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Two new Madagascan frog species of the *Gephyromantis* (*Duboimantis*) *tandroka* complex from northern Madagascar

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We describe two new frog species of the Madagascar-endemic genus *Gephyromantis*, belonging to the *G. tandroka* complex in the subgenus *Duboimantis*. *Gephyromantis (Duboimantis) saturnini* sp. nov. is known from specimens collected at Ampotsidy, in the District de Bealanana of the Région Sofia of northern Madagascar. It is a large and genetically distinct species with small interocular tubercles and indistinct femoral glands that emits calls in series composed of couplets and triplets. Morphologically and bioacoustically, it is most similar to *G. tandroka*, but genetically it was recovered as sister to *G. schilfi*, from which it is separated by an uncorrected p-distance of 5.1 % in the mitochondrial 16S rRNA gene. *Gephyromantis (Duboimantis) grosjeani* sp. nov. was collected on the Sorata massif, in the District de Vohemar of the Région Sava of northern Madagascar. It is a medium-sized species with large and distinct femoral glands, which are a distinctive characteristic from other members of this complex. Genetically, it is distinguished from all other *Gephyromantis* species by uncorrected p-distances of at least 5.1 % in the 16S rRNA gene.

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INTRODUCTION

The Madagascar-endemic mantellid frog genus *Gephyromantis* is currently divided into six subgenera: *Asperomantis* Vences, Köhler, Pabijan, Bletz, Gehring, Hawlitschek, Rakotoarison, Ratsoavina, Andreone, Crottini & Glaw, 2017, *Duboimantis* Glaw & Vences, 2006, *Gephyromantis* Methuen, 1920, *Laurentomantis* Dubois, 1980, *Phylacomantis* Glaw & Vences, 1994, and *Vatomantis* Glaw & Vences, 2006. The most diverse of these subgenera is *Duboimantis*, with 14 described species (Scherz *et al.* 2017*b*). *Duboimantis* has its centre of diversity in northeastern Madagascar (Kaffenberger *et al.* 2012), and in some areas, as many as seven species can occur in sympatry – and up to three species in close syntopy (e.g. Marojejy: Raselimanana *et al.* 2000; Glaw & Vences 2007; Scherz *et al.* 2017*a*). *Duboimantis* frogs typically inhabit primary rainforest, with only few representatives (e.g., *G. granulatus*) sometimes occurring in degraded areas and secondary forest. Adult males range in size from snout-vent lengths of 27 mm to 53 mm (Glaw & Vences 2007). They are scansorial, often found during the day in the leaf litter on the forest floor, and at night perching in the vegetation whence the males emit their advertisement calls (Glaw & Vences 2000, 2001, 2007; Vences & Glaw 2001). As far as known, these frogs have endotrophic (non-feeding) tadpoles that probably hatch in terrestrial nests and at least sometimes are washed into streams where they complete metamorphosis (Randrianiaina *et al.* 2011). Species of *Duboimantis* tend to be difficult to distinguish morphologically, and although they are rather vocal and their loud calls are easily heard, in some of the species groups even bioacoustic differences require specific experience to tell apart.

During fieldwork on the Sorata massif in the District de Vohemar of the Région Sava of northern Madagascar in 2012, we encountered numerous specimens of a large *Duboimantis* species, which resembles *G. (D.) tandroka* (Glaw & Vences 2001). Analysis of a fragment of the 16S rRNA mitochondrial barcode gene region showed that these specimens are genetically separated from that species, and the clade they formed was designated as a new candidate species, *G. (D.)* sp. Ca32 (Scherz *et al.* 2017*a*). On a separate expedition to Ampotsidy, an area of mountains north of Beandrarezona in the District de Bealanana of the Région Sofia of northern Madagascar in 2015–2016, we collected three specimens of another large *Duboimantis* species which represent another undescribed candidate species dubbed *G. (D.)* sp. Ca30, which also has affinities to *G. (D.) tandroka* (Scherz *et al.* 2017*b*). Herein, we address the taxonomy of these two candidate species.

METHODS

Specimens were located in the field by following their calls or opportunistically found on nocturnal transects. When possible, specimens were photographed in situ and recorded calling prior to capture. Specimens were anaesthetized with aqueous MS 222 solution and subsequently killed with an MS 222 overdose, fixed with 90 % ethanol, and then transferred to 70 % ethanol for long-term storage. Tissue samples taken prior to fixation were deposited in 99 % ethanol for molecular study. Field numbers MSZC, FGZC and ZCMV refer to the zoological collections of Mark D. Scherz, Frank Glaw and Miguel Vences, respectively. Specimens were deposited in the Zoologische

Staatssammlung München (ZSM) and the amphibian collections of the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale (UADBA-A). Additional institutional abbreviations used are MNHN (Muséum National d'Histoire Naturelle, Paris), MRSN (Museo Regionale di Scienze Naturali di Torino) and ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn).

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Measurements were taken by MV to the nearest 0.1 mm using the standard scheme employed in other recent *Gephyromantis* species descriptions (Scherz *et al.* 2017*a*, *b*; Vences *et al.* 2017), provided here again for better comparability: 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 (TD), 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), hindlimb length from cloaca to tip of longest toe (HIL), forelimb length from axilla to tip of longest finger (FORL), hand length from the base of the hand to the length of the longest finger (HAL) and femoral gland granule number (FGG). Webbing formulae follow Blommers-Schlösser (1979); femoral gland terminology follows Glaw *et al.* (2000); skin ridge and tubercle terminology follows Vences & Glaw (2001).

Previous analyses (Scherz *et al.* 2017*a*, *b*) had attributed the two target candidate species to the *G. salegy* subclade recovered in the multigene analysis of Kaffenberger *et al.* (2012). We therefore added sequences of the mitochondrial 16S rRNA gene (16S) from Scherz *et al.* (2017*b*) for *Gephyromantis* sp. Ca30 to the alignment of Scherz *et al.* (2017*a*) which included all described species of this subclade, and complemented this dataset with newly obtained sequences of a second 16S rRNA fragment, and of a fragment of the 12S rRNA gene (12S) for this candidate species. We extracted DNA using a standard salt extraction protocol from samples of muscle tissue preserved in 99 % ethanol in the field, used polymerase chain reaction to amplify and sequence the target fragments, and sequenced these directly on an automated capillary DNA sequencer. Primers and amplification protocols used were as follows (Vences *et al.* 2003): 12S, primer 12SAL (AAACTGGGATTAGATACCCCACTAT), and 12SBH (GAGGGTGACGGGCGGTGTGT), 35 cycles of 94°C (45 s), 50°C (60 s), 74°C (120 s). 16S, primer 16SL3 (AGCAAAGAHYWWACCTCGTACCTTTTGCAT and 16SAH (ATGTTTTTGATAAACAGGCG), 94°C (90 s) followed by 33 cycles of 94°C (45 s), 55°C (45 s), 72°C (90 s). All new DNA sequences were submitted to GenBank (accession numbers MH307657–MH307659 and MH307662–MH307664).

For phylogenetic analysis based on model selection under the Bayesian Information Criterion in jModeltest 2 (Darriba *et al.* 2012), we implemented a HKY+G substitution model in Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. ML was run in MEGA7 (Kumar *et al.* 2016) and node support assessed with 2000 non-parametric ML bootstraps. BI was run in MrBayes 3.2 (Ronquist *et al.* 2012), with two parallel runs for 50 million generations, sampling every 1000th tree, and discarding 25 % of the sampled trees as burn-in. Chain mixing and stationarity were assessed by examining the standard deviation of split frequencies and by plotting the -lnL per generation using Tracer 1.5 software (Rambaut & Drummond 2007). Genetic divergences are quantified as uncorrected pairwise distances (p-distances).

Call recordings from Ampotsidy (District de Bealanana, Région Sofia, Madagascar) and Marojejy (District d'Andapa, Région Sava, Madagascar) were made on a Marantz PMD661 MKII with a Sennheiser ME66/K6 supercardioid microphone, at 44.1 kHz. Recordings from Sorata (District de Vohemar, Région Sava, Madagascar) were made on an Edirol R-09 with its internal microphone. Bioacoustic analysis was performed in Cooledit Pro 2.0 (Syntrillium Corp.). Air temperatures were measured to the nearest 0.1°C after recording using an infrared thermometer pointed in the general direction of the calling specimen when possible. Terminology of call descriptions follows Köhler *et al.* (2017).

RESULTS

Phylogenetic analysis of three segments of the mitochondrial 16S and 12S genes (fig. 1) produced a tree with relatively high Bayesian posterior probability values (PP) at most nodes, but moderate to low Maximum Likelihood bootstrap support (BS). *Gephyromantis* sp. Ca30 was recovered as sister to *G. (D.) schilfi* (Glaw & Vences 2000) with fairly high support (PP 1.0, BS 84 %) from which it is separated by an uncorrected p-distance of 5.1 % in the region of the 16S gene fragment typically used for the molecular taxonomic identification (barcoding) of Madagascan frogs (e.g. Vieites *et al.* 2009). *Gephyromantis (Duboimantis)* sp. Ca32 was recovered as sister to *G. tandroka* with high support (PP 1.0, BS 92 %), from which it is also separated by an uncorrected p-distance of 5.1 %. The recently described *G. (D.) tohatra* Scherz, Razafindraibe, Rakotoarison, Dixit, Bletz, Glaw & Vences, 2017 was recovered without support as sister to the clade containing *G. (D.)* sp. Ca30 and *G. (D.) schilfi*. Two clades were formed within *G. (D.) schilfi* corresponding to the two localities (Marojejy and Sorata) whence this species is known, but the genetic differences between these two clades were much lower (0.6–0.8 %; see Scherz *et al.* 2017*a*).

We compared the morphology of *G. (D.)* sp. Ca30 and *G. (D.)* sp. Ca32 to other members of the subgenus *Duboimantis*, and to *G. (D.) tandroka* and *G. (D.) schilfi* in particular as these were found to be their respective sister species. We found *G. (D.)* sp. Ca30 (SVL 39–43 mm in adult males) to be larger than *G. (D.) tandroka* (36–40 mm in adult males). Otherwise these two species are highly similar—far more so than *G. (D.)* sp. Ca30 to its sister species (as suggested by mitochondrial DNA) *G. (D.) schilfi*, which is much smaller (27–30 mm in adult males). Males of *Gephyromantis (D.)* sp. Ca32 are morphologically quite distinctive as they are characterised by large, distinct femoral glands, which are indistinct in most other members of the *G. (D.) tandroka* complex. We investigated the bioacoustics of the two candidate species in comparison to other members of the *G. tandroka* complex in the subgenus *Duboimantis* (fig. 2–3). To facilitate this comparison, we provide a new description of calls of *G. (D.) tandroka* recorded in 2005 (Vences *et al.* 2006) and 2016 (deposited in the Tierstimmenarchiv, DOI: 10.7479/vd5c-3waj).

