The anoles of the *Norops pachypus* complex are denizens of the cloud forest. At premontane and montane elevations in the highlands of Costa Rica and western Panama these lizards form a prominent portion of the local herpetofauna, and often are the most abundant reptile species. In order to shed some light on the taxonomy of these highland anoles, from 2006 to 2014 Gunther Köhler undertook extensive fieldwork in Costa Rica as a basis for the present contribution. Pictured here is an adult male *Norops tropidolepis* from Volcán Barva, Costa Rica.

Mesoamerican Herpetology
www.mesoamericanherpetology.com
Eagle Mountain PUBLISHING, LC
www.eaglemountainpublishing.com
ISSN 2373-0951
OPEN ACCESS
Version of record:urn:lsid:zoobank.org:pub:393D9383-0407-40A1-A179-A22E3A9E023D

Two new species of the *Norops pachypus* complex (Squamata, Dactyloidae) from Costa Rica

Gunther Köhler[1], Joseph Vargas[1], and Sebastian Lotzkat[1,2]

[1]*Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany. E-mail*: gkoehler@senckenberg.de (Corresponding author)

[2]*Goethe-University, Institute for Ecology, Evolution & Diversity, Biologicum, Building C, Max-von-Laue-Straße 13, 60438 Frankfurt am Main, Germany.*

Abstract: We describe two new species of anoles from Costa Rica, which previously have been referred to as *Norops pachypus* or *N. tropidolepis* by different authors: *Norops alocomyos* sp. nov. from the Pacific versant of the western portion of the Cordillera de Talamanca and the highlands south of Escazú, and *Norops leditzigorum* sp. nov. from the Cordillera de Tilarán, Volcán Rincón de la Vieja, and the western portion of the Cordillera Central. Both belong to a cluster of species related to *N. pachypus* and are most similar in external morphology to *N. tropidolepis*, from which they differ by molecular distances and in hemipenial morphology, as well as in subtle differences in male dewlap color and several scalation characters.

Key words: Cryptic species, DNA barcoding, hemipenial morphology, Lower Central America, 16S

Resumen: Se describen dos especies nuevas de anolis de Costa Rica, que anteriormente se han referido como *Norops pachypus* o *N. tropidolepis* por diferentes autores: *Norops alocomyos* sp. nov. de la vertiente Pacífica de la parte occidental de la Cordillera de Talamanca y de las tierras altas del sur de Escazú, y *Norops leditzigorum* sp. nov. de la Cordillera de Tilarán, Volcán Rincón de la Vieja y de la parte occidental de la Cordillera Central. Ambas pertenecen al grupo de especies relacionado a *N. pachypus* y son más similares en su morfología externa a *N. tropidolepis*. Sin embargo, difieren de esta última por distancias moleculares, en la morfología de los hemipenes y además presentan diferencias sútiles en la coloración de la papada gular en los machos y en varios caracteres de escamación.

Palabras Claves: Códigos de barra de ADN, especies crípticas, morfología del hemipene, Centroamérica Ístmica, 16S

Citation: Köhler, G., J. Vargas, and S. Lotzkat. 2014. Two new species of the *Norops pachypus* complex (Squamata, Dactyloidae) from Costa Rica. Mesoamerican Herpetology 1: 254–280.

Received: 12 November 2014; **Accepted:** 11 December 2014; **Published:** 26 December 2014.

INTRODUCTION

The anole fauna at premontane and montane elevations in the highlands of Costa Rica and western Panama is dominated by a group of ground anoles that are characterized by the presence of long legs (tip of the 4th toe of the adpressed hind limb usually reaching a point well anterior to the eye), narrow toe pads, male dewlaps that range from solid yellow over different patterns of yellow and red or orange to solid red, keeled dorsal scales on the head and body, usually two slightly enlarged middorsal scale rows, a striking lateral head pattern of dark brown and cream lines radiating from the eye, and a dark interorbital bar. Furthermore, males lack enlarged postcloacal scales, and the base of the tail in large males often is conspicuously swollen because of their large hemipenes.

From this point on, we refer to the species in this group as the *Norops pachypus* complex. For most of the 20th century, these anoles have been assigned to either *Norops* (or *Anolis*) *pachypus* (Cope, 1876) or *Norops* (or *Anolis*) *tropidolepis* (Boulenger, 1885). In recent years, several studies on the systematics and taxonomy of the Panamanian populations of the *Norops pachypus* complex have been published (Köhler et al., 2007; Poe and Ibañez, 2007; Lotzkat et al., 2011). Based on the evidence presented in these works, four species of anoles related to *N. pachypus* are recognized in western Panama: *N. benedikti* (Lotzkat, Bienentreu, Hertz and Köhler, 2011), *N. magnaphallus* (Poe and Ibañez, 2007), *N. pachypus*, and *N. pseudopachypus* (Köhler, Sunyer, Ponce and Batista, 2007). In contrast, the Costa Rican populations of the *Norops pachypus* complex have received little attention in the past several decades. Savage (2002) briefly discussed the distribution and morphological variation of the Costa Rican populations of these anoles, and used the degree of ventral keeling and male dewlap coloration in life as the principal criteria for species recognition. Basically, Savage (2002: 464, 467) characterized *N. pachypus* as "having mostly smooth ventrals" and a male dewlap that is "orange red, usually with a central yellow spot" in life, whereas he diagnosed *N. tropidolepis* as having "strongly keeled ventrals" and a male dewlap that is "deep purplish red to burgundy." Savage stated that "field observations of male dewlap color influenced" his treatment of these anoles, but his treatment became confusing when he assigned some populations from "elevations above 2,000 m in the Cordillera Central ... [that] have mostly smooth ventrals, and males' dewlaps are orange red" to *N. pachypus*. Recently, Bienentreu (2011) showed that the degree of ventral keeling was highly variable in all the populations of the *N. pachypus* complex from Costa Rica and Panama he examined, suggesting that this qualitative and, above all, subjectively scored character should not be relied upon for species identification. Furthermore, his DNA barcoding results showed that all of the Costa Rican populations with solid red dewlaps he examined were genetically divergent from those with yellow-blotched red dewlaps, regardless of the ventral keeling. Accordingly, Lotzkat et al. (2011) regarded the coloration of the male dewlap to be "of superior importance" in the separation of these otherwise cryptic species, and referred to all of the Costa Rican populations with solid red dewlaps (Fig. 1a, b) as *N. tropidolepis*. We follow Bienentreu (2011) and Lotzkat et al. (2011) in restricting the name *N. pachypus* to populations in which the red male dewlaps bear a central yellow blotch (Fig. 1d, e).

In order to shed some light on the taxonomy of these Costa Rican highland anoles, from 2006 to 2014 one of us (GK) undertook extensive fieldwork in Costa Rica as a basis for the present contribution. In this study, we evaluate the geographic variation of color in life, hemipenial morphology, scalation, morphometrics, and molecular genetics of these anoles, in order to clarify the taxonomic situation of the *Norops pachypus* complex in Costa Rica.

MATERIALS AND METHODS

Prior to preserving the specimens collected in the field, we took color photographs of each individual's extended dewlap. For this purpose, whenever possible we used the standard forceps of genuine Swiss Army knives, because their broad, flat apex protects even thin-skinned dewlaps from damage and functions as an approximate scale (width = 3 mm). Immediately after euthanasia, we determined the relative hind limb length by recording the point reached by the tip of the 4th toe when the extended hind limb is adpressed along the straightened specimen. Whenever possible, we everted the hemipenes of male specimens by injecting 70% ethanol into the hemipenial pockets after manually pre-everting the hemipenes. We preserved specimens by injecting a solution of 5–10 mL absolute (i.e., 36%) formalin in 1 L of 96% ethanol into the body cavity and thighs, after sprinkling the everted hemipenes and extended dewlaps with this solution, and stored them in 70% ethanol. We deposited the specimens collected in Costa Rica

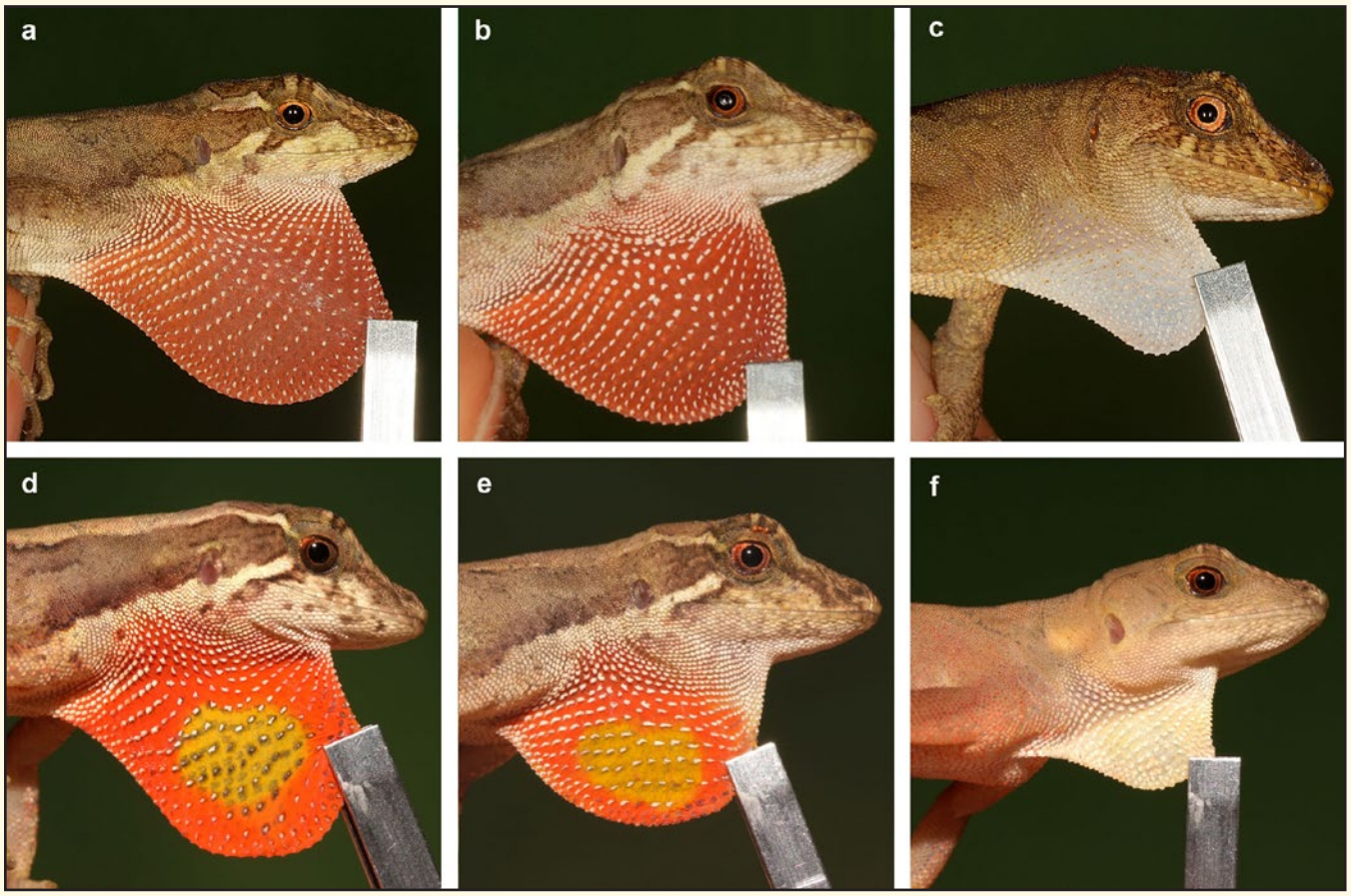

Fig. 1. Dewlaps in life: (a) *Norops tropidolepis* SMF 99289 (male); (b) *N. tropidolepis* SMF 93648 (male); (c) *N. tropidolepis* SMF 93647 (female); (d) *N. pachypus* SMF 93817 (male); (e) *N. pachypus* SMF 93815 (male); and (f) *N. pachypus* SMF 93814 (female).

in the collections of the Senckenberg Forschungsinstitut Frankfurt (SMF) and the Museo de Zoología, Universidad de Costa Rica (UCR), San José, Costa Rica. Abbreviations for the museum collections follow Sabaj Pérez (2014). We recorded the geographic coordinates and elevation by using Garmin GPS receivers with built-in altimeters. All of the coordinates are in decimal degrees and WGS 1984 datum, and all the elevations are in meters above sea level. The capitalized colors and color codes (the latter in parentheses) are those of Smithe (1975–1981) in the color descriptions of living specimens, and those of Köhler (2012) in the color descriptions of preserved material. We followed Köhler (2012) for the terminology of markings used in the color descriptions in life, and used Köhler (2014) for nomenclature and definitions of morphological characters. When variation in the bilateral symmetry of scale characters is present, they are given as right side/left side. The only abbreviation used for morphological characters is SVL (snout–vent length).

We cut tissue samples from the tip of the tail of selected individuals before they came into contact with formalin, stored them in 98% non-denatured ethanol, and deposited them in the tissue sample collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany. We extracted DNA following the protocol of Ivanova et al. (2006). To eliminate potential PCR-inhibiting contaminants, the tissue samples were incubated for 14 hrs in 200 µL low PBS buffer (20 µL PBS in 180µL of water) before overnight digestion with the vertebrate lysis buffer at 56°C. After extraction, the DNA was eluted in 50 µL TE buffer. A fragment of the mitochondrial 16S rRNA gene was amplified in an Eppendorf Mastercycler® pro using the following protocol: initial denaturation for 2 min at 94°C; followed by 40 cycles with denaturation for 35 s at 94°C, hybridization for 35 s at 48.5°C, and elongation for 60 s at 72°C; final elongation for 10 min at 72°C. The reaction mix for each sample contained 1 µL DNA template,

14 µL water, 2.5 µL PCR-buffer, 1 µL 25 mM $MgCl_2$, 4 µL 2.5 mM dNTPs (Invitrogen), 0.5 µL (containing 2.5 units) Taq Polymerase (PeqLab), and 1 µL of each primer (forward: L2510, 5'–CGCCTGTTTATCAAAAACAT–3'; reverse: H3056, 5'–CCGGTCTGAACTCAGATCACGT–3'; eurofins MWG Operon). We obtained a total of 40 16S sequences of the *Norops pachypus* complex, and added 15 sequences of other *Norops* (two *N. humilis* and 13 members of the *N. altae* complex) for comparison, as well as three *Dactyloa* and one *Sibon* species as outgroups (see Appendix 1 and species descriptions for specimens examined, and the GenBank accession numbers that follow their collection numbers in parentheses). We aligned the sequences with MUSCLE (Edgar, 2004) using the default settings in Geneious (Drummond et al., 2010). The manually refined final alignment of 59 sequences contained 547 positions, of which 148 were variable (excluding the outgroups). Using MEGA 5 (Tamura et al., 2011), we computed uncorrected pairwise genetic distances, determined TN93+G as the best-fitting substitution model using the Bayesian Information Criterion, and conducted a Maximum Likelihood (ML) analysis with 10,000 bootstrap replicates and gaps as a fifth character (i.e., using all sites). Using MrBayes 3.1.2, we conducted a Bayesian inference of phylogeny (BI; Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) running over 2×10^6 generations in two parallel runs with four chains each, sampled trees every 1,000 generations, and discarded the first 5% (burnin = 100) after verifying the previous convergence of the parallel runs by visually checking the logfile.

