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Descriptions of two new *Spinomantis* frogs from Madagascar (Amphibia: Mantellidae), and new morphological data for *S. brunae* and *S. massorum*

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ABSTRACT

New collections of *Spinomantis* frogs (Amphibia: Mantellidae: Mantellinae) have been made by us in northern Madagascar, and based on these collections we here describe two new species. One species, from northeastern Madagascar, has reduced dermal spines on the limbs and resembles *S. massorum*, but is diagnosed based on features including its shorter snout, proportionally longer hind limbs, reduced foot webbing, and different coloration. The other species, from the Tsaratanana Massif, is most similar to *S. peraccae*, but can be diagnosed based on features including its much larger body size, more extensive foot webbing and different coloration. We also redescribe two other poorly known species of *Spinomantis*: *S. brunae* and *S. massorum*. Both these rare species had been recently described based on a single and pair of type specimens respectively, and we here report on the morphology of new comparative material. For both the new and redescribed species, we summarize information on behavior, habits, individual variation, and distribution, and we also present a morphological identification key for the entire *Spinomantis* genus, which now includes 12 species. The new species from the Tsaratanana Massif is known only from a single site (Befosa River). Because this site is not protected within a reserve, we propose this forest be considered for inclusion within the ongoing protected area expansion program for Madagascar.

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INTRODUCTION

One of the most distinctive endemic frog genera in Madagascar is the genus *Spinomantis* (Mantellidae: Mantellinae). This genus includes mantelline species with well-developed dermal spines and fringing on the limbs, and species with bold and contrasting body markings (either dorsally or ventrally). However, the genus has been formally recognized only since 2006 (originally described as a subgenus by Dubois, 1992, with the type species *S. aglavei*), and currently includes 10 species (Glaw and Vences, 2006). These species are: *Spinomantis aglavei* (Methuen and Hewitt, 1913), *S. bertini* (Guibé, 1947), *S. brunae* (Andreone et al., 1998), *S. elegans* (Guibé, 1974), *S. fimbriatus* (Glaw and Vences, 1994), *S. guibei* (Blommers-Schlösser and Blanc, 1991), *S. massorum* (Glaw and Vences, 1994), *S. microtis* (Guibé, 1974), *S. peraccae* (Boulenger, 1896), and *S. phantasticus* (Glaw and Vences, 1997).

Although the *Spinomantis* species are generally distinctive, and there is growing molecular and karyotypic support for the monophyly of the group, the morphological diagnosis of *Spinomantis* has proven to be complicated, and there are no unique derived mantelline characters shared by all members (see Glaw and Vences, 2006). The current diagnosis of *Spinomantis* is based on an adult snout-vent length of 22–60 mm, rudimentary to complete webbing between toes (with the inclusion of *S. microtis*, see Andreone and Nussbaum, 2006), lateral metatarsalia connected or separated, inner and outer metatarsal tubercles (except *S. elegans*, with inner tubercle only), enlarged, triangular finger and toe disks, tibiotarsal articulation that may extend past snout tip (see below), type 2 femoral glands in adult males (as defined by Glaw et al., 2000) or else no male glands, female femoral glands absent, tibial glands absent, single or slightly bilobed subgular vocal sacs in males, maxillary teeth present, vomerine teeth present (except *S. bertini*), bifid tongue, diplasiocoelous vertebral column, and tympanum not sexually dimorphic in size. The genus is confined to humid regions of Madagascar; habits are arboreal and/or terrestrial, almost always found along streams, and activity is largely nocturnal. Tadpoles

(where known) are free swimming, developing in streams, with arboreal species depositing eggs on leaves overhanging water.

Spinomantis currently includes two informal groupings: the terrestrial stream-edge dwelling species: *S. bertini*, *S. brunae*, *S. elegans*, *S. guibei*, and *S. microtis*; and the nocturnal arboreal species: *S. aglavei*, *S. fimbriatus*, *S. massorum*, *S. fimbriatus*, *S. peraccae*, and *S. phantasticus*. All species in the latter grouping, with the exception of *S. peraccae*, have distinctive dermal spines on the hind limbs, which appear to make them more cryptic during their daytime hiding posture on tree trunks or the ground (Glaw and Vences, 1997; Raxworthy, personal obs.). Partly because of this cryptic behavior and morphology, relatively few specimens of *Spinomantis* have been collected, and most species are represented in collections by only small series of individuals (e.g. Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994, 1997; Andreone et al., 1998; Andreone and Nussbaum, 2006). As a result of this rarity, for most species within this genus, we currently lack detailed information for species distributions, sexual dimorphism, and even individual variation.

However, based on new *Spinomantis* material that we have recently collected, we here undertake a partial revision of the group by describing two new species from the arboreal nocturnal group that were collected in northern Madagascar, and redescribed two other species that are currently poorly known: *Spinomantis brunae* which was originally described based on just a single holotype (Andreone et al., 1998), and *S. massorum*, which was originally described based on two type specimens (Glaw and Vences, 1994).

MATERIALS AND METHODS

FIELDWORK

Amphibians were surveyed in Madagascar during the austral summer (between January and April) for the period of peak rainfall and for months with above mean annual temperatures (Jury, 2003). Frogs were collected by searching the ground and vegetation up to approximately 6 m height, during both the day, and at night using headlamps. The majority of searching was done close to new

trails made during the study, although ridges and riverbanks were also used to orient search paths. Photographs of representative specimens were taken soon after capture to record natural coloration. All color descriptions were based on diurnal photographs taken of captured animals. The following information was recorded at the time of capture for each individual: date, time, longitude, latitude, elevation (recorded using a GPS, altimeter, or 1:100,000 topographic maps), and microhabitat. Voucher specimens were euthanized and fixed in 10% buffered formalin and later transferred to alcohol. Livers and/or thigh muscles were removed from representative specimens and frozen in liquid nitrogen or preserved in alcohol or buffer. The field tag series abbreviations are: APR, Achille. P. Raselimanana; RAN, Ronald A. Nussbaum; RAX, Christopher J. Raxworthy; and standard institutional abbreviations are as listed in Leviton et al. (1985) and UADBA, University of Antananarivo Department of Animal Biology. Specimens have been deposited at the following three collections: AMNH (American Museum of Natural History, Department of Herpetology), UADBA (University of Antananarivo, Department of Animal Biology) and UMMZ (University of Michigan, Museum of Zoology).

MORPHOLOGY

Measurements were made on specimens preserved in 70% ethanol. All measurements were recorded to the nearest 0.1 mm by AC using either an electronic caliper (Mitutoyo Absolute Digimatic, Model CD-6" CS) or a reticle and binocular microscope. Sex and maturity was determined based on examination of gonads and secondary sexual characters (male femoral glands and vocal sacs): male (M), female (F), and juvenile (J). Femoral gland types follow Glaw et al. (2000). Other morphological abbreviations and measurements are as follows. Snout-vent length (SVL) measured in dorsal view from snout tip to cloacal opening, with the body gently extended if needed on a flat surface; head width (HW) measured in dorsal view at widest point (typically between eye and tympanum); head length (HL) measured in lateral view from

snout tip to mouth corner; eye diameter (ED), measured horizontally in lateral view from orbit margins, tympanum diameter (TD) measured horizontally in lateral view; eye-nostril distance (END) measured as the shortest distance between the center of the nostril and eye margin; nostril-snout distance (NSD) measured as the shortest distance between the center of the nostril to snout tip; internostril distance (NND) measuring dorsally between the center of each nostril; forearm length measured from center of elbow to center of wrist; thigh length measured from cloaca to center of knee; femoral gland length (FGL) measured as the longest length on gland; femoral gland width measured at widest length on widest gland; lower leg length measured from center of knee to proximal point of tarsus; foot length including tarsus (FTL) measured in ventral view from proximal point of tarsus to tip of longest toe disk; maximum pad width of toe 3 measured in dorsal view at widest point, extended to maximum width if not flat; terminal phalange width measured in dorsal view at most distal point basal to toe disk; metatarsal tubercle length measured at longest length; number of forelimb dermal spines (FS) counted as the number of points on dermal fringing, including any spines on hand; number of hind limb dermal spines (HS) counted as the number of points on the dermal fringing, including any spines on foot; and longest hind limb dermal spine (LHS), measured perpendicular to limb to tip of dermal spine point. Only dermal protrusions > 0.1 mm were classed as dermal spines, with counts per limb based on the maximum shown by each specimen.

Webbing extent was recorded by extending the digits, and scoring the phalanges lacking webbing using the formula described by Savage and Heyer (1997): 0 = webbing reaching end of the terminal phalange, and phalanges free of webbing recorded in 0.25 increments. The point of web termination was defined as the area where webbing ended or became parallel with the phalange.

REDISCRPTION OF TWO SPECIES

The following two *Spinomantis* species were originally described based on either a single specimen (*S. brunae*) or two specimens (*S.*

massorum) (see introduction). Based on new material, we here redescribe these species to include additional morphological variation. The redescription of *S. brunae* is based on eight new specimens: six adult males and the first known juveniles, and the redescription of *S. massorum* is based on 15 new specimens, including eight adult males, the first known female, and four juveniles.

Spinomantis brunae (Andreone et al., 1998)

Figures 1A–B, 2

Mantidactylus brunae Andreone et al., 1998
Spinomantis brunae: Glaw and Vences, 2006

HOLOTYPE: MRSN A1649 from between the villages of Isaka-Ivondro and Eminiminy, Andohahela Strict Reserve, Toliara (Tulear) Province, elevation about 600 m, 24°45'30"S, 46°51'15"E.

SPECIMENS EXAMINED: UMMZ 198404–11 (RAN 36211, RAN 36241–3, RAN 36279, RAN 36375, RAN 36517, RAN 36540), collected 19–28 December 1990, at Ampamakiesiny Pass, Tolagnaro Fivondronana, Toliara Province, Madagascar, between 700–800 m, 46.85°E, –24.53°S, by J.B. Ramamanjato, A. Raselimanana, and C.J. Raxworthy.

DIAGNOSIS: A medium-sized *Spinomantis* (adult male SLV 32–35 mm), with type 2 femoral glands; vomerine teeth; a reticulated dorsal pattern composed of dark round spots on a lighter background; a dark throat with light spots; a singular subgular vocal sac in males; inner and outer metatarsal tubercles; SVL/FT \geq 1.4; webbing formula I 0.5 to 1 – 0.75 to 1 II 0 to 0.5 – 1 to 1.5 III 0.5 to 1 – 2 IV 2 – 0.25 to 0.75 V; and no dermal spines on fore or hind limbs (table 1).

