimbs brown with irregular darker markings and stripes. Femoral glands of adult males are consistently large and prominent. The femoral glands of ZSM 180/2005 have an extensive proximal granular gland field, while such a structure is not recognisable in ZFMK 60141. In external view an external central depression in the distal ulcerous macrogland component of the femoral glands can be seen, and in life, the glands are of yellowish colour. In females femoral glands cannot be recognised in preservative, but in life, rudimentary glands consisting of two or three small structures of similar size are recognisable (Fig. 74e, l).

Natural history.—Regularly found in clean, running waters, often in areas of highly disturbed and degraded rainforest, but also in springs and swamps within undisturbed rainforest. Near Moramanga calling males were heard and collected during the day, from a slowly moving small stream near degraded rainforest and with just some remaining trees close to the water.

Calls.—The advertisement call of *M. inaudax*, recorded on 23 June 2009, at Makira West, at an estimated air temperature of 20–25°C, consisted of a pulsed note, emitted isolated or in short series containing 5–7 calls (Fig. 75). Notes exhibit amplitude modulation, with call energy rapidly increasing from the beginning of the note, reaching its maximum after approximately one third of the note's duration. Pulse repetition rate within notes was highest at the beginning and decreases towards the note's end. Numerical parameters of 14 analysed calls were as follows: call duration (= note duration) 196–367 ms (268.6 ± 66.4 ms); 19–28 pulses per note (22.6 ± 3.9); pulse duration 3–6 ms (4.3 ± 0.9 ms); pulse repetition rate within notes 55.6–130.4 pulses/s (85.8 ± 23.9); dominant frequency 1146–1276 Hz (1200 ± 41 Hz); prevalent bandwidth 800–3400 Hz; call repetition rate (= note repetition rate) within series ca 75 calls/min.

Calls recorded on 25 March 2006 at the crossing of the Moramanga-Anosibe An'Ala and Besariaka roads, at an estimated air temperature of 20–25°C, were emitted in regular series and agreed perfectly in character with the calls described from Makira West above and differd only slightly in numerical parameters (n = 9): call duration (= note duration) 199–312 ms (254.9 ± 35.9 ms); 17–23 pulses per note (20.3 ± 2.2); pulse duration 3–7 ms (4.7 ± 1.1 ms); pulse repetition rate within notes 61.2–142.9 pulses/s (87.1 ± 28.9); dominant frequency 738–961 Hz (814 ± 72 Hz); prevalent bandwidth 500–3500 Hz; call repetition rate (= note repetition rate) within series ca 60–90 calls/min. The most significant difference was the lower dominant frequency which was possibly due to a larger SVL of the calling male.

Tadpoles.—The tadpole of *M. inaudax* was described under the name '*M. biporus*' by Knoll *et al.* (2007).

Distribution.—Endemic to the highlands and rainforests of the Northern Central East and Central Madagascar, also occurring at sites in the North West and Ambirano Regions (Fig. 7). This species is known from Ambohitantely, Ampotsidy, Andrangoloaka, Anjozorobe, Fierenana, the vicinity of Lake Alaotra, the western

slope of Makira, and the Moramanga-Anosibe An'Ala/Besariaka crossroad. Elevation range: 948–1580 m a.s.l.

Etymology.—Latin adjective meaning 'shy' or 'hesitant'. It is a third-declension one-termination adjective, and thus is effectively invariable with respect to the gender of the genus.

Mantidactylus manerana **sp. nov.**

Identity and justification.—A lineage of the *M. inaudax* clade, differing from *M. inaudax* by ≥3.5% uncorrected distance in the 16S gene (Table 2), and here considered to represent a distinct species due to the deep divergence in the phylogenomic tree (Fig. 5), and bioacoustics differences (Table 4). *Mantidactylus manerana* **sp. nov.** is comprised of three deep mitochondrial lineages, one from Marojejy (Ca16), one from Sorata, and one from Befanjana. These three lineages differ by a strong mitochondrial divergence of 3.1–4.1% uncorrected distance in 16S, but exhibit haplotype sharing in Rag-1, and do not differ substantially morphologically. Bioacoustic data are not available from the Sorata and Befanjana populations to assess whether these lineages are different in call characters. The presence of mitochondrial divergence among these allopatric lineages without substantial differentiation in available phenotypic data and with haplotype sharing in a nuclear-encoded gene leads us to recognise them as subspecies, and we in the following assign them the subspecies names *M. manerana manerana* **ssp. nov.**, *M. manerana fotaka* **ssp. nov.**, and *M. manerana antsanga* **ssp. nov.**

Diagnosis.—*Mantidactylus manerana* **sp. nov.** belongs to the *M. inaudax* clade and, together with two related lineages here considered as subspecies (described below), forms the sister species of *M. inaudax,* according to our phylogenomic analysis. See Table 4 for a list of diagnostic morphological characters. The combination of small to moderate body size (male SVL 25–38 mm, female SVL 28–38 mm), slightly granular dorsal skin with weakly expressed but clearly recognisable dorsolateral ridges, presence of white spots on flanks, and absence of a white marking on the snout tip, distinguishes *M. manerana* from species of the *M. betsileanus, M. curtus, M. fergusoni, M. tricinctus,* and *M. ulcerosus* clades. *M. stelliger* (*M. stelliger* clade) differs by smaller body size and less developed foot webbing. Species of the *M. biporus* clade differ as follows: *M. biporus* by larger body size, absence of dorsolateral ridges, fewer pulses per note and and higher pulse repetition rate in advertisement calls; *M. augustini* by longer hindlimbs and fewer pulses per note in advertisement calls; *M. bletzae* by a somewhat smaller body size and more developed foot webbing; *M. brevirostris* by less developed foot webbing and absence of dorsolateral ridges, and possibly by smaller body size; *M. eulenbergeri* by slightly smaller body size and smoother dorsal skin; *M. glosi* by smaller body size and shorter hindlimbs in comparison with most individuals of *M. manerana* **sp. nov.**, as well as shorter duration of advertisement calls (Table 4). The species is very similar morphologically to its sister species *M. inaudax* which, however, has less distinct dorsolateral ridges and fewer pulses per note in advertisement calls. For a distinction of the nominal subspecies, *M. m. manerana* from the other two subspecies recognised, see the diagnoses in the respective subspecies accounts below. A full list of molecular diagnostic sites in the 16S gene of *M. manerana* **sp. nov.** in pairwise comparisons to all other *Brygoomantis* species is provided as Supplementary appendix.

Distribution.—Occurs on mountains of the North East and in forests in the Northern Central East. This species is known from Ambatobe, Befanjana, Marojejy (from camp 2 upwards, i.e. above 700 m a.s.l.), Sahavontsira, and Sorata (from 1279 m a.s.l. upwards). Elevation range: 14–1599 m a.s.l.

Etymology.—The species name is derived from the Malagasy adjective manerana, meaning 'observed everywhere' (in a specific place), and refers to the rather common occurrence of this species on the Marojejy Massif. The species name is used as a noun in apposition.

Mantidactylus manerana manerana **ssp. nov.**

Identity and justification.—The nominal subspecies was previously considered as unconfirmed candidate species *M*. sp. 16 by Vieites *et al.* (2009), and *M*. sp. Ca16 by Perl *et al.* (2014). It was depicted as '*Mantidactylus* sp. aff. *biporus* "Andranofotsy"' by Glaw and Vences (2007).

Holotype.—ZSM 500/2016 (field number ZCMV 15162), adult male, collected by M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences, and J. Razafindraibe on 17 November 2016 at Camp 3 'Simpona', Marojejy National Park (14.43661°S, 049.74335°E, 1325 m a.s.l.), Sava Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of 16 paratypes: ZSM 209/2005 (FGZC 2881), adult male, ZSM 206/2005 (FGZC 2837) and ZSM 5064/2005 (ZCMV 2019), two adult females, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 16–17 February 2005 at the type locality; ZSM 208/2005 (FGZC 2847) and ZSM 207/2005 (FGZC 2846), two adult males, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 16 February 2005 above Camp 3 'Simpona', Marojejy National Park; UADBA uncatalogued (ZCMV 2017–2018, FGZC 2854), three unsexed specimens, UADBA uncatalogued (FGZC 2835), subadult, and UADBA uncatalogued (FGZC 2836), female, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 16–17 February 2005 around the type locality; UADBA uncatalogued (ZCMV 2087), male, collected by F. Glaw, M. Vences, and R.D. Randrianiaina on 18 February 2005 on the trail between Camp 1 'Mantella' and Camp 2 'Marojejia', Marojejy National Park (precise coordinates unavailable); UADBA uncatalogued (ZCMV 15190, ZCMV 15301, ZCMV 15302), three females, UADBA uncatalogued (ZCMV 15297), unsexed adult, UADBA uncatalogued (ZCMV 15303), subadult, with the same collection data as the holotype.

Diagnosis.—See diagnosis for the species, *M. manerana*, above; for distinction from the other two subspecies, see their diagnoses below.

TABLE 11. Morphometric measurements (all in mm) of voucher specimens of the *Mantidactylus inaudax* clade. Type status is given in square brackets after voucher number: HT, holotype; PT, paratype; LT, lectotype. An asterisk (*) marks lectotypes designated in the current paper. A hash (#) marks measurements taken by AH and thus not fully comparable with other measurements, all taken by MV. For abbreviations of measurements, see Materials and Methods. NM, not measured; NA, not applicable.

