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Source: Journal of Vertebrate Biology, 73(23074)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.23074

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2024, 73: 23074 DOI: 10.25225/jvb.23074

RESEARCH PAPER

Two new species of wood lizards (*Hoplocercinae*: *Enyalioides*) from Cordillera de Colán in north-eastern Peru

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Received 30 August 2023; Accepted 31 October 2023; Published online 31 January 2024

Abstract. Based on morphological features, genetic distances, and phylogenetic relationships, we report the discovery of two new species of *Enyalioides* from the montane forest of Cordillera de Colán in northern Peru. The first new species can be distinguished from its congeners by the combination of the following characters: scales immediately posterior to superciliaries on lateral edge of skull conical, slightly higher than adjacent scales; gular scales heterogeneous in size; scales on neck mostly large and conical; dorsal scales between dorsolateral crests covered by large, keeled, mucronate scales; scales on flanks tiny, tuberculate or granular, with scattered enlarged conical or tuberculate scales; ventral scales keeled or feebly keeled; caudal scales heterogeneous, increasing in size posteriorly on each segment; and marked sexual dichromatism. Among other features, the second new species differs from other *Enyalioides* in having a distinctively low vertebral crest; scales immediately posterior to superciliaries on lateral edge of skull barely projected and similar in height to adjacent scales; 56-71 vertebral scales from occiput to base of tail; dorsal scales feebly keeled and heterogeneous in size; ventral scales keeled; and caudal scales heterogeneous, increasing in size posteriorly on each segment. In addition, we present an updated identification key for species of *Hoplocercinae*.

Key words: Andes, *Enyalioides anisolepis*, Huancabamba Depression, lizards, River Marañón, Peruvian Yungas, systematics

Introduction

The Cordillera de Colán is a semi-isolated mountain range of moderate elevation (< 3,700 m) in the Amazonas Department, northern Peru (Venegas et al. 2021). Except for its southern connection with the Andean Cordillera Central, the Cordillera de Colán is surrounded by lowlands, with the rivers Chiriaco and Utcubamba along its margins. These rivers flow northward into the River Marañón, the main tributary

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of the upper River Amazon (Duellman & Pramuk 1999). The Cordillera de Colán is also located on the south-eastern part of the Huancabamba Depression (4-7° S), which consists of relatively low-elevation mountains and represents a major structural and physiographic break in the Andes (Sillitoe 1974, Duellman & Pramuk 1999, Quintana et al. 2017).

The herpetological exploration in the Cordillera de Colán is still rudimentary. Most of the currently known herpetofauna is composed of amphibians that were collected during an ornithological expedition by Louisiana State University (LSU) led by Thomas S. Schulenberg in 1978. The specimens collected in that expedition resulted in the description of seven species of frogs: *Gastrotheca abdita* Duellman, 1987, *Colostethus spilotogaster* Duellman, 2004, *Eleutherodactylus avicuporum* Duellman & Pramuk, 1999, *E. atrabracus* Duellman & Pramuk, 1999, *E. serendipitus* Duellman & Pramuk, 1999, *E. cuneirostris* Duellman & Pramuk, 1999, and *Telmatobius colanensis* Wiens, 1993. More recently, between 2019 and 2021, three herpetological expeditions led by P.J. Venegas along the western slope of Cordillera de Colán resulted in the discovery of four new species of frogs: *Gastrotheca gemma* Venegas, García-Ayachi, Echevarría, Paluh, Chávez-Arribasplata, Marchelie & Catenazzi, 2021, *Lynchius wayneholomonae* Venegas, García-Ayachi, Ormeño, Bullard, Catenazzi & Motta, 2021, *Oreobates colanensis* Venegas, García-Ayachi, Ormeño, Bullard, Catenazzi & Motta, 2021, and *Pristimantis paulpittmani* Venegas, García-Ayachi & Catenazzi, 2021. In contrast, the reptile fauna of this semi-isolated mountain ridge remains poorly known, and only one new lizard species, *Stenocercus dracopennatus* Venegas, García-Ayachi, Chávez-Arribasplata, Chávez, Wong & García-Bravo, 2020, has been described in recent years.

Among squamatan reptiles, the clade *Hoplocercinae* includes 20 currently recognized species of Neotropical iguanian lizards assigned to two genera: *Enyalioides* Boulenger, 1885 and *Hoplocercus* Fitzinger, 1843 (Torres-Carvajal et al. 2023). Among these, wood lizards and manticores (*Enyalioides*) occupy lowland tropical rainforests, including the Chocó and the western Amazon basin, with fourteen species (74%) occurring east of the Andes and five (26%) west of the Andes. Remarkably, the clade *Enyalioides* is one of the Neotropical lizard taxa with the highest recent species discovery rate, with a 47% growth in the total number of species during the last fourteen years (Torres-Carvajal et al. 2008, 2009, 2015, Venegas et al. 2011, 2013a, 2021). These discoveries are primarily the result of recent fieldwork in poorly explored areas of the Central and Northern Andes of Peru and Ecuador. In this paper, we describe two new species of *Enyalioides* from Cordillera de Colán based on morphological and phylogenetic evidence (Torres-Carvajal et al. 2023).

Material and Methods

Field techniques

Most lizards were captured manually via the complete species inventory technique (Scott 1994) during slow nocturnal (20:00 to 02:00 h) walks along trails and through the forest. Coordinates and elevation data were taken with a GPS (Garmin, WGS84). After specimens were euthanized with T61 (Intervet), we took muscle tissue samples from the left thigh and stored them in cryogenic vials (Axygen) containing 96% ethanol. Specimens were then fixed in 10% formalin for 48 hours and stored in 70% ethanol. Voucher specimens were deposited at the herpetological collection of the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru. Specimens were collected under permits RDG 110-2007-INRENA-IFFS-DCB, RDG 067-2019-MINAGRI-SERFOR-DGGSPFFS, and 010-2021-MIDAGRISERFOR-DGGSPFFS issued by the Ministry of Agriculture.

Morphological data

Snout-vent length (SVL) and tail length (TL) were measured with a ruler and recorded to the nearest millimetre. All other measurements (i.e. head width, length, and height; rostral and mental width and height) were made with digital callipers and recorded to the nearest 0.1 mm. Sex was determined by noting the presence of everted hemipenes or sexually dichromatic characters. We followed Torres-Carvajal et al. (2011) for the description of the new species, as well as for the terminology of scutellational characters and measurements. Specimens of other species of *Enyalioides* examined in this study are listed in Appendix 1. Institutional abbreviations correspond to Centro de Ornitología y Biodiversidad (CORBIDI), Museo de Historia Natural San Marcos (MUSM), Lima, Peru, and Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador.

Genetic data

We obtained 41 sequences of the mitochondrial gene subunit II of NADH dehydrogenase (ND2) from GenBank to calculate uncorrected genetic distances among Hoplocercinae species. These sequences represent all known species of Hoplocercinae, including three samples of the species described

in this paper. Sample CORBIDI 21351, which corresponds to one of the new species described below, was excluded from this analysis as it had a high percentage of missing data (34.2%). GenBank accession numbers are listed in Table 2 of Torres-Carvajal et al. (2023).

Results

The taxonomic conclusions of this study are based on the observation of morphological features and colour patterns, genetic distances, and the phylogenetic tree recently presented by Torres-Carvajal et al. (2023). This information is considered species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998, 2007).

Enyalioides cyanocephalus sp. nov. Figs. 1-3
Enyalioides sp. 2 – Torres-Carvajal et al. (2023)
Proposed common name in English: blue-headed wood lizards
Proposed common name in Spanish: lagartijas de palo de cabeza azul

Holotype: CORBIDI 20781, an adult male from Uriarte (5.49099° S, 78.36703° W, 2,045 m, WGS 84), District Aramango, Bagua Province, Department Amazonas, Peru, collected on 13 August 2019 by P.J. Venegas.

Paratypes: Department Amazonas: Bagua Province: District Aramango: CORBIDI 20724 and 20726, juvenile females, and CORBIDI 20737, adult female, from Nueva Esperanza (5.48520° S, 78.34658° W, 1,559 m, WGS 84), collected between 9-11 August 2019 by P.J. Venegas and J.C. Chávez-Arribasplata; CORBIDI 22495 and 22496, juvenile females, CORBIDI 22497, juvenile male, CORBIDI 22498, adult female, CORBIDI 22499-501, three adult males, from Cataratas de Nueva Esperanza (5.49059° S, 78.33768° W, 1,705 m, WGS 84), collected on December 2019 by A. Marchelie; Bagua Province: District Imaza: CORBIDI 25410, 25430, 25433, 25493, adult females, and CORBIDI 25432, 25469, 25471, 25492, adult males, from Alto Wawas (5.38368° S, 78.28972° W, 1,234 m, WGS 84), collected between 8-10 June 2023 by L.A. García-Ayachi, J. Odar, S. Bullard, J. Valencia and E. Quispe; Bongara Province: District Yambrasbamba: CORBIDI 24920-22, 24938-40, four males and two females, from Perla del Imaza (5.61956° S, 77.97228° W, 1,566 m, WGS 84), collected between 17-19 March 2023 by P.J. Venegas L.A. García-Ayachi, S. Bullard, J. Valencia and E. Quispe.

