



Research article

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Two new *Pandanus* frogs (*Guibemantis*: Mantellidae: Anura) from northern Madagascar

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⁴[urn:lsid:zoobank.org:author:A354F4A8-FDD9-4072-9C27-DC17B6ED3664](https://zoobank.org/author:A354F4A8-FDD9-4072-9C27-DC17B6ED3664)

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Abstract. We describe two new frog species of the genus *Guibemantis* Dubois, 1992 (Mantellidae) from northern Madagascar. Both species are placed in the subgenus *Pandanusicola* Glaw & Vences, 1994 and, like most of their relatives, appear to only inhabit the leaf axils of *Pandanus* plants. *Guibemantis albomaculatus* sp. nov. is distinguished from other closely related species by light colored dorsolateral stripes and abundant small white spots found on its flanks and limbs. *Guibemantis woosteri* sp. nov. also has light-colored dorsolateral stripes and small white spots, but differs by having strongly banded forelimbs and a reddish coloration around the eye orbits. Mitochondrial DNA sequences corroborate the identity of these two new species, which appear to be regional endemics in northern and north-eastern Madagascar, respectively. These descriptions bring the species count in *Pandanusicola* to thirteen.

Keywords. Amphibia, *Pandanusicola*, new species, taxonomy, Madagascar

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Introduction

Madagascar has long been known as a center of species richness and endemism, and no group better exemplifies this than amphibians. The island has 350 currently described species of frogs (AmphibiaWeb 2018), except for two introduced species [*Hoplobatrachus tigerinus* (Daudin, 1802) and *Duttaphrynus melanostictus* (Schneider, 1799)] and one other species also occurring on the Mascarenes and Seychelles [*Ptychadena mascareniensis* (Duméril & Bibron, 1841)], all of these are endemic to the island (Glaw & Vences 2007; Andreone 2014). In addition, numerous genetically divergent lineages have already been identified as candidate species awaiting taxonomic revision (Vieites *et al.* 2009; Perl *et al.* 2014), and despite decades of taxonomic work, new species are still being regularly described.

One example of a taxonomically long neglected group with a high proportion of undescribed diversity is the subgenus *Pandanusicola* Glaw & Vences, 1994 of the genus *Guibemantis* Dubois, 1992 (Mantellidae). These small frogs are inhabitants of the water-filled leaf axils of *Pandanus* plants (except for two pond-breeding species *G. liber* (Peracca, 1893) and *G. tasifotsy* Lehtinen, Glaw, Andreone, Pabijan & Vences, 2012), are often drably colored and have inconspicuous advertisement calls. As with many other amphibians in Madagascar and in other tropical regions, molecular analyses have suggested the presence of taxonomically undescribed but genetically well-differentiated lineages (Lehtinen *et al.* 2007; Vieites *et al.* 2009). Presently, there are eleven species in this subgenus, four of which have been described or resurrected recently (Lehtinen *et al.* 2011, 2012; Vences *et al.* 2013; Bletz *et al.* 2018). Most of these species were from south-eastern or central-eastern Madagascar, whereas many of the unstudied new lineages of *Pandanusicola* come from localities in the northern portion of the island, an area of high environmental heterogeneity and high degrees of local endemism in many groups of amphibians and reptiles (e.g., Brown *et al.* 2016). Herein, we describe two additional new species of *Pandanusicola* which apparently are restricted to northern Madagascar.

Material and methods

Morphological measurements

The following morphological measurements were taken with digital calipers to the nearest 0.1 mm:

ED	=	horizontal eye diameter
END	=	eye-nostril distance
FGL	=	femoral gland length (in males only)
FGW	=	femoral gland width (in males only)
FL	=	femur length
FOL	=	foot length
HAL	=	hand length
HL	=	head length
HW	=	head width
IND	=	internarial distance
IOD	=	interorbital distance
LAL	=	lower arm or forearm length
NSD	=	nostril-snout tip distance
SVL	=	snout-vent length
TD	=	horizontal tympanum diameter
TL	=	tibia length
W3FD	=	maximum width of the third finger disc
W4FD	=	maximum width of the fourth toe disc

When mean values are presented, they are followed by the standard deviation (SD). Abbreviations and definitions of morphological features follow Vences & Glaw (2005), except where noted above. We also examined all specimens for the presence, position and/or shape of the inner and outer metatarsal tubercles, subarticular tubercles, lateral metatarsalia, canthus rostralis, tongue, vomerine teeth, and the supratympanic fold. Finger and toe webbing was quantified following Blommers-Schlösser (1979). Femoral gland terminology follows Glaw *et al.* (2000). Overall dorsal and ventral coloration and skin texture were also assessed in detail for each specimen.

Institutional abbreviations

MNHN	=	Muséum national d'Histoire naturelle, Paris, France
UADBA	=	Université d'Antananarivo, Département de Biologie Animale (currently Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo), Antananarivo, Madagascar
UMMZ	=	University of Michigan, Museum of Zoology, Ann Arbor, USA
ZFMK	=	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMA	=	Zoologisch Museum Amsterdam (transferred to Naturalis Biodiversity Center in Leiden), Netherlands
ZSM	=	Zoologische Staatssammlung München, Germany

FGMV, FGZC and ZCMV refer to F. Glaw and M. Vences field numbers.

Laboratory and phylogenetic reconstruction methods

We used standard salt extraction (Bruford *et al.* 1992) to extract genomic DNA from muscle tissue samples preserved in 99% ethanol and sequenced a segment of the 16S rRNA gene using primers and protocols as in Vences *et al.* (2013). PCR products were cleaned with enzymatic purification: incubation with 0.15 units of Shrimp Alkaline Phosphatase (SAP) and 1 unit of Exonuclease I (New England Biolabs) for 15 min at 37°C followed by 15 min at 80°C. Purified PCR products were sequenced on an automated DNA sequencer (Applied Biosystems, ABI 3130XL). Sequencing reactions (10 µl) contained 0.2 or 0.3 µl of PCR product, 0.5 µl of BigDye 3.1 (Applied Biosystems) and 0.3 µmol of primer. Sequences were checked and edited in the software CodonCode Aligner 3.7.1 (CodonCode Corporation, Dedham, MA, USA). Newly determined sequences were submitted to GenBank (accession numbers MH279456–MH279469).

We aligned sequences to those from previous studies (representing all valid species of *Guibemantis*) in MEGA, version 7 (Kumar *et al.* 2016). Pairwise genetic distances were calculated with the same software. We determined the best-fitting substitution model (SYM+I+G) by the Bayesian Information Criterion in jModelTest 2.1.4 (Darriba *et al.* 2012). We computed a phylogenetic tree by Bayesian inference with MrBayes 3.2 (Ronquist *et al.* 2012). Results of two independent runs of 50 million generations, each comprising four Markov Chains (three heated and one cold), were sampled every 10000 generations. Chain mixing and stationarity was assessed by examining the standard deviation of split frequencies and by plotting the -lnL per generation using Tracer 1.5 software (Rambaut & Drummond 2007). Results were combined to obtain a 50%-majority rule consensus tree and the respective posterior probabilities of nodes, after discarding 25% of the generations as burn-in (all compatible nodes with probabilities < 0.5 kept). In addition, we computed a Maximum Likelihood tree with a simpler substitution model (Kimura-2-Parameter) in MEGA 7 to avoid possible over-parametrization, and tested robustness of nodes with 500 non-parametric bootstrap replicates.

