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

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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.

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KEYWORDS
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.
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 ddH₂O 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.

| Taxon          | Voucher and locality                                      | GenBank accession number |   |
|----------------|----------------------------------------------------------|--------------------------|
| Anolis aeneus  | USNM 319162: Grenada: St George,:West end of Grand Anse Bay | JN112719^a                |
|                | JBL 442: Grenada: St George: Grand Anse Bay              | –                        | JN112592^a                |
| 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   | MHNL 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–T 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. calima      | MRC 118: Colombia: Valle del Cauca: on road to San Antonio, Television Tower | JN112724^a | JN112669^a | JN112597^a |
| A. calima      | MRC 119: Colombia: Valle del Cauca: on road to San Antonio, Television Tower | JN112725^a | JN112670^a | JN112598^a |
| A. casilda     | JMS 214: Panama: Chiriqui: near STRI–Fortuna Biological Station | JN112726^a | AY909745^a | 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 |

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<td>KM598668f</td>
<td>KM598700d</td>
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<td>Fazenda Experimental Catuaba</td>
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<td>POE 3162: Colombia: Valle de Cauca: km 18 on road</td>
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<td>–</td>
<td>see belowc</td>
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<td>from Cali to Buenaventura</td>
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<td><em>A. euskalerri</em></td>
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<td>JNN12737a</td>
<td>JNN12678a</td>
<td>JNN12610a</td>
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<td></td>
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<td>MBLUZ 935: Venezuela: Zulia: Sierra de Perijá, Villa</td>
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<td>JNN12738a</td>
<td>JNN12679a</td>
<td>JNN12611a</td>
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<td></td>
<td>del RosaRío</td>
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<td><em>A. extremus</em></td>
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<td>USNM 321945: St Lucia: Castries Quarter: grounds of</td>
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<td>JNN12739a</td>
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<td>JNN12612a</td>
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<td>Cunard La Toc Hotel</td>
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<td><em>A. fasciatus</em></td>
<td>QCAZ 10192: Ecuador: Los Ríos: Palenque Research Station</td>
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<td>KU316033g</td>
<td>KU316046g</td>
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<td><em>A. festae</em></td>
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<td>JNN12740a</td>
<td>JNN12680a</td>
<td>JNN12613a</td>
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<td>of Hosteria Tundaloma</td>
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<td><em>A. fitchi</em></td>
<td>QCAZ 6742: Ecuador: Napo: Pacto Sumaco</td>
<td>JNN12741a</td>
<td>JNN12681a</td>
<td>JNN12614a</td>
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<td><em>A. fitchi</em></td>
<td>QCAZ 6910: Ecuador: Tungurahua: Río Verde</td>
<td>JNN12742a</td>
<td>JNN12682a</td>
<td>JNN12615a</td>
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<td>QCAZ 6862: Ecuador: Pichincha: Mindo, on road to</td>
<td>JNN12743a</td>
<td>JNN12683a</td>
<td>JNN12616a</td>
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<td><em>A. fraseri</em></td>
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<td>JNN12744a</td>
<td>JNN12684a</td>
<td>JNN12617a</td>
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<td>Bilsa Biological Station, Río Ducha</td>
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<td><em>A. frenatus</em></td>
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<td>JNN12745a</td>
<td>–</td>
<td>JNN12618a</td>
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<td><em>A. frenatus</em></td>
<td>MHLU 15119 (MHLU–T 676): Colombia: Antioquia: San</td>
<td>JNN12746a</td>
<td>JNN12685a</td>
<td>JNN12619a</td>
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<td>Luis, Río Claro, El Refugio Natural Reserve</td>
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<td>QCAZ 6851: Ecuador: Pichincha: El Placer, on road to</td>
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<td>JNN12686a</td>
<td>JNN12620a</td>
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<td>Mariposas de Mindo to Mindo Garden</td>
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<td>QCAZ 6884: Ecuador: Pichincha: El Placer, on road to</td>
<td>JNN12748a</td>
<td>JNN12687a</td>
<td>JNN12621a</td>
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<td>Conchacato, Río Chisiche</td>
