Acta Herpetologica 16(2): 63-87, 2021
DOI: 10.36253/a_h-10742

A new species of the genus *Noblella* (Amphibia: Strabomantidae) from Ecuador, with new information for *Noblella worleyae*

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Submitted on: 2021, 31st March; revised on: 2021, 22nd July; accepted on: 2021, 23rd July
Guest Editor: Aaron M. Bauer

Abstract. We describe a new species of terrestrial-breeding frog of the genus *Noblella* from the northwestern slopes of the Andes of Ecuador, in the province of Pichincha, Ecuador, and report a new locality for the recently described *N. worleyae*. We include a detailed description of the osteology of both species and discuss their phylogenetic relationships. The new species is differentiated from other species of *Noblella* by having discs of fingers rounded, without papillae; distal phalanges only slightly T-shaped; toes slightly expanded and rounded distally, without papillae; dorsum uniform brown with irregular suprainguinal dark brown marks; venter yellowish cream, ventral surfaces of legs and thighs reddish to brownish cream; and dark brown throat. The new locality for *N. worleyae* is located in Los Cedros Reserve, an area highly threatened by mining. We highlight the importance of protecting endemic species of small vertebrates in northwestern Ecuador.

Keywords. Frog, Los Cedros Biological Reserve**,** endemism, Imbabura, Mindo, Pichincha, phylogeny.

INTRODUCTION

The amphibian diversity in the tropical Andes is outstanding (Duellman, 1988; Myers et al., 2000; Hutter et al., 2013, 2017). Each year, several species are described from montane forests of this biodiversity hotspot (e.g., Rojas-Runjaic et al., 2018; Guayasamin et al., 2019; Paez and Ron, 2019; Reyes-Puig et al., 2019b; Santa-Cruz et al., 2019; Yanez-Muñoz et al., 2019; Acevedo et al., 2020; Ospina-Sarria et al., 2020; Lehr et al., 2021). Most described species from Ecuador belong to the hyper-diverse genus *Pristimantis* (Paez and Ron, 2019; Reyes-Puig et al., 2020a), but diversity in other anuran taxa has also increased considerably (e.g., *Osornophryne*, *Hyloscirtus*, *Noblella*, Centrolenidae; Mueses-Cisneros et al., 2010; Cisneros-Heredia and Gluesenkamp,

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

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2010; Yánez-Muñoz et al., 2010a; Páez-Moscoso and Guayasamin, 2012; Almendáriz et al., 2014; Guayasamin et al., 2017a, 2019; Reyes-Puig et al., 2019c).

Terrestrial-breeding frogs of the genus *Noblella* Barbour 1930 are minute-size anurans (SVL < 22 mm), morphologically differentiated by having terminal discs on digits not or barely expanded, discs and circumferential grooves present distally (except in *N. duellmani*), terminal phalanges narrowly T-shaped, pointed tips of at least Toes III–IV, and an inner tarsal tubercle (De La Riva et al., 2008; Hedges et al., 2008; Duellman and Lehr, 2009). However, phylogenetic relationships of *Noblella* are not fully resolved and its monophyly is uncertain (De la Riva et al., 2017; Santa-Cruz et al., 2019). As currently defined, *Noblella* includes 16 species, fourteen distributed in the Andes of Ecuador, Peru, and Bolivia, and two (*N. losamigos* and *N. myrmecoides*) in the Amazonian lowlands from southeastern Colombia, Ecuador, Peru, Bolivia, and western Brazil (Frost, 2021). During the last 15 years, the number of species in the genus has doubled; and four new species have been described since 2019 (Catenazzi and Ttito, 2019; Reyes-Puig et al., 2019c, 2020b; Santa-Cruz et al., 2019). Currently, the total number of species of the genus *Noblella* is 16, distributed in ten species in Peru, seven in Ecuador, three in Bolivia, and one in Colombia and Brazil (Frost, 2021).

Andean species of the genus *Noblella* show a high level of endemicity, with very restricted distributions. While some species of *Noblella* may apparently be able to survive in environments modified by humans (e.g., *N. duellmani*, *N. losamigos*, *N. lochites*, *N. naturetrekii*; Duellman and Lehr, 2009; Reyes-Puig et al., 2019c; Santa-Cruz et al., 2019); most species (e.g., *N. coloma, N. heyeri, N. personina, N. pygmaea*; Lynch, 1986; Guayasamin and Terán-Valdez, 2009; Harvey et al., 2013) seem to depend on undisturbed forest. Three species of *Noblella* have been described from western Ecuador, all from mature mountain forests: *Noblella heyeri* (Lynch, 1986) occurs in southwestern Ecuador and extreme northwestern Peru; *Noblella coloma* Guayasamin and Terán-Valdez, 2009 is known from its type locality and surroundings (Rio Guajalito and Chiriboga area; Ron et al., 2019); and *Noblella worleyae*, a recently described species is known just from seven specimens, all found in mature forest in the Río Manduriacu Reserve, province of Imbabura, Ecuador (Reyes-Puig et al., 2020b).

While the Ecuadorian Andes have suffered serious habitat destruction and fragmentation caused by expansion of deforestation, agriculture, mining, among others (Castellanos et al., 2011; Roy et al., 2018; Guayasamin et al., 2019; Lessmann et al., 2019; Ortega et al., 2021), there are still some areas with mature forests that have not been exploited due to their complex topography, difficult access, private protection, or preservation for touristic activities. Unfortunately, all such sites are under strong anthropogenic pressure, including mining concessions and the expansion of agricultural boundaries, among others (Cuesta et al., 2017; Roy et al., 2018; Guayasamin et al., 2019; Ortega et al., 2021). These privileged areas have proven to keep an extremely high cryptic diversity of small vertebrates and contain the last remnant populations of numerous threatened species (Cisneros-Heredia and Yanez-Muñoz, 2010; Reyes-Puig et al., 2010, 2019a, 2019b; Yánez-Muñoz et al., 2010b, 2018; Guayasamin et al., 2018, 2019, 2020; Sánchez-Nivicela et al., 2018; Barrio-Amorós et al., 2020).

During the last five years, we have carried out surveys on the western slopes of the Andes in the provinces of Imbabura and Pichincha, Ecuador. As a result of this continuous effort, we found a new species of leaf-litter frog of the genus *Noblella*, which we describe herein based on a combination of morphological, molecular, and osteological features. We also document new information on distribution, external morphology and osteology for the recently described *Noblella worleyae*, information that was not described in detail in the original description. We also include intraspecific variation that will allow complete full with members of the same genus in the future.

MATERIALS AND METHODS

Taxonomy

We followed the family taxonomy proposed by Heinicke et al. (2018) and, also we revised De la Riva et al. (2017) and Barrietos et al. (2021). For identifying species, we assumed the unified species concept (De Queiroz, 2005, 2007). Information for species comparisons was extracted from the original descriptions and cited once at the beginning of the comparison.

Study area and fieldwork

Over the last three years (i.e., 2018–2020), we have carried out field surveys at several localities in montane forests of northwestern Ecuador, mainly in the provinces of Imbabura and Pichincha. Specimens of two different species of *Noblella* were found in Mindo (province of Pichincha) and Los Cedros Biological Reserve (province of Imbabura). Mindo is a small town renowned for its adventure and nature-based touristic activities; thus the area has numerous reserves that protect cloud forests (Arteaga-Navarro et al., 2013). Los Cedros Biological Reserve is a protected area that contains 6,879 hectares

of premontane humid tropical forest and cloud mountain forest. This reserve is located south of the Cotocachi-Cayapas Ecological Reserve (state protected area), and is also recognized by its endemic microfauna (Hutter and Guayasamin, 2015). Collected specimens were euthanized with benzocaine, fixed in 8% formalin, and preserved in 75% ethanol. Liver and leg muscle tissue samples were collected from all individuals prior to preservation. Tissues were preserved in 95% ethanol and stored at -20°C at the Laboratorio de Biología Evolutiva USFQ. Specimens were deposited in the Museo de Zoología, Universidad San Francisco de Quito, Ecuador (ZSFQ).

DNA extraction, amplification, and sequencing

We obtained new DNA sequences of *Noblella* sp. nov. (ZSFQ 050–051). DNA was extracted from muscle or liver tissue following the protocol by Peñafiel et al. (2019). Standard polymerase chain reaction (PCR) was performed to amplify a fragment of the mitochondrial gene 16S rRNA, using a combination of the following primers: 16L10, 16H36E, 16L34, 16H47 (Heinicke et al., 2007). Amplicons were sequenced in both directions by the Macrogen Sequencing Team (Macrogen Inc., Seoul, Korea).

The new sequences were assembled and edited with Geneious 7.1.7 (GeneMatters Corp). After assemblage, the sequences were combined with sequences from GenBank for all species of *Noblella* and representatives of the genera within the Terrarana clade (sensu Hedges et al., 2008), including *Barycholos* Heyer 1969, *Bryophryne* Hedges, Duellman & Heinicke 2008, *Craugastor* Cope 1862, *Haddadus* Hedges, Duellman & Heinicke 2008, *Holoaden* Miranda-Ribeiro 1920, *Ischnocnema* Reinhardt & Lutken 1862, *Lynchius* Hedges, Duellman & Heinicke 2008, *Niceforonia* Goin & Cochran 1963, *Oreobates* Jiménez de la Espada 1872, *Qosqophryne* Catenazzi, Mamani, Lehr, von May 2020, *Phrynopus* Peters 2873, *Pristimantis* Jiménez de la Espada 1870, *Psychrophrynella* Hedges, Duellman & Heinicke 2008, and *Microkayla* De la Riva, Chaparro, Castroviejo-Fisher, Padial 2017. GenBank codes are shown in our inferred phylogenetic tree (Fig. 1).

Phylogenetic analyses

Phylogenetic relationships were inferred using maximum likelihood as the optimality criterion. The final matrix, with 52 terminals, was aligned with MAFFT v.7 (Multiple Alignment Program for Amino Acid or Nucleotide Sequences: http://mafft.cbrc.jp/alignment/software/), with the Q-INS-i strategy. MacClade 4.07 (Maddison and Maddison, 2005) was used to visualize the alignment, which contained a total of 492 bp. Phylogenetic analyses were performed under the ML criteria in GARLI 2.01 (Genetic Algorithm for Rapid Likelihood Inference; Zwickl, 2006) for the mitochondrial gene 16S. GARLI uses a genetic algorithm that finds the tree topology, branch lengths, and model parameters that maximize lnL simultaneously (Zwickl, 2006). Individual solutions were selected after 10,000 generations with no significant improvement in likelihood, with the significant topological improvement level set at 0.01. Then, the final solution was selected when the total improvement in likelihood score was lower than 0.05, compared to the last solution obtained. Default values were used for other GARLI settings, as per recommendations of the developer (Zwickl, 2006). Bootstrap support was assessed via 1,000 pseudoreplicates under the same settings used in tree search. Pairwise genetic distances between species (uncorrected-p) for gene 16S were calculated with PAUP 4a (Swofford et al., 1996).

External morphology

Diagnosis and description of the new species follow formats proposed by Duellman and Lehr (2009) and Lynch and Duellman (1997). For comparisons, we examined specimens of other species of *Noblella* (see Appendix I). We followed the sequence of characters proposed by Guayasamin and Terán-Valdez (2009). We measured preserved specimens using digital calipers to the nearest 0.01 mm. These measurements are: snout to vent length (SVL), from the tip of the snout to the cloaca; head length (HL), measured from tip of snout to anterior edge of tympanum; head width (HW), measured at midorbital region; horizontal diameter of the eye (ED); eye–nostril distance (EN), from anterior ocular angle to posterior edge of nostril; horizontal diameter of tympanum (TD); minimum interorbital distance (MIOD); minimum eyelid width (MWE); hand length (LH), from posterior edge of palmar tubercle to tip of third digit; shank length (LS), from the tip of the ankle to the knee; and foot length (LF), from posterior edge of external metatarsal tubercle to tip of Toe IV. We determined sexual maturity by the presence of vocal slits or extended vocal sacs in males and by the presence of eggs or convoluted oviducts in females. Detailed illustrations of the head, hands and feet were done with Adobe InDesign ©.

Osteology

Osteological descriptions were based on one specimen of the new species (ZSFQ 050) and one of *Noblella worleyae* (MZUTI 1709). Both specimens were scanned using a high-resolution micro-computed tomography (micro-CT) desktop device (Bruker SkyScan 1173, Kontich, Belgium) at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK, Bonn, Germany). To avoid movements during scanning, specimens were placed in a small plastic container and mounted with styrofoam. Acquisition parameters comprised: An X-ray beam (source voltage 43 kV and current 114 μA) without the use of a filter; 800 projections of 500 ms exposure time each with a frame averaging of 5 recorded over a 180° continuous rotation (rotation steps of 0.3 degrees), resulting in a scan duration of 49 min; a magnification setup generating data with an isotropic voxel size of 19.16 μm (MZUTI 1709) and 14.55 μm (ZSFQ 050), respectively. The CT-dataset was reconstructed with N-Recon software (Bruker MicroCT, Kontich, Belgium) and rendered in three dimensions using CTVox for Windows 64 bits version 2.6 (Bruker MicroCT, Kontich, Belgium). Osteological

terminology follows Trueb (1973), Duellman and Trueb (1994), Fabrezi and Alberch (1996), Guayasamin and Terán-Valdez (2009), Scherz et al. (2017), and Suwannapoom et al. (2018). Cartilage structures were omitted from the osteological descriptions because micro-CT does not render cartilage.