Results

The starting point of our species delimitation procedure in *Pandanusicola* frogs is an assessment of their variation in mitochondrial DNA. Our tree based on 16S sequences (Fig. 1) agrees with previous

analyses of relationships among *Pandanusicola* in that it does not satisfyingly resolve most of the nodes within the subgenus, but it is here included mainly to illustrate the amount of genetic divergence among species, as represented by the branch lengths in the tree. The tree recovered the previously assessed relationships (*G. flavobrunneus* Blommers-Schlösser, 1979 sister to *G. pulcher* (Boulenger, 1882) and *G. punctatus* (Blommers-Schlösser, 1979) in a clade with the recently described *G. milingilingy* Bletz, Scherz, Rakotoarison, Lehtinen, Glaw & Vences, 2018). Our analysis includes single representatives of all described species of *Pandanusicola*, as well as multiple samples for the two target lineages from northern Madagascar. We found all individuals of the target lineages forming genetically homogeneous monophyletic groups, representing (1) individuals from the Marojejy Massif, and (2) individuals from the Manongarivo and Montagne d'Ambre Massifs (see map in Fig. 2). Samples from Montagne d'Ambre and Manongarivo differed by only shallow divergences of 0.2% (uncorrected pairwise distances in the

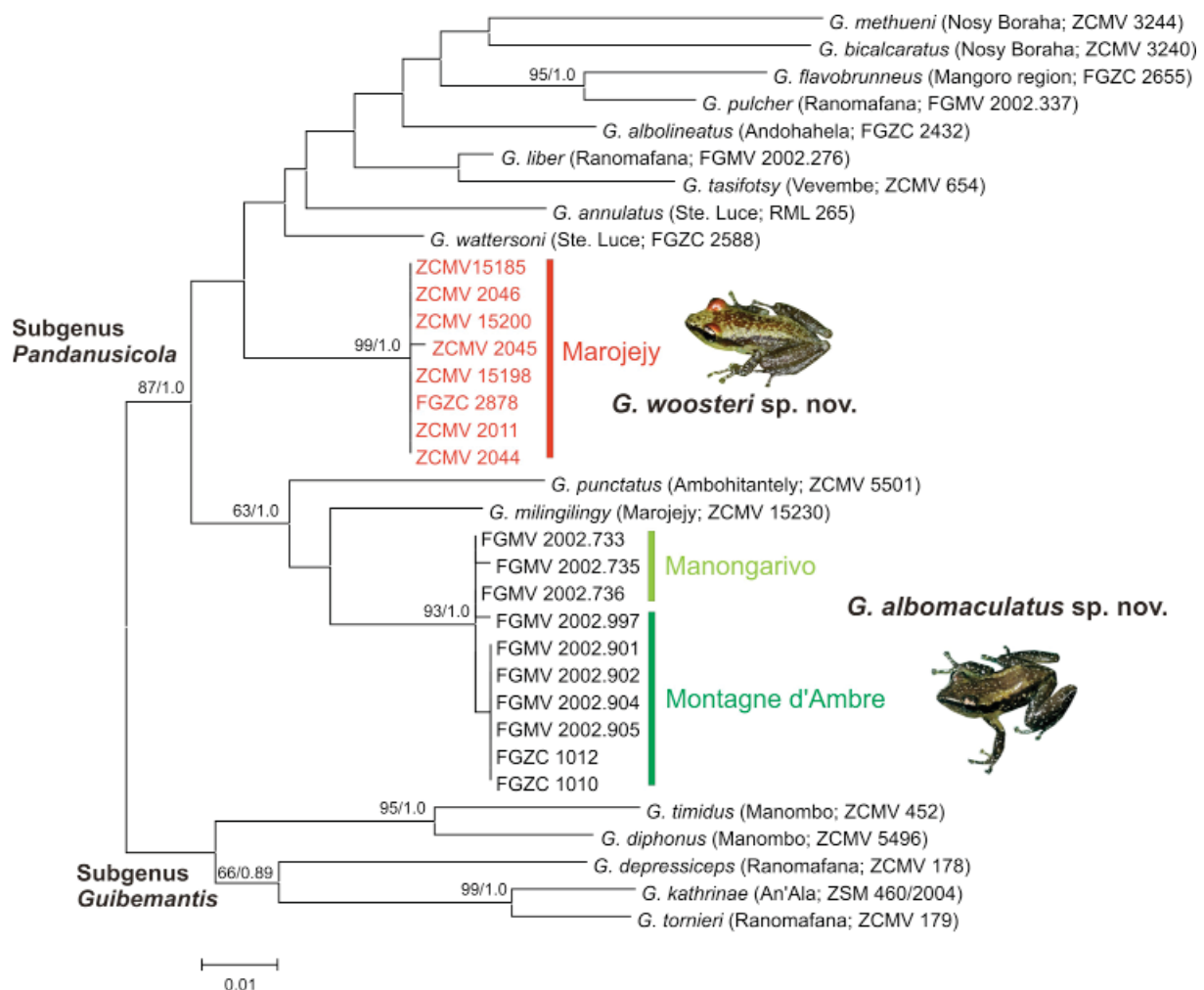


Fig. 1. Maximum Likelihood tree of species in the genus *Guibemantis* Dubois, 1992, subgenus *Pandanusicola* Glaw & Vences, 1994 (rooted with the nominal subgenus). The tree is based on an analysis of 535 bp of the mitochondrial 16S rRNA gene and contains representatives of all valid species of *Guibemantis*. Numbers at nodes are bootstrap proportions from a Maximum Likelihood bootstrap analysis (500 replicates) in percent (BP), and posterior probabilities (PP) from Bayesian Inference (only shown for nodes with either BP > 60% or PP > 0.95). Inset photos show the two new species described herein.

16S gene). The Ambre/Manongarivo lineage was placed sister to *G. milingilingy*; it differed from this species by 4.0–4.3%, and by >5% from all other species including *G. punctatus* which bears some morphological similarities (see below). The Marojejy lineage had the lowest distance to *G. wattersoni* Lehtinen, Glaw & Vences, 2011 (4.1%) and to the morphologically highly distinct *G. liber* (4.8%), and >5% to all other species.

Phylogenetically, the Marojejy lineage had an unresolved position in the tree, splitting from a rather basal node within *Pandanusicola*. The Montagne d'Ambre/Manongarivo lineage was placed in a clade with *G. milingilingy* and *G. punctatus*. In both cases, the long branches of these lineages are indicative of a substantial genetic divergence to all other valid species of the subgenus.

The combined evidence from the high genetic divergences of these lineages in the 16S gene, clearly above the 3% threshold proposed to define candidate species in Malagasy frogs (Vieites *et al.* 2009), their unresolved phylogenetic position suggesting they are not close relatives of any described species,

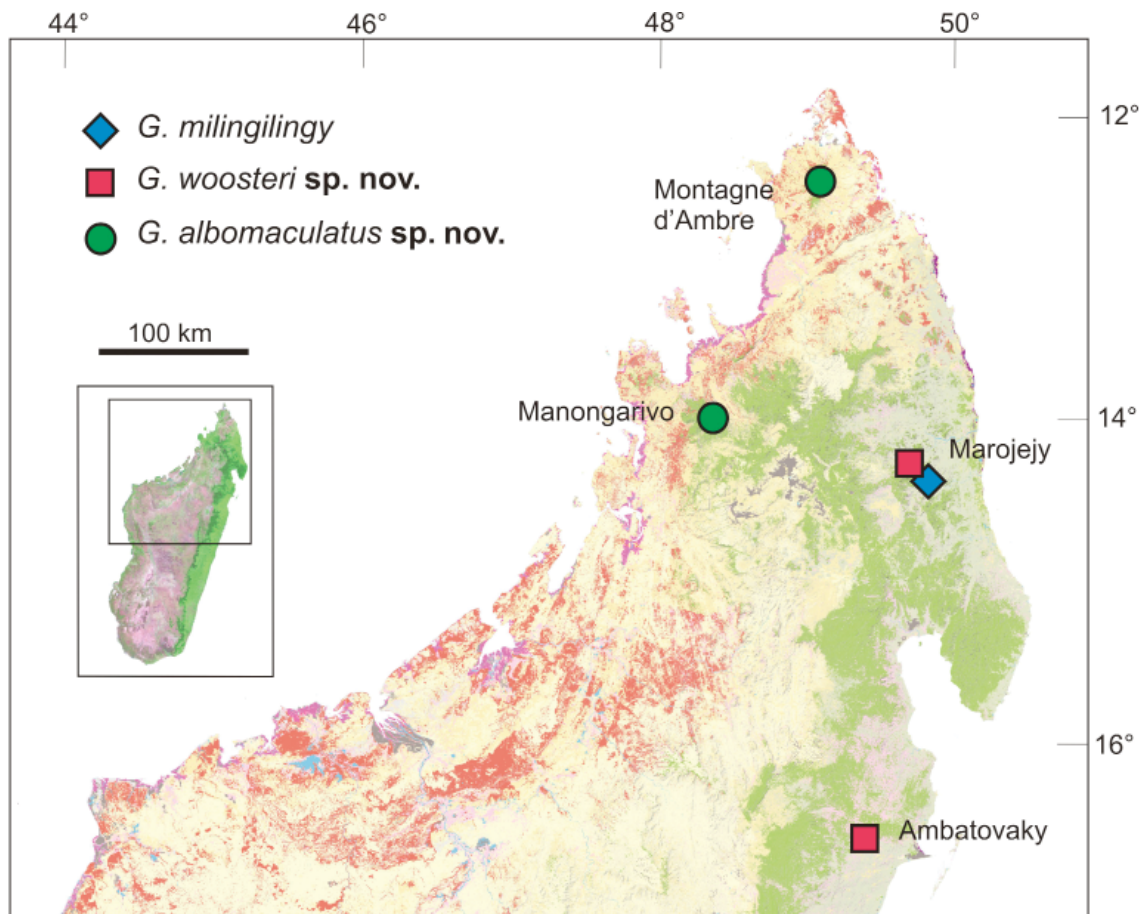


Fig. 2. Map of northern Madagascar, showing mostly verified distribution records of the two species of *Guibemantis* Dubois, 1992 described herein, and of the recently described *G. milingilingy* Bletz, Scherz, Rakotoarison, Lehtinen, Glaw & Vences, 2018. The locality Ambatovaky is only based on similarities in coloration and is in need of confirmation. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry forest.