In evaluating whether multiple species exist within a certain species complex, we followed the unified species concept (de Queiroz, 2007). As lines of evidence for species delimitation, we applied a phenotypic criterion (external morphology: coloration, morphometrics, and scalation, as well as hemipenial morphology) and a criterion for reproductive isolation. For the latter, we employed the genetic distinctness of the 16S rRNA gene that has been used widely in DNA barcoding studies of tropical herpetofauna (e.g., Vieites et al., 2009; Jansen et al., 2011). In evaluating the uncorrected p-distances calculated for our sample, we oriented ourselves on the values published in recent barcoding studies on Central American anoles (Bienentreu, 2011; Köhler et al., 2012, 2014; Lotzkat et al., 2013) and those calculated for Lower Central American Norops in the Ph.D. dissertation of SL (S. Lotzkat, unpublished), as well as in the relative positions that the clades in question assume in the inferred phylogenetic trees.

To assess the distinctness of the populations that were most recently (Bienentreu, 2011; Lotzkat et al., 2011) referred to as *Norops* (or *Anolis*) *tropidolepis*, we separated the examined material according to the phylogenies inferred from the 16S barcodes, hemipenial morphology, and geography, into Operational Taxonomic Units (OTUs), as follows (Figs. 2–4):

OTU 1: Cordillera de Tilarán.

OTU 2: the western portion of the Cordillera Central from Parque Nacional Juan Castro Blanco in the west to about Costa Rican highway 708, which crosses the Cordillera Central coming from Grecia to Bajo los Toros.

OTU 3: the central and eastern portion of the Cordillera Central, including Volcán Poás and Volcán Barva.

OTU 4: Volcán Irazú.

OTU 5: the western portion of the Cordillera de Talamanca, excluding populations in the Santa María de Dota and San Gerardo de Dota valleys.

OTU 6: the highlands of Escazú (Cerros de Escazú).

OTU 7: the Santa María de Dota and San Gerardo de Dota valleys in the western portion of the Cordillera de Talamanca.

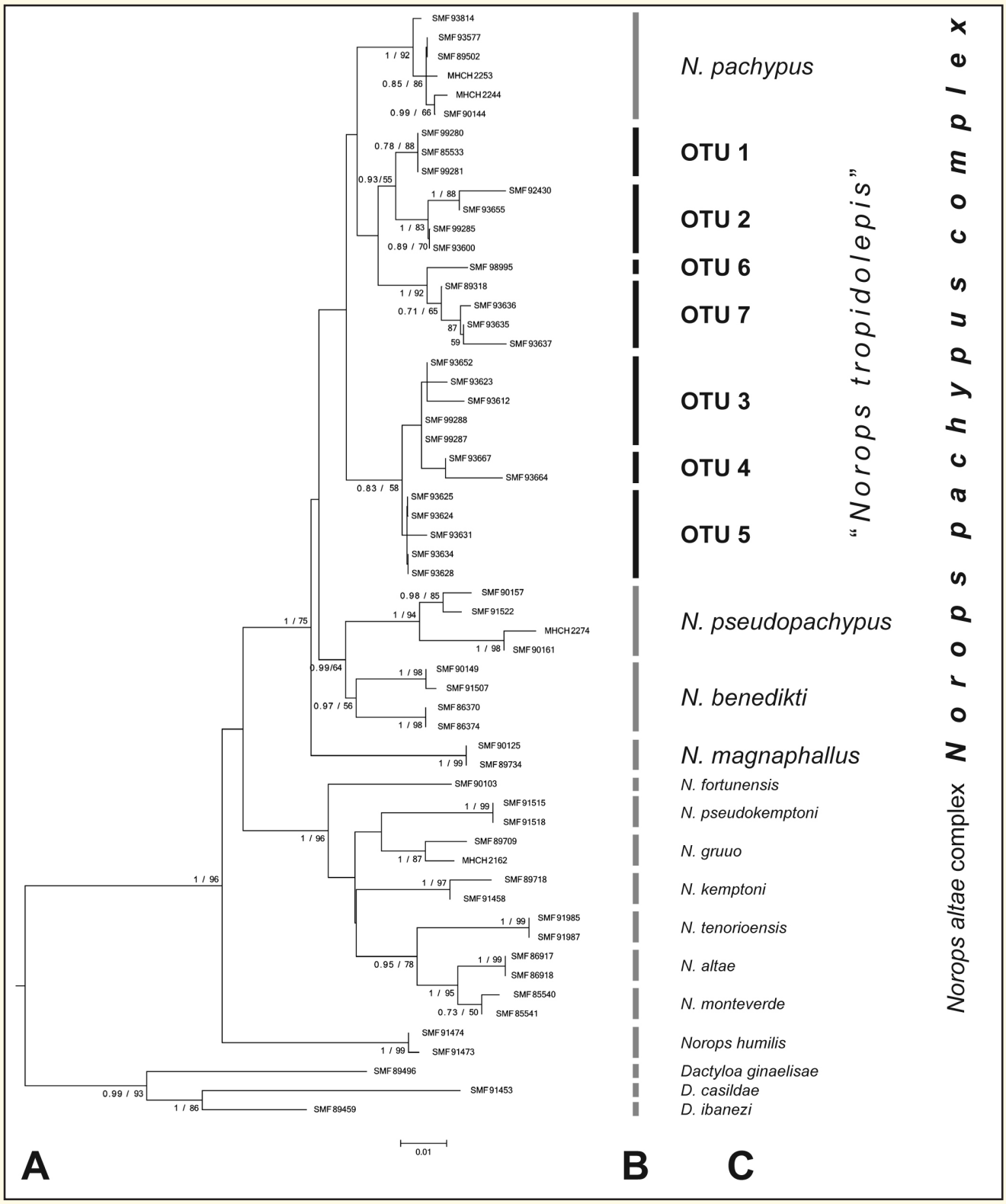

Fig. 2. Results of molecular genetic analyses. (A) Consensus tree from Maximum Likelihood analysis of 16S rRNA sequences (the distant outgroup *Sibon noalamina* is not shown). Only bootstrap values above 50% are shown, and are preceded by Bayesian posterior probabilities at nodes that also were recovered in the Bayesian inference of phylogeny. The scale bar refers to substitutions per site. (B) Delimitation of the nominal species (gray bars) and OTUs among anoles formerly referred to *Norops tropidolepis* (black bars) that are specified in (C).

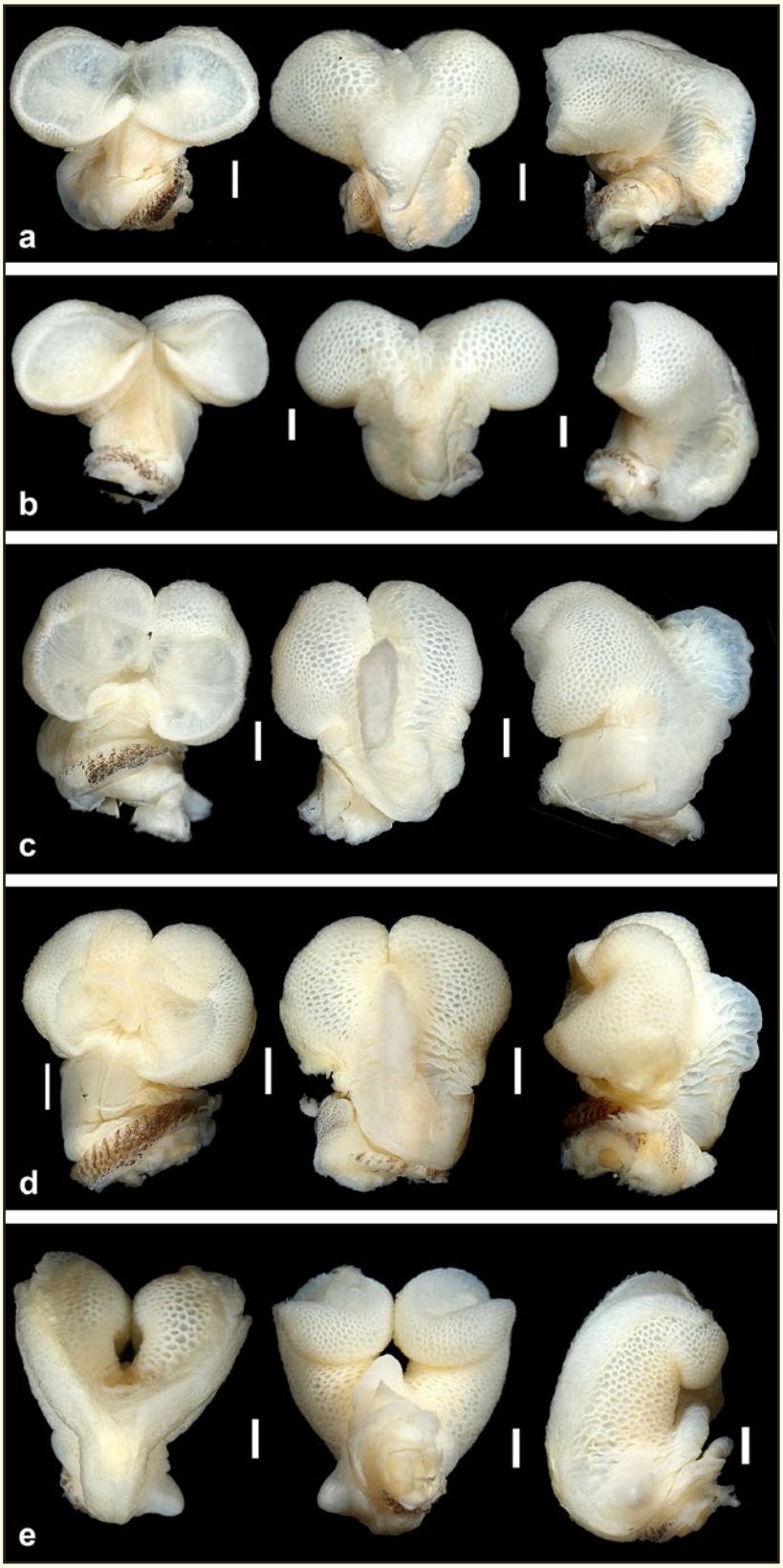

Fig. 3. Hemipenes of (a) *Norops leditzigorum* (SMF 99283); (b) *N. leditzigorum* (SMF 99284); (c) *N. tropidolepis* (SMF 99288); (d) *N. tropidolepis* (SMF 93667); and (e) *N. alocomyos* (SMF 93636); sulcate view left, asulcate view in center, lateral view right. Scale bars equal 1.0 mm.

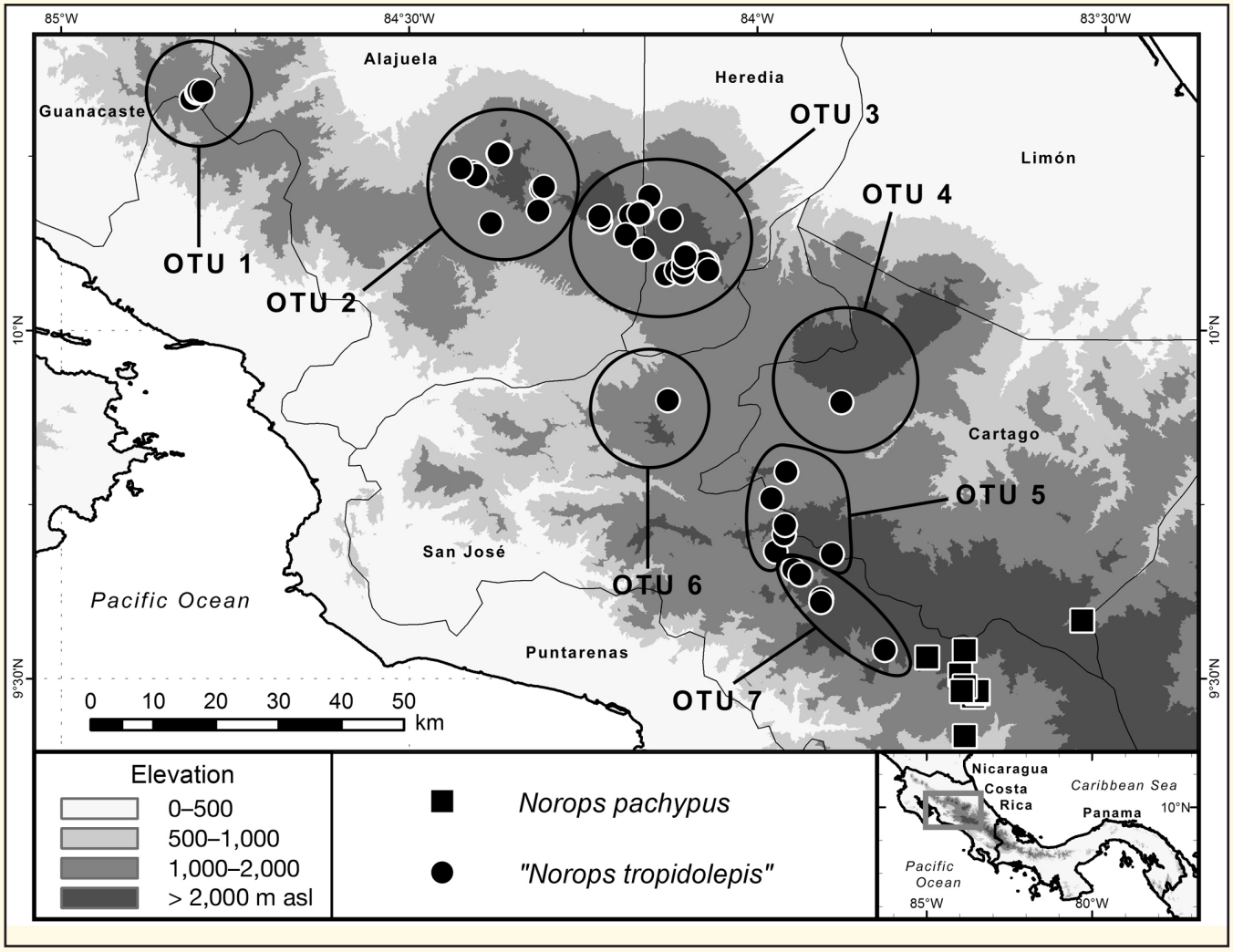

Fig. 4. Map of central Costa Rica showing localities where we collected specimens of *Norops pachypus* and anoles formerly referred to *N. tropidolepis*, as well as our designation of OTUs for the latter.