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<td><em>A. ginaelisae</em></td>
<td>SMF 89737: Panama: Chiriquí: Bajo Mono, Sendero La</td>
<td>JX083225</td>
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<td><em>A. griseus</em></td>
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<td>JNN12749a</td>
<td>AY296170b</td>
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<td><em>A. heteroderm</em></td>
<td>MHLU 11396 (MHLU–T 323): Colombia: Caldas: Manizales,</td>
<td>JNN12750a</td>
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<td>MRC 145: Colombia: Huila: Palestina, La Guajira, La</td>
<td>JNN12752a</td>
<td>JNN12688a</td>
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<td>Riviera Private Reserve</td>
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<td><em>A. huilae</em></td>
<td>MRC 146: Colombia: Huila: Palestina, Jericó, El Silencio</td>
<td>JNN12753a</td>
<td>JNN12691a</td>
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<td>Coffee plantation</td>
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<td><em>A. huilae</em></td>
<td>MRC 149: Colombia: Huila: Palestina, Jericó, El</td>
<td>JNN12754a</td>
<td>JNN12692a</td>
<td>JNN12627a</td>
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<td></td>
<td>Silencio Coffee plantation</td>
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<td><em>A. hyacinthogularis</em> sp. nov.</td>
<td>QCAZ 14135: Ecuador: Zamora Chinchipe:</td>
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<td>MG159790a</td>
<td>MG159798a</td>
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<td><em>A. hyacinthogularis</em> sp. nov.</td>
<td>QCAZ 14136: Ecuador: Zamora Chinchipe:</td>
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<td>MG159791a</td>
<td>MG159797a</td>
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<td><em>A. ibaneri</em></td>
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<td>see belowc</td>
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<td><em>A. insignis</em></td>
<td>JMR 3744: Colombia</td>
<td>JNN12755a</td>
<td>AY296145c</td>
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<td>MVUP 2021: Panama, Chiriquí, Reserva Forestal Fortuna</td>
<td>JNN12756a</td>
<td>JNN12693a</td>
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<td><strong>A. jacare</strong></td>
<td>MHNLB 17237: Venezuela: Táchira: Paramo Grande and La Grita, on road between Sabana la Negra, on road between Sabana Grande and La Grita, La Guacharita</td>
<td>JN112759(^a) JN112695(^a) JN112630(^a)</td>
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<td><strong>A. jacare</strong></td>
<td>MHNLB 17870: Venezuela: Merida: Antonio Pinto Salinas, Santa Cruz de Mora, La Macana</td>
<td>JN112757(^a) JN112694(^a) JN112629(^a)</td>
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<td><strong>A. kunayalae</strong></td>
<td>POE 1970: Panama: Coclé: El Copé: Parque Omar Torrijos</td>
<td>see below(^c) see below(^c) –</td>
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<td><strong>A. latifrons</strong></td>
<td>MHCH 2787: Panama: Darién: Serrania de Pirre</td>
<td>KP975514(^i) – –</td>
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<td><strong>A. latifrons</strong></td>
<td>MHCH 2788: Panama: Emberá–Wounán: Pavarandó, Camp 3 cerro garra garra</td>
<td>KP975513(^i) – –</td>
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<td><strong>A. latifrons</strong></td>
<td>POE 3172: Colombia: Valle de Cauca: trails from Chuchero (near Buenaventura)</td>
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<td>QCAZ 10173: Ecuador: Zamora Chinchipe: Parque Omar Torrijos</td>
<td>MG159788(^<em>) MG159793(^</em>) –</td>
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<td><strong>A. lososi</strong></td>
<td>QCAZ 14125: Ecuador: Zamora Chinchipe: San Francisco Research Station</td>
<td>MG159789(^<em>) MG159794(^</em>) –</td>
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<td><strong>A. lososi</strong></td>
<td>QCAZ 14132: Ecuador: Zamora Chinchipe: San Francisco Research Station</td>
<td>– MG159795(^*) –</td>
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<td><strong>A. luciae</strong></td>
<td>USNM 321960: St Lucia: Castries: grounds of Cunard La Toc Hotel</td>
<td>JN112760(^a) JN112697(^a) JN112631(^a)</td>
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<td><strong>A. maculigula</strong></td>
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<td><strong>A. maia</strong></td>
<td>MHCH 2783: Panama: Emberá–Wounán: Bajo pequeño, camp3 Pechito parao</td>
<td>KP975528(^i) – –</td>
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<td><strong>A. microtus</strong></td>
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<td><strong>A. nasofrontalis</strong></td>
<td>LOD 1383: Brazil: Espirito Santo: Santa Teresa, Reserva Biológica Augusto Ruschi</td>
<td>KU316037(^g) – MF004398(^i) MF004397(^i)</td>
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<td><strong>A. neblininus</strong></td>
<td>USNM 322912: Venezuela: Amazonas: Río Negro, Cerro de la Neblina, 12.5 km NNW of pico Phelps (= pico Neblina)</td>
<td>JN112763(^a) JN112700(^a) JN112634(^a)</td>
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<tr>
<td><strong>A. nicefori</strong></td>
<td>J. Renjifo 2537</td>
<td>– AF055948(^b) –</td>