Calls of one male *G. (D.) tandroka* (ZSM 417/2016; fig. 2–3) were recorded on 17 November 2016 at 19 h 15 at an estimated air temperature of 17°C, at the type locality, Camp 3 in Marojejy, ca. 1300 m a.s.l. A call consists of a single pulsatile note, with a call (or note) duration of 77–94 ms (88 ± 5 ms; *N* = 10), repeated for long periods with regular inter-call intervals of 1542–2034 ms (1721 ± 128 ms; *N* = 10). Each call (or note) consists of approximately 21–24 indistinct pulses (22.5 ± 1.4; *N* = 10), without silent interval between them. Pulse intensity decreases towards the end of the call. The dominant frequency is between 2885–3100 Hz (3048 ± 81 Hz; *N* = 10). The approximate prevalent bandwidth is between 1100–5900 Hz, with relevant energy bands also between 6000–9000 Hz.

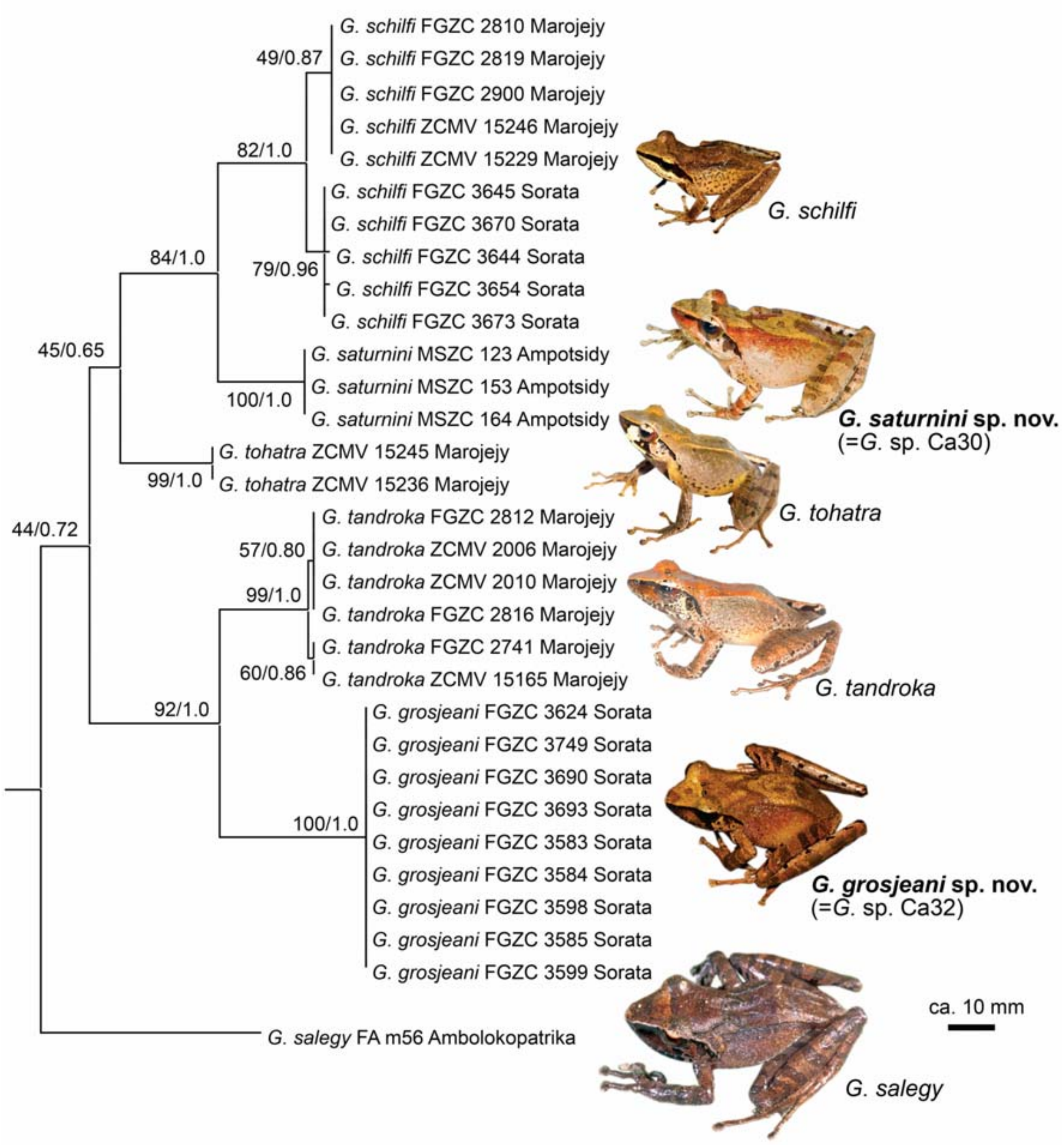

Figure 1. Maximum Likelihood tree based on 1106 bp of the mitochondrial 12S and 16S rRNA gene fragments, showing phylogenetic relationships of the two new species to their closest relatives among *Gephyromantis*. Support values at nodes are ML likelihood bootstrap values and BI posterior probabilities. *Gephyromantis granulatus* was used as outgroup (removed for better graphical representation). Inset photos show representative individuals of the target species, size of the pictures roughly to scale.

Additional calls were recorded on 16 February 2005 at the same site, at an air temperature of ca. 21°C (fig. 2–3). This recording, available in Vences *et al.* (2006), is of poorer quality and was done with a tape recorder. Calls are in general similar to those recorded in 2016, but the calls of various males in a chorus all have longer call durations, caused by a noisy ‘tail’ at the end which might be artefactual. The calls are pulsatile, but single pulses cannot be reliably recognized. Temporal and spectral measurements of one male (N = 10 calls) are as follows: call duration 113–152 ms (123 ± 14 ms), inter-call interval duration 1877–2447 ms (2226 ± 207 ms), dominant frequency 2842–3186 Hz (3082 ± 116 Hz), approximate prevalent bandwidth 1200–5500 Hz. In very large and persistent choruses, heard over numerous nights in 2005 and 2016, we do not recall hearing multi-note calls from *G. tandroka.*

Calls recorded from two individuals of *G. (D.)* sp. Ca30 (ZSM 61/2016 and 62/2016; fig. 2–3) were highly similar to one another, and, although similar note-for-note to the calls of *G. (D.) tandroka,* differ strongly in call structure, being typically composed of pairs or triplets of notes except the first few calls, compared to the single-note calls of that species. In this respect they resemble more closely the calls of *G. zavona* and *G. leucomaculatus* (Vences *et al.* 2006). They bear little similarity to the calls of *G. (D.) schilfi*, which are long, highly pulsed single-note calls (Glaw & Vences 2000; Vences *et al.* 2006). Calls from a single individual of *G. (D.)* sp. Ca32 were more similar to *G. (D.) tandroka* in call structure, being also composed of single calls (fig. 2–3), but differed in other call parameters, especially in call and inter-call interval duration; for details see below.

In light of their strong genetic differentiation together with morphological and bioacoustic differences from all described species of the *G. tandroka* complex in the subgenus *Duboimantis*, we describe *G. (D.)* sp. Ca30 and *G. (D.)* sp. Ca32 as new species:

Gephyromantis (Duboimantis) saturnini sp. nov.

(fig. 1–7, Table 1)

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Gephyromantis (Duboimantis) sp. Ca30 – (Scherz *et al.* 2017*a*, *b*)

Specimens allocated to new species

Holotype

ZSM 61/2016 (MSZC 0123), an adult male collected in the eastern parcel of the Ampotsidy mountains (14.4133°S, 48.7175°E, 1450 m a.s.l.), District de Bealanana, Région Sofia, northern Madagascar, at 18 h 30 on 31 December 2015 by M. D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D. H. Nomenjanahary and J. Rabearivony.

Paratypes

UADBA-A 61674 (ex-ZSM 66/2016, MSZC 0164), an adult male collected between 20 h 30 and 21 h 55 on 7 January 2016 in the western parcel of the Ampotsidy mountains (14.4123°S, 48.7118°E, 1481 m a.s.l.), and ZSM 62/2016 (MSZC 0153), an adult male collected at 23 h 50 on 6 January 2016 in the eastern parcel of the Ampotsidy mountains (14.4134°S, 48.7173°E, 1476 m a.s.l.), District de Bealanana, Région Sofia, northern Madagascar, by M. D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D. H. Nomenjanahary and J. Rabearivony.