RESULTS

Besides minor differences, the consensus trees from our BI and ML analyses of 16S sequence data show largely congruent topologies with the same terminal clades recovered in each. The results of our analyses reveal a high degree of genetic differentiation among several populations formerly referred to as *Norops tropidolepis* (Fig. 2, Table 1), which form three major genetic clusters (each comprising 2–3 of our OTUs) that together with *N. pachypus* constitute a tetratomy in the Bayesian consensus tree. These three clusters are separated by mean genetic distances of 3.0–4.0% from each other, and by mean genetic distances of 3.3–6.6% from the other currently recognized species of the *N. pachypus* complex. Geographic distance by itself is not responsible for these genetic distances, as evidenced by the low genetic differentiation between our OTUs 1 and 2 (1.5–2.4%, mean 1.8%), between OTUs 3, 4 and 5 (0.4–2.3%, mean values 0.8–1.4%), as well as between OTUs 6 and 7 (1.0–2.1%, mean 1.5%), respectively. We take this high level of genetic differentiation among these three genetic clusters as evidence for a lack of gene flow, and conclude that these three clusters are species level units. Thus, we recognize three species among the Costa Rican anoles formerly referred to as *N. tropidolepis*: Species A (OTUs 1 and 2), Species B (OTUs 3, 4, and 5), and Species C (OTUs 6 and 7). This three species hypothesis is supported by the results of our analysis of hemipenial morphology. Males of our OTU 7 (our Species C) are unique among all the OTUs, as well as among all

Table 1. Mean values of uncorrected *p*-distances among the 16S rRNA fragments of dactyloid lizards analyzed in this study. Values in the lower-left matrix are mean distances between nominal species and our seven OTUs formerly referred to *Norops tropidolepis*, whereas those in the upper-right matrix consider the three Costa Rican species with solid red dewlaps as delineated in this study (*N. leditzigorum* = OTUs 1 + 2; *N. tropidolepis* = OTUs 3 + 4 + 5; *N. alocomyos* = OTU 7). The separating diagonal shows the mean values within OTUs and species in **bold** face (***bold italics*** for the two Costa Rican species with solid red dewlaps comprising more than one OTU).

	Dactyloa ginaelisae	*D. casildae*	*D. ibanezi*	*Norops humilis*	*N. pseudokemptoni*	*N. kemptoni*	*N. fortunensis*	*N. tenorioensis*	*N. gruuo*	*N. altae*	*N. monteverde*	*N. magnaphallus*	*N. pseudopachypus*	*N. benedikti*	*N. pachypus*	OTU 1	OTU 2	OTU 3	OTU 4	OTU 5	OTU 6	OTU 7
D. ginaelisae	—															0.130		0.132				0.139
D. casildae	0.093	—														0.136		0.139				0.135
D. ibanezi	0.069	0.063	—													0.120		0.136				0.128
N. humilis	0.129	0.139	0.127	**0.0019**												0.081		0.070				0.082
N. pseudokemptoni	0.141	0.149	0.137	0.088	**0.0019**											0.088		0.079				0.096
N. kemptoni	0.134	0.138	0.128	0.089	0.066	**0.0076**										0.083		0.080				0.083
N. fortunensis	0.137	0.134	0.125	0.079	0.063	0.059	—									0.079		0.073				0.087
N. tenorioensis	0.142	0.146	0.131	0.098	0.062	0.051	0.061	**0.000**								0.092		0.091				0.096
N. gruuo	0.134	0.133	0.122	0.086	0.043	0.054	0.042	0.051	**0.0134**							0.082		0.078				0.092
N. altae	0.145	0.160	0.139	0.099	0.061	0.063	0.062	0.046	0.058	**0.000**						0.087		0.085				0.082
N. monteverde	0.146	0.149	0.135	0.093	0.052	0.060	0.052	0.042	0.041	0.020	**0.0038**					0.086		0.083				0.088
N. magnaphallus	0.119	0.136	0.130	0.087	0.099	0.083	0.088	0.086	0.091	0.080	0.087	**0.000**				0.052		0.053				0.056
N. pseudopachypus	0.131	0.136	0.126	0.091	0.098	0.083	0.087	0.086	0.087	0.086	0.086	0.062	**0.0221**			0.057		0.057				0.066
N. benedikti	0.129	0.137	0.126	0.084	0.087	0.076	0.082	0.090	0.080	0.085	0.084	0.055	0.048	**0.0181**		0.042		0.044				0.050
N. pachypus	0.125	0.130	0.119	0.068	0.094	0.085	0.082	0.092	0.087	0.086	0.088	0.046	0.055	0.047	**0.0042**	0.035		0.033				0.036
OTU 1	0.128	0.135	0.121	0.078	0.091	0.082	0.078	0.092	0.081	0.085	0.082	0.048	0.051	0.040	0.031	**0.000**	***0.0133***	0.040			0.032	0.030
OTU 2	0.132	0.137	0.119	0.084	0.085	0.083	0.079	0.093	0.082	0.089	0.089	0.054	0.061	0.044	0.037	0.018	**0.0111**					
OTU 3	0.133	0.139	0.135	0.061	0.073	0.078	0.067	0.086	0.072	0.084	0.080	0.051	0.055	0.043	0.030	0.037	0.048	**0.0032**		***0.0081***		
OTU 4	0.141	0.153	0.146	0.081	0.090	0.084	0.080	0.100	0.087	0.091	0.090	0.060	0.062	0.050	0.040	0.039	0.050	0.012	**0.0130**		0.037	0.036
OTU 5	0.126	0.134	0.134	0.074	0.080	0.079	0.077	0.092	0.081	0.083	0.082	0.052	0.057	0.042	0.033	0.029	0.038	0.008	0.014	**0.0038**		
OTU 6	0.132	0.130	0.123	0.083	0.093	0.084	0.088	0.092	0.088	0.081	0.087	0.057	0.060	0.050	0.036	0.031	0.033	0.039	0.042	0.033	—	
OTU 7	0.139	0.135	0.128	0.082	0.096	0.083	0.087	0.096	0.092	0.082	0.088	0.056	0.066	0.050	0.036	0.029	0.031	0.038	0.040	0.032	0.015	**0.0067**

the species currently recognized in the *N. pachypus* complex, by the presence of very long lobes (vs. short, bulky lobes), a closed sulcus spermaticus on the apical branches (vs. sulcus spermaticus opening into one or two broad fields void of ornamentation at the base of the apex), and a conical processus on sulcal side of the base of the truncus (vs. no such processus). Males of our OTUs 1 and 2 (our Species A) differ from males of our OTUs 3, 4, and 5 (our Species B) by the presence of a more distinctly bilobed hemipenis with two clearly distinct broad fields void of ornamentation at the base of the apex (vs. these two fields are less clearly separated, rather forming one large concave area), and by lacking a large asulcate cusp-like processus (vs. present). Furthermore, the dewlap of adult males of our Species A is purplish red, whereas those of our Species B and C are orange red (Figs. 1, 6, and 12). In morphometric characters and in scalation, these three species are more conservative and not easily differentiated (Table 2). Subtle differences among most of these species are evident, however, supporting the recognition of each of these as a distinct species.

Table 2. Selected measurements, proportions, and scale characters of *Norops alocomyos*, *N. leditzigorum*, and *N. tropidolepis*. Range is followed by mean value and standard deviation in parentheses.

		Norops alocomyos ♂3, ♀4	***Norops leditzigorum*** ♂10, ♀10	***Norops tropidolepis*** ♂19, ♀7
Maximum SVL	Males	49.0	51.0	53.0
	Females	54.1	52.5	53.0
Tail length / SVL	Males	1.76–1.91 (1.85 ± 0.11)	1.68–2.02 (1.87 ± 0.14)	1.72–2.24 (2.01 ± 0.15)
	Females	1.96–1.96 (1.96 ± 0.00)	1.62–1.90 (1.73 ± 0.09)	1.68–1.81 (1.74 ± 0.09)
Vertical diameter of tail / horizontal diameter of tail	Males	0.77–1.25 (1.01 ± 0.34)	0.88–1.32 (1.10 ± 0.11)	1.03–1.64 (1.23 ± 0.15)
	Females	1.05–1.25 (1.17 ± 0.09)	1.03–1.25 (1.15 ± 0.11)	1.08–1.38 (1.24 ± 0.13)
Axilla–groin distance / SVL	Males	0.40–0.41 (0.41 ± 0.01)	0.37–0.41 (0.39 ± 0.01)	0.33–0.42 (0.38 ± 0.02)
	Females	0.40–0.43 (0.42 ± 0.01)	0.35–0.45 (0.40 ± 0.03)	0.35–0.45 (0.40 ± 0.03)
Head length / SVL	Males	0.25–0.28 (0.26 ± 0.02)	0.25–0.27 (0.26 ± 0.01)	0.25–0.28 (0.26 ± 0.01)
	Females	0.24–0.26 (0.24 ± 0.01)	0.23–0.31 (0.26 ± 0.02)	0.24–0.27 (0.26 ± 0.01)
Head length / head width	Males	1.52–1.67 (1.60 ± 0.10)	1.44–1.88 (1.62 ± 0.13)	1.25–1.72 (1.55 ± 0.10)
	Females	1.51–1.57 (1.54 ± 0.03)	1.47–1.64 (1.58 ± 0.05)	1.42–1.65 (1.57 ± 0.09)
Snout length / SVL	Males	0.10–0.13 (0.11 ± 0.02)	0.10–0.12 (0.11 ± 0.01)	0.10–0.14 (0.11 ± 0.01)
	Females	0.10–0.12 (0.11 ± 0.01)	0.10–0.12 (0.11 ± 0.01)	0.10–0.14 (0.12 ± 0.01)
Snout length / head length	Males	0.41–0.46 (0.43 ± 0.03)	0.36–0.47 (0.43 ± 0.04)	0.40–0.51 (0.44 ± 0.03)
	Females	0.41–0.44 (0.43 ± 0.01)	0.37–0.49 (0.44 ± 0.04)	0.43–0.50 (0.45 ± 0.03)
Shank length / SVL	Males	0.29–0.33 (0.30 ± 0.01)	0.24–0.28 (0.26 ± 0.01)	0.24–0.30 (0.27 ± 0.01)
	Females	0.24–0.26 (0.25 ± 0.01)	0.24–0.29 (0.26 ± 0.01)	0.25–0.28 (0.26 ± 0.01)
Shank length / head length	Males	1.05–1.17 (1.11 ± 0.08)	0.93–1.08 (1.02 ± 0.04)	0.99–1.13 (1.06 ± 0.04)
	Females	1.00–1.06 (1.03 ± 0.03)	0.89–1.11 (1.01 ± 0.07)	0.93–1.05 (0.99 ± 0.05)
Number of medial dorsal scales in one head length	Males	32–54 (43.0 ± 15.6)	38–78 (53.2 ± 11.2)	34–62 (46.9 ± 10.04)
	Females	42–52 (46.0 ± 4.3)	40–64 (46.6 ± 6.8)	34–52 (41.7 ± 6.0)

Number of medial ventral scales in one head length	Males	34–38 (36.0 ± 2.8)	32–44 (39.4 ± 4.0)	30–50 (37.6 ± 5.1)
	Females	28–34 (30.5 ± 2.5)	28–40 (33.4 ± 4.4)	28–38 (34.0 ± 4.0)
Number of medial dorsal scales between levels of axilla and groin	Males	57–74 (65.5 ± 12.0)	70–97 (82.8 ± 8.7)	53–92 (71.9 ± 11.0)
	Females	80–91 (85.3 ± 5.6)	70–99 (83.0 ± 0.9)	65–90 (78.3 ± 10.2)
Number of medial ventral scales between levels of axilla and groin	Males	59–63 (61.0 ± 2.8)	51–70 (59.7 ± 7.0)	46–66 (55.2 ± 5.4)
	Females	46–51 (49.3 ± 2.4)	48–64 (55.5 ± 4.5)	46–64 (53.1 ± 6.2)
Number of scales around midbody	Males	124–142 (133.0 ± 12.7)	122–160 (140.0 ± 13.2)	122–182 (140.5 ± 13.7)
	Females	136–142 (139.0 ± 2.6)	134–174 (146.4 ± 12.1)	128–166 (144.0 ± 12.3)
Subdigital lamellae on Phalanges II–IV of Toe IV		22–25 (23.0 ± 1.1)	19–27 (22.3 ± 2.1)	17–24 (21.3 ± 1.5)
Subdigital lamellae on distal phalanx of Toe IV		8–9 (8.2 ± 0.4)	7–10 (8.9 ± 1.0)	7–10 (8.7 ± 1.0)
Number of scales between supraorbital semicircles		2–5 (3.2 ± 1.2)	3–5 (4.0 ± 0.7)	2–6 (3.8 ± 0.9)
Number of scales between interparietal plate and supraorbital semicircles		3–3 (3.0 ± 0.0)	3–5 (3.8 ± 0.8)	2–5 (3.5 ± 0.7)
Number of scales between subocular scales and supralabials		1–2 (1.7 ± 0.5)	1–2 (1.4 ± 0.4)	1–2 (1.4 ± 0.5)
Number of supralabials to level below center of eye		6–7 (6.4 ± 0.5)	5–8 (7.0 ± 0.8)	5–9 (7.0 ± 0.9)
Number of infralabials to level below center of eye		6–7 (6.4 ± 0.5)	6–8 (7.0 ± 0.9)	5–9 (7.2 ± 1.0)
Total number of loreals		34–67 (53.2 ± 11.1)	35–72 (51.8 ± 12.1)	30–77 (54.2 ± 12.1)
Number of horizontal loreal scale rows		6–9 (7.3 ± 1.2)	6–10 (7.9 ± 1.1)	6–11 (8.2 ± 1.2)
Number of postrostrals		6–7 (6.7 ± 0.5)	5–9 (7.0 ± 0.9)	5–8 (6.8 ± 0.9)
Number of postmentals		5–7 (6.2 ± 0.8)	5–8 (6.2 ± 0.7)	4–9 (6.2 ± 1.0)
Number of scales between nasals		6–8 (6.8 ± 0.8)	6–10 (8.5 ± 1.3)	5–10 (8.1 ± 1.4)
Number of scales between 2nd canthals		10–12 (11.0 ± 0.6)	12–17 (13.9 ± 1.5)	9–14 (11.4 ± 1.6)
Number of scales between posterior canthals		10–12 (11.0 ± 0.6)	12–18 (15.1 ± 1.6)	10–15 (12.5 ± 1.4)

Our Species B includes specimens from the type locality of *N. tropidolepis* (i.e., Volcán Irazú; our OTU 4); thus, this is the valid name for this species. The type locality of the nominal species *N. curtus* Boulenger 1898 is from the area of our OTU 5 (*N. tropidolepis sensu stricto*); thus, *N. curtus* remains in the synonymy of *N. tropidolepis*. No names are available for our Species A and C, so we describe each as a new species below.

Norops alocomyos sp. nov.

Figs. 3e, 5–8

***Holotype*:** SMF 93635 (KP209362), adult male, from along the road between Santa María de Dota and Copey, 9.65696°N, 83.94831°W, elev. 1,720 m asl, Provincia de San José, Costa Rica; collected by Gunther Köhler on 21 February 2010; original field number GK-2405.

***Paratypes*:** Collected by Gunther Köhler on 21 February 2010. All from Provincia de San José, Costa Rica: SMF 93636 (KP209363), along the road between Santa María de Dota and Copey, 9.64955°N, 83.93845°W, elev. 1,850 m; SMF 93637 (KP209364), 93638–41, along the road between Copey and Providencia, 9.61539°N,

83.90802°W, elev. 2,370 m; SMF 93642, along the road between Copey and Providencia, 9.61008°N, 83.90865°W, elev. 2,540 m. SMF 93636–37, 93642 are adult males, the remaining paratypes are adult females.

***Referred specimens*: COSTA RICA**—SAN JOSÉ: San Gerardo de Dota, 9.54097°N, 83.81694°W, elev. 2,125 m: SMF 89318 (KP209353), UCR 20137.