Spinomantis brunae can be distinguished from all other *Spinomantis* species by the following characters. *S. aglavei*, *S. fimbriatus*, *S. massorum*, *S. tavaratra* sp. nov., and *S. phantasticus* all have hind limb dermal spines that are absent in *S. brunae*. *Spinomantis bertini* is much smaller (males SVL 22–23 mm), and has only rudimentary webbing on the hind feet. *Spinomantis elegans* and *S. microtis* are larger (male SVL 34–60 mm) and males lack femoral glands. In addition, *S.*

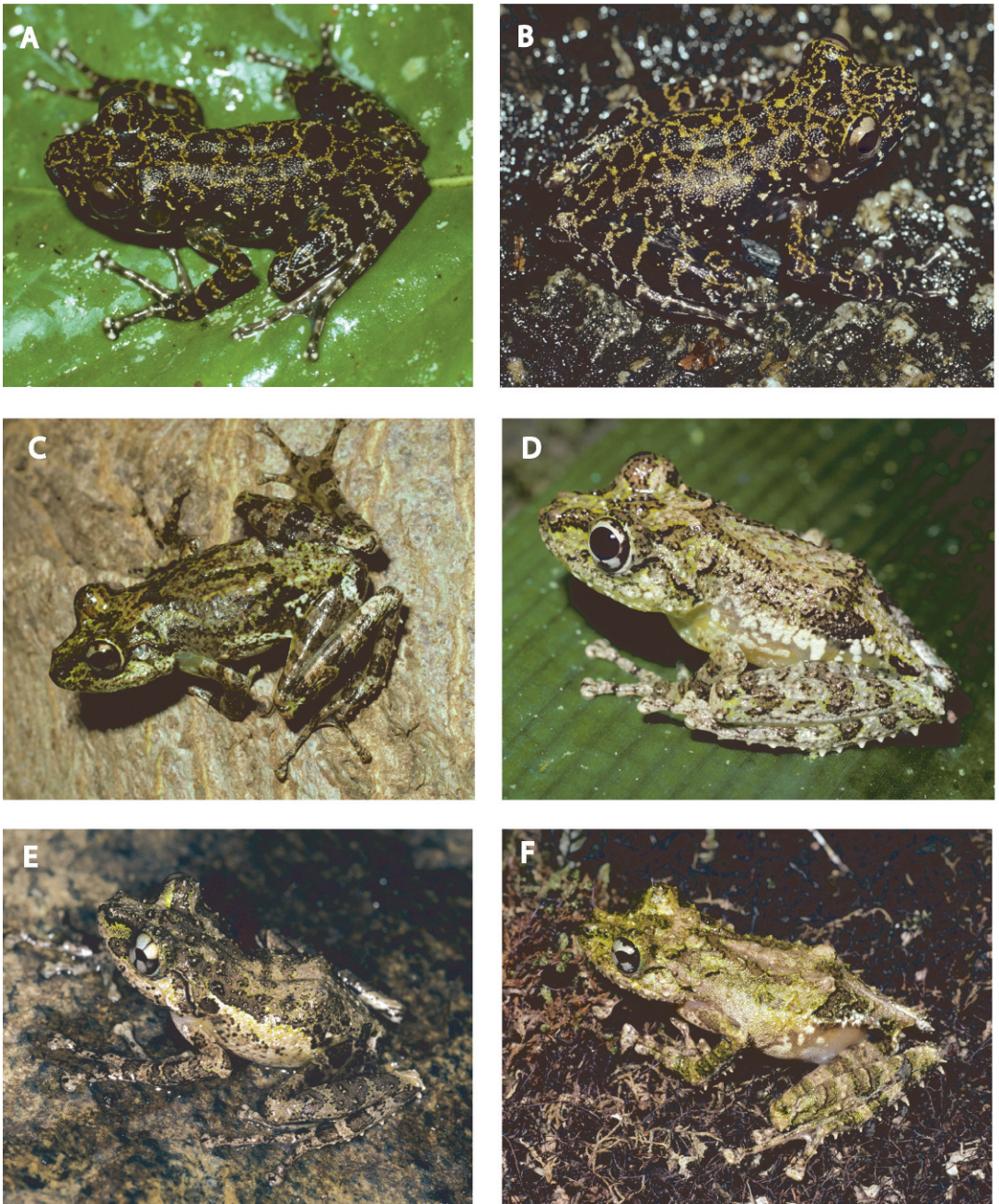
elegans lacks an outer metatarsal tubercle, and *S. microtis* has completely webbed feet. *Spinomantis guibei* has distinctive markings: the ventral limbs are white with black blotches, and the dorsal body has longitudinal dark lines (both marking features absent in *S. brunae*). *Spinomantis guibei* also has more reduced webbing: the 4th internal toe has 3 phalanges without webbing compared to 1–2 for *S. brunae*. *Spinomantis nussbaumi* sp. nov., and *S. peraccae* can be distinguished from *S. brunae* by their large adult male body size (SVL 35–57 mm); throat color (*S. nussbaumi* sp. nov. brilliant white with dark spots, *S. peraccae* pale yellowish white with or without dark spots); and smaller foot in relation to body size (*S. nussbaumi* sp. nov. and *S. peraccae* SVL/FT \leq 1.4).

DESCRIPTION OF UMMZ 198411: Adult male in an excellent state of preservation with a singular subgular vocal sac, distinct femoral glands, and mature testes, measuring 6.0 \times 0.9 mm, and whitish yellow in color.

Head dorsally finely granular and lacking an interocular longitudinal ridge. Head 1.18 times wider than long. Head length 0.32 times SVL. Canthus rostrum with a rounded edge. A weak ridge starts posterior to nostril and runs through the loreal region to the lower anterior eye orbit. Internarial distance 0.30 times head width. Nostrils open laterally. Pupil round. Eye to nostril distance 1.87 times nostril to snout distance and 0.86 times eye diameter. Tympanum well defined, diameter 0.61 times eye diameter. Supratympanic ridge arches smoothly from posterior of eye to above the forelimb insertion point. Vomerine teeth present, vomerine bone triangular in shape.

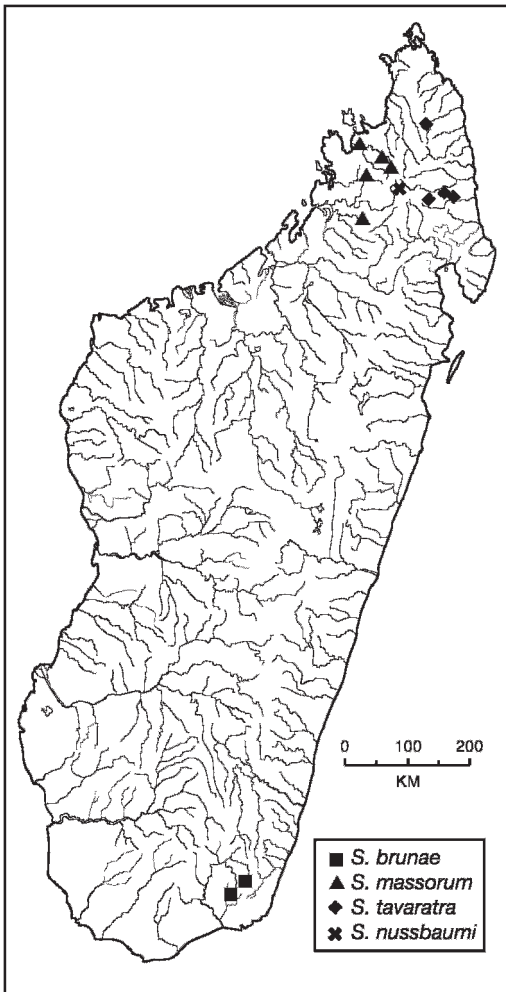
Arms slender and smooth with forearm length 0.24 times SVL. No dermal spines on arms, legs, or body. Hand length (including disks) 0.32 times SVL and free of webbing. Relative finger lengths 1 < 2 < 4 < 3. Fingers and toes with enlarged, triangular disks. Disk of third toe two times wider than terminal phalange. Body dorsally granular. Flanks and belly weakly granular. No enlarged tubercles on body or around anal region.

Tibio-tarsal extension reaches past snout. Thigh length 0.51 times SVL. Ventral surface of thigh granular, and all other leg surfaces smooth. Type 2 oval femoral glands clearly



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Fig. 1. Photos of selected live *Spinomantis* species. **A.** *Spinomantis brunae*, UMMZ 198405, Ampamakiesiny Pass (photo: C.J. Raxworthy). **B.** *S. brunae*, UMMZ 198407, Ampamakiesiny Pass (photo: C.J. Raxworthy). **C.** *S. massorum*, UMMZ 212362, Antsahabe River, Manongarivo Special Reserve (photo: C.J. Raxworthy). **D.** *S. massorum*, AMNH A167941, Ramena River, Tsaratanana Strict Nature Reserve (photo: C.J. Raxworthy). **E.** *S. tavaratra*, new species, AMNH A167937, Sorata Mountain (photo: C.J. Raxworthy). **F.** *S. aglavei*, UMMZ 212374, Andringitra Strict Nature Reserve (photo: C.J. Raxworthy).



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Fig. 2. Localities for the new and redescribed *Spinomantis* species.

differentiated and distended, measuring 8.7×3.5 mm, separated by 0.8 mm. Approximately 90 granules with no central pore visible in external view. Approximately 300 touching granules in internal view. Granules translucent with opaque centers. Lower leg 0.55 times SVL. Foot, including tarsus, 0.73 times SVL. Inner and outer metatarsal tubercles present on foot, with round outer metatarsal tubercle 0.4 mm in diameter and elliptical inner metatarsal tubercle 1.3 mm in length. Relative toe lengths $1 < 2 < 3 < 5 < 4$. Foot webbing **I** 1 – 1 **II** 0.5 – 1.25 **III** 0.75 – 2 **IV** 2 – 0.75 **V**.

COLORATION IN PRESERVATIVE: Head and dorsum pale brown, with a reticulated pattern of dark brown spots (approximately the diameter of the tympanum) closely spaced together. Iris dark brown. Tympanum light brown. Flanks dark brown with light brown small spots. Arms with five dorsal dark brown transverse stripes of uneven width. Legs light brown with 12 dark brown transverse stripes of uneven width. Some of the broader pale brown bands contain within them additional darker brown blotches. In the natural resting posture, the dorsal stripes on the hind limbs line up to form three longitudinal stripes. Ventral arms and legs light brown. Throat light brown with yellowish-white spots. Venter brown. Femoral glands light brown in external view and yellowish white in internal view.

COLORATION IN LIFE: The dorsal pale brown coloration (in preservative) is olive green in life, and the pale flank spots are white in life. The digit and toe pads are each marked

TABLE 1

Morphometric data for *Spinomantis brunae*. All measurements in mm. MRSN specimen data from Andreone et al., (1998).