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<td><strong>A. orcesi</strong></td>
<td>QCAZ 9692: Ecuador: Napo: 2.3 km north of turnoff to Baeza</td>
<td>KU316041(^g) KU316052(^g) –</td>
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<td><strong>A. otongae</strong></td>
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<td>KJ854221(^k) KJ854207(^k) KJ854214(^k)</td>
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<td><strong>A. otongae</strong></td>
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<td><strong>A. panilis</strong></td>
<td>QCAZ 10178: Ecuador: Esmeraldas: Mache Chindu Reserve, Bilsa Biological Station</td>
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<td><strong>A. philopunctatus</strong></td>
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<td><strong>A. philopunctatus</strong></td>
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<td>A. bimaculatus</td>
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<td>JN112781&lt;sup&gt;4&lt;/sup&gt;</td>
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<td>Palmetto Point: east of Boyd’s</td>
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<td>A. capito</td>
<td>SMF 97094: Panama: Guna Yala: Ridge,</td>
<td>KP975519&lt;sup&gt;2&lt;/sup&gt;</td>
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<td><strong>A. podocarpus</strong></td>
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<td>JN112703&lt;sup&gt;3&lt;/sup&gt;</td>
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<td>A. poecilopus</td>
<td>SMF 9711: Panamá: Darién: Río Cana, Cana field station, Chimenea trail</td>
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<td>A. poei</td>
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<td>A. princeps</td>
<td>MRC 135: Colombia: casidae cí: Bajo Baudó, Pilizá</td>
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<td>A. princeps</td>
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<td>A. princeps</td>
<td>QCAZ 6892: Ecuador: Los Ríos: Centro Científico Río Palenque</td>
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<td>QCAZ 9735: Ecuador: Pichincha: Mindo</td>
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<td>A. pseudotigrinus</td>
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<td>A. punctatus</td>
<td>MHNLS 17698: Venezuela: Amazonas: Atures, 12 km south of Puerto Ayacucho</td>
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<td>MRC 123: Colombia: Chocó: Quibdó, Tunutunendo</td>
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<td>A. purpureascens</td>
<td>MRC 134: Colombia: Chocó: Bajo Baudó, Pilizá</td>
<td>JN112731&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. richardi</td>
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<td>JN112770&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. soinii</td>
<td>QCAZ10163: Ecuador: Loja: Zamora – Loja road</td>
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<td>JN112778&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>JN112715&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>MHUA 11562 (MHUA–T 704): Colombia: Antioquia: Anorí, El Roble, La Forzosa forest</td>
<td>JN112779&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. tigrinus</td>
<td>MHNLS 17863: Venezuela: Vargas: on road Junquito–Colonía Tovar</td>
<td>JN112772&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. transversalis</td>
<td>MTR 28583: Brazil: Acre: Senator Guiomard, Fazenda Experimental Catuaba</td>
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<td>KM598688&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. transversalis</td>
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<td>JN112711&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. trinitatis</td>
<td>USNM 321992: St. Vincent: St George: Villan town</td>
<td>JN112774&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. tropidogaster</td>
<td>MHCH 2646: Panamá: Darién: Laguna de Matusagari, Agus Calientes</td>
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<td>KP975526&lt;sup&gt;6&lt;/sup&gt;</td>
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<td>A. vanzolinii</td>
<td>QCAZ 6926: Ecuador: Sucumbíos: Santa Bárbara, La Bretaña sector, on road between El Playón and El Carmelo</td>
<td>JN112775&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>JN112712&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. ventrimaculatus</td>
<td>MRC 091: Colombia: Valle del Cauca: La Cumbre, Chicoral, La Minga property</td>
<td>JN112776&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>JN112713&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. ventrimaculatus</td>
<td>MRC 112: Colombia: Valle del Cauca: on road to San Antonio, Television Tower</td>
<td>JN112777&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>JN112714&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>A. williamsmuttermeierorum</td>
<td>QCAZ 10170: Ecuador: Morona Santiago: close to Plan de Milagro</td>
<td>see below&lt;sup&gt;5&lt;/sup&gt;</td>
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<td>see below&lt;sup&gt;5&lt;/sup&gt;</td>
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<td>A. williamsmuttermeierorum</td>
<td>QCAZ 10170: Ecuador: Morona Santiago: close to Plan de Milagro</td>
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Table 1. (Continued).