Diagnosis: Enyalioides cyanocephalus can be distinguished from other species of *Enyalioides*, except its sister species *E. anisolepis* Torres-Carvajal, Venegas & de Queiroz, 2015 (Torres-Carvajal et al. 2023), by the combination of the following characters: 1) scales immediately posterior to superciliaries, on the lateral edge of skull, conical, slightly higher than adjacent scales; 2) gular scales heterogeneous in size; 3) scales on neck conical dorsally and conspicuously larger than the granular scales on the sides; 4) dorsal scales between dorsolateral crests covered by strongly carinate projected scales surrounded by tiny granular scales; 5) scales on flanks tiny, tuberculate or granular, with scattered enlarged conical or tuberculate scales; 6) ventral scales keeled or feebly keeled; 7) tail laterally compressed; 8) caudal scales heterogeneous, increasing in size posteriorly on each segment; 9) venter immaculate in adult males; and 10) marked sexual dichromatism with background dorsal colouration green in males (Fig. 1) and brown or greenish brown in females (Fig. 2).

Enyalioides cyanocephalus resembles *E. anisolepis* in having a green dorsal background in males and brown in females, dorsum and gular region with scales that are heterogeneous in size, and an orange patch on the gular region in males. Moreover, both species occur in close proximity as *E. anisolepis* is known from the Amazon slope of the Andes in extreme southern Ecuador and northern Peru at 724-1,742 m (Torres-Carvajal et al. 2015). Nevertheless, *E. cyanocephalus* can be distinguished from *E. anisolepis* (state of character in parentheses) by having scales on dorsal aspect of neck mostly large and conical (the dorsal aspect of neck with few scattered large conical scales) (see Fig. 3A, B), dorsum of body between dorsolateral crests mostly covered by large, keeled, mucronate scales (dorsum of body between dorsolateral crests with scattered large, keeled, non-mucronate scales) (see Fig. 3C, D), and belly and ventral surface of thighs immaculate (with scattered brown spots in adult males).

Other species of *Enyalioides* that possess scattered and projected large scales on dorsum are *E. cofanorum* Duellman, 1973, and *E. heterolepis* Bocourt, 1874. *Enyalioides cofanorum* occurs east of the Andes in Colombia, Ecuador, and Peru at elevations between 100 and 1,230 m (Torres-Carvajal et al. 2011). *Enyalioides cyanocephalus* differs from *E. cofanorum* in having gular scales and dorsal scales of hind limbs heterogeneous in size (homogeneous), and by lacking a dark patch on gular region (a black patch in both sexes). *Enyalioides heterolepis* occurs in Panama and the Pacific slope of the Andes of Ecuador and Colombia (Torres-Carvajal et al. 2011). *Enyalioides*

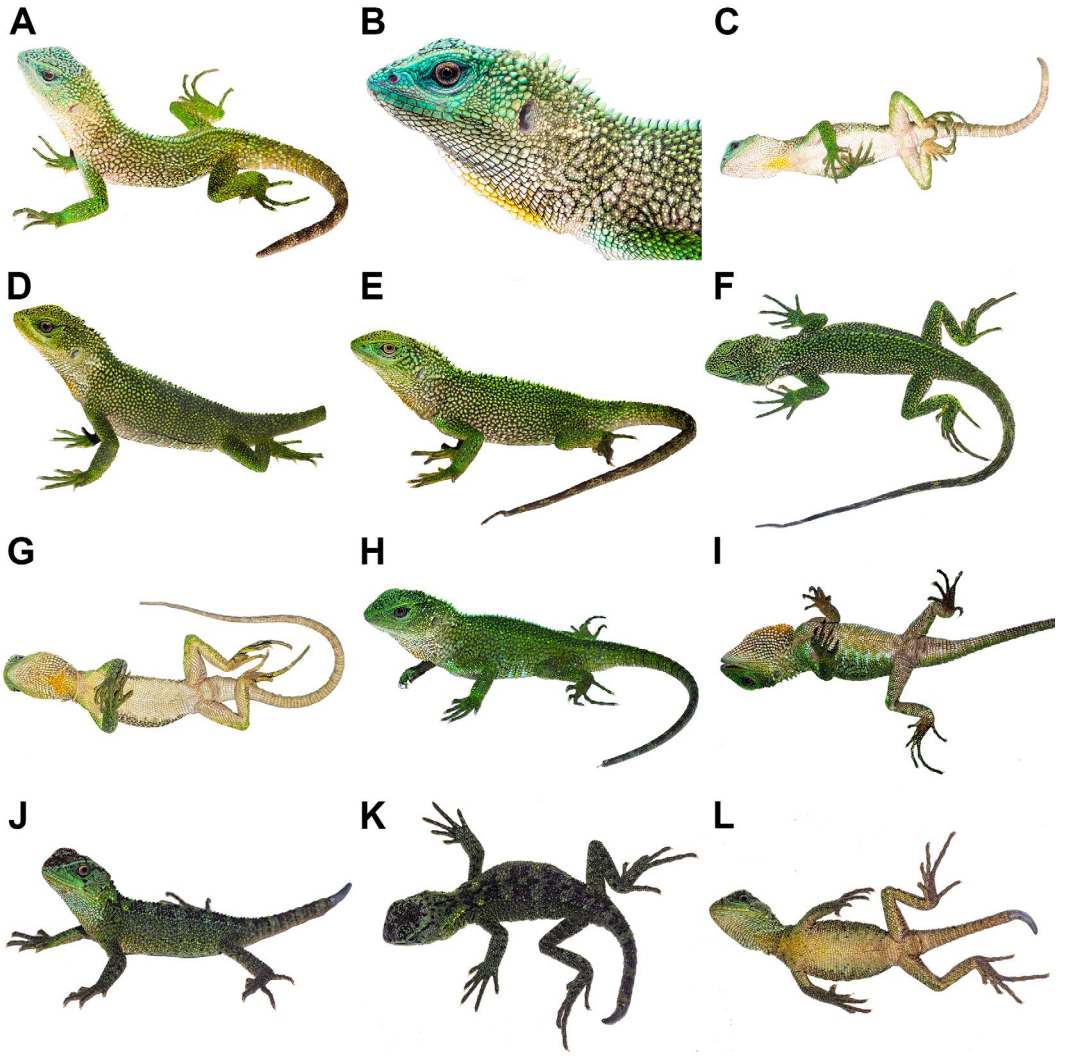

Fig. 1. Male specimens of *Enyalioides cyanocephalus* sp. nov.: (A-C) adult male holotype CORBIDI 20781, SVL = 121 mm; (D) adult male CORBIDI 22501, SVL = 106 mm; (E-G) adult male CORBIDI 22499, SVL = 114 mm; (H-I) adult male CORBIDI 22500, SVL = 100 mm; and (J-L) juvenile male CORBIDI 22497, SVL = 65 mm (photo Axel Marchelie).

cyanocephalus can be distinguished from *E. heterolepis* by having a taller vertebral crest with the vertebral scales on neck at least three times higher than those between the hindlimbs (a lower vertebral crest with vertebral scales on neck maximum twice as high as those between hindlimbs), venter immaculate (with a medial black patch), and by lacking enlarged projected scales on hind limbs (present).