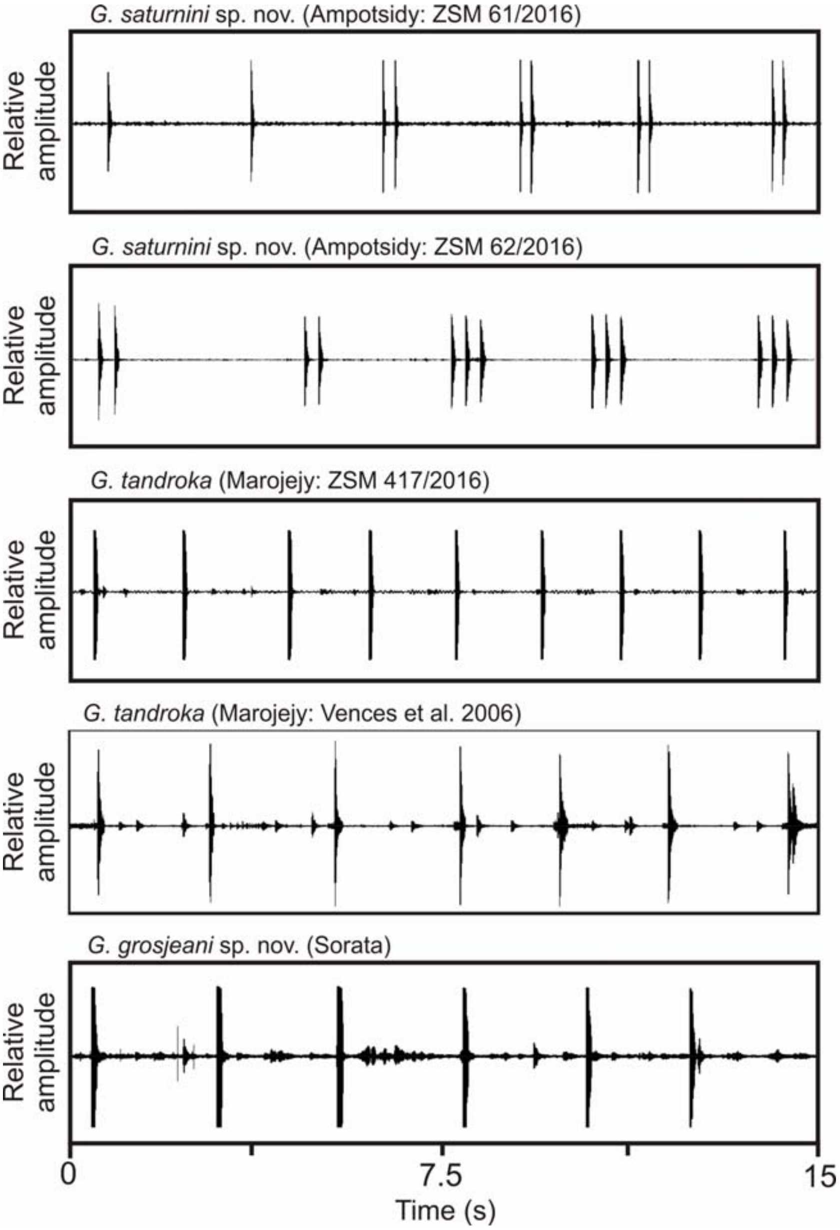

Figure 2. Comparative oscillograms of parts of call series of some representative of the *G. tandroka* complex in the subgenus *Duboimantis*. The figure shows the typical pattern of multi-note calls in *Gephyromantis (Duboimantis) saturnini* sp. nov. vs. *G. (D.) tandroka* and *G. (D.) grosjeani* sp. nov. The recording of *G. tandroka* from 2005 (taken from Vences *et al.* 2006) is of a chorus of multiple specimens; for visualization, the amplitude of calls of other specimens was strongly reduced to highlight the calls of the specimens closest to the microphone.

Diagnosis

A *Gephyromantis* species assigned to the subgenus *Duboimantis* on the basis of its fairly smooth skin, interocular tubercles, large body size and presence of inner and outer dorsolateral folds. *Gephyromantis saturnini* is characterised by the following unique suite of characters: (1) large body size (SVL 39.4–42.8 mm in adult males), (2) paired subgular vocal sacs, (3) HIL/SVL 1.79–1.87, (4) TD/ED 0.48–0.56, (5) presence of inner and outer dorsolateral folds, (6) reticulated low ridges on the dorsum, (7) distinct interocular tubercles, (8) indistinct femoral glands consisting of 9–16 faint granules. It is furthermore characterised by advertisement calls consisting of 1–3 pulsatile notes, emitted in series of 7–8 calls.

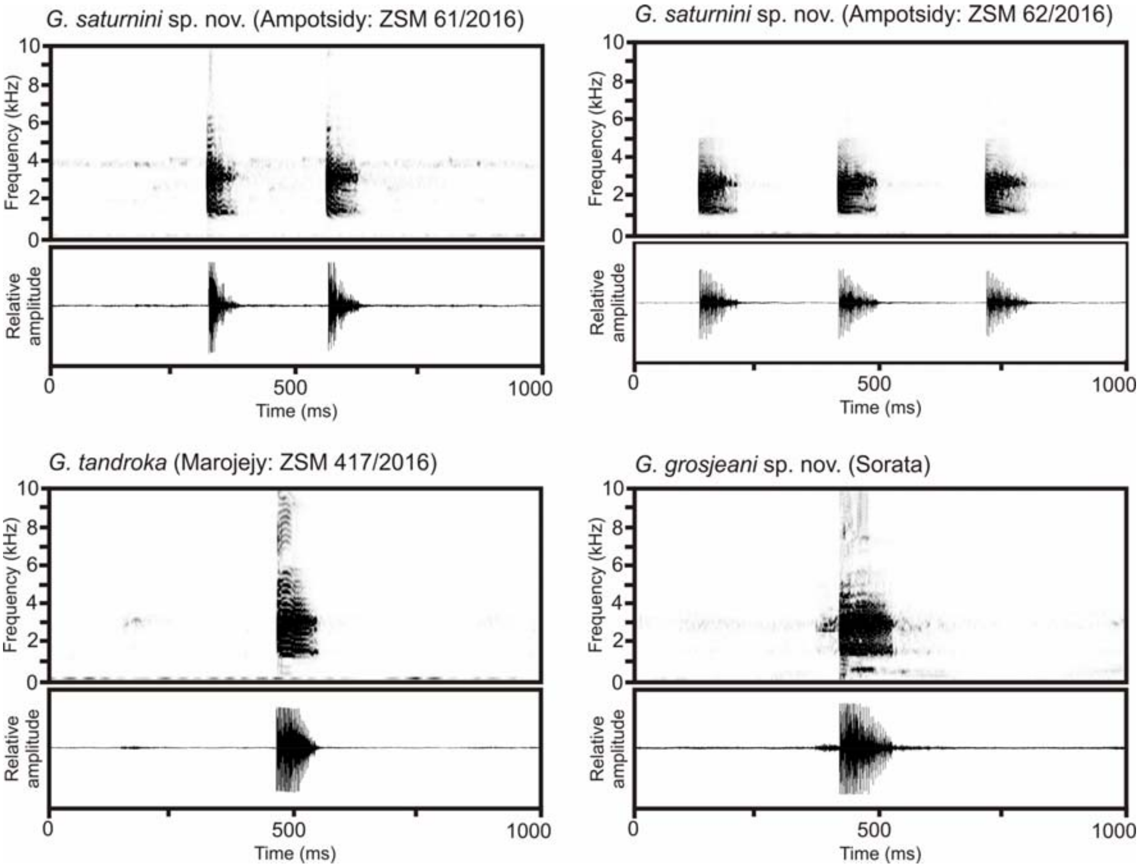

Figure 3. Comparative spectrograms and oscillograms of calls of some representatives of the *G. tandroka* complex in the subgenus *Duboimantis*.

Comparisons

Within the genus *Gephyromantis*, *G. saturnini* may be distinguished from all members of the subgenus *Gephyromantis* on the basis of much larger body size (SVL 39.4–42.8 mm vs. 20–33 mm); from all members of the subgenus *Asperomantis* on the basis of generally larger body size (SVL 39.4–42.8 mm vs. 26.6–40.7 mm); from all members of the subgenus *Phylacomantis* on the basis of the presence of distinct dorsolateral ridges (vs. absent or discontinuous), indistinct femoral glands (vs. distinct), more slender body shape and absence of outer metatarsal tubercle (vs. presence); from all members of the subgenus *Laurentomantis* on the basis of much larger body size (SVL 39.4–42.8 mm vs. 20–34 mm), smooth skin (vs. highly granular to rugose); and from all members of the subgenus *Vatomantis* on the basis of much larger body size (SVL 39.4–42.8 mm vs. 23–31 mm), lack of greenish skin colouration (vs. presence) and less slender limbs. Within the subgenus *Duboimantis*, it may be distinguished from *G. (D.) cornutus* (Glaw & Vences, 1992) and *G. (D.) redimitus* (Boulenger, 1889) by the possession of paired subgular vocal sacs (vs. single); from *G. (D.) luteus* (Methuen & Hewitt, 1913), *G. (D.) sculpturatus* (Ahl, 1929) and *G. (D.) plicifer* (Boulenger, 1882) by less webbed toes, lack of concave black suprascapular markings (vs. usually present) and presence of only diminutive heel spines (vs. distinct heel spines); from *G. (D.) moseri* (Glaw & Vences, 2002) by the much less rugose dorsum and smaller supraocular tubercles; from *G. (D.) salegy* (Andreone, Aprea, Vences & Odierna, 2003) and *G. (D.) redimitus* by considerably smaller body size (SVL 39.4–42.8 mm vs. 46–53 mm); from *G. (D.) schilfi*, *G. (D.) tschenki* (Glaw & Vences, 2001) and *G. (D). tohatra* by much larger body size (SVL 39.4–42.8 mm vs. 27–36 mm); from *G. (D.) zavona* (Vences, Andreone, Glaw & Randrianirina, 2003), *G. (D.) leucomaculatus* (Guibé, 1975) and *G. (D.) granulatus* (Boettger, 1881) by the presence of distinct interocular tubercles (vs. absence). From the most similar species, *G. (D.) tandroka*, *G. (D.) saturnini* may be distinguished by generally larger adult male size (SVL 39.4–42.8 mm vs. 35.6–40.1 mm; see Table 1).

Bioacoustically, *G. (D.) saturnini* most strongly resembles *G. (D.) tandroka* to the human ear, but differs consistently in call series structure (1–3 notes per call vs. always single-note calls). Its call series structure resembles more strongly *G. (D.) leucomaculatus* and *G. (D.) zavona* in this respect, but it differs from *G. (D.) zavona* in having a maximum of three notes per call (vs. up to five) and a lower dominant frequency (2497–2670 Hz vs. 3171–3785 Hz); and from *G. (D.) leucomaculatus* in having a longer inter-note interval within two-note calls (150–237 ms vs. 83–116 ms) and a lower dominant frequency (2497–2670 Hz vs. 2917–3168 Hz). To compare the calls by ear to other members of the subgenus *Duboimantis*, the reader is referred to our deposited calls and those available from Vences *et al.* (2006), which are also available online at www.fonozoo.com.

Genetically, the species is distinguished from all other species of *Gephyromantis* by uncorrected p-distances of at least 5.1 % in the analysed 16S rRNA gene fragment.

Table 1. Morphometric measurements of examined specimens of *Duboimantis*. For abbreviations, see Methods section. HT marks the holotype, PT the paratypes of the respective species. Measurements for *G. (D.) salegy* are from Andreone *et al.* (2003), *G. (D.) tohatra* are from Scherz *et al.* (2017*a*) and *G. (D.) schilfi* are from Glaw & Vences (2000) and Scherz *et al.* (2017*a*).