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<td>JN112782&lt;sup&gt;a&lt;/sup&gt; JN112717&lt;sup&gt;a&lt;/sup&gt; JN112651&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>A. cuvieri</td>
<td>REG 2104: Puerto Rico: Arecibo: Reserva Foresta Cambalache</td>
<td>JN112783&lt;sup&gt;a&lt;/sup&gt; AF055973&lt;sup&gt;b&lt;/sup&gt; JN112652&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>A. equestris</td>
<td>USNM 337647: Cuba: La Habana: Playa Jibacoa</td>
<td>JN112784&lt;sup&gt;a&lt;/sup&gt; AF055978&lt;sup&gt;b&lt;/sup&gt; JN112653&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>A. limifrons</td>
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<td>KP975523&lt;sup&gt;i&lt;/sup&gt; – –</td>
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<td>A. lucius</td>
<td>USNM 498030: Cuba: Cienfuegos: Cienfuegos Botanical Garden</td>
<td>JN112785&lt;sup&gt;a&lt;/sup&gt; AF055962&lt;sup&gt;b&lt;/sup&gt; JN112654&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>JBL 455: Dominican Republic: Peravia: between Baní and El Recodo</td>
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<td>USNM 321891: Puerto Rico: Humacao: Caribbean National Forest, Sierra de Luquillo, 13.3 km south of Palmer (=Mameyes)</td>
<td>JN112787&lt;sup&gt;a&lt;/sup&gt; AF055976&lt;sup&gt;b&lt;/sup&gt; JN112656&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>A. sagrei</td>
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<td>A. smaragdinus</td>
<td>USNM 549537: The Bahamas: South Bimini Island: vicinity of airport</td>
<td>JN112788&lt;sup&gt;a&lt;/sup&gt; JN112718&lt;sup&gt;a&lt;/sup&gt; JN112658&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Polychrus marmoratus</td>
<td>SNOMNH 36693: Brazil: Pará: approx. 101 km south and 18 km east Santarem, Agropecuaria Treviso LTDA</td>
<td>JN112789&lt;sup&gt;a&lt;/sup&gt; AF528738&lt;sup&gt;i&lt;/sup&gt; JN112659&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Pristidactylus scapulatus</td>
<td>PT 4810: Argentina: Río Negro, 2 km south Esperanza</td>
<td>JN112790&lt;sup&gt;a&lt;/sup&gt; AF528732&lt;sup&gt;i&lt;/sup&gt; JN112660&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Urostrophus gallardoi</td>
<td>FBC 0036: Argentina: Córdoba, aprox. 2 km south L. V. Marsilla</td>
<td>JN112791&lt;sup&gt;a&lt;/sup&gt; AF528735&lt;sup&gt;i&lt;/sup&gt; JN112661&lt;sup&gt;a&lt;/sup&gt;</td>
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<sup>a</sup>Castañeda and de Queiroz (<2011>)
<sup>b</sup>Jackman et al. (<1999>)
<sup>c</sup>Poe et al. (<2017); sequences available at stevenpoe.net
<sup>d</sup>Creer et al. (<2001>)
<sup>e</sup>Nicholson et al. (<2005>)
<sup>f</sup>Prates et al. (<2015>)
<sup>g</sup>Poe et al. (<2015>)
<sup>h</sup>Harmon et al. (<2003>)
<sup>i</sup>Batista et al. (<2015>)
<sup>j</sup>Prates et al. (<2017>)
<sup>k</sup>Ayala–Varela et al. (<2014>)
<sup>l</sup>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 Emílio 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, Rio Branco, Brazil; USNM, National Museum of Natural History, Washington 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)
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 supraciliary 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.