and their differentiation in color pattern from other *Pandanusicola* (see below), suggest a status of independent evolutionary lineages warranting description as new species. In the following we formalize this conclusion and describe these lineages as *Guibemantis albomaculatus* sp. nov. and *G. woosteri* sp. nov.

Description of new species

Order Anura Fischer von Waldheim, 1813
Family Mantellidae Laurent, 1946
Genus *Guibemantis* Dubois, 1992
Subgenus *Pandanusicola* Glaw & Vences, 1994

***Guibemantis albomaculatus* sp. nov.**

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Figs 1–4

Suggested common name: White-spotted Malagasy *Pandanus* Frog.

Diagnosis

Assigned to the subgenus *Pandanusicola* of the genus *Guibemantis* based on its small body size, phytotelm-breeding habitats (in *Pandanus* plants), moderate webbing between toes, connected lateral metatarsalia, the presence of both inner and outer metatarsal tubercles, type 2 femoral glands in males, and DNA sequence similarities (Glaw & Vences 2006). The new species is characterized by the unique combination of the following characters: (1) male SVL 18.9–22.9 mm, female SVL 20.9–26.7 mm, (2) two conspicuous parallel light-colored dorsolateral lines on the dorsum, (3) small white spots on the darkly colored arms, legs and flanks, (4) dark ventral surfaces to hands and feet, (5) distinct rostral stripe and (6) orange femoral glands.

Etymology

The specific epithet is used as a descriptive adjective and refers to the small white spots present on the arms, legs and flanks.

Material examined

Holotype

MADAGASCAR: adult ♂, Montagne d'Ambre National Park, northern Madagascar [geographical coordinates not taken, but most likely from a *Pandanus* plant very close to the Gîte d'étape (12.5270° S, 49.1720° E, 1055 m a.s.l.) or less likely from the Voie des mille arbres (ca 12.5200° S, 49.1756° E, 1052 m a.s.l.)], 18 Feb. 2003, F. Glaw, R.D. Randrianiana and A. Razafimanantsoa leg. [ZSM 0895/2003 (FGMV 2002.905)] (Fig. 3).

Paratypes (n = 19)

MADAGASCAR: 5 specs, Manongarivo Special Reserve, 20 Feb. 1992, C.J. Raxworthy, A. Raselimanana and J.B. Ramanamanjato leg. (UMMZ 212592–212596); 1 spec., Montagne d'Ambre National Park, Antomboka River, 1150 m a.s.l., 15 Nov. 1991, C.J. Raxworthy, A. Raselimanana and J.B. Ramanamanjato leg. (UMMZ 212585); 3 specs Montagne d'Ambre National Park, Antomboka River, 950 m a.s.l., 21 Nov. 1991, C.J. Raxworthy, A. Raselimanana and J.B. Ramanamanjato leg. (UMMZ 212587, UMMZ 212588, UMMZ 212591); 2 specs Manongarivo Special Reserve, “Camp 0”, 13.9756° S, 48.4267° E, 688 m a.s.l., 1–2 Feb. 2003, F. Glaw, R.D. Randrianiana and M. Vences leg. [ZSM 0816/2003 (FGMV 2002.735), ZMA 19582 (FGMV 2002.733)]; 1 spec., same collecting data as for preceding (UADBA uncatalogued, FGMV 2002.736); 1 spec., Montagne d'Ambre National

Park, 12.5275° S, 49.1725° E, 1010 m a.s.l., 19 Mar. 2000, F. Glaw, K. Schmidt and M. Vences leg. [ZSM 496/2000 (FGMV 2000.356)]; 4 specs, Montagne d'Ambre National Park, same collection data as for holotype [ZSM 0893/2003 (FGMV 2002.0901), ZSM 0894/2003 (FGMV 2002.0904), UADBA uncatalogued (FGMV 2002.902), and ZMA 19660 (FGMV 2002.997)]; 1 ♀ [UADBA uncatalogued (FGZC 1010)] and 1 juv. [UADBA uncatalogued (FGZC 1012)], Montagne d'Ambre National Park, Voie des mille arbres, 12.5167° S, 49.1767° E, 1050 m a.s.l., 23 Feb. 2007, F. Glaw, P. Bora, H. Enting, J. Köhler and A. Knoll legs.

The six paratypes from UADBA and ZMA were not available for morphometric comparison, but were sequenced and attributed genetically to *G. albomaculatus* sp. nov. (see Fig. 1).

Description of the holotype

Adult male. Head longer than wide and slightly wider than body; snout rounded in dorsal, ventral and lateral views; canthus rostralis rounded; nostrils much nearer to tip of snout than to eye, internarial distance 83% of interorbital distance; tympanum distinct 42% of horizontal eye diameter; dark supratympanic fold present from posterior edge of eye around the tympanum nearly to the arm insertion; one small round patch of vomerine teeth medial between eye and choanae on either side of head; tongue damaged, shape of tip unknown. Arms thin, lower arm is 91% of hand length; relative finger length $1 < 2 < 4 < 3$, finger discs moderately enlarged and squared off at tips in a rounded 'T' shape, only traces of webbing between fingers, subarticular tubercles prominent. Hindlimbs relatively thin, femur length 85% of tibia length, foot length 83% of tibia length; lateral metatarsalia connected; inner metatarsal tubercle oblong in shape (0.6 mm in length, 0.3 mm in width); outer metatarsal tubercle round (0.4 in diameter); webbing formula between toes 1(1) 2i(1) 2e(1) 3i(2) 3e(1.5) 4i(3) 4e(3) 5(1.5); relative length of toes $1 < 2 < 5 < 3 < 4$; toe discs moderately enlarged, width of fourth toe disc 58% of width of third finger disc. Femoral glands distinct, oblong in shape (4.4 mm long, 1.7 mm wide) with approximately 35 granules contained inside. Cloaca not clearly recognizable; skin is finely granular dorsally, more roughly granular ventrally. There is also a patch of whitish granules on the belly. For morphometric measurements see Table 1.

After seven years in preservative, the dorsal background coloration is medium brown which contrasts with the darker brown flanks. Two prominent light dorsolateral lines separate the medium brown color of the dorsum from the dark brown of the flanks. A single, relatively thick rostral stripe is present. Dorsal color of arms, legs, hands and feet is medium brown with abundant small white spots throughout. Vague light annuli are found on some digits just proximal to the finger and toe discs but are not prominent. Toe and finger discs have a similar dark coloration as the dorsal surface of the hands and feet, except for the discs of fingers I and II, which have a much lighter coloration. Venter is cream with abundant brown spots along jawline, chin and especially on the ventral surface of the hindlimbs. The pupil appears black and the iris is white.

Coloration in life

The life coloration of the holotype is unknown. However, based on photographs of live individuals from Manongarivo and Montagne d'Ambre (Fig. 4), there appear to be a number of coloration differences compared to preserved material. In life, the iris color is gold or bronze (white or gray in preservative). Portions of the arms and fingers as well as lateral areas of the head have a yellow or yellow-green color in life (beige in preservative). The more lightly colored toe and finger discs are a dull yellow (beige or whitish in preservative). The ventral skin is largely translucent such that chest and belly musculature and bones in the limbs are easily visible (not apparent in preservative). In males, femoral glands (type 2, as defined by Glaw *et al.* 2000) appear orange in life. Sexually mature males also possess a distinct white coloration on the lateral portions of the throat. A color photograph of a specimen of this species from Manongarivo is shown in Glaw & Vences (2007: 203, fig. 4).