Specimen #	SEX	SVL	ED	TD	END	NSD	NND	FTL	FGL	FS	HS
MRSN A1649 ^a	M	32.3	5.4	2.8	2.5	3.8	?	23.6	8.6	0	0
UMMZ 198405	M	34.6	4.3	2.6	4.0	1.9	3.7	24.2	8.5	0	0
UMMZ 198407	M	34.8	4.2	2.4	3.7	1.8	3.6	25.6	8.8	0	0
UMMZ 198408	M	32.4	3.9	2.3	3.7	1.8	3.4	23.9	8.6	0	0
UMMZ 198409	M	34.1	4.2	2.5	3.9	1.5	3.5	20.0	8.6	0	0
UMMZ 198410	M	34.4	4.1	2.5	3.7	1.7	3.3	24.9	9.1	0	0
UMMZ 198411	M	33.5	4.3	2.6	3.7	2.0	3.9	24.5	8.7	0	0
UMMZ 198404	J	18.5	2.6	1.2	2.1	1.0	2.0	13.3	-	0	0
UMMZ 198406	J	21.6	3.0	1.3	2.5	1.1	2.7	16.9	-	0	0

^aHolotype.

with a pair of white spots. The iris is creamy white in color.

VARIATION: Morphometric variation is summarized in table 1, which includes the holotype. All specimens agree with the description of UMMZ 198411 with the following exceptions. Femoral glands vary in size from 8.5–9.1 mm in length and 3.4–3.7 mm width, separated by 0.8–1.3 mm, with approximately 75–110 granules visible in external view. Inner metatarsal tubercle range from 1.2–1.4 mm in length. Foot webbing variation: **I** 0.5 to 1 – 0.75 to 1 **II** 0 to 0.5 – 1 to 1.5 **III** 0.5 to 1 – 2 **IV** 2 – 0.25 to 0.75 **V**. The holotype END and NSD measurements given by Andreone et al. (1998) are not within the range of the adult males examined by us (see table 1), possibly due to difference in measurement methodology.

Characters of adult females are unknown. Juveniles UMMZ 198404 and 198406 have poorly defined supratympanic ridges, yellowish-white venters in preservation, and a dorsal pattern of reticulate spots that are not as closely spaced together compared to the adult coloration.

DISTRIBUTION: Known only from humid forests in the Anosy Mountains, SE Madagascar, between 600–800 m elevation.

REMARKS: One UMMZ specimen was collected during the day (1100 hours) on a leaf, but all others were collected at night (2100–2300 hours) on leaves, branches, or rocks. All specimens were found in close proximity to small fast-flowing streams, in areas with large to massive rock boulders and rock crevices at the waters edge. One male (RAN 36729, UMMZ 198408) was found vocalizing at 2100 hours on a branch at 0.5 m height off the ground by a small stream. The call is a short one-second pulse, sounding like a rapid metallic trill, which is repeated every 5–10 seconds.

Spinomantis massorum
(Glaw and Vences, 1994)

Figures 1C–D, 2, 3

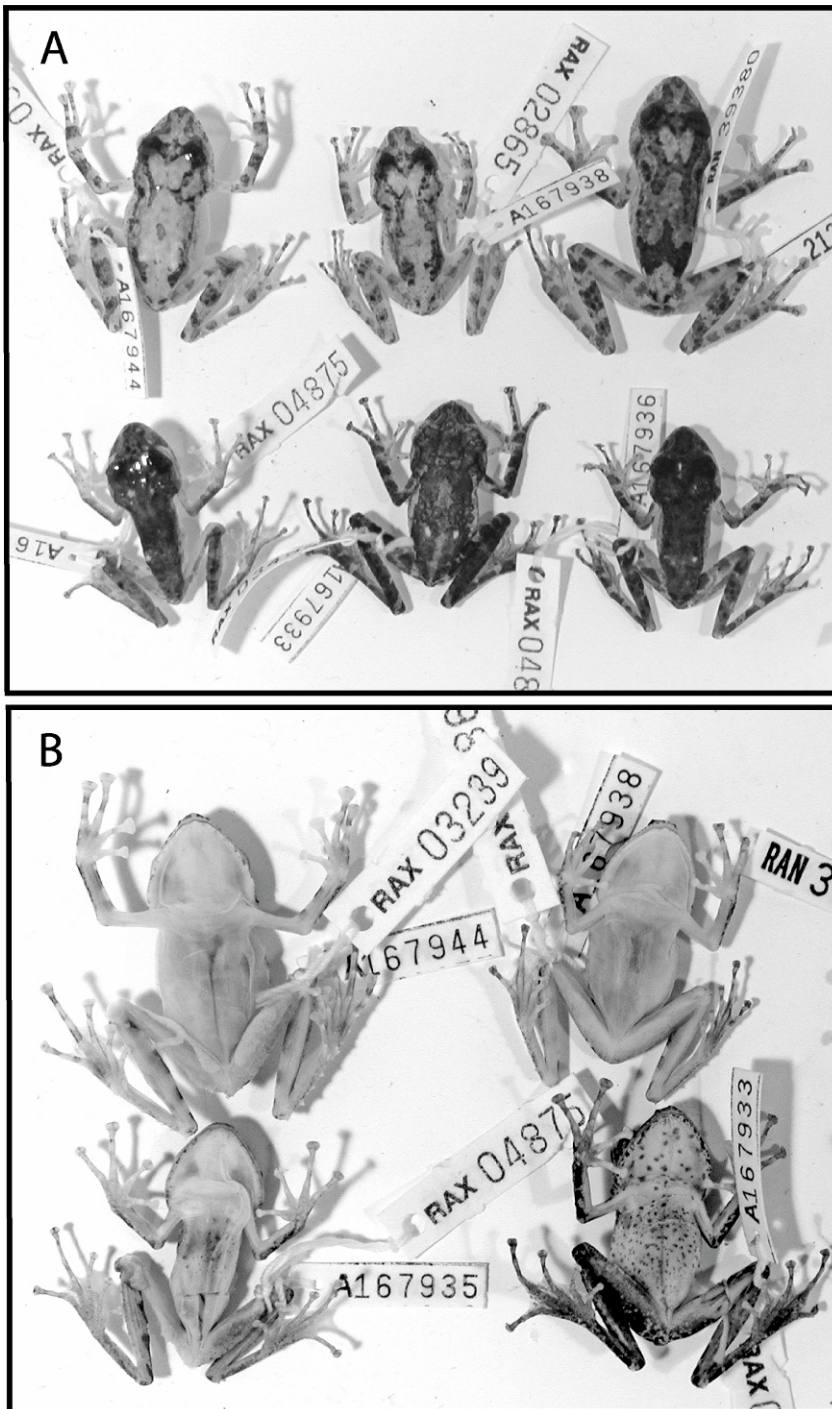
Mantidactylus massi Glaw and Vences, 1994
Mantidactylus massorum: Vences et al., 2003
Spinomantis massorum: Glaw and Vences 2006

HOLOTYPE: ZFMK 57442 from Benavony (near Ambanja), about 300 m altitude.

SPECIMENS EXAMINED: AMNH A167938–39 (RAX 2865, 2959), collected 11–12 April 2001, at Ramena River Camp, Tsaratanana Reserve, Ambanja Fivondronana, Antsiranana Province, 740 m, 13°55′04″S, 48°53′16″E, by S.D. Mahaviasy, N. Rabibisoa, C.J. Raxworthy, A. Razafimanantsoa, and A. Razafimanantsoa; AMNH A167940–41 (RAX 2965–66) as AMNH A167938, except 12 April 2001, 1150 m; AMNH A167942–45 (RAX 3190, 3238–39, 3298), collected 15–19 April 2001, at Antsaravy Ridge, Tsaratanana Reserve, Ambanja Fivondronana, Antsiranana Province, 1050–1200 m, 13°55′34″S, 48°54′21″E, by S.D. Mahaviasy, N. Rabibisoa, A. Razafimanantsoa, and A. Razafimanantsoa; AMNH A167946 (RAX 6581), collected 2 April 2003 at Irony River Relict Forest, Antsohihy Fivondronana, Mahajanga Province, 950 m, 14°45′8″S, 48°29′41″E, by S.D. Mahaviasy, N. Rabibisoa, and C.J. Raxworthy; UMMZ 212358–63 (RAN 39379–80, 39434–37), collected 1–4 March 1992 at Antsahabe River, Manongarivo Reserve, Ambanja Fivondronana, Antsiranana Province, 650 m, 48.342° E 14.433° S, by J.B. Ramamanjato, A. Raselimanana, and C.J. Raxworthy.

DIAGNOSIS: A medium-sized *Spinomantis* (adult male SLV 33–42 mm), type 2 femoral glands in adult males; vomerine teeth; no dark markings on throat or venter; a singular subgular vocal sac in males; adult NSD > 2.1 mm, inner and outer metatarsal tubercles; a tibio-tarsal extension that reaches between the eye and nostril, 1–2 phalanges free of webbing on the exterior 4th toe; and simple dermal spines < 1 mm in length (table 2).

Spinomantis massorum can be distinguished from the following species: *S. peraccae*, *S. brunae*, *S. elegans*, *S. microtis*, *S. bertini* and *S. nussbaumi* sp. nov. by the presence of dermal spines on the tarsus. *Spinomantis massorum* can be distinguished from *S. phantasticus* by the lack of supraocular dermal spines \geq 0.5 mm and lack of other prominent spines on the head or dorsum. *Spinomantis massorum* can be distinguished from *S. aglavei* and *S. fimbriatus* by adult dermal spines on its hind limbs that do not exceed 1 mm in length (Glaw and Vences, 1997); and lacking dermal spines with multiple points. *Spinomantis massorum* can be distinguished from *S. tavaratra* sp. nov. by a lack of markings on venter and



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Fig. 3. *Spinomantis massorum* and *S. tavaratra*, new species. **A.** Dorsal views of *S. massorum* (above, left to right): AMNH A167944, 167938, UMMZ 212359; and *S. tavaratra*, new species (below, left to right): AMNH A167935, 167933, 167936. **B.** Ventral views of *S. massorum* (above, left to right): AMNH A167944, 167938; and *S. tavaratra*, new species (below, left to right): AMNH A167935, 167933.

TABLE 2
Morphometric data for *Spinomantis massorum*. All measurements in mm. ZFMK specimen data from Glaw and Vences (1994, 1997).