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
Mantidactylus inaudax **bona species** (Ca17)																			
MZUT An727.1 [LT*]	NA	F		32.1	12.7	12.4	4.9	3.5	2.2	2.0	3.3	17.7	8.5	47.9	21.8	15.4	13.5	NA	NA
ZSM 180/2005	FGZC 2146	M	Ambohitantely	26.2	10.2	10.5	3.7	4.1	1.9	1.8	2.6	14.1	6.8	34.4	16.6	11.8	10.2	4.5	1.7
ZFMK 60142 #	NA	F	Ambohitantely	26.9	11.8	9.4	3.8	2.6	2.2	2.1	3.2	9.1	7.8	NM	NM	11.0	11.0	NA	NA
ZMA 19310 #	FGMV 2002.2435	F	Fierenana	33.1	13.3	12.7	5.2	3.3	2.7	2.1	4.1	11.3	9.1	NM	NM	14.6	14.6	1.6	1.3
ZMA 19311 #	FGMV 2002.2439	F	Fierenana (pitfall forest)	27.4	11.3	9.9	3.8	3.1	2.3	1.9	3.3	11.4	8.6	NM	NM	13.8	13.6	1.6	1.4
ZMA 19314 #	FGMV 2002.2429	F	Fierenana (Camp)	27.5	11.5	9.9	4.0	3.0	2.1	1.7	3.0	10.9	8.6	NM	NM	14.0	14.5	1.2	1.2
ZMA 19331 #	FGMV 2002.2441	F	Fierenana (pitfall forest)	27.0	11.1	9.6	3.8	3.0	2.1	1.9	3.2	11.4	8.8	NM	NM	13.6	13.7	1.5	1.2
ZSM 181/2005	FGZC 2147	F	Ambohitantely	29.4	11.0	11.2	4.0	3.1	2.3	1.8	2.8	15.5	7.5	40.2	19.3	13.1	11.6	NA	NA
ZMA 19341 #	FGMV 2002.2252	F?	Fierenana (Camp)	33.6	12.9	11.5	4.7	3.6	2.4	1.9	3.8	11.9	9.9	NM	NM	15.7	15.4	1.7	1.2
ZFMK 60141 #	NA	M	Ambohitantely	21.7	9.8	7.8	3.2	2.9	1.7	1.7	2.5	8.5	6.4	NM	NM	9.7	10.1	2.2	1.6
ZMA 19343 #	FGMV 2002.2423	M	Fierenana (Camp)	27.4	11.0	9.6	3.7	3.4	2.1	1.8	3.3	10.0	8.7	NM	NM	12.5	12.3	2.7	2.0
ZMA 19345 #	FGMV 2002.2251	M	Fierenana (Camp)	25.8	10.5	9.4	3.8	3.2	2.1	1.7	3.0	9.5	7.6	NM	NM	11.3	11.0	3.0	2.2
ZSM 1768/2008	ZCMV 8869	M	Forest fragment Brieville	25.7	10.6	10.5	4.0	3.6	2.3	1.8	3.2	15.0	6.7	38.2	17.6	12.1	10.4	2.7	1.9
ZSM 363/2010	FGZC 4358	M	Fanamby Forest, Anjozorobe	23.7	9.0	9.1	3.4	3.4	2.2	1.6	2.3	13.0	6.8	31.6	15.2	10.7	9.4	2.9	2.1
ZSM 398/2006	ZCMV 3259	M	Moramanga-Anosibeanala	30.0	10.7	11.9	4.3	3.6	2.3	2.1	3.3	15.8	8.3	42.2	20.7	14.5	11.5	2.8	2.2
ZSM 548/2009	ZCMV 11213	M	Makira West	22.7	8.7	9.5	3.8	3.3	2.2	1.5	2.4	13.5	7.0	33.9	16.5	11.7	9.8	4.4	2.0

...Continued on the next page

TABLE 11. (Continued)

Voucher	Field number	Sex	Locality	SVL	HW	HL	ED	HTD	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW
ZSM 85/2016	MSZC 0161	M	Ampotsidy	29.1	11.2	12.2	4.2	3.8	2.3	2.2	3.4	15.9	8.2	40.1	19.2	13.5	11.4	3.2	3.0
ZSM 88/2016	MSZC 0178	M	Ampotsidy	28.4	10.4	11.4	4.2	3.9	2.1	1.7	3.0	15.5	8.0	38.3	18.2	12.9	11.0	5.3	2.2
Mantidactylus manerana manerana **ssp. nov.** (Ca16)																			
ZSM 500/2016 [HT]	ZCMV 15162	M	Marojejy	27.5	10.2	11.0	3.9	3.3	2.8	1.8	3.0	16.0	8.5	40.7	18.6	12.9	12.0		
ZSM 206/2005 [PT]	FGZC 2837	F	Marojejy Camp Simpona	29.4	10.7	11.5	4.3	2.6	2.5	1.9	2.8	17.4	7.7	44.0	19.3	13.8	12.9	NA	NA
ZSM 5084/2005 [PT]	ZCMV 2019	F	Marojejy Camp Simpona	28.0	11.2	11.0	3.6	2.8	2.7	1.8	2.8	17.6	8.1	45.2	20.3	14.8	13.4	1.2	1.2
ZSM 207/2005 [PT]	FGZC 2846	M	Marojejy Camp Simpona	26.0	10.3	10.3	4.0	3.2	2.5	1.7	2.6	14.9	6.3	37.5	17.1	11.9	10.8	3.4	2.2
ZSM 208/2005 [PT]	FGZC 2847	M	Marojejy Camp Simpona	26.8	10.4	10.8	3.5	3.0	2.4	1.9	3.0	16.3	7.7	41.2	18.3	13.0	11.6	3.3	2.0
ZSM 209/2005 [PT]	FGZC 2881	M	Marojejy Camp Simpona	25.0	9.4	9.4	3.3	2.2	2.1	2.0	2.7	15.8	7.2	37.6	16.8	11.7	11.4	3.6	1.9
Mantidactylus manerana fotaka **ssp. nov.**																			
ZSM 1588/2012 [HT]	FGZC 3776	M	Sorata	26.2	10.2	10.3	3.8	3.5	2.5	1.8	2.8	13.7	6.9	36.8	17.5	12.1	10.5	4.6	2.3
ZSM 1587/2012 [PT]	FGZC 3770	F	Sorata	29.2	11.4	11.3	3.9	2.7	2.3	1.8	2.8	15.7	7.8	39.5	18.7	12.7	11.6	1.4	1.0
Mantidactylus manerana antsanga **ssp. nov.**																			
MRSN A5633 [HT]	FAZC 13371 (ACZC 10079)	F	Sahavontsira	37.5	13.0	14.1	5.2	3.6	2.7	2.6	3.7	21.3	9.6	53.0	25.1	17.3	15.8	NA	NA

FIGURE 76. *Mantidactylus manerana manerana* **sp. nov.** from Marojejy in life, in dorsolateral and ventral view. (a,b) Adult male (holotype ZSM 500/2016 = ZCMV 15162), photographed in 2016. (c,d). Adult male (ZSM 209/2005 = FGZC 2881), photographed in 2005. (e,f) Adult male (ZSM 207/2005 = FGZC 2846), photographed in 2005.