RESULTS

Phylogenetic relationships and genetic distances (Fig. 1)

The inferred phylogeny shows that the new species described herein is part of a clade composed of taxa distributed along the western slopes of the Ecuadorian Andes. This clade is composed by the new species *Noblella* sp. nov., *Noblella coloma* Guayasamin and Terán-Valdez, 2009, and *N. worleyae* Reyes-Puig, Maynard, Trageser, Vieira, Hamilton, Lynch, Culebras, Kohn, Brito and Guayasamin, 2020. Uncorrected p genetic distances are as follow: *N. coloma* (QCAZ 40579) and the new species (ZSFQ 050) = 5.1%; *N. coloma* (QCAZ 40579) and *N. worleyae* (ZSFQ 550–551) = 8.3%; *N. worleyae* (ZSFQ 550–551) and the new species (ZSFQ 050) = 1.2%.

Generic placement

We place the new species in the genus *Noblella* based on morphological and molecular evidence (Fig. 1). Morphologically, we assign the new species to the genus *Noblella,* as defined by Hedges et al. (2008), based on possession of the following traits: head not wider than body; cranial crests absent; tympanic membrane differentiated (undifferentiated in *N. duellmani*, *N. naturetrekii* and *N. madreselva*); dentigerous processes of vomers absent; terminal discs on digits not or barely expanded; discs and circumferential grooves present distally (absent in *N. duellmani*); terminal phalanges narrowly T-shaped; Finger I shorter than, or equal in length to, Finger II; Finger IV containing two phalanges in *Noblella carrascoicola* (De la Riva and Köhler, 1998), *N. lochites* (Lynch, 1976b), *N. losamigos* (Santa-Cruz et al., 2019), *N. myrmecoides* (Lynch, 1976b), *N. naturetrekii* (Reyes-Puig et al., 2019c), and *N. ritarasquinae* (Köhler, 2000) and three phalanges in *N. coloma* (Guayasamin and Terán-Valdez, 2009), *N. duellmani* (Lehr, Aguilar, and Lundberg, 2004), *N. heyeri* (Lynch, 1986), *N.* sp. nov., *N. lynchi* (Duellman, 1991), *N. madreselva* (Catenazzi, Uscapi, and von May, 2015), *N. personina* (Harvey, Almendáriz, Brito-M., and Batallas-R., 2013), *N. peruviana* (Noble, 1921), *N. pygmaea* (Lehr and Catenazzi, 2009), and *N. thiuni* (Catenazzi and Ttito, 2019); Toe III shorter than Toe V (except in *N. naturetrekii* and *N. worleyae*); tips of at least toes III–IV acuminate; subarticular tubercles not protruding; dorsum pustulate or shagreen; venter smooth; SVL less than 22 mm.

Systematic accounts

Noblella mindo new species.
Noblella coloma Arteaga et al. (2013).
Figs. 2–8
LSID urn:lsid: lsid:zoobank.org:act:3B7741EF-BF26-4589-B231-73F198AA1218
Proposed standard English name. Mindo Leaf Frog
Proposed standard Spanish name. Rana Noble de Mindo
Holotype. ZSFQ 050 (Fig. 2–6), adult female, collected in El Cinto, 11 Km E from Mindo town, Mindo (0.09022°S, 78.818581°W; 1,673 m; Fig. 2), province of Pichincha, República del Ecuador, by Melissa Costales, Matthijs Hollanders and Emilia Peñaherrera on 08 July 2017.
Paratypes (2 females, 2 males). Adult males (ZSFQ 049, 051) and adult females (ZSFQ 304–305) collected at the type locality (same data as holotype), by Melissa Costales on 04 October 2015.

Etymology

The specific name "mindo" is a word of unknown meaning in Panzaleo, an extinct pre-Columbian language of northern Ecuador (Jijón y Caamaño 1940). It is used as a noun in apposition, and alludes to the valley of Mindo, where the type locality of the new species is located. The remnant forests of this emblematic valley protect several species of endemic amphibians and reptiles such as *Pristimantis mindo, Noblella mindo*, and *Anolis proboscis*.

Diagnosis

Noblella mindo sp. nov. (Figs. 3–8) presents the following characteristics: (1) skin of dorsum finely shagreen, skin on venter smooth, discoidal fold slightly defined, discoidal and thoracic folds absent; (2) tympanic annulus and membrane visible externally, supratympanic fold inconspicuous (Figs. 3, 4); (3) snout short (eye-to-nostril distance 57% of eye diameter), rounded in dorsal and lateral views (Fig. 3); (4) eyelids without tubercles; (5) dentigerous processes of vomers absent; (6) vocal slits and sac present, nuptial pads not visible; (7) fingers not expanded distally, finger tips rounded, without papillae (Fig. 3); Finger I shorter than Finger II (Fig. 3); (8) distal phalanges slightly T-shaped, phalangeal formula of hands: 2-2-3-3 (Fig. 7); (9) supernumerary palmar tubercles present (slightly visible) mostly at the base

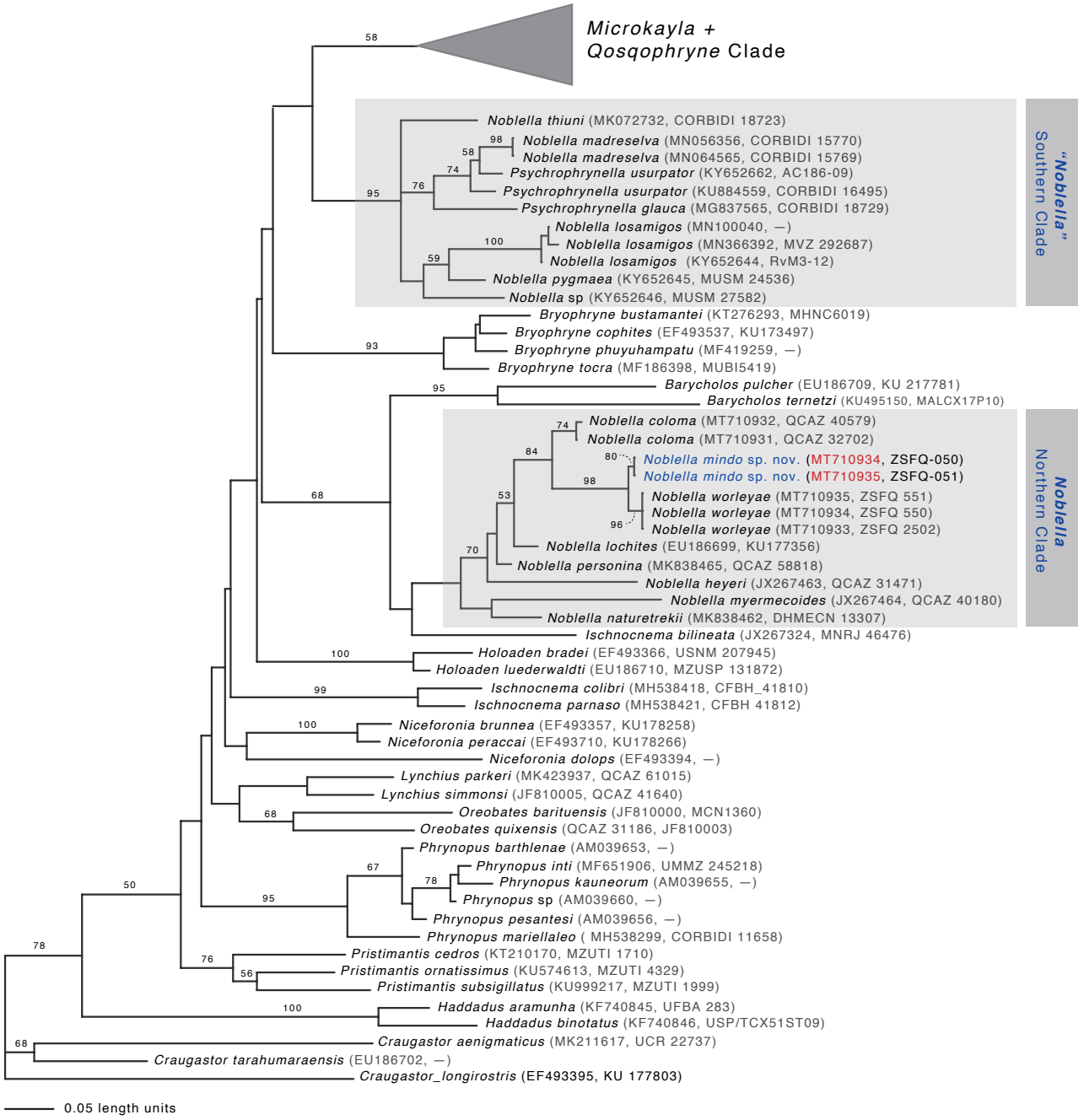

Fig. 1. Phylogeny of *Noblella* (light gray boxes) showing the relationships of *N. mindo* sp. nov. The phylogeny was inferred based on mitochondrial (16S) DNA sequences (16S; 52 terminals, 492 bp) and under the Maximum likelihood criterion. For each individual, museum catalog number or, if unavailable, GenBank accession number is shown.

of the digits, ulnar tubercles diminutive and rounded, subarticular tubercles rounded; circumferential grooves absent; (10) one tarsal tubercle elongated and subconical (Fig. 3); two prominent metatarsal tubercles (inner tubercle 3–4 times size of external); toes slightly expanded and rounded distally, without papillae; (11) Toe V shorter than Toe III, supernumerary plantar tubercles absent, distal portions of circumferential grooves not visible; (12) phalangeal formula of feet: 2-2-3-4-3 (Fig. 7); (13) in life, uniform brown dorsum, cream middorsal, longitudinal line distinct and present in all individuals, dark brown suprainguinal marks, white rictal gland,

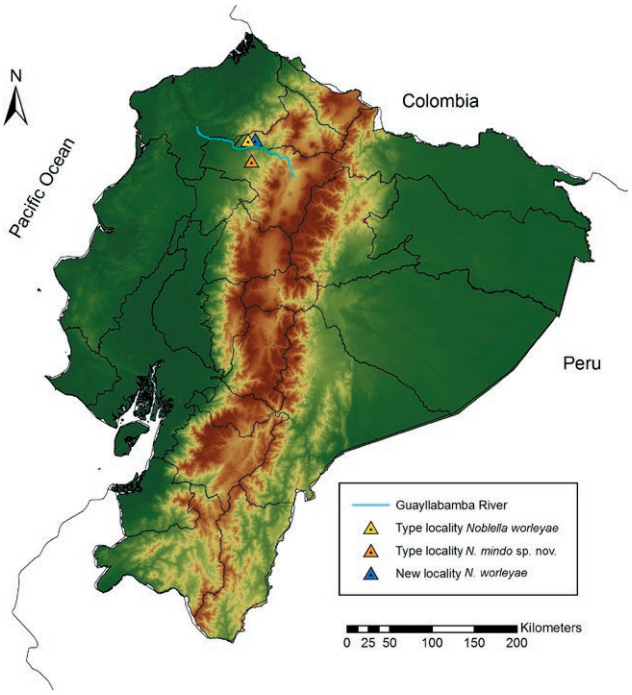

Fig. 2. Distribution of *Noblella mindo* sp. nov and *N. worleyae* in Ecuador.

flanks with dark brown band narrowing towards groin, dotted with white, light groin, with low concentration of melanophores, dark brown throat, chest and ventral surfaces of arms with a white cross formed by a longitudinal, fine line running from chin to chest crossing a similar line departing from midventral surface of each forelimb, yellowish-cream venter, reddish-copper iris with minute turquoise scattered dots (Fig. 4); (14) SVL in adult males 16.5–17.0 mm (mean 16.7 mm, n = 2), SVL in adult females 18.3–19.5 mm (mean 19.0 mm, n = 3).