Specimen #	SEX	SVL	ED	TD	END	NSD	NND	FTL	FGL	FS	HS	LHS
ZFMK 57442 ^a	M	36.7	4.5	1.8	4.1	3.2	?	26.0	9.1	?	9	<1.0
AMNH A167938	M	33.1	4.2	1.5	3.8	2.5	3.6	23.1	8.2	2	7	0.2
AMNH A167944	M	35.4	4.0	1.7	4.0	2.3	4.0	27.4	9.5	4	10	0.5
UMMZ 212358	M	42.2	3.7	1.8	4.4	2.4	4.0	28.9	9.7	1	7	0.6
UMMZ 212359	M	41.4	4.3	1.7	4.5	2.2	3.4	28.4	10.2	0	7	0.5
UMMZ 212360	M	42.1	4.2	1.9	5.1	2.3	4.0	29.4	11.3	1	8	0.6
UMMZ 212361	M	37.7	4.5	1.9	4.5	2.8	4.1	28.3	8.2	4	8	0.6
UMMZ 212362	M	39.5	4.1	1.9	4.4	2.7	3.9	28.8	10.3	0	7	0.7
UMMZ 212363	M	40.4	4.6	1.9	4.6	2.8	4.2	29.5	11.2	2	10	0.6
ZFMK 57443#	M	33.5	3.9	1.5	4.1	2.5	?	?	9.5	?	?	<1.0
AMNH A167943	F	37.9	3.9	1.7	4.7	2.6	4.4	27.8	-	5	10	0.4
AMNH A167940	MJ	28.6	3.5	1.2	3.4	2.1	3.2	20.6	-	3	9	0.3
AMNH A167941	MJ	30.3	3.5	1.3	3.4	2.4	3.4	22.4	-	2	9	0.3
AMNH A167945	FJ	30.8	3.5	1.2	3.5	2.2	3.5	22.1	-	5	9	0.4
AMNH A167946	FJ	33.1	4.3	1.5	3.7	2.6	3.8	24.3	-	4	9	0.3
AMNH A167939	J	25.5	3.3	1.1	2.9	1.8	2.8	19.2	-	1	7	0.2
AMNH A167942	J	29.6	3.6	1.1	3.7	2.3	3.4	20.3	-	7	9	0.2

^aHolotype.

throat (*S. tavaratra* sp. nov. with dark spots on venter and throat); a longer adult snout (*S. massorum* with NSD > 2.1 mm; *S. tavaratra* sp. nov. NSD < 2 mm); a tibio-tarsal extension that reaches between the eye and nostril (*S. tavaratra* sp. nov. tibio-tarsal extension may extend past snout); and more developed webbing on toe 4 (*S. massorum* 0.75 to 2; IV: 1 to 2; *S. tavaratra* sp. nov. 2 to 2.5; IV: 2 to 2.5).

DESCRIPTION OF AMNH A167944: Adult male in an excellent state of preservation with a singular subgular vocal sac, distinct femoral glands, and mature testes, measuring 2.2 × 1.0 mm, and whitish yellow in color. The skin, femoral gland, and muscle have been removed from the right thigh for a tissue sample.

Head width 1.33 times wider than long, head length 0.30 times SVL. Canthus rostrum with a rounded edge. Scattered tubercles on the snout and dorsal posterior regions of the head. A weak ridge starts posterior to nostril and runs through the loreal region to the lower anterior eye orbit. Internarial distance 0.29 times head width. Nostrils open laterally. Pupil round. Eye to nostril distance 1.74 times nostril to snout distance and equal to eye diameter. Tympanum well defined, diameter 0.43 times eye diameter. Supratympanic ridge

present and broken, arching unevenly from posterior of eye to above mouth corner. Vomerine teeth present, vomerine bone elliptical in shape.

Arms slender and smooth with forearm length 0.25 times SVL, with four dermal spines up to 0.2 mm in length forming a line from elbow to wrist. Hand length (including disks) 0.36 times SVL with a trace of webbing between digits, never extending beyond basal phalange. Relative finger lengths 1 < 2 < 4 < 3. Fingers and toes with enlarged triangular disks. Disk of third toe 1.7 times wider than terminal phalange. No dermal spines on body. Dorsum and flanks weakly granular. Venter weakly granular. Four enlarged tubercles positioned ventral to the cloaca.

Tibio-tarsal extension reaches between eye and snout. Thigh length 0.55 times SVL. Dorsal hind limbs with weakly developed tubercles, and smooth ventrally. Clearly differentiated and distended type 2 oval femoral glands, measuring 9.5 × 2.5 mm, and separated by 1.7 mm. Externally each gland includes approximately 120 granules with no central pore. Internally there are approximately 120 opaque centered granules in contact with each other. Lower limb 0.56 times SVL. On the posterior surface of the tarsus to fifth

toe there are eight simple dermal spines, measuring <1.0 mm in length. Foot, including tarsus 0.77 times SVL. Ventral foot granular. Inner and outer metatarsal tubercle, with round outer metatarsal tubercle 0.4 mm in diameter and elliptical inner metatarsal tubercle 2.1 mm in length. Relative toe lengths $1 < 2 < 5 < 3 < 4$. Foot webbing **I** 0.75 – 1 **II** 0 – 1.25 **III** 0.5 – 2 **IV** 2 – 0.75 **V**.

COLORATION IN PRESERVATIVE: Head dorsally and laterally brownish yellow with a dark brown transversal intraocular stripe and a brown blotchy band on the supratympanic ridge and canthus rostrum. Lower lip bordered by small dark brown spots. Iris dark brown. Dorsum brownish yellow, with a dark brown “W” marking on the shoulder region, and an isolated brown spot in the middle of the back. Posterior dorsal pelvic region marked with four dark brown spots forming an approximate square pattern. Flanks yellowish white with a brown blotchy dorsolateral line. Arms brownish yellow with four dorsal dark brown transverse stripes of uneven width. Legs brownish yellow with nine dark brown transverse stripes of uneven width. When in sitting posture, dorsal stripes on the hind limbs line up, forming three longitudinal stripes. Dermal spines pale yellow. Throat and ventral body yellowish white and unspotted. Ventral arms yellowish white. Ventral thigh light brown, which fades to yellowish white on the lower limb. Femoral glands yellowish white in external and internal view.

COLORATION IN LIFE: The iris is creamy white in color, with a brown border that includes short bars radiating in toward the pupil. Surrounding the brown border is a thin green iris ring. The dorsal body coloration includes green pigment in areas that are brownish yellow in preservation. The lower flanks and groin area have silvery blotches. The hind limb dermal spines are white.

VARIATION: Morphometric variation is summarized in table 2. All specimens agree with AMNH A167944 with the following exceptions. The vomerine bone of all other specimens is triangular in shape. Dermal tubercles ventral to the vent may be absent (AMNH A167938). Femoral glands vary in size from 8.2–11.3 in length and from 2.4 to 3.9 mm width, separated by 1.7 to 4.7 mm,

with approximately 50 to 120 granules visible in external view. Inner metatarsal tubercle range from 1.2 to 1.6 mm in length. Foot webbing variation: **I** 0 to 1 – 0.75 to 1.25 **II** 0 to 0.5 – 1 to 1.5 **III** 0 to 1 – 0.75 to 2 **IV** 1 to 2 – 0.25 to 1 **V**. Female AMNH A167943 lacks femoral glands. Juveniles AMNH A167939–42, and A167945–46 lack femoral glands but have fore- and hind limb dermal spines present similar in number, placement, and size to those of adults.

DISTRIBUTION: Known only from humid forests in NW Madagascar, in the Sambirano Region, between 300–1200 m elevation.

REMARKS: This species was found active at night between 2000–2100 hours, on leaves, vertical rock surfaces, branches, and tree trunks, up to 2.5 m height above the forest floor, but always at the edges of small streams or rivers. Three specimens were also found during the day by streams: one crouched on a rock surface, and the other two found among grass on the ground.

NEW SPECIES DESCRIPTIONS

Spinomantis tavaratra, new species

Figures 1E, 2, 3

HOLOTYPE: AMNH A167935 (RAX 4875), adult male, collected 11 April 2002 at Sorata Mountain, Vohemar Fivondronana, Antsiranana Province, 1300 m, 13°41'9"S 49°26'31"E, by S.D. Mahaviasy, N. Rabibisoa, and C.J. Raxworthy.

PARATYPES: AMNH A167936–37 (RAX 4876, 4962), collection data as the holotype except A167937, collected 12 April, 2002; AMNH A167933–34 (RAX 3494, RAX 3508), collected 6–7 December 2001, Ambolokopatrika River, Betaolana Corridor Forest, Andapa Fivondronana, Antsiranana, 1250 m, 14°31'53"S, 49°25'37" E by S.D. Mahaviasy, N. Rabibisoa, A. Rakotozafy, A. Razafimanantsoa, and A. Razafimanantsoa; AMNH A157066 (APR 380) and AMNH A157069 (APR 440), collected 15–17 October 1996, Andampimbazaha Cascade, a tributary of Manantenina River, 10 km NW from Manantenina village, Marojejy Strict Nature Reserve, Sambava Fivondronana, Antsiranana Prov-

TABLE 3
Morphometric data for *Spinomantis tavaratra*, new species. All measurements in mm.

Specimen #	SEX	SVL	ED	TD	END	NSD	NND	FTL	FGL	FS	HS	LHS
AMNH A167935 ^a	M	32.8	4.2	1.2	3.8	1.9	3.3	24.5	5.5	0	5	0.4
AMNH A157066	M	30.5	4.2	1.0	3.2	1.5	3.0	22.7	4.1	3	8	0.5
AMNH A157071	M	35.4	4.5	1.6	3.9	1.7	3.4	25.2	5.5	1	7	0.7
AMNH A167934	M	32.8	3.7	1.3	3.7	2.0	3.3	24.3	6.5	0	6	0.4
UMMZ 212365	M	35.4	4.5	1.4	3.8	1.7	3.4	26.3	7.2	0	8	0.7
UMMZ 212366	M	34.5	4.0	1.3	3.7	1.7	3.4	24.7	6.7	1	8	0.6
UMMZ 212367	M	33.7	3.9	1.4	3.9	1.9	3.4	26.2	5.8	0	8	0.6
UMMZ 212368	M	36.0	4.3	1.4	4.0	1.9	3.4	25.7	5.7	3	8	0.5
AMNH A157070	F	33.3	4.4	1.3	4.2	2.0	3.6	26.9	-	2	9	0.7
AMNH A157072	F	33.0	3.8	1.3	3.9	1.8	3.1	26.6	-	4	11	0.4
AMNH A157073	F	32.5	3.4	1.2	3.7	1.5	2.9	24.7	-	1	8	0.8
AMNH A167933	F	32.3	4.1	1.3	3.5	2.0	3.4	27.0	-	0	9	0.3
AMNH A167936	F	31.6	3.9	1.1	3.5	2.0	3.5	24.3	-	0	7	0.3
AMNH A167937	F	33.2	3.9	1.0	3.6	1.9	3.6	25.6	-	0	5	0.2
AMNH A157069	MJ	26.3	4.1	1.0	3.1	1.8	2.8	20.7	-	1	8	0.6
UMMZ 212364	J	20.5	3.1	0.6	2.7	1.2	2.5	14.9	-	3	7	0.3

^aHolotype.

ince, 700–780 m, 14°26.0'S, 49°45.7'E, by A.P. Raselimanana; AMNH A157070–73 (APR 722, 752, 754, 812) collected 24–27 October 1996, Ambavanaomby, 11 km NW from Manantenina village, Marojejy Strict Nature Reserve, Sambava Fivondronana, 1100–1180 m, 14°26.2'S, 49°44.5'E, by A.P. Raselimanana; UMMZ 212364–66 (RAN 39769, 39776, 39855) collected 21–24 November 1992 at the Manantenina River in the Marojejy Reserve, Sambava Fivondronana, Antsiranana Province, 650–700 m, 14.43°S, 49.76°E, by R. A. Nussbaum, C. J. Raxworthy, A. Razafimanantsoa, and A. Razafimanantsoa; UMMZ 212367–68 (RAN 39969–70) collected 27–30 November 1992 at Marojejy Reserve, Sambava Fivondronana, Antsiranana Province, 1300 m, 14.43°S, 49.76°E, by R. A. Nussbaum, C. J. Raxworthy, A. Razafimanantsoa, and A. Razafimanantsoa.