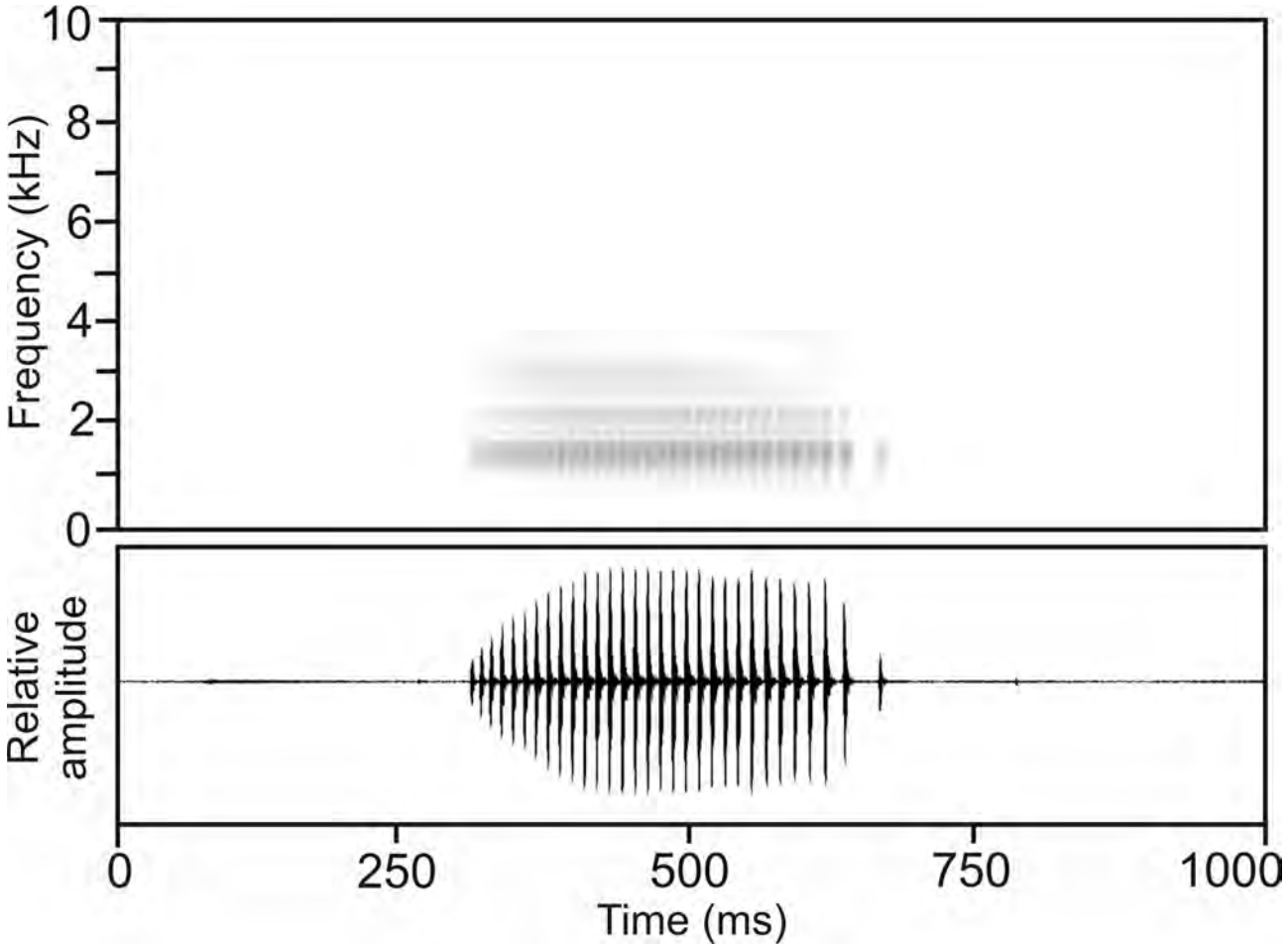

FIGURE 77. Audiospectrogram and corresponding oscillogram of one advertisement call of the holotype of *Mantidactylus manerana manerana,* recorded on 17 November 2016 at Camp Simpona, Marojejy National Park (ca 20°C air temperature). Recording bandpass-filtered at 350–6000 Hz.

Description of the holotype.—Adult male in excellent state of preservation (Fig. 73). Tissue from left thigh removed. Body rather stout. Head as wide as body. Snout rounded in dorsal view. Nostrils directed laterally, not protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, large, wider than high, horizontal diameter of tympanum 85% of horizontal eye diameter. Supratympanic fold distinct, beginning straight above, with gentle 45° bend midway towards insertion of forelimb. Tongue ovoid, distinctly bifid posteriorly. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot slightly longer than tibia (108%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle very small but recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4i(2.25), 4e(2.25), 5(0.75). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, slightly glandular dorsolaterally. Two weakly expressed, discontinuous dorsolateral ridges on anterior part of dorsum. Ventral side smooth. Femoral glands small but distinct in external view.

Colour in preservative: dorsally brown, with a dark patch posteriorly between eyes which anteriorly is bordered by a light band. Weakly defined light dorsolateral bands. Numerous distinct contrasted white spots on flanks and laterally on head. An anteroventrally directed white line on the upper lip starts mid-eye. A small white patch on the tip of the snout. Fingers and toes with alternating pattern of light and dark colour. Relatively distinct dark crossbands on limbs. Ventrally beige, with rather contrasted brown pigmentation on throat and chest with light spots and vermiculations, including a median light line on throat, and alternating light-dark pattern ventrally on lower lip. In life, colour was similar to the state in preservative but in general more vivid and contrasted. The white spots on flanks were very contrasted. The lighter parts on the dorsum were light brown. Ventrally silvery white except the darker areas on throat and chest. Femoral glands with a very slight yellow-orange shade.

Variation.—Variation in measurements is given in Table 11. See Fig. 76 for colouration in life and its variation. There is weak sexual size dimorphism

(confirmed male SVL 25.0–27.5 mm [n = 4] vs confirmed female SVL 28.0–29.4 mm [n = 2]). Males appear to have only slightly larger tympanum sizes than females (HTD/ED ratio is 60–78% in females, 67–86% in males). Femoral glands of males are relatively small but distinct in life, with a yellowish or orange shade, and with both a distal ulcerous macrogland and a proximal granular gland field recognizable.

Natural history.—Poorly known. Calling specimens were collected at dusk from a stream in primary rainforest.

Calls.—The advertisement call of *M. manerana manerana*, recorded from the holotype on 17 November 2016, 17:20 h, at Camp Simpona, Marojejy National Park, ca 20°C air temperature, consisted of a pulsed note, emitted isolated or in short series (Fig. 77). Notes exhibit amplitude modulation, with call energy constantly increasing from the beginning of the note, reaching its maximum after approximately one third of the note's duration. Pulse repetition rate within notes was highest at the beginning and decreased towards the note's end. Numerical parameters of eight analysed calls were as follows: call duration (= note duration) 260–363 ms (292.2 ± 37.4 ms); 26–31 pulses per note (27.9 ± 1.8); pulse duration 3–5 ms (4.5 ± 0.7 ms); pulse repetition rate within notes 62.5–115.9 pulses/s (93.9 ± 15.6); dominant frequency 1452–1539 Hz (1498 ± 30 Hz); prevalent bandwidth 720–5300 Hz; call repetition rate (= note repetition rate) within series ca 30 calls/min.

Tadpoles.—The tadpole of *M. manerana manerana* was described under the name '*M.* sp. aff. *biporus* "Marojejy"' by Schmidt *et al.* (2009).

Distribution.—Microendemic to the Marojejy massif (Fig. 7). This subspecies is known exclusively from high elevation in Marojejy National Park (from Camp 2 'Marojejia' to above Camp 3 'Simpona'). Elevation range: 615–1576 m a.s.l.

Mantidactylus manerana fotaka **ssp. nov.**

Identity and justification.—This lineage was newly identified in this study. It is characterized by a high divergence in 16S but haplotype sharing in Rag-1 with the nominal form, *M. manerana manerana*, which occurs allopatrically and lacks strong morphological differentiation, and is therefore described here as a new subspecies.

Holotype.—ZSM 1588/2012 (FGZC 3776), adult male, collected by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F. M. Ratsoavina, and A. Razafimanantsoa on 1 December 2012 at a campsite in the Sorata Massif (13.6851°S, 049.4417°E, 1279 m a.s.l.), Sava Region, Madagascar. A 16S barcode sequence of the holotype was obtained in this study and was included in the analysis.

Paratypes.—A total of four paratypes: ZSM 1587/2012 (FGZC 3770), adult female, and UADBA uncatalogued (FGZC 3777), unsexed, with same collection data as holotype; ZSM 1586/2012 (FGZC 3753), male, and UADBA uncatalogued (FGZC 3639), adult female, collected by the same collectors as the holotype on 28–30 November 2012 in bamboo forest above Sorata campsite (ca 13.6752°S, ca 49.4410°E, ca 1485 m a.s.l.).

Diagnosis.—*Mantidactylus manerana fotaka* **ssp. nov.** is a lineage here considered as subspecies of *M. manerana* due to its high morphological similarity. It is the direct sister group of *M. m. manerana* according to our phylogenomic analysis. See Table 4 and the diagnosis of *M. manerana* above for for a list of diagnostic morphological characters and of differences to other species of *Brygoomantis*. Morphologically, this poorly known taxon appears to differ from the nominal subspecies, *M. m. manerana*, by shorter hindlimbs (Table 4). A full list of molecular diagnostic sites in the 16S gene of *M. manerana fotaka* **ssp. nov.** in pairwise comparisons

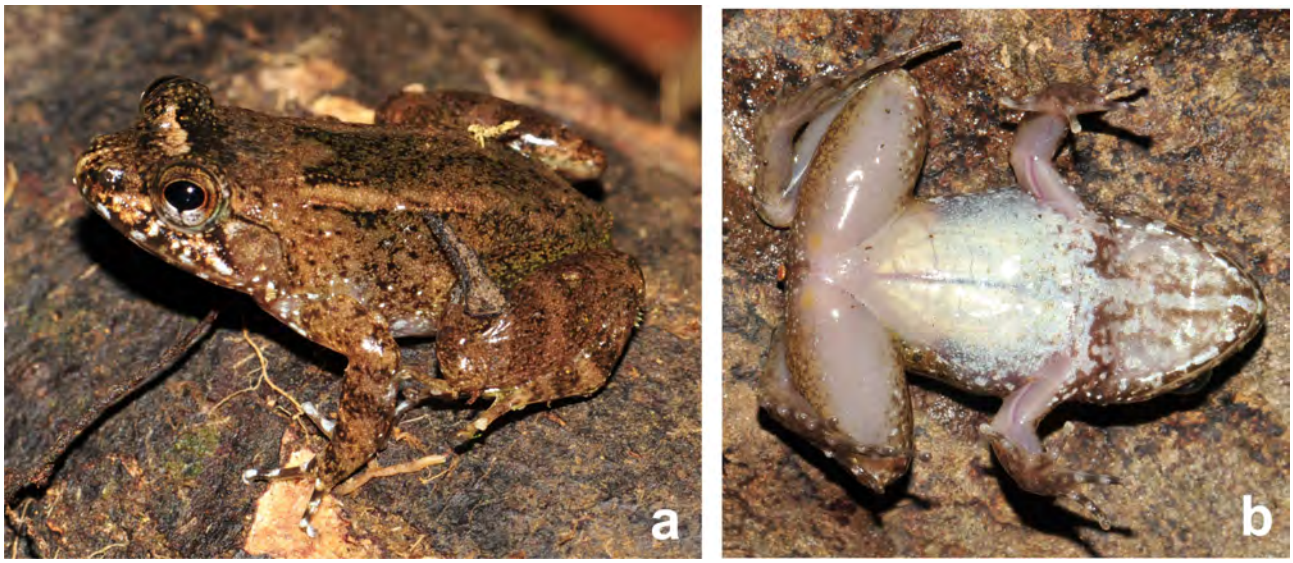

FIGURE 78. *Mantidactylus manerana fotaka* **ssp. nov.** in life. (a,b) Adult female from Sorata in dorsolateral and ventral view. Specimen probably corresponding to a voucher deposited in the UADBA collection.

to all other *Brygoomantis* species and subspecies is provided as Supplementary appendix.

