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Two new Andean species of *Anolis* lizard (Iguanidae: Dactyloinae) from southern Ecuador

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ABSTRACT
We describe two new species of *Anolis* lizard that are sympatric on the Amazonian slopes of the Andes of southern Ecuador at elevations between 1440 and 1970 m. The new species may be distinguished from other *Anolis* by external anatomy, mitochondrial divergence and dewlap colour. We estimate the phylogenetic positions of the new species using Bayesian analysis of DNA sequence data including all species of *Dactyloa*-clade *Anolis* for which DNA data are available. *Anolis hyacintogularis* sp. nov. is sister to *Anolis calimae*, whereas *Anolis lososi* sp. nov. is sister to *Anolis williamsmittermeierorum*, herein reported for Ecuador for the first time. Individuals of both new species were collected within a protected area in southern Ecuador, Podocarpus National Park, which suggests that at least some populations of these species are well protected.
www.zoobank.org/urn:lsid:zoobank.org:pub:E55FA804-E3FD-4412-8FEB-5234E29E272D

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Andes; Anoles; phylogeny; South America; systematics

Introduction

The approximately 400 described species of anole lizards (*Anolis*) have proliferated extensively in the Americas (Uetz 2017). The ecology, physiology and evolution of anoles have been studied extensively in the West Indies (Losos 2009), but the mainland forms are less well known. Documenting species diversity in the mainland clades is a necessary step towards understanding the diversity of the entire anole clade.

Anolis is the most species-rich clade traditionally recognized as a genus in Ecuador, with 40 species reported to date (Torres-Carvajal et al. 2017). The diversity of anole lizards in Ecuador is greatest west of the Andes, with more than twice the number of species that occur east of the Andes (27 and 13 species, respectively). Five new species of *Anolis* have been described from Ecuador during the last 6 years, as a result of both careful examination of existing collections (e.g. Ayala–Varela et al. 2014) and recent collecting in poorly explored areas (Ayala-Varela and Torres-Carvajal 2010). Herein, we contribute to this growing body of taxonomic knowledge

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Supplemental data can be accessed here.

with the description of two distinctive new species of *Anolis* endemic to the southeastern slopes of the Ecuadorian Andes. We present morphological and molecular evidence supporting recognition of the new species.

Material and methods

Morphological and colour data

All voucher specimens of the new species described in this paper were deposited in the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ). Other specimens examined are listed in the Appendix.

We follow previously proposed terminology for external characters by Williams et al. (1995) and Poe (2004). Scale counts were made on the left side if applicable. Fifteen morphological measurements were taken with digital callipers to the nearest 0.1 mm: head length, head width, head height, humerus length, ulna length, femur length, tibia length, snout–vent length (SVL), tail length, snout length, ear opening measured vertically, interparietal length, interorbital distance, dewlap length and height. Regenerated or broken tails were not measured. Sex was determined by the presence of everted hemipenes and enlarged postcloacal scales in males (assumed to be absent in females).

In addition to describing colour in life, we measured spectral radiance (reflectance and transmittance) of the gular sac of males and females. We measured reflectance using a bifurcated fibre optic probe connected to a portable Jazz spectrometer (Ocean Optics) following Fleishman et al. (2009), and used a tubular holder of 3.5 mm diameter cut at 45° relative to the surface. Transmittance was measured using two fibres by positioning the probes at an angle of 90° with respect to the plane of the gular sac, and attaching a collimated lens to the light source. Measurements were taken in five sections of the gular sac: close to the head, close to the base of the sac, close to the abdomen, approximate centre of sac, and outermost edge of the dewlap. Radiance of the dewlap was calculated by summing the transmittance and reflectance as per Leal and Fleishman (2004).

Statistical analyses

One of the new species described herein is very similar in morphology to *Anolis williamsmittermeierorum*. We used *t*-tests to evaluate quantitative differences between these species. Statistical analyses were performed in JMP 9.0 (SAS Institute Inc.).

DNA sequence data

Total genomic DNA was digested and extracted from liver or muscle tissue using a guanidinium isothiocyanate extraction protocol. Tissue samples were first mixed with Proteinase K and a lysis buffer and digested overnight before extraction. DNA samples were quantified using a Nanodrop® ND-1000 (NanoDrop Technologies, Inc.), re-suspended and diluted to 25 ng/µl in ddH$_2$O before amplification.

Using primers and amplification protocols from the literature (Kumazawa and Nishida 1993; Folmer et al. 1994; Macey et al. 1997; Schulte and Cartwright 2009) we obtained DNA sequences of the nuclear gene recombination-activating gene 1 (*RAG1*), as well as the mitochondrial genes Cytochrome c oxidase I (*CO1*) and a continuous fragment including the NADH dehydrogenase subunit 2 (*ND2*), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, and the origin of the light-strand replication (*Ol*), for three individuals each of the two new species described herein. In addition we used published DNA sequence data from individuals from two *Anolis* clades: 62 species of *Dactyloa* and 13 species of *Digilimbus* (Poe et al. 2017). Sequences from outgroup taxa *Polychrus*, *Pristidactylus* and *Urostrophus* were used to root the trees. Gene regions of taxa included in phylogenetic analyses along with their GenBank accession numbers are shown in Table 1.

Phylogenetic analyses

Editing, assembly and alignment of sequences were performed with Geneious 7.1.7 (Biomatters Ltd. 2014). Genes were combined into a single data set with 11 partitions, three per protein coding gene (*RAG1*, *ND2*, *CO1*) corresponding to each codon position,

Table 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions included in this study. Accession numbers for new sequences generated in this study are marked with asterisks.

		GenBank accession number		
Taxon	Voucher and locality	COI	ND2	RAG1
Anolis aeneus	**USNM 319162**: Grenada: St George,:West end of Grand Anse Bay	JN112719[a]	–	JN112592[a]
	JBL 442: Grenada: St George: Grand Anse Bay	–	AF055950[b]	–
A. aequatorialis	**QCAZ 6855**: Ecuador: Pichincha: Mindo, on road from Mariposas de Mindo to Mindo Garden	JN112720[a]	JN112662[a]	JN112593[a]
A. aequatorialis	**QCAZ 6883**: Ecuador: Pichincha: El Placer, on road to Conchacato, Río Chisinche	JN112721[a]	JN112663[a]	JN112594[a]
A. agassizi	**KEN 2004–2**: Colombia: Gorgona Island	JN112722[a]	JN112667[a]	JN112595[a]
A. anatoloros	**MHNLS 17872**: Venezuela: Barinas: San Isidro	JN112723[a]	JN112668[a]	JN112596[a]
A. anchicayae	**POE 3194**: Colombia: Valle de Cauca: Pianguita, behind Villas de Pianguita	–	see below[c]	–
A. anoriensis	**MHUA 11568 (MHUA–T 715)**: Colombia: Antioquia: Anorí, Cañadahonda	JN112736[a]	JN112666[a]	JN112609[a]
A. anoriensis	**MHUA–T 517**: Colombia: Antioquia: Anorí, El Retiro, Alto de La Forzosa	JN112735[a]	JN112665[a]	JN112608[a]
A. apollinaris	**POE 4407**: Colombia: Cundimarca: northwest of San Francisco	–	see below[c]	–
A. bonairensis	**LSUMZ 5468**	–	AF317070[d]	–
A. calimae	**MRC 118**: Colombia: Valle del Cauca: on road to San Antonio, Television Tower	JN112724[a]	JN112669[a]	JN112597[a]
A. calimae	**MRC 119**: Colombia: Valle del Cauca: on road to San Antonio, Television Tower	JN112725[a]	JN112670[a]	JN112598[a]
A. casildae	**JMS 214**: Panama: Chiriquí: near STRI–Fortuna Biological Station	JN112726[a]	AY909745[e]	JN112599[a]
A. chloris	**QCAZ 6877**: Ecuador: Pichincha: La Unión del Toachi, Centro de Interpretación Ambiental Otongachi, Otonga Foundation	JN112727[a]	JN112671[a]	JN112600[a]
A. chloris	**QCAZ 6920**: Ecuador: Esmeraldas: San Lorenzo, grounds of Hosteria Tundaloma	JN112728[a]	JN112672[a]	JN112601[a]
A. danieli	**MHUA 11564 (MHUA–T 711)**: Colombia: Antioquia: Anorí, Cañadahonda	JN112732[a]	JN112676[a]	JN112605[a]
A. danieli	**MHUA 11567 (MHUA–T 714)**: Colombia: Antioquia: Anorí, Cañadahonda	JN112733[a]	JN112677[a]	JN112606[a]
A. dissimilis	**UFAC 0084**: Brazil: Acre: Senador Guiomard, Fazenda Experimental Catuaba	–	KM598667[f]	KM598699[f]

(*Continued*)

Table 1. (Continued).