DIAGNOSIS: A medium-sized *Spinomantis* (adult male SLV 30–36 mm), with type 2 femoral glands in adult males; a singular subgular vocal sac in males; NSD < 2 mm; dark spots on throat and venter; inner and outer metatarsal tubercles; vomerine teeth; a tibio-tarsal extension that extends beyond the nostril to beyond the snout tip, 2 to 2.5 phalanges free of webbing on the exterior 4th toe, and simple dermal spines < 1 mm length along the posterior margin of the tarsus (table 3).

Spinomantis tavaratra can be distinguished from the following species: *S. peraccae*, *S. brunae*, *S. elegans*, *S. microtis*, *S. bertini*, and *S. nussbaumi* sp. nov. by presence of dermal spines on the tarsus. *Spinomantis tavaratra* can be distinguished from *S. phantasticus* by the lack of supraocular dermal spines ≥ 0.5 mm and lack of other prominent spines on the head or dorsum. *Spinomantis tavaratra* can be distinguished from *S. aglavei* and *S. fimbriatus* (see table 4) by its dermal spines on its hind limbs that do not exceed 1 mm in length (*S. aglavei* and *S. fimbriatus* spines exceed 1 mm, Glaw and Vences, 1997); absence of dermal spines with multiple points (*S. aglavei* spines with multiple points); smaller SVL (*S. tavaratra* SLV 30–36 mm, *S. aglavei* 40–51 mm, *S. fimbriatus* 36–39 mm); and tibio-tarsal extension that may extend beyond the nostrils (*S. aglavei* and *S. fimbriatus* to nostrils). *Spinomantis tavaratra* can be distinguished from *S. massorum* by the shorter snout (*S. tavaratra* NSD < 2 mm; *S. massorum* NSD > 2.1 mm); dark markings on venter and throat (*S. massorum* lacks dark markings on venter and throat); a tibio-tarsal extension that may extend past the nostril (*S. massorum* tibio-tarsal extension reaches between the eye and nostril); and less developed webbing on toe 4 (*S. tavaratra* 2 to 2.5:IV:2 to 2.5, *S. massorum* 0.75 to 2:IV:1 to 2).

TABLE 4
 Morphometric data for *Spinomantis aglavei*, *S. fimbriatus*, and *S. phantasticus*. All measurements in mm.
 ZFMK specimen data from Glaw and Vences (1994, 1997).

Specimen #	SEX	SVL	ED	TD	END	NSD	NND	FTL	FGL	FS	HS	LHS
<i>S. aglavei</i>												
AMNH A157067	M	41.3	4.7	1.4	5.1	2.3	4.0	28.6	8.1	12	26	1.6
AMNH A175866	M	47.5	5.0	1.4	6.1	2.9	4.2	35.1	9.9	13	26	1.3
ZFMK 46021	M	47.1	4.6	1.7	5.7	3.4	?	?	9.4	?	?	?
ZFMK 52727	M	48.2	?	2.0	?	?	?	?	10.7	?	?	?
ZFMK 57439	M	45.0	5.3	1.9	5	3.6	?	?	9.3	?	?	?
ZFMK 60002	M	40.5	4.6	0.7	4.2	3.7	?	?	8.1	?	?	?
TM 10073 ^a	F	43.0	5.0	2.1	5.3	3.5	?	?	-	?	?	?
AMNH A157068	F	43.7	5.0	1.5	5.5	2.9	4.2	32.9	-	10	34	1.3
AMNH A175865	F	45.2	5.3	1.6	5.6	2.6	4.2	31.9	-	17	31	1.4
UMMZ 212374	F	46.0	4.7	1.5	4.7	2.6	3.6	28.6	-	7	23	1.0
UMMZ 212357	F	37.7	4.0	1.3	4.6	2.2	3.7	26.1	-	9	24	1.1
UMMZ 214216	F	43.1	4.5	1.3	5.2	2.6	4.1	31.1	-	11	25	1.5
ZFMK52728	F	51.2	5.9	2.0	4.2	3.6	?	?	-	?	?	?
AMNH A175867	MJ	35.1	4.0	1.5	4.0	1.9	3.4	25.1	-	9	8	0.7
UMMZ 212369	MJ	40.3	3.5	1.4	4.1	2.0	3.4	28.6	-	11	24	1.2
AMNH A157065	J	31.6	3.9	1.4	4.1	1.8	3.3	20.3	-	7	18	1.1
AMNH A167908	J	25.1	3.4	0.9	3.4	2.1	2.9	17.5	-	5	7	1.1
<i>S. fimbriatus</i>												
ZFMK 57441 ^a	M	38.6	4.5	1.7	3.7	3.3	?	29	8.3	5	11	> 1
ZFMK 57440	M	36.6	4.5	1.9	3.7	3.2	?	?	8.0	?	?	> 1
<i>S. phantasticus</i>												
ZFMK 60000 ^a	M	37.9	4.0	1.4	4.1	2.9	?	?	10.7	?	?	> 1
ZFMK 60001	M	35.5	4.3	1.5	3.9	3.0	?	?	11.3	?	?	> 1
ZFMK 62208	M	37.7	4.3	1.8	4.0	3.1	?	?	11.3	?	?	> 1
AMNH A167952	M	36.2	3.8	1.4	4.5	2.8	3.9	28.0	10.9	10	15	1.2

^aHolotype.

DESCRIPTION OF HOLOTYPE: Adult male in a good state of preservation with vocal sac, distinct femoral gland, and mature testes measuring 3.6×0.9 mm, and whitish yellow in color. The skin, femoral gland, and muscle have been removed from the right thigh for a tissue sample.

Head laterally and dorsally with scattered weak tubercles. Head 1.19 times wider than long. Head length 0.33 times SVL. Canthus rostrum sharp edged. A weak ridge starts posterior to nostril and runs through the loreal region to the lower anterior eye orbit. Internarial distance 0.26 times head width. Nostrils open laterally. Pupil round. Eye to nostril distance two times nostril to snout distance and 0.89 times eye diameter. Tympanum well defined, diameter 0.28 times eye diameter. Supratympanic ridge present and uniform, arching from posterior of eye to above

the forelimb insertion point. Vomerine teeth present, vomerine bone triangular in shape.

Arms slender and smooth with forearm length 0.25 times SVL. No dermal spines on arms or body. Hand length (including disks) 0.37 times SVL with no webbing. Relative finger lengths $1 < 2 < 4 < 3$. Fingers and toes with enlarged triangular disks. Disk of third toe two times wider than terminal phalange. Dorsum and flanks smooth with a few rounded tubercles concentrated on the posterior dorsal region of the head and the posterior dorsal region of the body. Venter weakly granular.

Tibio-tarsal extension reaches between nostrils and snout tip. Thigh length 0.52 times SVL. Ventral surface of thigh granular, all other leg surfaces but with some scattered tubercles. Type 2 oval femoral glands differentiated and distended, measuring $5.5 \times$

1.8 mm. Approximately 40 granules with no central pore visible in external view. In internal view, 47 opaque granules, some with translucent perimeters. Lower leg 0.54 times SVL. Foot, including tarsus, 0.75 times SVL. Four simple dermal spines, <1.0 mm in length, approximately evenly spaced and increasing in size proximally on the posterior margin of the tarsus. Inner and outer metatarsal tubercles present, with round outer metatarsal tubercle 0.5 mm in diameter and elliptical inner metatarsal tubercle 1.8 mm in length. Relative toe lengths $I < 2 < 5 < 3 < 4$. Foot webbing: **I** 1 – 1.5 **II** 1 – 1.75 **III** 1.25 – 2.5 **IV** 2.5 – 1 **V**.

COLORATION IN PRESERVATIVE: Head dorsally and laterally reddish brown with scattered small brown spots, with larger dark brown spots concentrated on the canthus rostrum and supratympanic ridge, and a dark brown band between the eyes. Iris dark brown. Dorsum reddish brown with darker brown spots. Flanks yellowish white with faint brown spots. Arms with two dorsal broken grayish-brown transverse stripes. Legs with nine broken grayish-brown transverse stripes of uneven width. When in sitting posture, dorsal stripes on the hind limbs line up, forming three longitudinal stripes. Ventral arms and legs yellowish white with brown small spots. Throat yellowish white with lower lip bordered by grayish-brown spots. Venter yellowish white with scattered fine dark brown spots on the chest. Femoral glands brown in external view and white in internal view.

COLORATION IN LIFE: Some of the reddish-brown pigment on the dorsal surface of the head and body is pale green in life. The flanks are silvery white with pale yellowish-green fine spots. The tarsal spines are white. The iris is silvery white, with dark brown radiating bands, and a pale blue iris ring.

VARIATION: Morphometric variation is summarized in table 3. All specimens agree with the holotype description with the following exceptions. The presence of tubercles on the dorsum, head, and flanks range from being sparsely dispersed, as in AMNH A167934, to frequent, as in UMMZ 212366. The supratympanic ridge is reduced and broken in AMNH A157070–71, A157073, and UMMZ 212368. The tibio-tarsal exten-

sion may extend beyond the snout tip (AMNH A157070, A157072; UMMZ 212366–67). Simple dermal spines may be present on the posterior surface of the forearm (table 3). Dermal spines on the hind limb range from approximately uniform in spacing and size, as in the holotype, to alternating in size, with dermal spines generally reduced in size distally. Femoral glands 4.1–7.2 mm in length and 1.8–3.1 mm in width, separated by 2.4 to 3.5 mm, with approximately 20 to 40 granules visible in external view. Inner metatarsal tubercle range from 1.0 to 1.8 mm in length. Foot webbing variation: **I** 0.5 to 1 – 0.75 to 1.5 **II** 0 to 1 – 0.5 to 2 **III** 0.5 to 1.25 – 2 to 2.5 **IV** 2 to 2.75 – 0.75 to 1 **V**.