Description of the holotype.—Adult male in excellent state of preservation (Fig. 73). Tongue removed as tissue sample. Body stout. Head as wide as body. Snout rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, large, wider than high, horizontal diameter of tympanum 92% of horizontal eye diameter. Supratympanic fold distinct, beginning straight above, with gentle ca 60° bend midway, following edge of tympanum. Tongue removed. Maxillary teeth present. Vomerine teeth form two rounded aggregations, positioned posterolateral to choanae. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II≤IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (115%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle small but recognisable. Webbing formula: 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.75), 4i(2.5), 4e(2.25), 5(0.75). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, slightly glandular dorsolaterally. Two weakly expressed, discontinuous dorsolateral ridges on anterior part of dorsum. Ventral side smooth. Femoral glands relatively small but distinct, with a distal ulcerous macrogland as well as a proximal granular gland field recognisable in external view.

Colour in preservative: dorsally almost uniformly brown. Only a few white spots along flanks and laterally on head. A small white patch on tip of snout. Reatively distinct dark crossbands on limbs. Fingers and toes with alternating pattern of light and dark colour. Ventrally light beige, with rather contrasted brown pigmentation on throat and chest with light spots and vermiculations, including a median light line on throat, and light-dark pattern ventrally on lower lip. Colour of holotype in life not documented.

Variation.—Variation in measurements is given in Table 11. See Fig. 78 for colouration in life. There may be some sexual size dimorphism, but our sample size is small (confirmed male SVL 26.2 mm [n = 1] vs confirmed female SVL 29.2 mm [n = 1]). In females, small, yellowish gland rudiments are visible.

Natural history.—Largely unknown. Specimens were collected from an area of disturbed rainforest.

Calls.—The call of this subspecies has not been recorded.

Tadpoles.—The tadpole of this subspecies has not been described.

Distribution.—Apparently microendemic to the Sorata massif (Fig. 7). Elevation range: 1398–1599 m a.s.l.

Etymology.—The subspecies name is derived from the Malagasy word fotaka, meaning 'mud', in reference to the microhabitat in which this and other *Brygoomantis* dwell. The name is used as a noun in apposition.

Mantidactylus manerana antsanga **ssp. nov.**

Identity and justification.—This lineage was previously considered as unconfirmed candidate species *M*. sp. 15 by Vieites *et al.* (2009), and *M*. sp. Ca15 by Perl *et al.* (2014). It is characterized by a high divergence in 16S but haplotype sharing in Rag-1 with the nominal form, *M. manerana manerana*, which occurs allopatrically. Little is known about this form, with limited data on morphology and no data on bioacoustics or colour in life. We therefore describe it here as subspecies.

Holotype.—MRSN A5633 (FAZC 13371, ACZC 10079), adult female, collected by F. Andreone, F. Mattioli, and J.E. Randrianirina on 24 January 2006 in Sahavontsira (ca 16.91°S, 049.22°E), Analanjirofo Region, Madagascar. A 16S barcode sequence of the holotype was included in the analysis

Diagnosis.—*Mantidactylus manerana antsanga* **ssp. nov.** is a lineage here considered as subspecies of *M. manerana* due to its high morphological similarity. It is the sister group of the clade comprising *M. m. manerana* and *M. m. fotaka* according to our phylogenomic analysis. See Table 4 and the diagnosis of *M. manerana* above for a list of diagnostic morphological characters and of differences to other species of *Brygoomantis*. Morphologically, this poorly known taxon may differ from the other two subspecies by larger body size (SVL of the only examined female 38 mm, vs 28–29 mm female SVL in the other two subspecies). It may also differ from the nominal subspecies by slightly shorter hindlimbs and more developed foot webbing (Table 4). A full list of molecular diagnostic sites in the 16S gene of *M. manerana antsanga* **ssp. nov.** in pairwise comparisons to all other *Brygoomantis* species and subspecies is provided as Supplementary appendix.

Description of the holotype.—Adult female in excellent state of preservation (Fig. 73). Fourth toe of right foot removed as tissue sample. Body stout. Head as wide as body. Snout rounded in dorsal and lateral views. Nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye. Canthus rostralis weakly recognisable, slightly concave; loreal region slightly concave. Tympanum distinct, moderately sized, as wide as high, horizontal diameter of tympanum 69% of horizontal eye diameter. Supratympanic fold recognisable above the tympanum, slightly curved, not recognisable posterior to tympanum. Tongue ovoid, distinctly bifid posteriorly. Maxillary teeth present. Vomerine teeth form two prominent rounded aggregations, positioned posterolateral to choanae and almost as large as these. Choanae rounded. Subarticular tubercles single. Inner and outer metacarpal tubercles present. Fingers without webbing. Relative length of fingers: I<II<IV<III. Finger discs slightly enlarged. Nuptial pads absent. Foot longer than tibia (110%). Lateral metatarsalia separated. Inner metatarsal tubercle present. Outer metatarsal tubercle indistinct but recognisable. Webbing formula: 1(0.5), 2i(1), 2e(0.5), 3i(1.75), 3e(1), 4i(2.25), 4e(2), 5(0.25). Relative length of toes: I<II<V<III<IV. Skin on the upper surface smooth, with two weakly expressed dorsolateral ridges. Two equally sized femoral gland rudiments recognisable ventrally on each thigh.

TABLE 12. Current and proposed new IUCN Red List conservation status assessment of all *Mantidactylus* subgenus *Brygoomantis* species. DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, NA = not assessed, EOO = Extent of Occurrence. NA = not applicable, while B1ab(iii) and B2ab(iii) are Red List criteria (IUCN 2012).

Species	Former EOO (km^2)	Current Status (2022)	New Approx. EOO (km^2)	# Threat-defined locations	Extent and quality of habitat declining	Proposed Status	Applied IUCN Criteria
M. curtus	NA	LC	3720	8	yes	VU	B1ab(iii)
M. alutus	NA	LC	23880	9	yes	LC	NA
M. ambohimitombi	260	DD	22910	8	yes	LC	NA
M. bourgati	1313	EN	200	1 (Andringitra)	yes	EN	B1ab(iii)
M. madecassus	1290	EN	40	1 (Andringitra)	yes	CR	B1ab(iii)
M. pauliani	12	CR	12	1 (Ankaratra)	yes	CR	B1ab(iii)+2ab(iii)
M. mahery	NA	NA	2191870	>10	yes	LC	NA
M. ulcerosus	NA	LC	41950	>10	yes	LC	NA
M. bellyi	NA	LC	12850	>10	yes	LC	NA
M. schulzi	NA	NA	200	2	yes	EN	B1ab(iii)
M. steinfartzi	NA	NA	1010	3	yes	EN	B1ab(iii)
M. betsileanus	NA	LC	96130	>10	yes	LC	NA
M. noralottae	992	DD	60	1 (Isalo)	yes	CR	B1ab(iii)
M. tripunctatus	NA	NA	800	7	yes	VU	B1ab(iii)
M. incognitus	NA	NA	3360	6	yes	VU	B1ab(iii)
M. jonasi	NA	NA	31260	>10	yes	LC	NA
M. katae	NA	NA	39050	>10	yes	LC	NA
M. kortei	NA	NA	90	2	yes	EN	B1ab(iii)
M. riparius	NA	NA	220	1 (Isalo)	yes	EN	B1ab(iii)
M. fergusoni	NA	NA	22475	>10	yes	LC	NA
M. georgei	NA	NA	7540	9	yes	VU	B1ab(iii)
M. jahnarum	NA	NA	222	1 (Nosy Boraha)	yes	EN	B1ab(iii)
M. marintsoai	NA	NA	420	3	yes	EN	B1ab(iii)
M. tricintus	7838	VU	2920	4	yes	EN	B1ab(iii)
M. grubenmanni	NA	NA	21660	6	yes	NT	NA
M. gudrunae	NA	NA	890	5	yes	EN	B1ab(iii)
M. biporus	NA	LC	720	2	yes	EN	B1ab(iii)
M. augustini	NA	NA	2600	3	yes	EN	B1ab(iii)
M. bletzae	NA	NA	700	2	yes	EN	B1ab(iii)
M. brevirostris	NA	NA	565	2	yes	EN	B1ab(iii)
M. eulenbergeri	NA	NA	1060	5	yes	EN	B1ab(iii)
M. glosi	NA	NA	30	2	yes	EN	B1ab(iii)
M. stelliger	NA	NA	180	2	yes	EN	B1ab(iii)
M. inaudax	NA	NA	49920	8	yes	LC	NA
M. manerana	NA	NA	13700	4	yes	VU	B1ab(iii)

Colour in preservative: dorsally brown with some indistinct darker markings, and triangular more distinct dark marking between eyes. More irregularly dark-light marbled on flanks, and some lighter spots on upper lip and underneath the eye. Weakly defined dark crossbands on limbs. Fingers and, less expressed, toes with alternating pattern of light and dark colour. Ventrally beige, without any dark pigmentation except for a light-dark pattern ventrally on lower lip. Colour in life not documented.

Natural history.—Largely unknown. Specimens were collected from rainforest.

Calls.—The call of this subspecies has not been recorded.

Tadpoles.—The tadpole of this subspecies has not been described.