***Diagnosis*:** A medium-sized (maximum SVL 49.0 mm in males, 54.1 mm in females) species (our Species C of the *Norops pachypus* complex) of the genus *Norops* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to *N. benedikti*, *N. magnaphallus*, *N. pachypus*, *N. pseudopachypus*, *N. tropidolepis*, and a species described below (our Species A of the *Norops pachypus* complex). These six species and *N. alocomyos* are differentiated from all other anoles by the presence of a combination of narrow toe pads, long legs (tip of the 4th toe of the adpressed hind limb usually reaching a point anterior to the eye), a dark interorbital bar, a striking lateral head pattern of dark brown and cream lines radiating from the eye, usually at least the indication of a lyriform marking on the occipital region, keeled dorsal scales on head and body, smooth to weakly keeled ventral scales at midbody, and a lack of enlarged postcloacal scales in males. *Norops alocomyos* can be distinguished from the other six species in the *Norops pachypus* complex by a distinctive hemipenial morphology that includes very long lobes (vs. short, bulky lobes), a closed sulcus spermaticus on the apical branches (vs. a sulcus spermaticus that opens at the base of the apex into one or two broad fields void of ornamentation), and a conical processus on the sulcal side of the base of the truncus (vs. no such processus). *Norops alocomyos* can be differentiated further from *N. benedikti*, *N. pachypus*, and *N. pseudopachypus* by the presence of a uniform purplish red male dewlap in life (vs. a male dewlap mostly orange yellow, or red with a yellow central blotch and/or yellow margin, at least anteriorly).

***Description of the holotype*:** Adult male, as indicated by everted hemipenes and presence of moderate-sized dewlap; snout–vent length 46.5 mm; tail length 25.0 mm, tail incomplete; tail slightly compressed in cross section, tail height 2.5 mm, tail width 2.0 mm; axilla to groin distance 18.8 mm; head length 11.7 mm, head length/snout–vent length ratio 0.25; snout length 4.8 mm; head width 7.0 mm; longest toe of adpressed hind limb reaching to nostril; shank length 13.7 mm, shank length/head length ratio 1.17; longest finger of extended forelimb reaching about 4.7 mm beyond tip of snout; longest finger of adpressed forelimb reaching about 2.2 mm beyond anterior insertion of hind limbs; scales on snout keeled, uni- to multicarinate; 7 postrostrals; 7 scales between nasals; scales in distinct prefrontal depression distinctly keeled, uni- to multicarinate, keels mostly directed longitudinally or obliquely; supraorbital semicircles differentiated, separated by a minimum of 5 scales; supraorbital disc composed of 7–8 moderately enlarged keeled scales, mostly unicarinate; circumorbital series incomplete, one enlarged supraorbital scale in contact with supraorbital semicircles; 4 elongated superciliaries, anterior one longest; 5–6 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; interparietal plate distinctly enlarged, 1.3 × 0.6 mm (length × width), surrounded by moderate-sized scales; 3 scales present between interparietal plate and supraorbital semicircles; canthal ridge distinct, composed of 5 large (posterior) and 3 small (anterior) canthal scales; 11 scales present between second canthals; 11 scales present between posterior canthals; 36/37 keeled loreal scales in a maximum of 6 horizontal rows; subocular scales keeled, in a single row, one subocular scale in contact with supralabial series; 6/7 supralabials to level below center of eye; ear opening 0.9 × 1.9 mm (length × height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals; 7/6 infralabials to level below center of eye; sublabials undifferentiated; slightly keeled granular scales present on chin and throat; dewlap moderate-sized, extending well onto chest, anterior insertion at level of anterior border of orbit, posterior insertion at level of axilla, with about 10–12, somewhat irregular, partially interrupted gorgetal-sternal rows of 17–21 scales per row; dorsum of body with keeled, subimbricate scales, 2 medial rows of slightly enlarged scales, largest dorsal scales about 0.44 × 0.28 mm (length × width); about 32 medial dorsal scales in one head length; about 57 medial dorsal scales between axilla and groin; lateral scales slightly heterogeneous with single, mostly paler, slightly enlarged scales (0.25 mm in diameter) scattered among keeled, granular scales, the latter about 0.20 mm in diameter; ventrals at midbody weakly keeled, subimbricate, about 0.45 × 0.35 mm (length × width); about 34 ventral scales in one head length; about 63 ventral scales between axilla and groin; about 142 scales around midbody; caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; no enlarged postcloacal scales; no tube-like axillary pocket; scales on dorsal surface of forelimb strongly keeled, mucronate and imbricate; digital pads dilated, dilated pad about 2 times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 22/22 lamellae under phalanges II–IV of 4th toe; 9/8 scales under distal phalanx of 4th toe.

Fig. 5. *Norops alocomyos* in life. (a) SMF 93642 (male); and (b) SMF 93641 (female).

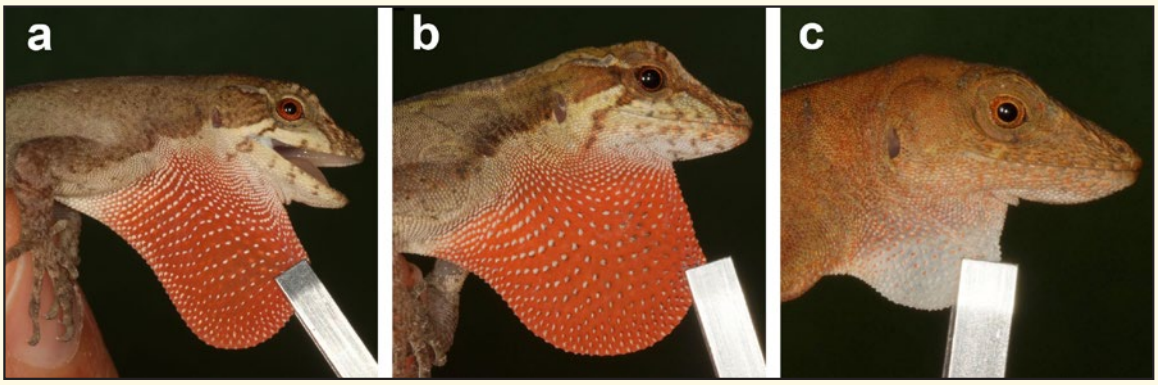

Fig. 6. Dewlaps of *Norops alocomyos* in life: (a) SMF 93635 (male); (b) SMF 93636 (male); and (c) SMF 93640 (female).

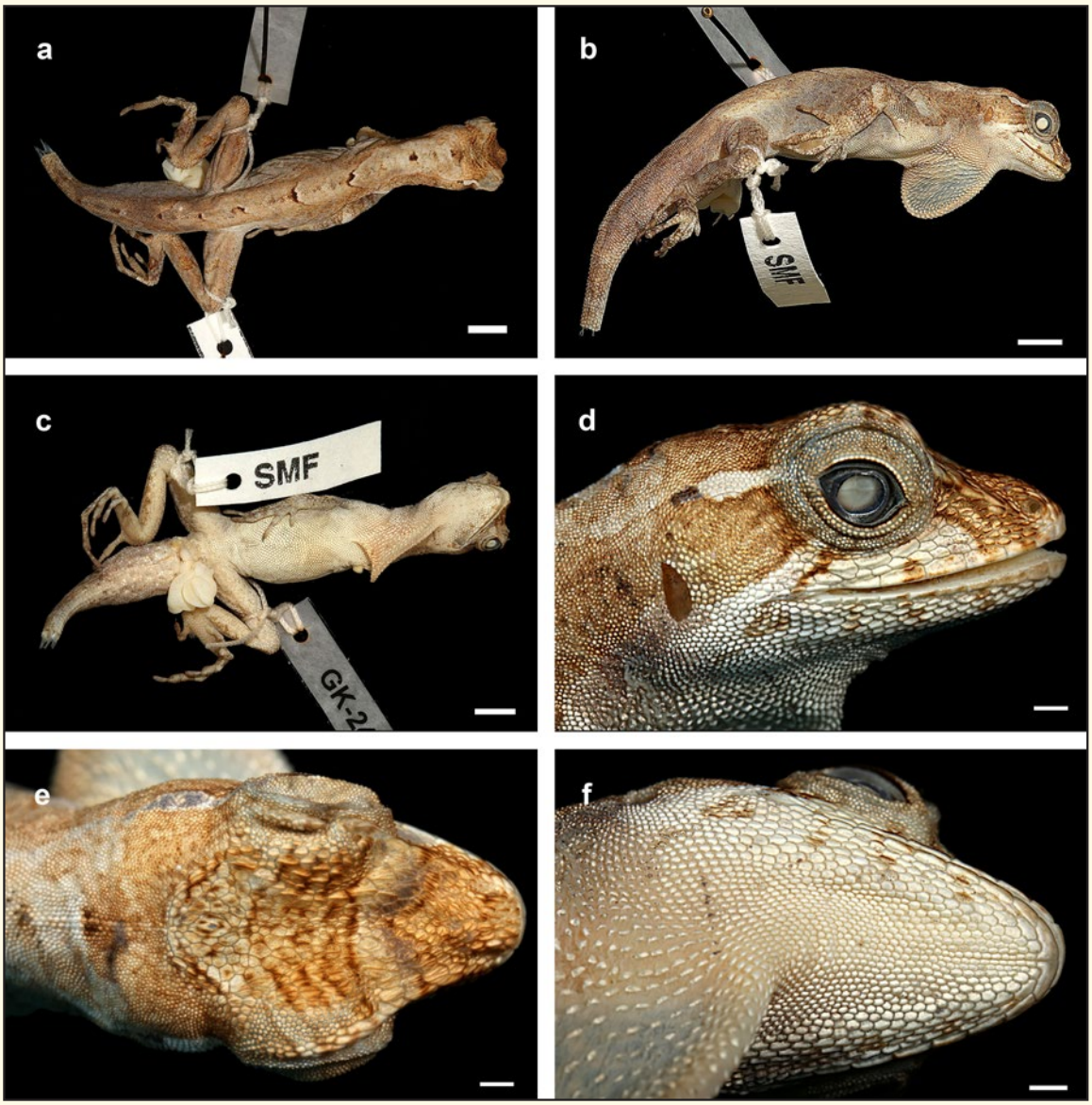

Fig. 7. Holotype of *Norops alocomyos* (SMF 93635): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; and (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively.

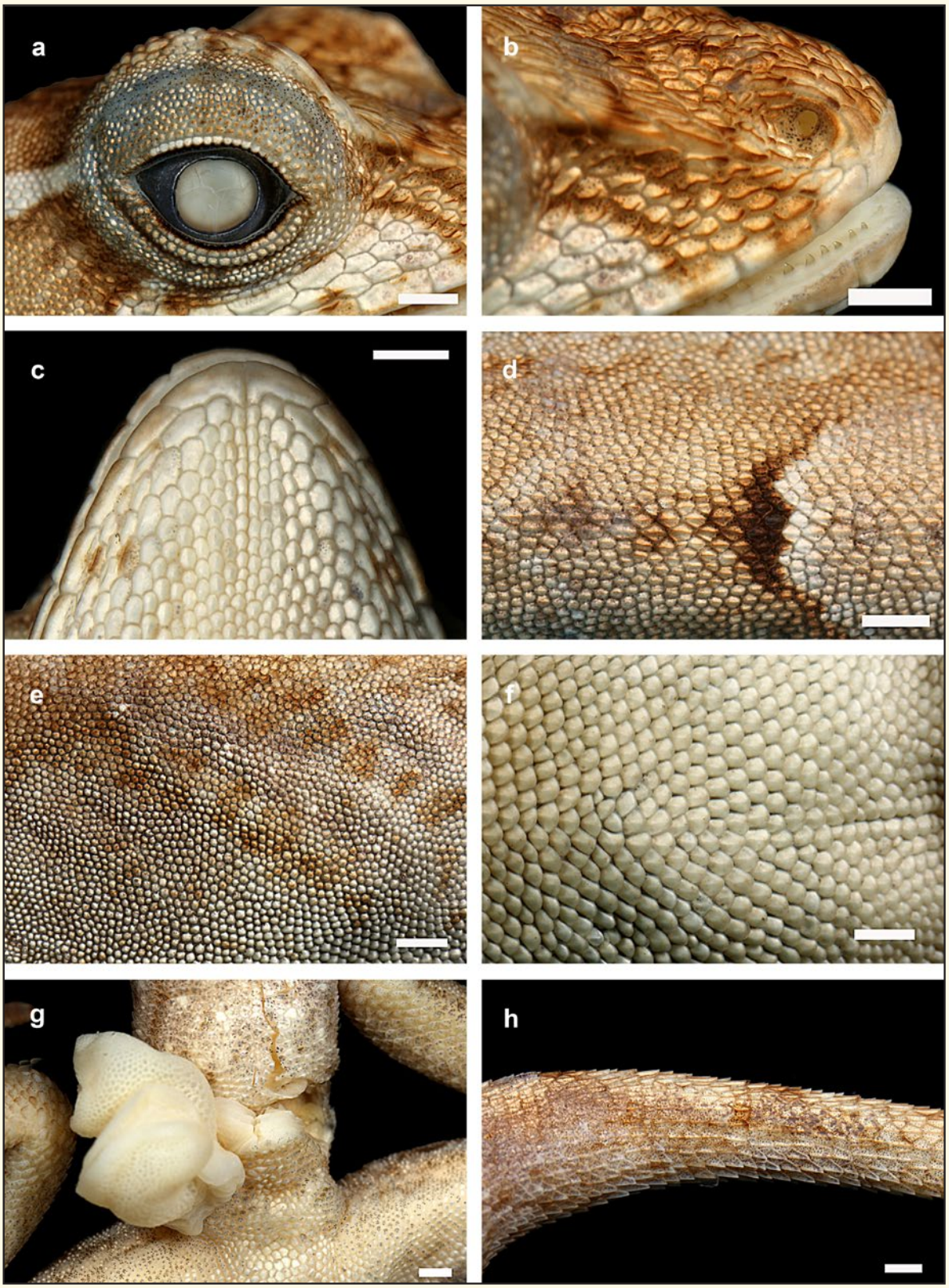

Fig. 8. Holotype of *Norops alocomyos* (SMF 93635): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region ; (e) flank region; (f) midventer; (g) cloacal region; and (h) lateral view of tail. Scale bars equal 1.0 mm.

Fig. 9. Habitat of *Norops alocomyos* near San Gerardo de Dota, Costa Rica.

The completely everted hemipenis is a large bilobate organ with well-developed, long lobes; sulcus spermaticus bordered by well-developed sulcal lips and bifurcating at base of apex with the branches continuing as closed furrows to the tip of the lobes where they open into small concave areas, one on each lobe; no asulcate ridge-like processus present; a conical processus present at base of truncus on sulcate side; lobes strongly calyculate, truncus with transverse folds.

The dewlap coloration in life was recorded as Peach Red (94).

After more than four years in preservative, the coloration was recorded as follows: dorsal ground color Smoke Gray (266) with Sepia (286) chevrons; lateral surface of head Raw Umber (22) with Cream White (52) stripes radiating out from eye; an Olive Horn Color (16) preocular bar, edged with Burnt Umber (48); ventral surfaces Pale Buff (1) slightly suffused with Smoke Gray (266); dewlap Pale Pinkish Buff (3) with Pale Buff (1) gorgetals.

