

New species of *Blaesodactylus* (Squamata: Gekkonidae) from Tsingy karstic outcrops in Ankarana National Park, northern Madagascar

TEPPEI JONO^{1,2,5}, AARON M. BAUER³, IAN BRENNAN^{3,4} & AKIRA MORI¹

¹*Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606-8502, Japan*
E-mail address: mjusinondo@gmail.com

²*Present Address: Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, Sichuan 610041, P.R. China*

³*Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA*

⁴*Evolution, Ecology, and Genetics, Research School of Biology, The Australian National University, Canberra, ACT, Australia*

⁵*Corresponding author*

Abstract

We describe a new gecko of the genus *Blaesodactylus* from a karstic outcrop in deciduous dry forest of Ankarana National Park, northern Madagascar. *Blaesodactylus microtuberculatus* sp. nov., the fifth recognized species of *Blaesodactylus*, is distinguished from all other congeners, *B. ambonihazo*, *B. antongilensis*, *B. boivini* and *B. sakalava* by a combination of small, homogeneous gular granules, unspotted venter and lack of tubercles on distal part of original tail. Mitochondrial (ND2 and ND4) and nuclear (RAG-1) DNA identify a consistent divergence between *B. microtuberculatus* and its allotopic sister species *B. boivini*. We highlight habitat partitioning in these allotopic congeners where *Blaesodactylus microtuberculatus* inhabits karstic outcrops in Tsingy massif, and *B. boivini* dwells on tree trunks in deciduous dry forest.

Key words: Squamata, Gekkonidae, Madagascar, *Blaesodactylus microtuberculatus* sp. nov.

Introduction

Genus *Blaesodactylus* Boettger, 1893 comprises relatively large sized nocturnal gekkonid, endemic to Madagascar (Glaw & Vences 2007; Greenbaum *et al.* 2007). Greenbaum *et al.* (2007) confirmed the reciprocal monophyly of *Blaesodactylus* and its sister taxon, *Homopholis* Boulenger, 1885 from continental Africa. The genus *Blaesodactylus* includes *B. antongilensis* (Böhme & Meier 1980), *B. boivini* (Duméril 1856), *B. sakalava* (Grandison 1867), and the recently described *B. ambonihazo* Bauer, Glaw, Gehring & Vences, 2011, from Ankafantsika, northwestern Madagascar. All four of these species are common where they occur, inhabiting dry deciduous forests or rain forests, and usually occupying tree trunks (Glaw & Vences 2007; Ikeuchi *et al.* 2014).

During fieldwork in 2012, we collected and observed several *Blaesodactylus* specimens from karstic outcrops and tree trunks in Ankarana National Park, northern Madagascar. One specimen collected from a karstic outcrop is morphologically distinct from the others collected from tree trunks. Here, we describe the former specimen as a new *Blaesodactylus* species; the fifth member of this endemic Madagascan genus. This new taxon is the sister species of its allotopic (*sensu* Rivas 1964) congener, *B. boivini*, and therefore, is of special interest as an additional example of localized endemism to karstic massifs in Madagascan geckos.

Material and methods

Sampling. Field surveys were conducted from 2 to 5 December 2012, in dry deciduous forest in Ankarana National Park, Antsiranana Province, northern Madagascar. Excursions into forested habitats included both day and night searches of trees and outcrops for specimens. We collected *Blaesodactylus* when possible, and recorded the geographic coordinates and time of observation for all individuals, including both inaccessible and captured

ones. Tissue samples were collected from liver or toes and stored in 95% ethanol and voucher specimens were fixed in 10% formalin, and later preserved in 70% ethanol. Specimens studied in detail were deposited in the Kyoto University Museum (KUZ), Kyoto, Japan, and associated field numbers are AMP, AFP (T. Jono) and Ad (A. Mori).

Molecular phylogenetics. We extracted genomic DNA from liver or toe tissue of eight *Blaesodactylus* samples. New sampling comprises three of the four currently recognized species: *B. ambonihazo*, *B. boivini* and *B. sakalava* as well as a single specimen of a new species described herein (Table 1). We also incorporated sequence data from additional *Blaesodactylus* specimens, including *B. antongilensis*, previously generated by Greenbaum *et al.* (2007) and Bauer *et al.* (2011) and from the closely related genera *Homopholis*, and *Geckolepis* (Greenbaum *et al.* 2007; Gamble *et al.* 2012). Genomic DNA was isolated from ethanol-preserved tissues via Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, California, USA). Segments of the mitochondrial loci ND2 (NADH dehydrogenase subunit 2; 1355 bp) and ND4 (NADH dehydrogenase subunit 4; 593 bp) and nuclear locus RAG-1 (recombination activating gene 1; 1098 bp) were amplified in 25 mL reactions with published primer pairs for ND2 (METF1, CO1R1), ND4 (ND4F1, LeuR1), and RAG-1 (RAG1-396, RAG1-397) (Arévalo *et al.* 1994; Macey *et al.* 1997; Groth & Barrowclough 1999). Polymerase chain reaction followed standard conditions across all loci: denaturation at 95°C for two minutes, followed by 34 cycles of: denaturation at 95°C for 35 s, annealing at 48°C for 35 s, and 1.5 m extension at 72°C. Amplified products were visualized on 1.5% agarose gels, and successful amplifications were purified using AMPure magnetic bead system (Agencourt Bioscience, Beverly, Massachusetts, USA). Sequencing reactions used ABI Prism BigDyeTerminator (Applied Biosystems, Foster City, California, USA), primer pairs for ND2 (METF1, ND2F17, TRPR3, CO1R1), ND4 (ND4F1, LeuRNA) and RAG-1 (RAG1-F700, RAG1-R700), and product was purified using Agencourt CleanSeq magnetic bead system (Agencourt Bioscience). Sequencing was carried out on an ABI 3730 automated sequencer for electrophoresis, and electropherograms were imported into Geneious 7.0 (Drummond *et al.* 2011). Sequences were manually aligned in TextWrangler v. 4.5 (Bare Bones Software, North Chelmsford, Massachusetts, USA). Appropriate evolutionary models (ND2: GTR+Γ+I, RAG1: HKY+Γ) were assessed using jModelTest 2 (Darriba *et al.* 2012). Final alignments were uploaded to the CIPRES Science Gateway (Miller *et al.* 2012) for Maximum Likelihood (ML) analysis using RAxML 8.0 (Stamatakis *et al.* 2005), and Bayesian Inference (BI) using MrBayes 3.2.3 (Huelsenbeck & Ronquist 2001). ML analysis was run for 100 independent tree searches, and 1000 bootstrap replicates using a general time reversible (GTR) model with gamma (Γ) distributed rate variation among sites. ML topologies of the individual ND2 and RAG-1 genes were congruent and were combined to form a concatenated dataset, partitioned by gene. BI analysis of the concatenated dataset implemented appropriate evolutionary models assessed by jModelTest2, with 2 runs for 100 million generations and 4 chains, and the first 25% of sampled trees discarded as burn-in. ML and BI topologies of the concatenated, partitioned dataset were identical. New sequences have been deposited in GenBank (see Table 1).