Females AMNH A157070, A157072–73, A167933, and A167936–37 lack femoral glands. AMNH A167933 is a gravid female with at least 25 visible eggs (up to 2.4 mm diameter) seen in ventral internal view. Juveniles AMNH A157069 and UMMZ 212364 lack femoral glands, but have fore- and hind limb dermal spines present similar in number and placement to those of adults.

UMMZ 212364 has very fine brown spotting on the venter. AMNH A167933 has silver-colored longitudinal stripes on the canthus rostrum, between the eyes, and dorsolaterally on the body. The dorsum dark brown blotches and spots loosely define a postocular “W” in UMMZ 212366–67. The dark spotting on the venter may extend to the throat (AMNH A167933 and A167936).

ETYMOLOGY: The specific name *tavaratra* refers to the Malagasy word for “the north”. This name is used as a nonlatinized specific epithet, and is given in reference to the known distribution of this species in northern Madagascar.

DISTRIBUTION: Known only from humid forests in NE Madagascar, between 650–1300 m elevation. Most specimens have been collected from the Marojeje Massif (including the Betaolana corridor), but the species is known to occur as far north as the Sorata Massif.

REMARKS: All specimens were collected at night, between 1800 and 2300 hours, in areas by the edges of rivers and small fast-flowing streams. Animals were found on leaves, branches, and tree trunks, at heights of 0.8–4.0 m above the forest floor.

Glaw and Vences (1997) report on four male specimens (ZFNK 59900, 59926–28) from 700 m elevation at Marojejy that may represent additional *S. tavaratra* material based on their SVL of 31–34 mm. Although these authors attributed these specimens to *S. fimbriatus* (type locality Andasibe, 500 km south of Marojejy), they also noted the small body size and differences in the call of these Marojejy specimens compared to the Andasibe *S. fimbriatus*.

Spinomantis nussbaumi, new species

Figures 2, 4, 5

HOLOTYPE: AMNH A167949 (RAX 5934), adult male, with muscle and skin removed from left thigh for a tissue sample, collected 27 February 2003, Befosa River–Antetikalam-bazaha, Tsaratanana Massif, Bealanana Fivondronana, Mahajanga Province, 1650 m, 14°10'27"S, 48° 56'42"E, by S.D. Mahaviasy, N. Rabibisoa, and N. Rakotozafy.

PARATYPES: AMNH A167947–48 (RAX 5824, 5933), A167950–51 (RAX 5975–76), collection data as the holotype except AMNH A167947, 24 February 2003, 1580 m; AMNH A167950–51, 28 February 2003, 1620 m.

DIAGNOSIS: A large-sized *Spinomantis* (adult male SLV 47–57 mm), with type 2 femoral glands that in preservative are lighter in coloration than the surrounding skin in breeding males; vomerine teeth; END/NSD \leq 1.8; dorsal body pattern composed of irregular darker shaped blotches; throat white (in life and preservative); a singular subgular vocal sac in males; SVL/FT \leq 1.4; inner and outer metatarsal tubercles; well-developed foot webbing, with only 0.25–0.5 of the distal phalange free of webbing on the exterior margin of toe 3, and only 1.0–1.5 distal phalanges free of webbing on the internal edge of toe 4.

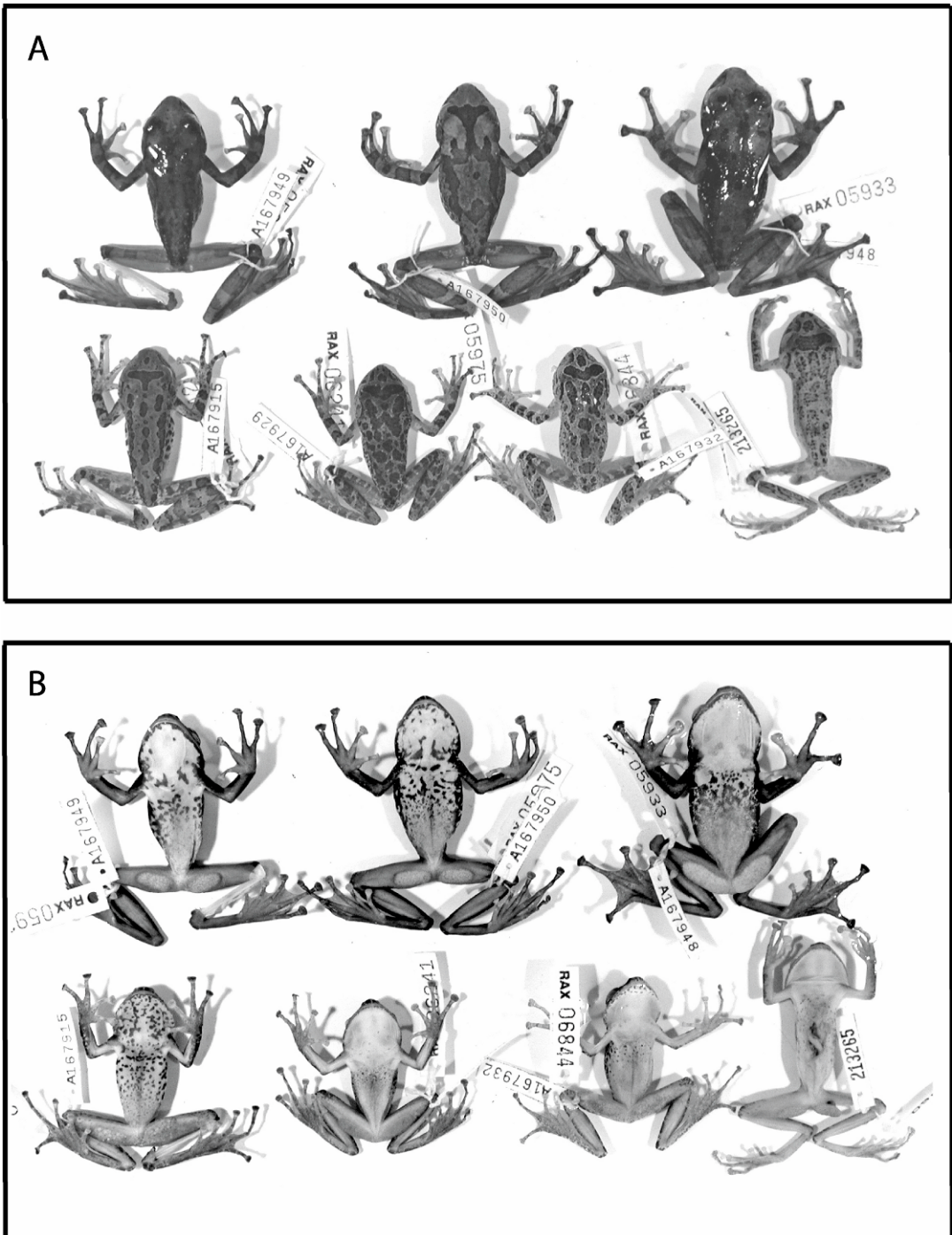
Spinomantis nussbaumi can be distinguished from all other *Spinomantis* species by the following characters. *Spinomantis aglavei*, *S. fimbriatus*, *S. massorum*, *S. tavaratra*, and *S. phantasticus* all have hind limb dermal spines that are absent in *S. nussbaumi*. *Spinomantis bertini* is much smaller (males SVL 22–23 mm), and has only rudimentary webbing on the hind feet. *Spinomantis elegans* and *S.*

microtis lack male femoral glands, and in addition, *S. elegans* lacks an outer metatarsal tubercle and *S. microtis* has completely webbed feet. *Spinomantis guibei* has distinctive markings: the ventral surface of the limbs are white with black blotches and the dorsal body has longitudinal dark lines, both of which are absent in *S. nussbaumi*. *Spinomantis guibei* also has more reduced webbing: the internal margin of toe 4 has three phalanges without webbing compared to 1–1.5 for *S. nussbaumi*. *Spinomantis brunae* can be distinguished by its smaller adult male body size (SVL 32–35 mm), reticulated dorsal body pattern, dark throat color, proportionally shorter snout (*S. brunae*, END/NSD $>$ 1.8, *S. nussbaumi* END/NSD \leq 1.8), and proportionally shorter foot length (*S. brunae* SVL/FT \geq 1.4, *S. nussbaumi* SVL/FT \leq 1.4). *S. peraccae* can be distinguished by its smaller adult male SLV (*S. peraccae* 35–46 mm, *S. nussbaumi* 47–57 mm; table 5) pale yellow throat color in preservative, less-developed toe webbing with the exterior margin of toe 3 with 0.75–1.0 phalanges without webbing (*S. nussbaumi* 0.25–0.5), and femoral gland color that is the same as the surrounding skin in preservative.

DESCRIPTION OF HOLOTYPE: Adult male in an excellent state of preservation with a singular subgular vocal sac, distinct femoral glands, and mature whitish-yellow testes, measuring 7.9 \times 1.7 mm. A tissue sample of muscle has been removed from the left thigh.