Voucher	Type status	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL
Gephyromantis tandroka (Marojejy) - males														
MNHN 1973.922	PT	38.9	13.1	14.5	2.2	4.8	3.4	2.2	3.7	26.6	13.0	74.4	32.8	21.8
MNHN 1973.924	HT	38.7	13.2	14.6	2.4	4.8	3.5	1.9	3.9	26.0	12.7	70.2	32.9	21.9
MNHN 1973.927	PT	38.8	14.0	15.6	2.4	5.1	3.8	2.3	3.5	26.3	12.7	73.3	32.8	21.9
MNHN 1973.929	PT	38.8	13.1	15.0	2.4	5.2	3.8	2.4	4.1	23.3	12.5	73.5	31.7	22.1
ZSM 321/2005 (FGZC 2812)		35.6	12.9	14.2	2.7	5.0	3.6	2.0	3.8	24.3	12.3	65.5	29.8	20.3
ZSM 322/2005 (FGZC 2816)		37.0	13.1	15.2	2.7	5.0	4.0	2.1	3.8	23.9	11.1	66.7	28.9	18.7
ZSM 417/2016 (ZCMV 15165)		40.1	14.8	16.0	2.6	6.1	4.1	2.1	4.4	26.7	13.4	74.3	32.4	22.4
Gephyromantis grosjeani (Sorata) - males														
ZSM 1553/2012 (FGZC 3749)	PT	36.1	12.3	14.1	2.8	5.3	3.8	1.8	4.0	23.9	12.0	70.9	31.3	21.2
ZSM 1554/2012 (FGZC 3584)	HT	38.4	13.0	14.2	2.6	4.5	3.6	2.1	3.4	24.8	12.1	70.9	32.2	22.1
Gephyromantis saturnini (Bealanana) - males														
ZSM 61/2016 (MSZC 123)	HT	39.4	13.4	14.7	2.8	5.0	4.1	2.5	4.7	24.0	12.5	73.7	32.5	21.9
ZSM 62/2016 (MSZC 153)	PT	41.7	13.7	15.3	2.4	5.0	4.2	2.3	4.2	24.1	12.0	74.5	33.9	22.9
UADBA-A61674 (ex-ZSM 66/2016, MSZC 164)	PT	42.8	14.5	15.8	2.8	5.5	4.3	2.4	4.3	26.2	13.2	77.6	35.1	24.0
Gephyromantis tohatra (Marojejy) - male														
ZSM 422/2016 (ZCMV 15245)	HT	32.7	9.5	12.0	1.9	4.5	3.3	2.7	3.8		11.0			18.2
Gephyromantis salegy (Ambolokopatrika) - males														
MRSN A2038	HT	47.8	16.2	18.0	3.0	5.9	4.7	2.8	4.5	29.4	14.4	86.5	38.7	25.9
MRSN A2043	PT	45.8	15.5	16.5	2.5	5.2	5.0	2.2	4.4	29.8	13.6	84.4	37.9	25.3
ZSM 48/2011 (ex-MRSN A2044)	PT	47.0	15.5	17.2	3.0	5.3	5.1	2.5	4.2	29.9	14.1	88.3	38.2	26.7
Gephyromantis schilfi (Marojejy) - male														
ZFMK 59885	HT	29.0			1.9	3.8								
ZSM 415/2016 (ZCMV 15246)		29.8	9.5	11.6	1.9	4.6	2.9	2.5	2.6		9.3			16.5

Voucher	Type status	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL
Gephyromantis tandroka (Marojejy) - females														
MNHN 1973.912	PT	43.2	14.9	16.4	2.9	5.1	4.1	2.5	4.6	29.2	13.9	81.8	36.2	24.2
MNHN 1973.926	PT	44.7	15.3	16.7	2.8	5.4	4.4	2.5	4.2	28.8	14.5	84.1	37.6	24.5
MNHN 1973.928	PT	39.8	13.3	14.8	2.2	5.1	3.8	2.3	3.8	25.8	12.6	78.4	34.3	22.4
ZFMK 59894	PT	39.6	15.0	16.5	2.3	5.4	4.3	2.7	4.7	27.0	13.6	80.1	36.0	23.1
ZSM 937/2000	PT	41.5	15.3	16.6	2.3	5.6	4.3	2.6	4.3	28.3	14.0	85.0	38.1	24.3
ZSM 320/2005 (FGZC 2741)		39.8	13.6	15.8	3.2	5.4	4.2	2.2	3.9	27.3	12.4	78.7	34.2	22.1
Gephyromantis grosjeani (Sorata) - females														
ZSM 1552/2012 (FGZC 3693)	PT	41.0	13.8	15.3	2.9	5.4	3.8	2.5	4.7	25.5	13.3	83.2	36.9	25.0
ZSM 1555/2012 (FGZC 3585)	PT	40.8	13.5	15.5	2.7	4.6	3.7	2.4	4.0	25.7	12.2	77.5	33.2	22.4
Gephyromantis salegy (Ambolokopatrika) - females														
MRSN A2039	PT	49.3	16.3	17.8	2.8	6.1	5.1	2.7	4.2	29.8	14.8	90.8	39.5	26.0
MRSN A2040	PT	44.6	15.0	16.8	2.6	6.0	4.5	2.6	4.4	28.4	13.2	86.4	39.0	24.7
MRSN A2041	PT	47.0	15.5	16.9	2.5	5.4	4.8	2.3	4.6	30.3	14.9	89.5	39.8	26.9
MRSN A2046	PT	50.1	16.8	19.0	2.6	5.6	5.0	2.7	4.5	33.0	15.3	97.1	43.0	28.5
MRSN A2045	PT	43.3	14.7	17.2	2.8	-	5.3	-	3.7	28.6	13.5	87.4	39.1	25.2
Gephyromantis tandroka (Marojejy) - subadult														
MNHN 1973.93	PT	33.9	11.6	13.0	2.4	4.3	3.4	1.9	3.6	23.8	11.1	72.3	32.3	20.0

Description of holotype ZSM 61/2016, adult male

Specimen in a good state of preservation, a tissue sample taken from the left thigh. SVL 39.4 mm. For other measurements see Table 1. Body somewhat gracile; head longer than wide, not as wide as body (body is somewhat inflated in preservative); snout pointed in dorsal and lateral view; nostrils directed laterally, protruding slightly, much nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region concave and weakly oblique; tympanum distinct, oval, its horizontal diameter 56 % of eye diameter; supratympanic fold distinct, weakly curved, from the posterior corner of the eye to above the insertion of the arm; tongue fairly broad, posteriorly bifid; vomerine teeth clearly distinct, arranged in two small aggregations on either side of the midline of the palate at the level of the anterior edge of the eye, posteromedial to choanae; choanae small and rounded and laterally displaced. Dark, translucent dermal fold below each jaw starting at the level of the anterior edge of the eye. Arms slender, subarticular tubercles single, highly distinct; outer metacarpal tubercle small and oval and inner metacarpal tubercle small; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth; finger discs distinctly enlarged, round, nuptial pads absent. Hindlimbs slender; lateral metatarsalia slightly separated distally with webbing; subarticular tubercles highly distinct; inner metatarsal tubercle distinct, anteriorly oriented, outer metatarsal tubercle absent; webbing formula of foot according to the scheme of Blommers-Schlösser (1979) 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.25), 4i(2.5), 4e(2.25), 5(1); relative toe length 1 < 2 < 3 < 5 < 4, third toe much shorter than fifth; toe discs distinctly enlarged. Skin dorsally granular, with two pairs of distinct dorsolateral ridges, corresponding to the inner and outer ridges of Vences & Glaw (2001), one pair running from the posterior of the eye to the suprascapular region, and the other pair along the dorsolateral ridge of the body; between these ridges over the dorsum posterior to the head is a reticulated pattern of fine ridges; a small pair of interocular spines is present, and each eye is adorned with two small supraocular spines; a diminutive dermal flap is present on the heel; ventral skin smooth on chin and forelimbs, but highly granular on the abdomen and ventral thighs. Femoral glands indistinguishable in the fixed specimen, but visible from images of the specimen in life (fig. 4): type 2 sensu Glaw *et al.* (2000), 4.6 mm long, 2.2 mm wide (measured in internal view), consisting of 16 granules on the right thigh and 15 on the left thigh.

In life (fig. 4) the dorsum was a light mocha, with rust markings on the upper flanks, in a W-shaped marking on the mid-dorsum, on the lateral head and posterior surface of the eyes, and in an oblong patch over the hips. The light colouration of the dorsal surface of the head continued as a medial rostral stripe visible in ventral and anterior view. The inner and outer dorsolateral folds were not remarkably coloured. A mottled dark line was present between the eyes, with black around the interocular tubercles. The larger of the two supraocular spines was also surrounded in black. A thin black stripe was present from the nostril to the eye along the canthus rostralis, and the lower edge of the supratympanic fold and the tympanum itself were dark brown. A further dark brown marking was present on the upper lip below the eye. The limbs exhibited extensive crossbanding: the forelimb had one faint crossband on the upper arm, and three crossbands on the lower arm, each of the rust colour of the dorsum, with black on the inner surface; the fingers lacked crossbands but had black flecks, without any distinctive colouration of the distal discs. The hindlimbs had five crossbands of dark brown tinged with rust and black on the thigh, six on the shank, three on the tibiotarsus, and two on the foot. The chin was mottled translucent and light yellow ventrally, only slightly darker on the vocal sacs, becoming translucent over the pectoral region, and then cream over the abdomen, in turn fading to egg-yolk yellow near the hip and over the surface of the thighs. The thighs were distally flecked with brown, the lower legs mottled yellow, beige and brown. The foot was mocha brown ventrally with tinges of rust on the subarticular tubercles. The hand was also brown ventrally, but its tubercles were cream in colour.

After roughly two years in preservative, the colour pattern is unchanged, but the colour itself has faded (fig. 5). Dorsally, areas that were light mocha have become grey to silver, with light grey dorsolateral ridges, while areas that were rust in life are now mauve. Both the chin and the pectoral region have lost their translucence and the colouration on the chin has become darker, and the W-shaped marking on the mid-dorsum has faded but is still visible. All traces of yellow in the ventral colouration has been replaced by a dirty cream.