Comparisons (Fig. 6, Table 1)

Noblella mindo sp. nov. differs from its congeners by the presence of rounded fingertips, without papillae; distal phalanges slightly T-shaped; toes slightly expanded and rounded distally, without papillae; dorsum uniform brown with middorsal cream line, suprainguinal marks dark brown, rictal gland white, light groin, throat and chest dark brown with white cross, and venter yellowish cream. *Noblella mindo* sp. nov. is most similar and closely related to *N. coloma* and *N. worleyae* (Fig. 1), but they differ as follows (characters of *N. mindo* sp. nov. in parentheses): *Noblella coloma* has all finger tips acuminate (all rounded), dark middorsal line (light), dark rictal gland (white), orange to reddish-venter (yellowish-cream), dark groin (light), uniform dark brown throat, chest and ventral surfaces of arms (dark brown with white cross), ulnar tubercles absent (diminutive and rounded), and smaller body size of 16.0 mm SVL in adult female (18.3–19.5 mm SVL in adult females); the new species (characters of *N. mindo* sp. nov. in parentheses) is distinguished from *Noblella worleyae* has finger tips slightly acuminate on Fingers I and IV and acuminate on Fingers II and III (rounded), T-shaped distal phalanges (slightly T-shaped), prootic and exoccipital fused to form otoccipital (separated), sphenethmoid well-ossified and ventrally fused at midline (moderately ossified, ventrally fused at midline in posterior half and separated in anterior half). For more comparison's information see Table 1.

Noblella mindo sp. nov. has three phalanges on Finger IV like *N. duellmani* (Lehr, Aguilar and Ludenberg, 2004), *N. heyeri* (Lynch, 1986), *N. lynchi* (Duellman, 1991), *N. madreselva* (Catenazzi, Uscapi and von May, 2015), *N. personina* (Harvey, Almendáriz, Brito, and Batallas, 2013), *N. peruviana* (Noble, 1921), *N. pygmaea* (Lehr and Catenazzi, 2009), and *N. thiuni* (Catenazzi and Ttito, 2019), but they differ as follows (characters of *N. mindo* sp. nov. in parentheses): *Noblella duellmani* has dorsal skin pustular (finely shagreen), tympanum membrane and annulus absent (present), upper eyelid bearing small tubercles (absent), ulnar tubercles coalesced into low folds (diminutive and round, not forming a fold), outer edge of tarsus bearing row of low and elongate tubercles (absent), tips of Fingers I-II slightly expanded and tips of Fingers III–IV slightly acuminate (all finger tips rounded), venter brown with tan mottling (yellowish-cream), and larger body size of 20.0 mm SVL in adult female (18.3–19.5 mm SVL in adult females); *Noblella heyeri* has dorsal skin weakly pustulate (finely shagreen), snout subacuminate in dorsal view (round), ulnar tubercles distinct and round (diminutive, round), toe tips slightly acuminate (round), venter brown with cream fleck (yellowish-cream), and smaller body size of 13.1–15.9 mm SVL in adult females (18.3–19.5 mm SVL in adult females); *Noblella lynchi* has dorsal skin pustular (finely shagreen), snout subacuminate in dorsal view (round), ulnar tubercles coalesced into low folds (diminutive and rounded, not forming a fold), outer edge of tarsus bearing row of low and elongate tubercles (absent), toe tips weakly acuminate (round), and venter brown with fine cream flecks (yellowish cream); *Noblella madreselva* has dorsal skin with small tubercles (finely shagreen), tympanic membrane not differentiated and tympanic annulus barely visible below skin (well-differentiated), upper eyelid with minute tubercles (absent), toe tips weakly acuminate (rounded), venter black with large and irregularly shaped white mark (yellowish-cream), and smaller body size of 17.6 mm SVL in adult female (18.3–19.5 mm SVL in adult females); *Noblella*

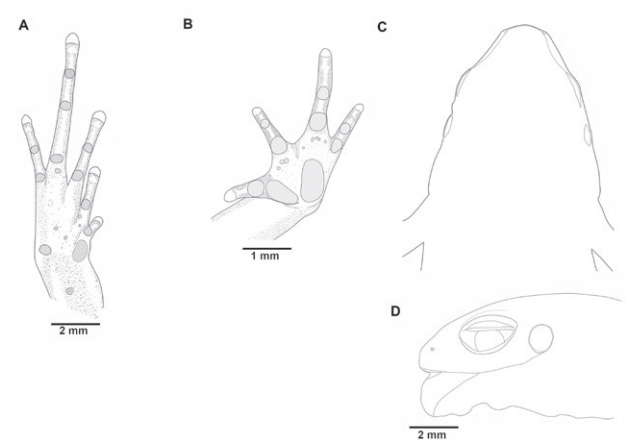

Fig. 3. *Noblella mindo* sp. preserved holotype, ZSFQ 050, adult female, SVL = 18.3 mm. **(A)** Foot in ventral view. **(B)** Hand in ventral view. **(C)** Head in dorsal view. **(D)** Head in lateral view. Illustrations by Carolina Reyes-Puig.

personina has dorsal skin smooth with pustules (finely shagreen), snout subtruncate in profile (round), finger and toe tips acuminate with papillae (round, lacking papillae), venter white (yellowish-cream), and smaller body size of 15.6–17.9 mm SVL in adult females (18.3–19.5 mm SVL in adult females); *Noblella peruviana* has tympanic membrane not differentiated (differentiated), toe tips slightly acuminate (round), and venter tan (yellowish cream); *Noblella pygmaea* has dorsal skin tubercular (finely shagreen), thoracic fold present (absent), dorsolateral fold on anterior half of body present (absent), upper eyelid bearing small tubercles (absent), minute tubercle on heel present (absent), toe tips pointed (round), venter pale grayish brown (yellowish-cream), and smaller body size of 11.3–12.4 mm SVL in adult females (18.3–19.5 mm SVL in adult females); *Noblella thiuni* has thin dorsolateral folds visible on anterior half of body (absent), tympanic membrane not differentiated (differentiated), fingertips bulbous (round), ulnar tubercles absent (present, diminutive and round), venter copper reddish with a profusion of silvery spots (yellowish cream), and smaller body size of 11.0 mm SVL in male (16.5–17 mm in adult females). *Noblella carrascoicola* (De la Riva and Köhler, 1998), *N. lochites* (Lynch, 1976b), *N. losamigos* (Santa-Cruz et al., 2019), *N. myrmecoides* (Lynch, 1976b), *N. naturetrekii* (Reyes-Puig et al., 2019c), and *N. ritarasquinae* (Köhler, 2000) are easily differentiated from *N. mindo* sp. nov. by having two phalanges on Finger IV instead of three.

Description of the holotype

Adult female (ZSFQ 050); head narrower than body, its length 40.8% of SVL; head longer than wide; head width 31.1% of SVL; snout round in dorsal and lateral

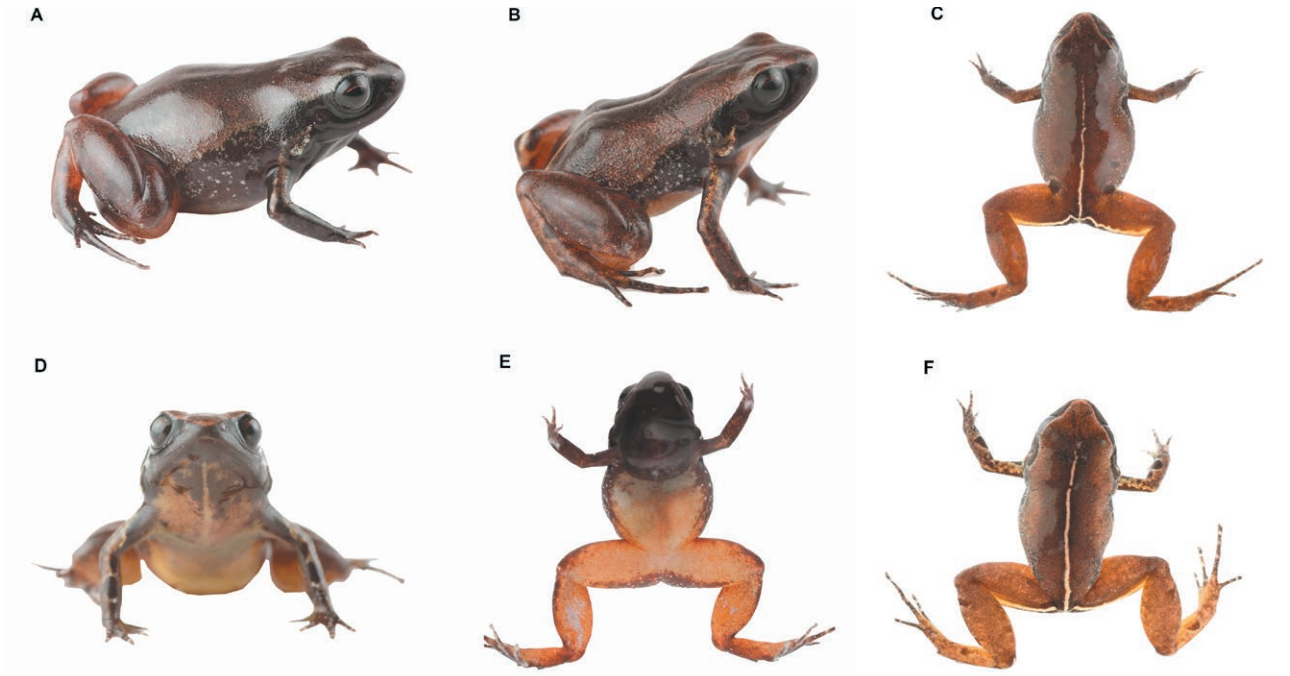

Fig. 4. Color patterns of *Noblella mindo* sp. nov. in life. **(A, C)** Dorso-lateral and ventral patterns of holotype, ZSFQ 050, adult female, SVL = 18.3 mm. **(B, D)** Dorsolateral and ventral patterns of paratype, ZSFQ 051, adult male, SVL = 16.9 mm. Photos by Matthijs Hollanders.

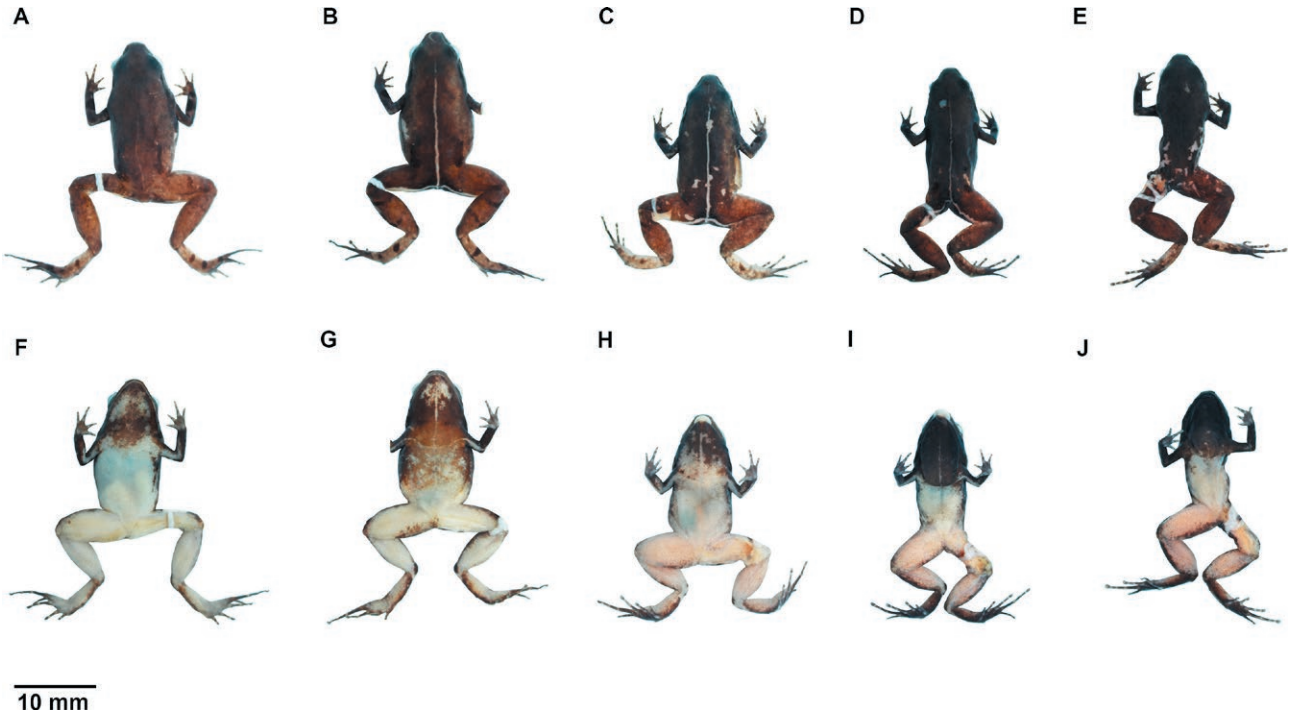

Fig. 5. Color variation of preserved *Noblella mindo* sp. nov. in (**A–E**) dorsal and (**F–J**) ventral views: **(A, F)** ZSFQ 305, paratype, adult female, SVL = 19.5 mm; **(B, G)** ZSFQ 304, paratype, adult female, SVL = 19.2 mm; **(C, H)** ZSFQ 050, holotype, adult female, SVL = 18.3 mm; **(D, I)** ZSFQ 051, paratype, adult male, SVL = 17.0 mm; **(E, J)** ZSFQ 049, paratype, adult male, SVL = 16.5 mm. Photos by David Brito-Zapata and Carolina Reyes-Puig.

views; canthus rostralis straight, slightly concave in profile; loreal region slightly concave; upper eyelid 45.6% of interorbital distance; eye-nostril distance 54.8% of eye diameter; tympanum visible externally, tympanic membrane differentiated from surrounding skin; supratympanic fold indistinct. Dentigerous processes of vomers absent and vomerine teeth absent; choanae laterally oriented; tongue longer than wide, elongated, partially notched posteriorly.