Distribution.—Widespread in the Northern Central East (Fig. 7). Currently known from Sahavontsira, Babitanety and Antsahataloka in the Befanjana forest, and Ambatobe. Elevation range: 14–466 m a.s.l.

Etymology.—The subspecies name is derived from the Malagasy word antsanga, meaning 'trash and mud deposited by flood water', in reference to the riparian habits of this species (and other *Brygoomantis* species). The name is used as a noun in apposition.

Conservation status

Of the previously described species of *Mantidactylus* subgenus *Brygoomantis*, six were hitherto assessed as Least Concern, one was Vulnerable, two were Endangered, one

was Critically Endangered, and two were Data Deficient (Table 12). One species (*M. schulzi*) was scientifically named after the latest update to the amphibian Red List and was consequently not yet assessed. However, the definition of most of these species has been adjusted here, and a thorough reassessment of all members of the subgenus is therefore needed.

We provide new proposed IUCN Red List statuses in Table 12, based on the other data presented therein, including approximate Extent of Occurrence (EOO), number of threat-defined locations, declining habitat, and other threats. This resulted in 10 species listed as Least Concern, one as Near Threatened, five as Vulnerable, 16 as Endangered, and three as Critically Endangered. All species are currently affected by on-going decline in extent and quality of habitat. No species of *Brygoomantis* is frequently marketed in the pet trade, and none are consumed by people, as far as we know. They are susceptible to and threatened by the pathogenic fungus *Batrachochytrium dendrobatidis* (*Bd*) (Bletz *et al.* 2015), but no mass-mortality event of any amphibian that could be connected with *Bd* has yet been recorded in Madagascar. All threatened species are assessed following IUCN criterion B1ab(iii); *M. pauliani* is also assessed under B2ab(iii) in accordance with its current assessment (IUCN SSC Amphibian Specialist Group 2016).

Discussion

Doubling the documented diversity of *Brygoomantis*

With this revision of the *Mantidactylus* subgenus *Brygoomantis* we have more than doubled the known diversity of this clade, raising it from 14 to 35 described species (plus six subspecies, including nominate subspecies). Our integrative approach, based on data from morphology, bioacoustics, and mitochondrial and nuclear genetics and genomics—including sequences from the name-bearing type specimens of 16 of the existing 20 scientific names—has yielded two revalidated species, three redefined species, one modified junior synonymy, and 20 species new to science. In other words, we have completely refurbished the taxonomy of *Brygoomantis*. This brings new light to numerous aspects of their evolution, biogeography, and conservation, which we elaborate on below.

Defining species in *Brygoomantis* was a challenge in several respects. The phylogenetic signal from the 16S rRNA mitochondrial marker typically used for putative species identification of frogs (Vieites *et al.* 2009) was often poor, and the signal from the Rag-1 nuclear marker frequently used to assess concordance between nuclear and mitochondrial signature revealed extensive inter-species allele sharing and patterns clearly different from those of the mitochondria. Compared to a similar-scale revision of the microhylid frog genus *Stumpffia* (Rakotoarison *et al.* 2017), these single-locus datasets were much more difficult to interpret. The reasons for different allele sharing patterns in nuclear-encoded genes may be multifaceted and are unknown in Malagasy amphibians; they may be related to factors as disparate as effective population sizes (large sizes favoring incomplete lineage sorting) and strength of premating barriers (weak barriers, e.g. similar advertisement calls, favouring hybridisation and cross-species gene flow). In our study, the addition of genomic sequence capture data made the phylogenetic and thereby taxonomic resolution of *Brygoomantis* much more straightforward. In fact the phylogenomic tree largely confirmed assignment of specimens to lineages suggested by the mitochondrial analysis, but as expected had much stronger support for deeper nodes. The phylogenomic analysis also highlighted one instance where we suspect there could be interspecific gene flow or mitochondrial capture (e.g. between *M. katae* and *M. tripunctatus*), and the Phylonetwork analyses supported two cases of reticulated evolution in the *M. curtus* clade. More such cases may exist (especially in the *M. curtus* clade—see species accounts of *M. ambohimitombi* and *M. curtus*) but at this time cannot be ascertained due to the lack of FrogCap data for several crucial specimens, such as for instance the type series of *M. ambohimitombi.*

It was necessary to slightly adjust our taxonomic approach from the genus *Stumpffia* in *Brygoomantis* in order to accommodate these complications. One of the key differences in our approach here to that taken in the *Stumpffia* revision was to incorporate subspecies, a taxonomic category that has been deprecated by many herpetologists in the past two decades due to its poor conceptual definition, despite its obvious advantages to flexibly categorize and provide formal names to genetically or morphologically differentiated geographic units within species (Hawlitschek *et al.* 2012; Hillis 2020). Our decision to apply the subspecies category was informed by the recent discussion of the role of subspecies in the new understanding of the process of speciation by de Queiroz (2020). De Queiroz argued that subspecies and species are differences in degree and not in kind, and that subspecies may still be at an early stage in the process of speciating, so that their evolutionary independence is not yet fully established.

To put this into practice, we adopted a strategy wherein allopatric lineages with strong mitochondrial but not nuclear differentiation and without obvious differentiation in phenotype (either calls or morphology) were named as subspecies. In most cases, the taxa we recognised as subspecies show considerably less genetic differentiation than the vast majority of species-level units we recognize in *Brygoomantis.* However, there is no strict 'cut-off threshold' of genetic differentiation that would separate species from subspecies-level units. Rather, an integrative approach with the inclusion and evaluation of additional lines of evidence is needed to make this judgement. See also Köhler (2021) and Hillis (2022) for additional comments on this matter. Therefore, the documentation of several *Brygoomantis* species pairs that are separated by relatively low genetic distances in the 16S rRNA mitochondrial marker but differ strikingly by male advertisement calls is not surprising. For instance, *Brygoomantis* contains at least two species

pairs with 16S distances at or below the threshold of 3% used by Vieites *et al.* (2009) to delimit candidate species of Malagasy frogs: *M. schulzi* and *M. steinfartzi* (16S p-distance = 2.6–3.1%) and *M. fergusoni* and *M. jahnarum* (2.0–3.1%).

Our work resulted in a total of six subspecies (including the nominal lineages). This approach allowed us to put names on lineages of particular evolutionary interest, which can be investigated and tested as taxonomic hypotheses in the future. Not naming these evolutionary lineages would result in an underestimation of diversity, whereas the recognition of them as full species would be premature.

Despite our effort to recognise lineages as subspecies when evidence was insufficient for convincingly delimiting them as species, in some cases the available data was insufficient even for this option—for instance, when the evidence is limited to single sequences without associated voucher specimens available for examination, or when the provenance of samples requires confirmation. Among the species containing substantial mitochondrial variation (>3% 16S distance) and thus needing further taxonomic study are *M. bletzae, M. georgei, M. grubenmanni, M. gudrunae, M. inaudax, M. jonasi, M. jahnarum*, and *M. tricinctus*.

We hope that this significant stride forward in the taxonomy of these small-bodied brown frogs showcases the power of modern taxonomic methods and recent conceptual advances, and may also serve as a case study for similar monographic compilations by other organismic groups in the future.

Definitive assignment of old names

Hillis (2019) predicted the future would 'bring a synthesis of many older practices (careful sampling, with attention to reproductive isolation, contact zone analysis, and geographic variation) with the new powerful analysis of genomic data sets, leading to a re-evaluation and reversal of much of the recent overly enthusiastic splitting of geographically variable species.' (p. 3). In this work on the *Mantidactylus* subgenus *Brygoomantis*, we have striven towards realisation of that future.

Our taxonomic revision of *Brygoomantis* was founded first and foremost on careful examination of the assignment of the existing 20 available names for members of this subgenus to genetic lineages of the clade. This resulted in the definitive assignment of 16 of these names to genetic lineages, with revisions or confirmation of several cases of synonymy. Because this was done based on genetic sequences from the name-bearing types, the assignments can be considered definitive. The only exceptions would be (i) in cases where there is substantial intraspecific genetic variation and the names could in future be revalidated for one of those lineages if they are elevated to the species level; (ii) if they are cases of mitochondrial introgression; or (iii) if the sequences were erroneous. While these are difficult to rule out (especially contamination and assembly errors, see Scherz *et al.* 2020), they are nevertheless unlikely.

Although there were 20 names available for *Brygoomantis*, the existing names covered only a fraction of the species diversity of the subgenus, and several were confirmed to be synonyms. Consequently, even though we were able to reverse some of the 'overly enthusiastic splitting', as Hillis (2019) put it, of Ahl (1929 '1928') and Angel (1930) (placing three of their names into synonymy), we wound up having to produce 24 new names for the hidden diversity of this clade. This was inescapable in such a diverse clade, but we do not think that discovery of such large amounts of undescribed diversity will be the general rule in all other groups of animals or plants. In many cases the same approach that we have taken here is likely to substantially reduce the number of valid taxa; for instance, in plants, where oversplitting has been notoriously pervasive, and already only ca 33% of all available species-level names are considered accepted (in zoological nomenclature 'valid') names (worldfloraonline.org, accessed 22 December 2021). Indeed, we advocate for conservative approaches that make as much use of existing names as possible (Scherz *et al.* 2021), and employ a parsimony of taxonomic changes (Scherz *et al.* 2017b), to avoid overloading the entire community of biological scientists with new, unnecessary nomenclatural changes (which also discredit taxonomy and taxonomists).