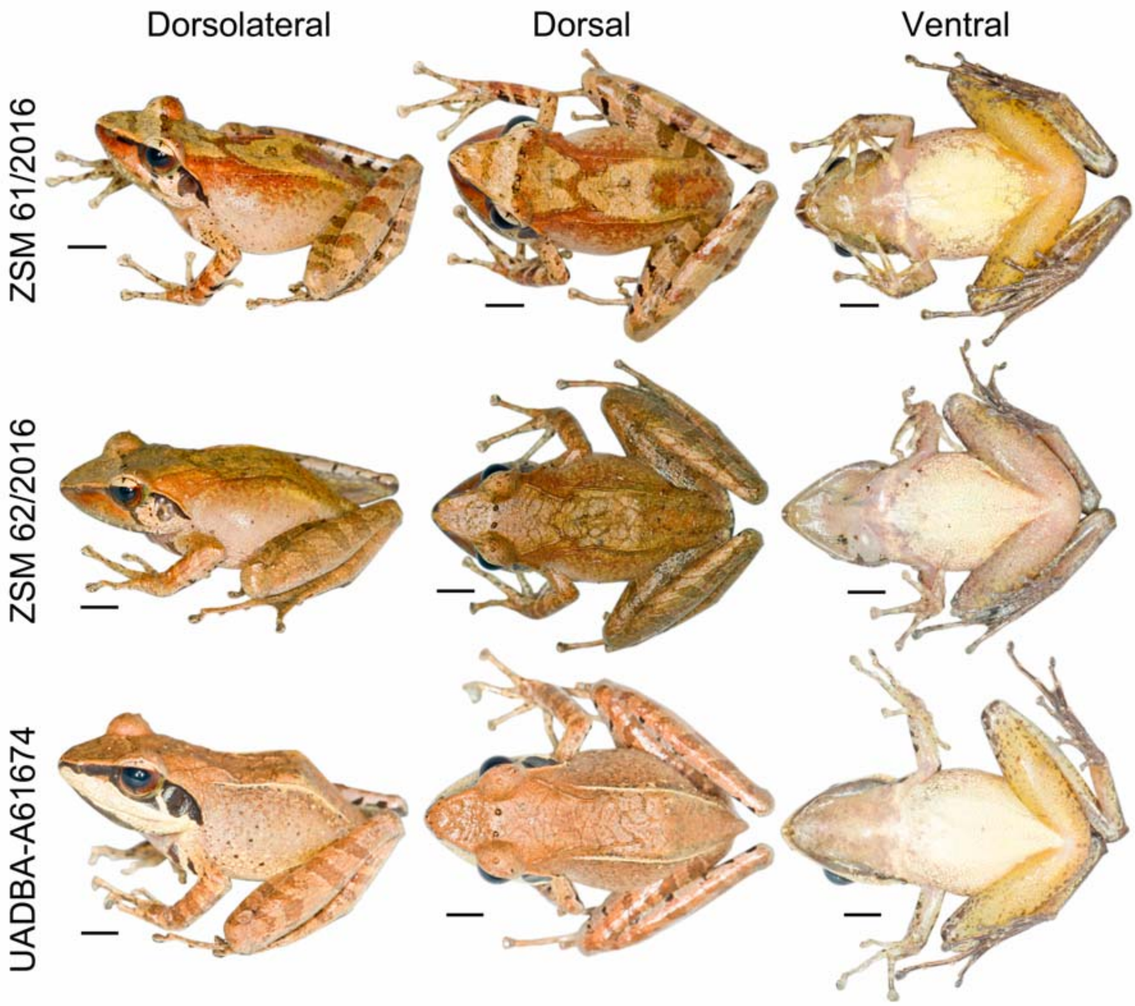

Figure 4. Type series of *Gephyromantis saturnini* sp. nov. in dorsolateral, dorsal and ventral view. Scale bars indicate 5 mm. Femoral gland granules (FGG): ZSM 61/2016, 15 left/16 right, ZSM 62/2016, 10/9, UADBA-A 61674, 13/10.

Morphological and chromatic variation

In morphology, the paratypes strongly resemble the holotype; for variation in measurements, see Table 1. Webbing formula varies in 3e (1 in the paratypes vs. 1.25 in the holotype) and 5i (0.75–1 in the paratypes). The femoral glands are equally poorly distinguishable in all specimens, but can be identified with strong magnification (fig 6); the number of granules varies from 9–16, but they are always indistinct.

Although they are consistently brown in overall colour, the colour patterns of the type specimens are highly varied (fig. 4), and only a few characteristics are consistent: the dark canthal stripe is consistently present in the type series, though much thicker in UADBA-A 61674 than the other paratypes. Crossbands are always present on the limbs, but the number is variable. The ventral abdomen is consistently cream in colour, and the mottling of the thighs distally is also fairly consistent among the specimens. The rostral stripe is present in all of the type series.

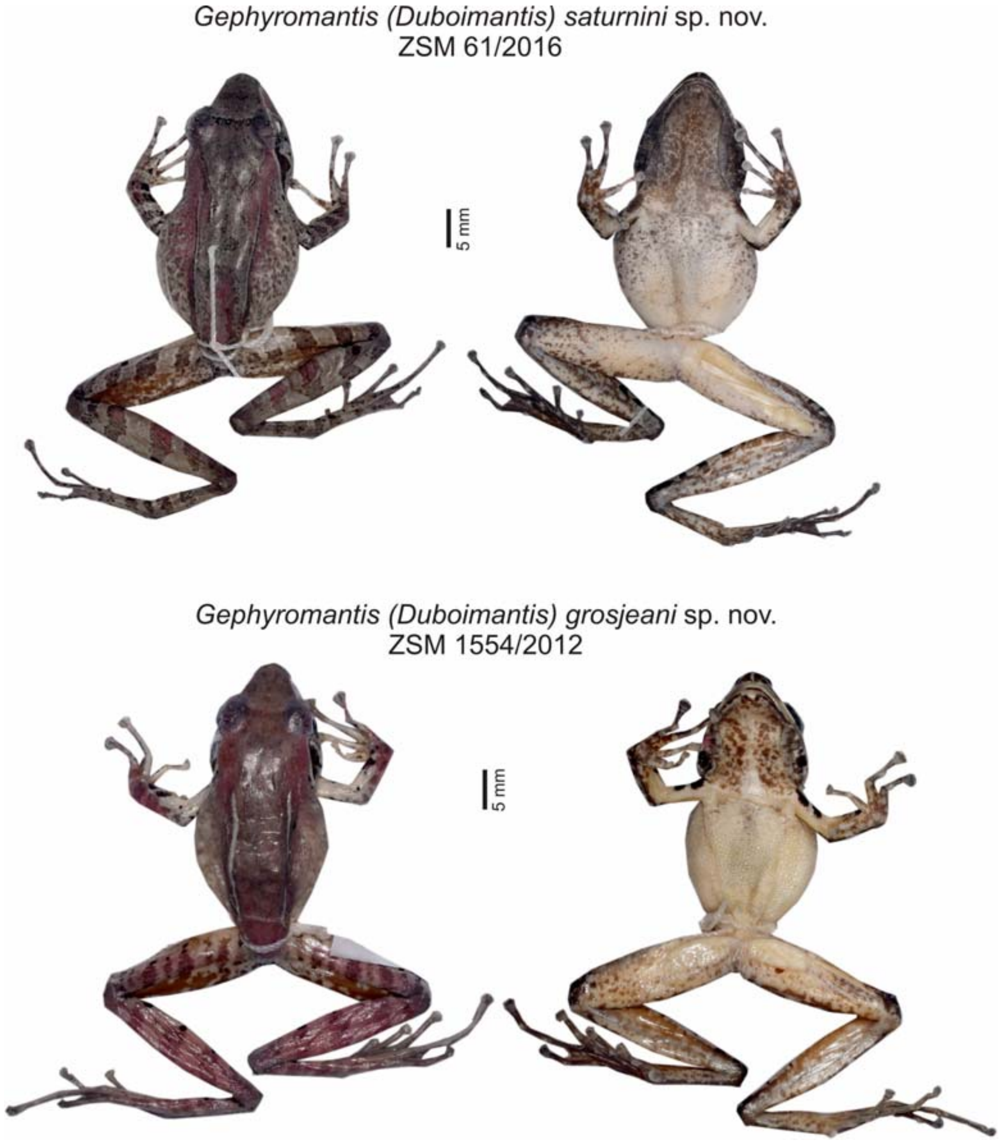

Figure 5. Holotypes of *Gephyromantis (Duboimantis) saturnini* sp. nov. (ZSM 61/2016) and *G. (D.) grosjeani* sp. nov. (ZSM 1554/2012) in dorsal (left) and ventral (right) view.

Bioacoustics

The calls of two recorded individuals consisted of pulsatile notes, which were arranged in note groups of 1–3 notes, and these note groups emitted in a finite series of 7–8 note groups. We here define each note group as a call. In this definition, calls are thus arranged in call series consisting of 7–8 calls, and each call consists of 1–3 notes. In the holotype ZSM 61/2016 (recorded on 31 December 2015 at 18 h 30, air temperature unknown), two call series contained calls with 1–2 notes, and lasted 22.7 s (7 calls) and 27.3 s (8 calls). Note duration was 56–78 ms (63 ± 6 ms; $N = 10$), and each note consisted of 12–18 very poorly distinguishable pulses (16 ± 2; $N = 10$), without silent intervals between them. Inter-call interval duration was 2054–8436 ms (3912 ± 2246 ms; $N = 10$) and decreased toward the end of the call series, i.e., calls were repeated faster and contained more notes towards the end of a call series. Within two-note calls, the interval duration between notes was 150–181 ms (165 ± 12 ms; $N = 8$). Dominant frequency was between 3057–3227 Hz (3100 ± 57 Hz; $N = 10$), approximate prevalent bandwidth is between 1000–4500 Hz.

The calls of paratype ZSM 62/2016 (recorded on 6 January 2016 at 23 h 45 at an air temperature of 15.9°C) were very similar; one call series of 7 calls was available for analysis. Of these, the first two calls had 1 note, the third and fourth call had two notes and the last three calls had three notes each. As in the holotype, inter-call interval duration decreased toward the end of the call series. Temporal and spectral measurements were as follows: Note duration 87–100 ms (91 ± 5 ms; $N = 12$), inter-call interval duration 2158–5944 ms (3500 ± 1385 ms; $N = 6$), inter-note interval within one call 199–237 ms (209 ± 13 ms; $N = 8$), dominant frequency 2497–2670 Hz (2583 ± 45 Hz; $N = 10$), approximate prevalent bandwidth 1000–5000 Hz.

