Evolutionary Systematics. 4 2020, 79–108 | DOI 10.3897/evolsyst.4.57578

PENSOFT

EVOLUTIONARY SYSTEMATICS

Four new species of *Stenocercus* Duméril & Bibron, 1837 (Squamata, Iguania) from the Department of Amazonas in northeastern Peru

Pablo J. Venegas[1,2], Luis A. García-Ayachi[1,2], Juan C. Chávez-Arribasplata[1,2], Germán Chávez[1,2], Iván Wong[3], Antonio García-Bravo[2,4]

1 *Instituto Peruano de Herpetología (IPH), Augusto Salazar Bondy 136, Urb. Higuereta, Surco, Lima, Perú*

2 *División de Herpetología, Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita No. 105 Of. 202, Urb. Huertos de San Antonio, Surco, Lima, Perú*

3 *Macanche RAM, Urb. 06 de Setiembre Mz. H, lote 20, Piura, Perú*

4 *Escuela de Ingeniería Forestal, Facultad de Ingeniería y Ciencias Agrarias, Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas. Calle Higos Urco N342-350-356. Amazonas, Perú*

http://zoobank.org/361BA656-C8DC-4F1D-A7B8-A167E95B2BB9

Corresponding author: Pablo J. Venegas (pvenegas@corbidi.org)

Academic editor: Alexander Haas ♦ **Received** 13 August 2020 ♦ **Accepted** 3 November 2020 ♦ **Published** 18 November 2020

Abstract

The tropical Andes are known to be the richest and most diverse place on earth. This mountainous region covers almost one third of the Peruvian territory, and its herpetofauna remains poorly known. The lizard genus *Stenocercus* Duméril & Bibron, 1837 contains 69 species and most of them occur in the tropical Andes, although some exist as high as 4000 m a.s.l. The examination of newly collected material from the Andes of northern Peru in the Department of Amazonas reveals four new species of *Stenocercus* which we describe below. Of these four new species, three inhabit the ecoregion of Peruvian Yungas at elevations of 1460 to 2370 m a.s.l., and one the Marañón dry forest ecoregion at elevations of 1340 to 1470 m a.s.l. Additionally, we provide new data about coloration, natural history and distribution of the poorly known *S. aculeatus* O'Shaughnessy, 1879; and discuss the identity of some populations of *S. prionotus* Cadle, 2001 and *S. scapularis* Boulenger, 1901.

Key Words

Andes, herpetofauna, Marañón dry forests, montane forest, morphology, Peruvian Yungas

Introduction

With the creation of conservation biology, at the end of the seventies, as a new field of research, new and striking terms such as "biodiversity" or "hotspots" were coined to highlight the importance of biological diversity and areas with a high species richness and endemism, respectively. The tropical Andes, a name currently applied to the hotspot that encompasses the Andean mountains between Venezuela and Bolivia, are known to be the most diverse region on earth (Myers et al. 2000). This mountainous region covers almost one third of the Peruvian territory, running from north to south with an average height of 4000 m a.s.l. (Peñaherrera del Aguila 1989). The general landscape includes snow-topped mountains, canyons and valleys. The wide altitudinal range of the Andes also houses diverse habitats as altitude changes including tropical rainforests at 500 to 1500 m a.s.l., cloud forests ranging from 800 to 3500 m a.s.l.; and the highest altitudes of 3000 to 4800 m. a.s.l. contain páramos and grasslands extending up to snow (Duellman and Lehr 2009).

New species of reptiles and amphibians are frequently discovered in the Peruvian Andes especially when remote regions are surveyed (e.g. Cadle 1991; Duellman and Wild 1993; Duellman and Venegas 2005; Chávez et al. 2011; Venegas et al. 2013; Lehr et al. 2017). The Department of

Amazonas in northern Peru is located along the northern portion of the central Andes and possesses a complex topography that in association with its climate pattern results in a wide variety of vegetation formations (Duellman and Pramuk 1999). The herpetological exploration of the Department of Amazonas has been fruitful since the decade of the seventies with the discovery of 38 species of anurans in the genera: *Atelopus* Duméril & Bibron, 1841 (Lötters et al. 2004), *Centrolene* Jiménez de la Espada, 1872 (Twomey et al. 2014), *Dendropsophus* Fitzinger, 1843 (Duellman 1982), *Gastrotheca* Fitzinger, 1843 (Duellman 1987, 2013; Duellman et al. 2014; Duellman and Venegas 2016), *Hyloscirtus* Peters, 1882 (Rivera-Correa et al. 2016), *Hyloxalus* Jiménez de la Espada, 1870 (Rivero 1991; Morales and Schulte 1993; Morales 1994; Duellman 2004), *Noblella* Barbour, 1930 (Duellman 1991), *Phyllomedusa* Wagler, 1830 (Cannatella 1982), *Pristimantis* Jiménez de la Espada, 1870 (Duellman 1990; Duellman and Pramuk 1999), *Rhinella* Fitzinger, 1826 (Duellman and Schulte 1992), *Telmatobius* Wiegmann, 1834 (Wiens 1993), *Scinax* Wagler, 1830 (Duellman and Wiens 1993); and 15 species of reptiles of the genera: *Ameiva* Meyer, 1795 (Koch et al. 2013), *Epictia* Gray, 1845 (Koch et al. 2015), *Morunasaurus* Dunn, 1933 (Köhler 2003), *Petracola* Doan & Castoe, 2005 (Echevarria and Venegas 2015), *Pseudogonatodes* Ruthven, 1915 (Huey and Dixon 1970); *Phyllodactylus* Gray, 1828 (Venegas et al. 2008; Koch et al. 2016), *Phyllopezus* Peters, 1878 (Koch et al. 2006), and *Stenocercus* Duméril & Bibron, 1837 (Fritts 1972; Cadle 1991; Venegas et al. 2016).

Currently the tropical Andes faces many threats and the most important by far are human activities including mining, logging, construction, agriculture and cattle ranching (Myers et al. 2000). The inter-Andean valleys of the Department of Amazonas are severely degraded and fragmented by human migration, agriculture and livestock (Venegas 2007). This is especially conspicuous in montane forests on the mountain slopes, particularly along the Chiriaco, Marañón and Utcubamba valleys. Therefore, documenting the biodiversity of the Department of Amazonas is a hard race against time.

Lizards of the *Stenocercus* clade are one of the most geographically and ecologically widespread taxa currently ranked as a genus in South America (Torres-Carvajal 2007a). The genus contains 71 species that occur at elevations between 0–4000 m a.s.l. in the Andes and adjacent lowland areas from northern Venezuela and Colombia to central Argentina, with some species in the Atlantic lowlands between southern Brazil and central Argentina, and others in northeastern Brazil (Torres-Carvajal 2007b; Uetz et al. 2020; Venegas et al. 2020). Peru is the country with the highest species richness in the genus *Stenocercus* with 59% of the species' diversity. However, the taxonomy of *Stenocercus* in this country has remained problematic. In the past the major problems in the taxonomy of *Stenocercus* were the use of multiple generic names to describe new species, different specific epithets for the same described species, and some early descriptions are very brief, making identification difficult (Torres-Carvajal 2007a). Although in the last three decades the alpha taxonomy of *Stenocercus* was noticeably improved with high level descriptions and extensive taxonomic revisions (e.g Cadle 1991, 1998, 2001; Torres-Carvajal 2000, 2007a), and the advances in molecular systematics resolved the monophyly of the genus showing its diversification (Torres-Carvajal et al. 2006; Torres-Carvajal 2007b; Teixeira et al. 2016); identifying species of *Stenocercus* from Peru by physical examination remains a challenge. Additionally, the coloration in life and intraspecific variation in most of the Peruvian species remain poorly known. On the other hand, some species like *S. chrysopygus* Boulenger, 1900, are known to possess intraspecific variation among populations that merits careful examination and phylogenetic analysis (Fritts 1974; Cadle 1998; Schluter 2000; Torres-Carvajal 2007b). In fact, several undescribed species remain in herpetological collections awaiting formal description and new species are discovered in the Peruvian Andes continuously (Venegas et al. 2013, 2014a, 2016, 2020; Köhler and Lehr 2015).

In order to contribute to the knowledge of the scarcely known herpetofauna of the Peruvian Andes, we conducted several herpetological surveys of the montane environments of the Andes of northern Peru, especially in the Department of Amazonas. In this paper, we describe four new species of *Stenocercus* from that department and present new data regarding taxonomy, natural history, and distribution of *S. aculeatus* O'Shaughnessy, 1879. This contribution increases the number of *Stenocercus* species known from Peru to 47.

Materials and methods

Ethics and research

This study was carried out in accordance with the guidelines for use of live amphibians and reptiles in field research (Beaupre et al. 2004), compiled by the American Society of Ichthyologists and Herpetologists (ASIH) and the Society for the Study of Amphibians and Reptiles (SSAR). Specimens collected for this study are covered by the following research permits (given by the Ministerio de Agricultura) that include permanent scientific collection of live specimens: 110-2007-INRENA-IFFS-DCB, 118-2007-INRENA-IFFS-DCB, 071-2008-INRENAIFFSDCB, 020-2009-AG-DGFFS-DGEFFS, 424-2010-AG-DGFFS-DGEFFS, 287-2011-AG-DGFFS-DGEFFS, 186-2014-MINAGRI-DGFFS/DGEFFS, 0581-2011-AG-DGFFS-DGEFFS, 295-2017-SERFOR/DGGSPFFS, 299-2017-SERFOR/DGGSPFFS, and 067-2019-MINAGRI-SERFOR-DGGSPFFS.

Field techniques

Lizards were captured by hand or noosing with a fishing rod. Coordinates and elevation were taken with a GPS

(Garmin, WGS84). All collected specimens were euthanized with T61, fixed in 10% formalin for 48 hours and permanently stored in 70% ethanol. Voucher specimens were deposited at the herpetological collection of the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru.

Morphological data

Measurements of snout-vent length (SVL) and tail length (TL) were taken with a ruler and recorded to the nearest 1 mm. All other measurements were made with digital calipers and recorded to the nearest 0.1 mm. Sex was determined by noting the presence of hemipenes and dimorphic phenotypic characters such as height of the vertebral crest and the ventral pattern. Data on scutellation of all species of *Stenocercus* compared herein was taken from Torres-Carvajal (2007a) and Cadle (1991). Specimens reviewed for comparison are housed at CORBIDI and the Museo de Zoología, Pontificia Universidad Católica de Ecuador, Quito (QCAZ), and are listed in Appendix I. The abdominal skeleton was examined by dissection of specimens (all paratypes): CORBIDI 18661, CORBIDI 18876, CORBIDI 21090, and CORBIDI 21367. We follow the terminology of Cadle (1991) and Torres-Carvajal (2000; 2004; 2007a) for characters included in the description. The volume of oviductal eggs was calculated by the formula for a prolate spheroid $V = 4/3\ \pi\ (\text{length}/2)\ (\text{width}/2)^2$ (Torres-Carvajal 2007a).

Species delimitation

The taxonomic conclusions of this study are based on the observation of morphological features and color patterns as evidence to infer the existence of species (Frost and Kluge 1994; de Queiroz 1998, 2007). This information is considered as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998, 2007).

Results

Stenocercus catherineae sp. nov.

http://zoobank.org/ADE1DCF5-09B3-45A5-B107-FBF536F2FC72

Figs 1–3

Type material. Holotype:

PERU • ♂, adult; Amazonas Department, Bongará Province, Florida District, Huembo; 5°51.47’S, 77°58.75’W; 2090 m a.s.l.; 09 Dec. 2019; P.J. Venegas and L.A. García-Ayachi leg.; CORBIDI 21365.

Paratypes:

PERU • 1 ♂, 1 ♀, adults, collected with the holotype; CORBIDI 21366-67 • 1 ♂, juvenile; Amazonas Department, Bongará Province, Cuispes District, Cuispes; 5°55.49’S, 77°56.94’W; 1850 m a.s.l.; 8 Mar. 2017; G. Chávez leg.; CORBIDI 18662 • 1 ♀, 1 ♂, adults; Amazonas Department, Bongará Province, Valera District, Cocachimba; 6°2.76’S, 77°53.55’W; 1460 m a.s.l.; 22 May 2007; by P.J. Venegas leg.; CORBIDI 501-02.

Diagnosis. *Stenocercus catherineae* sp. nov. differs from other species of *Stenocercus* except for *S. aculeatus*, *S. angulifer* Werner, 1901, *S. huancabambae* Cadle, 1991, *S. philmayi* sp. nov., *S. prionotus* Cadle, 2001, and *S. scapularis* Boulenger, 1901 by having: (1) projecting-angulate temporals, (2) laterally oriented nostrils; (3) dorsal and lateral scales of body similar in size, and (3) scales on posterior surface of thighs keeled and imbricate.

Stenocercus aculeatus, *S. angulifer*, *S. prionotus*, and *S. scapularis* can be easily distinguished from *S. catherineae* sp. nov. by having strongly keeled ventrals, whereas in the new species ventrals are feebly to moderately keeled. *Stenocercus aculeatus*, *S. angulifer* and *S. scapularis* also have a dorsolateral crest (absent in *S. catherineae* sp. nov.); and *S. prionotus* lacks a postfemoral mite pocket (present in *S. catherineae* sp. nov.). *Stenocercus catherineae* sp. nov. differs from *S. philmayi* sp. nov. by having smaller dorsal scales with 43 to 53 vertebrals and 46 to 59 scales around midbody versus 32 to 38 vertebrals and 34 to 45 scales around midbody in *S. philmayi* sp. nov. The gular region in adult males of *S. catherineae* sp. nov. is black, whereas in *S. philmayi* sp. nov. it is cream.

The new species is most similar to *S. huancabambae* (Fig. 4A, B) with which it shares ventral scales strongly keeled, like the rest of the aforementioned species, and a strongly compressed tail. Furthermore, both species are geographically close at the northern extreme of the central Andes in the Department of Amazonas (Cadle 1991; Torres-Carvajal 2007b). Nevertheless, the new species can be distinguished from *S. huancabambae* (characters in parentheses) by having the parietal eye not visible through the interparietal cornea (visible); postfemoral mite pocket as a distinct, deep slit-like opening (shallow slit-like opening, Fig. 3); dark patch covering most of the gular region of adult males present (absent); black patch on ventral surface of neck absent (present as a circular or elongate blotch, Fig. 4B); and a strongly compressed tail in adult males (very strongly compressed tail as a tape-like along its proximal two thirds).

At the locality of Cuispes, and probably also in Huembo, *S. catherineae* sp. nov. and *S. flagracanthus* sp. nov. exist in sympatry; however, both species are strikingly different. *S. flagracanthus* sp. nov. has a relatively short tail armed with projecting spines, whereas *S. catherineae* sp. nov. has a long tail, compressed laterally, and a projecting vertebral crest.

Definition. (1) Maximum SVL in males 83 mm ($n = 3$); (2) SVL in females 75 mm ($n = 2$); (3) vertebrals 43–53; (4) paravertebrals 62–73; (5) scales around midbody 46–59; (6) supraoculars 4; (7) internasals 4–6; (8) postrostrals 2–4; (9) loreals 5–6; (10) gulars 22–26; (11) subdigitals on Finger IV 18–21; (12) subdigitals on Toe IV 25–30; (13) posthumeral mite pocket present as a deep

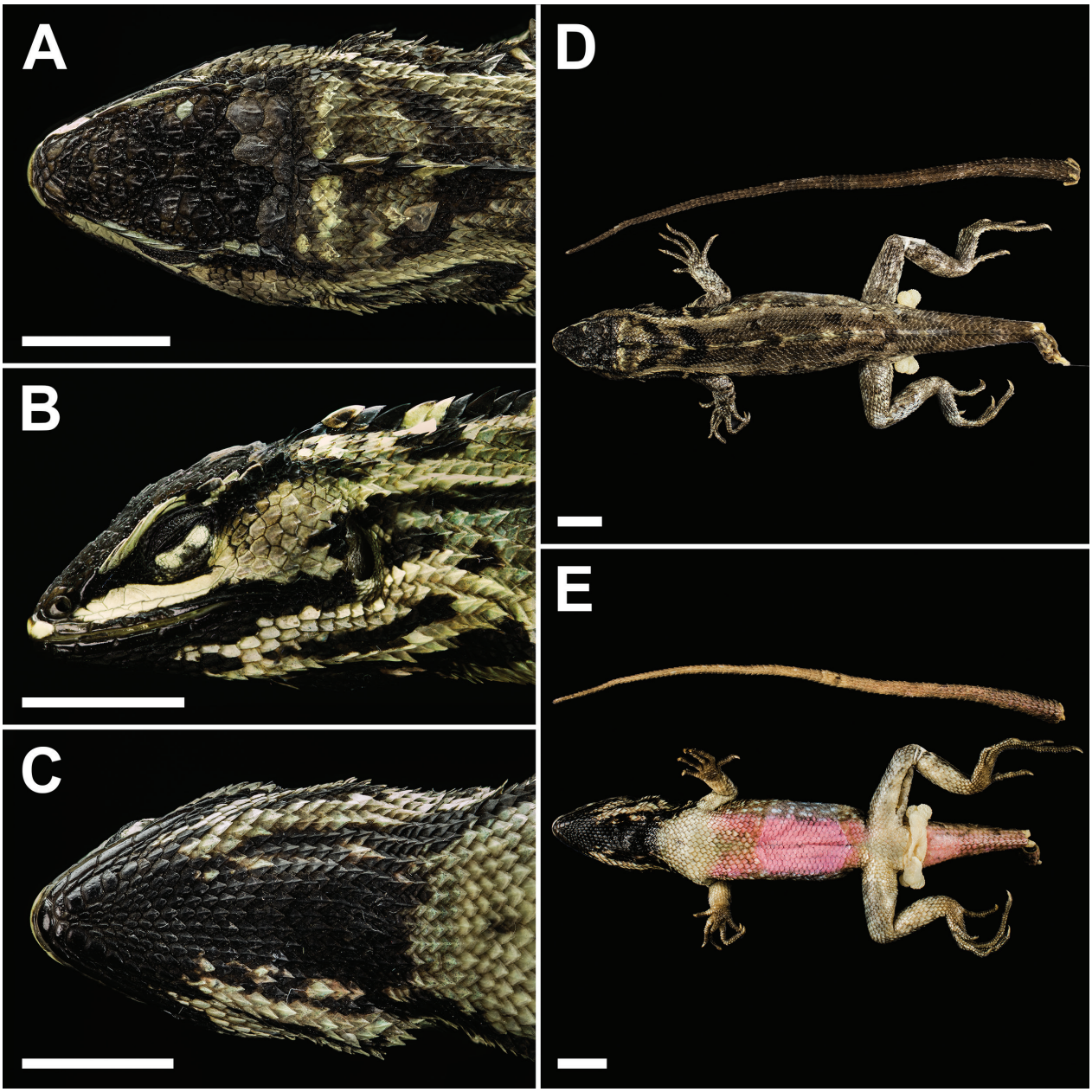

Figure 1. *Stenocercus catherineae* sp. nov. preserved holotype, adult male, SVL 82 mm (CORBIDI 21365): dorsal (**A**), lateral (**B**), and ventral (**C**) views of the head; dorsal (**D**) and ventral (**E**) views of the entire specimen. Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

depression with a wide opening [Type 3 of Torres-Carvajal (2007b)]; (14) postfemoral mite pocket present as a distinct pocket with a posteroventrally oriented slit-like opening [Type 2 of Torres-Carvajal (2007b)]; (15) parietal eye not visible through interparietal cornea in any specimens (n = 6); (16) scales on occipitoparietal region large, multicarinate, not imbricate; (17) projecting angulate temporals present; (18) row of enlarged supraoculars present, occupying most of supraocular region; (19) scales on frontonasal region and supraoculars slightly imbricate, multicarinate; (20) preauricular fringe present, short; (21) neck folds absent; (22) lateral and dorsal nuchals similar in size; (23) posterior gulars rhomboidal, projected posteriorly, keeled and imbricate, not notched; (24) lateral and dorsal body scales similar in size; (25) vertebrals larger than adjacent paravertebrals, forming a distinct vertebral crest; (26) dorsolateral crest absent; (27) ventrals keeled, imbricate, mucronate; (28) scales on posterior surfaces of thighs keeled, imbricate, mucronate; (29) inguinal granular pocket absent; (30) inguinal groove absent; (31) preanals not projecting; (32) tail strongly compressed laterally in adult males; (33) tail length 65–70% of total length; (34) caudal whorls per autotomic segment three; (35) caudals not spinose; (36) dark brown stripe extend-