It may appear paradoxical that we argue against oversplitting while our work more than doubles the species number in *Brygoomantis* and names multiple species based on an initial genetic species delimitation derived from genetic distances. In this context, it is important to reiterate that in many cases, the species considered herein also differ in the male advertisement call, and that the phylogenomic data robustly placed several morphologically similar lineages into different major subclades within the genus, thereby providing conclusive evidence that they represent distinct species. In addition, it is important to highlight that genetic distances, if correctly interpreted, are more than just a subjective, phenetic yardstick that can be deliberately used to define any differentiated unit as distinct species. The essential point is that genetic distances are roughly proportional to evolutionary time, as was recognised early on by Zuckerkandl and Pauling (1965), and more importantly, to the degree of reproductive incompatibility and thus reduction and eventual cessation of gene flow (Dufresnes *et al.* 2021; Malone & Fontenot 2008). This allows for the interpretation of genetic distances in a probabilistic framework (Kollár *et al.* 2022): the higher the genetic distance, the more genomic incompatibilities across a mass of genes two lineages will have accumulated (Dufresnes *et al.* 2021), which translates into a higher probability that these incompatibilities will have led to a disruption of gene flow and hence, to completion of speciation. Interestingly, for neobatrachian frogs, various studies applying radically different approaches have independently identified a threshold of about 3% distance in the mitochondrial 12S and 16S markers as indicative of some degree of reduction of gene flow (Dufresnes *et al.* 2021; Fouquet *et al.* 2007; Malone & Fontenot 2008; Vacher *et al.* 2020); it can therefore be concluded that

lineages with distances distinctly greater than 3% have a high probability of having completed speciation, as in the case of most *Brygoomantis*. In turn, lineages with <3% 16S distance have a lower probability of being distinct species, and thus require additional scrutiny, such as in our case *M. jahnarum* and *M. fergusoni* (2.0–3.1% pairwise 16S distance), which we considered as species due to the drastic differences in their advertisement calls.

The use of a single marker for species delimitation involves the risk of wrongly assigning individuals to species in cases of introgressive hybridization with mitochondrial capture. Recent studies have demonstrated how gene flow in tropical frogs can lead to the illusion of numerous cryptic species, and thereby to severe overestimations of species numbers using only mitochondrial distances (Chan *et al.* 2020, 2022). In *Brygoomantis*, we could have expected a high prevalence of this phenomenon due to the extensive allele sharing in Rag-1. However, surprisingly, the phylogenomic analysis overall suggested very similar relationships as the mitochondrial tree, thus validating the assignment of individuals to lineages based on 16S. Nevertheless, a few intriguing cases require further study, including *M. katae* and *M. tripunctatus*, two species with strongly divergent calls that appear to be closely related in the molecular analyses (Figs 2 and 5). We suspect that the apparent paraphyly of *M. katae* in the phylogenomic tree might be caused by introgressive hybridization with mitochondrial capture, i.e. the southernmost records of *M. katae* would possibly refer to *M. tripunctatus* with a mitochondrial genome captured from *M. katae*. Furthermore, we also suspect hybridization may have affected the lineages of the *M. curtus* clade, especially *M. curtus* and *M. ambohimitombi* where the morphological differentiation does not appear to match the genetic relationships. For instance, our taxon jacknifing results suggests possible gene flow between *M. curtus* and *M. ambohimitombi marefo* at Itremo, a hypothesis that requires additional scrutiny from more extensive data sets with inclusion of more individuals. Lastly, the deviant call of a *M. betsileanus* individual from Betampona may indicate hybridization phenomena in this region where a large number of *Brygoomantis* co-occur. Here, we did not perform dedicated introgression tests and hybrid zone analyses given that our phylogenomic sampling is too small for meaningful hypothesis testing. However, our study has served to point to the above cases as being of high interest for such studies in the future, thereby informing the sampling design for future phylogenomics.

Morphological variation and diagnosis

For most frogs, only adult (reproductive, calling) males and females (ovigerous in amplexus) are collected because the species are rare and/or secretive (e.g. treefrogs in canopy), and other life stages rarely encountered. *Brygoomantis* are ubiquitous and are commonly encountered jumping next to streams and swamps during day and night. Therefore, large collections of these species have been made in the past, consisting of specimens whose reproductive maturity is unknown. As a result, in many cases it has been uncertain whether morphological comparisons, especially concerning females without obvious externally visible secondary sexual characters, are being based on subadults or adults; whether sexual dimorphism can be properly assessed; and whether putative differences between species (e.g. body size or sexually dimorphic characters such as femoral glands or horizontal tympanum diameter) can be meaningfully compared.

Adding to this uncertainty, we encountered substantial intraspecific variation in numerous *Brygoomantis* species. For example, in some species of the *M. curtus*, *M. biporus* and *M. inaudax* clades, individuals of several species are characterized by conspicuously short and rounded snouts, but our measurements did not result in clear-cut, non-overlapping differences between species although these were quite obvious when examining large series of individuals in the field. This remarkable variability may be caused by numerous factors, including (i) an ontogenetic change undergone by all individuals, so that the perceived variability could be an artefact of missing information on the age of each individual (at least one species of *Brygoomantis* [*Mantidactylus fergusoni*] is known to reach three to five years of age, and species of other subgenera of *Mantidactylus* live up to eight years; Tessa *et al.* 2017); (ii) intraspecific genetic variation; or (iii) a plastic ontogenetic response to individual environmental conditions during development. Testing such hypotheses would help to disentangle the relative role of genetics and environment in generating the variability we observe. This, in turn, may be key to understanding the surprising diversity of *Brygoomantis* and their evolutionary radiation across Madagascar.

Phenotypic plasticity is known to be an important substrate for some adaptive radiations (Härer *et al.* 2017; Muschick *et al.* 2011; Schneider & Meyer 2017), and environment likely plays at least a partial role in generating morphological variation in *Brygoomantis*. It is well known that conditions experienced by tadpoles can strongly affect their ontogenetic trajectory (McCollum & Van Buskirk 1996; Pfennig 1990). Larval conditions also affect, and may canalise, adult developmental trajectories (Ficetola & de Bernardi 2006; Relyea 2001; Stamper *et al.* 2008), but current evidence pertains mostly to adult body size and limb length, and to colour pattern at least in salamanders (Sanchez *et al.* 2019); snout length, which is obviously quite highly variable within some *Mantidactylus* species, has not been noted to vary in these cases. As far as we know, the impact of environmental conditions on developmental trajectory in frogs has not been investigated for other points in ontogeny (e.g. as post-metamorphosed juveniles), but we hypothesise that the potential for trajectory change diminishes as full maturity is approached. However, the possibility for post-maturity changes remains unknown. In addition to plasticity, phenotypic flexibility, i.e. reversible intra-individual changes (Forsman 2015; Piersma & Drent 2003), has been suggested for some frogs that undergo strong transitions between aquatic and terrestrial forms (Martinazzo *et al.* 2011). No such plasticity or flexibility studies have been carried out in *Mantidactylus*, but we

expect that they, too, exhibit at least some degree of plasticity. Currently we have no evidence that phenotypic flexibility might play a role in *Mantidactylus*.

Whatever the cause, the result of the elevated phenotypic variability that we observe in *Brygoomantis* is a challenge for field diagnosis and taxonomic identification, especially of existing museum material without genetic or bioacoustics data. It also hinders the drafting of clear morphological diagnoses in those frogs that would allow identifying all individuals of a species. How to deal with overlapping metric characters in species delimitation and diagnosis is an unsolved question. It is clear that sample sizes are highly relevant, and truly 'diagnostic' characters in morphometrics between closely related species might be exceedingly rare; if large numbers of specimens are examined, it is likely that exceptional individuals will be found whose morphometry will match that of other species. The same might also apply to many qualitative (categorical) characters. A purely statistical comparison of individual traits (i.e. statistically significant differences in a morphometric ratio) can be useful for species delimitation, but will not always be useful for diagnosis as, for example, even exceedingly small, almost unnoticeable morphometric differences can be statistically different among two samples with large sample sizes of hundreds or thousands of individuals. On the other hand, a non-overlapping diagnostic difference can be meaningless if only two or three individuals are compared, because it will remain uncertain if the difference indeed serves to reliably distinguish individuals of the two lineages once sample size is increased. One solution could be a kind of 'diagnostic power analysis' of a data set, analogous to a Power analysis in statistics, but extended to quantify not only the sample sizes needed to statistically detect an effect, but also to quantify the probability and extent of overlap between values; such a statistical approach could serve as an indicator of the value of a character to really distinguish a pair of lineages. However, for most tropical species, including Malagasy frogs, we know few specimens, very often just one or two, precluding any such statistical approaches in the near future. Moreover, current policies limit the collection of specimens to just two per species per locality in Madagascar, hampering morphological analyses of variation.

Employing multivariate statistics as part of a species delimitation pipeline may also be a useful way to overcome strong intraspecific morphological variability (Buitrago Aristizábal *et al.* 2020). However, these have substantial limitations for use on animals because the relevant data can be difficult to collect from living individuals, and even from museum specimens they are time-consuming to generate, require large sample sizes per species, and can suffer strongly from measurer-effect (or preservation liquids and techniques; see also Bernal & Clavijo 2009; Watters *et al.* 2016). Results may also still be unsatisfactory. Indeed, for this work we performed exploratory Principal Component Analyses based on our morphometric datasets, and found little signal for species, or even clade, differentiation (consequently those analyses are not shown). This may be because our sample sizes per species were relatively small, and/or the number of traits analysed was low, but it may also simply be impossible to distinguish these taxa morphometrically, precisely because intraspecific variability is so great. Inclusion of additional qualitative characters might help, but these too are often variable. Additionally, we have strong reservations about the use of these methods for formal diagnosis of species that are as conservative in external morphology as are most *Brygoomantis* species. However, as we start to unravel highly cryptic lineages where genetic data suggest there are numerous species that are practically indistinguishable morphologically, we may have to overcome these reservations.