Morphology. The following measurements were taken with a digital caliper following the methods of Bauer *et al.* (2002, 2003): crus length (CrusL); ear length (EarL); eye to ear distance (EyeEar); forearm length (ForealL); head depth (HeadD); head length (HeadL); head width (HeadW); internarial distance; interorbital distance (shortest distance between left and right superciliary scale rows); orbital diameter (OrbD); snout to eye distance (SnEye); snout-vent length (SVL); tail length (Taill); trunk length (TrunkL). Values were reported to the nearest 0.1 mm. Measurements and scale counts are based on right side of animals unless otherwise noted. Scale counts and external observations of morphology were made using a dissecting microscope (Leica S8AP0, Leica Microsystems Inc., IL, USA). Meristic values recorded were scale rows around midbody; number of longitudinal rows of tubercles at midbody; ventral scales across the venter between the ventrolateral folds at midbody; number of supralabials; number of infralabials; subdigital lamellae of manus; subdigital lamellae of pes. Comparisons were made with museum specimens of congeneric species (see Appendix) and with data reported in the relevant systematic and faunistic literature (e.g., Duméril, 1856; Angel 1942; Russell 1978; Böhme & Meier 1980; Glaw & Vences 2007, Schönecker 2008; Bauer *et al.* 2011). Photographs of the specimens were taken with a Casio EXILIM EX-F1 (Casio Computer Co., LTD., Tokyo, Japan) mounted on a dissecting microscope or with a Nikon 1 camera (Nikon Co., Tokyo, Japan) using Adobe Illustrator CS2.

TABLE 1. List of specimens included in the molecular analyses with corresponding GenBank accession numbers. Newly obtained sequences have KM series accession numbers. Museum acronyms for material cited in Greenbaum *et al.* (2007) (EU series accession numbers): CAS—California Academy of Sciences, MCZ—Museum of Comparative Zoology, Harvard University, WRBM—William Roy Branch Madagascar Field Series, ZSM—Zoologische Staatssammlung München.

Species	Specimen No.	Locality	Latitude	Longitude	GenBank Accession No.		
					ND2	ND4	RAG-1
<i>Blaesodactylus ambonihazo</i>	ZSM 469/2001	Madagascar, Mahajanga Province, Ankafantsika NP	16°18'S	46°49'E	EU054254	EU054182	EU054230
<i>B. ambonihazo</i>	2012 AMP152	Madagascar, Mahajanga Province, Ankafantsika NP	16°18'50"S	46°49'02"E	KM580361	KM850990	KM580366
<i>B. ambonihazo</i>	2012 AMP153	Madagascar, Mahajanga Province, Ankafantsika NP	16°18'50"S	46°49'02"E	KM580362	KM850991	KM580367
<i>B. ambonihazo</i>	2012 AMP154	Madagascar, Mahajanga Province, Ankafantsika NP	16°18'50"S	46°49'02"E	KM580359	KM850992	KM580368
<i>B. ambonihazo</i>	2012 AMP155	Madagascar, Mahajanga Province, Ankafantsika NP	16°18'50"S	46°49'02"E	KM580360	KM850993	KM580369
<i>B. antongilensis</i>	ZSM 410/2005	Madagascar, Nosy Mangabe	15°29'S	49°46"E	EU054253	EU054181	EU054229
<i>B. boivini</i>	ZSM 263/2004	Madagascar, Montagne des Français	12°19'S	49°20"E	EU054252	EU054180	EU054228
<i>B. boivini</i>	KUZ 069429	Madagascar, Antsiranana Province, Ankarana NP	12°57'49"S	49°08'36"E	KM580364	KM850994	KM580370
<i>B. boivini</i>	KUZ 069430	Madagascar, Antsiranana Province, Ankarana NP	12°57'25"S	49°07'10"E	KM580365	KM850995	KM580371
<i>B. sakalava</i>	WRBM 18	Madagascar, Toliara Province, Will's Track	22°58'05"S	43°37'37"E	EU054251	EU054179	EU054227
<i>B. microtuberculatus</i> sp. nov.	KUZ 069431	Madagascar, Antsiranana Province, Ankarana NP	12°57"S	49°07"E	KM580363	KM850996	KM580372
<i>Homopholis mulleri</i>	CAS 234119	South Africa, Limpopo Province, Farm Brenhilda	22°40'11"S	29°29'51"E	EU054241	EU054169	EU054217
<i>H. wahlbergii</i>	MCZ R-184488	South Africa, Limpopo Province, Farm Kagama	24°04'02"S	28°26'16"E	EU054243	EU054171	EU054219