Description of holotype: Adult male (Fig. 1A-C); SVL = 110 mm; TL = 112 mm (13 mm regenerated); maximum head width = 23.3 mm; head length = 29.3 mm; head height = 20.2 mm; dorsal head scales feebly carinate or multicarinate, those in the parietal region conical, projected dorsally; scales immediately posterior to superciliaries conical and dorsally projected, forming an indistinct longitudinal row of six (left) or five (right) scales that extends posteriorly over supratemporal region; temporal scales small, conical or tuberculate, juxtaposed; three enlarged pretympanic scales, bottom one feebly carinate and pointed, the middle one tuberculate and larger than the rest, and upper one conical; superciliaries 12; canthals five; postrostrals five; supralabials 10 if counted to a point right below middle of eye, and 14 if counted to commissure of mouth; rostral (3.3 mm wide × 1.3 mm high) about twice as wide as adjacent supralabials; single longitudinal row of lorilabials between suboculars and supralabials at level of middle of eye, longitudinal rows of lorilabials anterior to this point two; loreal region with small, smooth and keeled, juxtaposed scales; nasal at level of supralabials III and IV; infralabials nine (left) or eight (right) if counted to a point right below middle of eye, and 13 if counted to commissure of mouth; mental (3.4 mm wide × 1.7 mm high) wider and higher than adjacent infralabials; postmentals two; gulars projected; gular fold complete midventrally;

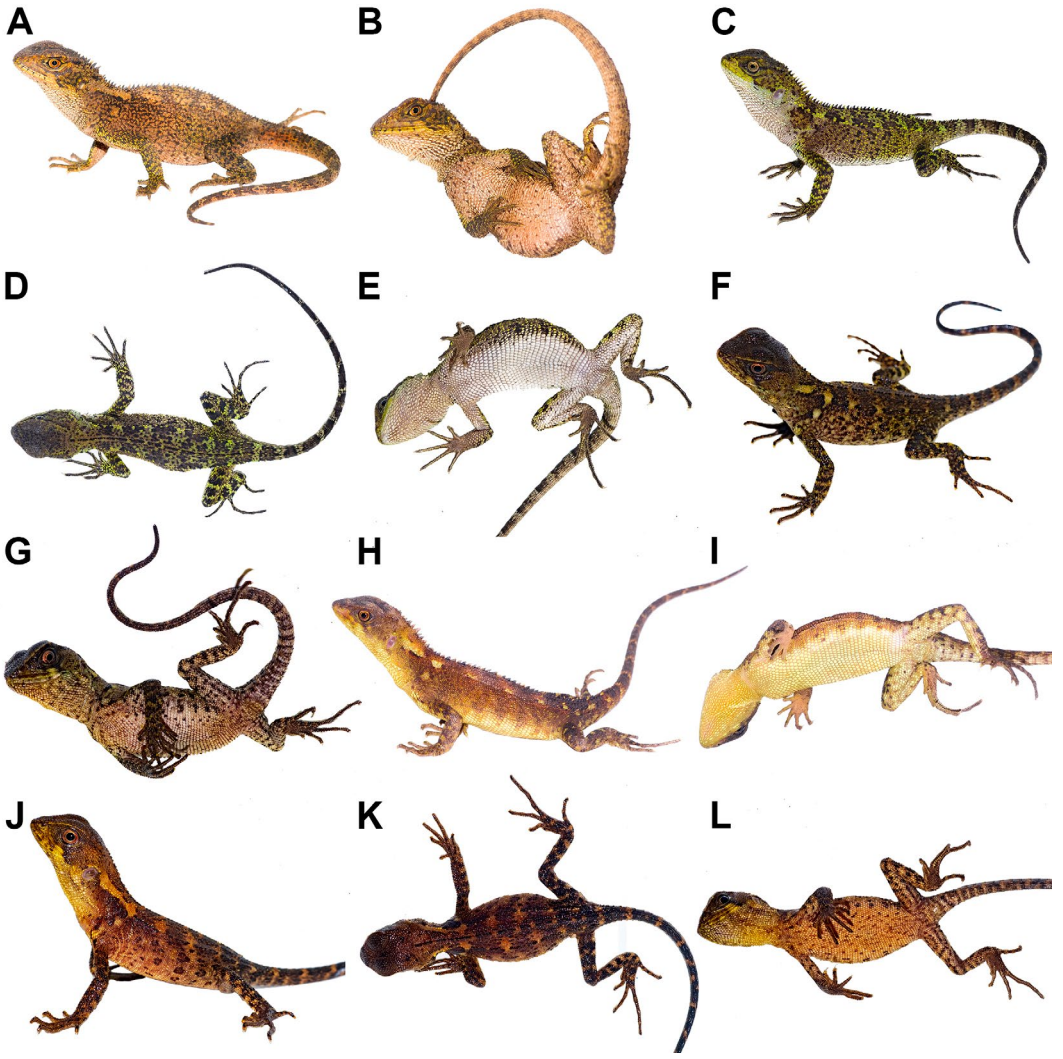

Fig. 2. Female specimens of *Enyalioides cyanocephalus* sp. nov.: (A-B) adult female CORBIDI 20737, SVL = 112 mm; (C-E) adult female CORBIDI 22498, SVL = 102 mm; (F-G) juvenile female CORBIDI 22495, SVL = 46 mm; (H-I) adult female CORBIDI 20726, SVL = 102 mm; and (J-L) juvenile female CORBIDI 22496, SVL = 44 mm (photo Axel Marchelie).

gular region expanded; neck with a few longitudinal and oblique folds.

Vertebral crest strongly projected and decreasing in size posteriorly, with vertebral on neck at least three times taller than those between hindlimbs; crest bifurcates at a point approximately 10 mm posterior to cloaca, and extends onto tail about ¼ its length; flanks between fore and hind limbs with dorsolateral and ventrolateral longitudinal folds, oblique folds present only on inguinal region; axillary region with one vertical fold; scales on dorsolateral folds slightly larger than adjacent flank scales giving the fold the appearance of a low crest; scales between dorsolateral folds and vertebral crest covered mainly by large, keeled, mucronate scales surrounded by tiny granular scales; neck and scapular region covered by large conical scales dorsally and granular scales laterally, with a lateral row of large conical scales; flank scales granular or tuberculate with scattered large conical or tuberculate scales, with the largest scales about ten times the size of the smallest ones; axillary region with conical scales; ventral scales imbricate, keeled, rhomboidal, with a posterior mucron; ventrals large, about three times the area of smallest dorsals.

Limb scales keeled and imbricate, dorsally and ventrally homogeneous in size on forelimbs; scales on dorsal and posterior aspects of thighs heterogeneous in size, with most scales about half the size of those on anterior and ventral aspects; scales on posterior surface of thighs covered by tiny granular or tuberculate scales with scattered large conical scales; scales on dorsal surface of shanks strongly keeled, projected, homogeneous in size; subdigitals on finger IV 21; subdigitals on toe IV 27; two femoral pores on left leg, one on right leg; tail laterally compressed and gradually tapering posteriorly; caudal scales strongly

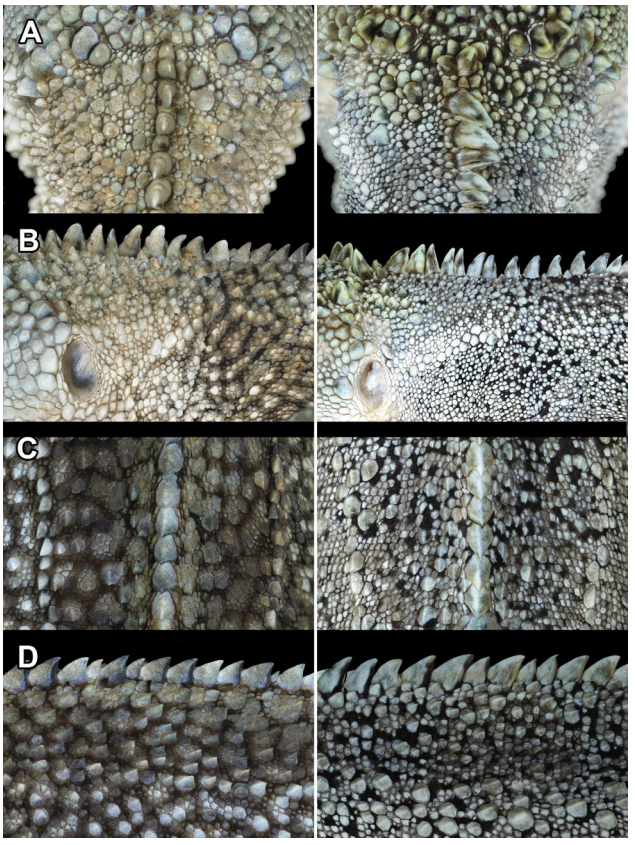

Fig. 3. Dorsal aspect of neck and dorsum of *Enyalioides cyanocephalus* sp. nov. (left), CORBIDI 20781, SVL = 121 mm, and *E. anisolepis* (right), CORBIDI 24321, SVL = 110 mm: (A) dorsal view of neck, (B) lateral view of neck, (C) dorsal view of the middle portion of dorsum between dorsolateral crests, and (D) lateral view of the middle portion of dorsum between vertebral crest and dorsolateral crest (photo Luis A. García-Ayachi).

keeled and imbricate, increasing in size posteriorly on lateral and dorsal aspects of each caudal segment; caudals larger ventrally than dorsally; individual caudal segments three scales long ventrally and six scales long dorsally.