Following our initial observation of morphological variation in many *Brygoomantis* species, we have decided to restrict our morphological comparisons to a limited number of characters. Several characters such as vomerine teeth, webbing, subarticular tubercles, lingual papillae, internal femoral gland structure, or shoulder girdle have in the past been used to characterize species of different subgroups of *Mantidactylus*, and may show diagnostic differences among *Brygoomantis* species. However, scoring these characters often depends heavily on the state of fixation and preservation of vouchers (e.g. webbing or tubercles), requires semi-destructive sampling (e.g. internal femoral gland structure, or internal oral structures in strongly fixed specimens where widely opening the mouth is difficult), or time- and cost-intensive micro-CT scanning (to assess skeletal features such as shape of shoulder girdle elements). Obtaining reliable data for these characters for a representative number of individuals (i.e. to understand their intraspecific variation) is very time consuming and often not achievable as it would require destructive examination of valuable voucher specimens, and in many cases, simply too few reliably identified vouchers are available. We anticipate that future detailed morphological and osteological assessments in *Brygoomantis*, are likely to yield additional diagnostic characters, but we emphasize that examination of multiple specimens (with known ontogenetic stage, i.e. subadults vs adults, and sex), if possible from various populations, is necessary to reliably assess the diagnostic value of these characters.

Of course, diagnosis of species by means of unique DNA sequences (DNA barcoding) is an increasingly popular means to identify species. This is particularly useful in the face of extreme phenotypic variability, and can help to increase the pace of species discovery and naming especially in hyperdiverse and morphologically cryptic taxa (Cook *et al.* 2010; Renner 2016). This is currently an active area of development and debate in the taxonomic community, ranging in extent from supplements to morphological diagnoses (González Gutiérrez *et al.* 2013; Jörger & Schrödl 2013; Santiago *et al.* 2020) to the exclusive basis of species diagnosis (e.g. Meierotto *et al.* 2019). The latter form has received extensive criticism (Ahrens *et al.* 2021; Zamani *et al.* 2021). Recent turbo taxonomy approaches have used diagnoses consisting only of a consensus DNA sequence (Meierotto *et al.* 2019; Sharkey *et al.* 2021); in light of the requirement of Article

12.1 of the Code, according to which a valid name must be accompanied by 'a description or definition that states in words characters that are purported to differentiate the taxon', this practice rests on the assumption that a DNA sequence can be seen as a 'word'. The authors of the present study differ among each other in their view on this topic, but we agree on recommending, in case a molecular diagnosis is used, phrasing the differences in the form of clear character state differences, i.e. diagnostic nucleotide positions distinguishing a species from other species. After pioneering programs developed in a cladistic framework (Sarkar *et al.* 2008), software for this purpose is becoming increasingly available (Hütter *et al.* 2020; Merckelbach & Borges 2020), and some of the most recently published tools allows the user to define diagnostic combinations of various nucleotide positions (MolD; Fedosov *et al.* 2019), and the automated output of pairwise lists of diagnostic sites, relative to a reference sequence (DNAdiagnoser in iTaxoTools, the approach we have used herein; Vences *et al.* 2021).

We emphasize however that in the present study, we are using the list of molecular diagnostic sites merely to fulfil formal requirements (especially for those *Brygoomantis* species or subspecies where clear-cut morphological diagnostic features to other lineages could not be found), and therefore have relegated the extremely long list of pairwise diagnostic sites to an online supplementary table (by stating the presence of such sites, and referring to the online list, we fulfill the requirements of Article 12.1). Although it is clear that approaches to molecular diagnosis have the potential of yielding a large number of characters to formally distinguish species, it is still poorly explored how strongly this approach is influenced by intra-species variation, and certainly, many putatively diagnostic nucleotide positions identified for species with low sample sizes will later turn out to not be diagnostic, once that DNA sequences from more individuals and populations become available—especially in taxa with substantial intraspecific genetic variation, such as most amphibians. It also should be considered that, especially in taxa where the possibility of field diagnosis is desirable, a purely molecular diagnosis will exclude a substantial part of the interested community from the possibility of identifying species. For instance, there are currently strong limitations on the accessibility of sequencing facilities, especially in developing countries like Madagascar. Mobile sequencing technology is progressing rapidly, but remains extremely expensive—a single MinION flow cell costs $900, while, according to the World Bank (2022), the gross domestic product per capita in Madagascar is ~$500 USD per year! Until those prices drop precipitously, sequence-based species identification will remain inaccessible to the vast majority of the global population for the foreseeable future. Thus, while diagnoses based on DNA sequences have an enormous potential to make 'dark taxa' accessible to formal taxonomic revision, for taxonomic groups of more general interest, morphological, ecological, or other phenotypic traits should also be included in the diagnosis or description, wherever possible.

All of these considerations are key not only for our challenging frogs, but moreover for the future of taxonomy. Bioinformatic strides are being made that may take some pressure off of the taxonomist by helping to identify key traits to include in the diagnosis, or partly writing sections of the differential diagnosis itself (functions included in the iTaxoTools toolkit (Vences *et al.* 2021). It may be worthwhile to consider how approaches like taxonomic power analysis, multivariate statistics, and inclusion of DNA-based diagnoses can be integrated in a way that simplifies the workload of the taxonomist. A substantial part of the workload may be lifted by reducing the time needed for writing taxonomic treatments. However, it must be emphasised that taxonomic expertise—the experience and differentiating eye for what does and does not matter for species identification—is *indispensable* in this whole process, and we do not envisage a future where the taxonomist is supplanted by an automated process. Critical review of the outputs of software-based approaches will always be necessary in order to account for the strong variation that exists in species and the speciation process itself, as well as data limitations.

Surprising morphological convergence in *Brygoomantis*

Previous work on *Brygoomantis* named candidate species by their putatively closest relative (*M.* sp. aff. *betsileanus*, *M.* sp. aff. *biporus*; Glaw & Vences 2007) or informally referred to species complexes (e.g. *M. betsileanus* complex; Schmidt *et al.* 2009). Indeed, in the early stages of drafting this manuscript, we were still working with these species complexes identified primarily on the basis of morphology. But in the light of the phylogenomic analysis presented here (Fig. 5), it is clear that these species complexes do not reflect shared ancestry.

As is prevalent in anuran evolution as a whole (Moen *et al.* 2016), the mismatch between apparent morphological similarity and phylogeny implies extensive homoplasy in the evolution of overall morphology of *Brygoomantis*, as well as some cases of strong morphological divergence. For instance, it seems that *M. schulzi* and especially *M. steinfartzi* have converged on morphology more typical for the *biporus, inaudax* and *stelliger* clades, and do not closely resemble the larger *M. bellyi* and *M. ulcerosus* to which they are more closely related. All four members of the *M. ulcerosus* clade differ however from the members of the *M. betsileanus* and *M. fergusoni* clades among which they appear to be nested (Fig. 5), but it is important to note that the *M. betsileanus* clade moved to become sister of the *M. fergusoni* clade when *M. stelliger* is excluded from the analysis (see results of our taxon jacknifing analysis). This illustrates how even highly supported phylogenomic results may be influenced by certain 'rogue taxa', perhaps due to inter-clade gene flow.

The *M. curtus* clade is likewise rather derived in morphology compared to the rest of their closest relatives. *Mantidactylus mahery* within that clade also stands out, because it resembles *M. ulcerosus* and *M. bellyi* in many aspects of morphology, including the prominent orange-coloured femoral gland structures, but it is not at all closely related to those species.

Our new phylogenomic tree will enable future studies to look at morphological diversification and convergence of *Brygoomantis* species in an explicit phylogenetic framework. Of particular interest will be studies looking at the evolution of certain morphotypes, as well as those looking at skeletal elements of these frogs: it will be possible to assess whether the skeletons of the frogs show as much signal for convergence as we observe externally, or whether they reveal characters that show synapomorphies for the different clades (or at least a clearer phylogenetic signal) and thus conform better to the genomic phylogeny. Such studies coupled with more data on thermoregulation, microhabitat usage, morphological variation, and especially field trials regarding performance traits like leaping and swimming behaviour, will have major consequences for our understanding of the evolution of these frogs.

Larval morphology is also a major missing component of our knowledge of the diversification of *Brygoomantis*. Tadpoles reliably identified by DNA barcoding have been described for ten species (Knoll *et al.* 2007; Schmidt *et al.* 2009; Thomas *et al.* 2005), but they are still unknown for the remaining 25 species (71%). Wollenberg Valero *et al.* (2017) showed that the adult and larval morphology of mantellid frogs is genetically uncoupled. Thus, the tadpoles of *Brygoomantis* may yield different but complimentary patterns to adult morphological evolution, although we suspect that possible differences among related species will be subtle given the generalised and relatively uniform tadpole morphology apparent from the descriptions published so far.

A fresh look at *Brygoomantis* biogeography

This comprehensive revision of the diversity of *Brygoomantis* sheds new light on the diversification of one of Madagascar's most neglected frog groups. Although we have not endeavoured to undertake a formal analysis of the biogeography of these frogs, some emergent general patterns are already worth discussing and elaborating upon. Among these are (i) the spatial concentration of species richness, (ii) repeated geographic radiation, (iii) the geographical context of speciation in *Brygoomantis*, and (iv) the combination of microendemism vs widespread lineages.