Guibemantis woosteri sp. nov.
ZSM 5063/2005



Guibemantis albomaculatus sp. nov.
ZSM 895/2003

Fig. 3. Preserved holotype specimens of the two new species described herein, *Guibemantis woosteri* sp. nov. [ZSM 5063/2005 (ZCMV 2044)] and *G. albomaculatus* sp. nov. [ZSM 0895/2003 (FGMV 2002.905)], in dorsal and ventral view. Scale bars = 5 mm.

Variation

The new species is similarly sized to most other *Pandanusicola* (overall mean SVL 22.8 ± 2.1 mm, $n = 15$). Females appear to be larger on average than males (female mean SVL 24.0 ± 1.7 mm, $n = 9$; male mean SVL 21.3 ± 1.5 mm, $n = 6$). While all individuals seem to possess a dark rostral stripe, some individuals have an additional gold colored one medial to the first. The small white spots on the dorsal surface of the arms, legs and flanks also vary in coverage and density among individuals. Some individuals only possess them in abundance on the hindlimbs and sparingly elsewhere. Other individuals have an abundance of these spots not only on both limbs and the flanks, but also on the back and head as well. While yellowish dorsal coloration is present in all known individuals, the dorsal base color intermixed with it differs among individuals. Most individuals have a dorsal base color of medium to dark brown but one individual was notably lighter than other specimens examined (Fig. 4B). The prominence and length of the two parallel dorsal lines also varies among individuals, with those from Manongarivo typically being more distinct. Some individuals possess a small but distinct light-colored spot between the eyes, other individuals lack this feature. Many individuals possess no obvious markings on the dorsum but a few have several vague dark splotches. On the ventral surface, most individuals possess fine brown spots on the jawline and on the undersurface on the limbs. Other individuals have these spots on the throat and chest as well. No variation was observed in the webbing on the hand. However, webbing on the foot was variable for some digits (range, where variable, given in parentheses): 1(1) 2i(1) 2e(1) 3i(2) 3e(1–2) 4i(3) 4e(2.75–3) 5(1–2). The distinct light-colored annuli present before the terminal phalange of each digit, that are prominent in some *Pandanusicola*, are usually only weakly developed but can be conspicuous in some individuals.

Differential diagnosis

Among *Pandanusicola*, the new species is distinguished from *G. annulatus* Lehtinen, Glaw & Vences, 2011, *G. bicalcaratus* (Boettger, 1913), *G. flavobrunneus*, *G. liber*, *G. pulcher*, *G. punctatus* and *G. tasifotsy* by the presence of two conspicuous parallel light-colored dorsolateral lines, by the presence of small white spots on more darkly colored arms, legs and flanks and by large genetic differences. By comparison, *G. pulcher* is a characteristic bright green in color with large irregular dark dorsal spots; *G. bicalcaratus* is yellowish or brownish dorsally with usually relatively few irregularly shaped dark spots; *G. flavobrunneus* is much larger (up to 38 mm SVL; Glaw & Vences 2007) and is primarily yellow with extensive brown dorsal markings; *G. liber* is rather variable in coloration but tends to be brownish overall, the entire surface of the throat of males is bright white, and this species does not breed in *Pandanus* plants; *G. tasifotsy* does not breed in *Pandanus* either and has a copper metallic coloration on the nares and/or eye orbits and prominent white lateral blotches; *G. annulatus* and *G. punctatus* are cream or olive-colored (respectively) and have abundant small dark spots; *G. methueni* (Angel, 1929) and *G. wattersoni* can have parallel dorsolateral light colored lines on the dorsum but most individuals lack this feature and it is usually poorly developed in those individuals that possess it. Furthermore, *G. wattersoni* is primarily a yellow or light brownish frog dorsally and the flanks and legs in *G. wattersoni* are always lightly colored whereas they are typically very dark in the new species. In *G. methueni*, the ventral surfaces of the hands and feet are very lightly colored, whereas they are dark in the new species. *Guibemantis albolineatus* (Blommers-Schlösser & Blanc, 1991) lacks both vomerine teeth and a rostral stripe (both present in the new species), has a distinctly shaped snout that is square in dorsal and ventral view and is notably smaller in overall body size (see Table 1). The recently described *G. milingilingy* differs by lacking white spots (present in the new species), by having banded forelimbs (unbanded in the new species), by having yellow femoral glands in males (orange in the new species) and by having a mid-dorsal stripe (absent or poorly developed in the new species). No other described species of *Pandanusicola* has the combination of light colored parallel dorsal lines with small white spots on the dark unbanded arms, legs and flanks.

Table 1 (continued on next page). Morphometric data (in mm) of available specimens of the two new species, *Guibemantis albomaculatus* sp. nov. (n = 15), and *G. woosteri* sp. nov. (n = 14), as well as comparative specimens of *G. albolineatus* (Blommers-Schlösser & Blanc, 1991) (n = 7). HT = holotype, PT = paratype, LT = lectotype, PLT = paralectotype, SD = standard deviation; see Material and methods for other abbreviations.