Natural history and conservation status

Very little is known of the ecology of this species. Male specimens were collected at night, sitting on leaves in primary rainforest at 1.1–3 m above the ground. ZSM 61/2016 was collected 20 m from a small stream on a steep slope. The confirmed elevational range of the collected specimens is 1450–1481 m a.s.l. and we did not encounter them below 1400 m a.s.l. Our survey work above 1500 m a.s.l. was insufficient to be conclusive as to the upper ranges of the distribution of this species, but the Ampotsidy mountains have a maximum elevation of ca. 1860 m a.s.l.

At present this species is known from just three collected specimens, though several others were heard in the vicinity of the collected individuals at low density (MDS pers. obs.). It is known from one area of fragmented forests, which are in an active state of decline due to ongoing slash-and-burn agriculture, cattle grazing and logging. However, like other species collected in Ampotsidy (e.g. *Gephyromantis [Asperomantis] angano*, Scherz *et al.* 2017*b*; *Calumma gehringi*, Prötzel *et al.* 2017; *Uroplatus fotsivava*, Ratsoavina *et al.* 2017), we suspect that the species will occur more broadly within the poorly surveyed District de Bealanana. As such, any evaluation of its conservation status based on current knowledge is liable to dramatically overestimate its threat status: at present it qualifies as Critically Endangered under IUCN (2012) criterion B1ab(iii) due to its range of below 100 km^2 (B1) from one threat-defined location (a) undergoing active decline in extent and quality of its habitat (b[iii]). To avoid being inflationary, we recommend that the species be considered Data Deficient until further survey work has been conducted in the District de Bealanana.

Etymology

We dedicate this species of *Duboimantis* to Saturnin Pojarski, a pseudonym of Alain Dubois during his time as a late-night radio presenter on Radio Carbone 14, a ‘pirate’ station that was part of the free radio movement in France in the 1980s. Saturnin also makes an appearance in a children's book (Dubois & Ohler 2010) as a grandfather transmitting the enthusiasm for and knowledge of amphibian biology to his grandson, Augustin.

Figure 6. Femoral glands of male specimens of *Gephyromantis tandroka* ZSM 321/2005 (FGZC 2812), femoral gland granules (FGG) 24 left/21 right (above), *G. saturnini* sp. nov. Holotype ZSM 61/2016 (MSZC 123), FGG 16/15 (middle) and *G. grosjeani* sp. nov. (unidentified UADBA specimen), FGG, 41/34 (below). Note the much more distinct glands in the latter species.

Gephyromantis (Duboimantis) grosjeani sp. nov.

(fig. 1–3, 5–9, Table 1)

LSID: urn:lsid:zoobank.org:act:2D5B8810-A9CD-4363-A960-3F8AA6C61D41

Gephyromantis (Duboimantis) sp. Ca32 – (Scherz *et al.* 2017*a*)

Specimens allocated to new species

Holotype

ZSM 1554/2012 (FGZC 3584), an adult male collected at high elevation on the Sorata massif (13.67–13.69°S, 49.43–49.44°E, ca. 1400–1500 m a.s.l.), District de Vohemar, Région Sava, northern Madagascar, at night on 26 November 2012 by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F. M. Ratsoavina and A. Razafimanantsoa.

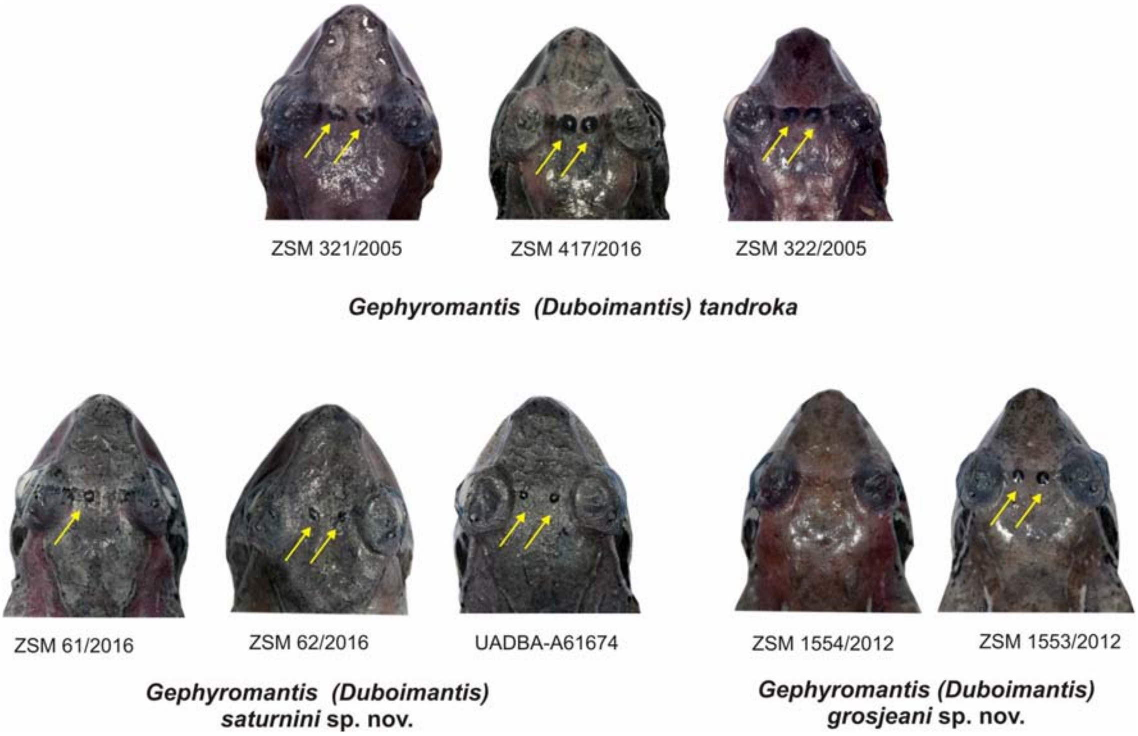

Figure 7. Heads of *Gephyromantis (Duboimantis) saturnini* sp. nov. and *G. (D.) grosjeani* sp. nov. in dorsal view compared to *G. (D.) tandroka*. Arrows indicate the interocular tubercles, which appear less expressed especially in *G. (D.) saturnini* sp. nov. than in *G. (D.) tandroka*.

Paratypes

ZSM 1555/2012 (FGZC 3585) and UADBA uncatalogued (FGZC 3583), two adult females and UADBA uncatalogued (FGZC 3599), an adult male with the same collection data as the holotype. ZSM 1553/2012 (FGZC 3749), a male, ZSM 1552/2012 (FGZC 3693), a female and UADBA uncatalogued (FGZC 3690), an unsexed individual, collected in bamboo forest above the campsite in Sorata (ca. 13.6752°S, ca. 49.4410°E, ca. 1485 m a.s.l.), District de Vohemar, Région Sava, northern Madagascar, at night between 28–30 November 2012 by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F. M. Ratsoavina and A. Razafimanantsoa. UADBA uncatalogued (FGZC 3598), an adult male collected above the campsite in Sorata (13.6829°S, 49.4419°E, 1312 m a.s.l.), District de Vohemar, Région Sava, northern Madagascar, at night on 26 November 2012 by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F. M. Ratsoavina and A. Razafimanantsoa.

Diagnosis

A *Gephyromantis* species assigned to the subgenus *Duboimantis* on the basis of its fairly smooth skin, interocular tubercles generally present, moderately large body size and presence of inner and outer dorsolateral folds. *Gephyromantis grosjeani* is characterised by the following unique suite of characters: (1) large body size (36.1–38.4 mm in adult males, 40.8–41.0 mm in adult females), (2) paired subgular vocal sacs, (3) HIL/SVL 1.84–2.03, (4) TD/ED 0.53–0.59, (5) presence of inner and outer dorsolateral folds, with the inner folds being generally weak, (6) reticulated low ridges on the dorsum, (7) large, distinct femoral glands in males consisting of 25–41 granules. It is furthermore characterised by advertisement calls consisting of pulsatile single-note calls arranged in undefined series.

Comparisons

Within the genus *Gephyromantis*, *G. grosjeani* may be distinguished from all members of the subgenus *Gephyromantis* on the basis of larger body size (SVL 36.1–41.0 mm vs. 20–33 mm); from all members of the subgenus *Asperomantis* by less rough dorsal skin, less distinct inner dorsolateral ridges, less pronounced supraocular spines and absence of a pale spot in the middle of the tympanum; from all members of the subgenus *Phylacomantis* on the basis of the presence of distinct dorsolateral ridges (vs. absent or discontinuous), more slender body shape and absence of outer metatarsal tubercle (vs. presence); from all members of the subgenus *Laurentomantis* on the basis of larger body size (SVL 36.1–41.0 mm vs. 20–34 mm), smooth skin (vs. highly granular to rugose); and from all members of the subgenus *Vatomantis* on the basis of much larger body size (SVL 36.1–41.0 mm vs. 23–31 mm), lack of greenish skin colouration (vs. presence) and less slender limbs. Within the subgenus *Duboimantis*, it may be distinguished from all species except *G. (D.) salegy*, *G. (D.) redimitus*, *G. (D.) plicifer* and *G. (D.) moseri* by larger and/or more distinct femoral glands in males. Additionally, it may be distinguished from *G. (D.) cornutus* and *G. (D.) redimitus* by the possession of paired subgular vocal sacs (vs. single); from *G. (D.) luteus*, *G. (D.) sculpturatus* and *G. (D.) plicifer* by less webbed toes, lack of concave black suprascapular markings (vs. usually present) and presence of only diminutive heel spines (vs. distinct heel spines); from *G. (D.) moseri* by the much less rugose dorsum and smaller supraocular tubercles; from *G. (D.) salegy* and *G. (D.) redimitus* by much smaller body size (SVL 36.1–41.0 mm vs. 46–53 mm); from *G. (D.) saturnini* by smaller adult male body size (36.1–38.4 mm vs. 39.4–42.8 mm) and less distinct inner dorsolateral folds; from *G. (D.) schilfi*, *G. (D.) tschenki* and *G. (D). tohatra* by larger body size (SVL 36.1–41.0 mm vs. 27–36 mm); from *G. (D.) zavona*, *G. (D.) leucomaculatus* and *G. (D.) granulatus* by the general presence of interocular tubercles (vs. absence). From the highly similar *G. (D.) tandroka*, it may be distinguished most reliably by the distinct femoral glands in males (fig. 6) and provisionally (due to low sample sizes) males may differ by slightly longer relative foot length (FOL/SVL 0.58–0.59 vs. 0.51–0.57) and females may differ by slightly longer relative forelimb length (FORL/SVL 0.62–0.63 vs. 0.64–69). The interocular spines of this species appear to be smaller and less distinct than those of *G. tandroka*, even when they are present (fig. 7).