Taxon	Voucher and locality	GenBank accession number		
		COI	ND2	RAG1
A. dissimilis	**UFAC 0089**: Brazil: Acre: Senador Guiomard, Fazenda Experimental Catuaba	–	KM598668[f]	KM598700[f]
A. eulaemus	**POE 3162**: Colombia: Valle de Cauca: km 18 on road from Cali to Buenaventura	–	see below[c]	–
A. euskalerriari	**MBLUZ 934**: Venezuela: Zulia: Sierra de Perija, Villa del RosaRío	JN112737[a]	JN112678[a]	JN112610[a]
A. euskalerriari	**MBLUZ 935**: Venezuela: Zulia: Sierra de Perijá, Villa del RosaRío	JN112738[a]	JN112679[a]	JN112611[a]
A. extremus	**USNM 321940**: St Lucia: Castries Quarter	–	AF317065[d]	–
	USNM 321945: St Lucia: Castries Quarter: grounds of Cunard La Toc Hotel	JN112739[a]		JN112612[a]
A. fasciatus	**QCAZ 10192**: Ecuador: Los Ríos: Río Palenque Research Station	KU316033[g]	KU316046[g]	–
A. festae	**QCAZ 6930**: Ecuador: Esmeraldas: San Lorenzo, grounds of Hosteria Tundaloma	JN112740[a]	JN112680[a]	JN112613[a]
A. fitchi	**QCAZ 6742**: Ecuador: Napo: Pacto Sumaco	JN112741[a]	JN112681[a]	JN112614[a]
A. fitchi	**QCAZ 6910**: Ecuador: Tungurahua: Río Verde	JN112742[a]	JN112682[a]	JN112615[a]
A. fraseri	**QCAZ 6862**: Ecuador: Pichincha: Mindo, on road to Mindo Garden at Muyu Mindala Hostal	JN112743[a]	JN112683[a]	JN112616[a]
A. fraseri	**QCAZ 6867**: Ecuador: Esmeraldas: Mache Chindú Reserve, Bilsa Biological Station, Río Ducha	JN112744[a]	JN112684[a]	JN112617[a]
A. frenatus	**JMS 192**: Panama: Chiriquí: near STRI–Fortuna Biological Station	JN112745[a]	–	JN112618[a]
A. frenatus	**MHUA 11519 (MHUA–T 676)**: Colombia: Antioquia: San Luís, Río Claro, El Refugio Natural Reserve	JN112746[a]	JN112685[a]	JN112619[a]
A. gemmosus	**QCAZ 6851**: Ecuador: Pichincha: Mindo, on road from Mariposas de Mindo to Mindo Garden	JN112747[a]	JN112686[a]	JN112620[a]
A. gemmosus	**QCAZ 6884**: Ecuador: Pichincha: El Placer, on road to Conchacato, Río Chisinche	JN112748[a]	JN112687[a]	JN112621[a]
A. ginaelisae	**SMF 89737**: Panama: Chiriqui: Bajo Mono, Sendero La Cascada	JX083225[c]	–	–
A. gorgonae	Unknown voucher: Colombia	–	see below[c]	–
A. griseus	**USNM 321983**: St Vincent: Saint Andrew: Kingston Botanical Gardens	JN112749[a]	AY296176[h]	JN112622[a]
A. heterodermus	**MHUA 11396 (MHUA–T 232)**: Colombia: Caldas: Manizales, Río Blanco	JN112750[a]	JN112689[a]	JN112623[a]
A. heterodermus	**MRC 145**: Colombia: Huila: Palestina, La Guajira, La Riviera Private Reserve	JN112752[a]	JN112688[a]	JN112625[a]
A. huilae	**MRC 146**: Colombia: Huila: Palestina, Jericó, El Silencio Coffee plantation	JN112753[a]	JN112691[a]	JN112626[a]
A. huilae	**MRC 149**: Colombia: Huila: Palestina, Jericó, El Silencio coffee plantation	JN112754[a]	JN112692[a]	JN112627[a]
A. hyacinthogularis sp. nov.	**QCAZ 14135**: Ecuador: Zamora Chinchipe: San Francisco Research Station	–	MG159790*	MG159798*
A. hyacinthogularis sp. nov.	**QCAZ 14136**: Ecuador: Zamora Chinchipe: San Francisco Research Station	–	MG159791*	MG159797*
A. hyacinthogularis sp. nov.	**QCAZ 14137**: Ecuador: Zamora Chinchipe: San Francisco Research Station	–	MG159792*	MG159796*
A. ibanezi	**POE 1966**: Panama: Coclé: El Copé: Parque Omar Torrijos	–	see below[c]	–
A. inderenae	**JMR 3744**: Colombia	JN112755[a]	AY296145[h]	JN112628[a]
A. insignis	**MVUP 2021**: Panama, Chiriquí, Reserva Forestal Fortuna	JN112756[a]	JN112693[a]	–

(*Continued*)

Table 1. (Continued).

Taxon	Voucher and locality	GenBank accession number		
		COI	ND2	RAG1
A. jacare	**MHNLS 17237**: Venezuela: Táchira: Paramo la Negra, on road between Sabana Grande and La Grita, La Guacharita	JN112759[a]	JN112695[a]	JN112630[a]
A. jacare	**MHNLS 17870**: Venezuela: Merida: Antonio Pinto Salinas, Santa Cruz de Mora, La Macana	JN112757[a]	JN112694[a]	JN112629[a]
A. kunayalae	**POE 1970**: Panama: Coclé: El Copé: Parque Omar Torrijos	see below[c]	see below[c]	–
A. latifrons	**MHCH 2787**: Panama: Darién: Serrania de Pirre	KP975514[i]	–	–
A. latifrons	**MHCH 2788**: Panama: Emberá–Wounáan: Pavarandó, Camp 3 cerro garra garra	KP975513[i]	–	–
A. latifrons	**POE 3172**: Colombia: Valle de Cauca: trails from Chuchero (near Buenaventura)	see below[c]	KU316036[g]	–
A. lososi sp. nov.	**QCAZ 10173**: Ecuador: Zamora Chinchipe: Romerillos Alto, 26 km N Zamora	MG159788*	MG159793*	–
A. lososi sp. nov.	**QCAZ 14125**: Ecuador: Zamora Chinchipe: San Francisco Research Station	MG159789*	MG159794*	–
A. lososi sp. nov.	**QCAZ 14132**: Ecuador: Zamora Chinchipe: San Francisco Research Station	–	MG159795*	–
A. luciae	**USNM 321960**: St Lucia: Castries: grounds of Cunard La Toc Hotel	JN112760[a]	JN112697[a]	JN112631[a]
A. maculigula	**MHUA 11558 (MHUA–T 705)**: Colombia: Antioquia: Frontino, Cuevas Peñitas, Don Luis property	JN112761[a]	JN112698[a]	JN112632[a]
A. maculigula	**MHUA 11559 (MHUA–T 706)**: Colombia: Antioquia: Frontino, Cuevas Peñitas, Don Luis property	JN112762[a]	JN112699[a]	JN112633[a]
A. maia	**MHCH 2782**: Panama: Guna Yala: from top of Ridge (Yarbir) to camp 2	KP975517[i]	–	–
A. maia	**MHCH 2783**: Panama: Emberá–Wounáan: Bajo pequeño, camp3 Pechito parao	KP975528[i]	–	–
A. microtus	**MVZ 204040**: Costa Rica: Cartago: Refugio Nacional Tapantí	KU316037[g]	AF055947[b]	–
A. nasofrontalis	LOD 1383: Brazil: Espirito Santo: Santa Teresa, Reserva Biológica Augusto Ruschi	–	MF004398[j]	MF004397[j]
A. neblininus	**USNM 322912**: Venezuela: Amazonas: Río Negro, Cerro de la Neblina, 12.5 km NNW of pico Phelps (= pico Neblina)	JN112763[a]	JN112700[a]	JN112634[a]
A. nicefori	**J. Renjifo 2537**	–	AF055948[b]	–
A. orcesi	**QCAZ 9692**: Ecuador: Napo: 2.3 km north of turnoff to Baeza	KU316041[g]	KU316052[g]	–
A. otongae	**QCAZ 11790**: Ecuador: Pichincha: Biological Reserve Otonga.	KJ854221[k]	KJ854207[k]	KJ854214[k]
A. otongae	**QCAZ 11791**: Ecuador: Pichincha: Biological Reserve Otonga	KJ854222[k]	KJ854208[k]	KJ854215[k]
A. parilis	**QCAZ 10178**: Ecuador: Esmeraldas: 4 km west Alto Tambo	KU316043[g]	KU316054[g]	–
A. peraccae	**QCAZ 6869**: Ecuador: Esmeraldas: Mache Chindú Reserve, Bilsa Biological Station	JN112764[a]	JN112701[a]	JN112635[a]
A. peraccae	**QCAZ 6879**: Ecuador: Pichincha: La Unión del Toachi, Centro de Interpretación Ambiental Otongachi, Otonga Foundation	JN112765[a]	JN112702[a]	JN112636[a]
A. philopunctatus	**Galo 132**: Brazil: Amazonas: Presidente Figueiredo	KM598669[f]	–	KM598701[f]
A. philopunctatus	**MTR 21474**: Brazil: Amazonas: Manaus	KM598670[f]	–	KM598702[f]
A. phyllorhinus	**MTR 977628**: Brazil: Mato Grosso: Colniza	KM598674[f]	–	KM598706[f]
A. phyllorhinus	**MTR 977664**: Brazil: Mato Grosso: Colniza	KM598675[f]	–	KM598707[f]

(*Continued*)

Table 1. (Continued).