Skin of dorsum finely shagreen, evident tubercles absent; skin on flanks smooth; venter smooth; discoidal fold slightly visible, dorsolateral folds and thoracic folds absent; diminutive rounded ulnar tubercles; palmar tubercle oval, about 2 times the size of the thenar tubercle; supernumerary palmar tubercles present, mainly at the base of the digits; proximal subarticular tubercles prominent, rounded; phalangeal formula 2-2-3-3; fingers not expanded distally, finger tips rounded, circumferential grooves absent; relative lengths of fingers: I < II < IV < III; forearm lacking evident tubercles.

Hindlimb lengths moderate, tibia length 49.3% of SVL; foot length 46.1% of SVL; dorsal surfaces of hindlimbs shagreen; tubercles on the heel absent; one prominent elongated tarsal tubercle on ventral surface of tarsus; two metatarsal tubercles, inner elongated conspicuous, outer subconical; proximal and distal subarticular tubercles well-defined; supernumerary tubercles absent. Toes slightly expanded and rounded distally; distal portions of circumferential grooves not visible; phalangeal formula 2-2-3-4-3; relative lengths of toes: I < II < V < III < IV.

Measurements of holotype (in mm)

SVL= 18.3, HL= 7.5, HW= 5.7, ED= 2.4, EN= 1.3, MWE= 1.5, TD= 0.9, MIOD= 3.4, LH= 3.4, LS= 9.0, LF= 8.4. For measurements of the type series (mm) see Table 2.

Color of holotype in life (Fig. 4)

Dorsum brown, grayish brown towards the flanks; well-defined cream middorsal stripe, extending from interparietal region to cloaca and continuing along posterior surfaces of hindlimb. Loreal region black, extending as homogeneous dark band to upper insertion of arm and into body flanks, narrowing towards groin and limited dorsally with a lighter brown line; flanks strongly light flecked; groin dark. Rictal gland white. Venter and ventral surfaces of hindlimbs yellowish cream; throat dark brown with large irregular yellowish cream marks and

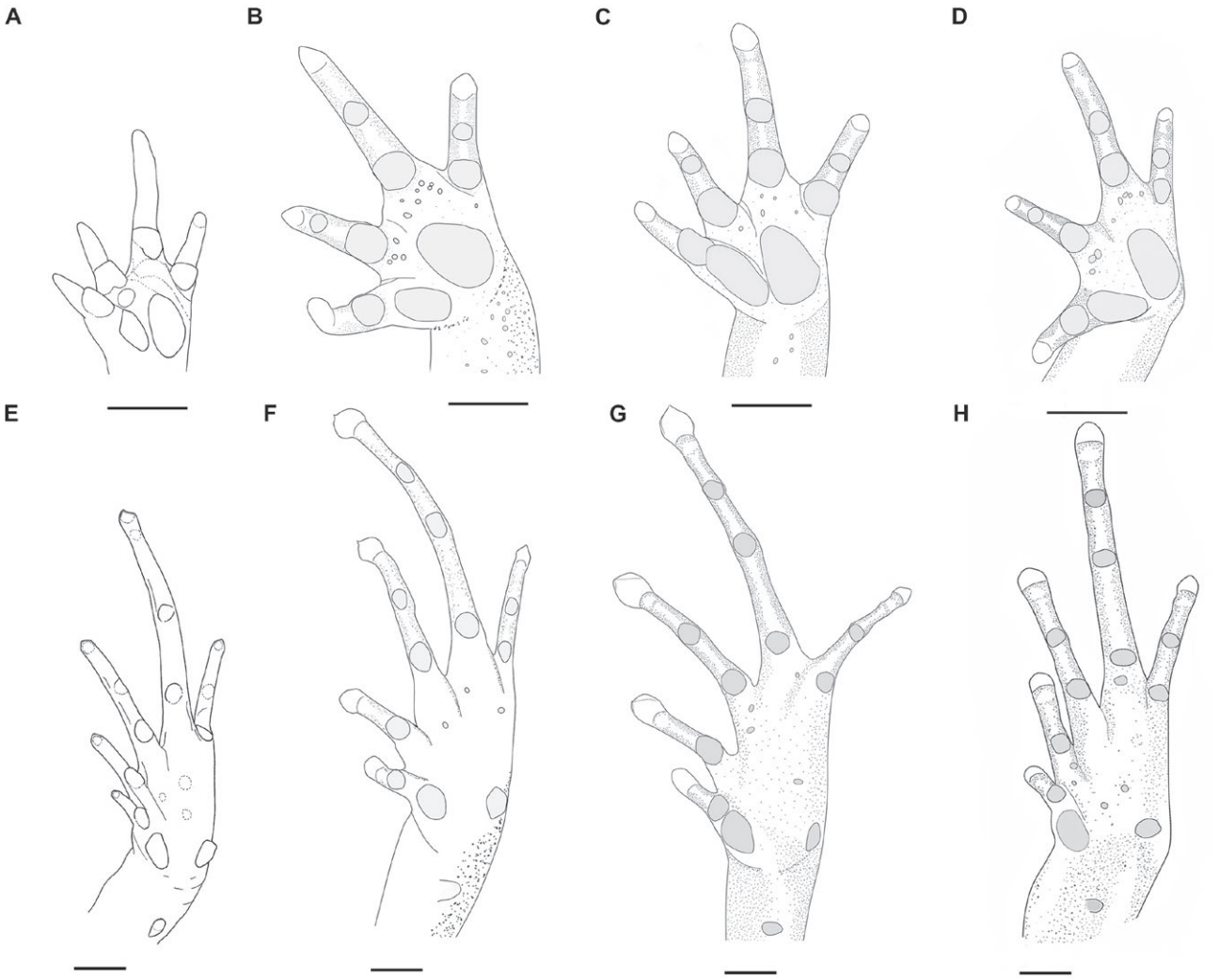

Fig. 6. Ventral views of **(A–D)** hands and **(E–H)** feet from three species of *Noblella*: **(A, E)** *Noblella coloma*, extracted from Guayasamin and Terán-Valdez (2009); **(B, F)** *N. worleyae* (holotype); **(C, G)** *N. worleyae* (ZSFQ 3851); **(D, H)** *N. mindo* sp. nov. (holotype). Scale bars = 1 mm. Illustrations by Carolina Reyes-Puig.

medium longitudinal line. Forelimbs ventrally yellowish cream with dark brown marks, dorsally light brown with dark brown marks; iris reddish copper with minute scattered turquoise dots. Hindlimbs like dorsum.

Color of holotype in ethanol (Fig. 5)

Dorsum brown, darker towards middorsum, well-defined middorsal line cream, extending from interparietal region to cloaca where stripe continues along posterior surface of thighs and pes. Dorsal surfaces of forelimbs brown with black spots. Labial bars absent; rictal gland light brown. Loreal region black, extending as homogeneous dark band to upper insertion of arm and into body flanks, narrowing towards groin; flanks strongly light flecked; groin dark. Dorsal surfaces of hindlimbs lighter brown than dorsum to cream with dark fleck and spots. Throat dark brown with cream irregular marks and medium longitudinal stripe. Chest, venter and ventral surfaces of thigh and crus cream.

Variation of color patterns and external morphology (Figs. 4–5)

Adult females ZSFQ 050, 304–305 and the adult male ZSFQ 051 exhibit a cream middorsal stripe extending from interparietal region to cloaca; stripe of ZSFQ 305 is thinner and faintly defined. Dark suprainguinal marks are faint in ZSFQ 049. Throat, chest and ventral surfaces of forelimbs are dark brown with a white cross formed by a longitudinal, fine line running from chin to chest, crossing a similar line departing from midventral

Table 1. Main diagnostic characters of three species of *Noblella* from northwestern Ecuador.

Species	Characters										Source
	Finger tips	Toe tips	Distal phalanges	Toes papillae	Ulnar tubercles	Venter and throat coloration	Prootic and exoccipital	Sphenethmoid	Length of transverse processes of Presacrals	Neural arch of Presacrals	
Noblella coloma	Acuminate	Slightly expanded and acuminate distally	T-shaped	Absent	Absent	Venter orange with minute white and brown spots	Separated	Well-ossified, ventrally not fused at midline	II, VIII<V–VII<IV<III	Presacrals III–V with raised medial ridge	Terán-Valdez and Guayasamin, 2009
N. worleyae	Slightly acuminate on Fingers I and IV and acuminate on Fingers II and III	Slightly expanded and slightly acuminate on Toes I and V, and cuspidate tips on Toes II–IV	T-shaped	Absent	Present	Venter yellowish cream with minute speckling; throat with irregular brown marks to homogeneously brown	Fused to form otoccipital	Well-ossified, ventrally fused at midline	II<V–VIII<IV<III	With raised medial ridge in all presacrals	Reyes-Puig et al., 2020 and this paper
N. mindo sp. nov.	Rounded	Slightly expanded and rounded distally	slightly T-shaped	Absent	Present	Throat, chest and ventral surfaces of arms dark brown with a white cross, venter yellowish cream	Separated	Moderately ossified, ventrally fused at midline in posterior half and separated in anterior half	V–VIII<II–IV<III	Presacrals III–VIII with raised medial ridge	This paper

Table 2. Measurements (in mm) of type series of *Noblella mindo* sp. nov. Ranges followed by mean and standard deviation in parentheses.

Characters	*Noblella mindo* sp. nov.	
	Females (n = 3)	Males (n = 2)
SVL	18.3–19.5 (19.0 ± 0.6)	16.5–17.0 (16.7 ± 0.3)
HL	7.1–7.5 (7.2 ± 0.2)	6.2–7.0 (6.6 ± 0.6)
HW	5.7–6.7 (6.3 ± 0.5)	5.37–5.4 (5.38 ± 0.02)
ED	2.2–2.5 (2.4 ± 0.2)	1.9–2.0 (1.95 ± 0.1)
EN	1.26–1.29 (1.28 ± 0.01)	1.21–1.22 (1.215 ± 0.01)
MWE	1.2–1.5 (1.3 ± 0.2)	1.1–1.2 (1.15 ± 0.01)
TD	0.8–1.2 (0.9 ± 0.2)	0.78–0.82 (0.8 ± 0.02)
MIOD	3.3–3.4 (3.3 ± 0.1)	3.0–3.4 (3.2 ± 0.3)
LH	3.5–3.9 (3.7 ± 0.2)	3.0–3.2 (3.1 ± 0.2)
LS	9.0–9.3 (9.1 ± 0.2)	7.7–8.0 (7.8 ± 0.2)
LF	8.4–9.0 (8.6 ± 0.4)	7.3–7.5 (7.4 ± 0.1)

surface of each forelimb (ZSFQ 050, 304, 774), longitudinal line on throat of ZSFQ 773 is faint, while cross is almost unnoticeable in holotype due to extensive light color of throat. Venter and ventral surfaces of hindlimbs are cream (ZSFQ 305), dirty cream with diffused irregular brown marks (ZSFQ 304), or pinkish cream (ZSFQ 049–051). The throat in females is cream (ZSFQ 304–305) or pinkish cream (ZSFQ 050) with large irregular dark brown marks; meanwhile in males it is homogenously dark brown with a slightly defined medium longitudinal stripe (ZSFQ 049, 051).

Osteology

Osteological description of *Noblella mindo* sp. nov. is based on micro-CT images of the adult female holotype (ZSFQ 050). Details of skull morphology and osteological aspects of hand and foot are presented in Fig. 7 and main skeletal features are shown in Fig. 8.