(i) Species richness and distribution of main clades

The highest concentration of *Brygoomantis* species is in the highlands of the Northern Central East and Southern Central East of Madagascar, and in the lowlands of the Northern Central East Madagascar (Fig. 8). In the West and North West regions of Madagascar, only a few species have been found, and these all occur in relict areas of elevated humidity, namely the limestone karsts of the Tsingy de Bemaraha, the canyons of Isalo, and the dry deciduous forests of Ankarafantsika (Fig. 7, Table 3). Several of the species that do occur in the West are found in multiple locations across the area, most of which are not connected by either watershed or forest, implying historical corridors for dispersal that no longer exist today. In this regard, *Mantidactylus mahery* is particularly remarkable, as it has the largest biogeographic range of any *Brygoomantis* species, stretching from Isalo in the South to Makira in the North East. How a frog requiring at least somewhat running water, a habitat that is very patchily distributed in the arid West, can achieve a range of this size in this part of the island is not clear, but it makes this species particularly interesting for future study.

Considering the increase in species introduced with this revision, it is likely that previous models of species richness and endemism for *Mantidactylus* (Brown *et al.* 2016) are no longer fully accurate. It will be interesting to see how these maps change as taxonomic work continues, and especially after revisions of the other subgenera, particularly of *Ochthomantis*, *Hylobatrachus* and *Chonomantis*, have been undertaken; we predict that northern Madagascar will emerge as a more important centre of both richness and endemism for the genus, shifting the emphasis from the east of Madagascar as recovered by Brown *et al.* (2016).

(ii) Repeated geographic radiation

Ecologically, most groups of *Brygoomantis* seem rather similar to one another. This makes the patterns of their diversification across Madagascar more interesting, because colonisation of new areas does not seem to have been tied to substantial changes in ecology or morphology.

The current phylogenetic patterns would agree with an origin of *Brygoomantis* in the South East of Madagascar. For instance, the *M. tricinctus* clade, largely restricted to this region, is sister to all other *Brygoomantis*, and the species in this clade with the southernmost occurrence (*M. gudrunae*) is sister to the other two species. Only the *M. ulcerosus* clade has its centre of species richness in northern Madagascar; all others are concentrated in central or eastern Madagascar. Several clades, such as the *M. biporus* and *M. inaudax* clades, have achieved remarkably similar biogeographic distribution independently, suggesting that they may have spread in waves across suitable habitat. To understand this in greater detail, an extensive biogeographic analysis will be needed.

Certain biogeographic regions of Madagascar are known to have stark turnover of lineages (Brown *et al.* 2014; Vences *et al.* 2009). In *Brygoomantis*, there are two cases where such a turnover is strongly observable, in connection with the Sambirano region and the mountain chain running between Tsaratanàna and Makira. The first is the sister species pair *M. bellyi*+*M. ulcerosus*: *M. bellyi* is only found to the northeast of the mountain chain, and *M. ulcerosus* is only found to the south of it. The lineages are sister to one another, but we are not aware of any site where they occur even in close parapatry. They exhibit a distinct differentiation in 16S rRNA, and differ in advertisement calls. The second is among the deep genetic lineages of *M. jonasi*. This species has the greatest intraspecific variation in Rag-1 alleles of all species we analysed, exhibiting 18 different alleles, some as many as 16 mutational steps away from one another (Fig. 4). *Mantidactylus jonasi*, as currently defined, occurs across the entire northern region of Madagascar, spanning the north and south of the Sambirano region. However,

there are two distinct and early diverging mitochondrial lineages within this species, one restricted to sites northeast of the Tsaratanàna–Makira mountain chain (e.g. Marojejy, Montagne d'Ambre, and Sorata), and the other to sites to the southwest of it (e.g. Ampotsidy, Bemanevika, Makira, and Manongarivo). These patterns conform to those observed e.g. in several lineages of frogs in the genera *Gephyromantis* (Scherz *et al.* 2017a, 2018; Vences *et al.* 2017) and *Stumpffia* (Rakotoarison *et al.* 2017, 2019), *Calumma* chameleons (Prötzel *et al.* 2017, 2018, 2020), *Uroplatus* geckos (Ratsoavina *et al.* 2017, 2020), and some *Microgale* tenrecs (Everson *et al.* 2020), adding to the growing understanding of the importance of this mountain chain in shaping the diversity of biotic communities in northern Madagascar. Analyses of whole communities in this area will be of great interest, to better understand how the landscape has affected diversification across the board in this topographically complex region.

(iii) The geographical context of speciation in *Brygoomantis*

The geographical context of speciation (i.e. sympatry, allopatry, and parapatry) is an important consideration in the understanding of species radiations, as some of the processes involved in the divergence of lineages can differ according to the level of co-occurrence among the diverging lineages (Nosil 2012). This is especially true for diverging lineages that do not differ strongly in ecology, as we apparently frequently observe in *Brygoomantis*. In cases where selection to adjust to different environments is not obvious, alternative drivers, such as genetic drift, or sexual selection, may explain the observed divergence and speciation.

The vast majority of sister lineages of *Brygoomantis* are allopatrically distributed, and it is therefore likely that genetic drift has had an important role in establishment of genome-wide differentiation of these species over time. However, there is at least one notable case of closely related lineages that are still found in sympatry or close parapatry: *Mantidactylus steinfartzi* and *M. schulzi* occur in narrow parapatry at two sites (separated by elevation; 751–1000 vs 688–730 m a.s.l., respectively). These two species are differentiated by advertisement call, colouration, and skin texture, in addition to genetic differentiation. This multimodal differentiation leaves the question of the origin of the two species open to much speculation. The differences in advertisement call suggest at least some role for sexual selection in their differentiation, but these signals may have diverged in any geographic context (e.g., reinforcement after secondary contact, or different routes of sexual selection in allopatry). A further interesting example to understand speciation processes in *Brygoomantis* may be the case of *M. ambohimitombi marefo* with its very low mitochondrial distances but distinct morphological differences to *M. a. ambohimitombi*, suggesting the possibility of incipient speciation by ecological specialization to more aquatic habits in *M. a. marefo*.

(iv) Microendemic and widespread species in *Brygoomantis*

Similar to other groups of Malagasy frogs, *Brygoomantis* exhibits an interesting combination of apparently microendemic and widespread species. The *M. betsileanus* clade alone consists of four species that are rather widespread, and four that appear to be restricted to very small ranges. The widespread *M. katae* is sister to the regionally endemic *M. tripunctatus*, while the three local endemics *M. kortei*, *M. noralottae* and *M. riparius* are closely related to one another. It is thus not clear whether range size of such lineages is phylogenetically correlated, or whether it is strongly lineage-specific and dynamic. Based on the overall patterns we observe, we suspect the latter to be the case; this is also probable for mantellids overall based on distribution of range sizes along their phylogeny (Wollenberg *et al.* 2011). Examples like that of the sister species *M. katae* (widespread) and *M. tripunctatus* (range restricted) also call for tests of possible peripatric speciation in these frogs, i.e. isolation and subsequent speciation of small populations at the range periphery of a widespread species, for which however Wollenberg *et al.* (2011) found no evidence across mantellids. Formal statistical analysis of such hypotheses based on updated phylogenies and taxonomies of *Brygoomantis* and other mantellids will be worthwhile in future studies. Such work might yield support for interpreting range sizes as intrinsic and possible adaptive characteristics of species and lead to an improved understanding of speciation mechanisms in tropical amphibians.

Conservation of little brown frogs

The heterogeneity of range size among frogs of the *Mantidactylus* subgenus *Brygoomantis* means that the conservation status of species in this clade is likewise variable. In association with our overhaul of this subgenus, we now have 35 species in need of reassessment. Above, we have provided preliminary information to enable the assessment of these species according to the IUCN Red List criteria (IUCN 2012). In total, we recommend assessing three species as Critically Endangered, 16 species as Endangered, five species as Vulnerable, one species as Near Threatened, and 10 species as Least Concern. All of the threatened species are assessed under criterion B, which pertains to the range of the species together with the quality of the habitat. For no species is there sufficient data on the population size or trends to provide assessments under any other criterion.

Mantidactylus pauliani has been identified as a priority species for conservation in the Sahonagasy Action Plan for 2016–2020 (Andreone *et al.* 2016). There are active efforts underway to monitor it together with *Boophis williamsi*, another endemic of the Ankaratra Massif, as well as conservation efforts for habitat restoration, raising public awareness, and generating alternative livelihoods for the local people (Rabemananjara *et al.* 2012). However, it remains one of the island's most threatened species.

The conservation of uncharismatic species is a well-known challenge in conservation biology (Muñoz 2007). Madagascar has many charismatic 'flagship' species, including lemurs, chameleons, and poison frogs, but small brown frogs are unlikely to be seen as attractive by the broad public. However, except for the few Critically

Endangered species, where directed management can be useful for their protection, in most cases, their survivorship can be ensured effectively by protection of their habitats. We therefore advocate for landscape-level conservation action, through better protection of existing forests, reforestation, and education of local communities on sustainable forestry practices, as potentially the most effective way to protect these little frogs.

Author contributions

Conceptualization: MV, MDS, MH, FG; Investigation: MV, MDS, CRH, AH, AC, MP; Formal analysis: MDS, MV, CRH, LR, JK; Validation: FG, AC; Resources: AC, TRF, GK, SHN, AO, AR, APR, ACR, MOR, GMR, JWS, DRV, FG; Writing - Original Draft: MDS, MV, JK; Writing - Review & Editing: All authors.

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