Results

For ND2 there were 584 variable sites, 375 of them informative; for ND4 there were 272 variable sites, 194 of them informative; and for RAG1 there were 57 variable sites, 40 of them informative. The concatenated ND2 + RAG-1 tree using *Homopholis* spp. as outgroups retrieves a pattern of relationships identical to that previously reported (Greenbaum *et al.* 2007; Bauer *et al.* 2011). *Blaesodactylus* sp. nov. is recovered as sister species to *B. boivini* (Fig. 1). All interspecific relationships except that of *B. sakalava* to *B. antongilensis* (69% bootstrap support, 0.97 posterior probability), receive 100% bootstrap support and a posterior probability of 1.0. The ND4 dataset was sensitive to outgroup selection, and topologies varied depending upon whether *Homopholis*, *Geckolepis*, or both were included in the analysis (not shown). When both genera were used as outgroups the clade *B. boivini* + *Blaesodactylus* sp. nov. was retrieved as the sister to remaining taxa, but with no support, but in all cases the new species received 100% bootstrap support as sister to *B. boivini*. On the basis of its genetic distinctiveness and the diagnostic morphological characters reported below, we here describe the distinctive specimen from Ankarana National Park as a new species.

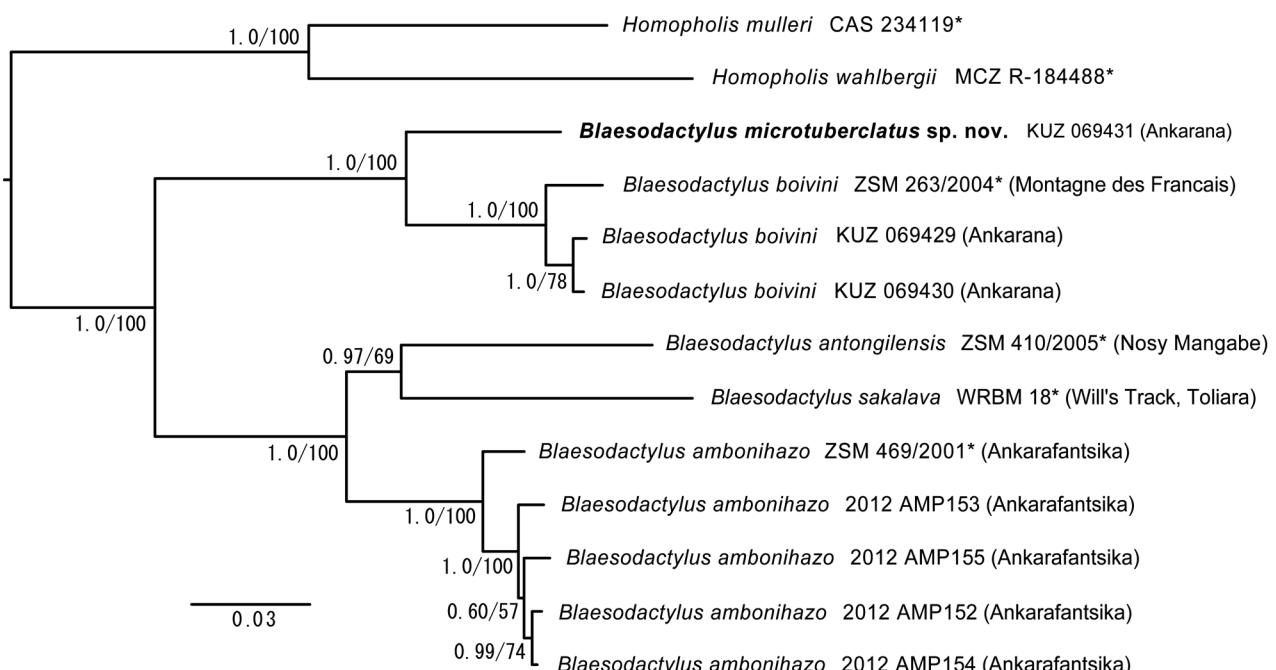


FIGURE 1. Results of a phylogenetic analysis of the concatenated mitochondrial ND2 gene and nuclear RAG-1 gene datasets. Values above branches are Bayesian Inference posterior probabilities/ Maximum Likelihood bootstrap supports. Localities and GenBank numbers are listed in Table 1. Data for specimens indicated with an asterisk are derived from Greenbaum *et al.* (2007). Sampling sites of *Blaesodactylus* specimens are shown in parentheses.

Blaesodactylus microtuberclatus sp. nov.

(Figs. 2A, 4A, 5A)

Holotype. KUZ069431 (field number AFP2012-002), adult male (Fig. 2A); Ankarana National Park, Antsiranana Province, northern Madagascar (12°57'S, 49°07'E; Fig. 3), collected by T. Jono and A. Mori on 4 December 2012.

Paratypes. None.

Etymology. The species epithet “*microtuberclatus*” refers to the presence of small tubercles, compared to all other congeners, on their trunk region.