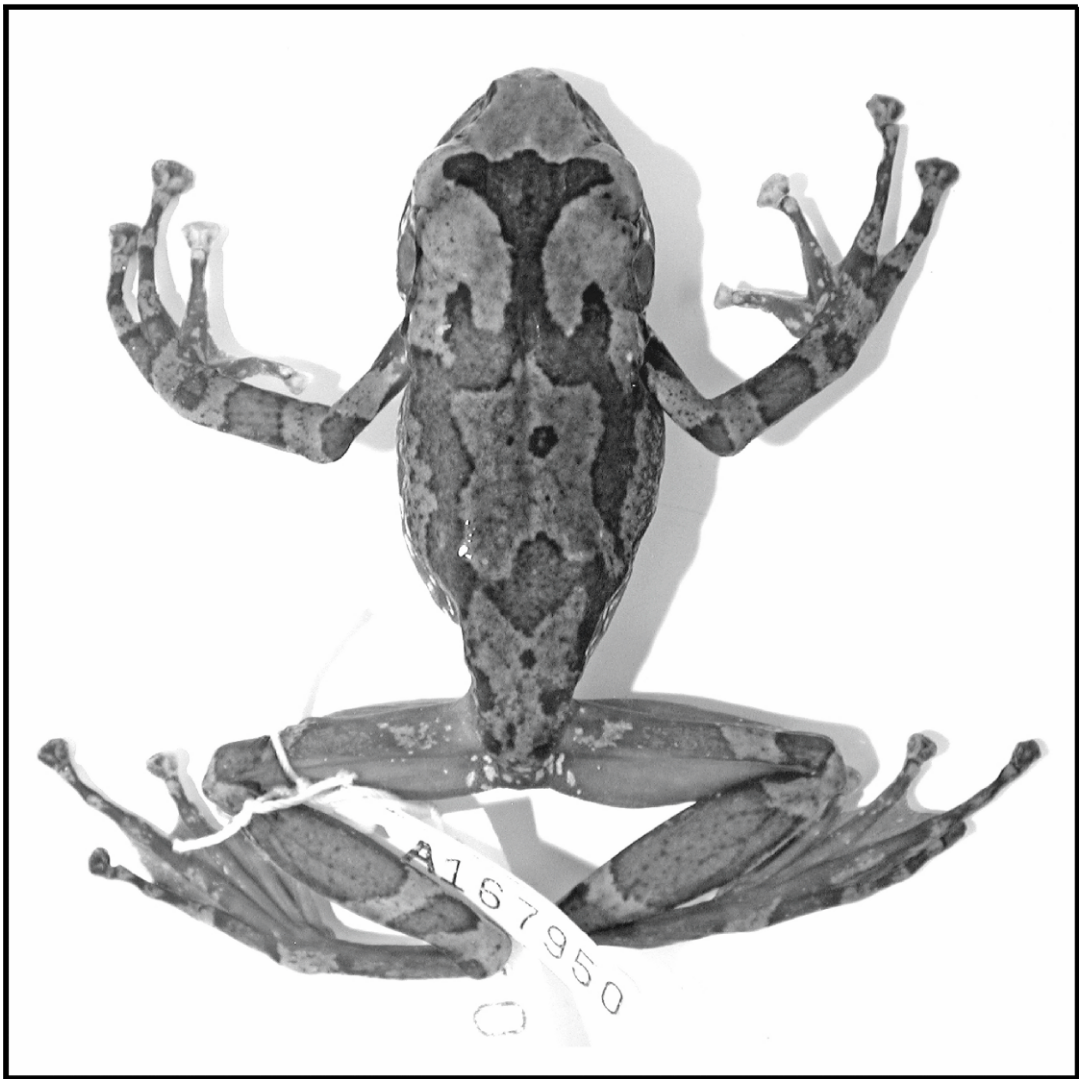
Head smooth dorsally, with a faint longitudinal intraocular ridge. Head width 1.41 times head length. Head length 0.26 times SVL. Canthus rostrum sharp edged. A weak ridge starts posterior to nostril and runs through the loreal region to the lower anterior eye orbit. Internarial distance 0.30 times head width. Nostrils open laterally. Pupil round. Eye to nostril distance 1.50 times nostril to snout distance and 0.85 times eye diameter. Tympanum well defined, diameter 0.56 times eye diameter. Supratympanic ridge present, arching smoothly from posterior of eye to above the forelimb insertion point. Vomerine teeth present and vomerine bone triangular in shape.

Arms slender and smooth with forearm length 0.25 times SVL. No dermal spines on arms, legs, or body. Hand length (including



Christopher J. Raxworthy

Fig. 4. *Spinomantis nussbaumi*, new species, and *S. peraccae*. **A.** Dorsal views of *S. nussbaumi*, new species (above, left to right): AMNH 167949, 167950, 167948; and *S. peraccae* (below, left to right): AMNH 167915, 167929, 167932, UMMZ 213265. **B.** Ventral views of *S. nussbaumi*, new species (above, left to right): AMNH 167949, 167950, 167948; and *S. peraccae* (below, left to right): AMNH 167915, 167929, 167932, UMMZ 213265.



Christopher J. Raxworthy

Fig. 5. Dorsal view of *Spinomantis nussbaumi*, new species AMNH A167950.

disks) 0.36 times SVL with a trace webbing between digits, never extending beyond basal phalange. Relative finger lengths $1 < 2 < 4 < 3$. Fingers and toes with enlarged, triangular disks. Disk of third toe 1.8 times wider than terminal phalange. Dorsum and flanks with fine granular skin. Venter weakly granular. No enlarged tubercles on body or around cloaca.

Tibio-tarsal extension reaches between eye and snout tip. Thigh length 0.49 times SVL. Ventral surface of thigh weakly granular, all other leg surfaces smooth. Type 2, oval femoral glands differentiated and distended,

measuring 9.8×5.0 mm, separated by 2.9 mm. In external view approximately 65 granules with no central pore visible. In internal view, approximately 120 granules. Granules translucent with opaque center. Lower leg 0.53 times SVL. Foot, including tarsus, 0.80 times SVL. Inner and outer metatarsal tubercles present, with round outer metatarsal tubercle 0.5 mm in diameter and elliptical inner metatarsal tubercle 2.1 mm in length. Relative toe lengths $1 < 2 < 5 < 3 < 4$. Foot webbing **I** 0.5 – 1 **II** 0.25 – 1 **III** 0.5 – 1.5 **IV** 1 – 0.75 **V**.

TABLE 5
Morphometric data for *Spinomantis nussbaumi*, new species, and *S. peraccae*. All measurements in mm. BM specimen data from Andreone *et al.*, (1998).

Specimen #	SEX	SVL	ED	TD	END	NSD	NND	FTL	FGL
<i>S. nussbaumi</i>									
AMNH A167949 ^a	M	47.9	4.6	2.6	3.9	2.6	5.3	38.3	9.8
AMNH A167947	M	47.8	4.3	3.1	4.1	2.6	5.2	36.8	9.7
AMNH A167948	M	56.4	6.1	3.5	4.7	3.3	6.1	42.3	15.5
AMNH A167950	M	50.2	4.8	3.1	4.0	3.7	5.6	38.2	9.9
AMNH A167951	M	47.5	4.9	2.9	3.7	3.6	5.3	36.9	9.2
<i>S. peraccae</i>									
BM 1947.2.9.7 ^a	F?	31.9	5.4	2.4	3.7	3.2	?	23.9	-
AMNH A167909	M	39.5	4.1	2.1	3.6	2.9	4.5	31.0	9.2
AMNH A167910	M	35.6	4.4	1.8	3.3	2.7	4.2	27.8	8.0
AMNH A167911	M	36.5	3.9	1.9	3.1	2.7	4.1	27.4	7.5
AMNH A167912	M	36.2	3.9	1.8	3.2	2.5	4.2	27.9	6.9
AMNH A167913	M	35.5	3.4	2.0	3.1	2.4	3.6	26.5	8.1
AMNH A167914	M	36.8	4.3	2.0	3.1	2.6	4.4	29.1	8.3
AMNH A167915	M	43.9	3.8	2.4	4.0	2.7	5.3	37.7	9.0
AMNH A167916	M	44.8	4.7	2.4	3.5	2.5	4.9	36.5	8.0
AMNH A167917	M	42.3	4.3	2.6	3.8	2.8	5.0	37.9	9.3
AMNH A167918	M	35.6	3.9	1.6	3.2	3.0	4.1	29.5	5.7
AMNH A167919	M	34.8	4.3	1.9	3.2	2.6	4.3	29.1	8.8
AMNH A167920	M	36.4	3.9	2.1	3.8	2.1	3.9	28.4	7.2
AMNH A167921	M	39.5	4.3	2.5	3.6	2.8	4.8	28.8	8.1
AMNH A167922	M	40.8	4.1	2.5	3.8	2.6	4.6	29.3	8.5
AMNH A167923	M	38.3	4.2	2.2	3.3	2.3	4.3	30.0	7.0
AMNH A167925	M	38.4	4.4	2.2	3.6	2.5	4.2	29.1	8.4
AMNH A167926	M	39.5	4.3	2.2	3.4	2.6	4.3	29.0	8.8
AMNH A167927	M	40.0	4.2	2.4	3.5	2.3	4.2	30.7	9.7
AMNH A167929	M	40.7	4.1	2.5	3.9	2.9	4.4	32.7	9.7
AMNH A167930	M	38.4	4.2	2.2	3.0	2.4	4.0	29.0	7.9
AMNH A167931	M	40.6	4.5	2.3	3.9	3.0	4.7	32.9	8.9
AMNH A167932	M	39.7	4.5	2.3	3.7	2.5	4.0	31.8	9.5
UMMZ 213265	M	45.9	5.3	2.3	4.3	2.9	4.6	33.0	7.8
UMMZ 213267	M	38.0	4.2	2.1	3.5	2.3	4.3	29.9	8.1
AMNH A167924	F	42.4	4.5	2.1	3.9	2.6	4.6	31.7	-
AMNH A167928	J	31.4	3.9	1.5	3.3	2.3	3.8	22.7	-

^aHolotype.

COLORATION IN PRESERVATIVE: Head dorsally and laterally dark brown with a darker brown, broken cross-shape marking on the posterior head, with the anterior arms of the cross reaching the supraocular regions. Iris dark brown. Tympanum light brown. Dorsum dark brown with darker brown spots forming two dorsolateral lines. Flanks dark brown with a yellowish-white spots. Arms brown with four dorsal darker brown transverse stripes of uneven width. Legs brown with nine darker brown transverse stripes of uneven width. When in sitting posture, dorsal stripes

on the hind limbs line up, forming three longitudinal stripes. Throat white with small dark brown spots mostly concentrated on the lower lip margin. Venter yellowish white with dark brown spots in the pectoral region and anterior belly, and fading into pale-brown points on the posterior belly. Ventral arms and legs uniform brown, except for the femoral glands that are paler brown.

COLORATION IN LIFE: As in preservative, except that some green and greenish-brown pigment is present in life, forming spots on the head and body.

VARIATION: Morphometric variation is summarized in table 5. All specimens agree with the holotype description with the following exceptions. The supratympanic ridge has a sharp bend posterior to the tympanum in AMNH A167950 and A167951. Femoral glands vary in size from 9.2–15.5 length \times 4.2–6.0 mm width, separated by 0.5–3.2 mm, with approximately 45 to 100 granules visible in external view. Inner metatarsal tubercles range from 1.5–1.9 mm in length. Foot webbing variation: I 0.25 to 0.5 – 1 II 0.25 – 1 to 1.25 III 0.25 to 0.5 – 1 to 1.5 IV 1 to 2 – 0.25 to 0.75 V.

AMNH A167947 and A167950 have a lighter grey-brown dorsum with more defined dark brown patterning. In these specimens there is a transverse intraocular stripe that connects to a medial longitudinal stripe that extends to the dorsal pectoral region. This longitudinal stripe then divides into two longitudinal dorsolateral stripes of uneven width that terminate at the lower back (fig. 5). AMNH A16750 also has small pale brown spots on the dorsal-posterior proximal region of each thigh. AMNH A167948 and A167951 have the intraocular transverse stripe and the medial stripe, and have scattered fine white spots on the posterior flanks. Spotting on the venter varies from a few small spots, as in AMNH A167947, to extensive blotching, as in AMNH A167948.

The female and juvenile morphology is unknown.

ETYMOLOGY: The specific name *nussbaumi* honors Ronald A. Nussbaum for his substantial contributions to our knowledge of the Malagasy herpetofauna.