Genetically, the species is distinguished from all other species of *Gephyromantis* by uncorrected p-distances of at least 5.1 % in the analysed 16S rRNA gene fragment.

The calls of *G. (D.) grosjeani* strongly resemble those of *G. (D.) tandroka*, but differ slightly in call duration (119–128 ms vs. 77–94 ms) and inter-call interval duration (1977–2720 ms vs. 1524–2034 ms), but the assessment of the diagnostic value of these differences requires additional data.

Description of holotype ZSM 1554/2012, adult male

Specimen in a good state of preservation, a tissue sample taken from the left thigh. SVL 38.4 mm. For other measurements see Table 1. Body somewhat gracile; head longer than wide, not as wide as body (body is somewhat inflated in preservative); snout pointed in dorsal view, rounded in lateral view; nostrils directed laterally, protruding slightly, much nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region concave and weakly oblique; tympanum indistinct, oval, its horizontal diameter 58 % of eye diameter; supratympanic fold distinct, curved, from the posterior corner of the eye to above the insertion of the arm; tongue fairly narrow, posteriorly bifid; vomerine teeth clearly distinct, arranged in two small aggregations on either side of the midline of the palate at the level of the anterior edge of the eye, posteromedial to choanae; choanae small and rounded and laterally displaced. Pigmented translucent dermal fold below each jaw starting at the level of the anterior edge of the eye. Arms quite stocky, subarticular tubercles single, highly distinct; outer metacarpal tubercle small and oval and inner metacarpal tubercle relatively well developed; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth; finger discs distinctly enlarged, round, nuptial pads absent. Hindlimbs slender; lateral metatarsalia separated distally with webbing; subarticular tubercles highly distinct; inner metatarsal tubercle distinct, anteriorly oriented, outer metatarsal tubercle absent; webbing formula of foot according to the scheme of Blommers-Schlösser (1979) 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4i(2.75), 4e(2.5), 5(1); relative toe length 1 < 2 < 3 = 5 < 4, third toe equal in length to fifth; toe discs distinctly enlarged. Skin dorsally smooth, with one pair of distinct dorsolateral ridges running from the suprascapular region to the hip, and weak suggestion of a pair of inner dorsolateral ridges as termed by Vences & Glaw (2001) only over the suprascapular region; interocular spines absent; two diminutive supraocular spines present; a diminutive dermal flap is present on the heel; skin smooth on chin, forelimbs and hindlimbs ventrally, but highly granular on the abdomen and lower flanks. Femoral glands distinct, large, type 2 sensu Glaw *et al.* (2000), 8.1 mm long, 3.6 mm wide (measured in external view), consisting of 37 granules on the right thigh and 31 on the left thigh (counted in internal view).

The colouration in life is unknown. After six years in preservative (fig. 5), the dorsum is grey-beige fading through salmon laterally onto grey flanks; the outer dorsolateral folds are cream. The lateral head is distinctly different in colour from the dorsum, with burnt umber patches over the tympanum, under the eye, along the canthus rostralis and around the nostril, separated by cream patches. The forelimb is cream in base-colour with thin blackish markings along the posterior edge of the upper forelimb, with salmon-grey crossbands with blackish internal markings from the hand to the elbow. The dorsal surface of the hand is externally the same salmon-grey colour, and internally cream. The dorsal hindlimb is light salmon in base colour with numerous mauve crossbands dorsally that darken to nearly black on the leading and trailing edges; there are roughly seven crossbands on the thigh, four or five on the shank and five becoming more indistinct on the foot; the toes lack crossbands. The hidden surfaces of the posterior thigh are a coffee brown towards the knee, becoming dappled with cream toward the cloaca, with a poorly-defined dark brown trapezoid below the cloaca. The ventral base colour is cream, immaculate over the abdomen and ventral surfaces of the forelimbs, but dappled with dark brown on the chin. The ventral surfaces of the hands and feet are a muddy grey. The thighs are cream with irregular small light brown spots all over except on the femoral glands ventrally, which are cream.

Morphological and chromatic variation

In morphology, the paratypes strongly resemble the holotype; for variation in measurements, see Table 1. Females are apparently larger than males (40.8–41.0 mm vs. 36.1–38.4 mm in males), but no other sexual dimorphisms are visible except the absence of the distinct femoral glands in females. Males have clearly bilobed subgular vocal sacs (fig. 8) The distinctiveness of the inner dorsolateral folds is variable, being distinct in ZSM 1552/2012, but weak or almost absent in the other specimens examined. Interocular tubercle presence is variable: present in ZSM 1552/2012 and 1553/2012, but absent in the holotype and ZSM 1555/2012 (fig. 7). The strength of the supraocular tubercles is slightly less variable, being small in all specimens, but exceptionally so in ZSM 1555/2012. Femoral glands vary in the number of granules (25–41) and the shape of the gland (fig. 6 & 9); the glands of ZSM 1553/2012 measure 5.4 mm long by 2.7 mm wide.

The dorsal colouration of this species is highly variable (fig. 9), while the ventral colouration is largely consistent, even between males and females except that the females lack the different colouration of the vocal sacs present in males. Dorsal base-colour ranges from the beige to salmon of the holotype to dark brown in preservative. The outer dorsolateral folds can be distinctly cream as in the holotype, or indistinct in colour as in ZSM 1552/2012. ZSM 1555/2012 differs dramatically in body colouration in having a strong colour border on the whole body between the dark brown dorsum and the light cream flanks. Laterally, the head can be solid black above with a white lip (e.g. ZSM 1553/2012) or wholly cream with only dark brown on the tympanum (ZSM

1555/2012). The number of crossbands on the limbs is wholly variable. When present, interocular tubercles are surrounded with blackish circles.

Bioacoustics

The advertisement call, recorded on 29 November 2012 at 20 h 30 at an elevation of ca. 1400 m a.s.l. in moderately disturbed primary montane forest (air temperature not recorded), consists of a single pulsatile note, with a call (= note) duration of 119–128 ms (121 ± 4 ms; *N* = 10 calls of one male), repeated for long periods with regular inter-call intervals of a duration of 1977–2720 ms (2363 ± 226 ms; *N* = 10). Each call (or note) consists of approximately 23–25 indistinct pulses (23.9 ± 0.7; *N* = 10), without clear silent interval between them. Pulse intensity decreases towards the end of the call, and pulses appear longer and more densely packed in the beginning of the call, becoming more distinct and more widely spaced toward the end. Dominant frequency is between 2713–3186 Hz (2936 ± 120 Hz; *N* = 10). Approximate prevalent bandwidth is between 1200–5800 Hz.

Figure 8. A calling male specimen of *Gephyromantis (Duboimantis) grosjeani* sp. nov. (specimen unidentified). Note the clearly bilobed subgular vocal sacs.

Figure 9. Photos in life of four specimens of *Gephyromantis (Duboimantis) grosjeani* sp. nov. from Sorata. (a–f) unidentified males (UADBA-A specimens) with femoral gland granule (FGG) numbers of (b) 41 left/34 right, (d) 31/34 and (f) 25/27; (g–h) female ZSM 1552/2012 (FGZC 3693).

Natural history and conservation status

Numerous male individuals were heard calling at night at the end of November, sitting on branches and leaves, especially of ferns, in disturbed primary rainforest and bamboo forest, ca. 1–3 m above the ground at an elevation of ca. 1300–1500 m a.s.l., but we suspect that the species will be distributed more widely in the poorly surveyed Sorata and Andravory regions and perhaps other high-altitude rainforests in northern Madagascar. Similarly to *G. saturnini* sp. nov. described above, an evaluation of the conservation status of *G. grosjeani* sp. nov. based on current knowledge is liable to dramatically overestimate its threat status: at present it qualifies as Critically Endangered under IUCN (2012) criterion B1ab(iii) due to its range of below 100 km^2 (B1) from essentially one threat-defined location (a) undergoing relative dramatic decline in extent and quality of its habitats (b[iii]). To avoid being inflationary, we recommend that the species be considered Data Deficient until further survey work has been conducted in surrounding rainforest areas.

Etymology

We dedicate this species to Stéphane Grosjean, who completed his PhD studies under the mentorship of Alain Dubois, in recognition of his valuable contributions to the knowledge of Madagascan frog larvae (e.g. Grosjean *et al.* 2007, 2011*a, b*).

DISCUSSION

The mitochondrial data on *Gephyromantis (Duboimantis) saturnini* suggests close affinities to *G. (D.) schilfi*, both in terms of uncorrected p-distance (5.1 %) and phylogenetic relationships (fig. 1). These two species however bear little resemblance to one another; *G. (D.) saturnini* is much more similar in appearance to *G. (D.) tandroka* (compare fig. 4 with fig. 10) and *G. (D.) grosjeani*, in terms of size, overall morphology and bioacoustics. Although it is at present poorly resolved, the position of *G. (D.) tohatra* outside of this clade is surprising, because that species is morphologically more similar to *G. (D.) schilfi* than is *G. (D.) saturnini*. These relationships suggest discordance between overall phenotype and mitochondrial sequence data, and therefore require further testing with sequences of nuclear genes. The observed discordance could be the result of one or more recent or ancient hybridisation events, which could be revealed by mitochondrial-nuclear gene tree discordance.

If our phylogeny is correct in representing relationships, the biogeography of this complex of frogs is interesting (fig. 11). The type localities of the two new species are separated by a mere ca. 112 km in a straight line, and the elevations of 1312–1500 m a.s.l. for *G. (D.) grosjeani* and 1450–1481 m a.s.l. for *G. (D.) saturnini* overlap, yet these two species are each more closely related to taxa in Marojejy (*G. [D.] grosjeani* to *G. [D.] tandroka*) and Marojejy plus Sorata (*G. (D.) saturnini* to *G. [D.] schilfi*), respectively. Marojejy is almost equally distant from both localities (90–120 km; see fig. 11). This suggests greater connectivity between Marojejy and Sorata, and Marojejy and the Bealanana area, than between Sorata and the Bealanana area. In other amphibian taxa we have found a similar level of isolation between species from Sorata and the Bealanana side of the Tsaratanana massif (Scherz *et al.* 2015; 2017*c*), and at present very few species are known to occur both in the Bealanana area and Sorata. Those that do occur at these two sites can also be found in Marojejy (e.g. *G. [Asperomantis] tahotra* Glaw, Köhler & Vences, 2011). Indeed, Sorata shares several species with Marojejy (Cramer *et al.* 2008; Scherz *et al.* 2017*c*, 2018; Prötzel *et al.* 2018). The emerging pattern suggests that the Tsaratanana massif, probably due to its great elevation, is acting as a barrier to gene flow between areas to its North-East and South-West, at least to species that occur at sufficiently low elevations to not have ring-shaped ranges including both sides of the massif. Gene flow along either side of the massif is less inhibited, resulting in the connectivity we see between Sorata and Marojejy and, to a lesser degree, the Bealanana area and Marojejy.