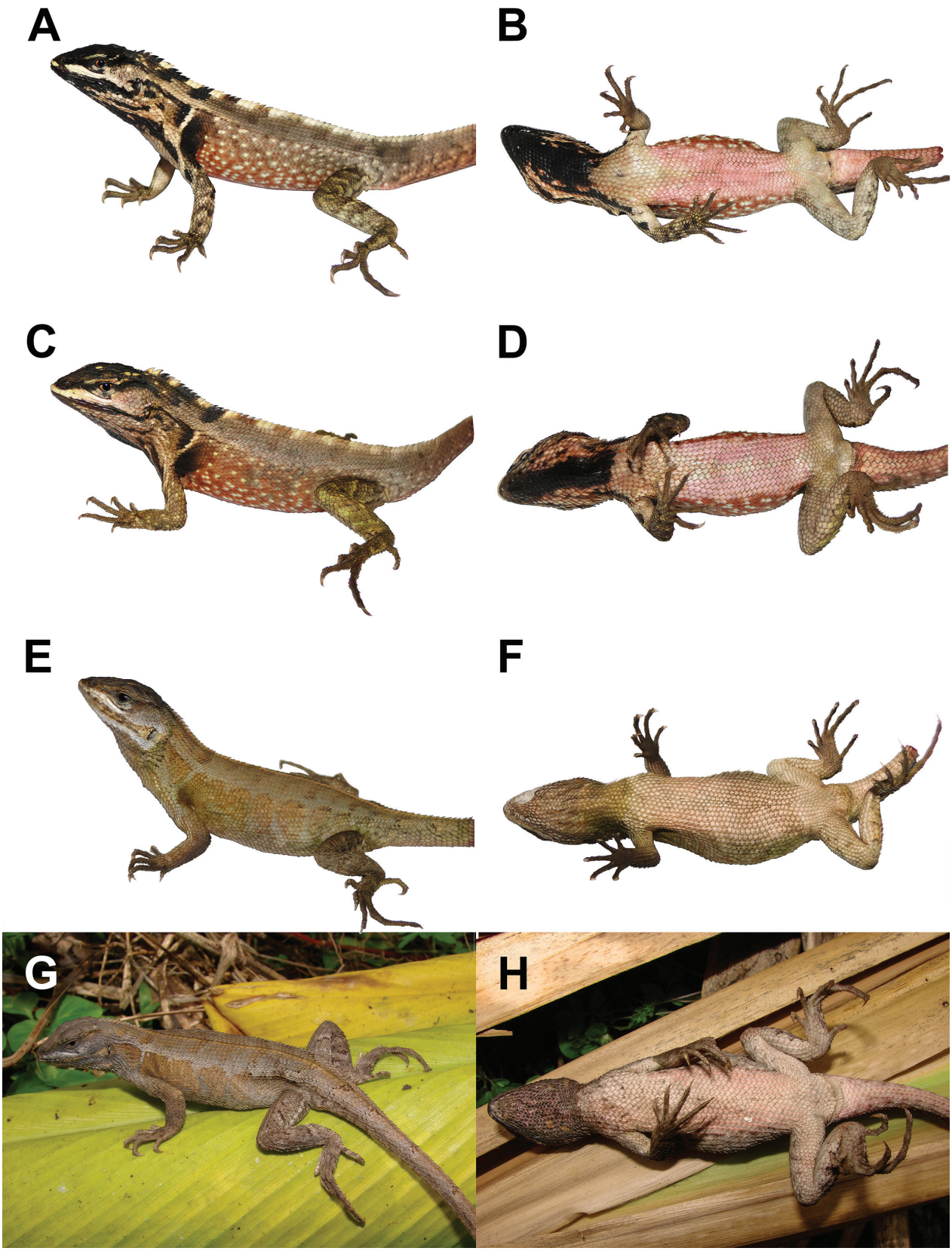

Figure 2. Dorsolateral and ventral views of *Stenocercus catherineae* sp. nov. in life: (**A**, **B**) holotype, adult male, SVL 82 mm (CORBIDI 21365); (**C**, **D**) adult male, SVL 79 mm (CORBIDI 21366); (**E**, **F**) adult female, SVL 75 mm (CORBIDI 21367); (**G**, **H**) adult female, SVL 75 mm (CORBIDI 501). Photographs by Pablo J. Venegas.

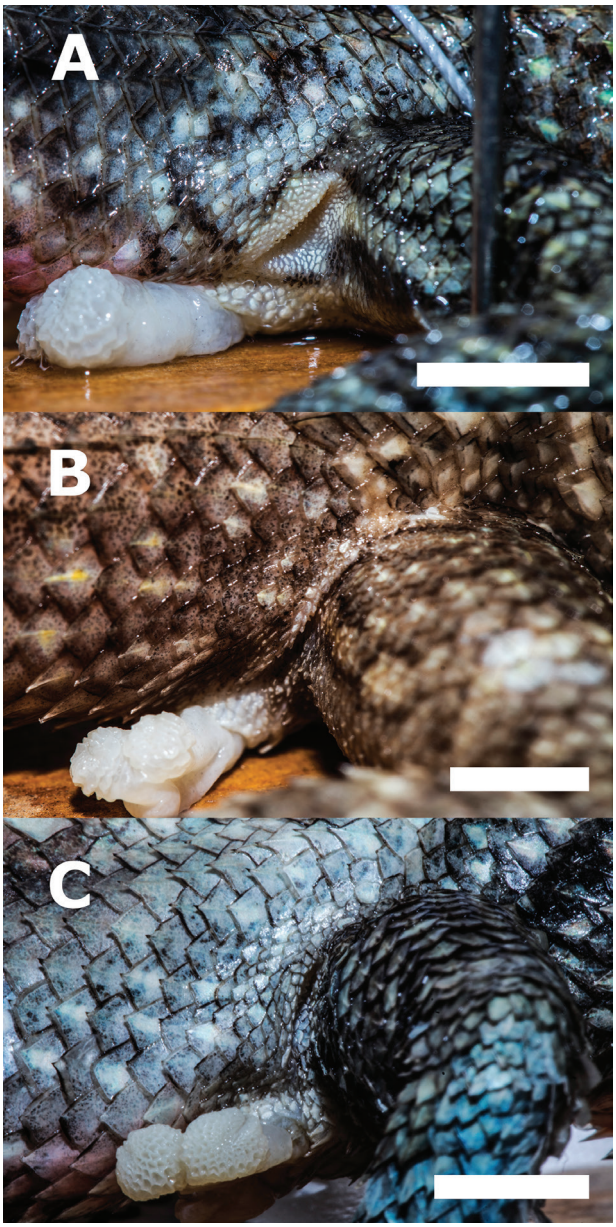

Figure 3. Lateral view of the postfemoral mite pocket in three species of *Stenocercus*: (**A**) *S. catherineae* sp. nov. (CORBIDI 21365), (**B**) *S. philmayi* sp. nov. (CORBIDI 21092), and (**C**) *S. huancabambae* (CORBIDI 19747). Photographs by Luis A. García-Ayachi. Scale bars: 5 mm.

ing anterodorsally from subocular region to supraciliaries always present; (37) dark patch extensively covering gular region of females present; (38) dark patch covering gular region in adult males present; (39) black patch on ventral surface of neck in adult males absent; (40) dark midventral longitudinal mark such as faint line, conspicuous stripe, or extensive patch in adult males absent; (41) dark patches on ventral surface of thighs in adult males absent; (42) two xiphisternal and three postxiphisternal pairs of inscriptional ribs fused medially, forming three chevrons (Pattern 6A of Torres-Carvajal 2004).

Description of the holotype. Adult male (Fig. 1); SVL 82 mm; TL 156 mm; maximum head width 15.7 mm; head length 18.7 mm; head height 12.8 mm; occipitals, parietals, interparietals, and postparietals large, multicarinate, slightly imbricate; parietal eye not visible; supraoculars in four rows, multicarinate, slightly imbricate, subequal in size; one canthal; canthal not in contact with the nasal; scales on frontonasal region slightly imbricate and multicarinate; internasals four; postrostrals three, two most lateral wider than long on each side, medial postrostrals as long as wide; supralabials four; infralabials five; loreals four; lorilabials in one row; preocular one, in contact with canthal; lateral temporals keeled, imbricate; gulars in 22 rows between tympanic openings; all gulars keeled, imbricate, apical pit absent; second infralabial not in contact with second and third sublabials; mental in contact with first pair of infralabials; lateral and dorsal scales of body and neck keeled, imbricate, mucronate; lateral and dorsal body scales similar in size; scales around midbody 46; vertebrals larger than dorsals, 43 scales on vertebral row, serrate vertebral crest present; paravertebrals 65; ventrals broad, rhomboidal, keeled, imbricate; preauricular fringe short, composed of three enlarged scales, all similar in size; antegular, gular, postauricular, oblique, supraauricular, longitudinal and antehumeral neck folds absent; limb scales keeled, imbricate; ventral scales of hindlimbs keeled and ventral scales of upper arms keeled, mucronate; lamellae on Finger IV 18; lamellae on Toe IV 27; tail strongly compressed laterally; caudals keeled, imbricate, mucronate; basal subcaudals keeled, imbricate; tail length 1.9 times SVL; posthumeral mite pocket present as a deep depression with a wide opening; postfemoral mite pocket present as a distinct deep pocket with a posteroventrally oriented slit-like opening; postfemoral region composed of imbricate, smooth scales that become keeled towards the tail.

Coloration in life (Fig. 2A, B). Dorsum pale brown with the first two chevrons over the vertebral line black and the rest slightly darker than the background; cream line extending vertically from the arm insertion to the scapular region surrounded by a black blotch; dorsal surface of limbs darker than the dorsum with faint dirty cream transverse bars; flanks reddish brown, including the tail, becoming red toward the venter and dotted with white; subocular and loreal regions creamy white; dorsal surface of head black with the superciliaries and rostral cream; labials, sublabials and mental black, extending as an irregular longitudinal stripe to the neck; gular region black with cream irregular blotches to the sides; a black irregular stripe extends from the gular region ventrolaterally to the arm insertion; ventral surface of neck, chest and forelimbs are dirty cream with a black spot ventrolaterally in the arm; belly and ventral surface of tail pink; pelvic region and ventral surface of hindlimbs dirty cream. The iris is reddish brown.

Coloration in preservative (Fig. 1D, E). It is similar to the coloration in life with the dorsal surface of trunk,

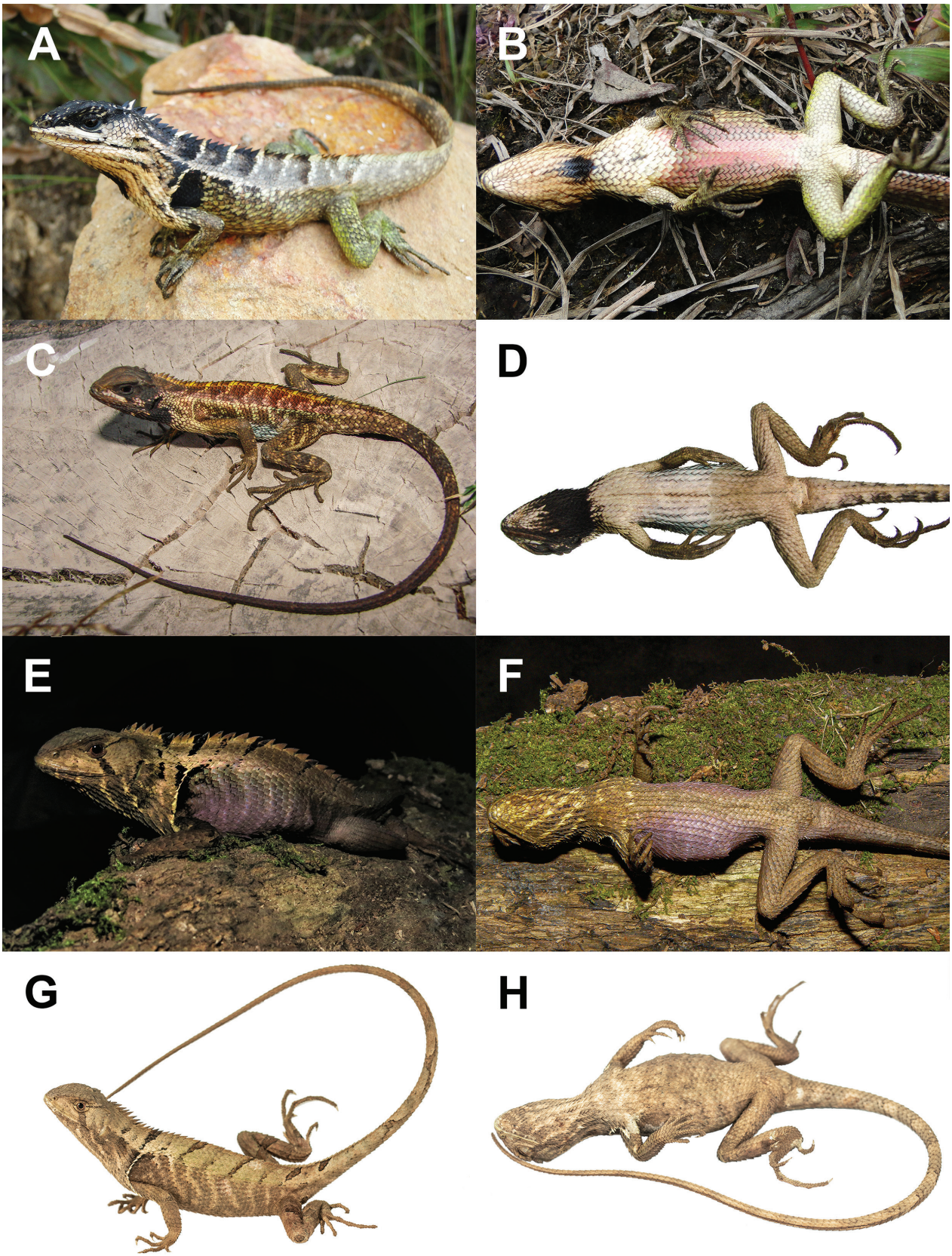

Figure 4. Dorsolateral and ventral views of adult males of three species of *Stenocercus*: (**A**, **B**) *S. huancabambae*, (**C**, **D**) *S. aculeatus*, (**E**, **F**) *S. prionotus* from northern-central Peru, and (**G**, **H**) *S. prionotus* from southern Peru. Photographs by: (**A-D**) Pablo J. Venegas, (**E**) Andy Barboza, (**F**) Diego Vasquez, and (**G, H**) German Chávez.

limbs and tail darker than in life. Moreover, the reddish coloration of the flanks almost disappears.

Intraspecific variation. Measurement and scutellation characters of *Stenocercus catherineae* sp. nov. are presented in Table 1. The second infralabial is in contact with the third sublabial in all specimens, and the first pair of postmentals are not in contact medially in two specimens (CORBIDI 501 and 21367). The three male paratypes are identical to the holotype, including a juvenile (CORBIDI 18662), varying only by having few scattered white dots on the head and, the black patch on the gular region extends to the ventral surface of the neck as a bold band (CORBIDI 21366) (Fig. 2C, D). Ventral scales in the juvenile male are strongly keeled and mucronate.

Sexual dimorphism is evident in adult individuals. In two adult female paratypes (Fig. 2E, H) dorsal coloration is dusty brown with cinnamon vertebral chevrons along the back and tail, and cinnamon blotches along the flanks; hindlimbs with scattered dark brown transverse stripes; head in both specimens are darker than the rest of body, being dark gray (CORBIDI 501) or dark brown (CORBIDI 21367); sides of head grayish white (CORBIDI 21367) or dark gray (CORBIDI 501) with the loreal and subocular region white, and labials brown. Ventral coloration is pale brown with the gular region dark brown (CORBIDI 21367) or dusty cream with the gular region dark gray (CORBIDI 501) but both specimens have a faint pink hue on belly and base of tail (Fig. 2F, H).

Distribution and natural history observations. *Stenocercus catherineae* sp. nov. is only known from three proximate localities at Huembo and Cuispes in the northern extreme of the Cordillera Central at the Río Utcubamba basin in the Department of Amazonas, at elevations between 1466 to 2085 m a.s.l. (Fig. 5). According to the terrestrial ecoregions of the world by Olson et al.

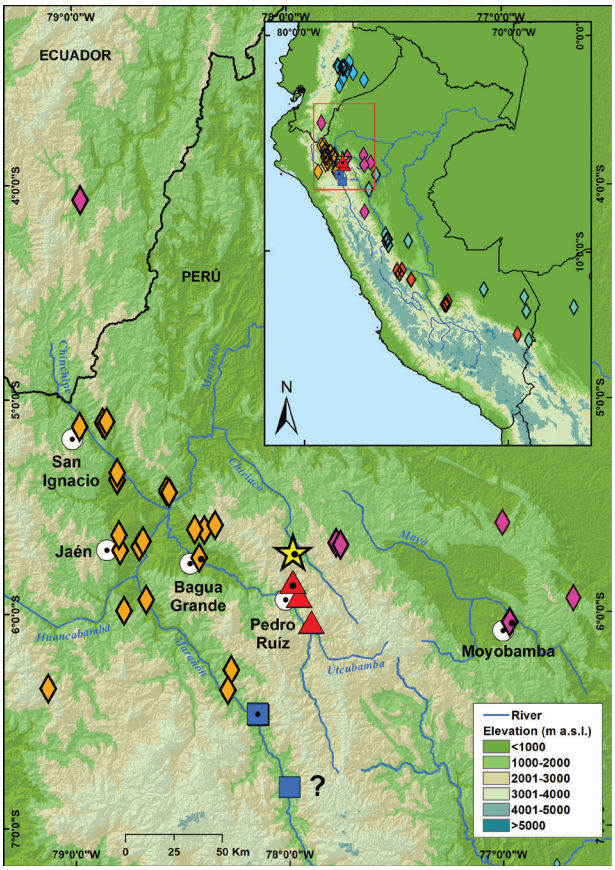

Figure 5. Distribution map of *S. catherineae* sp. nov. (red triangles), *S. dracopennatus* sp. nov. (yellow star), and *S. philmayi* sp. nov. (blue squares), and the similar species: *S. aculeatus* (fuchsia diamonds), *S. angulifer* (blue diamonds), *S. huancabambae* (orange diamonds), *S. prionotus* (turquoise diamonds), and *S. scapularis* (red diamonds). Symbols with a dot in the middle correspond to type localities. White circles with a dot are important cities for reference.

Table 1. Variation in scutellation and sexual dimorphism in snout-vent length (mm) of *Stenocercus aculeatus*, *S. catherineae* sp. nov., *S. dracopennatus* sp. nov., *S. philmayi* sp. nov., and their most similar species *S. angulifer* and *S. huancabambae*. Range followed by mean ± standard deviation is given for quantitative characters if applicable.

		S. aculeatus		*S. angulifer*	*S. catherineae*	*S. dracopennatus*	*S. huancabambae*	*S. philmayi*
Character	CORBIDI 1712	CORBIDI 11483	n = 5	n = 38	n = 6	n = 3	n = 32	n = 8
Scales around midbody	41	37	32–37	38–50	46–59	39–45	37–53	34–45
			35.00 ± 2.00	42.10 ± 2.37	53.00 ± 5.44	41.33 ± 3.21	43.94 ± 3.20	41.00 ± 3.70
Vertebrals	37	38	31–39	37–47	43–53	38–40	37–51	32–38
			35.20 ± 3.27	41.63 ± 2.25	47.33 ± 4.76	39.33 ± 1.15	43.39 ± 3.40	35.88 ± 1.96
Paravertebrals	50	53	41–48	37–57	62–73	53–57	48–64	49–59
			45.20 ± 2.95	50.42 ± 3.81	68.33 ± 4.37	54.67 ± 2.08	56.31 ± 3.74	55.14 ± 3.48
Gulars	20	18	15–18	16–20	22–26	19–20	18–28	20–24
			16.60 ± 1.14	18.47 ± 0.76	24.33 ± 1.63	19.33 ± 0.58	20.93 ± 1.64	21.75 ± 1.75
Supraoculars	5	4	4	4–5	4	4	3–6	4–5
			4	4	4	4	4	5
Internasals	5	4	4–5	4–8	4–6	4–5	4–7	3–5
			4	6	4	5	6	4
Subdigitals Finger IV	21	21	18–19	15–19	18–21	19–21	14–20	18–21
			18.80 ± 0.45	17.28 ± 1.11	19.33 ± 1.21	20.00 ± 1.00	16.81 ± 1.41	19.25 ± 1.16
Subdigitals Toe IV	31	27	23–27	19–25	25–30	26–28	20–28	28–31
			25.00 ± 1.58	22.84 ± 1.44	27.50 ± 1.64	27.00 ± 1.00	24.62 ± 1.56	29.25 ± 1.16
Tail length/total length	0.72	0.72	0.70 – 0.73	0.68–0.73	0.66–0.69 (n=5)	0.69–0.73	0.67–0.70	0.67–0.72 (n=7)
			0.71 ± 0.02	0.70 ± 0.02	0.67 ± 0.01	0.71 ± 0.02	0.69 ± 0.01	0.71 ± 0.02
Maximun SVL males	81	95	103	96	82	89	99	95
Maximun SVL females	unknown	unknown	91	82	75	unknown	75	74

(2001), this species occurs in the Peruvian Yungas ecoregion. The habitat at the type locality of *S. catherineae* sp. nov. is a steep area located on the sides of the Río Chido with presence of corn, coffee and fruit plantations, and some patches of secondary forest and shrub vegetation. Several individuals were observed basking on fallen tree trunks or at the base of bushes close to trails between 1000 and 1200 hours. When the lizards were disturbed, they ran to hide inside fern patches. No other lizards or reptiles were observed in sympatry.