Catalogue Number	Locality	Status	Sex	SVL	FL	TL	FOL	HL	HW	HAL	HAL/SVL	LLA	TD	ED	FGW	FGL	W3FD	W4TD	IOD	NSD	END	IND
<i>G. albomaculatus</i> sp. nov.																						
UMMZ 212592	Manongarivo	PT	♀	24.1	11.0	12.1	10.0	8.1	8.2	6.1	0.3	4.7	1.4	2.9	–	–	0.8	0.6	2.9	0.6	3.0	2.4
UMMZ 212593	Manongarivo	PT	♀	24.5	10.4	11.3	9.3	8.3	8.4	6.9	0.3	5.1	1.6	2.9	–	–	0.9	0.9	3.5	0.8	2.8	1.9
UMMZ 212594	Manongarivo	PT	♀	25.3	10.6	12.4	10.3	8.7	8.8	6.5	0.3	4.4	1.5	3.1	–	–	1.1	0.8	3.2	0.7	2.7	2.0
UMMZ 212595	Manongarivo	PT	♂	21.6	9.4	10.9	9.1	7.7	6.6	6.1	0.3	4.5	1.5	2.8	1.0	5.1	0.7	0.6	2.6	0.6	2.2	2.2
UMMZ 212596	Manongarivo	PT	♂	18.9	8.7	9.9	8.3	7.3	6.3	5.7	0.3	3.9	1.2	2.5	1.4	4.1	1.0	0.8	2.9	0.9	2.4	1.9
ZSM 0816/2003 / FGMV 2002.735	Manongarivo	PT	♂	22.4	10.2	11.1	9.3	7.8	7.5	5.7	0.3	5.2	1.3	2.9	–	–	1.2	1.0	3.3	0.9	2.7	2.3
UMMZ 212585	Montagne d'Ambre	PT	♂	22.9	10.1	10.5	9.3	7.7	7.9	6.0	0.3	5.7	1.5	2.8	1.3	4.9	0.9	0.8	3.4	0.7	2.7	2.2
UMMZ 212587	Montagne d'Ambre	PT	♀	24.3	11.1	12.0	10.5	9.2	8.4	6.4	0.3	4.7	1.3	3.1	–	–	0.9	0.6	3.2	0.7	2.9	1.5
UMMZ 212588	Montagne d'Ambre	PT	♂	20.0	9.2	9.5	8.0	6.7	6.9	4.7	0.2	3.6	1.2	2.5	1.5	3.7	0.9	0.6	2.9	0.9	2.4	1.8
UMMZ 212591	Montagne d'Ambre	PT	♀	26.7	11.3	12.8	11.0	9.7	9.3	6.6	0.2	5.1	1.2	2.9	–	–	0.7	0.5	3.1	0.5	2.9	2.2
ZSM 496/2000 / FGMV 2000.356	Montagne d'Ambre	PT	♀	22.2	9.5	10.4	9.4	6.7	7.9	5.5	0.2	4.7	1.2	2.8	–	–	1.1	0.6	3.0	0.9	2.5	2.3
ZSM 0874/2003 / FGMV 2002.869	Montagne d'Ambre	PT	♀	24.4	10.8	11.7	10.7	8.0	8.9	6.5	0.3	5.6	1.2	3.6	–	–	1.4	0.9	3.7	1.0	2.7	2.5
ZSM 0893/2003 / FGMV 2002.901	Montagne d'Ambre	PT	♀	23.3	9.4	10.6	10.1	7.8	7.7	6.5	0.3	4.9	1.1	2.8	–	–	1.2	0.8	3.6	0.8	2.4	2.4
ZSM 0894/2003 / FGMV 2002.904	Montagne d'Ambre	PT	♀	20.9	9.2	10.2	8.8	7.9	7.1	4.6	0.2	4.4	1.0	2.8	–	–	0.8	0.6	2.5	0.9	2.3	2.4
ZSM 0895/2003 / FGMV 2002.905	Montagne d'Ambre	HT	♂	22.0	9.0	10.6	8.8	7.1	7.6	5.6	0.3	5.1	1.1	2.6	1.4	4.4	1.2	0.7	2.9	0.8	2.3	2.4
<i>G. woosteri</i> sp. nov.																						
UMMZ 212601	Marojejy	PT	♂	21.8	10.2	11.4	9.9	7.9	7.0	6.1	0.3	5.1	1.3	3.2	1.4	4.8	0.9	0.7	2.9	1.0	2.5	2.0
UMMZ 212602	Marojejy	PT	♂	21.5	9.9	11.2	9.9	7.5	6.9	6.1	0.3	4.4	1.3	2.8	1.3	4.4	0.9	0.8	2.9	0.7	2.6	2.4
UMMZ 212604	Marojejy	PT	♂	21.8	9.8	11.0	10.1	8.5	7.3	5.7	0.3	4.6	1.4	3.2	1.5	4.7	0.9	0.6	2.6	0.8	2.2	1.9
UMMZ 212605	Marojejy	PT	♂	21.1	9.5	10.5	9.5	7.0	7.4	6.1	0.3	4.7	1.2	2.8	1.7	5.1	1.0	0.8	2.8	0.8	2.1	2.2
UMMZ 212606	Marojejy	PT	♂	20.4	9.6	11.0	9.2	7.7	7.0	5.7	0.3	4.7	1.5	2.9	1.4	4.1	1.1	0.7	3.2	0.7	2.2	2.1
UMMZ 212613	Marojejy	PT	♀	23.9	10.5	11.6	9.0	8.0	7.5	6.3	0.3	4.5	1.4	3.0	–	–	1.0	0.8	3.1	0.7	2.3	2.2
UMMZ 212615	Marojejy	PT	♀	23.0	10.4	11.7	10.5	8.0	8.0	6.6	0.3	5.2	1.5	3.3	–	–	1.0	0.9	2.8	1.0	2.2	2.7
UMMZ 212617	Marojejy	PT	♀	22.5	10.1	11.5	10.2	8.2	7.0	5.7	0.3	5.1	1.6	2.6	–	–	0.8	0.8	3.1	0.7	2.4	2.2
UMMZ 191339	Ambatovaky Reserve	–	♂	21.7	10.4	11.5	8.6	8.3	6.8	5.3	0.2	4.4	1.2	2.8	1.7	4.2	0.8	0.7	2.8	0.9	2.6	2.2
UMMZ 191340	Ambatovaky Reserve	–	♀	24.5	10.8	12.1	10.1	9.0	7.1	6.2	0.3	4.3	1.3	2.9	–	–	0.9	0.6	3.1	1.2	2.9	2.3
UMMZ 191343	Ambatovaky Reserve	–	♂	21.5	9.5	10.2	8.1	7.7	6.7	5.2	0.2	3.7	1.3	3.0	1.2	4.1	0.7	0.6	2.8	0.8	2.8	1.9

Table 1 (continued).

Catalogue Number	Locality	Status	Sex	SVL	FL	TL	FOL	HL	HW	HAL	HAL/SVL	LLA	TD	ED	FGW	FGL	W3FD	W4TD	IOD	NSD	END	IND
UMMZ 191344	Anbatovaky Reserve	–	♂	19.4	9.2	10.4	9.2	7.6	6.0	5.4	0.3	4.8	1.1	2.9	1.1	3.7	1.0	0.6	2.8	0.7	1.8	2.0
ZSM 5062/2005 / ZCMV 2011	Marojejy	PT	♂	20.8	10.3	10.6	9.0	6.9	7.3	6.0	0.3	5.1	1.1	3.1	1.6	5.0	1.1	0.8	2.2	0.7	2.3	2.3
ZSM 5063/2005 / ZCMV 2044	Marojejy	HT	♀	24.9	10.5	11.5	10.1	8.8	8.3	5.8	0.2	5.4	1.3	3.4	–	–	1.2	1.1	3.3	1.1	2.7	2.6
<i>G. albolineatus</i> (Blommers-Schlösser & Blanc, 1991)																						
ZSM 171/2005 / FGZC 2432	Andohahela	–	♂	21.3	9.5	10.9	9.7	6.4	7.6	7.2	0.34	5.1	1.2	2.8	1.8	5.0	1.3	1.2	3.2	1.2	2.2	2.4
ZSM 172/2005 / FGZC 2433	Andohahela	–	♂	20.9	10.0	10.7	9.9	6.6	7.4	7.1	0.34	5.1	1.0	2.8	2.1	5.7	1.0	0.9	2.9	1.3	2.1	2.6
MNHN 1972.2074	Andohahela	PT	♂	19.8	9.1	9.8	7.4	6.7	6.8	5.5	0.28	4.3	1.1	2.5	1.4	4.7	1.0	0.9	2.4	0.8	2.1	2.3
MNHN 1972.2082	Andohahela	PT	♀	19.0	8.0	9.8	8.9	7.4	6.9	5.5	0.29	4.7	1.1	2.6	–	–	0.9	0.8	2.8	0.6	2.1	2.3
MNHN 1972.2077	Andohahela	PT	♀	22.2	9.3	10.8	9.0	7.5	7.2	6.2	0.28	4.9	1.0	2.9	–	–	1.2	0.8	3	0.6	2.2	2.7
MNHN 1972.2079	Andohahela	PT	juv.	16.2	7.8	8.9	7.9	5.8	6.5	5.2	0.32	4.5	1.0	2.9	–	–	0.9	0.5	2.5	0.7	1.9	2.3
MNHN 1972.2080	Andohahela	PT	♀	18.9	9.1	9.5	8.2	5.7	6.4	5.6	0.30	4.4	1.0	2.5	–	–	1.0	0.7	2.5	0.8	2.0	2.4

Distribution

At present *G. albomaculatus* sp. nov. is known from rainforest habitats in two areas: the Manongarivo Special Reserve (type locality) and Montagne d'Ambre National Park, both in northern Madagascar (Fig. 2). The elevational range so far documented is from 950–1150 m.

Based on the limited knowledge of the distribution, we suggest a conservation status of "Data Deficient".