Taxon	Voucher and locality	GenBank accession number		
		COI	ND2	RAG1
A. podocarpus	**QCAZ 6047**: Ecuador: Loja: Parque Nacional Podocarpus, Romerillos Alto	JN112780[a]	JN112703[a]	–
A. poecilopus	**SMF 9711**: Panama: Darién: Rio Cana, Cana field station, Chimenea trail	KP975512[i]	–	–
A. poei	**QCAZ 3444**: Ecuador: Bolívar: Telimbela	KJ854223[k]	KJ854209[k]	KJ854216[k]
A. poei	**QCAZ 3448**: Ecuador: Bolívar: Telimbela	KJ854225[k]	KJ854211[k]	KJ854217[k]
A. princeps	**MRC 135**: Colombia: casildae có: Bajo Baudó, Pilizá	JN112768[a]	JN112706[a]	JN112639[a]
A. princeps	**QCAZ 6868**: Ecuador: Esmeraldas: Mache Chindu Reserve, Bilsa Biological Station	JN112766[a]	JN112704[a]	JN112637[a]
A. princeps	**QCAZ 6892**: Ecuador: Los Ríos: Centro Científico Río Palenque	JN112767[a]	JN112705[a]	JN112638[a]
A. proboscis	**QCAZ 9735**: Ecuador: Pichincha: Mindo	see below[c]	see below[c]	–
A. pseudotigrinus	**MTR 34789**: Brazil: Espirito Santo: Santa Teresa, Reserva Biológica Augusto Ruschi	–	MF004399[j]	MF004396[j]
A. punctatus	**MHNLS 17698**: Venezuela: Amazonas: Atures, 12 km south of Puerto Ayacucho	JN112769[a]	JN112707[a]	JN112640[a]
A. punctatus	**MPEG 24758**: Brazil: Pará: Oriximina, Porto Trombetas	–	KM598678[f]	KM598710[f]
A. purpurescens	**MRC 123**: Colombia: Chocó: Quibdó, Tutunendo	JN112730[a]	JN112674[a]	JN112603[a]
A. purpurescens	**MRC 134**: Colombia: Chocó: Bajo Baudó, Pilizá	JN112731[a]	JN112675[a]	JN112604[a]
A. richardii	**USNM 321792**: Grenada: St George: SW coast of Grand Anse Bay	JN112770[a]	JN112708[a]	JN112641[a]
A. roquet	**USNM 321824–5**: France: Martinique: Le Marin, Anse Mitan	JN112771[a]	JN112709[a]	JN112642[a]
A. soinii	**QCAZ10163**: Ecuador: Loja: Zamora – Loja road	see below[c]	KU316058[g]	–
A. sp. 1	**MHUA 11455**: Colombia: Santander: San Vicente de Chucurí, Centro, La Cartagena stream, El Castillo property	JN112778[a]	JN112715[a]	JN112649[a]
A. sp. 2	**MHUA 11562 (MHUA–T 704)**: Colombia: Antioquia: Anorí, El Roble, La Forzosa forest	JN112779[a]	JN112716[a]	JN112648[a]
A. tigrinus	**MHNLS 17863**: Venezuela: Vargas: on road Junquito–Colonia Tovar	JN112772[a]	JN112710[a]	JN112643[a]
A. transversalis	**MTR 28583**: Brazil: Acre: Senador Guiomard, Fazenda Experimental Catuaba	–	KM598688[f]	KM598722[f]
A. transversalis	**QCAZ 5936**: Ecuador: Orellana: Yasuní Scientific Station	JN112773[a]	JN112711[a]	JN112644[a]
A. trinitatis	**USNM 321992**: St. Vincent: St George: Villa town	JN112774[a]	AY296204[h]	JN112645[a]
A. tropidogaster	**MHCH 2646**: Panama: Darién: Laguna de Matusagarati, Aguas Calientes	–	KP975526[i]	–
A. vanzolinii	**QCAZ 6926**: Ecuador: Sucumbíos: Santa Bárbara, La Bretaña sector, on road between El Playón and El Carmelo	JN112775[a]	JN112712[a]	–
A. ventrimaculatus	**MRC 091**: Colombia: Valle del Cauca: La Cumbre, Chicoral, La Minga property	JN112776[a]	JN112713[a]	JN112646[a]
A. ventrimaculatus	**MRC 112**: Colombia: Valle del Cauca: on road to San Antonio, Television Tower	JN112777[a]	JN112714[a]	JN112647[a]
A. williamsmittermeierorum	**QCAZ 10170**: Ecuador: Morona Santiago: close to Plan de Milagro	see below[c]	see below[c]	–
Outgroups				
A. bimaculatus	**USNM 321912**: St Christopher: Trinity Palmetto Point: east of Boyd's	JN112781[a]	AF055930[b]	JN112650[a]
A. capito	**SMF 97094**: Panama: Guna Yala: Ridge, Yarbir	KP975519[i]	–	–

(*Continued*)

Table 1. (Continued).

Taxon	Voucher and locality	GenBank accession number		
		COI	ND2	RAG1
A. cupreus	**JMS 71**: Costa Rica: Guanacaste: OTS–Palo Verde Biological Station	JN112782[a]	JN112717[a]	JN112651[a]
A. cuvieri	**REG 2104**: Puerto Rico: Arecibo: Reserva Foresta Cambalache	JN112783[a]	AF055973[b]	JN112652[a]
A. equestris	**USNM 337647**: Cuba: La Habana: Playa Jibacoa	JN112784[a]	AF055978[b]	JN112653[a]
A. limifrons	**SMF 97099**: Panama: Comarca Ngäbe–Bugle: Isla Escudo de Veraguas	KP975523[i]	–	–
A. lucius	**USNM 498030**: Cuba: Cienfuegos: Cienfuegos Botanical Garden	JN112785[a]	AF055962[b]	JN112654[a]
A. marcanoi	**JBL 455**: Dominican Republic: Peravia: between Baní and El Recodo	JN112786[a]	AF055955[b]	JN112655[a]
A. occultus	**USNM 321891**: Puerto Rico: Humacao: Caribbean National Forest, Sierra de Luquillo, 13.3km south of Palmer (= Mameyes)	JN112787[a]	AF055976[b]	JN112656[a]
A. sagrei	**MVZ 217371**: United Kingdom: Cayman Islands: Little Cayman, McCoy's Lodge	–	–	JN112657[a]
A. smaragdinus	**USNM 549537**: The Bahamas: South Bimini Island: vicinity of airport	JN112788[a]	JN112718[a]	JN112658[a]
Polychrus marmoratus	**SNOMNH 36693**: Brazil: Pará: approx. 101 km south and 18 km east Santarem, Agropecuaria Treviso LTDA	JN112789[a]	AF528738[l]	JN112659[a]
Pristidactylus scapulatus	**PT 4810**: Argentina: Río Negro, 2 km south Esperanza	JN112790[a]	AF528732[l]	JN112660[a]
Urostrophus gallardoi	**FBC 0036**: Argentina: Córdoba, aprox. 2 km south L. V. Marsilla	JN112791[a]	AF528735[l]	JN112661[a]

[a]Castañeda and de Queiroz (2011)
[b]Jackman et al. (1999)
[c]Poe et al. (2017); sequences available at stevenpoe.net
[d]Creer et al. (2001)
[e]Nicholson et al. (2005)
[f]Prates et al. (2015)
[g]Poe et al. (2015)
[h]Harmon et al. (2003)
[i]Batista et al. (2015)
[j]Prates et al. (2017)
[k]Ayala–Varela et al. (2014)
[l]Schulte et al. (2003)
Museum abbreviations are LSUMZ, Louisiana Museum of Natural History, Louisiana, USA; MBLUZ, Museo de Biología de La Universidad del Zulia, Maracaibo, Venezuela; MHCH, Museo Herpetológico de Chiriquí, David, Chiriquí, Panama; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; MHUA, Museo de Herpetología, Universidad de Antioquia, Medellín, Colombia; MHUA–T, Colección de Tejidos Museo de Herpetología, Universidad de Antioquia, Medellín, Colombia; MPEG, Museu Paraense Emilio Goeldi, Belém, Brazil; MVUP, Museo de Vertebrados, Universidad de Panamá, Panama; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley, California, USA; SNOMNH, Sam Noble Oklahoma Museum of Natural History, Norman, USA; QCAZ, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; SMF, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany; UFAC, Universidade Federal do Acre, Río Branco, Brazil; USNM, National Museum of Natural History, Washinghton D.C., USA. Field numbers are FBC, PT, Félix B. Cruz; JBL, Jonathan B. Losos; JMR, Juan Manuel Renjifo; JMS, Jay M. Savage; KEN, Kirsten E. Nicholson; MRC, María del Rosario Castañeda; MTR, Miguel Trefaut Rodrigues; POE, Steve Poe; REG, Richard E. Glor.

one with all tRNAs, and one with the *Ol*. The optimal partition strategy along with the corresponding models of evolution were obtained in PartitionFinder 1.1.1 (Lanfear et al. 2012) under the Bayesian information criterion.