***Variation*:** The paratypes and referred specimens agree well with the holotype in general morphology and scalation (see Table 2). The coloration in life of the dewlap of an adult male (SMF 89318) from San Gerardo de Dota was recorded as uniform Scarlet (14) with white gorgetals.

***Natural history notes*:** All specimens in the type series of *Norops alocomyos* were encountered at night sleeping on the upper surface of leaves or on twigs, usually 0.2–0.7 m above the ground. Species recorded at the collecting sites of *N. alocomyos* were *N. intermedius* (Peters) and *Isthmohyla pseudopuma* (Günther).

***Geographic distribution*:** As presently understood, *Norops alocomyos* inhabits premontane and montane elevations (1,720–2,540 m) along the Pacific versant in the western portion of the Talamancan highlands of Costa Rica, specifically in the Santa María de Dota and San Gerardo de Dota valleys, as well as in the Escazú highlands (Fig. 10).

***Etymology*:** The specific name *alocomyos* is a compound noun formed from the Greek words *alox* (furrow) and *myo* (close), referring to the closed sulcus spermaticus in this species, which is unique among the known species in the *Norops pachypus* complex.

***Remarks*:** As shown in Fig. 2, our single specimen of OTU 6, the male SMF 98995, clusters together with our barcoded specimens of *Norops alocomyos*. Yet, this specimen does not exhibit the characteristic hemipenial phenotype of *N. alocomyos*. Thus, we refrain from including it in the referred specimens, but list it as *N.* cf. *alocomyos* in the Appendix (see discussion).

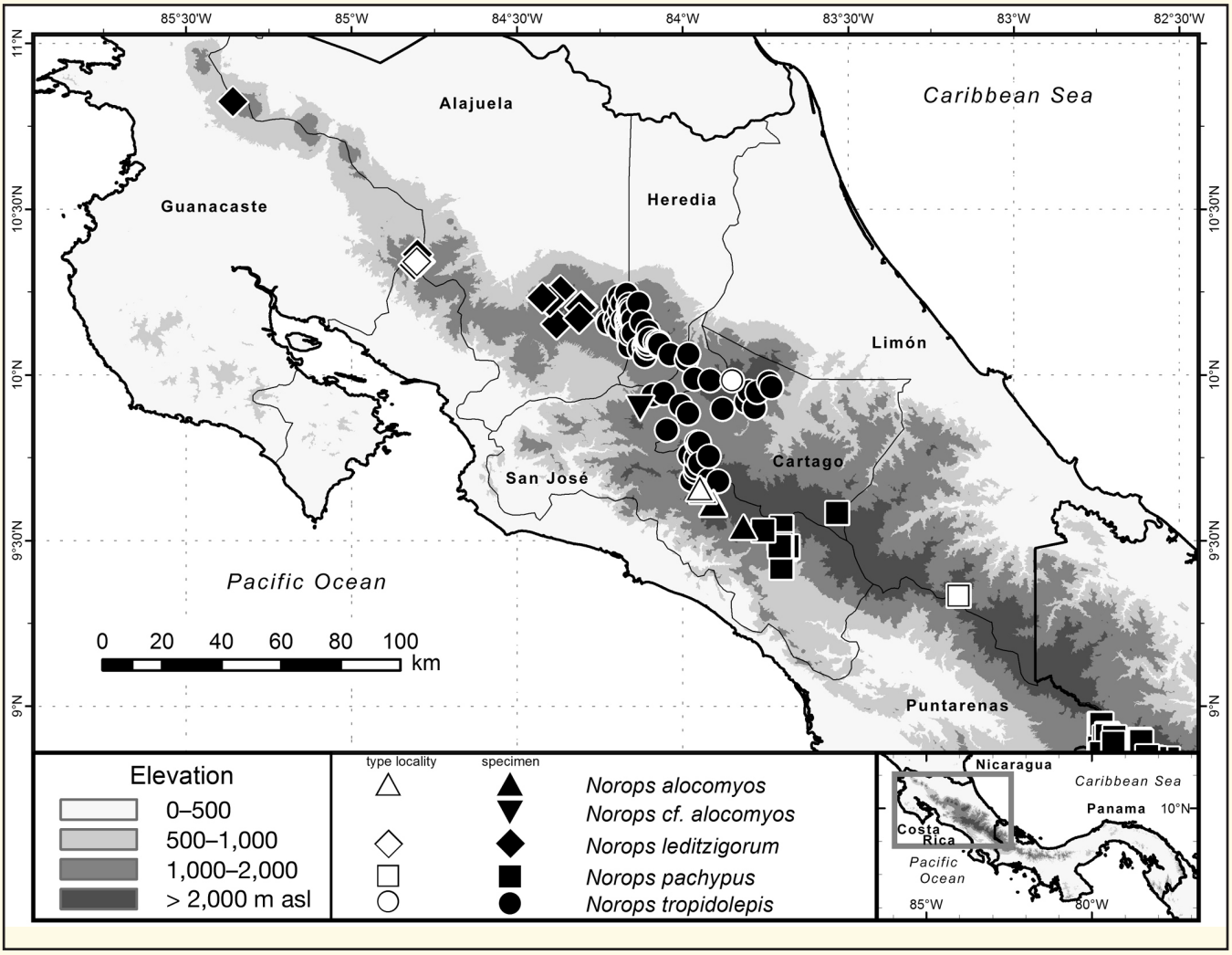

Fig. 10. Map indicating collecting localities of *Norops pachypus*, *N. tropidolepis*, and the two new species described herein in the highlands of Costa Rica and immediately adjacent western Panama. Each symbol can represent one or more adjacent localities.

Norops leditzigorum sp. nov.

Figs. 3a,b, 11–14

***Holotype*:** SMF 85538, adult male, from 4 km (on road) N Santa Elena, 10.34156°N, 84.80506°W, elev. 1,560 m asl, Provincia de Puntarenas, Costa Rica; collected by Gunther Köhler on 5 April 2006; original field number GK-1752.

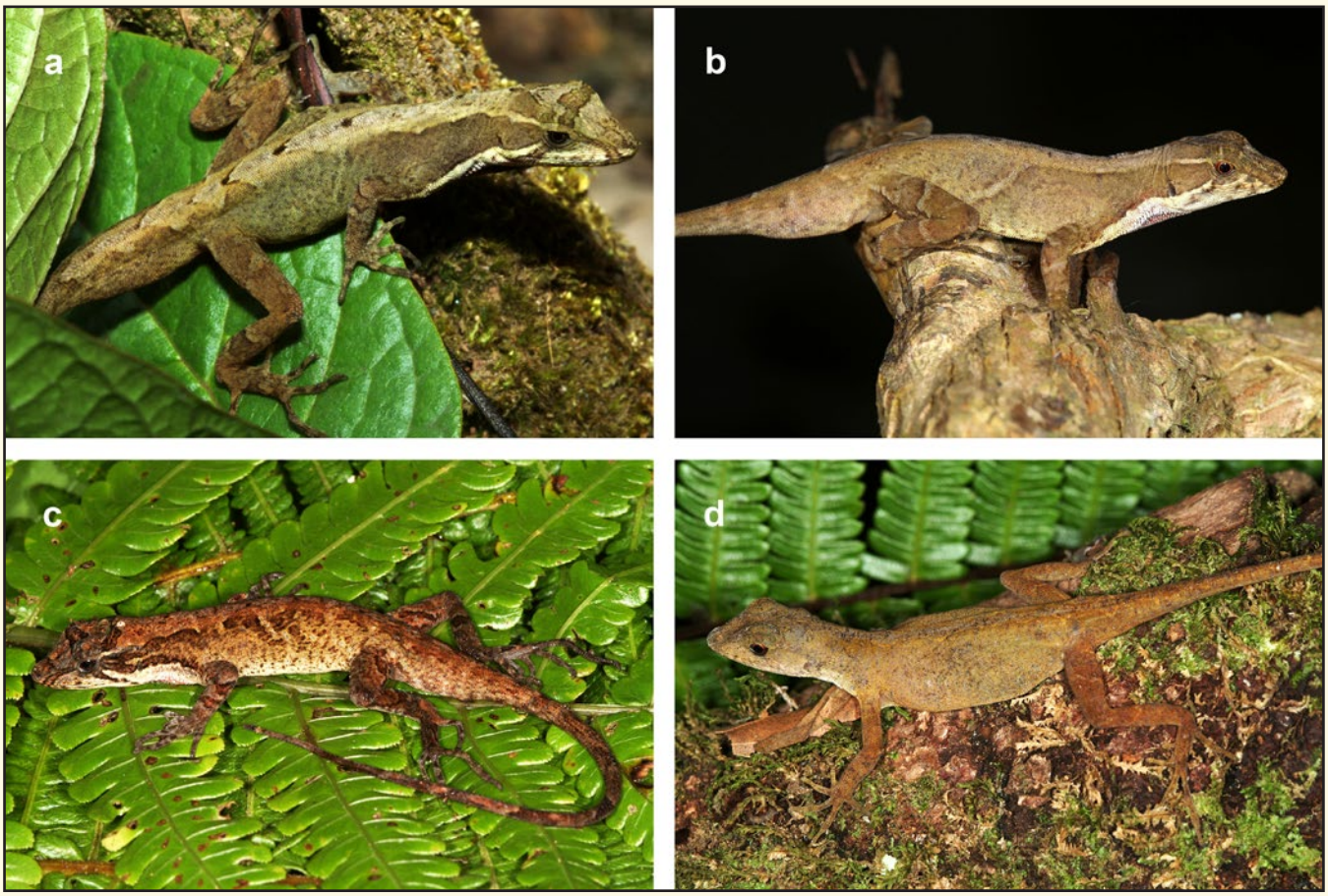

Fig. 11. *Norops leditzigorum* in life. (a) SMF 89346 (male); (b) SMF 99284 (male); (c) SMF 85532 (male); and (d) SMF 85533 (female).

***Paratypes*:** All collected by Gunther Köhler in Provincia de Puntarenas, Costa Rica: SMF 85539, same collecting data as holotype; SMF 89319–20, UCR 20140–43, 2 km N Santa Elena, 10.34181°N, 84.80444°W, elev. 1,550 m, collected on 17 February 2007; SMF 85532, 85533 (KP209352), 85534–37, 2.3 km N Santa Elena, 10.33189°N, 84.81289°W, elev. 1,575 m, collected on 5 April 2006; SMF 99283, near entrance to Reserva Santa Elena, 10.34308°N, 84.79720°W, elev. 1,640 m, collected on 28 October 2011; SMF 99280–81 (KP209370–71), 99282, Santa Elena, Sunset Hotel, 10.34384°N, 84.80268°W, elev. 1,580 m, collected on 28 October 2011. UCR 20142, SMF 85532–33, 85539, 89319–20, 99280, and 99283 are adult males, the remaining paratypes are adult females.

***Referred specimens*: COSTA RICA**—ALAJUELA: 1 km E Zapote at Río Tapezco, 10.22639°N, 84.40806°W, elev. 1,680 m: SMF 89346–50; Albergue Monterreal, 10.25417°N, 84.37127°W, elev. 1,775–1,880 m: SMF 91983–84, 99284, 99285 (KP209372), 99286, UCR 21259–61, 21343–50; Llano Bonito de Naranjo, 10.15391°N, 84.38287°W, elev. 1,560 m: SMF 93600 (KP209354); near Tapezco, 10.22290°N, 84.40384°W, elev. 1,665 m: SMF 93601–04; near Tapezco, 10.23275°N, 84.42628°W, elev. 1,460 m: SMF 93605–07; near Bajos del Toro, 10.20623°N, 84.30668°W, elev. 1,540 m: SMF 92430 (KP209367), 93660, 93662; road from La Luisa to Bajos del Toro, 10.20364°N, 84.30984°W, elev. 1,750 m: SMF 93655 (KP209366), 93656–59; road from La Luisa to Bajos del Toro, 10.17144°N, 84.31445°W, elev. 1,920 m: SMF 93663; GUANACASTE: Crest of Rincón de la Vieja: CRE 7613–15; PUNTARENAS: Monteverde, elev. 1,375–1,600 m: FMNH 236174, UTA R45923–24; 1 mi (= 1.6 km) before Monteverde Preserve: UTA R4543; Monteverde, near continental divide: UMMZ 131794 (1–15), 131795 (1–6), ZFMK 53888–89.

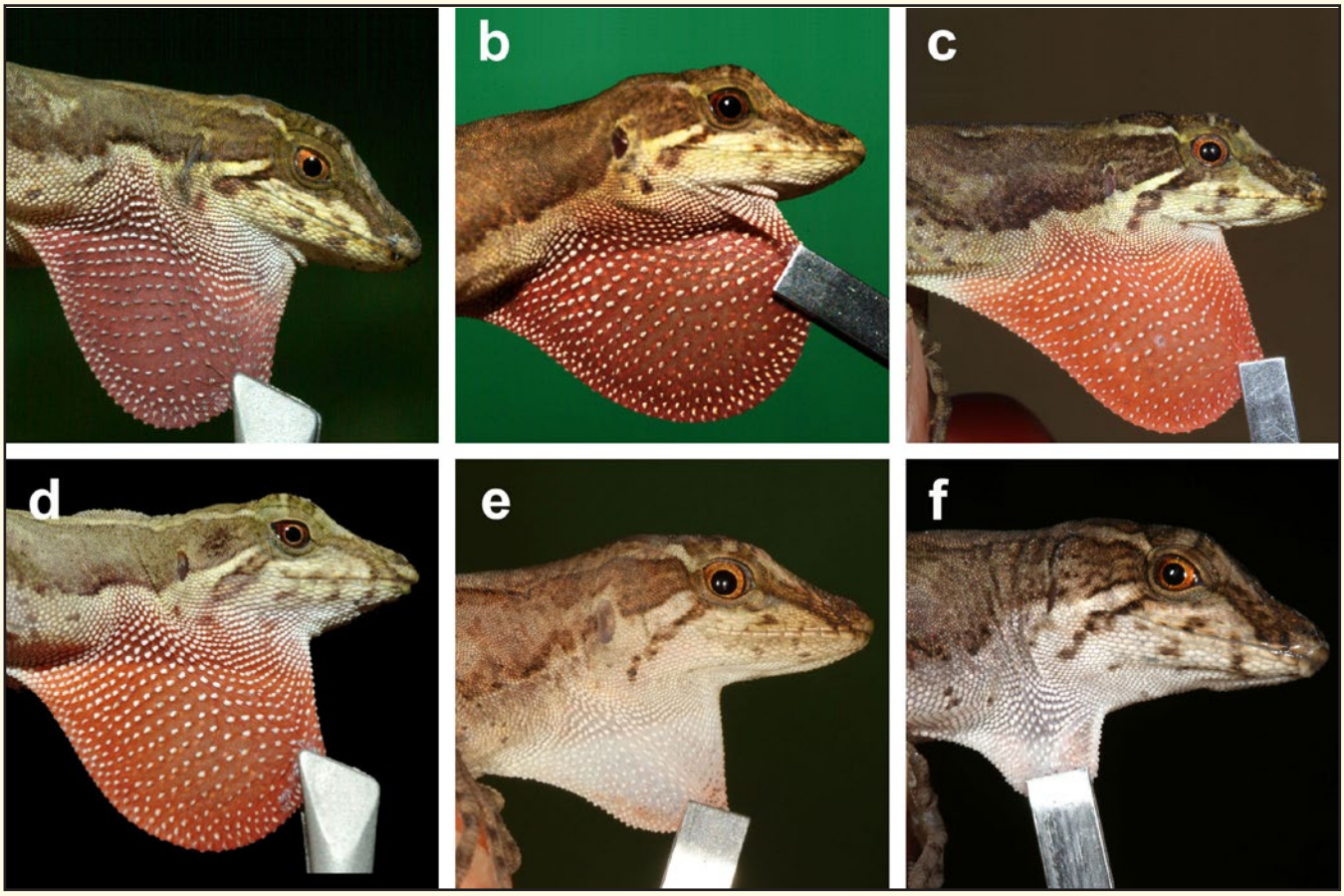

Fig. 12. Dewlaps of *Norops leditzigorum* in life: (a) SMF 89319 (male); (b) SMF 85532 (male); (c) SMF 99283 (male); (d) SMF 89346 (male); (e) SMF 93662 (female); and (f) (female).