Skull (Fig. 7)

Skull slightly longer than wide; widest part is at about where quadratojugal meets maxilla and is 89% of skull length. Rostrum short; distance from anterior edge of frontoparietals to anterior face of premaxilla is 16% of skull length. At level of midorbit, braincase is about 38% of maximum skull width. Braincase combines well- and poorly ossified elements. Frontoparietals are well-developed bones, distinctly longer than broad, slightly narrower anteriorly than posteriorly; narrowly separated along most of their length and only fused in anterior region. Boarder between frontoparietals and prootics not well-resolved in micro-CT scan. Ventrally, prootics in contact with parasphenoid alae. Prootics well-separated from each other. Exoccipitals approximate one another ventromedially and dorsomedially but still clearly separated with about same distance ventrally and dorsally; separated from frontoparietals. Anterolaterally, frontoparietals in contact with sphenethmoid. Sphenethmoid ventrally at midline separated in anterior half and fused in posterior half; posterior margin does not reach midpoint of orbit and is broadly separated from prootic and in ventral contact with parasphenoid. Cultriform process of parasphenoid well-ossified posteriorly, thinning anteriorly, and about 28% width of braincase at mid-orbit. Lateral margins of process approximately parallel. Parasphenoid alae long but poorly ossified at their lateral ends. Neopalatines very thin and long, articulate with sphenethmoid and approximate but not contact maxilla. Columella (or stapes) large and well-ossified. Due to tiny size and fine structure, septomaxilla is not well-resolved in micro-CT scan. Dorsal investing bones moderately developed. Nasals thin and broadly separated from one another, posteriorly in contact with anterior end of frontoparietals and posterolaterally in thin contact with maxilla. They curve ventrally towards their lateral edges. Small prevomers broadly separated from one another medially, their anterior edge almost contacts a long and thin posterior projecting ramus of septomaxilla. Maxillary arcade bears many small, poorly resolved teeth on premaxillae and maxillae. Premaxillae separated medially, and their anterodorsal alary processes rise divergent from midline but still distinctly separated from nasals. Premaxilla and maxilla in lateral contact, with anterior edge of maxilla slightly overlapping lateral edge of premaxilla. Pars palatina of premaxilla broad, with two well-defined processes: medial process thin and acuminate, running about parallel to its counterpart, being distinctly separated from it; lateral process about the same length, but slightly broader, especially at its truncate posterior ending. Maxilla long, its posterior end acuminate and in contact with quadratojugal. Triradiate pterygoid bears a long, curved anterior ramus oriented anterolaterally toward maxilla, with which it articulates at ventral boarder slightly anterior to midline of orbit. Posterior ramus of pterygoid about same length as medial ramus and both about half length of anterior ramus; however, posterior ramus more robust than other two. Edge of medial ramus overlaps lateral edge of prootic. Quadratojugal slender, almost straight and articulating anteriorly with maxilla and posterodorsally with ventral ramus of squamosal. Squamosal T-shaped, with a long laminar otic ramus; zygomatic ramus much shorter and slender; ventral ramus about same length as otic ramus, laminar and broad, increasing in width ventrally. Mandible slim and edentate. Mentomeckelians small, medial-

ly, and laterally slightly broadened, and separated medially by a narrow gap. Dentary long and thin, reaching to about anterior corner of orbit; it is posteriorly acuminate and overlapping angulospenial, seeming to be in contact with this bone for about the posterior half of its length; anteroventrally it contacts mentomeckelian bones. Angulosplenial long and arcuate. Coronoid process is a moderately long and slightly raised ridge. The only ossified portions of hyoid apparatus are two posteromedial processes, which are anteriorly slightly and posteriorly moderately expanded, approaching each other at anterior ends but being still moderately separated.

Postcranium (Fig. 8)

Eight presacral vertebrae. All presacrals non-imbricate. Presacral I longer than posterior vertebrae. All except Presacral I bear well-developed diapophyses. Transverse processes of Presacrals V–VIII similar in size, being the shortest and thinnest, those of Presacrals II and IV also about similar in size and being slightly larger, and those of Presacral III being the longest and widest of all transverse processes. Transverse processes of Presacrals II and VIII have slightly anterolateral orientation, those of Presacral III are laterally oriented and the others are slightly posterolaterally oriented. Neural arch of Presacrals III–VIII bears a raised medial ridge. Sacrum bears slightly expanded diapophyses. Urostyle long, slender, slightly shorter than presacral portion of vertebral column and bearing a well-pronounced dorsal ridge along most of its length, beginning at its anterior end. The bone has a bicondylar articulation with the sacrum. Pectoral girdle with well-ossified coracoids, clavicles, scapulae and cleithra. Suprascapular and sternum unossified and not visible in micro-CT scan, and omosternum hardly visible. Clavicles long and slim, oriented anteromedially, slightly curved, with medial tips touching each other. Laterally, clavicles firmly articulating with scapulae. Coracoids stout and glenoidal and sternal ends about equally expanded. Anterior edges of coracoids slightly curved, posterior edges almost straight. Medial tips of coracoids broadly separated from another. Scapula long, with a prominent pars acromialis not separated from pars glenoidalis. Cleithrum long, broader, and thicker at scapular boarder, thinning posteriorly. In pelvic girdle, long, slender iliac shafts bearing conspicuous dorsolateral ridges along most of their length, except anteriormost region. Ilia are fused posteriorly with ischium and pubis. Ischium stout, whereas pubis is thin and blade-like.

Manus and pes (Fig. 7)

All phalanges are ossified with a phalangeal formula for fingers and toes: 2-2-3-3 and 2-2-3-4-3, respectively. Order of finger length: I < II < IV < III, and that of toes: I < II < V < III < IV. Distal knobs present on terminal phalanges of all fingers and toes. Terminal phalanges of all toes and fingers narrower than penultimate phalanges of all toes and fingers, respectively. Carpus and tarsus not well-resolved in micro-CT scan. However, carpus seems to be composed of a radiale, ulnare, Element Y, ossified prepollex element, Carpal 2 and a large post-axial element probably representing a fusion of Carpals 3–5. Tarsus seems to be composed of two tarsal elements: Tarsal 1 and Tarsal 2 + 3, with latter being distinctly larger than Tarsal 1. A moderately large centrale and small ossified prehallux are also present. In ventral view, three sesamoids of subequal sizes are overlaying proximal end of Metatarsals IV–V, a further smaller sesamoid is overlaying parts of Tarsal 1.

Distribution and Natural History

Noblella mindo sp. nov. is only known from El Cinto (0.09022°S, 78.81858°W; 1,673 m), Mindo, province of Pichincha, Ecuador (Fig. 2). *Noblella mindo* sp. nov. inhabits secondary cloud forests, with the presence of palmito (*Bactris gasipaes*) plantations and trees that have emerged after the massive logging of forests in the area. These forests have a high humidity index, dense leaf litter layer, and abundant epiphytes. It has a restricted distribution; sampling activities were carried out in a range up to 3km around the type locality, and no individuals nor calls of *N. mindo* sp. nov. were recorded. The gecko *Lepidoblepharis conolepis* was found in sympatry. The locality is surrounded by livestock areas and within the type locality forest, there are trails used by farmers to move their livestock. The population of *Noblella mindo* sp. nov. could be impacted if livestock activity or deforestion expands. Three individuals (ZSFQ 049–051) were found active during the day between 10:00 and 11:00 am; all frogs were on the ground in a 2-meter depth hole.

Noblella worleyae Reyes-Puig, Maynard, Trageser, Vieira, Hamilton, Lynch, Culebras, Kohn, Brito, and Guayasamin 2020: New locality

Figs. 2, 9–12

New records (3 females, 1 male). All individuals were collected at different localities inside Los Cedros Biological Reserve: ZSFQ 3851 (Figs. 9–10), adult female and ZFSQ 3852, adult male, collected at 0.31501°N, 78.77943°W, 1,612 m (WGS84; Fig. 2), García Moreno, Cotacachi, province of Imbabura, by David Brito-Zapata and Martín Obando on 26 October 2019. MZUTI 1708, adult female, collected at 0.31125°N, 78.78095°W, 1,417 m, by Giusseppe Gagliardi and JMG on 13 March

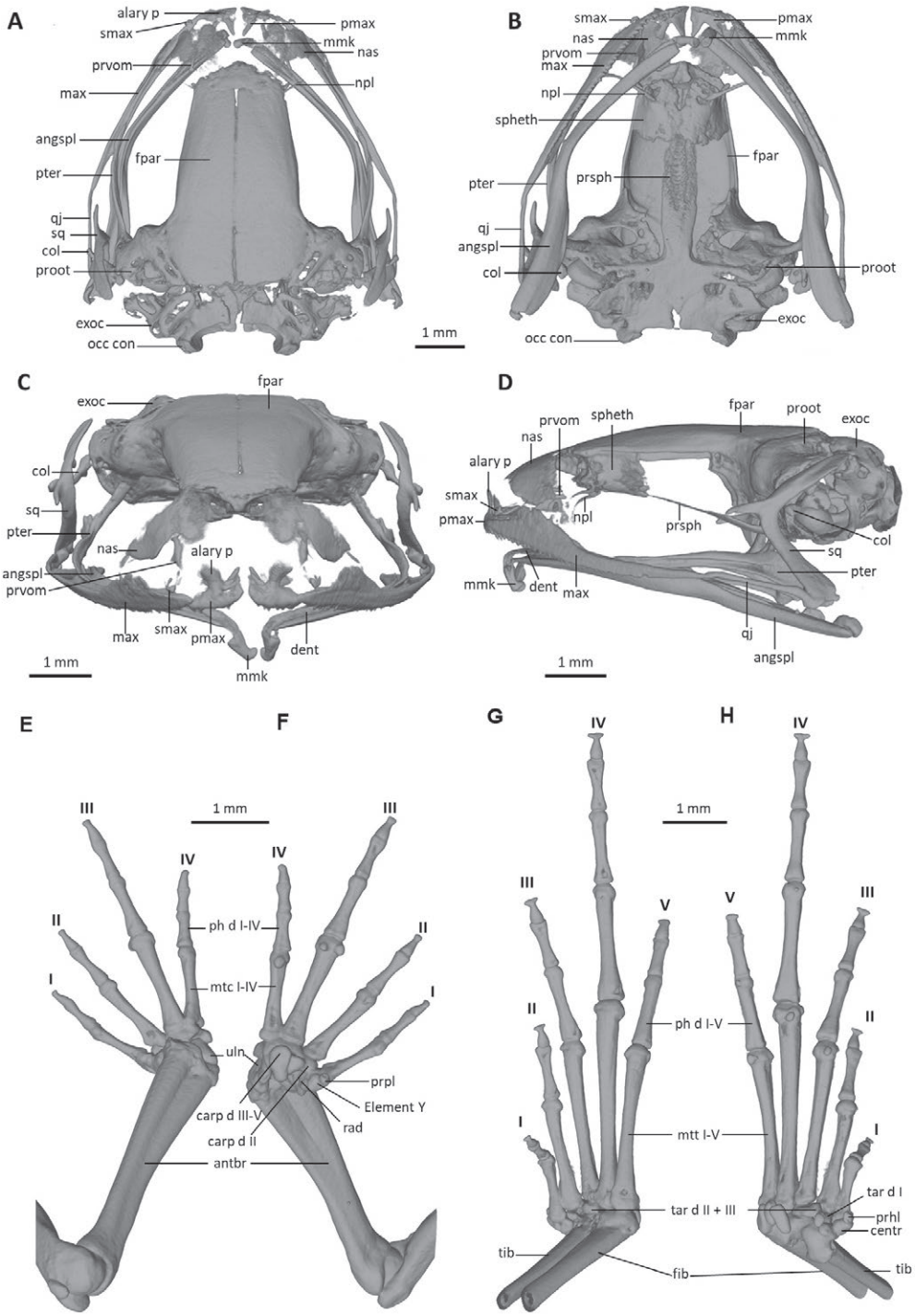

Fig. 7. Details of **(A–D)** skull morphology and osteological aspects of **(E–F)** hand and **(G–H)** foot of *Noblella mindo* sp. nov., ZSFQ 050, holotype, adult female. The skull is shown in **(A)** dorsal, **(B)** ventral, **(C)** frontal, and **(D)** lateral views. alary p = alary process, angspl = angulosplenial, col = columella, dent = dentary, fpar = frontoparietal, max = maxilla, mmk = mentomeckelian bone, nas = nasal, npl = neopalatine, occ con = occipital condyle, otoc = otoccipital (fused prootic and exoccipital), pmax = premaxilla, prsph = parasphenoid, prvom = prevomer, pter =pterygoid, qj = quadratojugal, smax = septomaxilla, spheth = sphenethmoid, sq = squamosal. The right hand is shown in **(E)** dorsal, and **(F)** palmar aspects; and the left foot in **(G)** dorsal, and **(H)** plantar aspects. Digits numbered I–V. antbr = os antebrachii (radius + ulna), carp d = carpale distale, cent = centrale, fib = fibulare, mtc = metacarpalia, mtt = metatarsalia, ph d I–IV = finger phalanges F1–F4, ph d I–V = toe phalanges F1–F5, prhl =prehallux, prpl = prepollex, rad = radius, tar d = tarsale distale, tib = tibiale, uln = ulnare. Images prepared by Claudia Koch.