Phylogenetic relationships were assessed under a Bayesian approach in MrBayes 3.2.0 (Ronquist and Huelsenbeck 2003). Four independent analyses were performed to reduce the chance of converging on a local optimum. Each analysis consisted of 10 million generations and four Markov chains with default heating values. Trees were sampled every 1000 generations resulting in 10,000 saved trees per analysis. Stationarity was confirmed by plotting the – ln *L* per generation in the program Tracer 1.6 (Rambaut et al. 2013). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman and Rubin 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. Adequacy of mixing was assessed by examining the acceptance rates for the parameters in MrBayes and the effective sample sizes in Tracer. After analysing convergence and mixing, 25% of the trees were discarded as 'burn-in' from each run. We then confirmed that the four analyses reached stationarity at a similar likelihood score and that the topologies were similar, and used the resultant 36,000 trees to calculate posterior probabilities (PP) for each bipartition on a Maximum Clade Credibility Tree in TreeAnnotator (Rambaut and Drummond 2016).

We calculated *ND2* genetic distances among all species in the clade *Dactyloa* included in this study using MEGA7 (Kumar et al. 2016) under the Maximum Composite Likelihood model (Tamura et al. 2004). The analysis involved 92 nucleotide sequences, and all positions containing gaps and missing data were eliminated.

Results and Discussion

Taxonomy

The taxonomic conclusions of this study are based on the study of external morphological features and colour pattern, as well as inferred phylogenetic divergences. We consider this information as species delimitation criteria following the evolutionary species concept (Simpson 1951, 1961; de Queiroz 1998, 2007).

Anolis hyacinthogularis sp. nov.
(Figures 1, 2)

Proposed standard English name: Blue dewlap anole
Proposed standard Spanish name: Anolis de saco azul

Holotype

QCAZ 14136 (Figure 1), adult male, Ecuador, Provincia Zamora Chinchipe, San Francisco Research Station, 03.971°S, 79.082°W, WGS84, 1441 m, 13 September 2015, collected by Andrea Narváez and Leonardo Cedeño.

Paratypes (4)

ECUADOR: Provincia Zamora Chinchipe: QCAZ 14135, juvenile female, same data as holotype, except 3.973°S, 79.078°W, 1823 m, 9 September 2015; QCAZ 14137, juvenile male, same data as holotype, except 3.973°S, 79.088°W, 1845 m, 15 September 2015; QCAZ 14450–51, adult males, San Francisco Research Station, 03.972°S, 79.084°W, 1919 m, 15 January 2016, collected by Fernando Ayala, Steven Poe and Chris Anderson.

Figure 1. Head of the holotype (QCAZ 14136) of *Anolis hyacinthogularis* sp. nov. in dorsal (top), lateral (middle), and ventral (bottom) views. Photographs by O. Torres-Carvajal. Scale bar = 5 mm.

Diagnosis

Anolis hyacinthogularis differs from other species of *Anolis* (clade *Dactyloa*) from Ecuador and Peru, except *Anolis dissimilis*, *Anolis festae* and *Anolis nigrolineatus*, by possessing a long tail, small size (SVL < 60 mm), short dewlap extending to the level of the arms, smooth head scales and by lacking a rostral proboscis. It differs from *A. festae* and *A. nigrolineatus* in lacking a black ventral stripe on the dewlap in males (dewlap stripe present in these species). *Anolis hyacinthogularis* is distinguished from *A. dissimilis* by having sky blue dewlap skin with horizontal rows of whitish cream scales agglomerated at the base in males (white to cream dewlap in males of *A. dissimilis*); seven or eight supralabials from snout to below centre of eye (11 in *A. dissimilis*), and a shorter head.

The *ND2* distance value (0.274) between *A. hyacinthogularis* and its closest relative *Anolis calimae* is comparable to DNA divergences between other species pairs of *Anolis* (Supplemental material).

Description of holotype (scores for paratypes in parentheses)

SVL 56.8 mm (56.3–56.9 mm); tail length 129.8 mm (132.0–142.0 mm); head length 14.9 mm (15.3–15.5 mm); head width 7.1 mm (7.0–7.4 mm); head height 6.6 mm (6.4–6.6 mm); humerus length 7.2 mm (6.5–7.2 mm); ulna length 5.8 mm (5.3–6.0 mm); femur length 10.7 mm (10.9–11.8 mm); tibia length 9.1 mm (8.3–9.7 mm); dewlap fold length 15.2 mm (14.2–14.5 mm); dewlap height 8.3 mm (7.1–7.8 mm); interparietal length 1.6 mm (1.5–1.7 mm); ear opening maximum length 0.6 mm (0.4 mm); snout length 7.0 mm (7.0–7.2 mm); interorbital distance 2.4 mm (2.5 mm).

Head scales smooth (smooth to rugose) on frontal region and on supraocular disc; 7 (6–9) scales between second canthals; 4 (6) scales, circumnasals included, bordering the rostral posteriorly; circumnasal in contact with rostral; supraorbital semicircles separated by 2 (3) scales; supraocular disc with one (2) enlarged scale; one short and elongate superciliary followed by a series of small scales; 4 (3–5) loreals; 30–37 (21–24) loreal scales; interparietal larger than ear opening, in contact with semicircles anteriorly; suboculars in contact with supralabials; 8 (7) supralabials counted from rostral to a point below centre of eye; 2 (4) postmentals; 4–5 enlarged sublabials in contact with infralabials.

Nuchal and dorsal crest absent; vertebral scales similar in size to adjacent scales; dorsal scales slightly keeled; 10 (9) mid-dorsal scales in a longitudinal segment representing 5% of SVL; flank scales homogeneous; ventral scales larger than dorsals, smooth, subimbricate and arranged in transverse rows; seven midventral scales in a longitudinal segment representing 5% of SVL.

Toepads overlapping the first phalanx in all toes; 17 (16) lamellae under third and fourth phalanges of fourth toe (counted in the manner of Williams et al. 1995); supradigital scales multicarinate; tail weakly compressed, with a single row of mid-dorsal scales not forming crest; enlarged postcloacal scales present in male specimens, absent in females.

Nuchal and dorsal folds absent in both sexes; dewlap small, extending posteriorly to fore limbs (also present in juvenile female); dewlap with six longitudinal single rows of scales similar in size to ventrals, separated by naked skin.

Variation in morphological characters in *A. hyacinthogularis* is presented in Table 2.

Colour in life

Holotype (Figure 2(a,b,g)): head, body, limbs and tail brown (background colour green before manipulation), with dark brown dots and flecks; lateral cream band extending from the lower portion of the head (loreal, supralabial and infralabial areas) to shoulder; dark brown lateral band (faint anteriorly) extending from suboculars to a point posterior to fore limbs; ventral scales cream, with brownish spots; six cream bands extend anterodorsally from ventral region onto flanks; tail with alternating dark and light brown bands; iris copper; ocular ring yellowish; dewlap skin sky blue, with horizontal rows of whitish cream scales agglomerated at the base.

Juvenile female (QCAZ 14135, Figure 2(c,d)): dorsum and head greenish brown; light brown mid-dorsal, longitudinal stripe, delimited by a parallel dark stripe on each side; supralabial and loreal areas light green; frontoparietal area brownish, with a cream