Colour in life of holotype (Fig. 1A-C). Dorsal and lateral aspects of head (including labial scales) are turquoise with scattered black scales dorsally; dorsal background of body, limbs and tail green with a black reticulated mantle on dorsum and flanks; scattered black scales on fore and hindlimbs; sides of neck and ventrolateral region dusty white with a greenish hue on the posterior half; vertebral crest pale green; ventral surface dusty white without spots, blotches or reticulations; skin between gular scales greyish white; yellow patch on posteromedial aspect of throat; ventral surface of tail dusty white at base and dirty cream from second quarter to tip of tail; iris brownish cream peripherally with dark brown reticulations and dark brown centrally with a thin golden ring around pupil.

Variation: Variation in meristic and morphometric characters of *E. cyanocephalus* is presented in Table 1. Caudal segments are 5-7 scales long laterally. Adult males of *E. cyanocephalus* show slight variation in colouration. The turquoise head and the smoky white colouration extending from the sides of the neck to the flanks are present in two of the eleven collected adult males. The head is bright green in CORBIDI 22501 (Fig. 1D) and water green in CORBIDI 22500 (Fig. 1H), and both specimens possess only the sides of neck and scapular region with a smoky white hue. Paratype CORBIDI 22500 has a greenish-white belly (Fig. 1I). Juvenile male CORBIDI 22497 has a dark green dorsum with black bands, greenish-cream gular region with a faint orange patch on its posterior margin, and brownish cream ventral surface of body, limbs and tail with scattered dark brown spots (Fig. 1J-L). The juvenile CORBIDI 22497 lacks the smoky white flanks with black reticulations observed in adult specimens.

Enyalioides cyanocephalus has a marked sexual dichromatism in background colouration (bright green in males *vs.* brown or greenish brown in females; see Figs. 1-2). Adult and juvenile females possess dark brown bands on dorsum with distinct pale brown interspaces and strongly spotted (with dark brown spots or semicircular blotches) flanks and limbs. Adult female CORBIDI 20737 is the only female specimen with the same black reticulations on flanks of adult males (Fig. 2A). Female specimens have a conspicuous dark brown banded tail and dorsal surface of limbs strongly marked by dark brown or black spots, flecks and bands (see Fig. 2). Except for one (CORBIDI 22498), all adult females bear a distinct postympanic pale brown or brownish-cream stripe along the neck. Ventral colouration in adult females varies from immaculate smoky white (CORBIDI 22498) (Fig. 2E) to yellowish cream (CORBIDI 20726) (Fig. 2I). In juvenile females, ventral colouration is brownish cream with or without scattered dark brown flecks (CORBIDI 22495). Two juvenile females (CORBIDI 20726 and 22496) have yellow gular regions.

The scales on hindlimbs can be slightly heterogenous in size on dorsal surface of thighs and homogeneous on dorsal surface of shanks as in the holotype, or conspicuously heterogeneous in size in both sexes (e.g. CORBIDI 20737 and 22500). However, adult females possess (CORBIDI 20726) or lack (CORBIDI 20737) conical projected scales on dorsal surface of thighs.

Distribution and natural history: Enyalioides cyanocephalus occurs in the north-western and south-eastern slopes of Cordillera de Colán in northern Peru (Amazonas Department), at elevations between 1,559 and 2,045 m (Fig. 4). It is known from four localities, two localities in the Río Marañón basin (Cataratas de Nueva Esperanza and Uriarte) and two localities in the Río Chiriaco basin (Alto Wawas and Perla del Imaza), within the Peruvian Yungas ecoregion (Olson et al. 2001). The general landscape in this area is composed of montane forest with scattered crops and pasture for cattle ranching. Specimens were found sleeping at night (7:00-12:00 h) between 0.2 and 1.8 m above ground on stems of bushes and plants near trails in primary forest.

Sympatric species of squamatan reptiles collected in the same survey include the lizards *Alopoglossus buckleyi* O'Shaughnessy, 1881, *Anolis fuscoauratus* D'Orbigny, 1837, *A. soinii* Poe & Yañez-Miranda, 2008, and *Pseudogonatodes peruvianus* Huey & Dixon, 1970; as well as the snakes *Chironius monticola* Roze, 1952, *Clelia clelia* Daudin, 1803, *Bothrocophias microphthalmus* Cope, 1875, *Bothrops pulcher* Peters, 1862, *Dipsas catesbyi* Sentzen, 1796, *D. peruana* Boettger, 1898, *Epicrates cenchria* Linnaeus, 1758, *Erythrolamprus janaleeae* Dixon, 2000, and *E. guentheri* Garman, 1883.

Etymology: The specific epithet is derived from the Greek words '*kyanos*', an adjective meaning blue, and '*cephalus*', a noun meaning head. This specific name is used as a noun in apposition and refers to the bluish head of the holotype specimen. Although only two adult males in the type series possessed a distinctive bluish head, the males of this species are commonly known by the local people in Cordillera de Colán as blue-headed chameleon, which leads us to think that males of *E. cyanocephalus* with bluish heads are not uncommon.

Remarks: Enyalioides cyanocephalus is nested in a strongly supported clade of 13 currently recognized species of *Enyalioides* as the sister taxon of *E. anisolepis* (Torres-Carvajal et al. 2023). All species in this clade – *E. anisolepis*, *E. azulae* Venegas, Torres-Carvajal, Duran & de Queiroz, 2013, *E. binzayedi* Venegas, Torres-Carvajal, Duran & de Queiroz, 2013, *E. cofanorum*, *E. cyanocephalus*, *E. feiruzae* Venegas, Chávez, García-Ayachi, Duran & Torres-Carvajal, 2021, *E. microlepis* O'Shaughnessy, 1881, *E. palpebralis* Boulenger, 1883, *E. praestabilis* O'Shaughnessy, 1881, *E. rubrigularis* Torres-Carvajal, de Queiroz & Etheridge, 2009, *E. rudolfarndti* Venegas, Duran, Landauro & Lujan, 2011, *E. sophiarothschildae* Torres-Carvajal, Venegas & de Queiroz, 2015, and the new species described below – are restricted to the eastern slopes of the Andes and adjacent lowlands. The uncorrected ND2 genetic distance between *E. cyanocephalus* and *E. anisolepis* is 0.036, slightly higher than between other species pairs with relatively small distances, such as *E. rudolfarndti*/*E. feiruzae* (0.024), *E. microlepis*/*E. cofanorum* (0.032), and *E. feiruzae*/*E. binzayedi* (0.033) (Table S1). ND2 genetic distances among all species of *Enyalioides* range between 0.024 (*E. rudolfarndti*/*E. feiruzae*) and 0.269 (*E. altotambo* Torres-Carvajal, Venegas & de Queiroz, 2015/*E. laticeps* Guichenot, 1855).

Enyalioides dickinsoni sp. nov. Figs. 5-6
Enyalioides sp. 1 – Torres-Carvajal et al. (2023)
Proposed common name in English: Dickinson's wood lizards
Proposed common name in Spanish: lagartijas de palo de Dickinson

Holotype: CORBIDI 21351, an adult male from Guayaquil (5.67157° S, 78.26106° W, 1,717 m, WGS 84), District Cajaruro, Utcubamba Province, Department Amazonas, Peru, collected on 5 December 2019 by S. Bullard.

Paratypes: Department Amazonas: Bagua Province: District La Peca: CORBIDI 738, an adult female from Chonza Alta (5.61330° S, 78.39674° W, 1,405 m, WGS 84), collected on 1 December 2007 by P.J. Venegas; de Utcubamba Province: District de Cajaruro: CORBIDI 21703, adult male, CORBIDI 21710, juvenile female, CORBIDI 21711, adult female, from La Unión (5.70613° S, 78.28547° W, 1,459 m, WGS 84), collected between 18-23 September 2019 by A. Marchelie.

Diagnosis: Enyalioides dickinsoni can be distinguished from all known species of *Enyalioides*, except *E. azulae*, by the combination of the following characters: 1) a distinctively low vertebral crest, with the crest on neck at most twice as high as the crest between hind limbs; 2) scales immediately posterior to superciliaries on lateral edge of skull barely projected and similar in height to adjacent scales; 3) 56-71 vertebral scales from occiput to base of tail; 4) dorsal scales feebly keeled and heterogeneous in size; 5) ventral scales keeled; 6) tail circular in cross-section; and 7) caudal scales heterogeneous, increasing in size posteriorly on each segment.