Diagnosis. A large sized (SVL 117.4 mm), robust-bodied *Blaesodactylus* with tail slightly longer than SVL (Fig. 2A). Snout elongate, gular granules small and homogenous, internarial region convex (Fig. 4A). 162 scale rows around midbody, 15–17 longitudinal rows of relatively small tubercles on dorsum. Fourth digit of pes with 21 undivided subdigital lamellae. No tubercles on tail dorsum; midventral subcaudal scales transversely enlarged,

about half width of tail. Body dorsum grayish, mid-dorsal row of five blotches, original tail weakly banded, venter pale, only gular region with very faint mottling (Fig. 4A).

Among its congeners *Blaesodactylus microtuberculatus* sp. nov. may be differentiated from *B. boivini* by its smaller dorsal tubercles (Fig. 5; ~3 times size of adjacent scales *versus* ~10 times), absence of caudal tubercles (Fig. 5; *versus* caudal tubercles ~4 times size of adjacent scales and present on more than half of the tail), uniform pale venter except for gular region (*versus* mottled with areas of dark pigmentation), and lower number of dorsal tubercle rows (15–17 *versus* 18–21). It differs from *B. sakalava* in its smaller dorsal tubercles (Fig. 5; ~3 times size of adjacent scales *versus* ~6 times, with tubercles finely keel), absence of caudal tubercles (Fig. 5; *versus* keeled tubercles ~6 times size of adjacent scales and present on more than half of the tail), wider midventral subcaudal scales (Fig. 5; about half width of tail *versus* less than one-third width of tail), and mottled gular region (Fig. 4; *versus* pale). It is distinguished from *B. ambonihazo* by its smaller dorsal tubercles (Fig. 5; ~3 times size of adjacent scales *versus* ~6 times), absence of caudal tubercles (Fig. 5; *versus* keeled tubercles ~3 times size of adjacent scales present on proximal ~40% of the tail), wider midventral subcaudal scales (Fig. 5; about half width of tail *versus* less than one-third width of tail), mottled gular region (Fig. 4; *versus* pale), lower number of dorsal tubercle rows (15–17 *versus* 17–21). It is distinguished from *B. antongilensis* by its lower number of dorsal tubercles (15–17 *versus* up to 24), and mottled gular region (Fig. 4; *versus* pale).