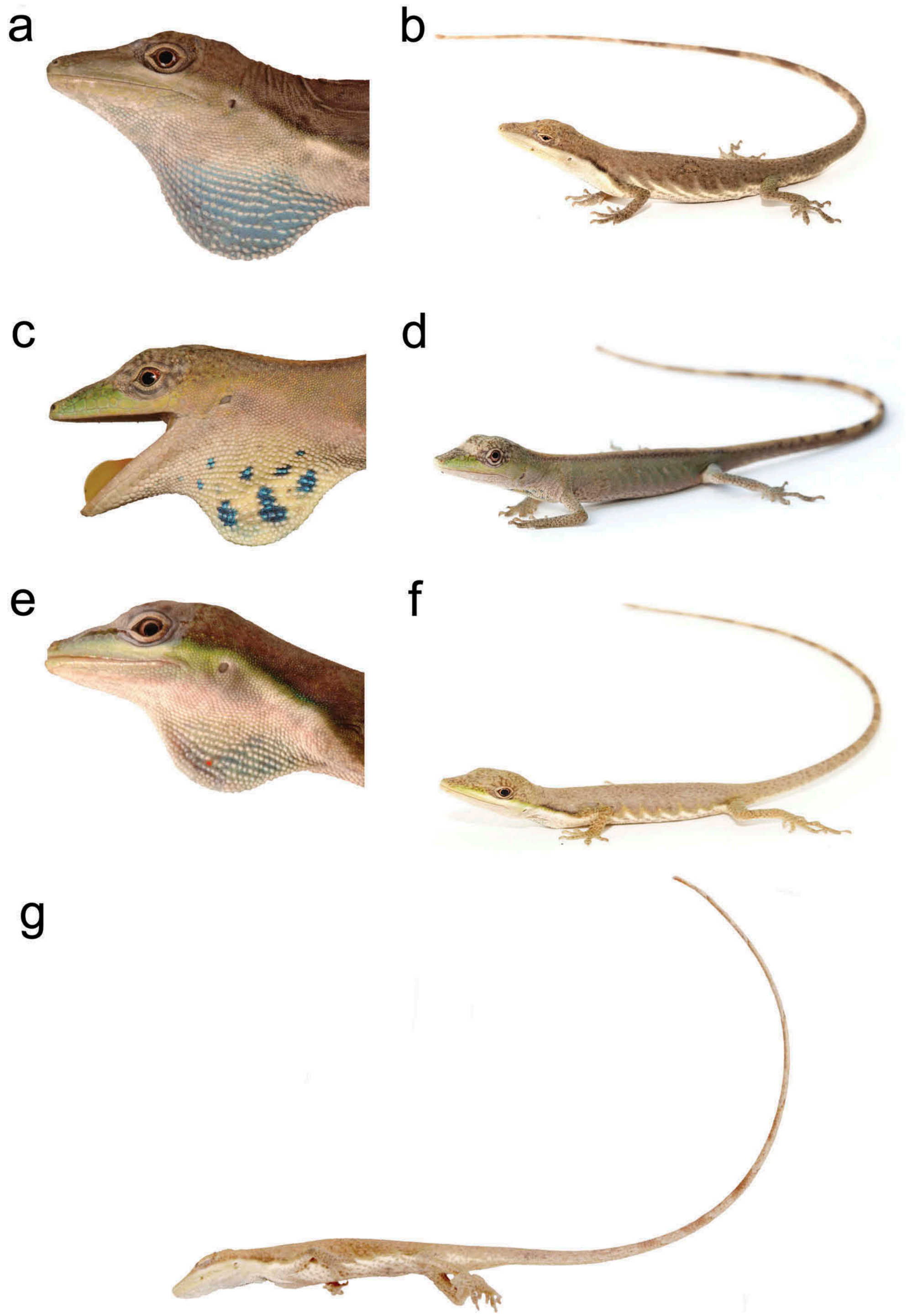

Figure 2. *Anolis hyacinthogularis* sp. nov. Holotype, adult male (SVL = 56.8 mm, QCAZ 14136, a, b, g), juvenile female (SVL = 36.5 mm, QCAZ 14135, c, d) and juvenile male (SVL = 34.6 mm, QCAZ 14137, e, f). Photographs by O. Torres-Carvajal (a, b, e, f, g) and A. Narváez (c, d).

transverse band; iris brownish copper; ocular ring cream; dewlap pale yellow, with irregular metallic blue (teal) patches; tongue yellow.

Juvenile male (QCAZ14137, Figure 2(e,f)): dorsum and head light brown with dark brown dots; black spots along the mid-dorsal portion of the body and legs; longitudinal greenish band extending from snout to shoulder, darker on neck; dewlap colour pattern similar to holotype. Some individuals had a green background colour.

Gular sac radiance

We obtained colour data from one female and four males measured *in vivo* on the day of collection. In males, the regions close to the head and the base are brighter than the edge, the section close to the abdomen, and the centre, which are more bluish (Figure 3). In males, radiation peaked on average at 500 nm (sky blue), increasing gradually from 400 nm to 570 nm, and decreasing slightly afterwards. Unlike males, the female exhibited the highest peak of reflectance (50%) at longer wavelengths, showing also a high reflectance (~40%) at wavelength values > 500 nm (Figure 3). The gular sac in both males and the female exhibited UV reflection (i.e. wavelength < 400 nm) in all measured areas.

Distribution and ecology

Anolis hyacinthogularis occurs on the Amazonian slopes of the Cordillera Real in southern Ecuador, Provincia Zamora Chinchipe, between 1440 and 1845 m (Figure 4). It is known from the upper basin of the Zamora river (Atlantic drainage) in evergreen lower montane forest (Homeier et al. 2008). This area has suffered from dramatic deforestation (Tapia-Armijos et al. 2015). All individuals of *A. hyacinthogularis* were collected at San Francisco Research Station, which lies near Podocarpus National Park. These collections within the park suggest that at least some populations of this species are well protected.

The new species occurs in sympatry with *Anolis lososi* sp. nov. and *Anolis soinii* at the type locality, where it shares the same microhabitat (sub-canopy twigs) with *A. lososi*. *Anolis soinii* has been observed to occupy open or partially open areas and lower, leafier perches such as ferns. All specimens of the new species were found sleeping at night between 20:00h and 02:00h on steep slopes of secondary and primary forest. Individuals were found perching on twigs or narrow leaves from 2 to 4 m above the ground. The smallest individual QCAZ 14137 (SVL = 36.64 mm; tail length = 63.19 mm) was collected on 15 September 2015.

Etymology

The specific epithet *hyacinthogularis* alludes to the blue dewlap of the male and derives from the Latin words *hyacinthus* (=blue), and *gula* (=throat).

Anolis lososi sp. nov.
(Figures 5, 6)

Proposed standard English name: Losos's anole
Proposed standard Spanish name: Anolis de Losos

Table 2. Summary of lepidosis, measurements (mm) and colour characters of *Anolis hyacinthogularis* sp. nov. and *Anolis lososi* sp. nov.

Character	*A. hyacinthogularis* sp. nov.	*A. lososi* sp. nov.
Maximum SVL in males	57	61
Maximum SVL in females	–	60
Ear height/head length	0.03–0.04 (3) 0.03	0.08–0.11 (4) 0.09
Tail length/SVL	2.28–2.50 (3) 2.37	1.21–1.31 (5) 1.25
Scales between second canthals	6–9 (3) 7.2	4–6 (7) 5.14
Postrostrals	4–6 (3) 4.6	3–6 (7) 4.57
Loreals	21–37 (3) 27.3	5–15 (7) 9.86
Supralabials from rostral to below centre of eye	7–8 (3) 7.7	5–8 (7) 6.43
Postmentals	2–4 (3) 2.5	2–4 (7) 3.57
Lamellae under phalanges III–IV of fourth toe	16–17 (3) 16.3	18–21 (7) 19.71
Length of dewlap in males/SVL	0.25–0.27 (3) 0.26	0.43–0.48 (4) 0.46
Length of dewlap in females/SVL	0.26 (1)*	0.35 (1)
Enlarged mid-dorsal crest	absent	absent
Dewlap colour in males	Sky blue skin with horizontal rows of whitish cream scales agglomerated at the base	Skin and scales white or cream
Dewlap colour in females	Pale yellow skin with irregular metallic blue (teal) patches	Bright yellow with round black blotches; scales pale orange
Throat colour	Pinkish, edges of mouth white	Black, edges of mouth bright yellow-orange

*juvenile.
Range and sample size (in parentheses) followed by mean are given.

Holotype

QCAZ 10173 (Figures 5, 6), adult male, Ecuador, Provincia Zamora Chinchipe, Romerillos Alto, 4.227°S, 78.939°W, WGS84, 1550 m, 18 December 2009, collected by Steven Poe, Levi Gray, Julian Davis, and Fernando Ayala.

Paratypes (23)

ECUADOR: Provincia Zamora Chinchipe: QCAZ 6850, San Francisco Research Station, 3.971°S, 79.078°W, 1970 m, 2 April 2005, collected by Kristin Roos, Alban Pfeiffer, Andy Fries, Ulf Soltau and Florian Werner; QCAZ 10171–72, road from Zamora to Loja, 3.970°S, 79.063°W, 1706 m, 17 December 2009, collected by Steven Poe, Levi Gray, Julian Davis and Fernando Ayala; QCAZ 10174–75, same collection data as holotype; QCAZ 14125, San Francisco Research Station, 3.973°S, 79.077°W, 1872 m, 9 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14126, San Francisco Research Station, 3.974°S, 79.078°W, 1883 m, 10 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14128, San Francisco Research Station, 3.973°S, 79.078°W, 1821 m, 11 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14129, San Francisco Research Station, 3.972°S, 79.077°W, 1912 m, 11 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14130, San Francisco Research Station, 3.972°S, 79.079°W, 1883 m, 11 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14132, San Francisco Research Station, 3.973°S, 79.078°W, 1857 m, 15 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14133, San Francisco Research Station, 3.973°S, 79.077°W, 1878 m, 15 September 2015, collected by Andrea Narváez and Leonardo Cedeño; QCAZ 14335–336, San Francisco Research Station, canal path, 3.972°S, 79.075°W, 1898 m, 12