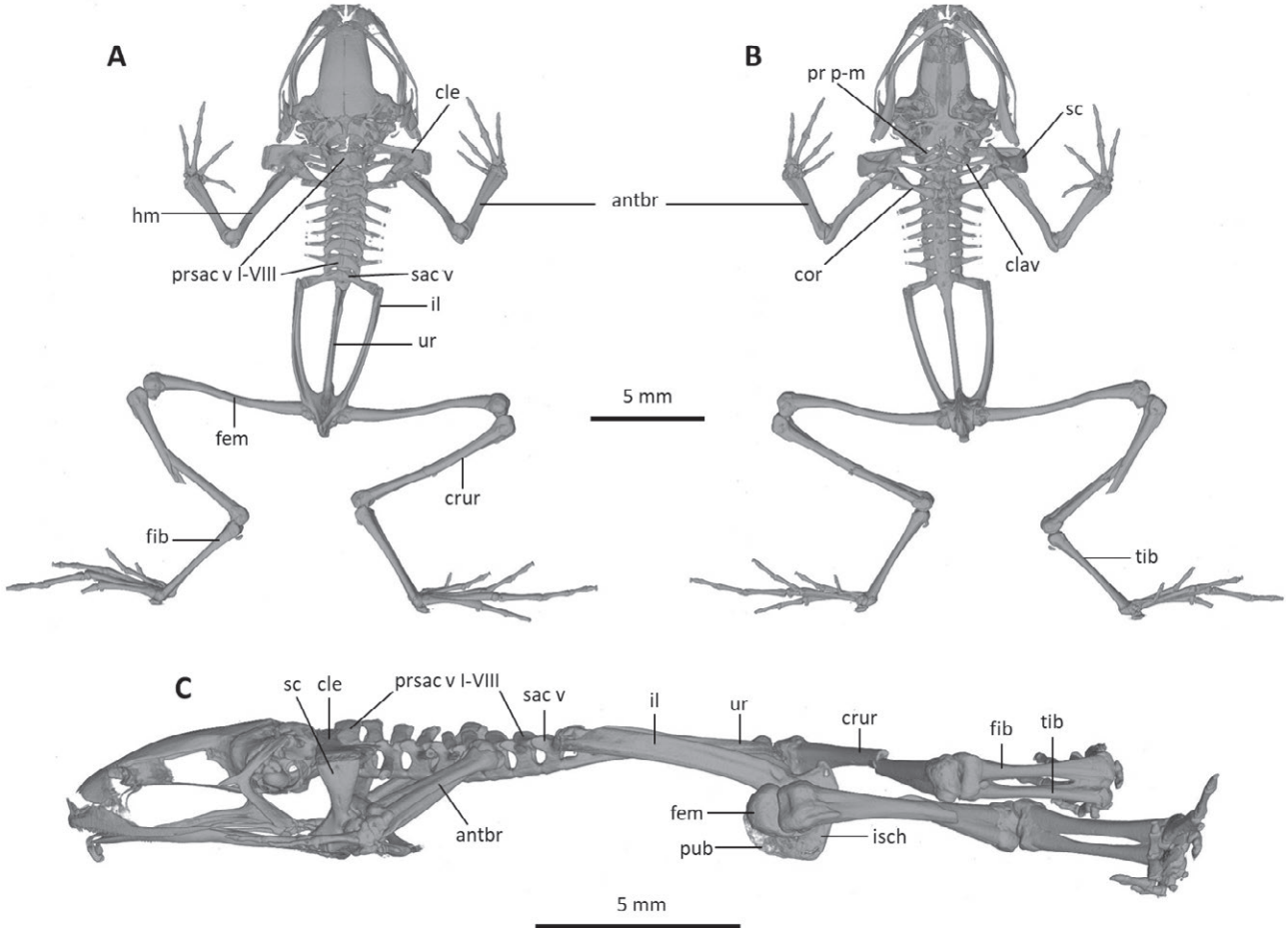

Fig. 8. Osteology of *Noblella mindo* sp. nov., ZSFQ 050, holotype, adult female. The full skeleton is shown in **(A)** dorsal, **(B)** ventral, and **(C)** lateral views. antbr = os antebrachii (radius + ulna), clav = clavicle, cle = cleithrum, cor = coracoid bone, crur = os cruris (tibia + fibula), fem = femoral bone, fib = fibulare, hm = humeral bone, il = ilium, isch = ischium, pr p-m = processus postero-medialis, prsac v = presacral vertebrae, pub = pubis, sac v = sacral vertebra, sc = scapula, ur = urostyle, tib = tibiale. Images prepared by Claudia Koch.

2012; MZUTI 1709, adult female, collected at 0.3184°N, 78.7837°W, 1,790 m, by Jaime Culebras and JMG on 15 March 2012.

Diagnosis

Specimens collected in Los Cedros reserve show morphological characters described for *Noblella worleyae* (Reyes-Puig et al., 2020; Figs. 6, 9–10) as follow (variation from original description in bold): (1) skin of dorsum finely shagreen, skin on venter smooth; (2) tympanic annulus and membrane visible externally, supratympanic fold inconspicuous; (3) snout, rounded in dorsal and lateral views; (4) eyelids without tubercles; (5) dentigerous processes of vomers absent; (6) vocal slits and vocal sac present, nuptial pads not visible; (7) fingers not expanded or slightly expanded distally, tips of Fingers I and IV rounded and tips of Fingers II and III slightly acuminate (originally described as tips of Fingers I and IV slightly acuminate, Fingers II and III acuminate), without papillae (Fig. 6), Finger I shorter than Finger II,(8); distal phalanges T-shaped (originally described as slightly T-shaped)**,** phalangeal formula of hands: 2-2-3-3 (Fig. 11); (9) supernumerary palmar tubercles few but present, ulnar tubercles diminutive and round (decreased by preservation effects), subarticular tubercles rounded, discs lacking circumferential grooves; (10) one tarsal tubercle, elongated and subconical, two metatarsal tubercles (inner tubercle 2 times size of external); toes slightly expanded distally and rounded on Toes I and V, cuspidate tips on Toes II–IV, papillae present on Toes II–IV (Fig. 6); (11) Toe V shorter than Toe III distal portions of circumferential grooves present on Toes II–V, supernumerary tubercles absent (12) phalangeal formula of feet: 2-2-3-4-3 (Fig. 11); (13) in life, dorsum brown, with two suprain-

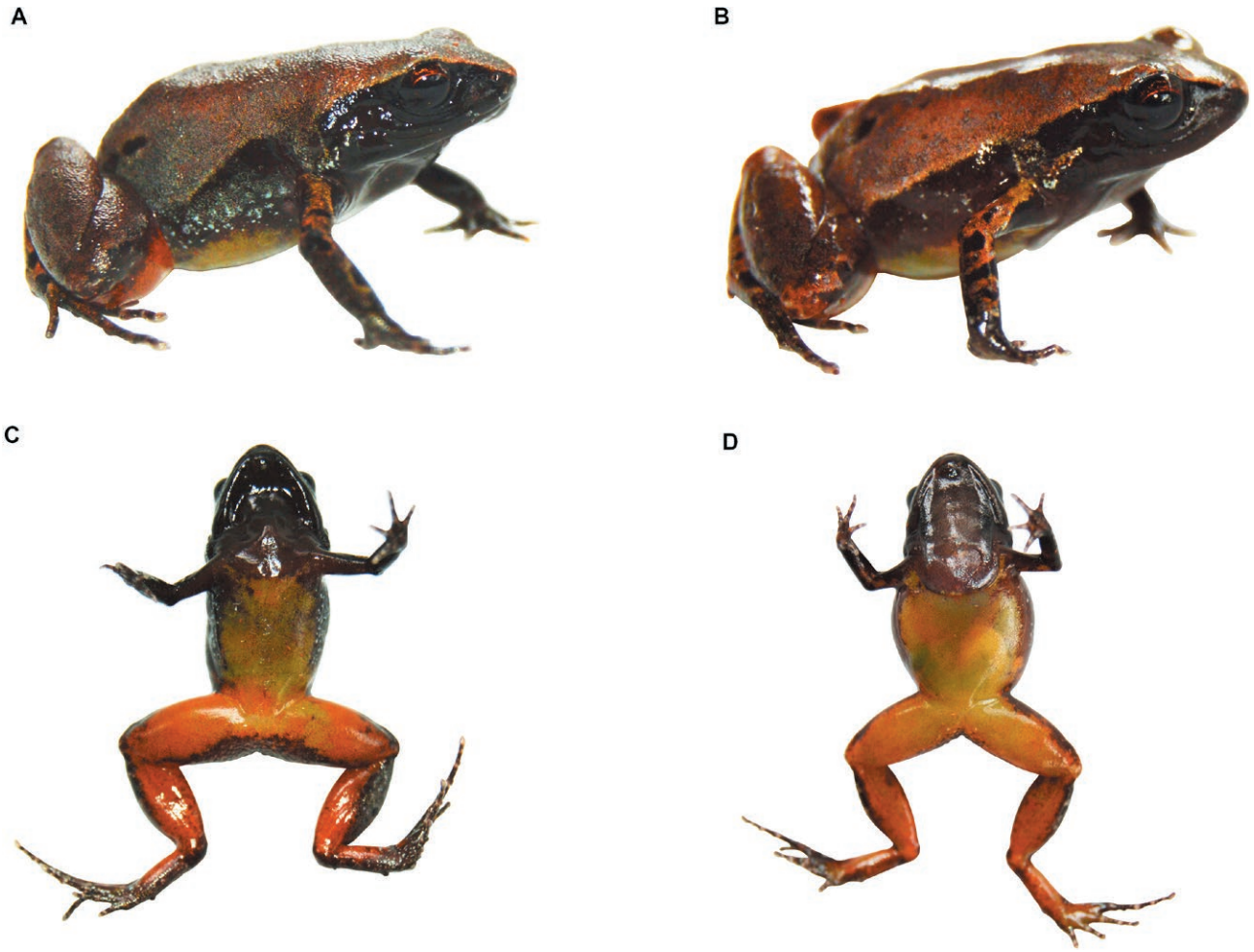

Fig. 9. Color pattern of *Noblella worleyae* in life: **(A, C)** Dorso-lateral and ventral patterns of ZSFQ 3851, adult female, SVL = 19.1 mm; **(B, D)** Dorsal and ventral patterns of ZSFQ 3852, adult male, SVL = 16.1 mm. Photos by David Brito-Zapata.

guinal dark brown marks; middorsal, longitudinal line faint cream; rictal gland dark brown; flanks with dark brown band narrowing towards groin and with clusters of turquoise specks towards ventral side; groin dark, with high concentration of melanophores; throat, chest and ventral surfaces of arms dark brown; venter yellowish cream, with brownish-orange tones on ventral surfaces of legs and thighs, iris reddish copper; (14) SVL in one adult male 16.1 mm; in adult females 19.1–20.4 mm (mean 19.8 mm, n = 3) (range originally described 18.1–19.1 mm).

Variation of color patterns and external morphology (Figs. 9–10)

Specimens of *Noblella worleyae* from Los Cedros Reserve vary from brown (MZUTI 1708–1709) to dark brown (ZSFQ 3851–3852). In preservative, specimen ZSFQ 3852 has a grayish-brown dorsal coloration. Black suprainguinal spots vary in size and may be diffused but are always present. All specimens exhibit a faint, cream middorsal stripe extending from the head to cloaca, but only in one specimen (MZUTI 1709) this line continues onto posterior surfaces of thigh, disappears in crus, and reappears in posterior surfaces of pes. Specimens MZUTI 1708 and ZSFQ 3852 have a homogenously dark brown throat like the holotype, but in MZUTI 1709 the throat is brown with scattered irregular cream marks. Ventral surfaces of thighs and crus of ZSFQ 3852 retain pinkish-cream color in preservative. Male ZSFQ 3852 exhibits an evident discoidal fold.

Osteology description

Osteological description of *Noblella worleyae* is based on micro-CT images of an adult female (MZUTI 1709). Details of skull morphology and osteological aspects of hand and foot are presented in Fig. 11 and main skeletal features are shown in Fig. 12.