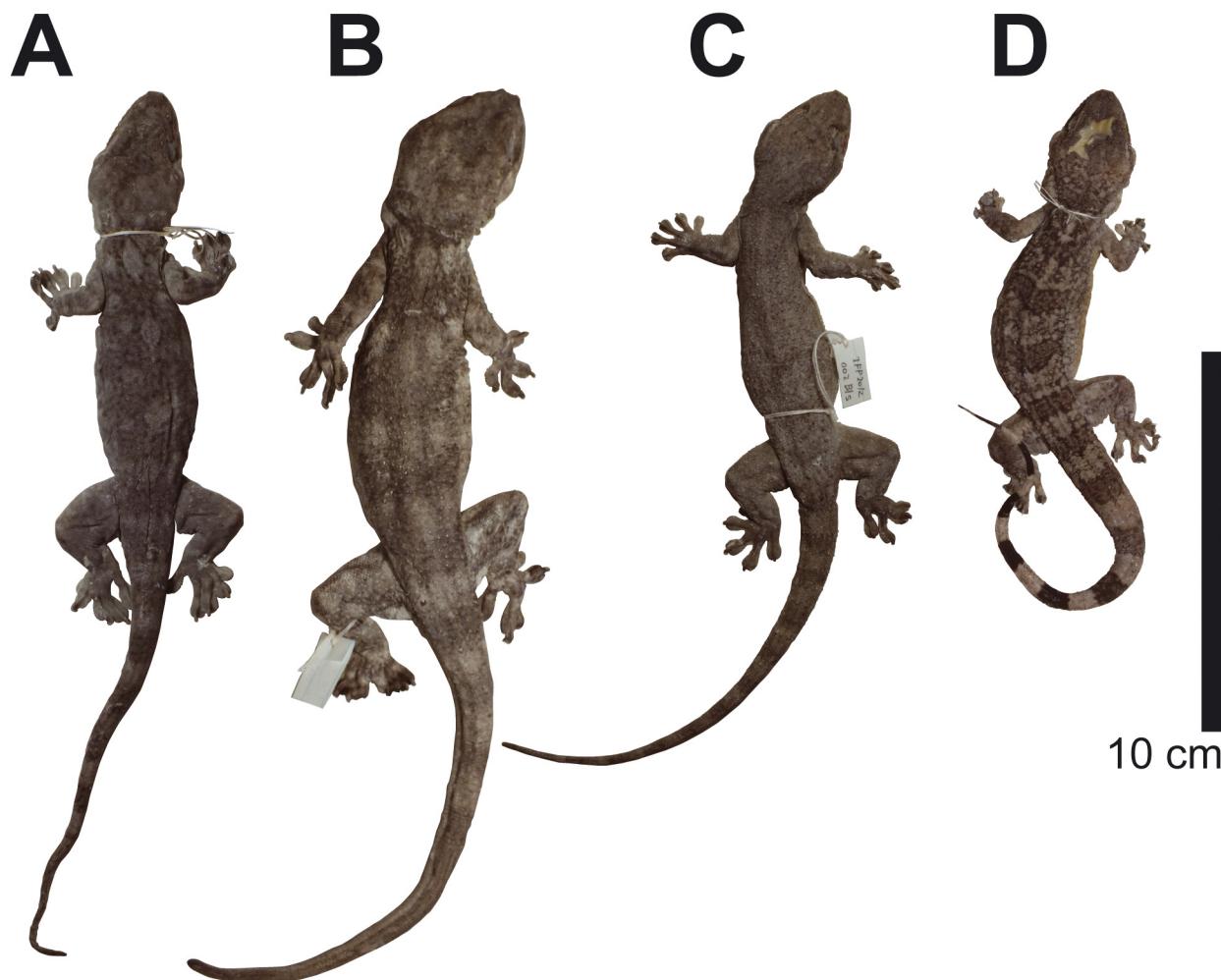


FIGURE 2. Holotype of *Blaesodactylus microtuberculatus* sp. nov. and representatives of three of its congeners. A. *B. microtuberculatus* sp. nov. (KUZ069431). B. *B. boivini* (KUZ069429). C. *B. sakalava* (KUZ069432). D. *B. ambonihazo* (KUZ069433).

Description of the holotype. KUZ069431, adult male. SVL 117.4 mm, TailL 134.2 mm (regenerated). Part of liver removed through mid-flank for tissue sample. Head relatively long (HeadL = 30.6 mm; HeadL/SVL = 0.26) and wide (HeadW = 23.6 mm; HeadW/HeadL = 0.77), depressed (HeadD = 12.7 mm; HeadD/HeadL = 0.42);

obviously broader than neck. Frontonasal region concave, snout elongate ($\text{SnEye} = 14.9 \text{ mm}$; $\text{SnEye}/\text{HeadL} = 0.49$), blunt, longer than eye diameter ($\text{OrbD} = 6.1 \text{ mm}$; $\text{OrbD}/\text{SnEye} = 0.41$); internarial distance 11.1 mm ; interorbital distance 4.6 mm ; scales on snout and forehead small, granular, and heterogeneous; scales on snout larger than those on occipital region except for scattered conical tubercles (~3 times size of adjacent scales); 24 scales across narrowest point of frontals, 52 between superciliary scale rows. Eye large ($\text{OrbD}/\text{HeadL} = 0.20$); pupil vertical with crenelated margins; superciliaries forming a short brilla fold with small spines at anterior and posterior margins. Ear opening obliquely oval, large ($\text{EarL} = 3.8 \text{ mm}$; $\text{EarL}/\text{HeadL} = 0.12$); eye to ear distance longer than diameter of eye ($\text{EyeEar} = 9.3 \text{ mm}$; $\text{EyeEar}/\text{OrbD} = 1.54$). Rostral quadrangular, much wider (5.2 mm) than high (2.5 mm), with no median groove. Enlarged supranasals separated by two internasal scales, one smaller scale (same size of snout granules) anteriorly, bordering rostral, and one larger scale (twice size of snout granules) posteriorly; rostral in contact with first supralabials, supranasals, and one internasal; nostrils round, each surrounded by supranasal, rostral, first supralabial, and a crescentic nasal, itself bordered posteriorly by 4 postnasal scales; 3–4 rows of small scales separate rim of orbit from supralabials. Mental pentagonal, wider (4.2 mm) than deep (2.7 mm); median pair of postmentals elongated (3.7 mm long), each bordered anteromedially by mental, medially in broad contact with other postmental along most of their entire length, but separated anteriorly by posterior tip of mental, and bordered anterolaterally by first infralabial, laterally by second postmental, posteriorly by 3 slightly enlarged chin scales grading posteriorly and laterally into smaller gular scales; 14 (right) to 13 (left) supralabials, 12 infralabials on both sides.