DISTRIBUTION: Known only from the type locality: Befosa River–Antetikalambazaha, Tsaratanana Massif, in northern Madagascar. This species was found in rainforest between 1580–1650 m elevation.

REMARKS: All specimens were collected at night between 2100–2330 hours, on leaves at 1–3 height, overhanging or at the edge of the Befosa River. AMNH A167947 was found calling at the time of capture. At higher elevation at Tsaratanana, we also found specimens of *S. peraccae*. However, the type locality for *S. peraccae* is Ivohimanitra (Boulenger, 1896) in southeast Madagascar

(Tanala Region), and based on the geographic variation that is evident within this complex, this suggests the potential for additional species diversity. To facilitate the diagnosis of *S. nussbaumi* compared to *S. peraccae*, we report morphometric variation within both species in table 4, which includes the holotype of *S. peraccae*. Additional morphological data for *S. peraccae* is given by Glaw and Vences (1994) and Andreone et al. (1998).

IDENTIFICATION KEY TO *SPINOMANTIS*

This key will identify *Spinomantis* species for all adult male specimens (the only representative material known for some species), although many characters should also identify female and juvenile specimens.

1. No dermal spines on hind limbs. 2
- Dermal spines present on hind limbs 8
2. Adult male SVL < 24 mm; rudimentary webbing on hind limbs; limbs with prominent and narrow dark transverse bands
. *Spinomantis bertini*
- Adult male SVL > 24 mm; developed webbing on hind limbs; limbs may lack prominent and narrow dark transverse bands. 3
3. Outer metatarsal tubercle absent; adult male SVL 52–60 mm; femoral glands absent in adult males; body dorsally marked by large distinct dark spots with pale borders.
. *Spinomantis elegans*
- Outer metatarsal tubercle present; adult male SVL 29–57 mm; femoral glands may be present in adult males; body dorsally may lack distinct dark spots with pale borders 4
4. Toes completely webbed; adult male SVL 34–56 mm; femoral glands absent in adult males *Spinomantis microtis*
- Toes incompletely webbed; adult male SVL 29–57 mm; femoral glands present in adult males 5
5. Ventral surface of hind limbs white with distinct large black spots; dorsal body with longitudinal black lines; adult male SVL 29–35 mm *Spinomantis guibei*
- Ventral surface of hind limbs not white and without distinct large black spots; dorsal body spotted, and usually lacks longitudinal black lines; adult male SVL 32–57 mm . . 6
6. Adult male SVL < 35 mm; body dorsally with a reticulated pattern of round dark spots; dark brown throat with light spots; NND/TD

- ≤ 1.5 ; END/NSD > 1.8 ; SVL/FTL ≥ 1.4 *Spinomantis brunae*
 — Adult male SVL > 34 mm; body dorsally lacks a reticulated pattern of round dark spots; light colored throat with dark spots; NND/TD ≥ 1.7 ; END/NSD ≤ 1.8 ; SVL/FTL ≤ 1.4 7
 7. Adult SVL 33–46 mm; interior surface of toe 3 with 1.5 to 2 phalanges free of webbing; yellowish-white throat in preservative; lower flanks light with dark spots; adult male femoral glands same color as surrounding skin *Spinomantis peraccae*
 — Adult SVL 47–56 mm; interior surface of toe 3 with 1 to 1.5 phalanges free of webbing; bright white throat in preservative (and life); lower flanks dark with white spots; adult male femoral glands lighter in color than surrounding skin *Spinomantis nussbaumi*
 8. Adult with dermal spines ≥ 0.5 mm in length above the eyes, and with prominent dermal spines on head and body *Spinomantis phantasticus*
 — Adult lacks dermal spines ≥ 0.5 mm in height above the eyes, and without prominent dermal spines on head and body 9
 9. Adults with dermal spines > 1 mm in length on tarsus; dermal spines may have multiple points; dermal spines always present on arms 10
 — Adults lacks dermal spines > 1 mm in length on tarsus; dermal spines on hind limb with single points; dermal spines may be absent on arms 11
 10. Adult male SLV ≥ 40 mm; END/NSD ≥ 1.5 *Spinomantis aglavei*
 — Adult male SLV < 40 mm; END/NSD < 1.5 *Spinomantis fimbriatus*
 11. No dark spots on throat or venter; adult NSD > 2.1 mm; tibio-tarsal extension reaches between the eye and nostrils; interior surface of toe 4 with 0.75 to 2 phalanges free of webbing; exterior surface of toe 4 with 1 to 2 phalanges free of webbing *Spinomantis massorum*
 — Dark spots on throat and/or venter; adult NSD < 2.1 mm; tibio-tarsal extension reaches nostrils to beyond snout tip; interior surface of toe 4 with 2 to 2.5 phalanges free of webbing; exterior surface of toe 4 with 2 to 2.5 phalanges free of webbing *Spinomantis tavaratra*

DISCUSSION

The behavior and habits that we report here for *S. brunae*, *S. massorum*, and the two new

species are all extremely similar, and these observations largely agree with previous records made for the other nocturnal and arboreal *Spinomantis* species (see Introduction). All these species appear to be restricted to humid rainforest habitat in close proximity to streams, and individuals may be found either on the ground or on leaves, branches, or vertical tree trunks. Males are found calling soon after dusk from perches, usually overhanging water, and it is likely that all these species deposit terrestrial egg clumps, either attached to leaves (see Glaw and Vences, 1997) or possibly rock surfaces overhanging water (as described for *S. microtis*, Andreone and Nussbaum, 2006). Our observations for *S. brunae* clearly show that this species should not be classified as a terrestrial species within this genus (cf. Glaw and Vences, 2006). The habits of the other terrestrial species: *S. bertini*, *S. elegans*, *S. guibei*, and *S. microtis* remain more poorly documented. All these species are restricted to humid habitats, and *S. microtis* is known to be restricted to water-splashed rock surfaces of fast-flowing streams (Andreone and Nussbaum, 2006; Raxworthy, personal obs.).

The development of well-developed dermal spines on the limbs for some nocturnal and arboreal *Spinomantis* species represents a unique character within mantellines (although some *Gephyromantis* species have tubercles or small triangular skin flaps on the limbs). *Spinomantis massorum* and *S. tavaratra* have dermal spines on the hind limbs but they never exceed 1 mm in length in the adult. The most pronounced dermal spines (exceeding 1 mm in length) are found in *S. aglavei*, *S. fimbriatus*, and *S. phantasticus*. The latter species also has well-developed dermal spines on the dorsal surface of the head and body. For the juvenile (subadult) *S. massorum*, *S. tavaratra*, and *S. aglavei* that we examined, we found that dermal spine arrangements were generally very similar to the adults in terms of numbers, placement, and shape. These preliminary results thus suggest that dermal spines may also be diagnostic for identifying subadult individuals. However, because it is also likely that newly developed metamorphs lack limb spines, these characters should be used with care for the identification of smaller juveniles.

The correspondence between dermal spine development, and behaviors that might take advantage of cryptic resting postures, such as crouching on moss or lichen-covered tree trunks, is not yet known for these species. However, we suspect that these dermal spines aid hiding from visual predators (e.g., birds) during the daytime period of inactivity, and thus may allow these species to occupy refuges not suitable to other species (for example, the exposed surfaces of tree trunks).

The phylogenetic relationships of the two new *Spinomantis* species have not yet been investigated; however, the phenetic similarity between *S. nussbaumi* and *S. peraccae* suggests they are closely related, and the tarsal spines of *S. tavaratra* (which are almost certainly apomorphic) suggest a close relation with the other arboreal and spiny species in this genus. As reported for other mantelline groups in northern Madagascar (Rabibisoa et al., in press; Rakotondrazafy and Raxworthy, in press), these two new species further confirm the high species diversity and localized endemism of amphibians in the Northern Highlands of Madagascar.

The distribution data we present here for *S. massorum* and *S. brunae* conform to the previously proposed patterns of endemism: *S. massorum* is currently confined to north-west Madagascar with a typical Sambirano distribution; and *S. brunae* continues to be known only from the Anosy Mountains in southeast Madagascar. For the new species: *S. tavaratra* has a distribution currently known only in northeast Madagascar, occurring as far south as the Marojejy Massif, which is similar to the northern distributions found in other mantelline species (e.g. see Blommers-Schlösser and Blanc, 1991; Rabibisoa et al., in press; Rakotondrazafy and Raxworthy, in press). By contrast, the single known locality for *S. nussbaumi* suggests it may be endemic to the central Tsaratanana Massif (it was not found at any of the surrounding surveyed sites, as listed by Rabibisoa et al., in press); the Tsaratanana Massif is also a well-known area of herpetological endemism (Raxworthy and Nussbaum, 1995, 1996, 1997, 2006).

Concerning conservation issues for these four *Spinomantis* species, three are known from the following reserves and consequently

appear to be well protected: *S. brunae*, Andohahela National Park (Andreone et al., 1998); *S. massorum*, Manongarivo Special Reserve and Tsaratanana Strict Nature Reserve; and *S. tavaratra*, Marojejy National Park. The fourth species: *S. nussbaumi* is only known from a single forested site that is currently outside the protected area of the Tsaratanana Strict Nature Reserve. The type locality, however, is on the main trail leading from Mangindrano village to the Maromokotro summit, and plans are being developed to include this forest within a new protected area, or extension of the original Tsaratanana Strict Nature Reserve (ANGAP, 2001). The discovery of this new species thus further strengthens the case for this forest to be conserved.

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APPENDIX 1

ADDITIONAL SPECIMENS EXAMINED

Spinomantis aglavei: Madagascar: Ankitsika Mountain, Antsiranana Province: AMNH A167908; Betampona Strict Reserve, Toamasina Province: AMNH A175865–67; Marojejy Reserve, Antsiranana Province: AMNH A157065, A157067–68, UMMZ 212357, 212369; Andringitra, Fianarantsoa Province: UMMZ 212374; Anjananaharibe-Sud Special Reserve, Antsiranana Province: UMMZ 214216; *Spinomantis phantasticus*: Madagascar: Ambolokopatrika River, Betaolana Corridor

Forest, Antsiranana Province: AMNH A167952; *Spinomantis peraccae*: Madagascar: Matsaborimaiky Lake, Tsaratanana, Mahajanga Province: AMNH A167909–14; Ambodinitaratanana, Tsaratanana, Antsiranana Province: AMNH A167915–18; Befosa River, Antetikalambazaha, Tsaratanana, Mahajanga Province: AMNH A167919–24; Matsaborimena, Bemanevika Lakes, Mahajanga Province: AMNH A167925–30; Lohanandroranga, Mahajanga Province: AMNH A167931–32; Marojejy Reserve, Antsiranana Province: UMMZ 213265; Matsabory (= Matsaborimaiky Lake), Tsaratanana, Mahajanga Province: UMMZ 213267.

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