At Cuispes only one individual was collected in the croplands close to the village. Other squamate reptiles collected with *S. catherineae* sp. nov. at Cuispes were *Atractus* sp. Wagler, 1828, *Dipsas palmeri* Boulenger, 1912, and *S. flagracanthus* sp. nov. At Cocachimba, the two specimens collected were found basking at 1000 hours on the base of rocky fences with bushes along a trail. An uncollected adult female was observed basking at 900 hours on a fallen wall of an abandoned house. The general landscape at Cocachimba is composed of croplands of corn, fruit and sugar cane bordered by rocky fences and some streams with narrow fringes of riverine forest or shrub vegetation. Other species of squamate reptiles collected with *S. catherineae* sp. nov. at Cocachimba were: *Atractus* sp., *Chironius exoletus* Linnaeus, 1758, *Mastigodryas boddaerti* Sentzen, 1796, and *Petracola angustisoma* Echevarría & Venegas, 2015.

The female paratype (CORBIDI 21367) collected during the rainy season (December 2019) had 2 well developed follicles, one in the left and the other in the right ovary. The sizes of these follicles are 10.83 × 9.67 mm and 10.99 × 9.53 mm; their volumes were 530.2 mm³ and 522.6 mm³, respectively.

Etymology. The specific name is a noun in the genitive case and is a patronym for Catherine Dupont, a Peruvian veterinary specialist in One Health, who is actively working searching and monitoring viruses and other zoonotic pathogens. The specific name of this lizard is in recognition of her passion for the natural world and its creatures, and her selfless support of the herpetological division of CORBIDI.

Stenocercus dracopennatus sp. nov.

http://zoobank.org/0F8C57E0-3F73-48C1-9596-3657BE465B7E

Figs 6–9

Type material. Holotype:

PERU • ♂, adult; Amazonas Department, Bongará Province, Yambrasbamba District, Yambrasbamba; 5°43.01'S, 77°58.61'W; 2370 m a.s.l.; 07 Sept. 2017; P.J. Venegas leg.; CORBIDI 18875.

Paratypes:

PERU • 2 ♂, adult and juvenile collected with the holotype; CORBIDI 18868,18876.

Diagnosis. *Stenocercus dracopennatus* sp. nov. differs from all species of *Stenocercus*, except for *S. aculeatus*, *S. angulifer*, *S. prionotus*, and *S. scapularis*, by having: (1) projecting angulate temporals, (2) laterally oriented nostrils, (3) dorsolateral crest (distinct on second half of body and base of tail in *S. prionotus*), (4) dorsal and lateral scales of body similar in size, (5) strongly keeled ventrals, and (6) scales on posterior surface of thighs keeled and imbricate.

However, *S. dracopennatus* sp. nov. can also be easily distinguished from *S. prionotus* (state of characters in parentheses) by having a low-lying vertebral crest (high and projected, Figs 4E, 9A) and postfemoral mite pocket as a slit-like opening (absent). Furthermore, *S. dracopennatus* sp. nov. differs from *S. scapularis* (state of characters in parentheses) by having a thin and inconspicuous subocular stripe (conspicuous and broad subocular stripe, Fig. 16), smooth infralabials and sublabials (keeled), a black patch covering the ventral surface of neck (absent), and 38 to 40 vertebrals (43 to 53).

Stenocercus dracopennatus sp. nov. can be readily distinguished from *S. angulifer* and *S. aculeatus* by having two canthals and a black patch covering the ventral surface of the neck (one canthal and a black patch extensively covering most of the gular region in the last two species, see Figs 4D, 7B, D). Additionally, *Stenocercus dracopennatus* sp. nov. differs from *S. aculeatus* (state of characters in parentheses) by having a longer snout (shorter, Fig. 8A, B), a low-lying vertebral crest (distinctly higher, Fig. 9A, B), a deeper posthumeral mite pocket (less deep, Fig. 8C, D), and cycloidal, smooth or feebly keeled dorsal scales at midbody between the dorsolateral crests with or without minute mucronations (lanceolate, strongly keeled and mucronate, Fig. 9C–F).

Definition. (1) Maximum SVL in males 89 mm (n = 3); (2) SVL in females unknown; (3) vertebrals 38–40; (4) paravertebrals 53–57; (5) scales around midbody 39–45; (6) supraoculars 4; (7) internasals 4–5; (8) postrostrals 2–5; (9) loreals 4–5; (10) gulars 19–20; (11) subdigitals on Finger IV 19–21; (12) subdigitals on Toe IV 26–28; (13) posthumeral mite pocket present as a deep depression with a narrow opening [Type 3 of Torres-Carvajal (2007b)]; (14) postfemoral mite pocket present as a distinct pocket with a posteroventrally oriented slit-like opening [Type 2 of Torres-Carvajal (2007b)]; (15) parietal eye not visible through interparietal cornea in any specimens (n = 3); (16) scales on occipitoparietal region large, feebly keeled or wrinkled, juxtaposed; (17) projecting angulate temporals present, two; (18) row of enlarged supraoculars occupying most of supraocular region present; (19) scales on frontonasal region feebly keeled, juxtaposed; (20) preauricular fringe present, distinct; (21) neck folds absent; (22) lateral and dorsal nuchals similar in size; (23) posterior gulars lanceolate, projected posteriorly, strongly keeled, mucronate and conspicuously imbricate; (24) lateral and dorsal body scales similar in size; (25) vertebrals larger than adjacent paravertebrals, forming a low vertebral crest; (26) dorsolateral crest present; (27) ventrals strongly keeled, imbricate, mucronate; (28) scales on posterior surfaces of thighs keeled, imbricate, mucronate; (29) inguinal granular pocket absent;

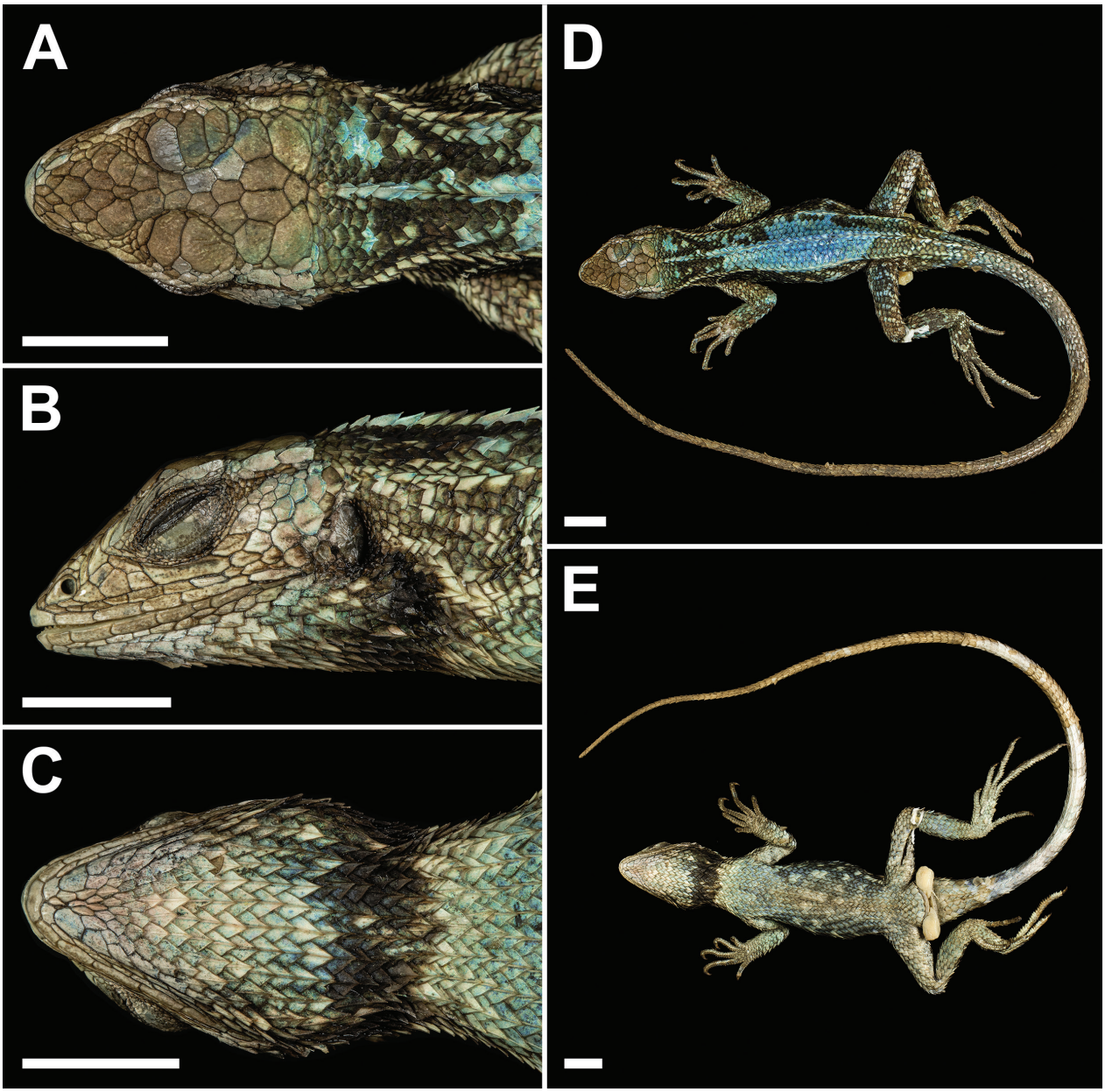

Figure 6. *Stenocercus dracopennatus* sp. nov. preserved holotype, adult male, SVL 79 mm (CORBIDI 18875): dorsal (**A**), lateral (**B**), and ventral (**C**) views of the head; dorsal (**D**) and ventral (**E**) views of the entire specimen. Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

(30) inguinal groove absent; (31) preanals projected; (32) tail compressed laterally in adult males; (33) tail length 68–72% of total length; (34) caudal whorls per autotomic segment three; (35) caudals not spinose; (36) dark brown stripe extending anterodorsally from subocular region to supraciliaries present, present only in juveniles; (37) dark patch extensively covering gular region of females unknown; (38) dark patch covering gular region in adult males absent; (39) black patch on ventral surface of neck in adult males present; (40) dark midventral longitudinal mark such as faint line, conspicuous stripe, or extensive patch in adult males absent; (41) dark patches on ventral surface of thighs in adult males absent; (42) two xiphisternal and three postxiphisternal pairs of inscriptional ribs fused medially, forming three chevrons (Pattern 6A of Torres-Carvajal 2004).

Description of the holotype. Male (Fig. 6); SVL 79 mm; TL 210 mm; maximum head width 16.4 mm; head length 20.5 mm; head height 13.5 mm; parietals, interparietals and postparietals large; interparietals keeled, parietals and postparietals barely rugose, juxtaposed; occipital small, barely wrinkled; parietal eye not visible; supraoculars in four rows, keeled, slightly imbricate, subequal in size; canthals two; canthal not in contact with the nasal; scales on frontonasal region slightly imbricate, keeled; internasals five; postrostrals five, the three on the middle longer than wide and one third longer than postrostrals on the sides; supralabials

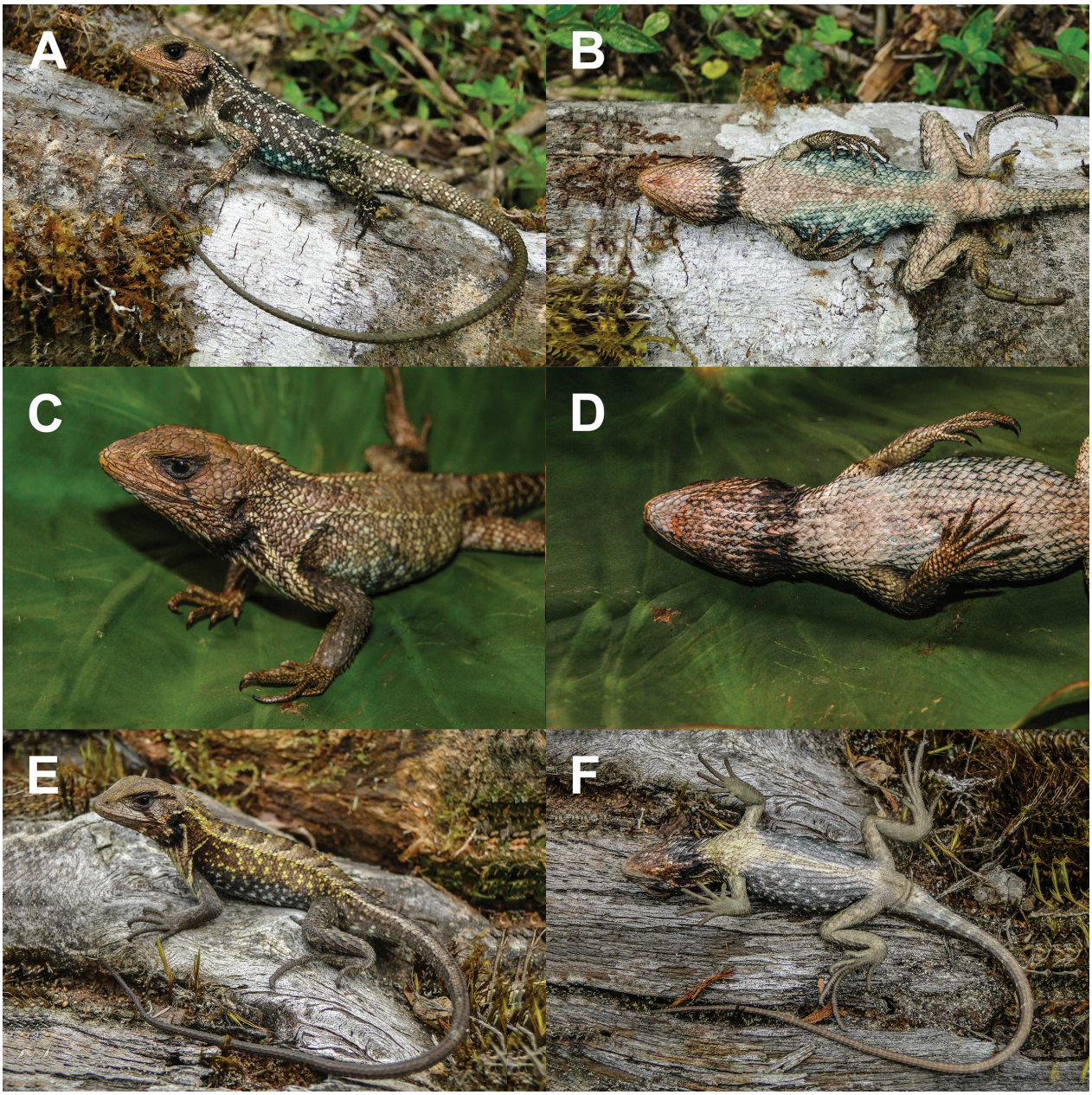

Figure 7. Dorsolateral and ventral views of *Stenocercus dracopennatus* sp. nov. in life: (**A**, **B**) holotype, adult male, SVL 79 mm (CORBIDI 18875); (**C**, **D**) adult male, SVL 88 mm (CORBIDI 18868); (**E**, **F**) juvenile male, SVL 56 mm (CORBIDI 18876). Photographs by Pablo J. Venegas.

five; infralabials seven; loreals five; lorilabials in one row; preocular one, in contact with second canthal; lateral temporals keeled, some of these with a minute mucron, imbricate; gulars in 19 rows between tympanic openings; all gulars keeled, mucronate, imbricate, posteriorly projected, apical pit absent; second infralabial in contact with first to third sublabials; mental in contact with first pair of infralabials; lateral and dorsal scales of body and neck keeled, imbricate, mucronate; lateral and dorsal body scales similar in size; scales around midbody 39; vertebrals larger than dorsals, 38 scales on vertebral row, low serrate vertebral crest present; paravertebrals 53; ventrals broad, rhomboidal, strongly keeled, mucronate, imbricate; preauricular fringe short, indistinct, composed of six small scales, all similar in size; antegular, gular, postauricular, oblique, supraauricular, longitudinal and antehumeral neck folds absent; limb scales strongly keeled, imbricate, mucronate; ventral scales of hindlimbs and upper arms strongly keeled and mucronate; lamellae on Finger IV 21; lamellae on Toe IV 28; tail compressed laterally; caudals keeled, imbricate, mucronate but without projected spines; basal subcaudals strongly keeled, imbricate; tail length 2.6 times SVL; posthumeral mite pocket present as a deep depression with a narrow opening; postfemoral mite pocket present as a distinct deep pocket with a curved slit-like opening bordering the thigh insertion; postfemoral region composed of imbricate, keeled scales.

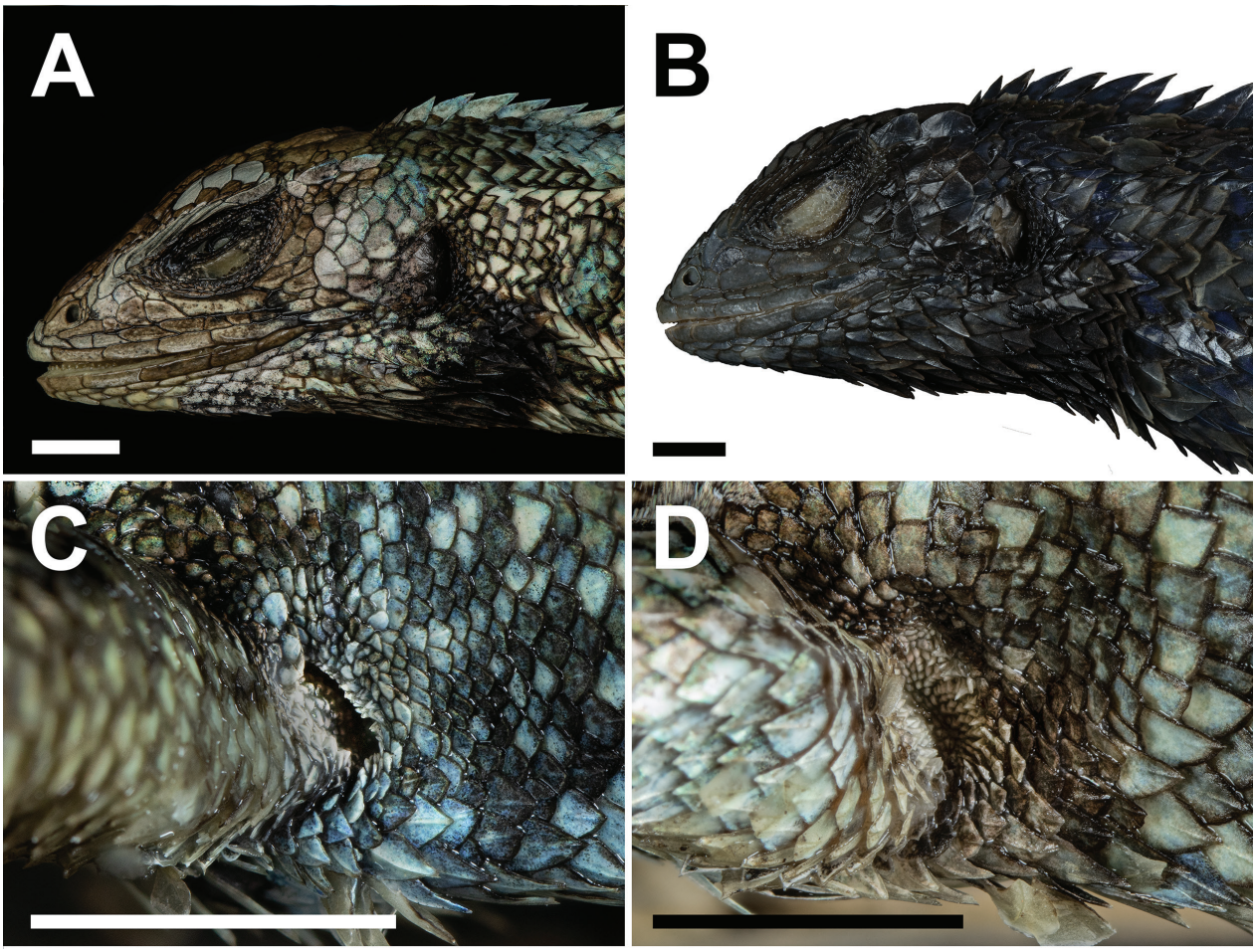

Figure 8. Lateral view of head and posthumeral mite pockets of adult male *Stenocercus* for comparison: (**A**) *S. dracopennatus* sp. nov. (CORBIDI 18868), (**B**) *S. aculeatus* (CORBIDI 11483), (**C**) *S. dracopennatus* sp. nov. (CORBIDI 18875), and (**D**) *S. aculeatus* (CORBIDI 1712). Photographs by Luis A. García-Ayachi. Scale bars: 5 mm.