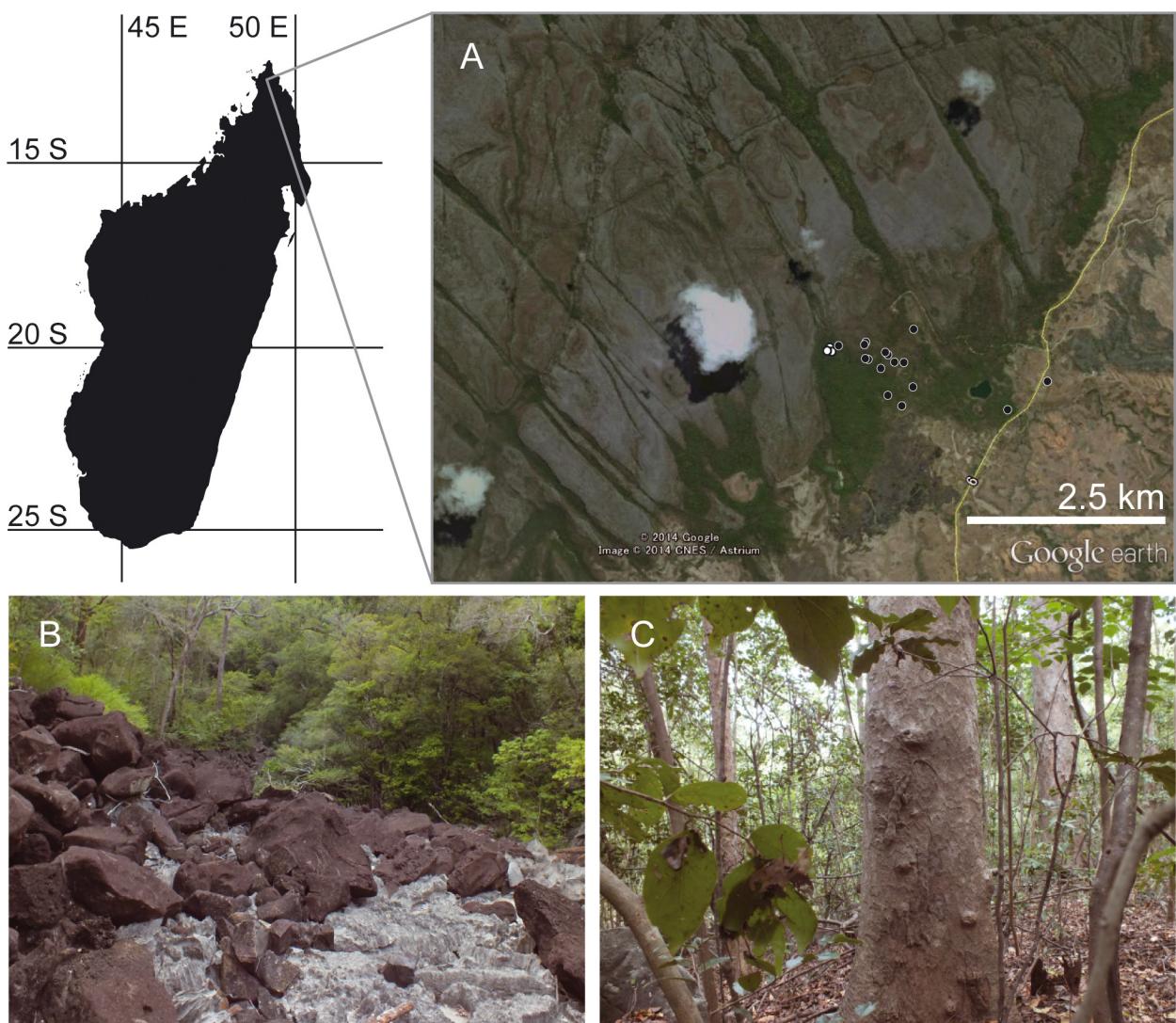


FIGURE 3. Localities and habitat of two allotypic *Blaesodactylus* spp. A. Map of Ankarana National Park. Note that the Tsingy karstic outcroppings are inside the forest. Open circle indicates the site where *B. microtuberculatus* sp. nov. was found and closed circles indicate the sites where *B. boivini* was found. B. Habitat of *B. microtuberculatus* sp. nov. C. Habitat of *B. boivini*.

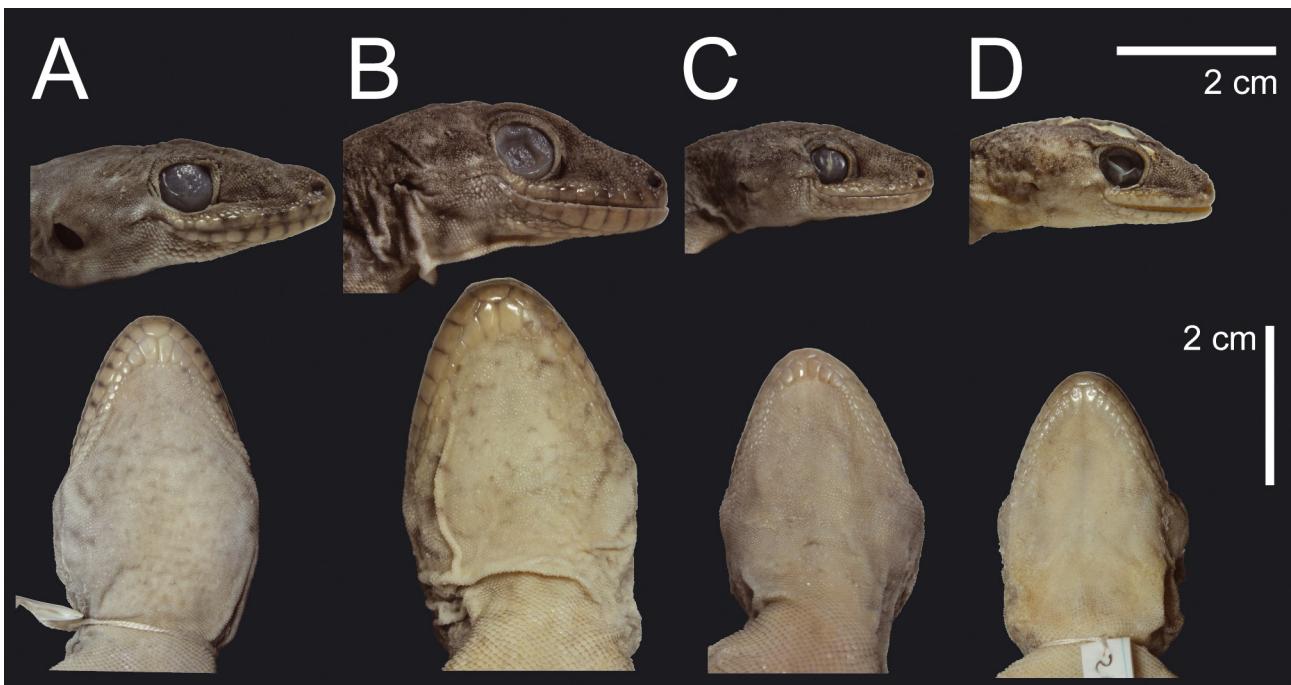


FIGURE 4. Lateral and ventral views of heads of *Blaesodactylus* spp. A. *B. microtuberculatus* sp. nov. (KUZ069431). B. *B. boivini* (KUZ069429). C. *B. sakalava* (KUZ069432). D. *B. ambonihazo* (KUZ069433).