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

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

**Holotype**

**Paratypes** (23)
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,
Diagnosis


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

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).
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 apicoventral 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*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>A. williamsmittermeierorum</em></th>
<th><em>A. lososi</em> sp. nov.</th>
<th>t-value</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scales between second canthals</td>
<td>3–6 (7) 5.29 ± 1.11</td>
<td>4–6 (7) 5.14 ± 0.69</td>
<td>0.29</td>
<td>0.78</td>
</tr>
<tr>
<td>Postrostrals</td>
<td>4–7 (6) 5.50 ± 1.05</td>
<td>3–6 (7) 4.57 ± 1.13</td>
<td>1.52</td>
<td>0.16</td>
</tr>
<tr>
<td>Loral rows</td>
<td>2–4 (7) 2.71 ± 0.76</td>
<td>2–3 (7) 2.29 ± 0.49</td>
<td>1.26</td>
<td>0.23</td>
</tr>
<tr>
<td>Loreals</td>
<td>9–21 (7) 13.71 ± 3.86</td>
<td>5–15 (7) 9.86 ± 3.24</td>
<td>2.03</td>
<td>0.07</td>
</tr>
<tr>
<td>Scales between interparietal and semicircles</td>
<td>0 (7) 0.0 ± 0.79</td>
<td>0–2 (7) 0.43 ± 0.79</td>
<td>−1.44</td>
<td>0.20*</td>
</tr>
<tr>
<td>Supralabials from rostral to below centre of eye</td>
<td>6–7 (7) 6.57 ± 0.54</td>
<td>5–8 (7) 6.43 ± 0.98</td>
<td>0.34</td>
<td>0.74</td>
</tr>
<tr>
<td>Postmentals</td>
<td>4 (7) 4 ± 0</td>
<td>2–4 (7) 3.57 ± 0.79</td>
<td>1.44*</td>
<td>0.20*</td>
</tr>
<tr>
<td>Sublabials in contact with infralabials</td>
<td>3–5 (7) 3.86 ± 0.90</td>
<td>2–5 (7) 3.14 ± 1.07</td>
<td>1.35</td>
<td>0.20</td>
</tr>
<tr>
<td>Lamellae under phalanges III–IV of fourth toe</td>
<td>17–19 (6) 17.67 ± 0.82</td>
<td>18–21 (7) 19.71 ± 0.95</td>
<td>−4.12</td>
<td>0.0017</td>
</tr>
<tr>
<td>Mid-dorsals in 5% SVL</td>
<td>7–9 (7) 7.86 ± 0.69</td>
<td>7–10 (6) 8.17 ± 1.17</td>
<td>−0.59</td>
<td>0.57</td>
</tr>
<tr>
<td>Midventrals in 5% SVL</td>
<td>6–8 (7) 6.86 ± 0.69</td>
<td>6–8 (6) 7.00 ± 1.10</td>
<td>−0.28*</td>
<td>0.79*</td>
</tr>
<tr>
<td>Enlarged mid-dorsal crest scales</td>
<td>Absent</td>
<td>Absent</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Dewlap colour in males</td>
<td>Pale brown skin with orange-peach at edge; white scales</td>
<td>White or milk white skin and scales</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Dewlap colour in females</td>