Coloration in life (Fig. 7A, B). Dorsal surface of the body is dusty brown with a greenish yellow hue on the pelvic region and tail; the vertebral and dorsolateral crests are yellowish with faint gray vertebral chevrons on the back, the posterior margin of each chevron is yellowish as well; antehumeral region with a dark brown vertical stripe with the anterior margin yellowish; flanks with diagonal rows of yellowish dots; limbs and proximal half of tail with transverse yellowish stripes; ventrolateral region turquoise; sides of head sepia and ocular region black. Ventrally, gular region sepia, ventral surface of neck covered by a black patch; chest, pelvic region and ventral surface of hindlimbs, and base of tail dirty cream with the sides of belly turquoise; proximal half of the tail is also dirty cream with transverse paler bands. The iris is dark brown.

Coloration in preservative (Fig. 6D, E). Similar to the coloration in life however the dorsal background and marks are paler than in life with a long patch of depigmentation on the back. The ventral surface turns bluish gray with scattered pale blotches on the belly.

Intraspecific variation. Measurements and scutellation characters of *Stenocercus dracopennatus* sp. nov. are presented in Table 1. The first pair of postmentals are not in contact medially in one specimen (CORBIDI 18868). The adult male paratype is larger than the holotype with 89 mm of SVL and its dorsal coloration is pale compared to the holotype, lacking the dark dorsal chevrons present in the holotype (Fig. 7C). The ventral pattern is identical to the holotype (Fig. 7D). The second paratype is a juvenile male (CORBIDI 18876) with the dorsum cinnamon and with the vertebral chevrons more contrasting than in the holotype; a distinct dark brown stripe extending anterodorsally from subocular region to supraciliaries; dots on the flanks of this juvenile specimen are yellow with the dots on the axillary region whitish and lacking the turquoise hue of the adult specimens (Fig. 7E). Ventrally, the gular region is dark sepia and the rest of body whitish cream with the sides of belly dark gray and not turquoise like in the adult (Fig. 7F). Females are unknown.

Distribution and natural history observations. *Stenocercus dracopennatus* sp. nov. is only known from the type locality, a summit near Yambrasbamba village at 2370 m elevation, located on the eastern slope of the Cordillera de Colán, at the Río Chiriaco basin, Department of Amazonas, Peru (Fig. 5). According to Peñaherrera del Aguila (1989) and Olson et al. (2001), the distribution of this new species occurs within the Yungas and Peruvian Yungas ecoregions, respectively. The new species inhabits

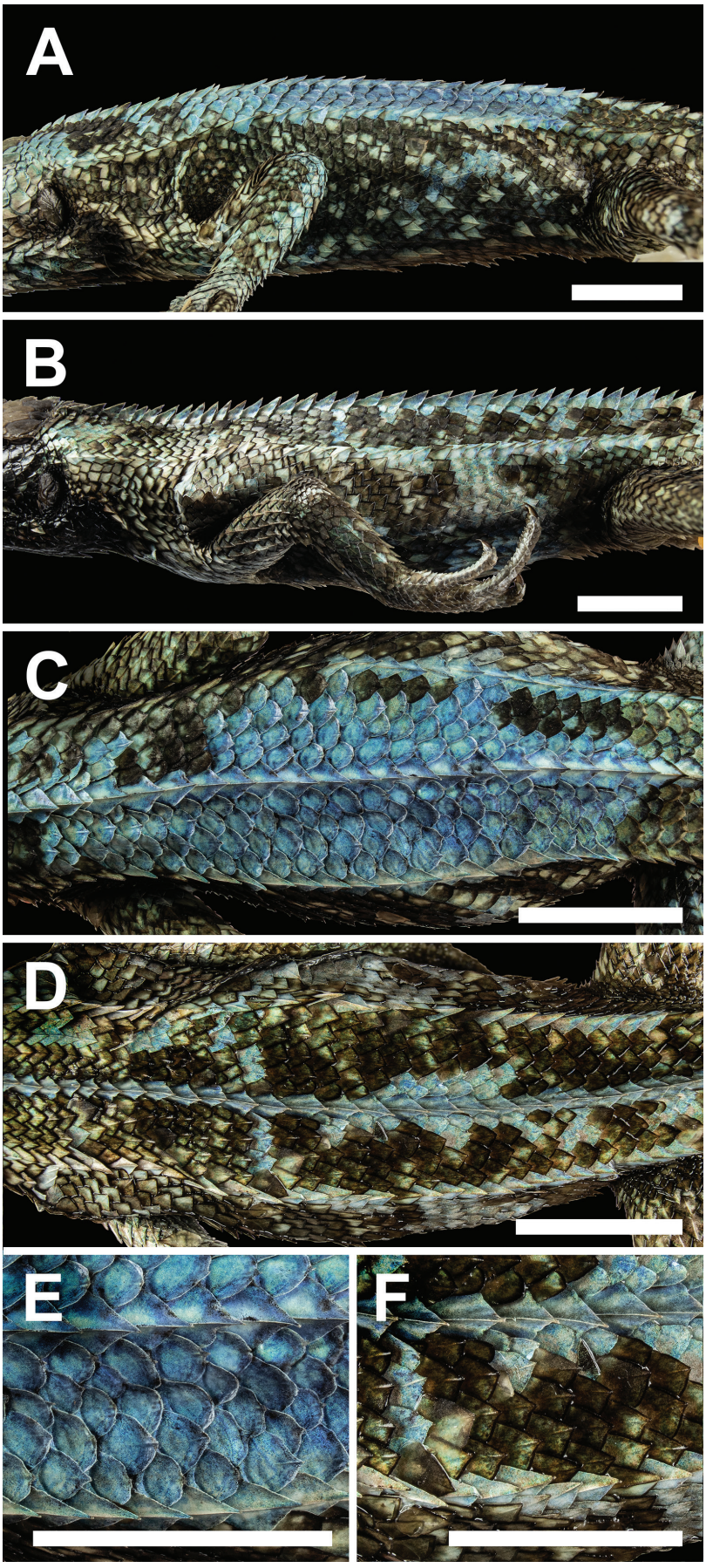

Figure 9. Lateral and dorsal views of adult males of *Stenocercus* for comparison: (**A**, **C**, **E**) *S. dracopennatus* (CORBIDI 18875) and (**B**, **D**, **F**) *S. aculeatus* (CORBIDI 1712). Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

a mountain top covered by a dwarf montane forest full of terrestrial and arboreal bromeliads on a white sand soil. Six individuals were observed basking on a sunny morning, between 1000 and 1100 hours, on the sand and on fallen branches and running to find refuge in patches of terrestrial bromeliads and long grasses. No other reptile species were found in sympatry with *S. dracopennatus* sp. nov.

Etymology. The specific epithet "*dracopennatus*" is a noun derived from two words in Latin, "*draco*" that means dragon, the mythological being, and "*pennatus*" that means feathered. The specific name is a noun in apposition and refers to the similarity between lizards and dragons, which in both Western and Chinese cultures are beings similar to reptiles like crocodiles or serpents. Moreover, due to the big scales of this new species that give it the appearance of being covered by feathers, we decided to name *S. dracopennatus* sp. nov. for its resemblance to an imaginary feathered dragon.

Stenocercus flagracanthus sp. nov.

http://zoobank.org/C2AE661B-A0E9-4E88-B3E3-E412E6F1E414

Figs 10, 11

Type material. Holotype:

PERU • ♂, adult; Amazonas Department, Bongará Province, Cuispes District, Cuispes village; 5°55.49'S, 77°56.94'W; 1850 m a.s.l.; 7 Mar. 2017; G. Chávez leg.; from farms adjacent to Cuispes village; CORBIDI 18658.

Paratypes:

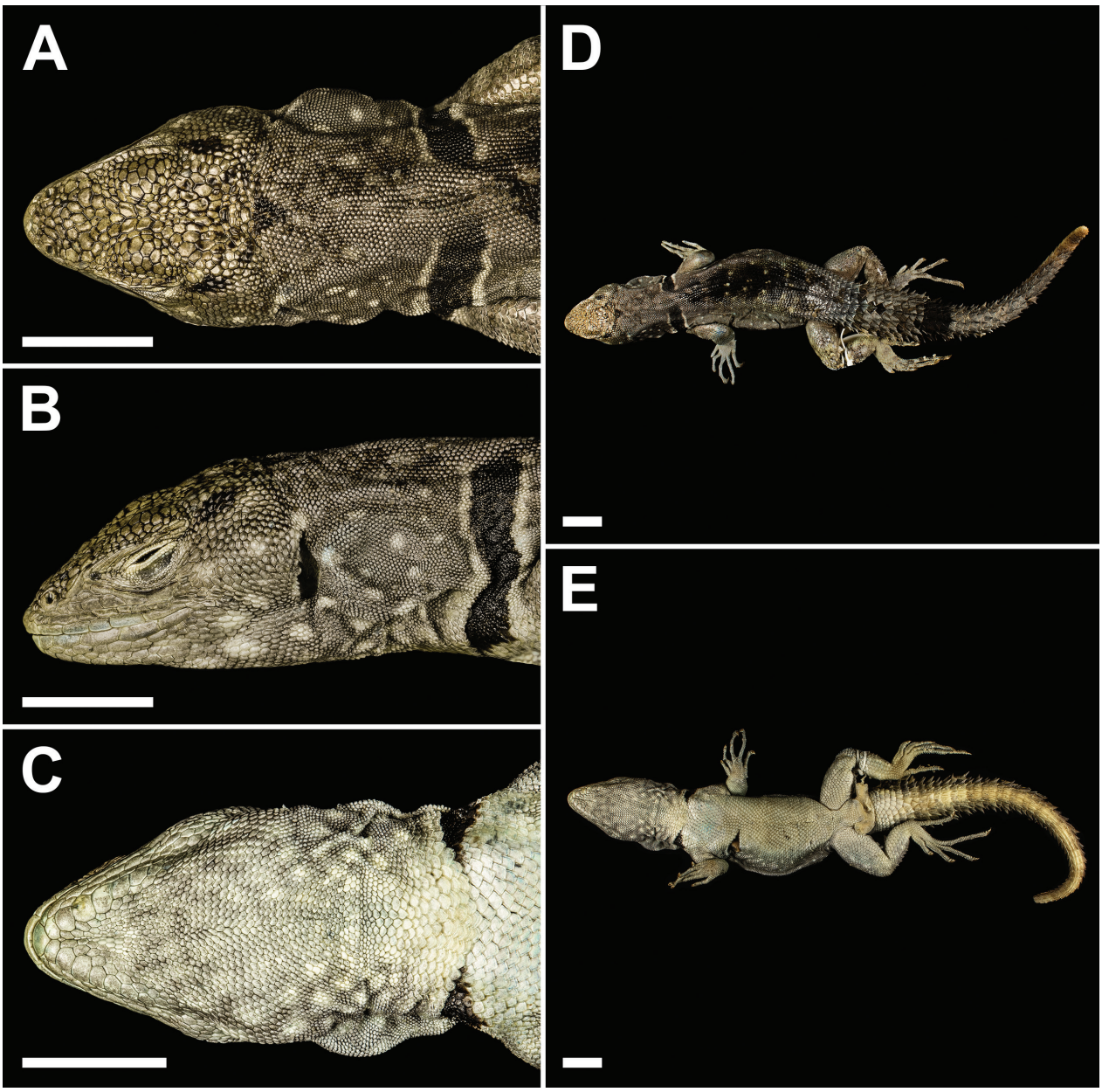

Figure 10. *Stenocercus flagracanthus* sp. nov. preserved holotype, adult male, SVL 75 mm (CORBIDI 18658): dorsal (**A**), lateral (**B**), and ventral (**C**) views of the head; dorsal (**D**) and ventral (E) views of the entire specimen. Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

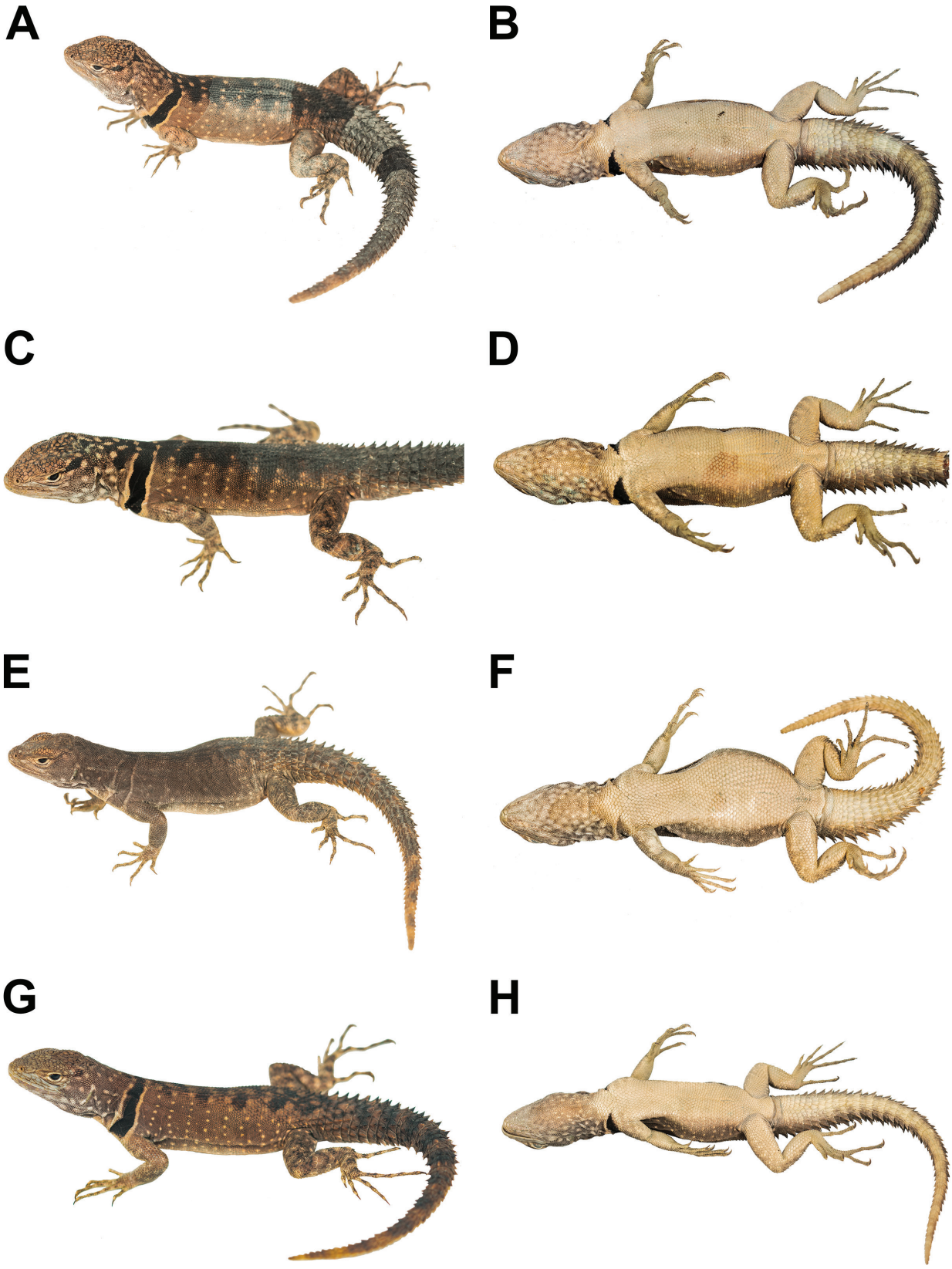

Figure 11. Dorsolateral and ventral views of *Stenocercus flagracanthus* sp. nov. in life: (**A**, **B**) holotype, adult male, SVL 75 mm (CORBIDI 18658); (**C**, **D**) adult male, SVL 72.9 mm (CORBIDI 18659); (**E**, **F**) adult female, SVL 68 mm (CORBIDI 18661); (**G**, **H**) sub adult male, SVL 61 mm (CORBIDI 18660). Photographs by German Chávez.

PERU • 2 ♂, 1 ♀, adults; collected with the holotype; CORBIDI 18659–61 • 2 ♂, adults, 1 juvenile; Amazonas Department, Bongará Province, Shipasbamba District, Canta Gallo; 5°55.43'S, 77°59.03'W; 1720 m a.s.l.; 27 Aug. 2017; A. García-Bravo leg.; CORBIDI 18748, 18749, 18750 • 1 ♀, adult; Amazonas Department,

Bongará Province, Cuispes District, Cuispes village; 5°55.79'S, 77°56.66'W; 1880 m a.s.l.; 25 Sept. 2019; L.A. García-Ayachi leg.; CORBIDI 22035.

Diagnosis. *Stenocercus flagracanthus* sp. nov. differs from all other species of *Stenocercus*, except from *S. arndti* Venegas, Echevarria & Alvarez, 2014, *S. bolivarensis* Castro & Ayala, 1982, *S. carrioni* Parker, 1934, *S. chlorostictus* Cadle, 1991, *S. crassicaudatus* Tschudi, 1845, *S. empetrus* Fritts, 1972, *S. eunetopsis* Cadle, 1991, *S. torquatus* Boulenger, 1885, and *S. simonsii* Boulenger, 1899 by having granular scales on the posterior surface of the thighs, a relatively short tail, caudals spinose and two caudal whorls per autotomic segment. Among the aforementioned species, *S. flagracanthus* sp. nov., possesses caudal scales with the most strongly projected mucrons. This difference is evident comparing *S. flagracanthus* sp. nov. with *S. carrioni*, *S. crassicaudatus*, *S. empetrus*, *S. eunetopsis*, and *S. simonsii*, and to a lesser degree comparing it with *S. arndti*, *S. chlorostictus* and *S. torquatus*. Moreover, the size of mucrons along the second half of the tail in *S. flagracanthus* sp. nov., is clearly alternating, with large mucrons followed by small mucrons per each caudal whorl. In the other species, this character is indistinct or only possible to observe at the distal extreme, like in *S. carrioni*. With the goal of facilitating the distinction between *S. flagracanthus* sp. nov. and the aforementioned species, herein, we provide more differences.

Stenocercus flagracanthus sp. nov. differs from *S. carrioni*, *S. chlorostictus* and *S. euneptopsis* by having dorsal scales of the neck granular and not keeled (keeled and imbricate in the three former species). *Stenocercus flagracanthus* sp. nov. can be easily distinguished from *S. crassicaudatus* and *S. empetrus* by having a distinct black antehumeral collar (faint or absent in the remaining species). *Stenocercus crassicaudatus*, *S. euneptopsis* and *S. simonsii* have longer tails than *S. flagracanthus* sp. nov. with 57 to 62%, 64 to 66%, and 57 to 63% versus 50 to 54% of total length, respectively. *Stenocercus flagracanthus* sp. nov. also differs from *S. crassicaudatus* by having fewer scales around midbody with 96 to 104 ($\bar{x}$ = 99.63) in the new species, and 97 to 121 ($\bar{x}$ = 108.87) in *S. crassicaudatus*. *Stenocercus flagracanthus* sp. nov. differs from *S. bolivarensis* by having granular lateral body scales versus strongly keeled and imbricate lateral body scales (Torres-Carvajal 2007b).

Males of *S. arndti* are easily distinguished from *S. flagracanthus* sp. nov. by having a bold black transverse band at midbody that extends ventrolaterally (absent in *S. flagracanthus* sp. nov.). *Stenocercus torquatus* can be distinguished from *S. flagracanthus* sp. nov. by having black nuchal bands, absent in *S. flagracanthus* sp. nov. Moreover, *Stenocercus torquatus* has more scales around midbody than *S. flagracanthus* sp. nov. (120 to 137, $\bar{x}$ = 116.96 versus 96 to 104, $\bar{x}$ = 99.63, respectively). *Stenocercus empetrus* can be easily separated from *S. flagracanthus* sp. nov. by the ventral coloration, venter yellowish-orange with black reticulations in the former and whitish gray without reticulations in *S. flagracanthus* sp. nov.

Stenocercus roseiventris D'Orbigny in Duméril & Bibron, 1837 and *S. marmoratus* Duméril & Bibron, 1837 share with *S. flagracanthus* sp. nov. the presence of caudal scales with strongly projected mucrons but differ by having the scales on the dorsal surface of neck and posterior surface of thighs imbricate and keeled.