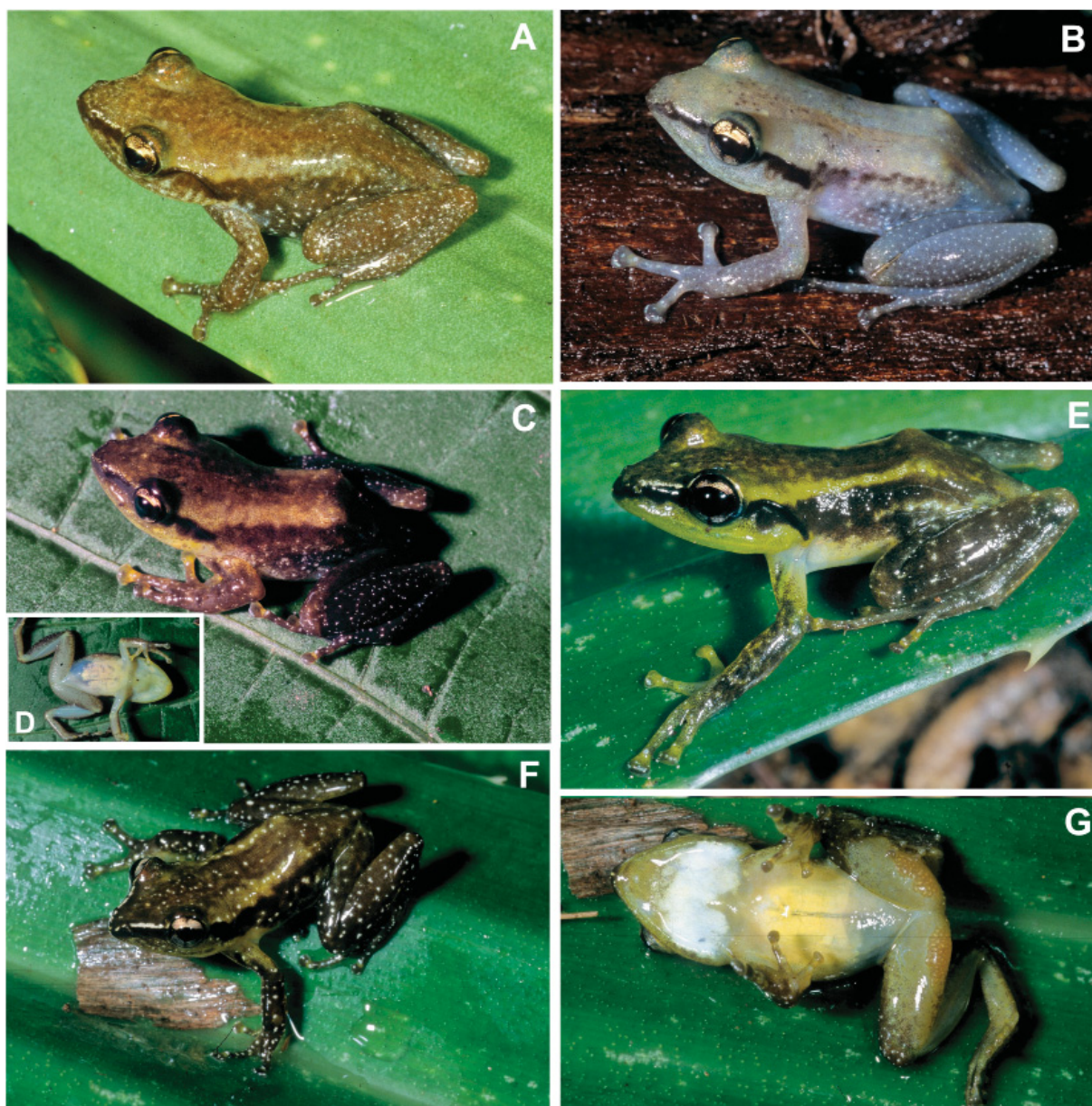


Fig. 4. *Guibemantis albomaculatus* sp. nov. in life. **A–B.** Two specimens with unknown sex or voucher numbers from Montagne d'Ambre. **C–D.** ♀, from Montagne d'Ambre, probably ZSM 894/2003 (FG/MV 2002.904). **e.** Specimen from Manongarivo with unknown sex or voucher number. **F–G.** ♂, from Manongarivo, ZSM 816/2003 (FG/MV 2002.735).

Natural history

Little is known of the natural history of this species. Specimens have only been collected from *Pandanus* plants and are probably obligate *Pandanus* breeders, like most other species in this group. Vocalizations have not been recorded and eggs and larvae have yet to be documented.

Available names and comparisons

The only available synonyms that could possibly be applied to this species are *Gephyromantis albogularis* Guibé, 1947 and *Gephyromantis variabilis* Millot & Guibé, 1951, both of which were confidently assigned to *Guibemantis liber* by Lehtinen *et al.* (2011).

Males of *Guibemantis liber* have a throat that is bright white over its entire surface. The whitish coloration on the throat of males in *G. albomaculatus* sp. nov. does not cover the entire surface nor is it as brightly white as in *G. liber*.

Remark

This species has been previously listed as *Guibemantis* sp. aff. *albolineatus* “Manongarivo” in Glaw & Vences (2007: 202–203), *Guibemantis bicalcaratus* (Manongarivo) in Lehtinen *et al.* (2007) and *Guibemantis* sp. Ca12 in Vieites *et al.* (2009) and Perl *et al.* (2014).

Guibemantis woosteri sp. nov.

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Figs 1–3, 5

Suggested common name: Wooster’s Malagasy *Pandanus* Frog.

Diagnosis

Assigned to the subgenus *Pandanusicola* of the genus *Guibemantis* based on its small body size, phytotelm-breeding habitats (in *Pandanus* plants), moderate webbing between toes, connected lateral metatarsalia, the presence of both inner and outer metatarsal tubercles, type 2 femoral glands in males, and DNA sequence similarities (Glaw & Vences 2006). The new species is characterized by the unique combination of the following characters: (1) male SVL 19.4–21.8 mm, (2) two fairly conspicuous parallel light-colored dorsolateral lines on the dorsum, (3) well-defined dark bars on the forearms and sometimes on the legs, (4) a conspicuous light area near the forearm insertion, (5) dark ventral surfaces to hands and feet, (6) thick, single dark rostral stripe, (7) distinctly reddish color dorsally surrounding the eyes, (8) white spots of the dorsum and limbs and (9) gray femoral glands in males.

Etymology

This new species is dedicated to the College of Wooster and its faculty, staff, students and alumni in celebration of 150 years of educational excellence.

Material examined

Holotype

MADAGASCAR: adult ♀, Marojejy National Park at “Camp Simpona”, 14.437° S, 49.743° E, 1326 m a.s.l., 18 Feb. 2005, F. Glaw, M. Vences and R.D. Randrianiana leg. [ZSM 5063/2005 (ZCMV 2044)] (Fig. 3).

Paratypes (n = 15)

MADAGASCAR: 8 adults, Manantenina River in Marojejy National Park, 700–1300 m a.s.l., Nov. 1992, R.A. Nussbaum, C.J. Raxworthy, A. Razafimanantsoa and A. Razafimanantsoa leg. (UMMZ 212601–

212602, UMMZ 212604–212606, UMMZ 212613, UMMZ 212615, UMMZ 212617); adult ♂, same data as for holotype [ZSM 5062/2005 (ZCMV 2011)]; 1 ♀, Marojejy National Park, Camp 3 “Simpona”, 14.4366° S, 49.7434° E, 1325 m a.s.l., 17 Nov. 2017, M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences and J. Razafindraibe leg. [ZSM 425/2016 (ZCMV 15185)]; 1 ♂ and 1 juv., Marojejy, between Camp 2 “Marojejia” and Camp 3 “Simpona”, no coordinates taken, 18 Nov. 2016, M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences and J. Razafindraibe leg. [ZSM 426/2016 (ZCMV 15198), UADBA uncatalogued (ZCMV 15200)]; 1 spec., Marojejy National Park, same data as for holotype, but collected on 16 Feb. 2005 [(FGZC 2878), UADBA uncatalogued]; 1 spec., same data as holotype (ZCMV 2045); 1 spec., same data as holotype, but collected above Camp Marojejia (ZCMV 2046).

The paratypes from UADBA were not available for morphometric comparison, but were sequenced and attributed genetically to *G. woosteri* sp. nov. (see Fig. 1).

Referred specimens

Based on similarity in coloration (no genetic data available), we also tentatively assign to this species the series UMMZ 191339–191340 and UMMZ 191343–191344; adults from Ambatovaky Special Reserve (600–800 m), collected by C.J. Raxworthy on 21 February 1990.

Description of the holotype

Adult female. Head longer than wide and slightly wider than body; snout rounded in dorsal, ventral and lateral views; canthus rostralis rounded; nostrils very near to the tip of snout, internarial distance 79% of interorbital distance; tympanum distinct 38% of horizontal eye diameter; very dark and prominent supratympanic fold present from posterior edge of eye around the tympanum nearly to the arm insertion; one small round patch of vomerine teeth medial between eye and choanae on either side of head; tongue stout and strongly bifid. Arms thin, lower arm is 93% of hand length; relative finger length $1 < 2 < 4 < 3$, finger discs moderately enlarged and squared off at tips in a rounded ‘T’ shape, only traces of webbing between fingers, subarticular tubercles prominent. Hindlimbs relatively thin, femur length 91% of tibia length, foot length 88% of tibia length; lateral metatarsalia connected; inner metatarsal tubercle oblong, (0.8 in length, 0.3 in width); outer metatarsal tubercle round (0.3 in diameter); webbing formula between toes 1(1) 2i(1) 2e(1) 3i(2) 3e(2) 4i(2.75) 4e(3) 5(1.5); relative length of toes $1 < 2 < 5 < 3 < 4$; toe discs moderately enlarged, width of fourth toe disc 92% of width of third finger disc. Cloaca not clearly recognizable; skin is finely granular dorsally, more coarsely granular ventrally. For morphometric measurements see Table 1. A sample of muscle was taken from right leg for genetic analysis.