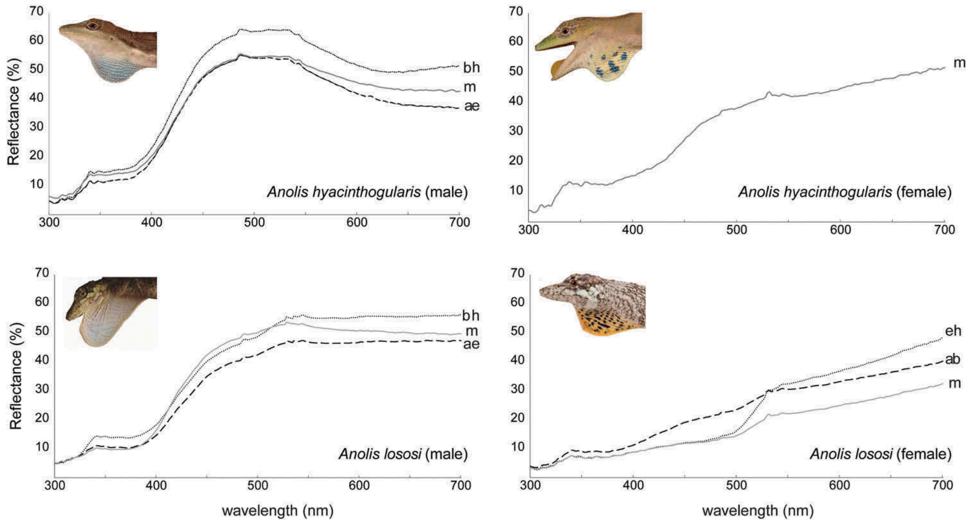

Figure 3. Radiance of the gular sac in males and females of *Anolis hyacinthogularis* sp. nov. and *Anolis lososi* sp. nov. Measured regions are gular sac base 'b', centre 'm', edge 'e', as well as regions close to the head 'h' and close to the abdomen 'a'. Photographs by A. Narváez and M. J. Quiroz.

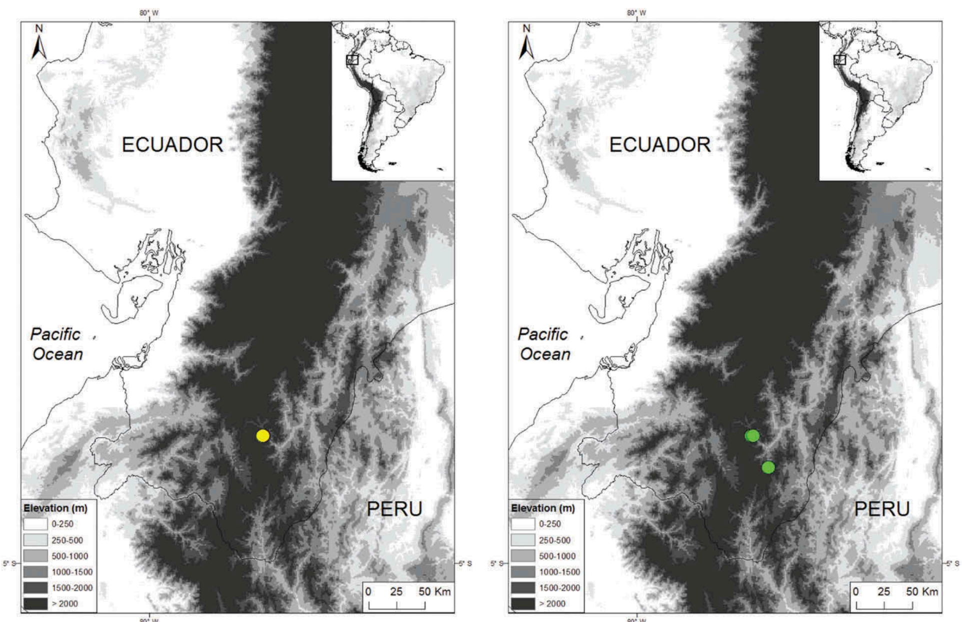

Figure 4. Distribution of *Anolis hyacinthogularis* sp. nov. (left) and *Anolis lososi* sp. nov. (right) in Ecuador.

January 2016, collected by Omar Torres–Carvajal, Diego A. Paucar and reptile class students; QCAZ 14337, San Francisco Research Station, Tarabita's path, 3.972°S, 79.079° W, 1848 m, 14 January 2016, collected by Fernando Ayala, Steven Poe and Chris Anderson; QCAZ 14434–439, San Francisco Research Station, 3.971°S, 79.079°W, 1789 m, 12 January 2016, collected by Fernando Ayala, Steven Poe and Chris Anderson; QCAZ 14611, San Francisco Research Station, 3.973°S, 79.077°W, 1872 m, 14 September 2015, collected by Andrea Narváez and Leonardo Cedeño; FHGO 1756, 3.6 km southwest from La Pituca, 4.156°S, 78.974°W, 1820 m, 24 April 1998, collected by Diego Almeida-Reinoso and Fernando Nogales-Sornosa.

Diagnosis

Anolis lososi differs from other species of *Anolis* (clade *Dactyloa*) from Ecuador and Peru, except *Anolis orcesi*, *Anolis peruensis* and *Anolis williamsmittermeierorum*, in having large smooth head scales, homogeneous lateral lepidosis, short limbs, short tail, and in lacking a rostral proboscis. *Anolis lososi* differs from *A. orcesi*, *A. peruensis* and *A. williamsmittermeierorum* in having differently coloured male and female dewlaps (*A. orcesi* male: yellow with greenish blue at base, female: orange; *A. peruensis* male: solid yellow, female: black; *A. williamsmittermeierorum* male: tan with peach-orange distal edge, female: black and white; *A. lososi* male: white, female: black and orange). *Anolis lososi*, *A. peruensis* and *A. williamsmittermeierorum* lack a vertebral crest (present in *A. orcesi*). *Anolis lososi* and *A. williamsmittermeierorum* have a black throat with bright yellow-orange mouth edges (grey in *A. peruensis* and black in *A. orcesi*).

Anolis lososi is most similar morphologically to *A. williamsmittermeierorum* in lepidosis. It can be further distinguished from *A. williamsmittermeierorum* in having a longer dewlap fold and more lamellae under phalanges III–IV of fourth toe (Table 3).

Finally, although the *ND2* genetic distance between *A. lososi* and its closest relative *A. williamsmittermeierorum* is relatively low (0.108), it is comparable to DNA divergences between other inarguable species pairs, such as *Anolis microtus* versus *Anolis insignis* (0.100) and *Anolis peraccae* versus *Anolis anchicayae* (0.107) (Figure 7; Supplemental material).

Description of holotype (scores for paratypes in parentheses)

SVL 61.4 mm (55.1–59.8 mm); tail length 77.2 mm (66.5–78.2 mm); head length 16.7 mm (14.0–16.7 mm); head width 8.5 mm (7.8–9.4 mm); head height 7.4 mm (7.1–7.8 mm); humerus length 8.4 mm (7.8–9.5 mm); ulna length 7.9 mm (5.3–7.9 mm); femur length 10.3 mm (9.6–10.6 mm); tibia length 9.7 mm (7.6–9.7 mm); dewlap length 29.1 mm (20.8–29.1 mm); dewlap height 13.4 mm (6.8–13.4 mm); interparietal length 2.2 mm (1.8–2.3 mm); ear opening vertical length 1.5 mm (1.3–1.5 mm); snout length 7.7 mm (7.0–7.7 mm); interorbital distance 2.1 (2.1–2.5 mm).

Head scales smooth (smooth to rugose); 4 (4 – 6) scales between second canthals; 6 (3 – 6) scales bordering the rostral posteriorly; circumnasal in contact with rostral (in contact or separated by one scale); supraorbital semicircles in contact; supraocular disc with 3 (3 – 5) abruptly enlarged scales; one short and rectangular superciliary followed by quadrangular scales (or small scales); 2 (2 – 3) loreal rows; 5 (5–15) loreal scales; interparietal smaller (smaller to similarly sized) than ear opening, in contact (separated by two small scales) with semicircles anteriorly; suboculars in contact with supralabials; 7 (6 – 8) supralabials counted up to a point below centre of eye; 2 (2 – 4) postmentals; 5 (2 – 5) enlarged sublabials in contact with infralabials.