Enyalioides dickinsoni differs from *E. azulae* (state of character in parentheses) by having 36-41 gular scales (45-57), ventral scales keeled or feebly keeled

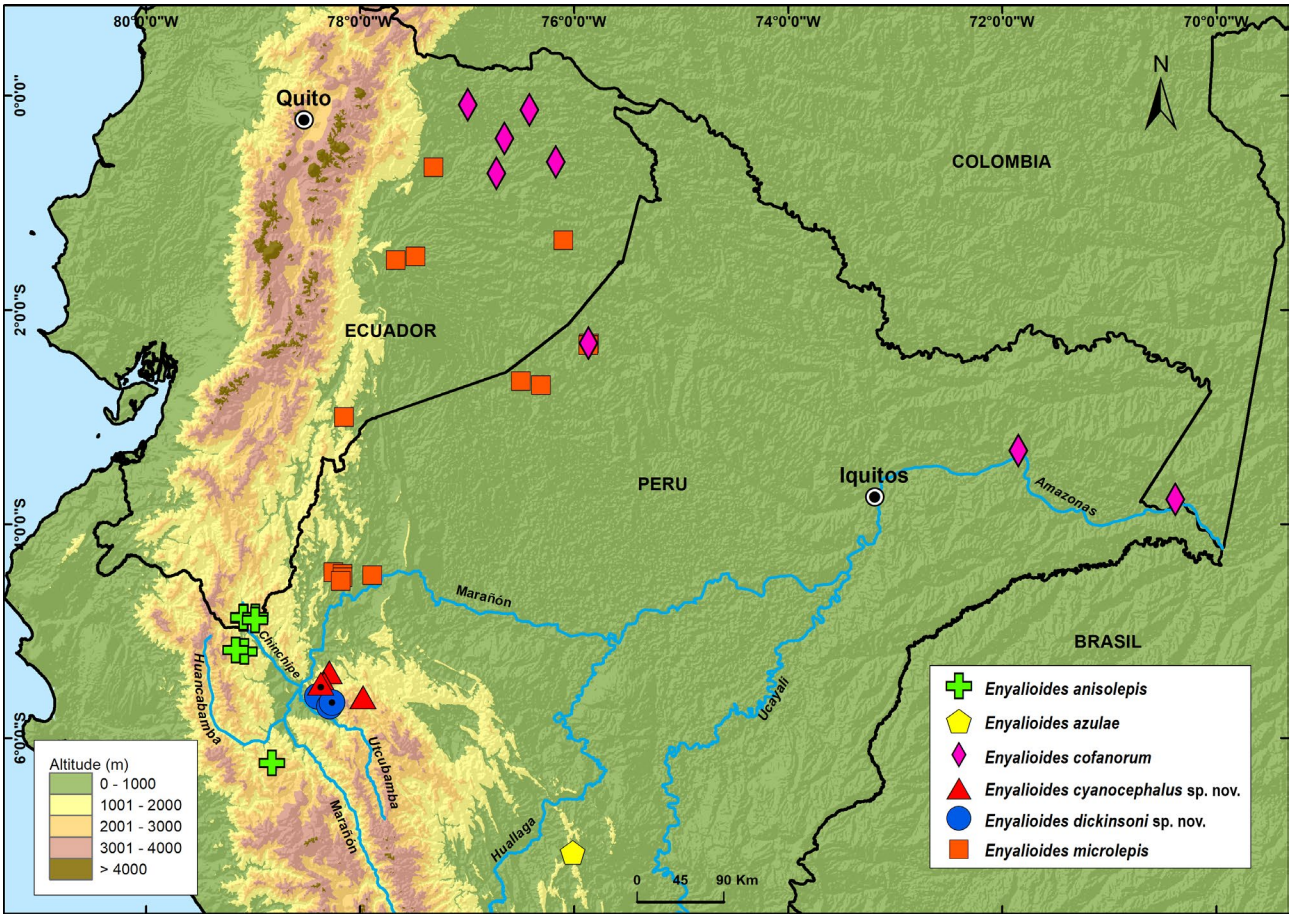

Fig. 4. Distribution of *Enyalioides anisolepis*, *E. azulae*, *E. cofanorum*, *E. cyanocephalus* sp. nov., *E. dickinsoni* sp. nov., and *E. microlepis* in Peru and Ecuador. Symbols with black dots are the type localities.

(strongly keeled), and a faint dirty white postympanic stripe extending up to the middle of neck in males (a conspicuous cream or white postympanic stripe extending to the scapular region). Other species, such as *E. cofanorum* and *E. microlepis*, are slightly similar to *E. dickinsoni* in general features, such as low crest, relatively small size (SVL between 100 and 130 mm), and a brownish dorsal colouration in both sexes. However, *E. dickinsoni* differs from *E. cofanorum* (state of character in parentheses) by lacking scattered, projecting, large dorsal scales between forelimbs and hindlimbs (present) and having a dark patch on gular region restricted to the posterior edge in males (a large dark patch covering most of gular region in both sexes). *Enyalioides dickinsoni* differs from *E. microlepis* in having 27-38 dorsal scales in a transverse row between dorsolateral crests at midbody (more than 40), keeled ventral scales (strongly keeled), and a brownish orange gular patch (light blue gular patch surrounding the black gular patch extending to level of eyes and neck sides).

Description of holotype: Male (Fig. 5A-C); SVL = 113 mm; TL = 172 mm; maximum head width = 25.5 mm; head length = 31.5 mm; head height = 22.3 mm; dorsal head scales keeled, those in parietal region projected dorsally; scales immediately posterior to superciliaries barely projected and slightly larger than adjacent scales; temporal scales small, tuberculate or keeled, juxtaposed; one noticeably enlarged pretympanic scale on top of anterodorsal edge of tympanic opening; superciliaries 14; canthals four; postrostrals four; supralabials nine if counted to a point right below middle of eye, and 18 if counted to commissure of mouth; rostral (3.3 mm wide × 1.3 mm high) about twice as wide as adjacent supralabials; two longitudinal rows of lorilabials between suboculars and supralabials at level of middle of eye, longitudinal rows of lorilabials anterior to this point 3-4; loreal region with small, smooth and keeled, juxtaposed scales; nasal at level of supralabials III and IV; infralabials eleven (left and right) if counted to a point right below middle of eye, and 16 (left) and 15 (right) if counted to commissure of mouth; mental (3.4 mm wide × 1.7 mm high) wider and higher than adjacent infralabials; postmentals three; gulars projected, low; gular fold complete midventrally; gular region expanded; neck with few ill-defined longitudinal and oblique folds.

Vertebral crest projected, low and decreasing in size posteriorly, up to two times higher on neck than between hind limbs; crest bifurcates at a point approximately 15 mm posterior to the cloaca and extends onto tail about ¼ its length; flanks between fore and hind limbs without folds; axillary region with three vertical folds; a row of enlarged scales along dorsolateral region, forming a dorsolateral crest; scales on dorsolateral row 3-4 times larger than adjacent scales; scales between dorsolateral crests and vertebral crest feebly keeled, increasing in size gradually towards vertebral crest, with scales near vertebral crest three times as large as the smallest ones; neck and scapular region with low conical scales, heterogeneous in size; flank scales ventral to dorsolateral crest feebly keeled, similar to paravertebrals, increasing in size gradually towards venter, with largest scales four times as large as smallest ones; axillary region with conical scales; ventral scales imbricate, feebly keeled on the chest and keeled on the belly, rhomboidal, with a posterior mucron; ventral scales more than five times the area of the smallest dorsal scales.

Limb scales keeled dorsally and ventrally, homogeneous in size on forelimbs; scales on dorsal and posterior aspect of thighs homogeneous in size, with most scales less than half the size of those on anterior and ventral aspects; scales on dorsal surface of shanks homogeneous in size and mucronate; subdigitals on finger IV 20; subdigitals on toe IV 24; femoral pores on left leg absent, one on right leg; tail cylindrical; caudal scales strongly keeled, imbricate and finely mucronate, increasing in size posteriorly on lateral and dorsal aspects of each caudal segment; caudals conspicuously larger ventrally than dorsally; individual caudal segments three scales long ventrally and seven scales long dorsally.