Body stout, relatively short (TrunkL = 47.2mm; TrunkL/SVL = 0.40) with moderately developed ventrolateral folds. Dorsal scales smooth, granular to conical and recumbent, juxtaposed; 162 scale rows around midbody, intermixed with enlarged, smooth rounded tubercles (~3 times size of adjacent scales, largest on flanks, and smallest in occipital region), extending from occipital regions to tail base; tubercles in 15–17 rows at midbody. Ventral scales much larger than dorsals, smooth, imbricate, free margin rounded, largest on abdomen except for rows immediately anterior to vent; 46 scale rows across venter between ventrolateral folds; gular region with relatively homogeneous, smooth, rounded to oval scales, juxtaposed anteriorly to subimbricate posteriorly. No precloacal or femoral pores, no enlarged femoral scales. Preaxial scalation of limbs subimbricate, postaxial granular, dorsal surface of limbs without tubercles. Scales of palms and soles smooth, flattened, round, subimbricate.

Limbs short and robust (ForeaL = 11.3 mm; ForeaL/SVL = 0.10; CrusL = 20.9 mm; CrusL/SVL = 0.18). Digits broadly dilated, distal portion of digits II–V free of pad, bearing a prominent recurved claw partly sheathed between a pair of scales, distal portion of digit I not free of pad, claw minute and lying in a groove in the adhesive pad; number of broad lamellae beneath each digit (10–17–21–21–15 manus; 15–14–17–21–17 pes); all lamellae, except distalmost slightly bowed, undivided except for distalmost lamellae of digit I; interdigital webbing weakly developed. Relative length of digits (manus): IV> III > III> II >V> I; (pes): IV>III > V> II > I.

Tail slender, approximately one-third length of whole tail regenerated, tapering to tip; somewhat longer than snout-vent length (Taill/SVL = 1.14), dorso-ventrally depressed. Tail base with 4 (right) and 3 (left) smooth cloacal spurs on each side, largest anteriormost. Scales of tail dorsum heterogeneous — rectangular to pentagonal or hexagonal, subimbricate; midventral subcaudal scales transversely enlarged and about half of tail width; tail clearly verticillate, each segment 8 dorsal scale rows and 3 transversely enlarged subcaudal scales in length; posterior edge of each segment without a row of enlarged tubercles. Regenerated portion of tail with some segmentation evident but scalation irregular. Hemipenes partly everted, but detailed morphology unobservable.

Coloration (in preservative). Body dorsum grayish without a series of crossbars, mid-dorsal row of five lighter color blotches, indistinctly separated from each other along the dorsal midline. Irregular dark vermiculation on dorsum. Flanks with some faint mottling. Limbs mottled. Tail with faint alternating dark-gray and light-gray bands. Head medium gray with beige labial scales, rictus, and posteroventral orbital margin. Venter cream anteriorly and light gray posteriorly; chin with very faint mottling. Palms and soles grayish. Coloration in life generally similar to that in preservative, but more contrasting.

Distribution. This species is currently known only from Ankarana National Park in northern Madagascar (Fig. 3A).

Natural history. The specimen was collected in Tsingy karstic outcropping surrounded by dry deciduous forest in Ankarana National Park at 22:19 on 4 December 2012 (Fig. 3A). It perched motionless on the surface of an outcrop (Fig. 3B). We were unable to capture two additional individuals, similar in appearance and morphological characteristics, which were found in a similar posture on limestones in the karstic outcropping. In the deciduous forest of this park (Fig. 3C), we found 16 individuals of *B. boivini* on tree trunks both in the daytime and at night, but no geckos similar to *B. microtuberculatus* were found in this habitat. The minimum distance between the locations of *B. microtuberculatus* and *B. boivini* was 11 m.