Low nuchal crest formed by conical scales; low body crest formed by conical scales alternating with smooth scales (crest present in adults of both sexes); dorsal scales

Figure 5. Head of the holotype (QCAZ 10173) of *Anolis lososi* sp. nov. in dorsal (top), lateral (middle), and ventral (bottom) views. Photographs by V. Chasiluisa. Scale bar = 5 mm.

smooth (smooth or swollen); 10 (7 – 9) mid-dorsal scales in a longitudinal segment representing 5% of SVL; flank scales more or less barely separated by skin; ventral scales similar in size to dorsals (ventrals larger than dorsals or similarly sized), smooth,

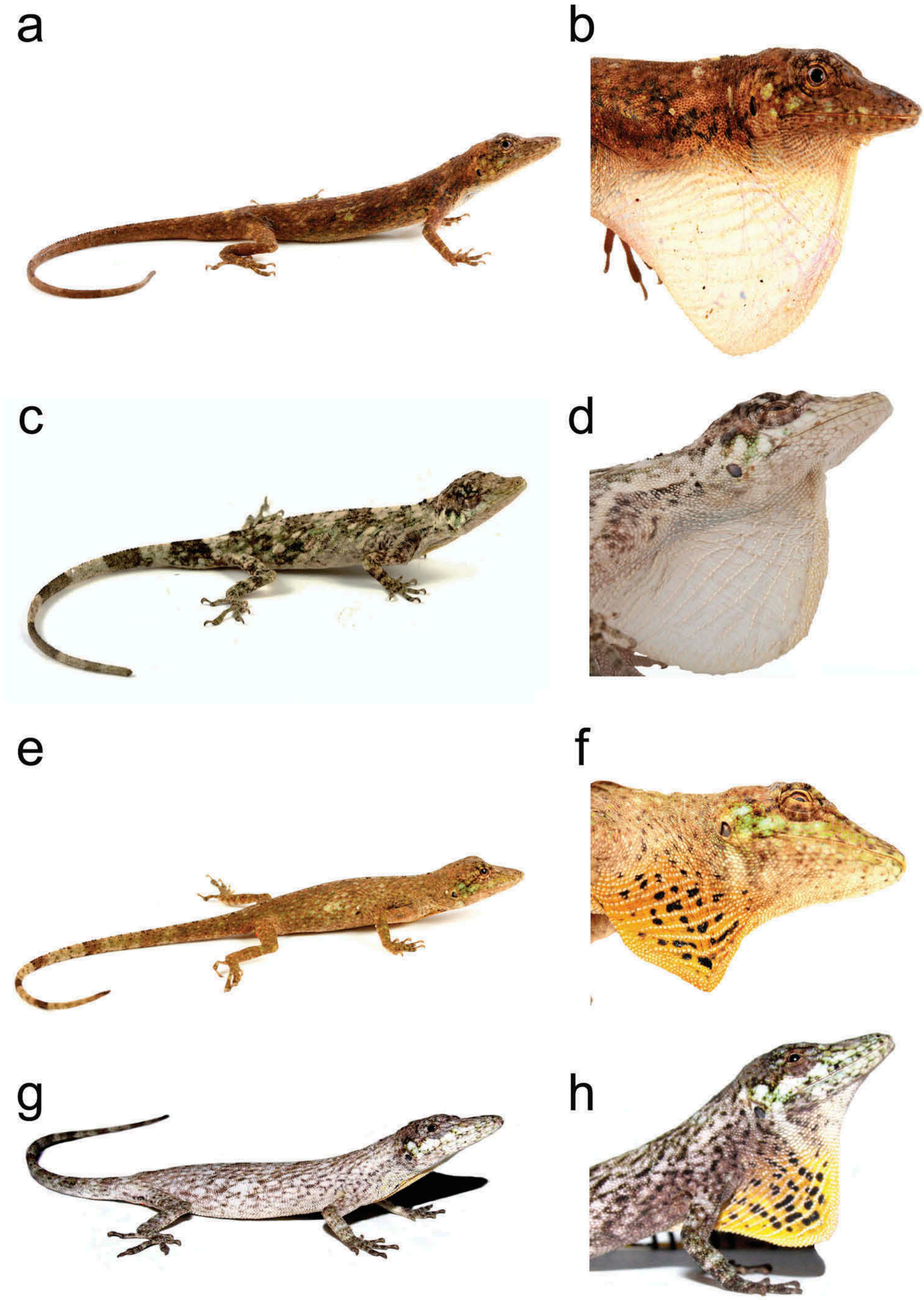

Figure 6. *Anolis lososi* sp. nov. Holotype, adult male (SVL = 61.4 mm, QCAZ 10173, a, b), adult male (SVL = 55.1 mm, QCAZ 10171, c, d), subadult female (SVL = 45.0 mm, QCAZ 10175, e, f), and adult female (SVL = 59.8 mm, QCAZ 10172, g, h). Photographs by O. Torres-Carvajal (a, b, e, f); F. Ayala (c, d, g, h).

imbricate (juxtaposed or subimbricate) and arranged in transverse rows; 8 (6 – 8) midventral scales in a longitudinal segment representing 5% of SVL.

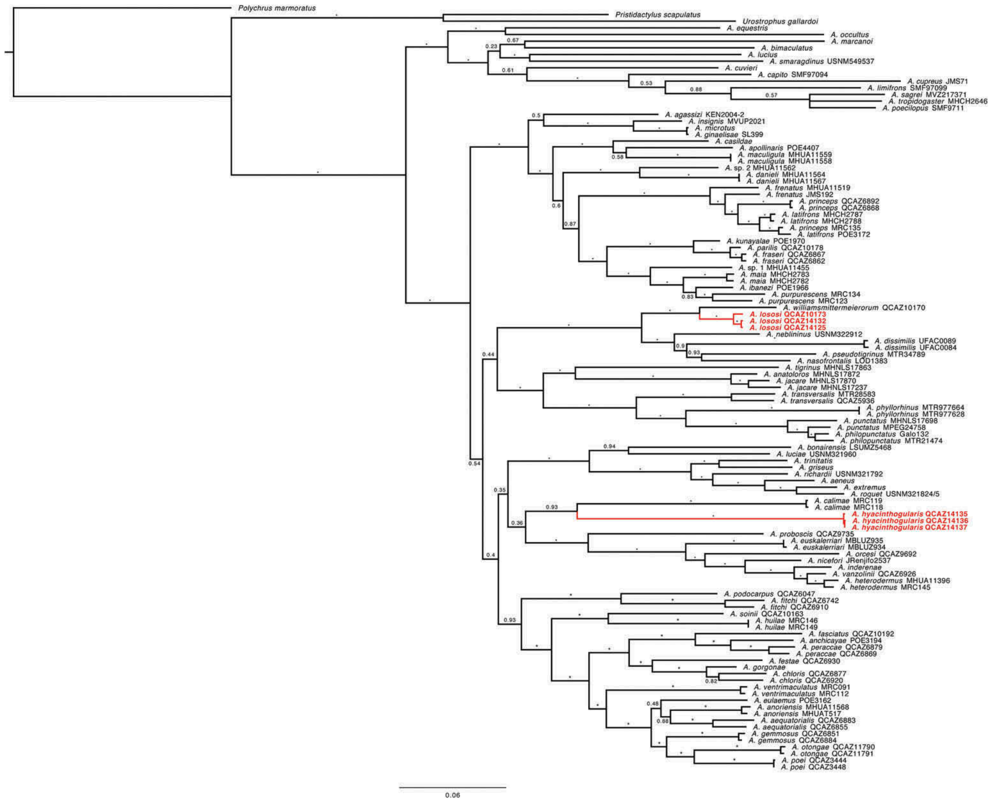

Figure 7. Phylogeny of Dactyloa including *Anolis hyacinthogularis* sp. nov. and *Anolis lososi* sp. nov. Maximum clade credibility tree obtained from a Bayesian analysis of 114 specimens, two mitochondrial genes (*COI, ND2*) and one nuclear gene (*RAG1*). Numbers above branches correspond to Bayesian posterior probability (PP) values; asterisks represent PP ≥ 0.95. GenBank accession numbers along with locality data are presented in Table 1 for all specimens included in this tree.

Toepads overlapping the first phalanx in all toes; 20 (18 – 20) lamellae under third and fourth phalanges of fourth toe; supradigitals smooth; tail weakly compressed, with a single row of mid-dorsal scales forming a serrate crest; enlarged postcloacal scales present (absent in females).

Nuchal and dorsal folds absent in both sexes; dewlap large, extending posteriorly behind fore limbs (same but slightly smaller in females), with six longitudinal single rows of scales similar in size to ventrals, separated by naked skin.

Variation in morphological characters in *A. lososi* is presented in Table 2.

Colour in life

Holotype (Figure 6(a,b); adapted from colour photos of stressed specimen): head, body, limbs and tail with brown, yellow and green marks giving a lichenous appearance; supralabials and infralabials with a dark brown speck each; light band extending from tympanum to axilla; body with four broad transverse dark bands from shoulder to sacrum, as well as reticulating brown lines and small black spots mid-dorsally; ventral surface of head, body, limbs and tail cream with a few brown dots; limbs with narrow transverse bands formed by yellow dots; tail with dark brown transverse bands; iris almond brown; dewlap skin and scales cream.

Adult male QCAZ 10171 (Figure 6(c,d), adapted from colour photos): general colour pattern similar but lighter than holotype; edge of mouth including jaw hinges bright orange; tongue russet brown. Several male specimens had pale blue apicogorgetal and apicosternal regions.

Adult female QCAZ 10175 (Figure 5(e,f); adapted from colour photos): head, body, limbs and tail pale dark tan (pale green lichenous appearance); head flanks with a blotch anteriorly to the tympanum light sap greenish grey; limbs with narrow transverse bands formed by dark olive dots; tail with dark brown transverse bands; body flanks with yellowish grey dots; ventral surface of head, body, limbs and tail whitish cream with dots

Table 3. Summary of lepidosis, measurements (mm) and colour patterns of *Anolis lososi* sp. nov. and *Anolis williamsmittermeierorum*.