After 13 years in preservative, the dorsal background coloration is a medium brown with the flanks much darker brown. Starting at the snout tip, there is a distinct color change along the dorsolateral area (medium brown medially, dark brown laterally). A few vague light spots are present, but there are no conspicuous dorsal markings. A thick, dark rostral stripe is present. The dorsal surface of arms, hands and fingers is medium brown with darker bands on the forearms. Dorsal surface of legs, feet and toes is a uniform medium brown with no obvious markings. The skin on the upper arms near the articulation with the body conspicuously lacks any coloration and this contrasts markedly with the more distal portions of the arm that are darker. Finger discs are fairly dark brown dorsally and ventrally with some lighter areas (especially fingers I and II). Toe discs are similar. Fairly obvious white annuli are present on many digits. Ventral surface cream with dark spots on jawline and ventral surface of thighs, hands and feet.

Coloration in life

The life coloration of the holotype is unknown. However, based on photographs of live individuals from Marojejy (Fig. 5), there are several clear coloration differences compared to preserved specimens. The small white spots, often prominent in life, are not usually obvious after preservation in alcohol. The iris, which is gold in life, is white or gray in preservative. The portions of the limbs, dorsum and head,

medium brown in preservative, appear yellowish-green in life. Moreover, at least some individuals have a prominent red color on the eye orbits; there is no indication of this in preservative. The ventral skin is semi-translucent in life such that chest and belly musculature are visible (not apparent in preservative). In males, femoral glands (type 2, as defined by Glaw *et al.* 2000) appear gray in life with large granules in the gland, each of which has a white spot (Fig. 5C). Sexually mature males also possess a white coloration on portions of the throat.

Variation

Like most *Pandanusicola*, this new species is small (overall mean 22.1 ± 1.6 mm SVL, $n = 14$). Females are larger (mean 23.8 ± 1.0 mm SVL, $n = 5$) than males (mean 21.1 ± 0.8 mm SVL, $n = 9$) on average. Some individuals have relatively few small white dorsal spots (primarily on the hindlimbs), while others have dense spots over much of the dorsal surfaces (contrast Fig. 5A and 5B). The light dorsolateral lines on the dorsum are conspicuous in some individuals but much less so in others. Dark spotting on the dorsum also varies from none to many. Dark bars on legs vary from reasonably distinct (Fig. 5A) to inconspicuous (Fig. 5B). Head coloration can be variable also, with several specimens having a distinctly lighter coloration anterior to the eyes than posterior and one specimen possessed a distinct interocular bar. Many, but not all, specimens had a distinct light spot in the middle of the snout. The

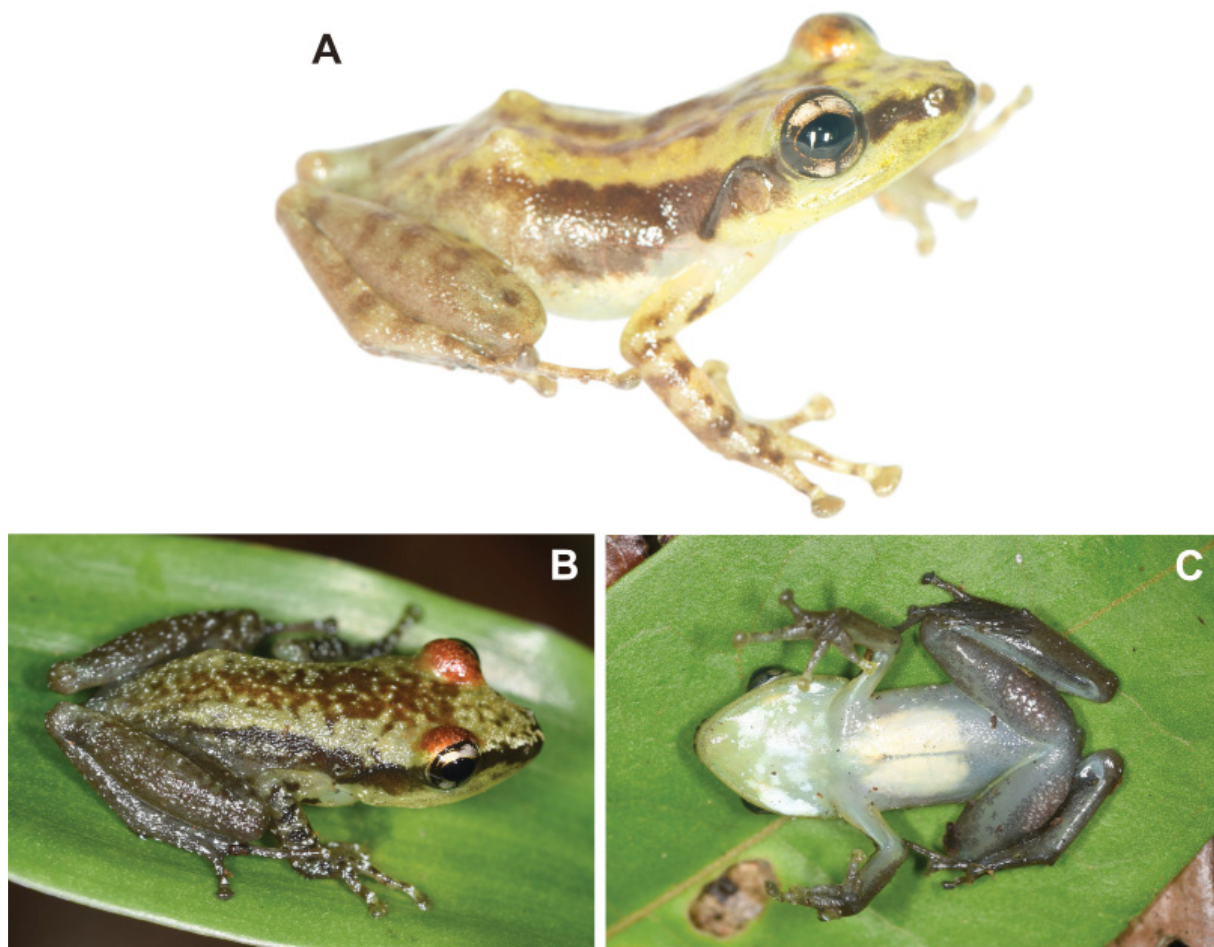


Fig. 5. *Guibemantis woosteri* sp. nov. in life. **A.** ZSM 425/2016 (ZCMV 15185) from Marojejy. **B–C.** ZSM 426/2016 (ZCMV 15198) from Marojejy in dorsolateral and ventral view.

color of the digits and toepads also varies. Some individuals have distinct dark bars on the digits and this seems to be an extension of the bars on the forearms. The color of the toepads is similarly variable with the pads on some digits being dark and other digits being light. A few individuals had indications of faint annuli on the digits proximal to the toepads or a second rostral line parallel to the first (as in *G. annulatus* and *G. wattersoni*), however, these are usually not well developed. Ventrally, coloration varies from having dark markings only along the jawline to individuals with dark spotting on the throat, chest and/or thighs. The ventral surfaces of the hands and feet are apparently always dark. One individual (UMMZ 212604) had especially rough granular patches on the belly, reminiscent of those recently described from *G. tasifotsy*. No variation was observed in the webbing on the hand. However, webbing on the foot was variable for some digits (range, where variable, given in parentheses): 1(1) 2i(1) 2e(1) 3i(2) 3e(1–2) 4i(2.5–3) 4e(2.5–3) 5(1–2).