Definition. (1) Maximum SVL in males 76.8 mm (n = 5); (2) maximum SVL in females 68.3 mm (n = 1); (3) vertebrals 83–97; (4) paravertebrals 95–111; (5) scales around midbody 96–104 (6) supraoculars 4–6; (7) internasals 4–6; (8) postrostrals 4–5; (9) loreals 4–7; (10) gulars 55–62; (11) lamellae on Finger IV 26–29; (12) lamellae on Toe IV 30–33; (13) posthumeral mite pocket present as one or more vertical folds or ridges [Type 1 of Torres-Carvajal (2007b)]; (14) postfemoral mite pocket distinct with slit-like opening [Type 2 of Torres-Carvajal (2007b)]; (15) parietal eye absent; (16) occipital scales small, smooth, juxtaposed; (17) projecting angulate temporal absent; (18) row of enlarged supraoculars occupying most of supraocular region absent; (19) scales on frontonasal region juxtaposed, smooth; (20) preauricular fringe short; (21) antegular, antehumeral, gular, longitudinal, oblique, postauricular, and supra-auricular neck folds present; (22) lateral nuchals and dorsals similar in size; (23) lateral body scales, granular, smaller than dorsals, becoming slightly imbricate toward the groin; (24) vertebrals slightly enlarged, forming a distinct row of scales from forelimbs to hindlimbs; (25) dorsolateral crest absent; (26) paravertebrals from the second third of dorsum, like the adjacent dorsals, becoming gradually larger, imbricate, keeled and mucronate toward the hindlimb insertion; (27) ventral scales smooth, imbricate; (28) scales on posterior surface of thighs granular; (29) prefemoral fold present; (30) inguinal groove present; (31) preanals not projected; (32) tail not compressed laterally; (33) tail relatively short (tail length 50–54% of total length); (34) caudal whorls per autotomic segment two; (35) tail strongly spinose; (36) postocular stripe present; (37) gular region in males grayish with cream dots; (38) gular region in females grayish with pale dots; (39) black patch on ventral surface of neck in adult males absent; (40) dark midventral stripe in adult males absent; (41) dark patch on ventral surface of thighs, vent and tail in adult males absent; (42) background color of dorsum pale brown in males and gray in females, but with distinct black transversal stripes in both sexes; (43) two post-xiphisternal pairs of inscriptional ribs, one long (not in contact midventrally) and the other short (Pattern 1B of Torres-Carvajal 2004).

Description of holotype. Male (Fig. 10); SVL 75.0 mm; TL 87.0 mm; maximum head width 16.0 mm; head length 19.0 mm; head height 12.4 mm; scales on parietal and occipital regions small, smooth, juxtaposed, subequal in size; parietal eye not visible: supraoculars smooth, juxtaposed; circumorbitals absent; canthals two; loreals six; postrostrals four; internasals five; supralabials five; infralabials five; lorilabials in one row; preocular divided into two scales, most dorsal in contact with poste-

rior canthal; lateral temporals granular; gulars in 56 rows between tympanic openings; all gulars cycloid, smooth, imbricated; second infralabial in contact with first and second sublabials; first pair of postmentals in contact; mental in contact with first pair of infralabials and first pair of postmentals; dorsal and lateral scales of neck granular until the level of arm insertion, becoming gradually enlarged, imbricate, keeled to strongly keeled, and mucronate toward the hindlimbs insertion; lateral scales of body granular becoming slightly imbricate and feebly keeled toward the groin; scales around midbody 101; vertebrals 97 enlarged, keeled on the second half of body, imbricate, forming indistinct vertebral row; paravertebrals adjacent to vertebrals row larger than dorsals, keeled, imbricate becoming larger and mucronate toward hindlimb insertion; paravertebrals 111; ventrals smooth, imbricate, nearly twice the size of the dorsals, only paravertebrals near hindlimb insertion are twice the size of ventrals; preauricular fringe short composed of five enlarged, granular scales; suprauricular, antehumeral, gular, longitudinal, oblique, antegular, postauricular and rictal neck folds present; dorsolateral, ventrolateral and prefemoral folds present; dorsal scales of forelimbs imbricate, feebly keeled; dorsal scales of hindlimbs imbricate, strongly keeled and mucronate; ventral humeral scales granular becoming imbricate toward to the forearm; ventral scales of forelimbs and hindlimbs smooth, imbricate; palmar and plantar scales imbricate, keeled; lamellae on Finger IV 29; lamellae on Toe IV 33; tail rounded (tail length 53% of total length); caudal scales keeled, strongly mucronate, imbricate; basal subcaudal scales smooth, imbricate; posthumeral mite pocket present as one or more vertical folds or ridges; postfemoral mite pocket distinct with slit-like opening.

Coloration in life (Fig. 11A, B). Dorsal surface pale brown spattered with dirty cream dots bearing a distinct black collar (incomplete dorsally) with dirty cream borders, broad black stripes without pale interspaces along dorsum, finely blotched with black on neck and limbs, and a middorsal triangular black blotch posterior to occiput; dorsal surface of head with black flecks; side of head with the loreal region, subocular scale, and jaws gray, supralabials and temporal region pale brown with a postocular black stripe; tail black with the distal quarter brown. Ventral surface creamy gray with the gular region gray with faint cream blotches better defined on the sides; tail surface at the distal half gray. Iris pale brown.

Coloration in preservative (Fig. 10D, E). Dorsal coloration gray, except on the head that remains brown, dots whitish cream, the borders of the collar white, and the black marks as in life. Ventral surface whitish cream with the gular region darker than in life.

Intraspecific variation. Measurements, scutellation, and other morphological characters of *Stenocercus flagracanthus* sp. nov. are presented in Table 2. Loreals 4–7; supralabials 4–6; infralabials 5; second infralabials in contact with third sublabials in 75% of specimens; first pair of postmentals in contact medially in all specimens. In one dissected paratype the pattern was two xiphisternal and two postxiphisternal pairs of inscriptional ribs, one long but not in contact midventrally and the other short [Pattern 1B; Torres-Carvajal (2004)].

The adult male paratypes ($n = 4$) are identical to the holotype (Fig. 11). Sexual dimorphism is noticeable in size, the single collected female (CORBIDI 18661) is smaller than males (Table 2). The black collar can be complete or incomplete and is present in both sexes, gray in the single female paratype and black in males. The dorsum in the female paratype is grayish brown; the dorsal black marks along the back of males are faint gray and black on the pelvic region and tail (Fig. 11E, F). The single juvenile specimen has the dorsum gray including the tail with a well-defined complete dark gray collar but without the transverse black stripes of the adult individuals and dorsal surface of head brown.

Distribution and natural history observations. *Stenocercus flagracanthus* sp. nov. is only known from two close localities, Cuispes village and Canta Gallo, both on the Amazon versant of the extreme northern portion of the central Andes in the Río Utcubamba basin (Department of Amazonas), at elevations of 1720 and 1880 m (Fig. 12). According to Peñaherrera del Aguila (1989) and Olson et al. (2001), the distribution of this new species occurs within the Yungas and Peruvian Yungas ecoregions, respectively. The habitat of *S. flagracanthus* sp. nov. lies within agricultural lands with a mixture of corn, fruit trees and coffee plantations, and also pastures for livestock. The area east of Cuispes village has some montane forest remnants in steep areas but no individual of *S. flagracanthus* sp. nov. was observed there. Also, the road between Cuispes and Shipasbamba pos-

Table 2. Variation in scutellation and sexual dimorphism in snout-vent length (mm) of *Stenocercus flagracanthus* sp. nov., and the similar species *S. crassicaudatus* and *S. torquatus*. Range followed by mean ± standard deviation is given for quantitative characters if applicable. Scale counts and measurements of *S. crassicaudatus* and *S. torquatus* were taken from Torres-Carvajal (2007a).

	S. flagracanthus	*S. crassicaudatus*	*S. torquatus*
Character	$n = 8$	$n = 31$	$n = 46$
Scales around midbody	96–104	97–121	102–137
	99.63 ± 2.88	108.87 ± 5.99	116.96 ± 8.21
Vertebrals	83–97	83–97	83–115
	89.38 ± 5.21	89.80 ± 3.74	98.86 ± 7.94
Paravertebrals	95–111	107–166	103–151
	100.13 ± 5.41	126.67 ± 12.21	124.05 ± 12.17
Gulars	55–62	44–55	47–67
	57.50 ± 2.20	49.57 ± 2.73	54.09 ± 4.58
Supraoculars	4–6	6–8	6–8
	5	6	7
Internasals	4–6	4–7	4–6
	5	6	4
Subdigitals Finger IV	26–29	23–32	22–29
	27.38 ± 1.19	28.53 ± 1.80	25.76 ± 1.49
Subdigitals Toe IV	30–33	26–38	26–32
	31.28 ± 1.06	33.00 ± 2.86	28.96 ± 1.55
Tail length/total length	0.51–0.54 (n = 7)	0.57–0.62	0.47–0.54
	0.52 ± 0.01	0.59 ± 0.01	0.51 ± 0.02
Maximun SVL males	77	95	84
Maximun SVL females	68	85	74

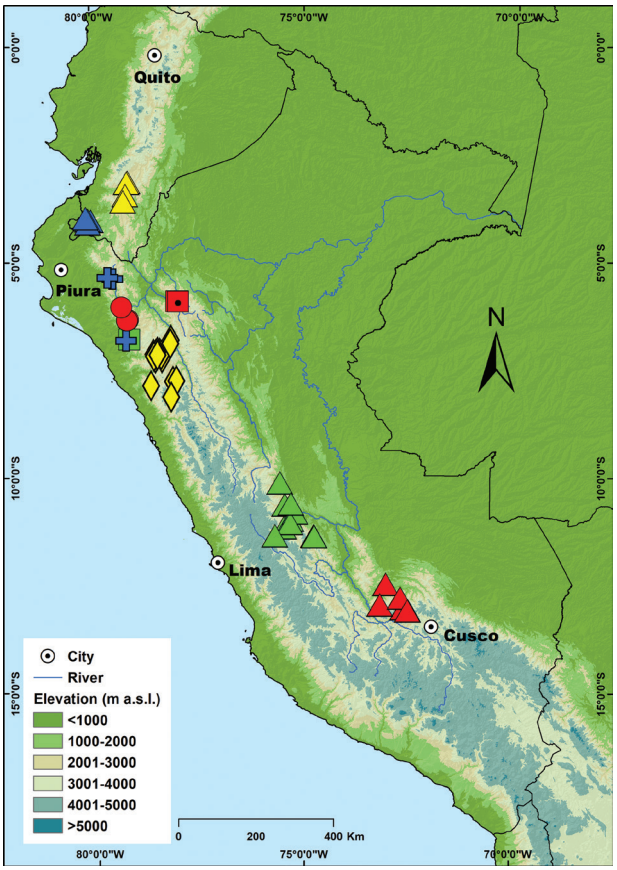

Figure 12. Distribution map of *Stenocercus flagracanthus* sp. nov. (red square) and its most similar species: *S. arndti* (red circles), *S. carrioni* (blue triangles), *S. chlorostictus* (blue crosses), *S. crassicaudatus* (red triangles), *S. empetrus* (yellow diamonds), *S. eunetopsis* (green square), *S. torquatus* (green triangles), and *S. simonsii* (yellow triangles). Symbol with a dot in the middle corresponds to type locality. White circles with a dot are important cities for reference.

sesses steep areas covered by montane forest, however our surveys in this zone remain superficial. Individuals were observed basking on house walls and roofs, using crevices as retreats and also on piles of firewood close to houses. One individual was found basking on a rocky fence close to a house.

The single female paratype collected during the rainy season (March 2017) had 2 well-developed follicles, one each in the left and right ovary. The sizes of these follicles are 18.65 × 9.80 mm and 18.88 × 10.25 mm; their volumes were 937.8 mm³ and 1038.6 mm³, respectively. *Stenocercus flagracanthus* sp. nov. was found sympatric with *S. catherineae* sp. nov., *Dipsas palmeri*, *Atractus* sp. and *Chironius exoletus*.

Etymology. The specific epithet "*flagracanthus*" is a noun in apposition derived from the Latin words "*flagrum*" (= whip, derived from "*flagellum*") and the Greek "*acanthos*" (= spine or thorn). It refers to the spiny tail of this new species of lizard that resembles the ancient Roman torture tool, the "flagrum", a whip-like instrument with accessories for inflicting damage.

Stenocercus philmayi sp. nov.

http://zoobank.org/82F392EA-A164-46F6-9461-1B197FE52804

Figs 13, 14

Type material. Holotype:

PERU • ♂, adult; Amazonas Department, Luya Province, Pisuquía District, Las Corontas; 6°28.54'S, 78°8.77'W; 1340 m a.s.l.; 15 Dec. 2019; I. Wong and A. García-Bravo leg.; CORBIDI 21092.

Paratypes:

PERU • 1 ♀, adult, 1 juvenile; collected with the holotype; CORBIDI 21090, 21093 • 2 ♂, adults, 2 juveniles; Amazonas Department, Luya Province, Pisuquía District, Las Corontas; 6°28.75'S, 78°8.52'W; 1470 m a.s.l.; 13 Dec. 2019; I. Wong and A. García-Bravo leg.; CORBIDI 21074, 21078, 21075, 21087 • 1 ♂, adult; Amazonas Department, Luya Province, Pisuquía District, Las Corontas; 6°28.79'S, 78°8.61'W; 1390 m a.s.l.; 13 Dec. 2019; I. Wong and A. García-Bravo leg.; CORBIDI 21077.

Diagnosis. *Stenocercus philmayi* sp. nov. differs from other species of *Stenocercus* except for *S. aculeatus*, *S. angulifer*, *S. catherineae* sp. nov., *S. dracopennatus* sp. nov., *S. huancabambae*, *S. prionotus*, and *S. scapularis* by having: (1) projecting-angulate temporals, (2) laterally oriented nostrils; (3) dorsal and lateral scales of body similar in size, and (3) scales on posterior surface of thighs keeled and imbricate. *Stenocercus aculeatus*, *S. angulifer* and *S. scapularis* differs from *S. philmayi* sp. nov. by having a dorsolateral crest (absent in *S. philmayi* sp. nov.). *Stenocercus prionotus* and *S. philmayi* sp. nov. share a prominent vertebral crest, however the former lacks a postfemoral mite pocket (present in *S. philmayi* sp. nov.). Adult males of *S. aculeatus* and *S. angulifer* can be easily distinguished from *S. philmayi* sp. nov. by having the gular region covered by a black patch (absent in the new species) and fewer gulars (15 to 18 in *S. aculeatus* and 16 to 20 in *S. angulifer* versus 20 to 24 in *S. philmayi* sp. nov.). The new species differs from *S. scapularis* by having fewer scales around midbody (34 to 45 in *S. philmayi* sp. nov. versus 52 to 70 in *S. scapularis* according with Torres-Carvajal (2007b)).

The new species shares the presence of two canthals with the geographically close *S. catherineae* sp. nov. and *S. dracopennatus* sp. nov. (all from the northern extreme of the central Andes in the Department of Amazonas). However, *S. philmayi* sp. nov. possesses conspicuously larger dorsal scales than *S. catherineae* sp. nov., resulting in 32 to 38 vertebrals and 34 to 45 scales around midbody (43 to 53 vertebrals and 46 to 59 scales around midbody in *S. catherineae* sp. nov.). Adult males of *S. catherineae* sp. nov. have a black patch covering most of the gular region (Fig. 2B, D) and *S. huancabambae* has a black elongate or circular patch covering the ventral surface of the neck (Fig. 4B), and both species share a pink coloration on the belly and the base of the tail (Fig. 2B, 4B); whereas the new species lacks a black or pink coloration on ventral surfaces (Fig. 14B, D). Additionally, *S. huan-*

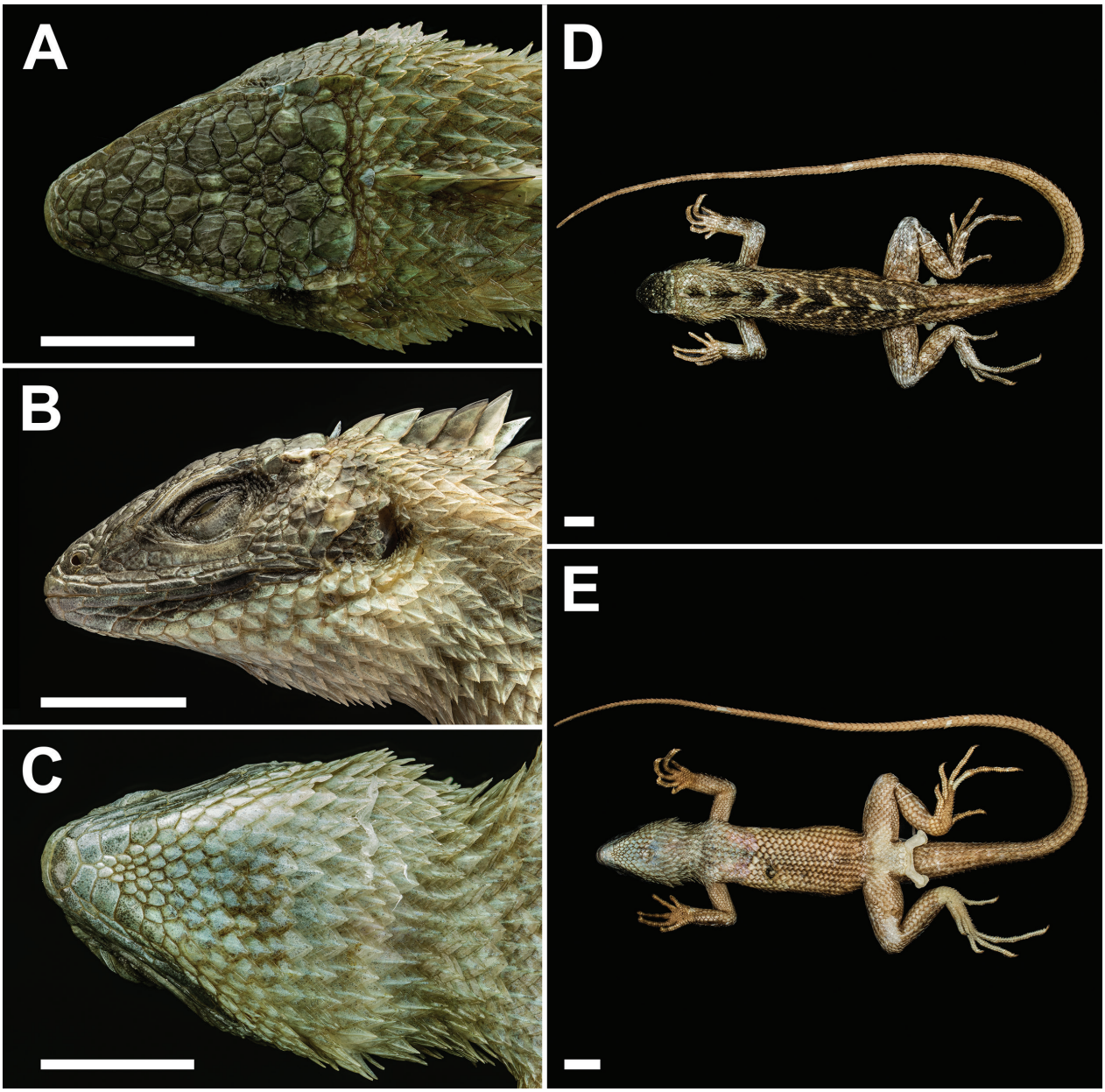

Figure 13. *Stenocercus philmayi* sp. nov. preserved holotype, adult male, SVL 95 mm (CORBIDI 21092): dorsal (**A**), lateral (**B**), and ventral (**C**) views of the head; dorsal (**D**) and ventral (**E**) views of the entire specimen. Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

cabambae possesses a very strongly compressed tail laterally compared to the compressed tail of *S. philmayi* sp. nov. In the case of *S. dracopennatus* sp. nov., it can be distinguished from *S. philmayi* sp. nov. (character state in parentheses) by having three occipitals (one), a black patch on the ventral surface of neck in adult males (dark coloration absent on ventral surface), and strongly keeled scales on the belly (keeled).