***Diagnosis*:** A medium-sized (maximum SVL 51.0 mm in males, 52.5 mm in females) species (our Species A of the *Norops pachypus* complex) of the genus *Norops* (*sensu* Nicholson et al. 2012), that is most similar in external morphology to *N. alocomyos*, *N. benedikti*, *N. magnaphallus*, *N. pachypus*, *N. pseudopachypus*, and *N. tropidolepis*. These six species and *N. leditzigorum* are differentiated from all other anoles by the presence of a combination of narrow toe pads, long legs (tip of the 4th toe of adpressed hind limb usually reaching a point anterior to the eye), a dark interorbital bar, a striking lateral head pattern of dark brown and cream lines radiating from the eye, usually at least the indication of a lyriform marking on the occipital region, keeled dorsal scales on head and body, smooth to weakly keeled ventral scales at midbody, and a lack of enlarged postcloacal scales in males. *Norops leditzigorum* can be distinguished from *N. benedikti, N. pachypus,* and *N. pseudopachypus* by the presence of a uniform purplish red male dewlap in life (vs. a male dewlap mostly orange yellow, or red with a yellow central blotch and/or yellow margin, at least anteriorly). *Norops leditzigorum* differs from *N. alocomyos* by a distinctive hemipenial morphology with short, bulky lobes (vs. very long lobes), a sulcus spermaticus opening at the base of the apex into two broad fields void of ornamentation (vs. a closed sulcus spermaticus on the apical branches), and no conical processus on sulcal side of the base of the truncus (vs. such a processus present). *Norops leditzigorum* differs from *N. tropidolepis* by the presence of a more distinctly bilobed hemipenis with two clearly distinct broad fields void of ornamentation at the base of the apex (vs. these two fields are less clearly separated, rather forming one large concave area) and by lacking a large asulcate cusp-like processus (vs. such a processus present). Furthermore, the dewlap of adult males of *N. leditzigorum* is purplish red, whereas that of *N. tropidolepis* is orange red.

***Description of the holotype*:** Adult male, as indicated by everted hemipenes and presence of moderate-sized dewlap; snout–vent length 48.5 mm; tail length 95.0 mm, tail complete; tail slightly compressed in cross section, tail

height 2.3 mm, tail width 1.8 mm; axilla to groin distance 18.5 mm; head length 12.9 mm, head length/snout–vent length ratio 0.27; snout length 5.4 mm; head width 7.7 mm; shank length 13.5 mm, shank length/head length ratio 1.05; longest finger of extended forelimb reaching about 3.9 mm beyond tip of snout; longest finger of adpressed forelimb reaching to anterior insertion of hind limbs; scales on snout keeled, mostly unicarinate; 7 postrostrals; 10 scales between nasals; scales in distinct prefrontal depression distinctly keeled, mostly unicarinate, keels mostly directed transversely; supraorbital semicircles differentiated, separated by a minimum of 4 scales; supraorbital disc composed of 6–7 moderately enlarged keeled scales, mostly multicarinate; circumorbital series incomplete, one

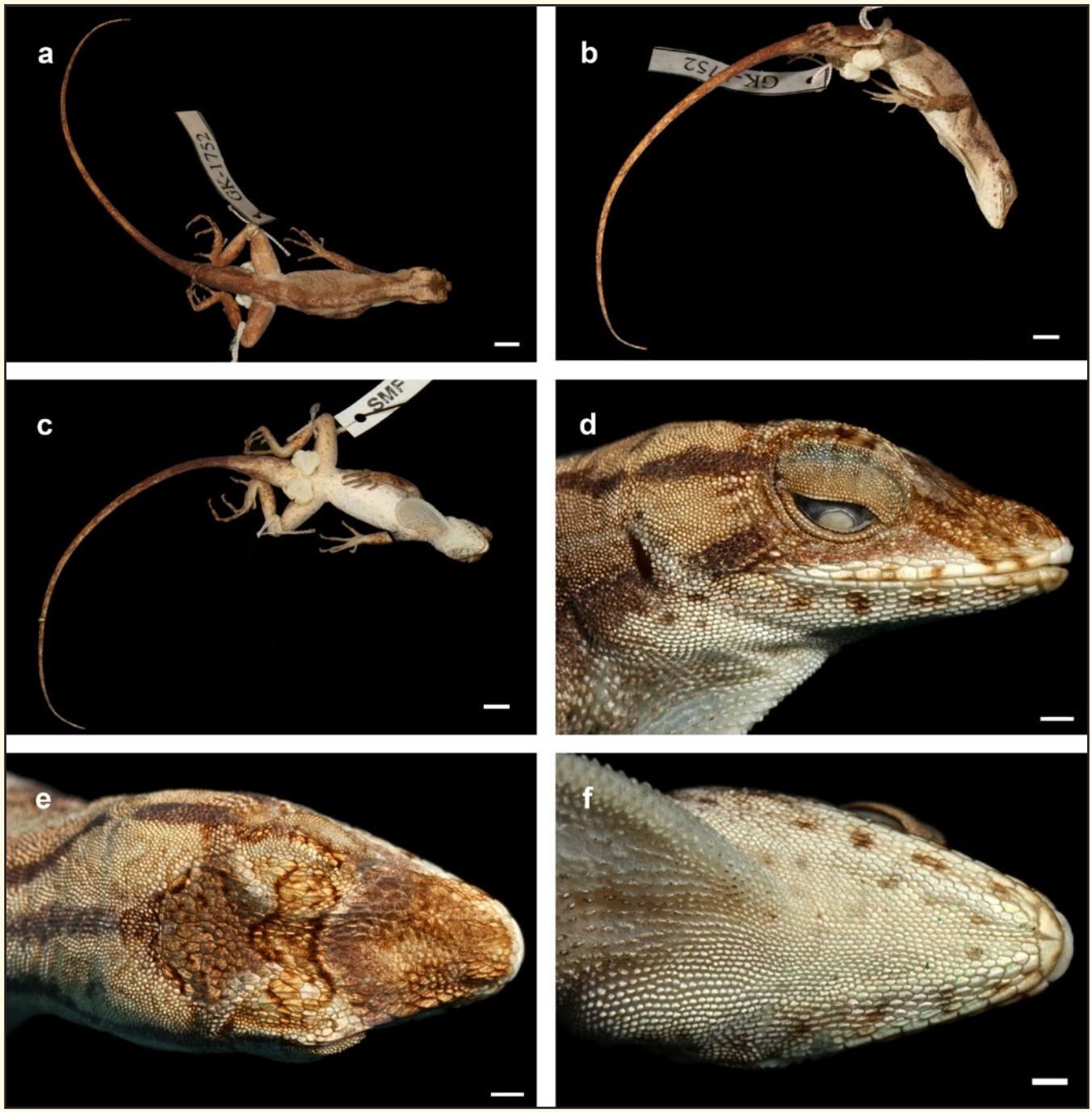

Fig. 13. Holotype of *Norops leditzigorum* (SMF 85538): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively.

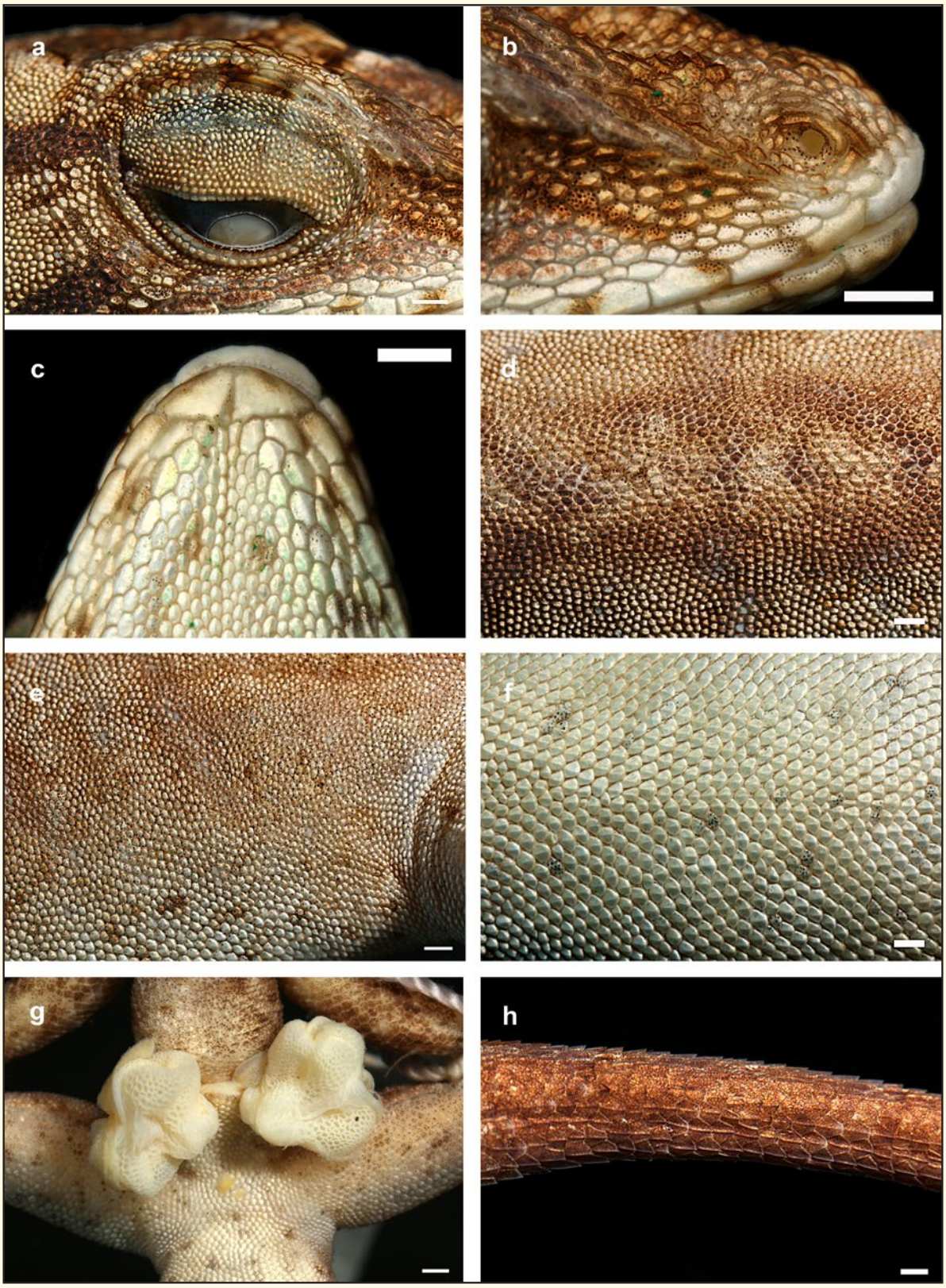

Fig. 14. Holotype of *Norops leditzigorum* (SMF 85538): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; and (h) lateral view of tail. Scale bars equal 1.0 mm.

enlarged supraorbital scale in contact with supraorbital semicircles; 4 elongated superciliaries, anterior one longest; 5–6 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; interparietal plate distinctly enlarged, 1.2 × 0.6 mm (length × width), surrounded by moderate-sized scales; 4 scales present between interparietal plate and supraorbital semicircles; canthal ridge distinct, composed of 5 large (posterior) and 3 small (anterior) canthal scales; 12 scales present between second canthals; 13 scales present between posterior canthals; 61/64 keeled loreal scales in a maximum of 8 horizontal rows; subocular scales keeled, in a single row, one subocular scale in contact with supralabial series; 9/8 supralabials to level below center of eye; ear opening 0.7 × 1.5 mm (length × height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals; 8/8 infralabials to level below center of eye; sublabials undifferentiated; strongly keeled granular scales present on chin and throat; dewlap moderate-sized, extending well onto chest, anterior insertion at level of anterior border of orbit, posterior insertion at level of axilla, with about 12–14, somewhat irregular, partially interrupted gorgetal–sternal rows of 17–20 scales per row; dorsum of body with keeled, subimbricate scales, 2 medial rows of slightly enlarged scales, largest dorsal scales about 0.40 × 0.30 mm (length × width); about 40 medial dorsal scales in one head length; about 70 medial dorsal scales between axilla and groin; lateral scales granular, pointed, homogeneous, about 0.16 mm in diameter; ventrals at midbody weakly keeled, subimbricate, about 0.35 × 0.45 mm (length × width); about 42 ventral scales in one head length; about 68 ventral scales between axilla and groin; about 146 scales around midbody; caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; no enlarged postcloacal scales; no tube-like axillary pocket; scales on dorsal surface of forelimb strongly keeled, mucronate and imbricate; digital pads dilated, dilated pad about 2 times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 24/23 lamellae under phalanges II–IV of 4th toe; 10/10 scales under distal phalanx of 4th toe.

The completely everted hemipenis is a stout bilobate organ with bulky, short lobes; the sulcus spermaticus is bordered by well-developed sulcal lips and opens at base of apex into two large concave areas void of ornamentation, one on each lobe; asulcate ridge-like processus shallow or absent; no conical processus present at base of truncus on sulcate side; lobes strongly calyculate, truncus with transverse folds.

After more than eight years in preservative, the coloration was recorded as follows: dorsal ground color Smoke Gray (267) with Brownish Olive (276) suffusions; dorsal surfaces of neck and temporal region Raw Umber (22); a Raw Umber (22) interorbital bar; ventral surfaces of head and body Pale Buff (1) slightly suffused with Olive Horn Color (16); ventral surfaces of limbs Drab (19); ventral surface of tail Raw Umber (22) with indistinct Cinnamon (21) bands; dewlap Smoke Gray (266) with Pale Buff (1) gorgetals.

***Variation*:** The paratypes and referred specimens agree well with the holotype in general morphology and scalation (see Table 2).

The coloration in life of the adult male paratype UCR 20142 was recorded as follows: dorsal ground color Raw Umber (123) grading into Raw Umber (223) in vertebral region; vertebral stripe bordered by Cinnamon (123A); ventral surfaces Tawny Olive (223D) with a suggestion of Citrine (51); dewlap uniformly Deep Vinaceous (4) with white gorgetals; iris Cinnamon-Rufous (40). The coloration in life of an adult male (SMF 89349) from 1 km E Zapote at Río Tapezco was recorded as follows: dorsal ground color Olive-Green (Auxiliary, 48) becoming paler towards vertebral region and with Sepia (119) chevrons; dorsal surface of head Tawny Olive (223D) with Raw Umber (123) interorbital bar; dorsal surface of tail Olive-Green (Auxiliary, 48) with Natal Brown (219A) bands; dewlap uniformly Mahogany Red (123B) with white gorgetals; iris Chestnut (32).