With the description of these two new species, we bring the subgenus *Duboimantis* to 16 described species. The centre of diversity of this subgenus is unquestionably northeastern Madagascar (Kaffenberger *et al.* 2012), although some members are more widespread throughout the east of the island (Glaw & Vences 2007). The new species described here conform to this pattern. Although all members of the *G. (D.) tandroka* complex are relatively high-elevation species, they are not as ecologically conserved as this might suggest. Forests above 1300 m a.s.l. in Marojejy (type localities of *G. [D.] schilfi*, *G. [D.] tohatra* and *G. [D.] tandroka*) are montane high-elevation forest with a low canopy and dense epiphyte coverage. The type locality of *G. (D.) grosjeani* is similar in these regards, but it occurs also in bamboo forest, which was not seen at this elevation in Marojejy. The forests of Ampotsidy from 1400–1600 m a.s.l. (type locality of *G. [D.] saturnini*) are rather humid forests, with little understory, a high canopy and relatively few epiphytes. This habitat is somewhat different from those of the other members of this complex, and its ecology may differ accordingly. More data are needed on its reproductive habits before we can draw conclusions to this effect however.

Finally, we are pleased to note that the type localities of both of the new species, as well as most members of the *G. (D.) tandroka* complex, are within the network of protected areas that have recently been expanding in northern Madagascar (Gardner *et al.* 2018, fig. 11). Although these protected areas are in relatively early states of establishment and as such the habitat within them is still liable to decline through anthropogenic activity, the future outlook is a positive one.

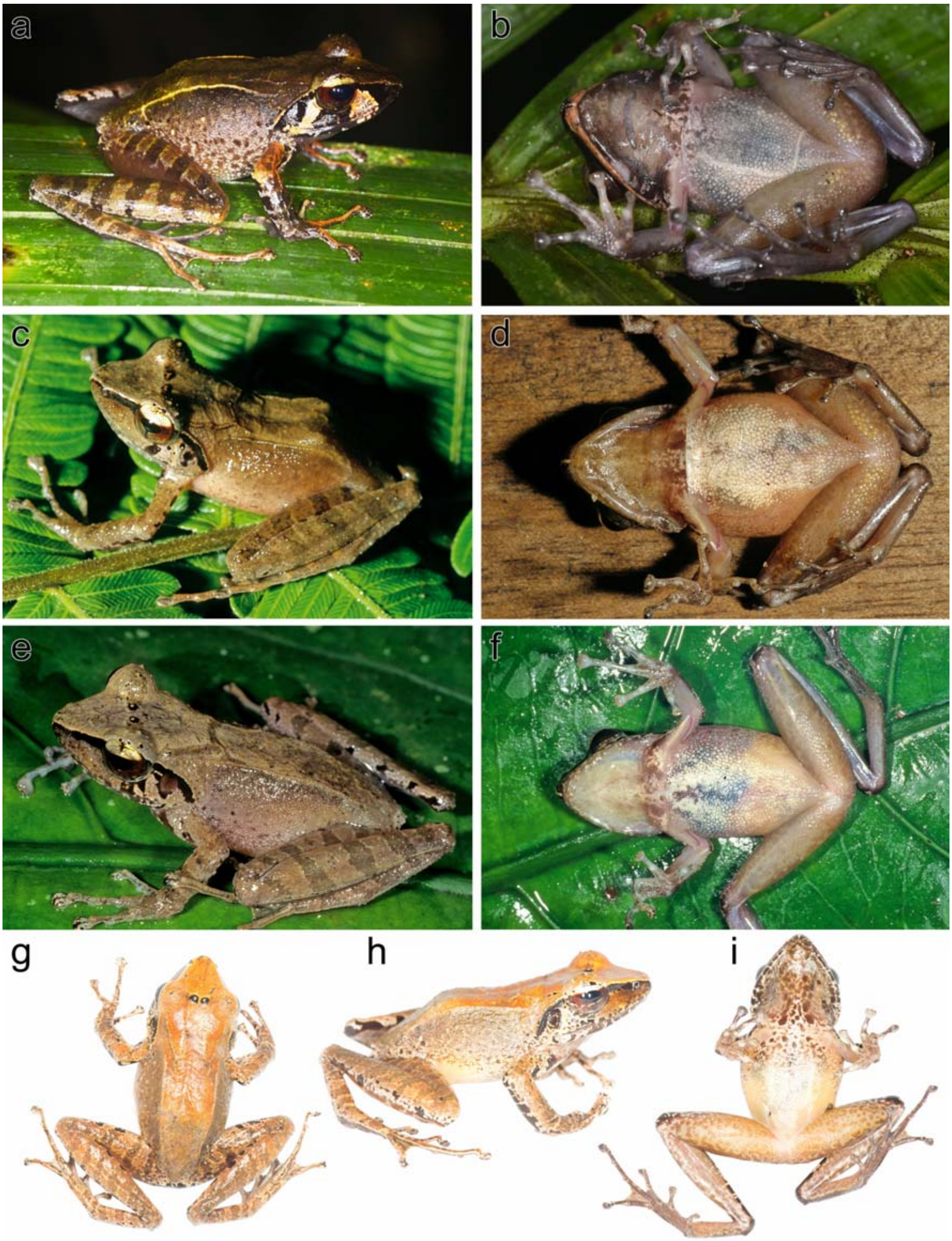

Figure 10. Photos in life of four specimens of *Gephyromantis (Duboimantis) tandroka* from Marojejy. (a,b) an uncollected male specimen photographed in 2016, femoral gland granules 10 left/8 right, (c,d) ZSM 321/2005 (FGZC 2812), FGG 23/21, (e,f) ZSM 937/2000, (g–i) ZSM 417/2016 (ZCMV 15165), FGG 18/12.

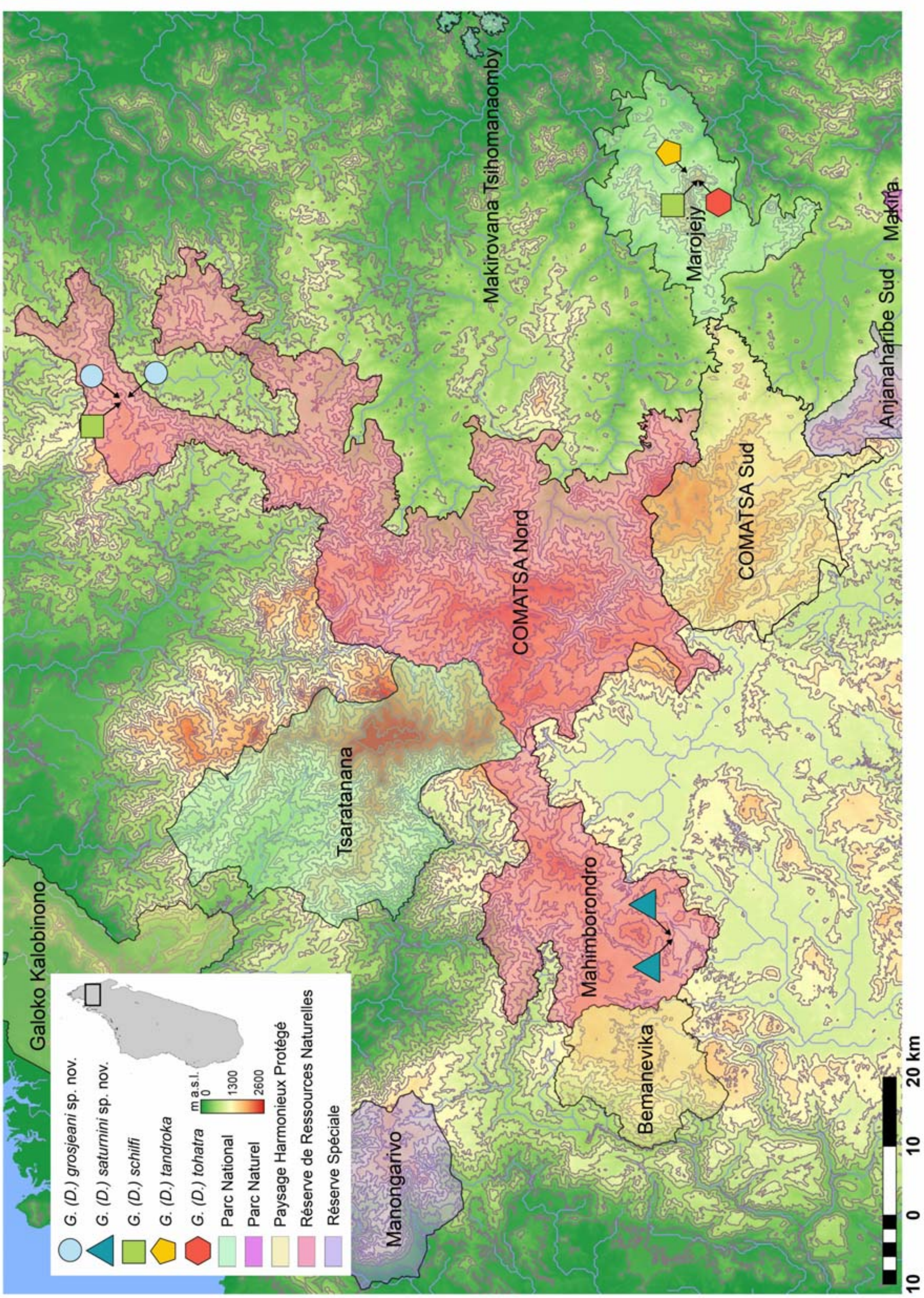

Figure 11. Map of current distribution records of the *Gephyromantis (Duboimantis) tandroka* species complex, with reference to the network of protected areas in northern Madagascar. Isolines indicate 200 m.

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