Definition. (1) Maximum SVL in males 95 mm (n = 4); (2) SVL in females 74 mm (n = 1); (3) vertebrals 32–38; (4) paravertebrals 49–59; (5) scales around midbody 34–45; (6) supraoculars 4–5; (7) internasals 3–5; (8) postrostrals 2–4; (9) loreals 4–6; (10) gulars 20–24; (11) subdigitals on Finger IV 18–21; (12) subdigitals on Toe IV 28–31; (13) posthumeral mite pocket present as a deep depression with a narrow opening [Type 3 of Torres-Carvajal (2007b)]; (14) postfemoral mite pocket present as a distinct pocket with a posteroventrally oriented slit-like opening [Type 2 of Torres-Carvajal (2007b)]; (15) parietal eye not visible through interparietal cornea in any specimens (n = 8); (16) scales on occipitoparietal region large, keeled, not imbricate; (17) projecting, angulate temporals present; (18) row of enlarged supraoculars occupying most of supraocular region present; (19) scales on frontonasal region not imbricate; (20) preauricular fringe present, distinct; (21) neck folds absent; (22) lateral and dorsal nuchals similar in size; (23) posterior gulars rhomboidal, projected posteriorly, keeled and con-

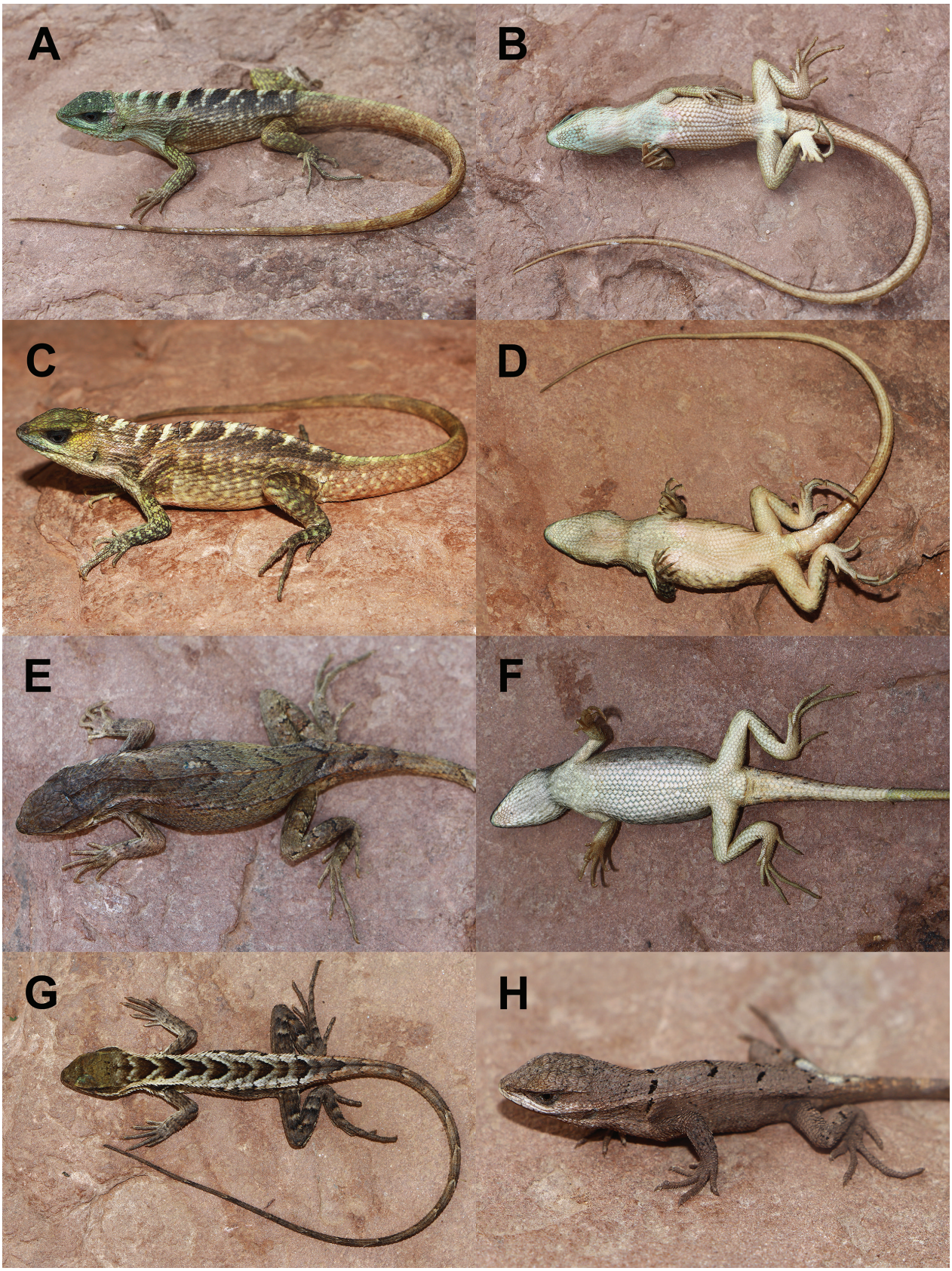

Figure 14. Dorsolateral and ventral views of *Stenocercus philmayi* sp. nov. in life: (**A**, **B**) holotype, adult male, SVL 95 mm (CORBIDI 21092); (**C**, **D**) adult male, SVL 86.0 mm (CORBIDI 21077); (**E**, **F**) adult female, SVL 74 mm (CORBIDI 21090); (**G**) juvenile male, SVL 55 mm (CORBIDI 21075); and (**H**) hatchling, SVL 33 mm (CORBIDI 21093). Photographs by Iván Wong.

spicuously imbricate, not notched; (24) lateral and dorsal body scales similar in size; (25) vertebrals larger than adjacent paravertebrals, forming a prominent vertebral crest; (26) dorsolateral crest absent; (27) ventrals keeled, imbricate, not mucronate; (28) scales on posterior surfaces of thighs keeled, imbricate, mucronate; (29) inguinal granular pocket absent; (30) inguinal groove absent; (31) preanals projected; (32) tail compressed laterally in adult males; (33) tail length 71–72% of total length; (34) caudal whorls per autotomic segment three; (35) caudals not spinose; (36) dark brown stripe extending anterodorsally from subocular region to supraciliaries absent; (37) dark patch extensively covering gular region of females absent; (38) dark patch covering gular region in adult males absent; (39) black patch on ventral surface of neck in adult males absent; (40) dark midventral longitudinal mark such as faint line, conspicuous stripe, or extensive patch in adult males absent; (41) dark patches on ventral surface of thighs in adult males absent; (42) two xiphisternal and three postxiphisternal pairs of inscriptional ribs fused medially, forming three chevrons (Pattern 6A of Torres-Carvajal 2004).

Description of the holotype. Male (Fig. 13); SVL 95 mm; TL 246 mm; maximum head width 17.5 mm; head length 22.5 mm; head height 15.4 mm; parietals, interparietals and postparietals large, parietals rugose and the rest of scales keeled, not imbricate; occipitals three, small, keeled; parietal eye not visible; supraoculars in five rows, keeled, slightly imbricate, subequal in size; canthals two; canthal in contact with the nasal; scales on frontonasal region slightly imbricate, keeled; internasals four; postrostrals four, both wider than long; supralabials five; infralabials six; loreals five; lorilabials in one row; preocular one, in contact with second canthal; lateral temporals keeled, imbricate; gulars in 20 rows between tympanic openings; all gulars keeled, imbricate, apical pit absent; second infralabial not in contact with second and third sublabials; mental in contact with first pair of infralabials; lateral and dorsal scales of body and neck keeled, imbricate, mucronate; lateral and dorsal body scales similar in size; scales around midbody 40; vertebrals larger than dorsals, 35 scales on vertebral row, prominent serrate vertebral crest present; paravertebrals 59; ventrals broad, rhomboidal, keeled, imbricate; preauricular fringe short, composed of four enlarged scales, all similar in size; antegular, gular, postauricular, oblique, supraauricular, longitudinal and antehumeral neck folds absent; limb scales keeled, imbricate, mucronate; ventral scales of hindlimbs and upper arms keeled and mucronate; lamellae on Finger IV 18; lamellae on Toe IV 31; tail compressed laterally; caudals keeled, imbricate, mucronate; basal subcaudals strongly keeled, imbricate; tail length 3.42 times SVL; posthumeral mite pocket present as a deep depression with a narrow opening; postfemoral mite pocket present as a distinct shallow pocket with a posteroventrally oriented slit-like opening; postfemoral region composed of imbricate, keeled scales.

Coloration in life (Fig. 14A, B)**.** Dorsal surface of body greenish gray with dark brown chevrons and narrow greenish white interspaces over the vertebral line; body flanks dusty brown splattered with whitish dots; dorsal surface of limbs olive green with scattered faint brown specks; dorsal surface of tail dusty brown with the crest greenish cream and faint cream transversal stripes; dorsal surface of head pale green with some scattered cream dots; sides of head greenish cream with the ocular region dark green; sides of neck greenish cream as the sides of head. Ventrally, gular region pale greenish cream; neck and chest paler than gular region; belly and tail cream with a tan hue; pelvic region pale cream and hindlimbs tan. The iris is dark brown.

Coloration in preservative (Fig. 13D, E)**.** Similar to the life coloration however the greenish hue on the dorsum is pale brown and dorsal surface of the head is dark gray. Ventrally, gular region and chest dusty gray with a bluish hue, the rest of body is dark tan with the pelvic region dark cream.

Intraspecific variation. Measurements and scutellation of *Stenocercus philmayi* sp. nov. are presented in Table 1. Second infralabial not in contact with third sublabial in any specimens, and first pair of postmentals not in contact medially in one specimen. The other adult male paratypes ($n = 3$) are identical to the holotype (Fig. 14C, D). Two juvenile males (CORBIDI 21087 and 21075) have the same dorsal pattern as adults (Fig. 14G) However, the dorsal surface of the head is brown, the greenish hue of the sides of head, neck and forearms is absent, and they possess a cream dorsolateral stripe that extends from the loreal region to the scapular region in CORBIDI 21087 and to the base of tail in CORBIDI 21075. Ventrally juvenile males are cream with scattered elongate pale gray blotches on neck, chest and sides of belly. The single hatchling paratype (CORBIDI 21093) has the dorsal surface dark brown with narrow black chevrons over the vertebral line and a longitudinal cream stripe from the loreal region to the scapular region (Fig. 14H). The dorsal surface of the hindlimbs also presents thin black bars. Ventral surface is cream without marks.

Sexual dimorphism is evident in adults. Dorsal coloration in a single female paratype (CORBIDI 21090) is dark brown with thin darker brown chevrons and darker thin brown bars on hindlimbs (Fig. 14E, F). Also present a longitudinal cream stripe from the loreal region to scapular region becoming faint from the temporal region. Ventral surface is completely cream without marks.

Distribution and natural history observations. *Stenocercus philmayi* sp. nov. is only known from Las Corontas in the northern portion of the central Andes at elevations of 1340–1470 m within the Río Marañón basin (Fig. 5). According to the terrestrial ecoregions of the world by Olson et al. (2001), this species inhabits the Marañón dry forests ecoregion and following the ecoregions of Brack-Egg (1986), the equatorial dry forest ecoregion. The general landscape in the habitat of *S. philmayi* sp. nov. is the ecotone between dry forest and

humid montane forest. The dry forest in this zone has high trees with a canopy between 4 and 6 m, dense understory vegetation and scattered patches of cacti. Individuals of *S. philmayi* sp. nov. were observed during sunny days between 800 and 1400 hours basking on fallen logs close to trails that border or cross patches of forest. One adult male specimen was collected basking in the understory vegetation at 1 m in height. Other individuals were observed basking on rocks in patches of cacti and also on rocky fences with bushes near houses. Additional squamate reptile species collected with *S. philmayi* sp. nov. were *Ameiva aggerecusans* Koch, Venegas, Rödder, Flecks & Böhme, 2013, *Microlophus stolzmanni* Steindachner, 1891, *Phyllodactylus pachamama* Koch, Flecks, Venegas, Bialke, Valverde & Rödder, 2016, *Epictia septemlineata* Koch, Venegas & Böhme, 2015, and *E. antoniogarciai* Koch, Venegas & Böhme, 2015.

Cadle (2001), reported an undescribed species of *Stenocercus* (represented by a single specimen), from 17 km ENE of Balsas village (6°49.00'S, 78°0.00'W) (Fig. 4) with similar features to *S. philmayi* sp. nov. The location of this specimen is 40.5 km to the south of the type locality of *S. philmayi* sp. nov. at an elevation of 1477 m, and lies also in the Marañón dry forests ecoregion.

The single female paratype collected during the rainy season (December 2019) had 2 eggs, one in the left and one in the right ovary. The sizes of these follicles are 19.71 × 9.44 mm and 19.81 × 8.40 mm; their volumes were 919.6 mm³ and 731.8 mm³, respectively.

Etymology. The specific epithet *philmayi* is a noun in the genitive case and is a patronym for Philip May (1946–2017), an American lichenologist and philanthropist, who was passionate about protecting biological diversity. During his life-time, his generous support of Nature and Culture International was instrumental to the protection of endangered ecosystems and endemic species in the Amazonas, Cajamarca, and La Libertad departments of Peru. Even after his death in 2018, his generosity has continued to protect Latin America's biodiversity through charitable bequests. This new species was discovered in one of the departments that May supported during his life, and naming it after him, honors May's enduring legacy as a champion of biodiversity.

Stenocercus aculeatus O'Shaughnessy, 1879

Figs 4C, D, 8B, 9B, D, F, 15

Note. An elusive species represented by five specimens in museum collections (Cadle 2001; Torres-Carvajal 2007a). Currently it is known from five localities at elevations of 723 and 1311 m between Zamora, in the Andes of southern Ecuador, and its southernmost record in Pampa Seca at Department of La Libertad in northern Peru (Cadle 2001; Torres-Carvajal and Carvajal-Campos 2009). No data about its natural history and coloration in life exist and probably due to its disjunct distribution more than one species is represented under its specific epithet.

Collecting specimens in the Andes of northern Peru for almost two decades, we acquired only two specimens of *S. aculeatus* in two locations of Abra Patricia at elevations of 1700 and 1990 m, just at the limits of the departments of Amazonas and San Martín (Fig. 5). Extending its altitudinal range by 679 m above its previously known record, Pampa Seca in the Mishollo Valley, at an elevation of 1311 m (Cadle 2001), one of the specimens (CORBIDI 1712) is also the first report for the Department Amazonas. Both specimens have scale counts similar to the description of Torres-Carvajal (2007a).

Abra Patricia is the pass between the Río Chiriaco and Río Mayo basins located in the Peruvian Yungas, according to Olson et al. (2001). It is a steep area mostly covered by humid montane forest with an abundance of orchids, bromeliads, lichens and *Chusquea* spp. Kunth, 1882. The forest at the base and on the slopes is 3 to 5 m of high, decreasing in height toward the tops. Some slopes are rocky and very steep with only shrubby vegetation or long grasses. The weather is rainy most of the year and hours with sun are usually limited.

One specimen (CORBIDI 11483) was collected by ornithologists of the Louisiana State University during an ornithological expedition to Abra Patricia in August 2002. The specimen is an adult male of 95 mm SVL preserved in ethanol with an overall dark gray coloration. Only a black patch extensively covering the gular region is dark enough to observe. Although no collecting data is available for this specimen the area where it was collected is a steep slope covered by montane forest near a cleared area for cattle ranching.

The second individual (Fig. 15) is another adult male (CORBIDI 1712) of 80 mm SVL and was collected by P.J. Venegas in October 2008. This specimen was encountered during the morning at 1000 hours on the top of long grass at a height of 50 cm in a flat area with scattered scrubs and grasses close to the road. The specimen was lethargic due to lack of sun, being easy to capture. The same day at 1200 hours three more individuals were observed: one male basking at the base of long grasses on a steep rocky wall close to the road and a couple were observed on a trail along a summit covered by scrub and scattered boulders to 200 m from the road. These individuals ran to hide at the base of dense scrub when they detected PJV getting closer, and were impossible to capture.

Coloration in life of adult males (CORBIDI 1712): dorsal surface (Fig. 4C) is dusty brown with a sepia hue on dorsum, bearing dark brown transverse bands with narrow cream interspaces; vertebral crest is greenish yellow with the tip of some spines brown; limbs and tail with faint cream transverse stripes; coloration of flanks similar to dorsum but with the ventrolateral region bluish; side of neck and arm insertion cream; dorsal surface of head dark brown with the occipital region darker; sides of head dark brown with the loreal and subocular region white, interrupted by a diagonal dark brown subocular stripe, snout dark brown, tympanic region and ventrolateral region of neck black. Ventrally (Fig. 4D), the anterior half

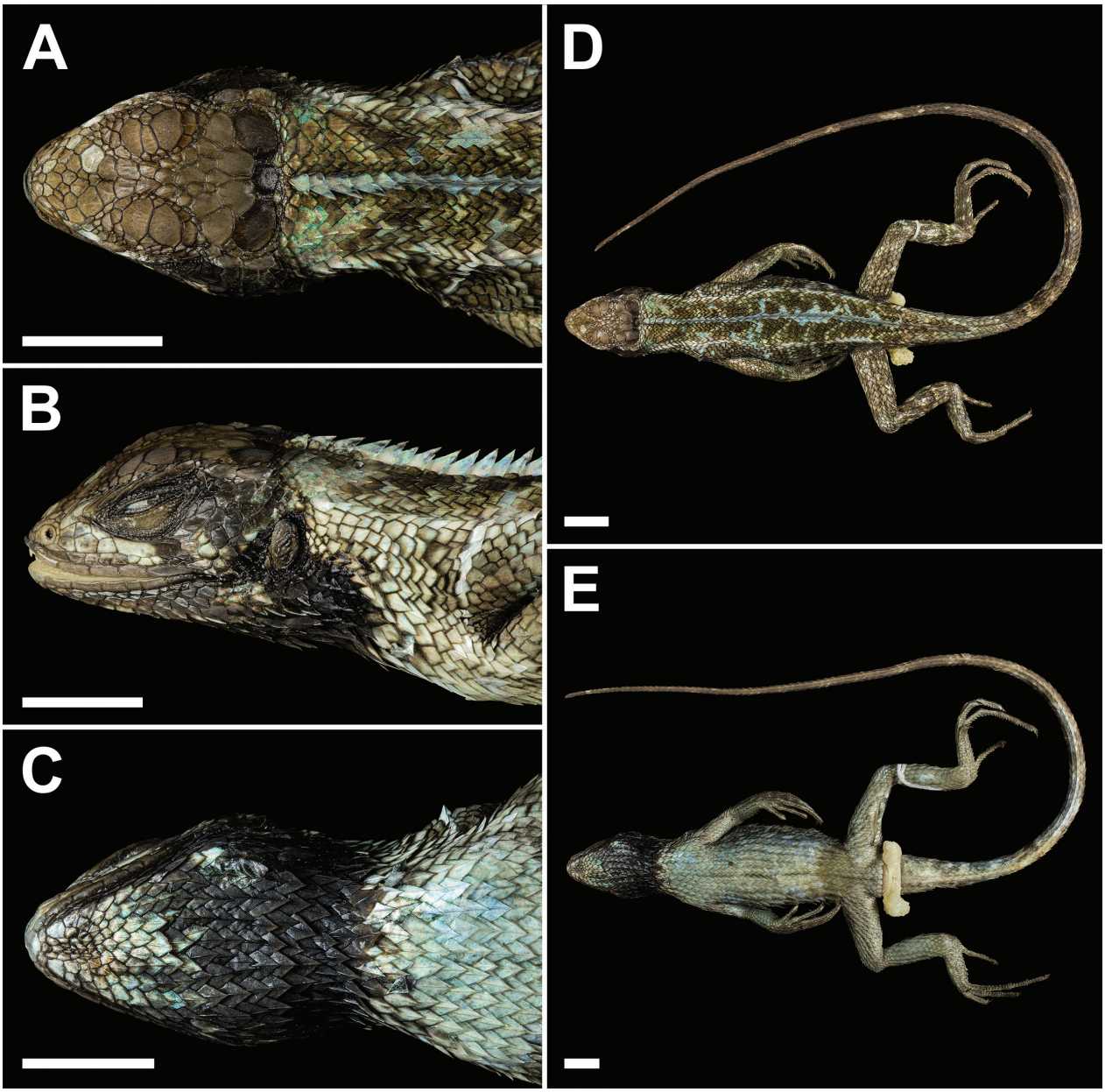

Figure 15. *Stenocercus aculeatus* preserved specimen, adult male, SVL 80 mm (CORBIDI 1712): dorsal (**A**), lateral (**B**), and ventral (**C**) views of the head; dorsal (**D**) and ventral (**E**) views of the entire specimen. Photographs by Luis A. García-Ayachi. Scale bars: 10 mm.

of the gular region dirty cream and the rest of the gular region and ventral surface of neck black; chest, forearms and belly brownish cream with a thin dark brown stripe from the chest to the end of belly, sides of belly bluish gray; pelvic region and ventral surface of hindlimbs tan, a cream blotch on the cloacal region; proximal half of tail creamy tan with faint brown transverse bands the rest of tail brown.

Discussion

Observations on the taxonomy and distribution of *Stenocercus aculeatus*, *S. prionotus* and *S. scapularis*.

Stenocercus aculeatus was a species briefly described in the past that generated confusion with other taxa, such as *S. angulifer*, due to the lack of specimens available in museum collections and the lack of data about its coloration in life (Cadle 2001; Torres-Carvajal 2000, 2007b); resulting in a species difficult to identify and to compare with similar species. Our two specimens of *S. aculeatus* reported here have similar scale counts to specimens reported by Torres-Carvajal (2007a), presenting a little variation in some counts, attributable to the low sample (n = 5) of *S. aculeatus* in the literature (see Table 1).