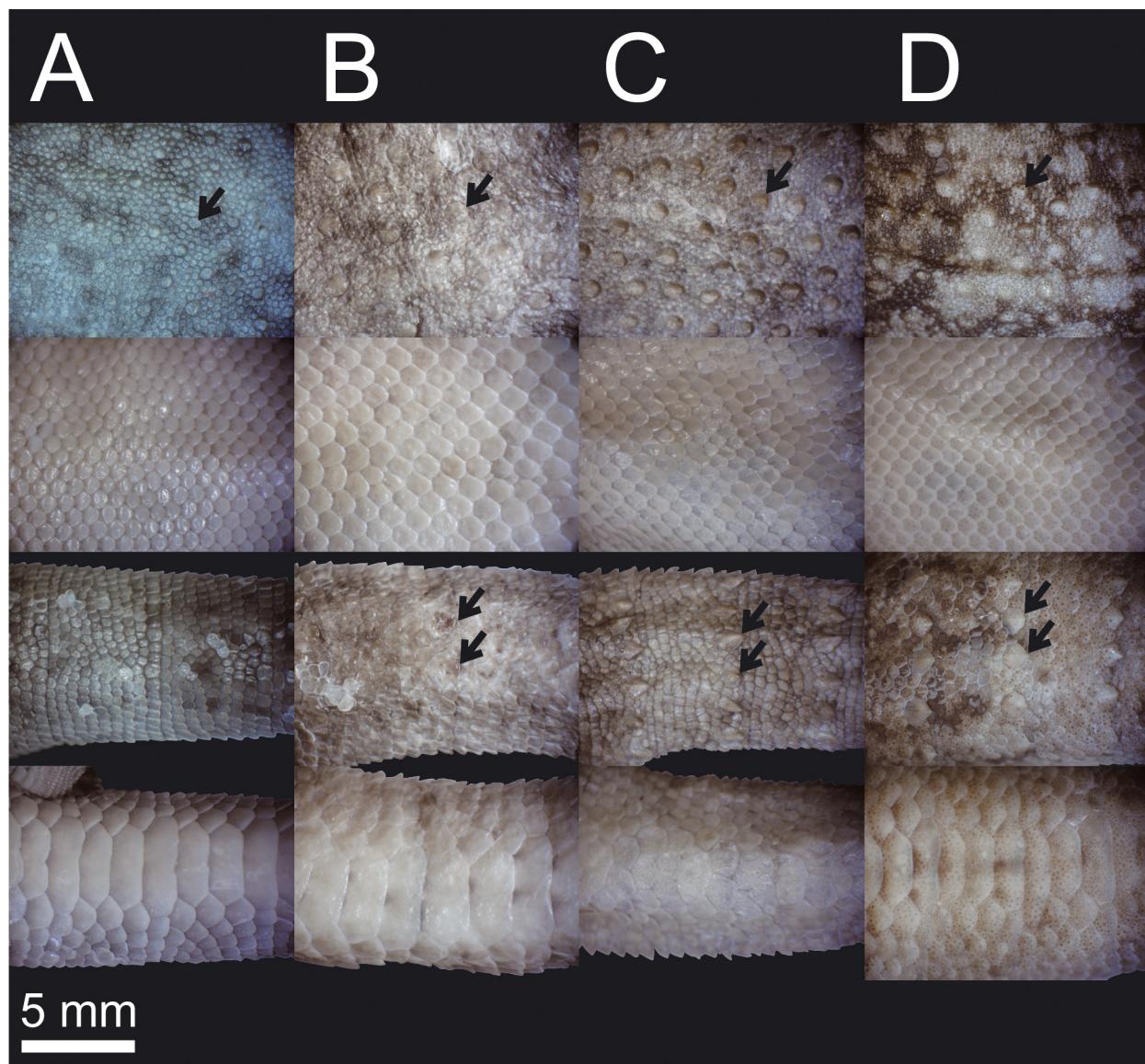


FIGURE 5. Dorsal, ventral, tail, and subcaudal scalations of *Blaesodactylus* spp. A. *B. microtuberculatus* sp. nov. (KUZ069431). B. *B. boivini* (KUZ069429). C. *B. sakalava* (KUZ069432). D. *B. ambonihazo* (KUZ069433). Arrows indicate tubercles. Magnification of all photos is identical.

Discussion

The description of *B. microtuberculatus* sp. nov. adds a distinctive new species to the genus *Blaesodactylus*. This species is distinguished from allotypic congener, *B. boivini*, both morphologically and genetically. *Blaesodactylus microtuberculatus* inhabits karstic outcrops, whereas *B. boivini* dwells on tree trunks in deciduous dry forests,

suggesting the existence of habitat partitioning between the two species. Molecular phylogenetic analysis retrieves *B. microtuberculatus* as the sister of *B. boivini*, with these two significantly divergent from the remaining species of this genus. In northern Madagascar, the landscape comprises a mosaic of heterogeneous habitats: interspersed dry deciduous forests and Tsingy karstic massif bordering savannas (e.g. Vences *et al.* 2009; Crottini *et al.* 2012; Glaw *et al.* 2014). Apparent habitat partitioning and the sister taxa relationship between *B. boivini* and *B. microtuberculatus* suggests the possibility that the mosaic of different habitats throughout the region may have facilitated local endemism. Invasion of the karstic massif habitat may have precipitated the speciation of *B. microtuberculatus* from the forest-living ancestral lineage. The Madagascan biota is characterized by a high degree of microendemism in many taxa (Kremen *et al.* 2008; Vences *et al.* 2009; Köhler *et al.* 2010). Several Madagascan gecko genera such as *Lygodactylus* Gray (Pasteur & Blanc 1973), *Paroedura* Günther (Nassbaum & Raxworthy 2000; Glaw *et al.* 2014) and *Phelsuma* Gray (Glaw *et al.* 2010) have lineages that have distributions restricted to Tsingy massifs. Bauer *et al.* (2011) reported the existence of deep mitochondrial divergence between Ifaty and Tsingy de Bemaraha populations of *B. sakalava*. This divergence is even greater than that seen between *B. microtuberculatus* sp. nov. and *B. boivini* and considering the major habitat differences between the two sites, spiny forests in Ifaty and Tsingy karstic massif in Tsingy de Bemaraha, this might represent a case of speciation parallel to that reported here in the *B. boivini*—*B. microtuberculatus* clade. Further studies are needed to clarify the habitat partitioning and the speciation processes in *Blaesodactylus*.

Considering that the Tsingy landscape is restricted to a small area, further investigation is necessary to determine the potentially limited range of this new species. Furthermore, deforestation for agriculture, logging and cattle grazing observed in the areas surrounding its habitat serves as an additional impetus to research. Taking both habitat destruction and its possibly limited distribution into consideration, *B. microtuberculatus* sp. nov. should probably be assigned to one of the threatened categories in the IUCN Red List. However, due to a paucity of current knowledge on this new species, we propose an IUCN Red List status of “Data Deficient” for the species.

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APPENDIX

Comparative specimens examined (all localities in Madagascar):

Blaesodactylus boivini: KUZ069429, Ankarana National Park, Antsiranana Province, northern Madagascar.

Blaesodactylus sakalava: KUZ069432, Ifaty, Toliara Province, southwestern Madagascar.

Blaesodactylus ambonihazo: KUZ069433 (field number: 2011-Ad-071), Ampondrabe, Ankarafantsika National Park, Mahajanga Province, northwestern Madagascar.