***Natural history notes*:** All specimens in the type series of *Norops leditzigorum* were encountered at night sleeping on the upper surface of leaves or on twigs, usually 0.2–0.6 m above the ground. Species recorded at the collecting sites of the type series of *N. leditzigorum* were *N. monteverde* (Köhler) and *Pristimantis cruentus* (Peters). At the type locality, patches of disturbed cloud forest are present on one side of the dirt road whereas on the other side of the road most of the forest has been transformed into pasture.

***Geographic distribution*:** As presently understood, *Norops leditzigorum* inhabits premontane and montane elevations in the Cordillera de Tilarán, in the western portion of the Cordillera Central, and on Volcán Rincón de la Vieja (Fig. 10). The species has been collected at elevations from 1,375 to 1,640 m in the Cordillera de Tilarán, and from 1,540 to 1,920 m in the western portion of the Cordillera Central.

***Etymology*:** The specific name is a patronym for the Leditzig family, Denmark, in recognition of the financial support of taxonomic research provided by Jørgen Leditzig through the BIOPAT initiative.

Fig. 15. Habitat at the type locality of *Norops leditzigorum.*

DISCUSSION

In recent years, DNA barcoding has been employed as a powerful tool in the recognition and delimitation of cryptic diversity, in general herpetofaunal contexts (e.g., Vieites et al., 2009; Jansen et al., 2011; Nagy et al., 2012) as well as for anoles in particular (Köhler et al., 2012, 2014; Lotzkat et al., 2013). The present study again corroborates the usefulness of this line of evidence that is independent of traditionally applied morphological criteria. While we do not advocate the uncritical application of threshold values of genetic distances for delimiting species, we recognize the usefulness of *p*-distance ranges provided by pioneering studies in evaluating whether a given divergence is to be interpreted as intra- or interspecific. In this context, the splitting of what has been called *Norops tropidolepis* in former studies of our group (Bienentreu, 2011; Lotzkat et al., 2011) into three species appears well-supported by 16S sequence data, given that interspecific *p*-distances between closely related but morphologically well-separable species of *Norops* have been found to be as low as 2% (Köhler et al., 2014; S. Lotzkat, unpublished; this study: *N altae* and *N. monteverde*). Moreover, although the genetic distances among members of the *N. pachypus* complex generally are at the lower end of interspecific distances in 16S barcodes of the genus *Norops* (Köhler et al., 2012, 2014; Lotzkat et al., 2013), the two new nominal species described herein appear more closely related to the morphologically well-distinguishable *N. pachypus* and to each other than to *N. tropidolepis* (to which they are much

more cryptic in their external morphology, and by which they are separated geographically), rendering their formal separation from the latter nomen desirable. Furthermore, apart from more subtle differences in scalation and dewlap coloration, the hemipenial morphology of the two new species strongly supports the conclusions drawn from the molecular results as a crucial second line of evidence.

Also in other aspects, the analysis of DNA barcodes in this study yields interesting results: The single representative of OTU 6 shows the mitochondrial (i.e., maternal) genotype of *Norops alocomyos* while exhibiting the hemipenial phenotype of the geographically neighboring *N. tropidolepis.* We interpret this phenomenon as evidence of hybridization between these two closely related species. In fact, we found this phenomenon (male phenotype of one species and maternally inherited genotype of another) along the contact zones of *N. limifrons* and *N. cryptolimifrons* (J. J. Köhler and S. Lotzkat, unpublished). Yet, herein it is documented for the first time as occurring in the *N. pachypus* complex, despite extensive barcoding of its Panamanian populations (Bienentreu, 2011; S. Lotzkat, unpublished). In view of these conclusions, we tentatively include the highlands south of Escazú in the distribution of *N. alocomyos* (though for now plotted as "*N.* cf. *alocomyos*" in Fig. 10)*,* expecting specimens "fully" attributable to this species to be collected in the course of future field surveys in that area.

Most species in the *Norops pachypus* complex are not separable by hemipenial morphology, but rather have hemipenes that are very similar among species, with short lobes and a sulcus spermaticus that opens at the base of the apex into one or two broad concave areas void of ornamentation. A remarkable exception is the long-lobed male copulatory organ of *N. alocomyos* that further differs from all other hemipenes among the species related to *N. pachypus* by the presence of a closed sulcus spermaticus on the lobes and of a conspicuous conical processus at the sulcate base of the apex, a hemipenial structure unknown in any anole species studied by GK thus far.

The recovered distribution of the Costa Rican species in the *Norops pachypus* complex might seem surprising at first examination. All three species with unicolored red male dewlaps are distributed across different highland systems that are separated by intervening lower areas with probably unsuitable habitat for these highland anoles. It can be assumed, however, that due to the generally lower temperatures during the glacial periods these lizards occurred at lower elevations than today, making a more continuous distribution likely. Thus, some of the present-day disjunct populations probably shared gene flow until some 15,000 years ago (Severinghaus and Brook, 1999), explaining the low genetic distances and lack of morphological differentiation, e.g., in *N. leditzigorum,* between the populations in the Cordillera de Tilarán and in the western Cordillera Central, or in *N. tropidolepis,* among the populations in the eastern Cordillera Central, Volcán Irazú, and in the western Cordillera de Talamanca.

Acknowledgements.—Javier Guevara Sequeira and Lourdes Vargas, SINAC Central, Ministerio del Ambiente y Energía (MINAE), San José, Costa Rica, issued the collecting and exportation permits. For the loan of and/or access to specimens, we thank Ted Daeschler and Ned Gilmore, Academy of Natural Sciences (ANSP), Philadelphia; Colin J. McCarthy, The Natural History Museum (BMNH), London; Alan Resetar, Field Museum of Natural History (FMNH), Chicago; Rafe Brown, Matt Buehler, and William E. Duellman, University of Kansas, Natural History Museum (KU), Lawrence; Federico Bolaños, Museo de Zoología, Universidad de Costa Rica (UCR), San José; Ronald A. Nussbaum and Greg Schneider, University of Michigan Museum of Zoology (UMMZ), Ann Arbor; Roy W. McDiarmid, Robert Wilson, and W. Ronald Heyer, National Museum of Natural History (USNM), Washington, D.C.; Jonathan A. Campbell and Carl J. Franklin, The University of Texas at Arlington (UTA), Arlington; Wolfgang Böhme, Zoologisches Forschungsinstitut und Museum A. Koenig (ZFMK), Bonn; and Frank Glaw and Michael Franzen, Zoologische Staatssammlung München (ZSM), Munich. For field assistance, we thank Julia Graap, Markus Gutpelet, Christoph Parsch, Heinz Schuh, and Javier Sunyer. For help with taking morphological data of anoles used in this study, we thank Marcel Haas and Alexia Wurster. We thank Kirsten E. Nicholson, Louis Porras, and Larry David Wilson for helpful comments and corrections on an early draft of this article.

Literature Cited

Bienentreu, J.-F. 2011. Phylogeographie mittelamerikanischer Saumfingerechsen aus dem *Anolis pachypus*-Komplex. Unpublished Diploma thesis, Goethe-Universität, Frankfurt am Main. Germany.

Boulenger, G. A. 1885. Catalogue of the Lizards in the British Museum (Natural History). 2nd ed. Vol. II. Taylor and Francis, London, England.

Cope, E. D. "1875" (1876). On the Batrachia and Reptilia of Costa Rica. Journal of the Academy of Natural Sciences of Philadelphia, ser. 2, 8: 93–154.

de Queiroz, K. 2007. Species concepts and species delimitation. Systematic Biology 56: 879–886.

Drummond, A. J., B. Ashton, M. Cheung, J. Heled, M. Kearse, R. Moir et al. 2010. Geneious v.4.8.5. (www.geneious.com; accessed 10 November 2011).

Edgar, R. C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5: 1–19.

Huelsenbeck, J. P., and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.

Ivanova, N. V., J. De Waard, and P. D. N. Hebert. 2006. An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6: 998–1,002.

Jansen, M., R. Bloch, A. Schulze, and M. Pfenninger. 2011. Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. Zoologica Scripta 40: 567–583.

Köhler, G. 2012. Color Catalogue for Field Biologists. Herpeton, Offenbach, Germany.

Köhler, G. 2014. Characters of external morphology used in *Anolis* taxonomy—Definition of terms, advice on usage, and illustrated examples. Zootaxa 3,774: 201–257.

Köhler, G., M. Ponce, J. Sunyer, and A. Batista. 2007. Four new species of anoles (genus *Anolis*) from the Serranía de Tabasará, west-central Panama (Squamata: Polychrotidae). Herpetologica 63: 375–391.

Köhler, G., A. Batista, M. Vesely, M. Ponce, A. Carrizo, and S. Lotzkat. 2012. Evidence for the recognition of two species of *Anolis* formerly referred to as *A. tropidogaster* (Squamata: Dactyloidae). Zootaxa 3,348: 1–23.

Köhler, G., R. Gómez Trejo Pérez, C. B. P. Petersen, and F. R. Méndez de la Cruz. 2014. A revision of the Mexican *Anolis* (Reptilia, Squamata, Dactyloidae) from the Pacific versant west of the Isthmus de Tehuantepec in the states of Oaxaca, Guerrero, and Puebla, with the description of six new species. Zootaxa 3,862: 1–210.

Lotzkat, S., J.-F. Bienentreu, A. Hertz, and G. Köhler. 2011. A new species of *Anolis* (Squamata: Iguania: Polychrotidae) formerly referred to as *A. pachypus* from the Cordillera de Talamanca of western Panama and adjacent Costa Rica. Zootaxa 3,125: 1–21.

Lotzkat, S., A. Hertz, J.-F. Bienentreu, and G. Köhler. 2013. Distribution and variation of the giant alpha anoles (Squamata: Dactyloidae) of the genus *Dactyloa* in the highlands of western Panama, with the description of a new species formerly referred to as *D. microtus*. Zootaxa 3,626: 1–54.

Nagy, Z. T., G. Sonet, F. Glaw, M. Vences, and J. Chave. 2012. First large-lcale DNA Barcoding assessment of reptiles in the biodiversity hotspot of Madagascar, based on newly designed COI primers. PLoS ONE 7: 1–11.

Nicholson, K. E., B. I. Crother, C. Guyer, and J. M. Savage. 2012. It is time for a new classification of anoles (Squamata: Dactyloidae). Zootaxa 3,477: 1–108.

Poe, S., and R. Ibañez. 2007. A new species of *Anolis* lizard from the Cordillera de Talamanca of western Panama. Journal of Herpetology 41: 263–270.

Ronquist, F., and J. P. Huelsenbeck. 2003: MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1,572–1,574.

Sabaj Pérez, M. H. (Ed.). 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Verson 3.0 (23 February 2012). American Society of Ichthyologists and Herpetologists, Washington, D.C., United States. (www.asih.org; accessed 02 December 2014).

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. The University of Chicago Press, Chicago, Illinois, United States.

Severinghaus, J., and E. Brook. 1999. Abrupt climate change at the end of the last glacial period inferred from trapped air in Polar ice. Science 286 (5441): 930–934.

Smithe, F. B. 1975–1981. Naturalist's color guide. Part I. Color guide. 182 color swatches. American Museum of Natural History, New York, New York, United States.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony methods. Molecular Biology and Evolution 28: 2,731–2,739.

Vieites, D. R., K. C. Wollenberg, F. Andreone, J. Köhler, F. Glaw, and M. Vences. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences of the United States of America 106: 8,267–8,272.

Appendix 1. Comparative material examined. For specimens with 16S sequences analyzed in this study, the GenBank accession number follows the collection number in parentheses.

Dactyloa casildae.—**PANAMA:** COMARCA NGÖBE-BUGLÉ: Río Flor, 8.5209°N, 81.7785°W, elev. 1,220 m: SMF 91453 (JX083231).

Dactyloa ginaelisae.—**PANAMA:** COMARCA NGÖBE-BUGLÉ: W slope Cerro Santiago, La Nevera, 8.4997°N, 81.7724°W, elev. 1,700 m: SMF 89496 (JX083226).

Dactyloa ibanezi.—**PANAMA:** VERAGUAS: Cerro Mariposa, 8.5100°N, 81.1166°W, elev. 880 m, SMF 89459 (JX083236).

Norops cf. *alocomyos*.—**COSTA RICA:** SAN JOSÉ: Altos de Escazú, Río Agres, 9.89972°N, 84.12861°W, elev. 1,534 m: SMF 98995 (KP209375).

Norops altae.—**COSTA RICA:** CARTAGO: 1 km E Coliblanco, 9.9544°N, 83.7717°W, elev. 1,654 m: SMF 86917–18 (KP209321–22).

Norops benedikti.—**COSTA RICA:** PUNTARENAS: Las Tablas, 8.9407°N, 82.7280°W, elev. 1,960 m: SMF 92134; **PANAMA:** BOCAS DEL TORO: N slope Cerro Pando, 8.9314°N, 82.7137°W, elev. 2,390 m: SMF 89744; N slope Cerro Pando, 8.9333°N, 82.7131°W, elev. 2,310–2,330 m: SMF 89745–89746, 90149 (holotype; KP209325); N slope Cerro Pando, 8.9354°N, 82.7128°W, elev. 2,280 m: SMF 90148; N slope Cerro Pando, between Río Clarito und Río Changena, 8.9887°N, 82.6749°W, elev. 1,820 m: SMF 91509; N slope Cerro Pando, Río Changena, 8.9785°N, 82.6901°W, elev. 1,640–1,660 m: MHCH 2108–2109, SMF 91505–91506; N slope Cerro Pando, tributary to Río Changena, 8.9474°N, 82.7098°W, elev. 1,990–2,000 m: SMF 91508, MHCH 2106–2107; N slope Cerro Pando, tributary to Río Changena, 8.9524°N, 82.7093°W, elev. 1,960 m: SMF 91507 (KP209326); Sendero Culebra, 8.8760°N, 82.4696°W, elev. 1,740 m: SMF 86374 (KP209324), 86375, 89274; Sendero el Pianista, 8.8411°N, 82.4246°W, elev. 1,650 m: SMF 86370 (KP209323), 86371–73; CHIRIQUÍ: Bajo Mono, 8.8333°N, 82.4833°W, elev. 1,820 m: SMF 85268; Jurutungo, 8.9083°N, 82.7168°W, elev. 2,010–2,100 m: SMF 85276, 85277; Jurutungo, 8.9109°N, 82.7144°W, elev. 2,060 m: SMF 85272, 85273; Jurutungo, 8.9111°N, 82.7159°W, elev. 2,020 m: SMF 89505; Jurutungo, 8.9114°N, 82.7129°W, elev. 2,070 m: SMF 89507; 8.9119°N, 82.7095°W, elev. 2,250 m: MHCH 2105; Jurutungo, 8.9121°N, 82.7096°W, elev. 2,200 m: SMF 89506; Alto Chiquero, 1 km W Estación de Guardaparques, 8.8453°N, 82.4958°W, elev. 1,920 m: SMF 85264, 85265, 85266, 85267.