The type locality of *S. aculeatus*, Moyobamba, at an elevation of 723 m (Cadle 2001; Torres-Carvajal 2007a) is the lower altitudinal range for the species. However, the other known localities lie at elevations between 915 and 1311 m (Cadle 2001; Torres-Carvajal 2007a; Torres-Carvajal and Carvajal-Campos 2009), and the specimens reported here from Abra Patricia are from 1700 to 1987 m,

making the exact location of the type locality in O'Shaughnessy (1879), doubtful. Moyobamba is a city located in the valley of the Río Mayo at low elevation between two major mountain ridges. The closer mountains to Moyobamba are located 5 and 8 km from the city, reaching heights of 900 and 1500 m, and are similar to the other places where *S. aculeatus* specimens were collected (e.g. Cerro Calzada is the most striking mountain near to Moyobamba). Although our new records of *S. aculeatus* are higher than the rest of previously known localities, the closer known localities from Moyobamba for *S. aculeatus* (i.e. the range between Moyobamba and Cahuapanas, and Icuta on the Balsapuerto-Moyobamba trail; see Cadle (2001)) lie in the Cordillera Escalera, a mountain ridge to the east of Moyobamba that divides San Martín and Loreto departments (Pitman et al. 2014). The habitats of the Cordillera Escalera at elevations above 1000 m have a similar herpetofauna to Abra Patricia and the upper basin of the Río Mayo (see Venegas et al. 2014b). In fact, summits of the Cordillera Escalera reach 2700 m (Pitman et al. 2014) a similar elevation to the mountains of Abra Patricia.

The geographical distribution of *S. aculeatus* still seems peculiar with a gap of approximately 276 km to the northernmost locality in Zamora in southern Ecuador (Torres-Carvajal and Carvajal-Campos 2009), and a gap of approximately 256 km to the southernmost locality in Pampa Seca (Río Mishollo valley) in the Department of La Libertad (Cadle 2001; Torres-Carvajal 2007a). Nevertheless, except for *S. aculeatus*, no other species of *Stenocercus* occurs to north and south of the Río Marañón (the main tributary of the upper Amazon) (see Torres-Carvajal 2007a), and according to Cadle (2001), no *Stenocercus* species was reported in herpetofaunal surveys in northern Amazonas Department on the Río Cenepa and the Río Santiago or in biological rapid assessment of the Cordillera del Condor of southern Ecuador and northern Peru; or in the Cordillera de Kampankis, a narrow mountain ridge between the Río Santiago and Río Morona (see Catenazzi and Venegas 2012). For the gap toward the southernmost locality in Pampa Seca, no evident barriers occur and montane habitats between 700 and 2000 m in this space are poorly known in herpetological terms. Although Torres-Carvajal and Carvajal-Campos (2009) did not show details or photographs of the specimen reported from Ecuador, the low sample size of specimens currently available for *S. aculeatus* in museums and the lack of DNA samples remains a barrier for understanding the variation and identity of this elusive species through its range.

In the process of diagnosing the new species described herein, we examined the morphology and distribution of *S. prionotus* and *S. scapularis*, both from the Peruvian Amazon foothills, and adjacent Amazon lowlands, including Bolivia for *S. prionotus* (Cadle 2001; Torres-Carvajal 2007b). As was shown by Cadle (2001), we also observed a conspicuous variation in the vertebral crest height and ventral coloration, between adult males of *S. prionotus* from populations of north-central Peru (Fig. 4E, F) and southern Peru and Bolivia (Fig. 4G, H). Both populations are separated by a gap between the Río Pachitea (Department of Huánuco) and Cocha Cashu (Department of Madre de Dios) (Cadle 2001). Although Cadle (2001) did not find significant statistical support for separating both populations based in a lower or higher number of vertebral scales as a reflection of their size, we suggest that populations from north-central Peru, southern Peru and Bolivia need to be treated as two allopatric and different species.

The sympatric relationships between species such as *S. aculeatus*, *S. prionotus* and *S. scapularis* were discussed by Cadle (2001) and remain poorly understood. Although the distributions of *S. aculeatus* and *S. prionotus* overlap in northern Peru, both species possess different altitudinal ranges, and *S. prionotus* occurs in lower elevations than *S. aculeatus*. Cadle (2001), mentioned possible places where *S. prionotus* and *S. scapularis* could be sympatric in central Peru but did not include southern Peru. However, the presence of *S. scapularis* in central Peru includes the distribution gap of *S. prionotus* (see Fig. 5) and we found clear variation in ventral coloration and head shape between populations of *S. scapularis* from central and southern Peru. Although we were not able to review adult males from central Peru, adult females from central and southern Peru (Fig. 16) can be distinguished (respectively): brown irises versus reddish irises, dark brown gular region versus pale lavender, brown belly with cream blotches vs. creamy tan belly with irregular transverse bands, and frontal region in profile gently raised versus abruptly raised (see Fig. 16E, F). The geographic gap between the central and southern populations lies in the Río Urubamba valley, which could well be a barrier, separating two different species.

Distributional patterns and morphological affinities between *S. aculeatus*, *S. catherineae* sp. nov., *S. dracopennatus* sp. nov., *S. huancabambae*, and *S. philmayi* sp. nov.

The interspecific phylogenetic relationships in *Stenocercus* are complex and morphologically heterogeneous. However, we discuss some conjectures originating on the basis of the morphological resemblance and the geographical proximity between *S. aculeatus*, *S. catherineae* sp. nov., *S. dracopennatus* sp. nov., *S. huancabambae*, and *S. philmayi* sp. nov. These five species are structurally similar (see Table 1); all of these species possess two xiphisternal and three postxiphisternal pairs of inscriptional ribs fused medially, forming three chevrons (Pattern 6A of Torres-Carvajal 2004) and are altitudinally segregated through the upper basin of the Río Marañón and its tributaries in the Huancabamba Deflection and the northern limit of the central Andes (see Fig. 4). While *S. huancabambae* inhabits dry deciduous forest at elevations of 200 to 1318 m along the Río Marañón and its tributaries, like the Río Utcubamba (Cadle 1991; Koch et al. 2018); *S. catherineae* sp. nov. occurs, like the former species, in the basin of the Río Utcubamba, but at higher elevations of 1460 and 2090 m, inhabiting montane forest; and *S. philmayi* sp. nov. occupies the ecotone be-

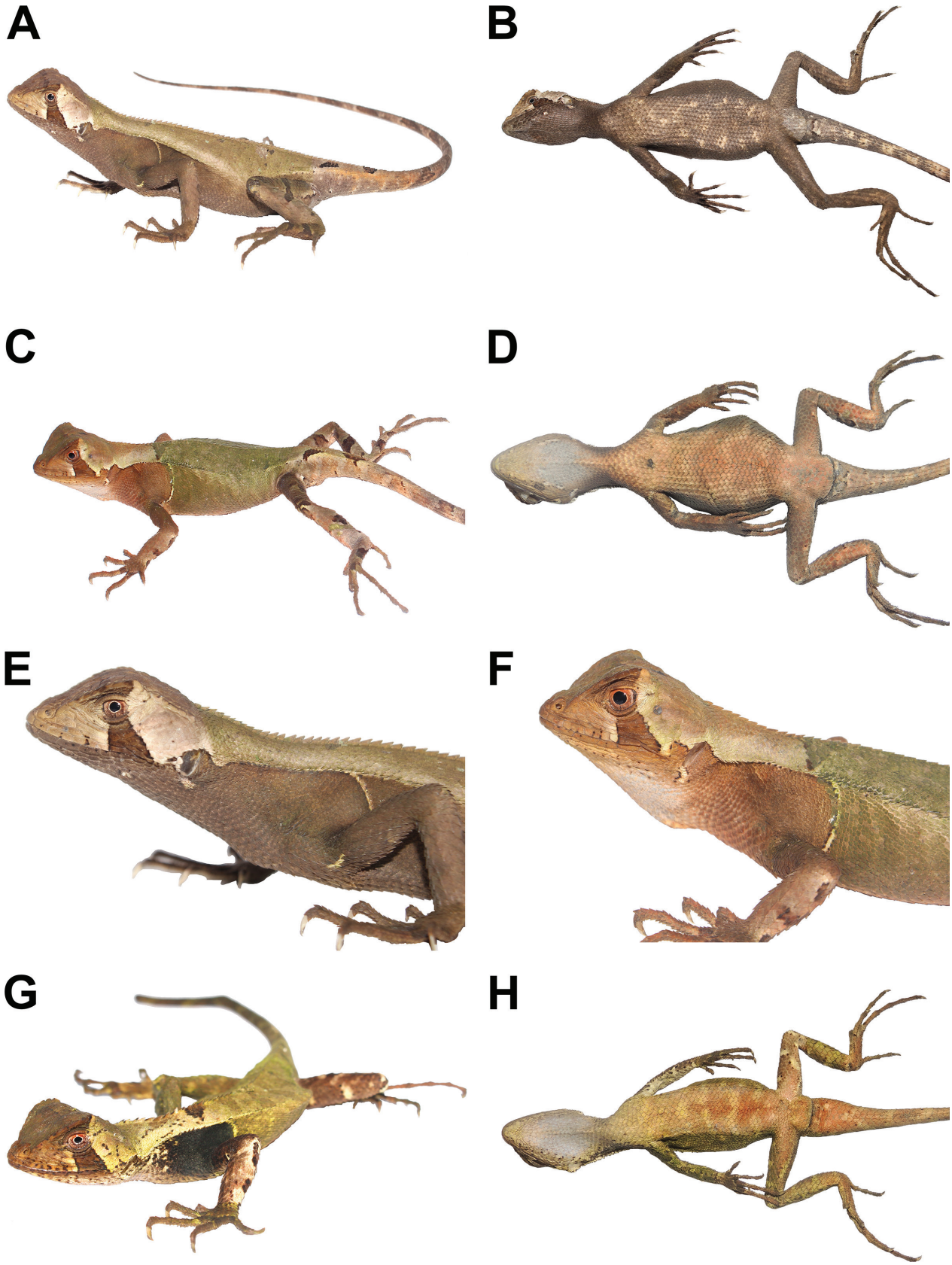

Figure 16. Dorsolateral and ventral views of *Stenocercus scapularis* in life: (**A**, **B**, **E**) adult female (CORBIDI 21983) from San Ramón, Department of Junín, Central Peru; (**C**, **D**, **F**) adult female (CORBIDI 17739) from La Convención, Department of Cusco, southern Peru; (**G**, **H**) adult male, (CORBIDI 17738) from La Convención, Department of Cusco, southern Peru. Photographs by Juan C. Chávez-Arribasplata.

tween dry Marañón forest and montane forest in terrain with denser understory than the habitat of *S. huancabambae*, at a close altitudinal range between 1340 to 1470 m. On the other hand, *S. dracopennatus* sp. nov. inhabits the highest elevation at 2370 m in the humid montane forest of the Río Chiriaco basin (a tributary of the Río Marañón), whereas *S. aculeatus* is nearby inhabiting the same type of forest up to 1970 m elevation on the divide between the Río Chiriaco and Río Mayo basins.

Although these species apparently possess allopatric distributions, they are distinguished externally by sexually dimorphic characters (e.g. height of crest, marks on flanks and ventral coloration on gular region and neck; see Cooper and Burns 1987; Watkins 1998) with a potential role in either intra or interspecific communication that suggests possible contact zones or sympatry in some areas. *Stenocercus huancabambae* and *S. catherineae* sp. nov. are very similar in squamation (e.g. both species possess one canthal in contrast to two canthals in the other two new species), structure and color pattern, and distinguished basically by the form and size of the black patch in the gular-neck region and the height of the tail. The flanks in the four species are characterized by bright flecks with different levels of contrast between species being subtle in *S. philmayi* sp. nov. and conspicuous in *S. dracopennatus* sp. nov. Additionally, height of the crest is identical in *S. catherineae* sp. nov., *S. huancabambae*, and *S. philmayi* sp. nov. but strikingly low in *S. dracopennatus* sp. nov. On the other hand, the height of the tail and its compressed form in *S. huancabambae* are strongly pronounced in contrast to the rest of the species. Although not well understood, the relation of tail height and visual signals in lizards could be involved in intrasexual aggression as is the height of the crest in iguanas (e.g. Watkins 1998). The aforementioned species are similar in size; however, the strikingly high tail of *S. huancabambae* makes it distinctively bigger in lateral view.

We suggest that these specific distinctions shown by males, are due to the abundance of closely related species in the same region –the northern portion of the central Andes– likely with contact zones. Morphological resemblance and particular distinctions concerning features related to inter-sexual selection in this assemblage of lizards are a result of close phylogenetic relationships owing to a recent process of vicariance driven by constant geological changes in the formation of a complex landscape like the Huancabamba Deflection and the central Andes (Vuilleumier 1969; Cadle 1991; Duellman and Pramuk 1999).

Conservation status

We describe four new species of *Stenocercus* only known either from a single locality or up to a maximum of three localities. *Stenocercus catherineae* sp. nov. is known from three geographically proximate localities in the Río Utcubamba basin. This species was abundant in the type locality, where several individuals were found basking close to a trail on a slope of second growth vegetation along the Río Chido, a tributary of the Río Utcubamba. The general landscape at the type locality is strongly impacted by agriculture and cattle ranching with some scattered patches of forest. The same degree of fragmentation is observed in the locality of Cocachimba where several individuals of *S. catherineae* sp. nov. were observed in bushes and on rocky fences delimiting croplands. However, at the locality of Cuispes only one individual of *S. catherineae* sp. nov. was collected whereas several individuals of *S. flagracanthus* sp. nov. were observed. The latter species is known from two close localities, both in the Río Utcubamba basin. However, all individuals observed were found in croplands and were using human construction as refuges (e.g. houses, rocky fences and piles of firewood).

Stenocercus philmayi sp. nov. is known only from its type locality and an unconfirmed locality (see Fig. 5) reported by Cadle (2001). We found that *S. philmayi* sp. nov. matches the identification key of Cadle (2001) as "*Stenocercus* new species", that is based on a single specimen that occurs 40.5 km to the south of the type locality of *S. philmayi* sp. nov., at a similar elevation and also in the Marañón dry forests ecoregion. Although we were unable to examine the specimen (ROM 16458) reported by Cadle (2001), we consider it possible that this specimen belongs to *S. philmayi* sp. nov., although this needs to be confirmed by examining the specimen or collecting more specimens at the same locality. The general habitat of this new species is better conserved than the habitat of *S. catherineae* sp. nov. and *S. flagracanthus* sp. nov.; and the main cause of habitat fragmentation in the type locality of *S. philmayi* sp. nov. are the clearings for coca (*Erythroxylum* sp. Browne, 1756), mango (*Mangifera indica*, Linnaeus, 1753a), and cacao (*Theobroma* sp. Linnaeus, 1753b). Nevertheless, *S. philmayi* sp. nov. is locally abundant and some individuals were observed near houses and croplands. Nevertheless, the distribution of this species remains known with certainty for a single locality. Finally, *S. dracopennatus* sp. nov. is also known from a single locality where only few individuals were observed. The general landscape is only impacted by a road and its habitat is on white sand soils so neither agriculture nor cattle ranching occur in the area; however, some slopes seem to have been burned in the past.

Stenocercus catherineae sp. nov., *S. flagracanthus* sp. nov., and *S. philmayi* sp. nov. inhabit croplands and use human-made buildings as refuges, as is well known for other species of *Stenocercus* (Dávila-Jativa and Cisneros-Heredia 2017). Although these habits showed a high degree of resilience in these species, we prefer to be cautious in giving them a conservation status, especially due to their poorly known geographical distribution. Thus, following the IUCN categories and criteria (IUCN 2012), we categorize these three species as Data Deficient (DD). On the other hand, in *S. dracopennatus* sp. nov., we have not observed adaptations for living in anthropic conditions and inasmuch as this species is known from a single locality, it must be considered as Data Deficient, too.

Acknowledgments

The primary research was made possible with the support of the Critical Ecosystem Partnership Fund (CEPF) (project number CEPF-109938) through the Fondo de Promoción de las Áreas Naturales Protegidas del Perú (PROFONANPE). However, the development of our CEPF project would not have been possible without the logistic support of Odile Sanchez and Claudia Zarate from PROFONANPE. Our field work was also supported by the Global Genome Initiative (GGBN-GGI). The expeditions where *Stenocercus catherineae* sp. nov. was discovered were funded by APECO under the research grant "Carlos Ponce del Prado Award (XI edition)". The expeditions to Cuispes and Las Corontas were funded by Nature and Culture International. We thank David Boyd and Angel Portocarrero ARA-Amazonas for their logistic support during the search for *S. philmayi* sp. nov. in Las Corontas. We are indebted to William W. Lamar for review and comments on an early version of this manuscript.

References

Barbour T (1930) A list of Antillean reptiles and amphibians. Zoologica 11: 61–116.

Beaupre SJ, Jacobson ER, Lillywhite HB, Zamudio K (2004) Guidelines for use of live amphibians and reptiles in field and laboratory research. Second ed. The American Society of Ichthyologists and Herpetologists, USA, 43 pp.

Boulenger GA (1885) Catalogue of the lizards in the British Museum (Natural History): Iguanidae, Xenosauridae, Zonuridae, Anguidae, Anniellidae, Helodermatidae, Varanidae, Xantusiidae, Teiidae, Amphisbaenidae. Order of the Trustees. London, 497 pp.

Boulenger GA (1899) Descriptions of new reptiles and batrachians collected by Mr. P.O. Simons in the Andes of Ecuador. The Annals and Magazine of Natural History 4: 454–457. https://doi.org/10.1080/00222939908678229

Boulenger GA (1900) Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. The Annals and Magazine of Natural History 6: 181–186. https://doi.org/10.1080/00222930008678355

Boulenger GA (1901) Further descriptions of new reptiles collected by Mr. P. O. Simons in Peru and Bolivia. The Annals and Magazine of Natural History 7: 546–549. https://doi.org/10.1080/00222930108678513

Boulenger GA (1912) Descriptions of new reptiles from the Andes of South America, preserved in the British Museum. The Annals and Magazine of Natural History 10: 420–424. https://doi.org/10.1080/00222931208693255

Brack-Egg E (1986) Las ecorregiones del Perú. Boletín de Lima 44: 57–70.

Browne P (1756) The Civil and Natural History of Jamaica un Three Parts. London, 278 pp.

Cadle JE (1991) Systematics of lizards of the genus *Stenocercus* (Iguania: Tropiduridae) from northern Perú: New species and comments on relationships and distribution patterns. Proceedings of the Academy of Natural Sciences of Philadelphia 143: 1–96.

Cadle JE (1998) New species of lizards, genus *Stenocercus* (Iguania: Tropiduridae), from Western Ecuador and Peru. Bulletin of the Museum of Comparative Zoology at Harvard College 155: 257–297.

Cadle JE (2001) A new species of lizard related to *Stenocercus caducus* (Cope) (Squamata: Iguanidae) from Peru and Bolivia, with a key to the" *Ophryoessoides* Group". Bulletin of the Museum of Comparative Zoology at Harvard College 157: 183–221.

Cannatella DC (1982) Leaf-Frogs of the *Phyllomedusa perinesos* Group (Anura: Hylidae). Copeia 1982: 501–513. https://doi.org/10.2307/1444649

Castro F, Ayala SC (1982) Nueva especie de (Sauria: Iguanidae) lagarto collarejo de la zona sur Andina de Colombia. Caldasia 13: 473–478.

Catenazzi A, Venegas PJ (2012) Anfibios y Reptiles/ Amphibians and Reptiles. In: Pitman N, Inzunza ER, Alvira D, Vriesendorp C, Moskovits DK, Campo A, Wachter T, Stotz DF, Noningo SS, Tuesta CE, Smith RC (Eds) Peru: Cerro de Kampankis Rapid Biological and Social Inventories Report 24. The Field Museum, Chicago, 106–117. [260–271, 348–365.]

Chávez G, Siu-Ting K, Duran V, Venegas PJ (2011) Two new species of Andean gymnophthalmid lizards of the genus *Euspondylus* (Reptilia, Squamata) from Central and Southern Peru. Zookeys 109: 1–17. https://doi.org/10.3897/zookeys.109.1304

Cooper JWE, Burns N (1987) Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Animal Behaviour 35: 526–532. https://doi.org/10.1016/S0003-3472(87)80277-4

Dávila-Jativa M, Cisneros-Heredia DF (2017) Use of human-made buildings by *Stenocercus* lizards (Iguania, Tropiduridae). Herpetology Notes 10: 517–519.

de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH (Eds) Endless Forms: Species and Speciation. Oxford University Press, 57–75 pp.

de Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56: 879–886. https://doi.org/10.1080/10635150701701083

Doan TM, Castoe TA (2005) Phylogenetic taxonomy of the Cercosaurini (Squamata: Gymnophthalmidae), with new genera for species of *Neusticurus* and *Proctoporus*. Zoological Journal of the Linnean Society 143: 405–416. https://doi.org/10.1111/j.1096-3642.2005.00145.x

Duellman WE (1982) A new species of small yellow *Hyla* from Peru (Anura: Hylidae). Amphibia-Reptilia 3: 153–160. https://doi.org/10.1163/156853882X00383

Duellman WE (1987) Two new species of Marsupial Frogs (Anura: Hylidae) from Peru. Copeia 1987: 903–909. https://doi.org/10.2307/1445553

Duellman WE (1990) A new species of *Eleutherodactylus* from the Andes of northern Peru (Anura: Leptodactylidae). Journal of Herpetology 24: 348–350. https://doi.org/10.2307/1565048

Duellman WE (1991) A new species of Leptodactylid Frog, genus *Phyllonastes*, from Peru. Herpetologica 47: 9–13.