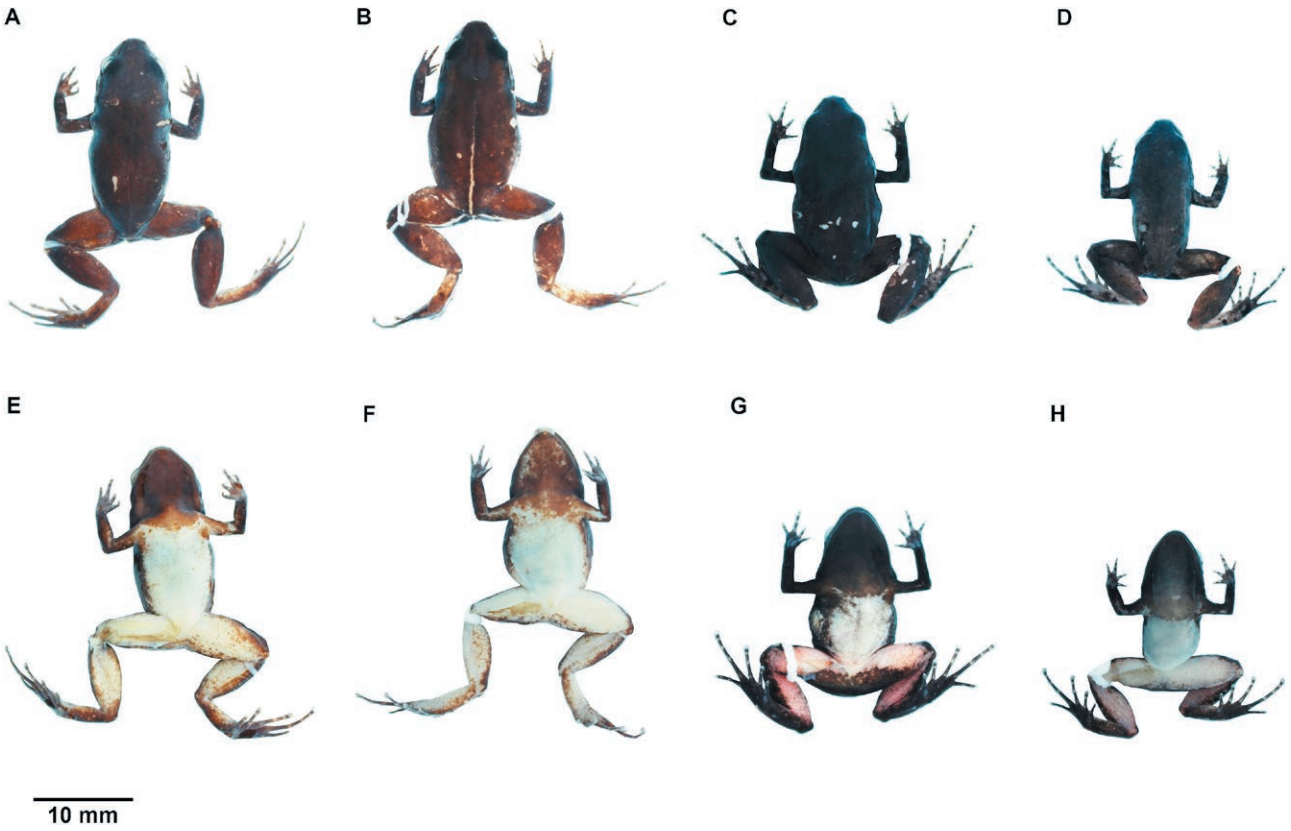

Fig. 10. Color variation of preserved *Noblella worleyae* in (**A–D**) dorsal and (**E–H**) ventral views: **(A, E)** MZUTI 1708, adult female, SVL = 20.4 mm; **(B, F)** MZUTI 1709, adult female, SVL = 19.9 mm; **(C, G)** ZSFQ 3851, adult female, SVL = 19.1 mm; **(D, H)** ZSFQ 3852, adult male, SVL = 16.1 mm. Photos by David Brito-Zapata and Carolina Reyes-Puig.

Skull (Fig. 11)

Skull almost as wide as long; widest part is at about where quadratojugal meets maxilla and is 97% of skull length. Rostrum short; distance from anterior edge of frontoparietals to anterior face of premaxilla is 18% of skull length. At level of midorbit, braincase is about 34% of maximum skull width. Braincase combines well- and poorly ossified elements. Prootic and exoccipital seem to be fused to form otoccipital. Frontoparietals are well-developed bones, distinctly longer than broad, slightly narrower anteriorly than posteriorly; narrowly separated along most of their length and only fused in anterior region. Posterior portion of braincase seems to be fully enclosed by partial fusion of frontoparietals with otoccipitals. However, there might still exist some traces of boarders between bones, but these parts are not well-resolved in micro-CT scans. Ventrally, otoccipitals are in contact with parasphenoid alae. Prootic part of otoccipitals are well-separated from each other. Exoccipital parts approximate one another ventromedially and dorsomedially but are still clearly separated with a broader ventral than dorsal gap between them. Anterolaterally, frontoparietals are in contact with sphenethmoid. Sphenethmoid is well-ossified and ventrally fused at midline; posterior margin almost reaches midpoint of orbit but is still broadly separated from prootic part of otoccipitals and is in ventral contact with cultriform process of parasphenoid. Cultriform process of parasphenoid is well-ossified posteriorly, thinning anteriorly, and about 31% of width of braincase at mid-orbit. Lateral margins of process are approximately parallel. Parasphenoid alae are long and well-ossified. Neopalatines are very thin and long, articulating with sphenethmoid dorsomedially and maxilla laterally. Columella (or stapes) is large and well-ossified. Because of tiny size and fine structure, septomaxilla is not well-resolved in micro-CT scan. Dorsal investing bones are moderately developed. Nasals are thin and broadly separated from one another, posteriorly in contact with anterior end of frontoparietals and posterolaterally in very thin contact with maxilla. They curve ventrally towards their lateral edges. Small prevomers are broadly separated from one another medially, their anterior edge approximates a long and thin posterior projecting ramus of septomax-

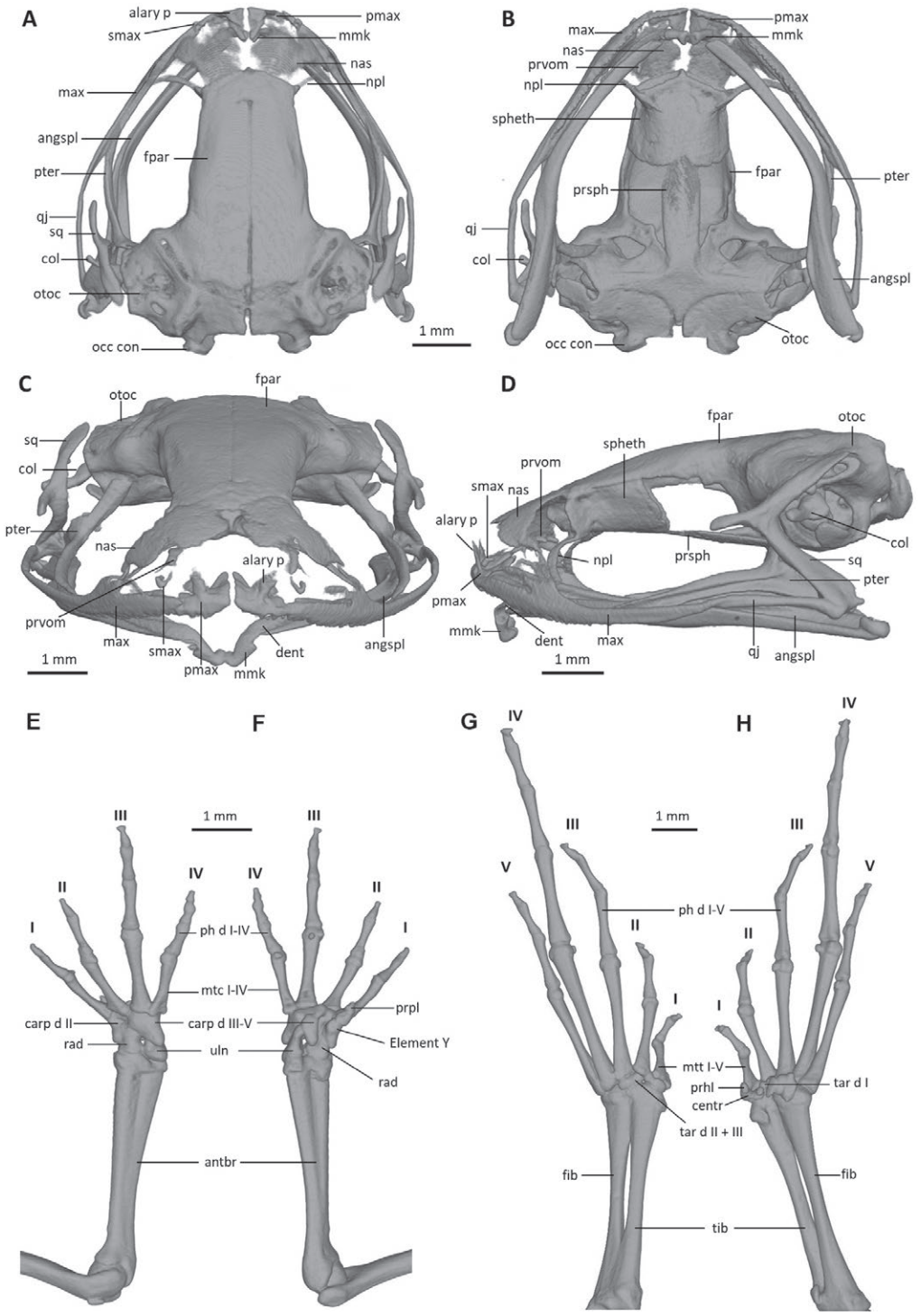

Fig. 11. Details of **(A–D)** skull morphology and osteological aspects of **(E–F)** hand and **(G–H)** foot of *Noblella worleyae*, MZUTI 1709. The skull is shown in **(A)** dorsal, **(B)** ventral, **(C)** frontal, and **(D)** lateral views. alary p = alary process, angspl = angulosplenial, col = columella, dent = dentary, fpar = frontoparietal, max = maxilla, mmk = mentomeckelian bone, nas = nasal, npl = neopalatine, occ con = occipital condyle, otoc = otoccipital (fused prootic and exoccipital), pmax = premaxilla, prsph = parasphenoid, prvom = prevomer, pter =pterygoid, qj = quadratojugal, smax = septomaxilla, spheth = sphenethmoid, sq = squamosal. The right hand is shown in **(E)** dorsal, and **(F)** palmar aspects; and the left foot in **(G)** dorsal, and **(H)** plantar aspects. Digits numbered I–V. antbr = os antebrachii (radius + ulna), carp d = carpale distale, cent = centrale, fib = fibulare, mtc = metacarpalia, mtt = metatarsalia, ph d I–IV = finger phalanges F1–F4, ph d I–V = toe phalanges F1–F5, prhl =prehallux, prpl = prepollex, rad = radius, tar d = tarsale distale, tib = tibiale, uln = ulnare. Images prepared by Claudia Koch.

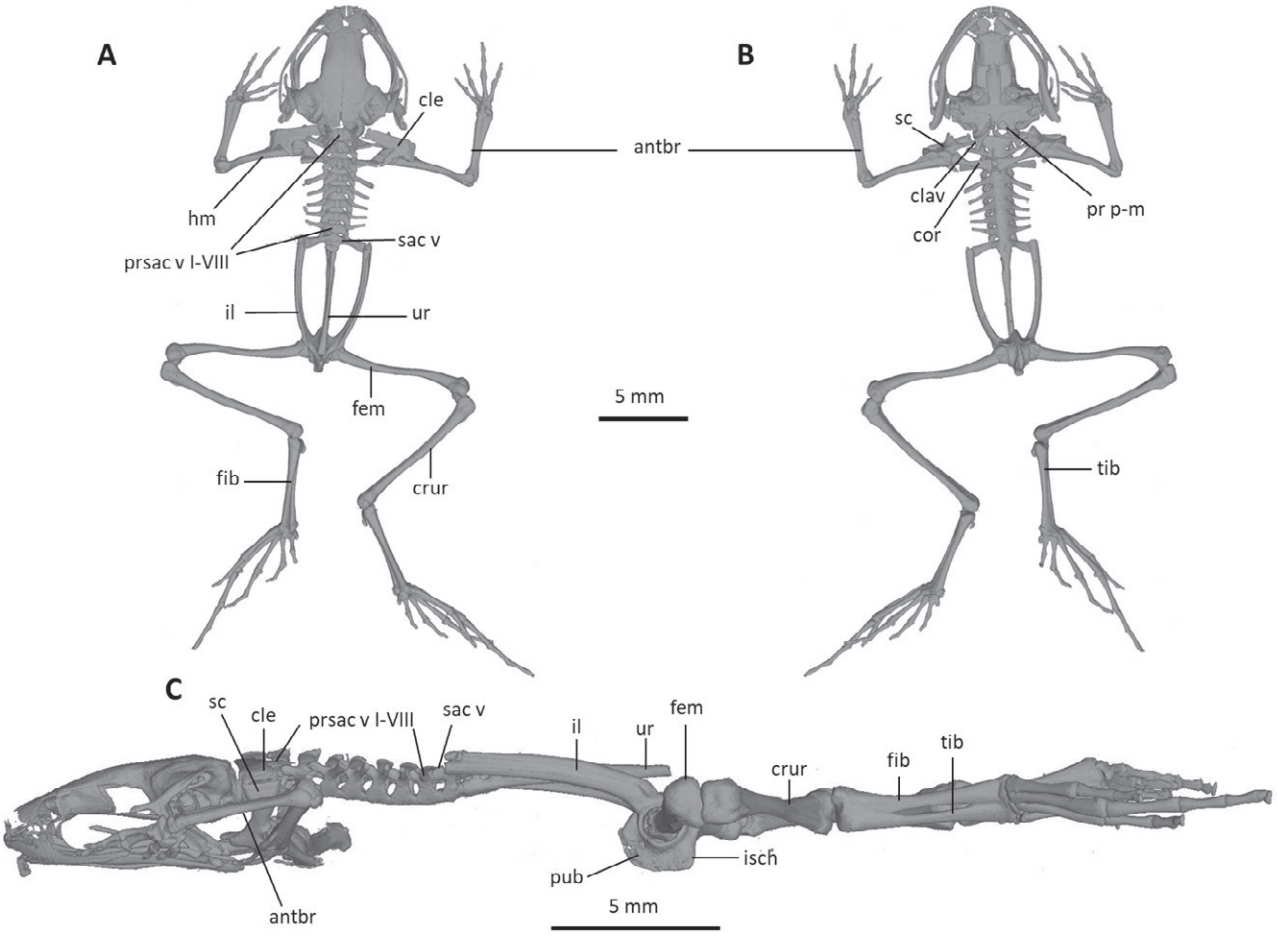

Fig. 12. Osteology of *Noblella worleyae,* MZUTI 1709, adult female. The full skeleton is shown in **(A)** dorsal, **(B)** ventral, and **(C)** lateral views. antbr = os antebrachii (radius + ulna), clav = clavicle, cle = cleithrum, cor = coracoid bone, crur = os cruris (tibia + fibula), fem = femoral bone, fib = fibulare, hm = humeral bone, il = ilium, isch = ischium, pr p-m = processus postero-medialis, prsac v = presacral vertebrae, pub = pubis, sac v = sacral vertebra, sc = scapula, ur = urostyle, tib = tibiale. Images prepared by Claudia Koch.