Colour in life of holotype (Fig. 5A-C). Dorsal and lateral aspect of head, including supralabials I-IV

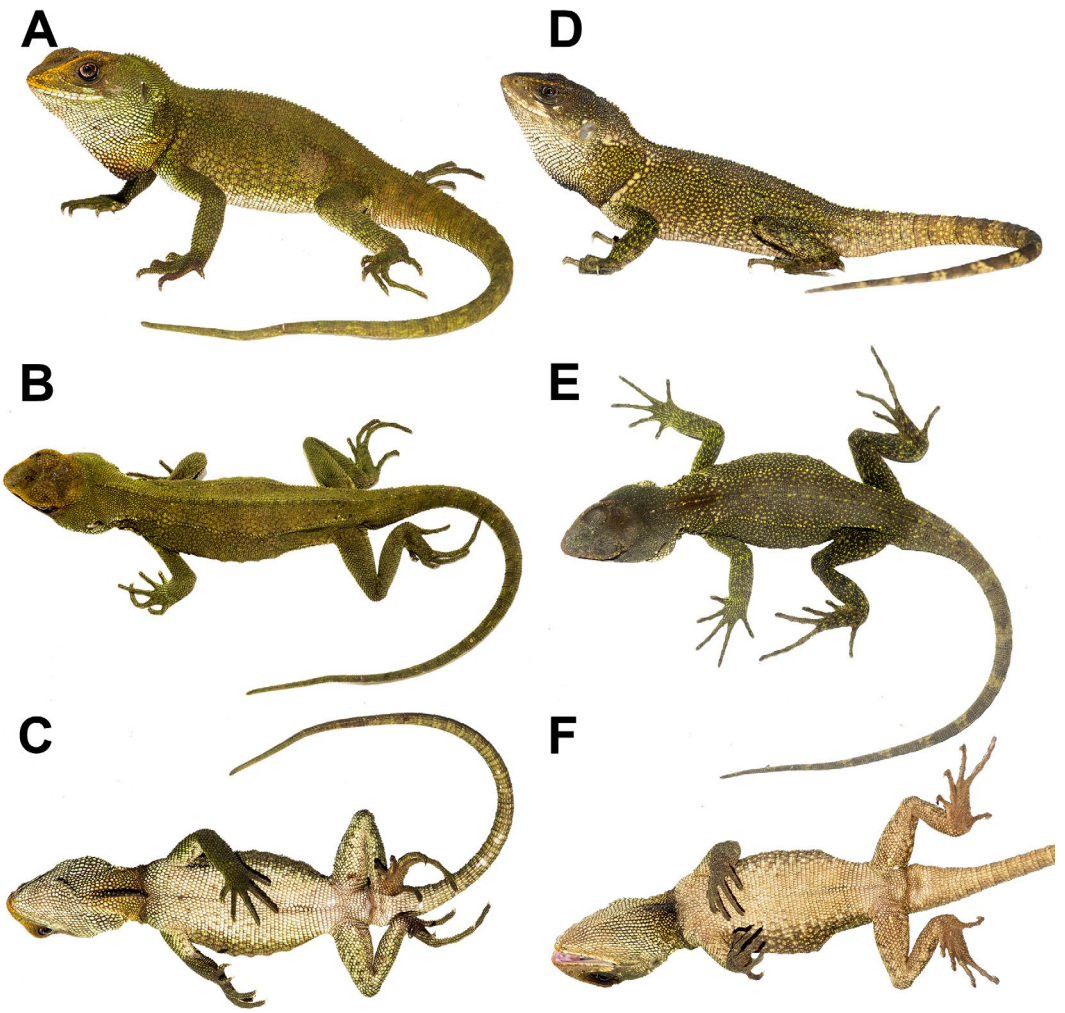

Fig. 5. Two adult male specimens of *Enyalioides dickinsoni* sp. n.: (A-C) holotype CORBIDI 21351, SVL = 113 mm; (D-F) CORBIDI 21703, SVL = 92 mm (photo Axel Marchelie).

greenish bronze; remaining labials and subocular blotch dirty white; dorsal background of body, vertebral crest, limbs, and tail greenish brown with a faint postympanic dirty white stripe on neck and brown reticulations on flanks; gular scales dirty white, the skin between them pale brown; posterior aspect of throat with brownish orange patch; chest and belly dirty white; ventral surface of limbs dirty white with a greenish tint and scattered brown spots; ventral surface of tail dirty white proximally and greenish brown distally; iris brownish cream peripherally with dark brown reticulations centrally; thin golden ring around pupil; sclera black; buccal mucosa pale pink with a slight purple hue on the tongue.

Variation: Variations in meristic and morphometric characters of *E. dickinsoni* are presented in Table 1. Caudal segments are 6-8 scales long laterally. The single adult male paratype (CORBIDI 21703) is similar in background colour to the holotype but varies in having dorsum and flanks splattered by bright green scales, a cream anthehumeral bar, the skin between gular scales dark grey, a black patch on the posterior aspect of throat, and the belly brownish cream (Fig. 5). This species has a slight sexual dichromatism in background colours (greenish bronze in males, brown in females; see Figs. 5-6). Moreover, female paratypes, including a juvenile (CORBIDI 21710), possess several skin folds on flanks and sides of neck including oblique, transversal, dorsolateral and lateral folds.

The colouration pattern of females is variable. An adult female (CORBIDI 738) possesses a dark brown dorsum with a row of pale greenish blotches, pale brown flanks splattered by pale greenish spots, and a postympanic pale green stripe along neck; while another adult female (CORBIDI 21711) has a uniform brown dorsum (Fig. 6A-B). A juvenile female

Table 1. Variation in meristic and morphometric characters. Range (first line) and mean ± standard deviation (second line) are given for quantitative characters, except when there was no variation. Sample size in parentheses for maximum SVL.

Character	*E. cyanocephalus* n = 19	*E. dickinsoni* n = 5
Vertebrals from occiput to base of tail	40-55 46.79 ± 4.72	56-71 62.20 ± 5.81
Dorsals in transverse row between dorsolateral crests at midbody	24-35 29.05 ± 2.80	27-38 33.40 ± 4.16
Ventrals in transverse row at midbody	22-37 25.74 ± 3.30	27-33 29.00 ± 2.45
Transverse rows of ventrals between fore and hind limb	33-47 38.16 ± 4.07	34-40 37.00 ± 2.24
Gulars	29-35 31.74 ± 1.91	36-41 38.80 ± 1.92
Infralabials	8-10 8.37 ± 0.60	8-10 9.00 ± 0.71
Supralabials	9-11 9.68 ± 0.58	9-9 9.00 ± 0.00
Canthals	4-5 4.95 ± 0.23	4-6 5.00 ± 0.71
Superciliaries	12-16 14.26 ± 1.15	13-16 14.60 ± 1.14
Subdigitals on finger IV	18-22 20.11 ± 1.63	18-20 19.20 ± 0.84
Subdigitals on toe IV	24-29 26.58 ± 1.68	24-27 25.20 ± 1.30
Tail length/total length	0.58-0.62 0.60 ± 0.01	0.56-0.60 0.59 ± 0.02
Maximum SVL (mm) males	116 (n = 8)	113 (n = 2)
Maximum SVL (mm) females	112 (n = 9)	97 (n = 3)