Duellman WE (2004) Frogs of the genus *Colostethus* (Anura; Dendrobatidae) in the Andes of northern Peru. Scientific Papers Natural History Museum, The University of Kansas 35: 1–49. https://doi.org/10.5962/bhl.title.8467

Duellman WE (2013) An elusive new species of Marsupial Frog (Anura: Hemiphractidae: *Gastrotheca*) from the Andes of northern Peru. Phyllomedusa 12: 3–11. https://doi.org/10.11606/issn.2316-9079.v12i1p3-11

Duellman WE, Schulte R (1992) Description of a new species of *Bufo* from northern Peru with comments on phenetic groups of South

American Toads (Anura: Bufonidae). Copeia 1992: 162–172. https://doi.org/10.2307/1446548

Duellman WE, Wiens JJ (1993) Hylid Frogs of the genus *Scinax* Wagler, 1830, in Amazonian Ecuador and Peru. Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 153: 1–57.

Duellman WE, Wild ER (1993) Anuran amphibians from the Cordillera de Huancabamba, northern Peru: systematics, ecology, and biogeography. Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 157: 1–53.

Duellman WE, Pramuk JB (1999) Frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae) in the Andes of northern Peru. Natural History Museum The University of Kansas 13: 1–78. https://doi.org/10.5962/bhl.title.16169

Duellman WE, Venegas PJ (2005) Marsupial Frogs (Anura: Hylidae: *Gastrotheca*) from the Andes of northern Peru with descriptions of two new species. Herpetologica 61: 295–307. https://doi.org/10.1655/04-105.1

Duellman WE, Lehr E (2009) Terrestrial breeding frogs (Strabomantidae) in Peru. Natur und Tier-Verlag GmbH, 384 pp.

Duellman WE, Venegas PJ (2016) Diversity of Marsupial Frogs (Anura: Hemiphractidae: *Gastrotheca*) in the northern Cordillera Central, Peru, with the descriptions of two new species. Phyllomedusa 15: 103–117. https://doi.org/10.11606/issn.2316-9079.v15i2p103-117

Duellman WE, Barley AJ, Venegas PJ (2014) Cryptic species diversity in Marsupial Frogs (Anura: Hemiphractidae: *Gastrotheca*) in the Andes of northern Peru. Zootaxa 3768: 159–177. https://doi.org/10.11646/zootaxa.3768.2.4

Duméril AMC, Bibron G (1837) Erpétologie Générale ou Histoire Naturelle Complete des Reptiles (Vol. 4). Libr. Encyclopédique Roret, Paris, 570 pp.

Duméril AMC, Bibron G (1841) Erpétologie Générale ou Histoire Naturelle Compléte des Reptiles (Vol. 8). Libr. Encyclopédique Roret, Paris, 784 pp.

Dunn ER (1933) Amphibians and reptiles from El Valle de Antón, Panamá. Occasional Papers of the Boston Society of Natural History 8: 65–79.

Echevarria LY, Venegas PJ (2015) A new elusive species of *Petracola* (Squamata: Gymnophthalmidae) from the Utcubamba basin in the Andes of northern Peru. Amphibian & Reptile Conservation 9: 26–33.

Fitzinger LJFJ (1826) Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologischen Museum's zu Wien. Wien: J. G. Heubner, 66 pp. https://doi.org/10.5962/bhl.title.4683

Fitzinger LJFJ (1843) Systema Reptilium. Fasciculus Primus. Braumüller et Seidel, Wien, 106 pp.

Fritts TH (1972) New species of lizards of the genus *Stenocercus* from Peru (Sauria: Iguanidae). Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 10: 1–21.

Fritts TH (1974) A multivariate evolutionary analysis of the Andean Iguanid Lizards of the genus *Stenocercus*. San Diego Society of Natural History 7: 1–86.

Frost DR, Kluge AG (1994) A consideration of epistemology in Systematic Biology, with special reference to species. Cladistics 10: 259–294. https://doi.org/10.1111/j.1096-0031.1994.tb00178.x

Gray JE (1828) Original figures and short systematic descriptions of new and unfigured animals. Spicilegia Zoologica 1: 1–3.

Gray JE (1845) Catalogue of the specimens of lizards in the collection of the British Museum. Trustees of die British Museum/Edward Newman, London, 289 pp.

Huey RB, Dixon JR (1970) A new *Pseudogonatodes* from Peru with remarks on other species of the genus. Copeia 1970: 538–542. https://doi.org/10.2307/1442282

IUCN (2012) Categorías y Criterios de la Lista Roja de la UICN: versión 3.1. Gland, Switzerlandand Cambridge, United Kingdom, 34 pp.

Jiménez de la Espada M (1870) Fauna neotropicalis species quaedam nondum cognitae. Jornal de Sciências, Mathemáticas, Physicas e Naturaes. Lisboa 3: 57–65.

Jiménez de la Espada M (1872). Nuevos batrácios Americanos. Anales de la Sociedad Española de Historia Natural. Madrid 1: 84–88.

Koch C, Venegas PJ, Böhme W (2006) A remarkable discovery: description of a big-growing new gecko (Squamata: Gekkonidae: *Phyllopezus*) from Northwestern Peru. Salamandra 42: 145–150.

Koch C, Venegas PJ, Böhme W (2015) Three new endemic species of *Epictia* Gray, 1845 (Serpentes: Leptotyphlopidae) from the Dry Forest of Northwestern Peru. Zootaxa 3964: 228–244. https://doi.org/10.11646/zootaxa.3964.2.4

Koch C, Venegas PJ, Santa Cruz R, Böhme W (2018) Annotated checklist and key to the species of amphibians and reptiles inhabiting the northern Peruvian dry forest along the Andean valley of the Marañón River and its tributaries. Zootaxa 4385: 001–101. https://doi.org/10.11646/zootaxa.4385.1.1

Koch C, Venegas PJ, Rödder D, Flecks M, Böhme W (2013) Two new endemic species of *Ameiva* (Squamata: Teiidae) from the Dry Forest of Northwestern Peru and additional information on *Ameiva concolor* Ruthven, 1924. Zootaxa 3745: 263–295. https://doi.org/10.11646/zootaxa.3745.2.6

Koch C, Flecks M, Venegas PJ, Bialke P, Valverde S, Rödder D (2016) Applying n-dimensional hypervolumes for species delimitation: unexpected molecular, morphological, and ecological diversity in the Leaf-Toed Gecko *Phyllodactylus reissii* Peters, 1862 (Squamata: Phyllodactylidae) from northern Peru. Zootaxa 4161: 41–80. https://doi.org/10.11646/zootaxa.4161.1.2

Köhler G (2003) A new species of *Morunasaurus* from Peru (Reptilia, Squamata, Hoplocercidae). Senckenbergiana Biologica 82: 1–7.

Köhler G, Lehr E (2015) Two new species of lizards of the genus *Stenocercus* (Iguania, Tropiduridae) from central Peru. Zootaxa 3956: 413–427. https://doi.org/10.11646/zootaxa.3956.3.6

Kunth PC (1882) Sur le genre bambusa. Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts. 95: 148–151.

Lehr E, Von May R, Moravec J, Cusi JC (2017) Three new species of *Pristimantis* (Amphibia, Anura, Craugastoridae) from Upper Montane Forests and High Andean Grasslands of the Pui Pui Protected Forest in Central Peru. Zootaxa 4299: 301–336. https://doi.org/10.11646/zootaxa.4299.3.1

Linnaeus C (1753a) Species Plantarum: Exhibentes Plantas Rite Cognitas ad Genera Relatas, cum Diferentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas. Tomo I. Berlin, 560 pp.

Linnaeus C (1753b) Species Plantarum: Exhibentes Plantas Rite Cognitas ad Genera Relatas, cum Diferentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas Tomo II. Berlin, 1200 pp.

Linnaeus C (1758) Systema Naturæ per Regna Tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differenti-

is, Synonymis, Locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiæ, 824 pp.

Lötters S, Schulte R, Duellman WE (2004) A new and critically endangered species of *Atelopus* from the Andes of northern Peru (Anura: Bufonidae). Revista Española de Herpetología 18: 101–109.

Morales V (1994) Taxonomía sobre algunos *Colostethus* (Anura: Dendrobatidae) de Sudamérica, con descripción de dos especies nuevas. Revista Española de Herpetología 8: 95–103.

Morales V, Schulte R (1993) Dos especies nuevas de *Colostethus* (Anura, Dendrobatidae) en las vertientes de la Cordillera Oriental del Perú y del Ecuador. Alytes 11: 97–106.

Meyer FAA (1795) Synopsis Reptilium: Novam Ipsorum Sistens Generum Methodum: nec non Gottingensium Huius Ordinis Animalium Enumerationem. Vandenhoek et Ruprecht, 32 pp. https://doi.org/10.5962/bhl.title.5025

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity Hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

O'Shaughnessy AWE (1879) XXXIII.–Descriptions of new species of lizards in the collection of the British Museum. The Annals and magazine of natural history 4: 295–303. https://doi.org/10.1080/00222937908679832

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial Ecoregions of the World: A new Map of Life on Earth. BioScience 51: 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Parker HW (1934) Reptiles and amphibians from southern Ecuador. The Annals and Magazine of Natural History 14: 264–273. https://doi.org/10.1080/00222933408654895

Peñaherrera del Aguila C (1989) Atlas del Perú. Instituto Geográfico Nacional, Lima, 400 pp.

Peters W (1878) Herpetologische Notizen. II. Bemerkungen über neue oder weniger bekannte Amphibien. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1877: 415–423.

Peters W (1882) Den Namen der Batrachiergattung *Hylonomus* in *Hyloscirtus* zu ändern und legte zwei neue Arten von Schlangen, *Microsoma notatum*, und *Liophis Ygraecum*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1882: 127–129. https://doi.org/10.5962/bhl.part.15223

Pitman N, Vriesendorp C, Alvira D, Markel JA, Johnston M, Inzunza ER, Pizango AL, Valenzuela GS, Álvarez-Loayza P, Homan J (2014) Peru: Cordillera Escalera-Loreto. Rapid Biological and Social Inventories Report 26. The Field Museum, 550 pp.

Rivera-Correa M, Garcia-Burneo K, Grant T (2016) A new red-eyed of stream treefrog of *Hyloscirtus* (Anura: Hylidae) from Peru, with comments on the taxonomy of the genus. Zootaxa 4061: 29–40. https://doi.org/10.11646/zootaxa.4061.1.3

Rivero JA (1991) New *Colostethus* (Amphibia, Dendrobatidae) from South America. Breviora 493: 1–28.

Ruthven AG (1915) Description of a new genus and species of lizard of the family Gekkonidae. Occasional Papers of the Museum of Zoology, University of Michigan 19: 1–3.

Schluter D (2000) The Ecology of Adaptive Radiation. Oxford University Press, Oxford, 288 pp.

Sentzen (1796) Ophiologische Fragmente. Meyer's Zoologische Archiv 2: 59–66.

Steindachner F (1891) Ueber neue und seltene Lacertiden aus der herpetologischen Sammlung des k. k. naturhistorisches Hofsmuseums. Annalen des K. K. Naturhistorischen Hofmuseums 6: 371–378.

Teixeira M, Prates I, Nisa C, Silva-Martins NSC, Strüssmann C, Rodrigues MT (2016) Molecular data reveal spatial and temporal patterns of diversification and a cryptic new species of lowland *Stenocercus* Duméril & Bibron, 1837 (Squamata: Tropiduridae). Molecular Phylogenetics and Evolution 94: 410–423. https://doi.org/10.1016/j.ympev.2015.09.010

The Reptile Database (2020) The Reptile Database. http://www.reptile-database.org [accessed on 02.06.2020]

Torres-Carvajal O (2000) Ecuadorian Lizards of the genus *Stenocercus* (Squamata: Tropiduridae). Scientific Papers Natural History Museum, the University of Kansas 15: 1–38. https://doi.org/10.5962/bhl.title.16286

Torres-Carvajal O (2004) The abdominal skeleton of Tropidurid Lizards (Squamata: Tropiduridae). Herpetologica 60: 75–83. https://doi.org/10.1655/03-15

Torres-Carvajal O (2007a) A taxonomic revision of South American *Stenocercus* (Squamata: Iguania) Lizards. Herpetological Monographs 21: 76–178. https://doi.org/10.1655/06-001.1

Torres-Carvajal O (2007b) Phylogeny and biogeography of a large radiation of Andean Lizards (Iguania, *Stenocercus*). Zoologica Scripta 36: 311–326. https://doi.org/10.1111/j.1463-6409.2006.00284.x

Torres-Carvajal O, Carvajal-Campos A (2009) Reptilia, Squamata, Iguanidae, *Stenocercus aculeatus*: Distribution extension and first record for Ecuador. Check List 5: 753–754. https://doi.org/10.15560/5.3.753

Torres-Carvajal O, Schulte II JA, Cadle JE (2006) Phylogenetic relationships of South American lizards of the genus *Stenocercus* (Squamata: Iguania): a new approach using a general mixture model for gene sequence data. Molecular Phylogenetics and Evolution 39: 171–185. https://doi.org/10.1016/j.ympev.2005.09.007

Tschudi JJV (1845) Reptilium conspectum quae in republica Peruana reperiuntur er pleraque observata vel collecta sunt in itenere. Archiv für Naturgeschichte 11: 150–170. https://doi.org/10.5962/bhl.part.7963

Twomey E, Delia J, Castroviejo-Fisher S (2014) A review of northern Peruvian Glassfrogs (Centrolenidae), with the description of four new remarkable species. Zootaxa 3851: 1–87. https://doi.org/10.11646/zootaxa.3851.1.1

Venegas PJ (2007) A new species of *Eleutherodactylus* (Anura: Leptodactylidae) from the Cordillera Central in northern Peru. Journal of Herpetology 41: 394–400. https://doi.org/10.1670/0022-1511(2007)41[394:ANSOEA]2.0.CO;2

Venegas PJ, Duran V, Garcia-Burneo K (2013) A new species of arboreal Iguanid Lizard, genus *Stenocercus* (Squamata: Iguania), from Central Peru. Zootaxa 3609: 291–301. https://doi.org/10.11646/zootaxa.3609.3.3

Venegas PJ, Echevarria LY, Alvarez SC (2014a) A new species of spiny-tailed iguanid lizard (Iguania: *Stenocercus*) from northwestern Peru. Zootaxa 3753: 47–58. https://doi.org/10.11646/zootaxa.3753.1.4

Venegas PJ, Gagliardi-Urrutia G, Odicio M (2014b) Anfibios y Reptiles/ Amphibians and Reptiles. In: Pitman N, Vriesendorp C, Alvira D, Markel JA, Johnston M, Inzunza ER, Pizango AL, Valenzuela GS, Álvarez-Loayza P, Homan J (Eds) Peru: Cordillera Escalera-Loreto Rapid Biological and Social Inventories Report 26. The Field Museum, Chicago, 127–138. [319–329, 470–481.]

Venegas PJ, Townsend JH, Koch C, Böhme W (2008) Two new sympatric species of Leaf-Toed Geckos (Gekkonidae: *Phyllodactylus*) from

the Balsas Region of the Upper Marañón Valley, Peru. Journal of Herpetology 42: 386–396. https://doi.org/10.1670/07-1341.1

Venegas PJ, Echevarria LY, Garcia-Burneo K, Koch C (2016) A new species of Iguanid Lizard, genus *Stenocercus* (Squamata, Iguania), from the Central Andes in Peru. Zootaxa 4205: 52–64. https://doi.org/10.11646/zootaxa.4205.1.4

Venegas PJ, Echevarría LY, García-Ayachi LA, Landauro CZ (2020) Two new Sympatric species of Stenocercus (Squamata: Iguania) from the inter-Andean valley of the Mantaro River, Peru. Zootaxa 4858: 555-575. https://doi.org/10.11646/zootaxa.4858.4.5

Vuilleumier F (1969) Pleistocene speciation in birds living in the high Andes. Nature 223: 1179–1180. https://doi.org/10.1038/2231179a0

Wagler J (1828) Auszüge aus seinem Systema Amphibiorum. Isis von Oken 21: 740–744.

Wagler J (1830) Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. München, Stuttgart and Tübingen: J. G. Cotta, 354 pp. https://doi.org/10.5962/bhl.title.108661

Werner F (1901) Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verhandlungen Zoologisch-Botanischen Gesellschaft in Wien 51: 593–614. https://doi.org/10.5962/bhl.part.4586

Watkins GG (1998) Function of a secondary sexual ornament: the crest in the South American iguanian lizard *Microlophus occipitalis* (Peters, Tropiduridae). Herpetologica 54: 161–169.

Wiegmann AFA (1834) Amphibien. In: Meyen FJF (Eds) Reise um die Erde ausgeführt auf dem Königlich Preussischen Seehandlungs-Schiffe Prinzess Louise, comandirt von Capitain W. Wendt, in den Jahren 1830, 1831 und 1832 von Dr. F. J. F. Meyen. Dritter Theil. Zoologischer Bericht, Berlin, 433–522 pp.

Wiens JJ (1993) Systematics of the Leptodactylid Frog genus *Telmatobius* in the Andes of northern Peru. Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 162: 1–76.

Appendix I

Material examined.

Stenocercus aculeatus – PERÚ: Amazonas: Bongará: Abra Patricia, CORBIDI 01712; San Martín: Rioja: Cerro Patricia, CORBIDI 11483.

Stenocercus arndti – PERÚ: Cajamarca: Chota: Quebrada Checos, CORBIDI 01680,01681,01685, Quebrada La Iraca, CORBIDI 01682–01684, 01686–01692.

Stenocercus carrioni – ECUADOR: Loja: Celica, Huajala QCAZ 10319, 10324, 10329.

Stenocercus chlorostictus – PERÚ: Piura: Ayabaca: Caserio de toronche – Comunidad de Olleros, CORBIDI 16891; Huancabamba: Canchaque, CORBIDI 19361–19366, 19368, 19369, 19382, 19383; Cajamarca: Santa Cruz: Agua Azul, MUSM 25821.

Stenocercus crassicaudatus – PERÚ: Cusco: Urubamba: Machu Picchu, CORBIDI 9058, MUSM 4905, 4906, 8691.

Stenocercus empetrus – PERÚ: La Libertad: Huamachuco MUSM 8658, 8675, 8677–8680; Santiago de Chuco: Shulgomopampa, CORBIDI 20534, 20535, 20536, 20537; Cajamarca: Cajamarca: MUSM 4909–10, La Colmena MUSM 8659, San Vicente MUSM 8676, Cerca al Cañon de Zangal, CORBIDI 01454, Aylambo, CORBIDI 06532, Cataratas de Llacanora, CORBIDI 08638.

Stenocercus eunetopsis – PERU: Cajamarca: Santa Cruz, Udima, MUSM 4018, 4022–4029.

Stenocercus huancabambae – PERÚ: Amazonas: Bagua: Chonza Alta (Bagua Chica), CORBIDI 00737, Comunidad Nativa Copallin, CORBIDI 05605, Utcubamba: Cumba, CORBIDI 05791, 05792, Luya: Playa Jumet, CORBIDI 11941, Huaranguillo, CORBIDI 11976; Cajamarca: Jaén: El Tupire (Santa Rosa de la Yunga), CORBIDI 01014–01027, Santa Rosa de la Yunga, CORBIDI 01035, 01889, 01920, Jaén, CORBIDI 01861, 01864, Bellavista, CORBIDI 05790, Bosque de Yanahuanca, CORBIDI 14844,14845, Chota: La Granja, CORBIDI 01693, Cutervo: Gotas de Agua, CORBIDI 01903, San Ignacio: Perico, CORBIDI 01930, 01931, 14061, Los Llanos, CORBIDI 19744, 19746, 19747, 19775.

Stenocercus prionotus – PERÚ: Huánuco: Huánuco: Dos Aguas, CORBIDI 6895, Malgotingo, CORBIDI 15001; Madre de Dios: Tambopata, CORBIDI 18599.

Stenocercus scapularis – PERÚ: Cusco: La Convención: Echarati, CORBIDI 06043, 17738, 17739, 17761, Santa Rosa de Cutivireni, CORBIDI 5431, Alto Shima, CORBIDI 9698, 9699, Chimparina, CORBIDI 18828; Junín: Satipo: Bosque rivereño, CORBIDI 21413, Chanchamayo: San Ramón, CORBIDI 21983.

Stenocercus simonsii – ECUADOR: Azuay: Giron, sendero El Salado, QCAZ 09636.

Stenocercus torquatus – PERÚ: Junín: Alto Yurinaqui, MUSM 8617–8619, Satipo: San Antonio, CORBIDI 21432, 21433, 21436, 21437, 21675–21677; Pasco: Oxapampa: Huampal, CORBIDI 7211, Bosque de Shollet, CORBIDI 9912.