Norops fortunensis.—**PANAMA:** CHIRIQUÍ: Reserva Forestal La Fortuna, Cerro Guayabo, 8.75477°N, 82.25338°W, elev. 1,200 m, SMF 90103 (KP209327).

Norops gruuo.—**PANAMA:** COMARCA NGÖBE-BUGLÉ: Buabidí/Alto Tugrí, 8.48195°N, 81.72097°W, elev. 1,200 m, SMF 89709 (KP209328); VERAGUAS: Cerro Mariposa, 8.51607°N, 81.11849°W, elev. 883 m, MHCH 2162 (KP209329).

Norops humilis.—**PANAMA:** BOCAS DEL TORO: between Río Clarito und Río Changena, 8.99207°N, 82.66598°W, elev. 1,665 m, SMF 91473 (KP209331); between Río Clarito und Río Changena, 8.99109°N, 82.67118°W, elev. 1,752 m, SMF 91474 (KP209330).

Norops kemptoni.—**PANAMA:** CHIRIQUÍ: Bajo Mono: Sendero La Cascada, 8.82504°N, 82.50206°W, elev. 1,866 m, SMF 89718 (KP209332); Reserva Forestal La Fortuna, near Lost & Found Ecohostel, 8.67443°N, 82.21611°W, elev. 1,434 m, SMF 91458 (KP209333).

Norops magnaphallus.—**PANAMA:** CHIRIQUÍ: Alto Jaramillo, Cerro Altrilleria, 8.7757°N, 82.3901°W, elev. 1,950–1,970 m: SMF 90121, 90122, MHCH 2226; Alto Jaramillo, Cerro Altrilleria, 8.7759°N, 82.3888°W, elev. 2,050 m: SMF 90125 (KP209334); Boquete, Volcáncito, 8.7841°N, 82.4748°W, elev. 1,570 m: SMF 89262; Bajo Mono: Sendero La Cascada, 8.8263°N, 82.4989°W, elev. 1,820–1,830 m: SMF 89727, MHCH 2231; Bajo Mono: Sendero La Cascada, 8.8262°N, 82.4990°W, elev. 1,830 m: SMF 90129, MHCH 2223, 2225; Bajo Mono: Sendero La Cascada, 8.8257°N, 82.5001°W, elev. 1,840 m: MHCH 2224; Bajo Mono: Sendero La Cascada, 8.8250°N, 82.5021°W, elev. 1,870 m: SMF 89728; Sendero los Quetzales, Quebrada de Silencio, 8.8494°N, 82.5154°W, elev. 2,130 m: SMF 89732; Sendero los Quetzales, Quebrada de Silencio, 8.8491°N, 82.5162°W, elev. 2,110 m: SMF 90126; Sendero los Quetzales, Refugio Las Rocas, 8.8480°N, 82.5196°W, elev. 2370 m: SMF 8,9734 (KP209335); Volcán Barú, 8.7909°N, 82.5142°W, elev. 2,580 m: SMF 90130; Volcán Barú: area de acampar Mamecillos, 8.8015°N, 82.513°W, elev. 2,580 m: SMF 90131.

Norops monteverde.—**COSTA RICA:** GUANACASTE: road from Santa Elena to Reserva Santa Elena, 10.33167°N, 84.77944°W, elev. 1,575 m: SMF 85540 (KP209336); road from Santa Elena to Reserva Santa Elena, 10.34139°N, 84.80500°W, elev. 1,560 m: SMF 85541 (KP209337).

Norops pachypus.—**COSTA RICA:** CARTAGO: Chirripo Grande: ANSP 29108 PUNTARENAS: Las Tablas: SMF 93577 (KP209339), 93578–81; SAN JOSÉ: Boquete Road camp, side of Cerro de la Muerte, elev. 2,000 m: FMNH 101824, 101827, 101836, 101843, 101849, KU 40672–73; above San Isidro del General: KU 40734; 18.5–18.8 km N San Isidro del General: KU 91775–79, 104072–76, UMMZ 117624 (1–3); 14.2 km N San Isidro del General: UMMZ 117746; 5.15 km N an Isidro del General: UMMZ 117610; S side Cerro de la Muerte, 9 km below División on Pan American Highway: UMMZ 149209–10; road from San Isidro de El General to Cerro de la Muerte: SMF 93814 (KP209338), 93815–17; **PANAMA:** CHIRIQUÍ: Cerro Punta, Finca La Tatica, 8.8778°N, 82.5835°W, elev. 2,000 m: SMF 89358, 89361; Cerro Picacho, Las Nubes, 8.8942°N, 82.6149°W, elev. 2,120 m: SMF 90141, MHCH 2246; Cerro Picacho, Las Nubes, 8.8936°N, 82.6158°W, elev. 2,230 m: SMF 90140; Cerro Picacho, Las Nubes, 8.8926°N, 82.6163°W, elev. 2,250 m: SMF 90139; Cerro Picacho, Las Nubes, 8.8961°N, 82.6170°W, elev. 2,300–2,310 m: SMF 90138, MHCH 2243; Cerro

Picacho, Las Nubes, 8.8915°N, 82.6174°W, elev. 2,260 m: MHCH 2244 (KP209341); Cerro Picacho, Las Nubes, 8.8969°N, 82.6187°W, elev. 2,360 m: MHCH 2242; Cerro Picacho, Las Nubes, 8.8986°N, 82.6195°W, elev. 2,350 m: SMF 90137; Jurutungo, 8.9120°N, 82.7182°W, elev. 1,890 m: SMF 89502 (KP209342); Jurutungo, 8.9067°N, 82.7259°W, elev. 1,890 m: MHCH 2252, 2253 (KP209343); Alto Respingo, 8.8416°N, 82.5345°W, elev. 2,550 m: SMF 90146; Alto Respingo, 8.8418°N, 82.5345°W, elev. 2,540 m: SMF 90147; Alto Respingo, 8.8416°N, 82.5346°W, elev. 2,560 m: SMF 90143, 90144 (KP209340); Alto Respingo, 8.8411°N, 82.5346°W, elev. 2,550 m: SMF 90145.

Norops pseudokemptoni.—**PANAMA:** COMARCA NGÖBE-BUGLÉ: Cerro Saguí, near Quebrada Juglí, 8.5636°N, 81.8217°W, elev. 1,960 m: SMF 91515 (KP209348); Río Flor, 8.5209°N, 81.7785°W, elev. 1,220 m: SMF 91518 (KP209349).

Norops pseudopachypus.—**PANAMA:** CHIRIQUÍ: Cerro Guayabo, 8.7751°N, 82.2398°W, elev. 1,790 m: SMF 90159, 90160; Cerro Guayabo, 8.7683°N, 82.2484°W, elev. 1,560 m: SMF 90161 (KP209345); Cerro Pata de Macho, 8.6793°N, 82.1930°W, elev. 1,810–1,860 m: SMF 90162, 90165; Cerro Pata de Macho, 8.6776°N, 82.1981°W, elev. 1,750 m: SMF 89524, 89753, MHCH 2279; Cerro Pata de Macho, 8.6776°N, 82.1981°W, elev. 1,760 m: MHCH 2274 (KP209344); Cerro Pata de Macho, 8.6761°N, 82.2006°W, elev. 1,630–1,660 m: SMF 90166, MHCH 2280; COMARCA NGÖBE-BUGLÉ: Cerro Saguí, near Quebrada Juglí, 8.5636°N, 81.8217°W, elev. 1,930–1,940 m: SMF 91520, MHCH 2286; Cerro Saguí, near Quebrada Juglí, 8.5642°N, 81.8221°W, elev. 2,030 m: SMF 91522 (KP209347); Cerro Santiago near La Nevera, 8.4954°N, 81.7673°W, elev. 1,810 m: SMF 89522, 90157 (KP209346), 90158; Cerro Santiago near La Nevera, 8.4989°N, 81.7682°W, elev. 1,580 m: MHCH 2282; Cerro Santiago near La Nevera, 8.5018°N, 81.7689°W, elev. 1,560 m: SMF 89519, 89521; La Nevera, 8.4997°N, 81.7724°W, elev. 1,700 m: SMF 89516, 89518; Quebrada Ardilla, 8.4968°N, 81.7221°W, elev. 1,580 m: SMF 89751, 89752, MHCH 2281.

Norops tenorioensis.—**COSTA RICA:** ALAJUELA: Volcán Tenorio, 10.70521°N, 85.03068°W, elev. 1,160 m: SMF 91985 (KP209350), 91987 (KP209351).

Norops tropidolepis.—**COSTA RICA:** ALAJUELA: 2 km E Poasito, 10.16533°N, 84.18253°W, elev. 1,940 m: SMF 93617; Isla Bonita: FMNH 101820–23, 101825–26, 101828–34, 101837–41, 101844–48, 101859, 101861–63; road from Carrizal to Vara Blanca, 10.11669°N, 84.16338°W, elev. 1,735 m: SMF 93623 (KP209356); Volcán Poás, 10.15600°N, 84.22564°W, elev. 2,210 m: SMF 93612 (KP209355), 93613–16; Volcán Poás, 10.16381°N, 84.22681°W, elev. 2,370 m: SMF 93651, 93652 (KP209365), 93653–54; S Poasito, 10.13731°N, 84.18882°W, elev. 1,720 m: SMF 93622; Villa Calas, 10.16925°N, 84.16732°W, elev. 1,813 m: SMF 92127, UCR 21314–16, 21321–23; near Villa Calas, 10.16845°N, 84.16856°W, elev. 1,800 m: SMF 93618; near Villa Calas, 10.15893°N, 84.1246°W, elev. 1,920 m: SMF 93611; CARTAGO: Volcán Irazú: BMNH 1885.3.24.4–9, UMMZ 59001 (1–2) ; Pacayas: KU 40683–84; 10 km S of Cartago on Costa Rica Route 2: USNM 244951; Finca QuIrazú, 4 mi (= 6.4 km) SW Cartago: KU 40687; Quebrada Honda, near Pacayas: KU 40674; Finca Coliblanco, Volcán Irazú: UMMZ 123634; Volcán Turrialba, S slope: UMMZ 117621; Volcán Turrialba Santa Cruz: KU 40685–86; Cerro Carpintera: ANSP 23936–38; Parque Nacional on Pan American Highway, S Cartago: KU 40675–76; Empalme: KU 40681–82; 5 km N El Empalme: KU 67143–44; 13 airline km SW from Cartago, 9.75862°N, 83.97994°W, elev. 1,930 m: SMF 93625 (KP209358), 93626; 7 mi (= 11.3 km) S Cartago on Pan American Highway: FMNH 167730, KU 40688–89; between Cartago and Cerro de la Muerte, elev. 3,010’ (= 917 m): FMNH 167728; Hotel Tapanti, 9.67872°N, 83.89279°W, elev. 2,520 m: SMF 93627; road from Cartago to San Isidro, 8 airline km SW from Cartago, 9.79679°N, 83.95853°W, elev. 1,850 m: SMF 93624 (KP209357); S slope of Volcán Irazú, 9.89689°N, 83.87952°W, elev. 1,875 m: SMF 93664 (KP209368), 93665–66, 93667 (KP209369); HEREDIA: 4 km (on road) N Vara Blanca: SMF 85531; Cerro Chompipe, 10.09776°N, 84.07294°W, elev. 2,613 m: SMF 93668–71; La Cruz: UCR 21253; Cinchona: FMNH 176861, 177278; Finca Heinz Hoffmann, Birri (Plan de Birri), 10.08017°N, 84.13114°W, elev. 1,630 m: SMF 93599; La Cruz: UCR 21253; near San Jose de la Montaña, 10.09433°N, 84.10598°W, elev. 2,040 m: SMF 93619–21, 93648–50; 2.7 km N San Jose de la Montaña: KU 67127; San Jose de la Montaña: KU 67126; near Vara Blanca, 5,200’ (= 1,585 m): FMNH 154423; road from San Jose de la Montaña to Birrí, 10.08169°N, 84.10616°W, elev. 1,810 m: SMF 93609; S slope of Volcán Barva, 10.08594°N, 84.116555°W, elev. 1,850 m: SMF 93608; S slope of Volcán Barva, 10.10915°N, 84.10056°W, elev. 2,260 m: SMF 93610; Volcán Barva, 10.10627°N, 84.10365°W, elev. 2,259 m: SMF 99287–88 (KP209373–74), 99289; Volcán Barva: ANSP 24530–36, 34748–51; Volcán Barva, Conde de Tattenbach: KU 40679–80, 40998; Volcán Barva, Los Angeles de Paso Llano, 10.10770°N, 84.10327°W, elev. 2,260 m: KU 67128–31, SMF 93643–47; Volcán Barva, near Rama sur Río Las Vueltas: KU 103911, 104016–49, UMMZ 128940; 8 km NE San Rafael: UMMZ 143758–60; SAN JOSÉ: Boquete road camp, side of Cerro de la Muerte, elev. 2,000 m: FMNH 101824, 101827, 101836, 101843, 101849; La Palma: ANSP 21449; La Carpintera: KU 40714–19; Guadalupe: KU 67134–35; La Hondura: ANSP 24523–29; Tablazo: ANSP 21918–19; road (CR 226) from Santa María de Dota to Interamericana, 9.68242°N, 83.97366°W, elev. 1,880 m: SMF 93628 (KP209359); road (CR 226) from Santa María de Dota to Interamericana, 9.70720°N, 83.96158°W, elev. 2,160 m: SMF 93630, 93631 (KP209360), 93632; road (CR 226) from Santa María de Dota to Interamericana, 9.72061°N, 83.96032°W, elev. 2,300 m: SMF 93633, 93634 (KP209361); San José: USNM 75442, 80906–11; highlands of San José: ZSM 288/1981/2; 2 km N Las Nubes: KU 67136–38; 2.6 km N Las Nubes: KU 67139–41.

Sibon noalamina.—**PANAMA:** COMARCA NGÖBE-BUGLÉ: Bosque Protector Palo Seco, headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, elev. 1,050 m: SMF 91539 (KP209376).

Gunther Köhler received a degree in Veterinary Medicine (Staatsexamen) at the University Gießen, Germany, in 1993, and a doctoral degree at Goethe University Frankfurt am Main, Germany, in 1995; since that time, he has been the Curator of Herpetology at the Senckenberg Research Institute, Frankfurt am Main, Germany. His research focuses on the Neotropical herpetofauna, primarily that of Central America and Mexico. To date, Gunther has authored 27 books and 178 research papers on amphibians and reptiles.

Joseph Vargas is a Costa Rican who obtained a Bachelors Degree in Biological Sciences at the Latin University of Costa Rica, Costa Rica, and currently is a research student at Senckenberg Research Institute, Frankfurt am Main, Germany. Joseph is specializing in the study of amphibians and reptiles from Costa Rica, and his research focuses on alkaloids, barcoding, biogeography, conservation, and taxonomy, as well as in the reproduction of amphibians and reptiles in captivity.

Sebastian Lotzkat studied Biology at Goethe-University Frankfurt, Germany, where he received his Diploma degree in 2007. Based at the Senckenberg Research Institute Frankfurt, he is currently finishing his Ph.D. project on the reptile fauna of mountainous western Panama. Besides his research on the integrative taxonomy, diversity, and biogeography of Central American herpetofauna, Sebastian is dedicated to the communication of biological topics to a broad audience through print and online publications, lectures, and excursions.