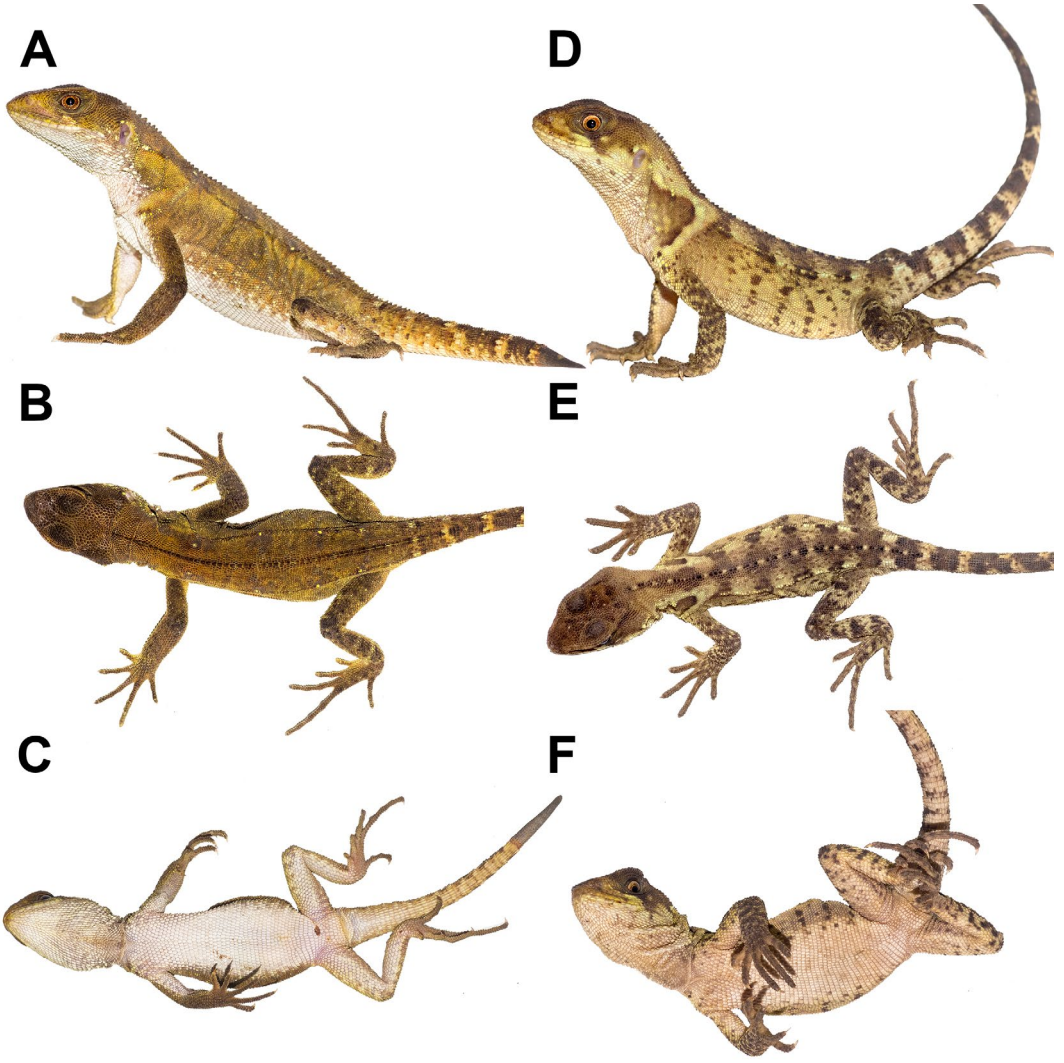

Fig. 6. Female specimens of *Enyalioides dickinsoni* sp. n.: (A-C) adult female CORBIDI 21711, SVL = 87 mm; (D-F) juvenile female CORBIDI 21710, SVL = 83 mm (photo Axel Marchelie).

(CORBIDI 21710) differs from the adult females by having a pale brown dorsum with dark brown transverse bars (Fig. 6D-E).

Distribution and natural history: Enyalioides dickinsoni occurs at elevations between 1,405-1,717 m on the western slope of Cordillera de Colán in the Andes of northern Peru (Fig. 4). It is known from three localities (Chonza Alta, La Unión and Guayaquil) along the Río Utcubamba basin, Peruvian Yungas ecoregion (Olson et al. 2001). The general landscape in this region includes croplands of coffee, cacao, and citrus, as well as pasture for cattle ranching on a matrix of secondary forest bisected by several rocky streams, some with narrow fringes of forest. Most specimens were found sleeping at night (7:00-12:00 h) between 0.4 and 1.5 m above ground on stems in coffee crops. Only one specimen was found during the day (10:00 h) in the base of a bush, which ran to hide under a large rock. Sympatric species of squamatan reptiles collected with *E. dickinsoni* include the lizards *A. fuscoauratus*, *Petracola* sp., *Polychrus peruvianus*, and *Stenocercus huancabambae* Cadle, 1991; and the snakes *B. microphthalmus*, *B. pulcher*, *D. peruana*, *Erythrolamprus festae* Peracca, 1897, and *E. janaleeae*.

Etymology: The specific name is a noun in the genitive form and is a patronym honouring Paul Bruce Dickinson (born 7 August 1958), who is best known as the lead singer of the legendary heavy metal band Iron Maiden, though he is also a music producer, entrepreneur, competitive fencer, novelist, aviator, broadcaster and the recipient of numerous honorary degrees and awards. In 2016, he flew a loggerhead sea turtle, *Caretta caretta*, that washed up on a Jersey beach to the Canary Islands in his private plane, thus contributing to the awareness and protection of this vulnerable species. We also highlight that Iron Maiden is a popular band among taxonomists and museum curators who appreciate rock music.

Remarks: Enyalioides dickinsoni is nested in a strongly supported clade of 13 currently recognized species of *Enyalioides* as sister to the clade *E. anisolepis*, *E. cyanocephalus* (Torres-Carvajal et al. 2023). All species in this clade – *E. anisolepis*, *E. azulae*, *E. binzayedi*, *E. cofanorum*, *E. cyanocephalus*, *E. feiruzae*, *E. microlepis*, *E. palpebralis*, *E. praestabilis*, *E. rubrigularis*, *E. rudolfarndti*, *E. sophiarothschildae*, *E. dickinsoni* – are restricted to the eastern slopes of the Andes and adjacent lowlands. The smallest uncorrected ND2 genetic distance between *E. dickinsoni* and other species of *Enyalioides* is 0.036 (*E. anisolepis*). The genetic distance between *E. dickinsoni* and *E. cyanocephalus*, the most proximate geographically, is 0.161 (Table S1). ND2 genetic distances among all species of *Enyalioides* range between 0.024 (*E. rudolfarndti*/*E. feiruzae*) and 0.269 (*E. altotambo*/*E. laticeps*).

Discussion

Including the two new species described herein, the herpetological exploration of the Andes from northern Peru in the last three decades has resulted in the discovery of 35 species of lizards belonging to ten genera (i.e. two species of *Ameiva* Meyer, 1795, one *Cercosaura* Wagler, 1830, six *Enyalioides*, two *Macropholidus* Noble, 1921, two *Petracola* Doan & Castoe, 2005, one *Pholidobolus* Peters, 1863, one *Polychrus* Linnaeus, 1758, three *Phyllodactylus* Gray, 1828, one *Phyllopezus* Peters, 1877, and sixteen *Stenocercus*) (Cadle 1991, 1998, 2001, Cadle & Chuna 1995, Torres-Carvajal 2005, Koch et al. 2006, 2011, 2013, 2016, Venegas et al. 2008, 2013a, b, 2014, 2016a, b, 2020, 2022, Echevarría & Venegas 2015, Echevarría et al. 2015, 2021, Torres-Carvajal et al. 2015, 2020, Rodríguez & Mamani 2020). Most of these species are known from a few localities restricted or adjacent to the Huacabamba Depression, which represents a complex orographic scenario where Andean mountain ranges are separated by deep valleys (Duellman & Pramuk 1999). This remarkable depression has been recognized as a major biogeographic barrier and a migration corridor (Vuilleumier 1969, Duellman 1979, Cadle 1991, Quintana et al. 2017). For example, the Huancabamba Depression seems to have impacted the radiation of several Andean lizard clades, such as *Stenocercus* Duméril & Bibron, 1837, *Riama* Gray, 1858, and *Pholidobolus* (Doan 2003, Torres-Carvajal 2007, Torres-Carvajal & Mafla-Endara 2013). Moreover, one lizard clade – *Macropholidus* – has radiated mostly within the Huacabamba Depression (Torres-Carvajal et al. 2020). Interestingly, phylogenetic and biogeographic analyses of Cercosaurinae lizards showed that the age of *Macropholidus* (12.36-18.90 mya) closely corresponds to the Middle Miocene (Torres-Carvajal et al. 2016), when the Andes had emerged to form the Huancabamba Depression (Quintana et al. 2017). Therefore, the Huancabamba Depression has also acted as a centre of origin and diversification, which explains the high diversity and endemicity of lizards in this area.

The rivers Marañón and Utcubamba form deep valleys covered by dry forest vegetation at lower elevations and seem to form an important biogeographical barrier for *Enyalioides* in the Huancabamba Depression. The distribution range of the two new species described in this paper is restricted to the east and north of the rivers Marañón and Utcubamba, respectively. By contrast, their close relative, *E. anisolepis*, occurs west of the Marañón. Moreover, the River Marañon represents approximately the southern limit of the clade (*E. rubrigularis* (*E. praestabilis* (*E. cofanorum*, *E. microlepis*))), which is the sister taxon of (*E. dickinsoni* (*E. anisolepis*, *E. cyanocephalus*)). These two clades together form the sister taxon of another clade occurring south of the Marañón (see Fig. 3 in Torres-Carvajal et al. 2023). In conclusion, the River Marañón seems to have acted as a major biogeographical barrier affecting the evolution of *Enyalioides* lizards.

Key to the 22 species of *Hoplocercinae*

The following key is a modification to the key presented by Torres-Carvajal et al. (2015) and is artificial in the sense that its structure does not necessarily reflect the order of branching in the phylogeny.