Character	*A. williamsmittermeierorum*	*A. lososi* sp. nov.	*t*-value	*p*
Scales between second canthals	3–6 (7) 5.29 ± 1.11	4–6 (7) 5.14 ± 0.69	0.29	0.78
Postrostrals	4–7 (6) 5.50 ± 1.05	3–6 (7) 4.57 ± 1.13	1.52	0.16
Loreal rows	2–4 (7) 2.71 ± 0.76	2–3 (7) 2.29 ± 0.49	1.26	0.23
Loreals	9–21 (7) 13.71 ± 3.86	5–15 (7) 9.86 ± 3.24	2.03	0.07
Scales between interparietal and semicircles	0 (7)	0–2 (7) 0.43 ± 0.79	−1.44*	0.20*
Supralabials from rostral to below centre of eye	6–7 (7) 6.57 ± 0.54	5–8 (7) 6.43 ± 0.98	0.34	0.74
Postmentals	4 (7) 4 ± 0	2–4 (7) 3.57 ± 0.79	1.44*	0.20*
Sublabials in contact with infralabials	3–5 (7) 3.86 ± 0.90	2–5 (7) 3.14 ± 1.07	1.35	0.20
Lamellae under phalanges III–IV of fourth toe	17–19 (6) 17.67 ± 0.82	18–21 (7) 19.71 ± 0.95	−4.12	**0.0017**
Mid-dorsals in 5% SVL	7–9 (7) 7.86 ± 0.69	7–10 (6) 8.17 ± 1.17	−0.59	0.57
Midventrals in 5% SVL	6–8 (7) 6.86 ± 0.69	6–8 (6) 7.00 ± 1.10	−0.28*	0.79*
Enlarged mid-dorsal crest scales	Absent	Absent	–	–
Dewlap colour in males	Pale brown skin with orange-peach at edge; white scales	White or milk white skin and scales	–	–
Dewlap colour in females	Dirty white skin with elongate black blotches; white scales	Brilliant yellow skin with round black blotches; pale orange scales	–	–
Throat colour	Black, edges of mouth bright yellow-orange	Black, edges of mouth bright yellow-orange	–	–
Head length	12.70–16.90 (6) 14.67 ± 1.66	14–16.7 (4) 15.50 ± 1.12	−0.87	0.41
Head width	7.50–10.10 (6) 8.75 ± 1.06	7.8–9.4 (4) 8.65 ± 0.68	0.17	0.87
Femur length	9.30–12.30 (5) 10.96 ± 1.36	9–10.60 (4) 9.88 ± 0.72	1.53*	0.17*
Tail length	66–80 (5) 71.40 ± 5.73	66.50–78.20 (4) 73.90 ± 5.30	−0.67	0.52
Interparietal length	1.90–2.70 (6) 2.28 ± 0.33	1.8–2.3 (4) 2.13 ± 0.22	0.83	0.43
Ear height	1–1.70 (6) 1.35 ± 0.27	1.3–1.5 (4) 1.45 ± 0.10	−0.69	0.51
Fourth toe length	7.10–8.50 (6) 7.78 ± 0.69	7.5–8.90 (4) 8.25 ± 0.66	−1.07	0.32
Fourth toe width	1.30–1.60 (5) 1.40 ± 0.12	1.20–1.40 (4) 1.30 ± 0.12	1.25	0.25
Dewlap fold length	15.60–22 (6) 18.60 ± 2.29	20.80–29.10 (4) 25.63 ± 4.03	−3.55	**0.0075**
Snout–vent length	48–65.50 (6) 54.75 ± 6.85	55.10–61.40 (4) 58.93 ± 2.69	−1.14	0.29
Maximum SVL	66	61	–	–

For each quantitative character, the *t*-value and corresponding *p*-value ($p < 0.05$ in bold) are given. Range and sample size (*n*) followed by mean ± standard deviation are given. Asterisks indicate that a *t*-test assuming unequal variances (i.e. $p < 0.05$, Levene test) was performed.

greyish brown; dewlap skin brilliant orange-yellow with round black blotches, appearing jaguar-striped; dewlap scales cream; iris moderate orange.

Gular sac radiance

We obtained and averaged colour data from four females and eight males measured *in vivo* on the day of collection. In males, the gular sac reflected more or less equally all sections of the visible spectrum, featuring cream-white colours – reflectance increased from 400 nm to 500 nm (55%), after which it remained steady (Figure 3). The centre exhibited a slight decrease on reflectance at high wavelength values. The base and region close to the head were brighter than the edge and the section close to the abdomen. In females, reflectance increased steadily with wavelength (Figure 3); orange-yellow patches were measured at the base, edge and in areas closest to the head and abdomen, whereas dark patches were measured at the centre. Males exhibited more UV reflection (i.e. wavelength <400 nm) in all measured areas than females.

Distribution and ecology

Anolis lososi occurs on the Amazonian slopes of the Cordillera Real in southern Ecuador, Provincia Zamora Chinchipe, between 1550 and 1970 m (Figure 4). It is known from the upper basin of the Zamora river (Atlantic drainage) in evergreen lower montane forest (Homeier et al. 2008). This area has suffered from dramatic deforestation (Tapia-Armijos et al. 2015). However, most individuals of *A. lososi* were collected within Podocarpus National Park, which suggests that at least some populations of this species are well protected.

Specimens of *A. lososi* were collected mainly in open areas. At the type locality, they were found along a secondary forest edge near a creek; at the San Francisco Research Station, they were collected along trails and in both primary and secondary forest gaps, and in disturbed areas. All individuals were found at night (19:00h and 24:00h) sleeping horizontally on twigs of bushes and trees, as well as on leaves of arboreal ferns between 2 and 8 m above ground. A male and female (QCAZ 10171–10172) were found together near a river (about 5 m from shore); they were 10 cm away from each other, 2 m above the ground, resting horizontally with their heads toward the distal end of the branch. This species occurs in sympatry with *A. podocarpus* and *A. soinii* at the type locality, and with *A. soinii* and *A. hyacinthogularis* at San Francisco Research Station.

Etymology

The specific epithet *lososi* is a noun in the genitive case and is a patronym for Jonathan B. Losos, who has dedicated his life to the study of anole lizards. After visiting Ecuador a few years ago, he inspired young Ecuadorian biology students who are undertaking pioneering studies on the ecology of these lizards.

Phylogenetic relationships

The Bayesian analysis estimated *A. hyacinthogularis* to be sister to *A. calimae*, an enigmatic species known from high elevations on the Pacific Andean slope in Colombia (Figure 7). The deep divergence between *A. hyacinthogularis* and other *Anolis*, including *A. calimae*, further supports the species status of *A. hyacinthogularis*. The broader affinities of these two species, whose sister relationship is strongly supported at posterior probability of 93%, are unclear. The sister relationship of these forms, on either side of the Andes, suggests additional complexity in the evolution of the Dactyloa clade of *Anoli*s (see Poe et al. 2017; Prates et al. 2017).

The closest included relative to *A. lososi* was estimated to be *A. williamsmittermeierorum* (Figure 7). These species possess large smooth head scales, short limbs and tail, and cryptic coloration and (as far as is known) behaviour. This 'twig' ecomorph, which is paralleled in the West Indies by species such as *Anolis insolitus* and *Anolis guazuma*, is observed in many species of the *Dactyloa* clade of *Anolis*. This condition may have evolved convergently within *Dactyloa* or, alternatively, as the ancestral ecomorph in *Dactyloa* or *Continenteloa* (i.e. *Dactyloa* excluding the *roquet* series in Poe et al. 2017; Prates et al. 2017).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix

Additional specimens examined

MCZ = Museum of Comparative Zoology, Harvard, United States. MSB = Museum of Southwestern Biology, University of New Mexico, United States. QCAZ = Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador, Ecuador. UNAP = Universidad Nacional de la Amazonia Peruana, Iquitos, Perú.

Anolis orcesi – Ecuador: *Provincia Napo*: Mt. Sumaco, 0.538°N, 77.626°W, MCZ 38937; Baeza-Borja road, access #3 to Río Quijos, near Hostería Cumandá, 0.477°S, 77.864°W, 1766 m, QCAZ 4502; 2.3 km north from Baeza deviation, 0.450°S, 77.890°W, 1819 m, QCAZ 9692–93; Río Quijos, 15.7 km north from Baeza deviation, 0.376°S, 77.819°W, 1584 m, QCAZ 9697; 30 km north from Baeza deviation, 0.292°S, 77.775°W, 1661 m, QCAZ 9705–06; 44.1 km north from Baeza deviation, 0.222°S, 77.735°W, 1662 m, QCAZ 9712–14. *Provincia Tungurahua*: 4.8 km southwest Río Negro, La Estancia road, Río Encanto´s path, 1.451°S, 78.227°W, 1800 m, QCAZ 4642; Río Verde, 1.403°S, 78.298°W, 1514 m, QCAZ 10156; Puyo-Baños road, 1.399°S, 78.364°W, 1638 m, QCAZ 10160.

Anolis williamsmittermeierorum – Perú: *Departamento San Martín*: Venceremos, approximately 96 km west Rioja, 5.6734°S, 77.7552°W, 1739 m, UNAP 02.000181 (holotype), 02.000180, 02.00189–90, MSB 72521–3.