<td>Dirty white skin with elongate black blotches; white scales</td>
<td>Brilliant yellow skin with round black blotches; pale orange scales</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Throat colour</td>
<td>Black, edges of mouth bright yellow-orange</td>
<td>Black, edges of mouth bright yellow-orange</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Head length</td>
<td>12.70–16.90 (6) 14.67 ± 1.66</td>
<td>14–16.7 (4) 15.50 ± 1.12</td>
<td>−0.87</td>
<td>0.41</td>
</tr>
<tr>
<td>Head width</td>
<td>7.50–10.10 (6) 8.75 ± 1.06</td>
<td>7.8–9.4 (4) 8.65 ± 0.68</td>
<td>0.17</td>
<td>0.87</td>
</tr>
<tr>
<td>Femur length</td>
<td>9.30–12.30 (5) 10.96 ± 1.36</td>
<td>9–10.60 (4) 9.88 ± 0.72</td>
<td>1.53*</td>
<td>0.17*</td>
</tr>
<tr>
<td>Tail length</td>
<td>66–80 (5) 71.40 ± 5.73</td>
<td>66.50–78.20 (4) 73.90 ± 5.30</td>
<td>−0.67</td>
<td>0.52</td>
</tr>
<tr>
<td>Interparietal length</td>
<td>1.90–2.70 (6) 2.28 ± 0.33</td>
<td>1.8–2.3 (4) 2.13 ± 0.22</td>
<td>0.83</td>
<td>0.43</td>
</tr>
<tr>
<td>Ear height</td>
<td>1–1.70 (6) 1.35 ± 0.27</td>
<td>1.3–1.5 (4) 1.45 ± 0.10</td>
<td>−0.69</td>
<td>0.51</td>
</tr>
<tr>
<td>Fourth toe length</td>
<td>7.10–8.50 (6) 7.78 ± 0.69</td>
<td>7.5–8.90 (4) 8.25 ± 0.66</td>
<td>−1.07</td>
<td>0.32</td>
</tr>
<tr>
<td>Fourth toe width</td>
<td>1.30–1.60 (5) 1.40 ± 0.12</td>
<td>1.20–1.40 (4) 1.30 ± 0.12</td>
<td>1.25</td>
<td>0.25</td>
</tr>
<tr>
<td>Dewlap fold length</td>
<td>15.60–22 (6) 18.60 ± 2.29</td>
<td>20.80–29.10 (4) 25.63 ± 4.03</td>
<td>−3.55</td>
<td>0.0075</td>
</tr>
<tr>
<td>Snout–vent length</td>
<td>48–65.50 (6) 54.75 ± 6.85</td>
<td>55.10–61.40 (4) 58.93 ± 2.69</td>
<td>−1.14</td>
<td>0.29</td>
</tr>
<tr>
<td>Maximum SVL</td>
<td>66</td>
<td>61</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

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 Anolis (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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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 Rio Quijos, near Hosteria Cumandá, 0.477°S, 77.864°W, 1766 m, QCAZ 9692–93; Rio Quijos, 15.7 km north from Baeza deviation, 0.450°S, 77.735°W, 1662 m, QCAZ 9712–14. Provincia Tungurahua: 4.8 km southwest Rio Negro, La Estancia road, Rio Encanto’s path, 1.451°S, 78.227°W, 1800 m, QCAZ 4642; Rio 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 Martin: 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.