1. Dorsal head scales flat, smooth, juxtaposed; vertebral crest absent or composed of a discontinuous row of enlarged scales that are longer than tall.....2
Dorsal head scales conical; vertebral crest present, composed by projecting scales that are taller than long.....5
2. Tail depressed, short (tail length < snout-vent length), with enlarged spiny scales dorsally and laterally .....*Hoplocercus spinosus*
Tail nearly round, moderate (tail length > snout-vent length), with rings of enlarged spiny scales.....3
3. Vertebral region of trunk without enlarged scales; tail with three scale rows separating the spiny whorls ventrally.....*Enyalioides groi*
Some vertebral scales in trunk region enlarged, forming a discontinuous longitudinal row; tail with two scale rows separating the spiny whorls ventrally.....4

4. Usually two femoral pores on each leg; two postmentals; females without streaks on throat.....*E. annularis*
Femoral pores 3-4 on each leg; usually four postmentals; females with dark streaks on throat.....*E. peruvianus*
5. Caudal scales homogeneous in size within each autotomic segment.....6
Caudal scales increase in size posteriorly within each autotomic segment.....7
6. Gular region in males white with a black medial patch.....*E. sophiarothschildae*
Gular region in males orange or dirty cream, with longitudinal brown, reddish-brown, bluish, or orange streaks, and a large brown or black medial blotch at the level of the gular fold.....*E. laticeps*
7. Laterally projecting superciliary flap present; vertebral crest usually discontinuous (absent on posterior part of neck).....*E. palpebralis*
Laterally projecting superciliary flap absent; vertebral crest continuous.....8
8. Scattered, conspicuous large scales on dorsum, flanks, and hind limbs present.....9
Scattered, conspicuous large scales on dorsum, flanks, and hind limbs absent.....11
9. Scattered large scales tetrahedral in shape; vertebrals on neck maximum twice as high as those between hind limbs.....*E. heterolepis*
Scattered large scales strongly keeled, not tetrahedral in shape; vertebrals on neck at least three times higher than those between hind limbs.....10
10. Dorsal aspect of neck with a few scattered large, conical scales; dorsals between dorsolateral crests include scattered large, keeled, non-mucronate scales; belly and ventral surface of thighs with scattered brown spots in adult males.....*E. anisolepis*
Dorsal aspect of neck covered mainly by large, conical scales; dorsals between dorsolateral crests mostly large, keeled, and mucronate; belly and ventral surface of thighs immaculate in adult males.....*E. cyanocephalus*
11. Ventrals smooth or feebly keeled.....12
Ventrals conspicuously keeled.....13
12. Gulars in males cream or yellow without black margins; usually one femoral pore on each leg.....*E. praestabilis*
Gulars in males bright orange or red, with black margins; usually two femoral pores on each leg.....*E. rubrigularis*
13. Dorsals heterogeneous in size, with scattered, tetrahedral, projecting scales (sometimes absent in males or juveniles); dorsolateral crests well developed between hind limbs.....*E. cofanorum*
Dorsals homogeneous in size, without projecting scales; dorsolateral crests inconspicuous or absent between hind limbs.....14
14. Dorsals smooth or slightly keeled.....15
Dorsals conspicuously keeled.....16
15. Scales on flanks heterogeneous in size, with a few enlarged, circular, keeled scales; iris bright red in both sexes; black patch under gular fold extending dorsally to form a short antehumeral bar in males.....*E. oshaughnessyi*
Scales on flanks almost homogenous in size; iris brown in both sexes; black medial patch on gular region not extending dorsally to form an antehumeral bar in males.....*E. altotambo*
16. Scales posterior to the superciliaries enlarged and pointed (relative to adjacent scales), forming a well-defined longitudinal row of distinctly raised scales across the lateral edge of the head in adults of both sexes.....17
Scales posterior to the superciliaries slightly or barely enlarged and not always pointed (relative to adjacent scales) without forming a well-defined longitudinal row of distinctly raised scales across the lateral edge of the head in adults of both sexes.....19
17. Scales along the lateral edge of the skull roof strongly projected, dorsals with prominent median keel; antehumeral orange blotch in adult males absent.....*E. binzayedi*
Scales along the lateral edge of the skull roof slightly projected; dorsals without prominent median keel.....18
18. Dorsals heterogeneous in size; 11-12 supralabials (means = 11.75); conspicuous antehumeral orange blotch in adult males.....*E. rudolfarndti*
Dorsals mostly homogeneous in size; 8-10 supralabials (means = 9.52); conspicuous antehumeral orange blotch in adult males.....*E. feiruzae*
19. White or cream spot posterior to tympanum usually present.....20
White or cream spot posterior to tympanum usually absent.....21
20. 41-54 (mean = 45.96 ± 3.49) dorsals in transverse row between dorsolateral crests at midbody; gular background in adult males light blue.....*E. microlepis*
27-38 (mean = 33.40 ± 4.16) dorsals in transverse row between dorsolateral crests at midbody; gular background in adult males brownish orange.....*E. dickinsoni*
21. Vertebral scales in neck region in adult males similar in size as vertebrals in pelvic region; 45-57 (mean = 51.13 ± 4.05) gulars.....*E. azulae*
Vertebral scales in neck region in adult males more than twice as high as vertebrals in pelvic region; 42-48 (mean = 44.40 ± 2.22) gulars.....*E. touzeti*

Acknowledgements

We are grateful to the Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP), especially to the professional personnel of the Santuario Nacional Cordillera de Colán and Reserva Comunal Chayu Nain: Christian Olivera, Jhonny D. Ramos, Gerlys Fernandez, Abner García, Victor Juep Bakuants, Ysmael Zurita Santos, Roger Vasquez Rojas, Timoteo Wasum Shakai and Efrain Tsamajain Yampii. We are also indebted to Geronimo Goicochea Nuñez and Humberto Palomino Rafael from Guayaquil for their support in the field. This research was funded by the Critical Ecosystem Partnership Fund (CEPF), with the project numbers CEPF-109938 and CEPF 113268, through the Fondo de Promoción de las Áreas Naturales Protegidas del Perú (PROFONANPE), and the Hollomon Price Foundation.

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Supplementary online material

Table S1. Uncorrected ND2 genetic distances among *Enyalioides* species (https://www.ivb.cz/wp-content/uploads/JVB-vol.-73-2024-VenegasP.J.-et-al.-Table-S1.xlsx).

Appendix 1. Specimens examined.
Enyalioides anisolepis – ECUADOR: Zamora-Chinchipe: bank of the River Mayo, 4.5 km ESE Zumba, 4.88605° S, 79.08738° W, 765 m, QCAZ 12537 (holotype), QCAZ 12521, QCAZ 12527, QCAZ 12528, QCAZ 12531; Nuevo Paraíso, 700 m NW on road to Las Tres Aguas, 4.87109° S, 78.97579° W, 1,742 m, QCAZ 12517; Chito, sector Los Planes, 4.89814° S, 78.98095° W, QCAZ 8395, QCAZ 8515, QCAZ 8428: PERU: Cajamarca: San Ignacio: Alto Ihuamaca-Namballe, 5.19448° S, 79.08048° W, 1,616 m, CORBIDI 870; El Sauce, Tabaconas Namballe National Sanctuary, 5.17897° S, 79.16347° W, 1,600 m, MUSM 20675.

Enyalioides azulae – PERU: San Martín: Picota: Chambirillo close to Checkpoint 16 of the Cordillera Azul National Park, 7.06913° S, 76.01422° W, 1,122 m, CORBIDI 06772 (holotype), 8825, 8826, 08786, 08790, 08791.

Enyalioides cofanorum – ECUADOR: Orellana: Vía Pompeya-Iro, 66 km from Pompeya, QCAZ 8035; Sucumbíos: La Selva lodge, 0.40000° S, 76.65000° W, QCAZ 3953, 3521.

Enyallioides heterolepis – ECUADOR: Esmeraldas: Alto Tambo, 253 m, QCAZ 5523; Bosque Protector La Chiquita, 30 km E San Lorenzo on road to Ibarra, QCAZ 3839; Corriente Grande, 70 m, QCAZ 3531; Loma Linda, Río Onzole, 95 m, QCAZ 3626; Mayronga, 100 m, QCAZ 2185-2186, 2263-2266; San Miguel de Cayapas, QCAZ 412; Los Ríos: Estación Biológica Río Palenque, 150-220 m, QCAZ 427; Santo Domingo de los Tsáchilas: 15 km NW La Florida, QCAZ 2844; Bosque Protector La Perla, QCAZ 2025–2026.

Enyalioides microlepis – PERU: Loreto: Pozo Runtusapa, MUSM 22264; Datem del Marañón: Andoas, 3.70433° S, 77.31283° W, 273 m, CORBIDI 01506, 01575; Capahuari Norte, 2.66425° S, 76.50123° W, 270 m, CORBIDI 04804; San Jacinto 2.33083° S, 75.86369° W, 160 m, CORBIDI 05120.

NOMENCLATURAL ACTS REGISTRATION ✷

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Publication LSID: urn:lsid:zoobank.org:pub: 51EB32EA-9DED-42F1-89F9-5C2109170353.

Nomenclatural act LSID: urn:lsid:zoobank.org:act:A521C0DC-EE55-46ED-B265-5EF985534C29.
urn:lsid:zoobank.org:act:zoobank.org/7F8AFE5A-6F7C-42B7-B1DB-CD122C49C734.