Differential diagnosis

Among *Pandanusicola*, the new species is distinguished from *G. annulatus*, *G. bicalcaratus*, *G. flavobrunneus*, *G. liber*, *G. pulcher*, *G. punctatus* and *G. tasifotsy* by the presence of two conspicuous parallel dorsolateral light-colored lines on the dorsum, by the presence of small white spots on more darkly colored arms, legs and flanks and by large genetic differences. By comparison, *G. pulcher* is a characteristic bright green in color with large irregular dark dorsal spots; *G. bicalcaratus*, is yellowish or brownish dorsally with usually relatively few irregularly shaped dark spots; *G. flavobrunneus* is much larger (up to 38 mm SVL; Glaw & Vences 2007) and is primarily yellow with extensive brown dorsal markings; *G. liber* is rather variable in coloration but tends to be brownish overall, the entire surface of the throat of males is bright white, and this species does not breed in *Pandanus* plants; *G. tasifotsy* does not breed in *Pandanus* either, and has a copper metallic coloration on the nares and/or eye orbits and prominent white lateral blotches; *G. annulatus* and *G. punctatus* are cream or olive-colored, respectively, and have abundant small, well-defined dark spots; *G. methueni* and *G. wattersoni* can have parallel light-colored dorsolateral lines on the dorsum but most individuals lack this feature and, if present, it is usually poorly developed. Furthermore, *G. wattersoni* is a yellow or light brownish frog dorsally and its flanks and legs are always lightly colored whereas they are typically dark in the new species. In *G. methueni*, the ventral surfaces of the hands and feet are very lightly colored, whereas they are dark in the new species. *Guibemantis albolineatus* lacks both vomerine teeth and a rostral stripe (both present in the new species), has a distinctly shaped snout that is square in dorsal and ventral view and is notably smaller in overall body size (see Table 1). The recently described *G. milingilingy* differs by lacking the characteristic white spots on the dorsum and limbs (versus presence), by lacking the reddish colored skin on the eye orbits (versus presence) and by having yellow femoral glands in mature males (gray in the new species). Finally, *G. woosteri* sp. nov. differs from *G. albomaculatus* sp. nov. in having well-defined dark bars on the forearms and sometimes on the legs, a conspicuous light area near the forearm insertion (both of which *G. albomaculatus* sp. nov. lacks) and gray femoral glands in males with distinct white spots (femoral glands are orange in male *G. albomaculatus* sp. nov.). No other described species of *Pandanusicola* has the combination of light colored parallel dorsolateral lines with small white spots on the legs and flanks and well-defined dark bars on the forearms.

Distribution

Currently, *G. woosteri* sp. nov. is reliably known only from mid-elevation rainforests in Marojejy National Park, the type locality, in the North-East of Madagascar (Fig. 2), from roughly 700–1325 m a.s.l. In addition, we here consider specimens from the Ambatovaky Special Reserve in the Northern Central East of the island as possibly belonging to this species (Fig. 2), but this identification requires confirmation by molecular data.

Based on the limited knowledge of the distribution, we suggest a conservation status of "Data Deficient".

Natural history

Only known from *Pandanus* plants. One adult female attributed to this species (UMMZ 212617) had four visible eggs in the body cavity (egg diameter 0.8 mm) and another (UMMZ 191340; from Ambatovaky) had six (egg diameter 1.8 mm) possibly suggesting a small clutch size. Tadpoles and breeding vocalizations are unknown.

Available names and comparisons

The only available synonyms that could possibly be applied to this species are *Gephyromantis albogularis* Guibé, 1947 and *Gephyromantis variabilis* Millot & Guibé, 1951, both of which were confidently assigned to *Guibemantis liber* by Lehtinen *et al.* (2011). *Guibemantis liber* males have a throat that is bright white over its entire surface. The whitish coloration on the throat of males in *G. woosteri* sp. nov. does not cover the entire surface nor is it as brightly white as in *G. liber*.

Remark

In Vieites *et al.* (2009) and Perl *et al.* (2014), the holotype of *G. woosteri* sp. nov. (ZSM 5063/2005 / ZCMV 2044) and one paratype (ZSM 5062/2005 / ZCMV 2011) were listed as two different candidate species (Ca15 and Ca17, respectively). However, the 16S sequence data reported here show them to be nearly identical genetically (Fig. 1) and they are also morphologically similar (Table 1). Thus, we consider them to be conspecific. In another earlier molecular analysis, Lehtinen *et al.* (2007) found the holotype of *G. woosteri* sp. nov. (ZSM 5063/2005) to be phylogenetically related to UMMZ 212597 (also from Marojejy) and UMMZ 212922 from Cap Est (in the same region, but further east on the coast). However, these forms are 7.3% and 8.1% different in the 12S and 16S mitochondrial genes (Lehtinen *et al.* 2007) and are morphologically distinct from *G. woosteri* sp. nov. We have, therefore, not included these specimens in the definition of *G. woosteri* sp. nov. as they likely represent additional undescribed taxa.

Discussion

The description of two new *Pandanusicola* herein brings the number of described species in *Guibemantis* to 18 (five in the subgenus *Guibemantis* and 13 in the subgenus *Pandanusicola*). However, numerous additional candidate species that are either highly divergent genetically or morphologically distinctive (or both) remain to be assessed, especially in *Pandanusicola* (Lehtinen *et al.* 2007; Vieites *et al.* 2009). Since these small frogs can be confusingly variable morphologically and tend not to vocalize very conspicuously, other characters may need to be evaluated to help assess the true diversity in this group.

One character that may be useful in this regard is the structure and the color of femoral glands in males. While the precise function of these structures remains unclear, they are sexually dimorphic and thus may be under selection as important mating barriers between species (Glaw *et al.* 2000). If this is true, they are likely to be useful in distinguishing closely related forms. In *Pandanusicola*, two species (*G. liber* and *G. tasifotsy*) have femoral glands that cover much of the thigh and do not have clear boundaries (Lehtinen *et al.* 2012). As far as is known in all other *Pandanusicola*, the femoral glands are smaller (often covering only a relatively small portion of the thigh). However, the size and distribution of granules within the femoral glands seem to vary substantially in different species. For example, in *G. albomaculatus* sp. nov., *G. methueni*, *G. milingilingy* and *G. woosteri* sp. nov., the granules are large (~ 30–36 granules per gland based on Figs 4G and 5C and photos in Lehtinen *et al.* 2011; Vences *et al.* 2013). By contrast, *G. punctatus* has ~65 granules per gland and *G. annulatus* has ~120 (based on photos in Lehtinen *et al.* 2011).

There also appear to be distinct differences among *Pandanusicola* species in femoral gland color, as well as in the contrast of the femoral gland color with that of the adjacent skin on the thigh. For example, in *G. milingilingy* the femoral glands are yellow (Bletz *et al.* 2018) and in *G. albomaculatus* sp. nov. they are orange (Fig. 4G), but in both cases they contrast markedly in color from the surrounding tissue. In *G. woosteri* sp. nov. the femoral glands are dark gray and in *G. methueni* and *G. wattersoni* they are beige, but in these cases they do not differ strongly in color compared to the adjacent area of the thigh. While it is likely that the appearance of the femoral glands differs depending on the time of year and the physiological state of the individual (Blommers-Schlösser 1979), these characters may nonetheless be useful to distinguish otherwise similar species. Femoral gland color and contrast as well as other coloration patterns not apparent in preserved specimens seem to be important in distinguishing many species of *Pandanusicola*. To help in this regard, we encourage others to take dorsal and ventral photographs of live individuals as standard practice when collecting specimens.

Our study increases the number of amphibian species endemic to northern Madagascar, a region where in-situ diversification processes have resulted in a high diversity of micro-endemic species in many groups (Brown *et al.* 2016). The example of *Guibemantis albomaculatus* sp. nov. also adds to the list of species that are known both from Montagne d'Ambre and from Manongarivo and/or Tsaratanana (Andreone *et al.* 2009). In some cases, the populations from these lineages have deep divergences [e.g., in *Gephyromantis ambohitra* (Vences & Glaw, 2001); Vences *et al.* 2017], whereas the divergences are very shallow in *G. albomaculatus* sp. nov. This may possibly suggest a recent gene flow of these frogs between the Ambre and Manongarivo massifs. A comparative analysis of more co-distributed species on these massifs, as well as their habitat requirements and elevational distributions, might allow the testing of hypotheses of past rainforest connections and dispersal corridors in northern Madagascar, as well as identifying intrinsic traits favoring such dispersal in frogs and other animals.

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