illa. Maxillary arcade bears many small, poorly resolved teeth on premaxillae and maxillae. Premaxillae are separated medially, and their anterodorsal alary processes rise divergent from midline but are still distinctly separated from nasals. Premaxilla and maxilla are in lateral contact, with anterior edge of maxilla slightly overlapping lateral edge of premaxilla. Pars palatina of premaxilla is broad, with two well-defined processes: medial process acuminate, and runs about parallel to its counterpart, being distinctly separated from it; lateral process is slightly shorter and broader. Maxilla is long, its posterior end acuminate and in contact with quadratojugals. Triradiate pterygoid bears a long, curved anterior ramus that is oriented anterolaterally towards maxilla, with which it articulates at ventral boarder anterior to midline of orbit. Posterior ramus of pterygoid is about same length as medial ramus and both are about half length of anterior ramus; however, posterior ramus is more robust than the other two. Edge of medial ramus overlaps lateral edge of prootic part of otoccipital. Quadratojugal is slender, slightly curved and articulates anteriorly with maxilla and posterodorsally with ventral ramus of squamosal. Squamosal is T-shaped with long laminar otic ramus; zygomatic ramus is much shorter and more slender; ventral ramus is about same length as otic ramus, laminar and broad, increasing in width ventrally. Mandible is slim and edentate. Mentomeckelians are small, medially and laterally slightly broadened, and medially contacting each other. Dentary is long and thin, reaching to about anterior corner of orbit; posteriorly acuminate and overlapping angulospenial, seeming to be in contact with this bone for most of its length, except the most anterior part; anteroventrally it contacts mentomeckelian bones. Angulosplenial is long and arcu-

ate. Coronoid process is a moderately long and strongly raised ridge. The only ossified portions of hyoid apparatus are two posteromedial processes, which are anteriorly slightly more expanded than posteriorly, approaching each other at anterior ends but being still distinctly separated.

Postcranium (Fig. 12)

Eight presacral vertebrae. All presacrals are non-imbricate. First presacral vertebra is longer than posterior vertebrae. All except Presacral I bear well-developed diapophyses. Transverse processes of Presacrals V–VIII similar in size and being the thinnest and second shortest, those of Presacral II being the shortest, and those of Presacral III being the longest and widest of all transverse processes. Transverse processes of Presacrals II and VIII have slightly anterolateral orientation, those of Presacrals III and VII are laterally oriented and others are slightly posterolaterally oriented. Neural arch of all presacrals bears a raised medial ridge. Sacrum bears slightly expanded diapophyses. Urostyle is long, slender, about similar in length as presacral portion of vertebral column and bearing a well-pronounced dorsal ridge along about two-thirds of its length, beginning at its anterior end, with a lateral foramen in anterior region. The bone has a bicondylar articulation with the sacrum. Pectoral girdle with well-ossified coracoids, clavicles, scapulae and cleithra. Suprascapular, omosternum, and sternum unossified and not visible in micro-CT scan. Clavicles are long and slim, oriented anteromedially, slightly curved, with medial tips approaching but not touching each other. Laterally, clavicles firmly articulating with scapulae. Coracoids are stout and glenoidal and sternal ends are about equally expanded. Anterior edges of coracoids are curved, the posterior edges are almost straight. Medial tips of coracoids are broadly separated from another. Scapula is long with a prominent pars acromialis that is not separated from pars glenoidalis. Cleithrum is long, broader and thicker at scapular boarder, thinning posteriorly. In pelvic girdle, long, slender iliac shafts bear conspicuous dorsolateral ridges along most of their length, except the anterior most region. Ilia is fused posterirly with ischium and pubis. Ischium is stout, whereas pubis is thinner and blade-like.

Manus and pes (Fig. 11)

All phalanges are ossified, with phalangeal formula for fingers and toes: 2-2-3-3 and 2-2-3-4-3, respectively. Order of finger length: I < II < IV < III, and that of toes: I < II < V < III < IV. Distal knobs seem to be absent on Finger I but are present on terminal phalanges of all other fingers and toes. Nevertheless, they are not well-resolved in micro-CT scans and are sensitive to thresholds used during reconstruction. Terminal phalanges of all toes and fingers are narrower than penultimate phalanges of all toes and fingers, respectively. Carpus and tarsus are not well-resolved in micro-CT scan. However, carpus seems to be composed of a radiale, ulnare, Element Y, ossified prepollex element, Carpal 2 and a large post-axial element probably representing a fusion of Carpals 3–5. Tarsus seems to be composed of two tarsal elements: Tarsal 1 and Tarsal 2 + 3, with latter being larger than Tarsal 1. A moderately large centrale and small ossified prehallux are also present. In ventral view, three sesamoids of subequal sizes overlaying proximal end of Metatarsals II–IV, a further smaller sesamoid overlaying parts of Tarsal 1 and proximal end of Metatarsal I.

Natural History

We report a new locality for *Noblella worleyae*: Los Cedros Biological Reserve, province of Imbabura, Ecuador (Fig. 2), at approximately 8.4 km in a straight line between the type locality of *N. worleyae* (i.e., Manduriacu Reserve). The individuals were found at several point-localities between 1,417–1,790 m of elevation. The reserve presents an important track of mature Low Montane Evergreen Forest. All specimens were collected at night between 7:00 and 11:50 pm and were found on the ground, in areas covered with abundant leaf litter. Individuals appeared inactive, because they were located by movement only when litter was removed. Syntopic species were *Pristimantis mutabilis* (Guayasamin et al., 2017b), *P. crenunguis*, (Lynch, 1976a) and *Alopoglossus viridiceps* (Torres-Carvajal and Lobos, 2014). *Noblella worleyae* seems to be a rare species at Los Cedros Biological Reserve. Only two individuals were found in two different surveys with known sampling effort. The first sampling was carried out between 22–25 August 2019, with five people for approximately nine hours per day. The second sampling was carried out between 26–30 October 2019, with two people for about nine hours per day. Individuals were found in the lower forest stratum, camouflaged extremely well in leaflitter and having an evasive behavior, similar to other *Noblella* species (Reyes-Puig et al., 2019c).

DISCUSSION

Our phylogenetic analyses (Fig. 1) agree with previous studies that have shown that southern species of *Noblella* (*N. losamigos*, *N. madreselva*, *N. pygmaea*, *N. thiuni*) are more closely related to species of *Psychrophrynella*, rather than to northern species of *Noblel-*

la (*N. coloma*, *N. heyeri*, *N. lochites*, *N. mindo* sp. nov., *N. myrmecoides*, *N. personina*, *N. worleyae*) (Reyes-Puig et al., 2019c, 2020; Santa-Cruz et al., 2019). *Noblella peruviana* is the type species of the genus, which, based on geography, is most likely part of the Southern Clade. However, since there are no sequences of *N. peruviana,* we refrain from proposing a new generic arrangement.

Species richness of the genus *Noblella* has increased dramatically over the last decade (Frost, 2020). About a decade ago, only three species of *Noblella* were known in Ecuador and no species had been described from the northwestern slopes of the Andes of Ecuador (Cisneros-Heredia and Reynolds, 2007). Nowadays, there are eight species of *Noblella* reported from Ecuador, including three from the western Ecuadorian Andes (*N. coloma*, *N. mindo* sp. nov., and *N. worleyae*) that form a distinct clade among the northern *Noblella* (Fig 1). The diversity of the genus *Noblella* has also increased in the Peruvian Andes, where in recent years three species been described, forming a clade with the previously described *Psychrophrynella* and *Noblella* (Catenazzi et al., 2015; Santa Cruz et al., 2019; Catenazzi and Ttito, 2019).

Our new records of *Noblella worleyae* from Los Cedros reserve add important intraspecific variation to the original description, in terms of its body size, coloration and shape of tips of the digits. In particular, variation in the fingertips was found, with tips of Fingers I and IV varying from slightly acuminate (original description) to rounded (data presented herein), and tips of Fingers II and III from acuminate (original description) to slightly acuminate (data presented herein). We also strengthen the original publication (Reyes-Puig et al., 2020) with a detailed description of the osteology of the species.

Diversification in *Noblella* seems be related with the linearity of the Andes, with allopatric and parapatric populations being separated by ecological and geographic barriers. In Ecuador, all species of *Noblella* are allopatric and most of them are restricted to very specific geographic areas. *Noblella mindo* sp. nov. occurs in low montane forest in the valley of Mindo, in the Nambillo River watershed, western slopes of the Pichincha Massif, northwestern Andes, at 1,673 m; while *N. worleyae* inhabits low montane forest in the Manduriacu-Los Cedros watersheds, southern slopes of the Toisan massif; and *N. coloma* is restricted to the cloud forests of the Río Guajalito watershed, western slopes of the Atacazo volcano. *Noblella worleyae* is separated from *N. coloma* and *N. mindo* sp. nov. by the Guayllabamba River Valley (Fig. 2), an important biogeographic barrier, especially for frog species with low vagility (Hillman et al., 2014). Although the valley of Mindo (type locality of *N. mindo* sp. nov.) and the valley of Guajalito (type locality of *N. coloma*) are ca. 20 km apart in straight line, they are in different watersheds, separated by the Nambillo River and complex orogeny caused by the Pichincha massif and the Atacazo volcano.

All species currently recognized under the genus *Noblella* are miniaturized frogs, among the smallest Neotropical vertebrates (Duellman and Lehr, 2009). They are cryptic and adapted to live amidst or under leaf litter in forests, where they are often overlooked by amphibian visual surveys, being easier to locate by their calls or through pitfall traps (Reyes-Puig et al., 2019c). Although some species may be abundant locally, most species appear to have low densities. For example, yearly surveys between 2000–2012 at the type locality of *N. coloma* produced only three records, while up to 20 individuals of *N. lochites* were found in 2014 at a single locality in the province of Zamora-Chinchipe (D. F. Cisneros-Heredia pers. obs.).

Most remnants of mature forests in the Andes of Ecuador are nowadays either inside public or private protected areas or persist due to their inaccessibility. Private conservation initiatives have become extremely important in Ecuador (Betancourt et al., 2018; Guayasamin et al., 2018, 2019; Reyes-Puig et al., 2019a, 2019b, 2019c), where public protected areas do not cover all critically important regions for biodiversity (Lessmann et al., 2014; Cuesta et al., 2017; Reyes-Puig et al., 2017).

Unfortunately, habitat loss due to unsustainable expansion of the agricultural frontier, mining and infrastructure projects have placed a heavy burden on several private reserves (Roy et al., 2018; Guayasamin et al., 2019). In the early 2000s, the region of Mindo was heavily threatened by the construction of an oil pipeline (Oleoducto de Crudos Pesados OCP). Fortunately, local, national and international protests managed to promote some actions to mitigate the largest impacts of the pipeline development. Eventually Mindo has transformed into one of the most popular ecotourism destinations in northwestern Ecuador, allowing several private protected areas to preserve large tracks of mature forest (Welford and Yarbrough, 2015). Unfortunately, twenty years later, history repeats itself, now at Los Cedros reserve, but this time with mining concessions, exploration and exploitation (Roy et al., 2018). Thus, biodiversity conservation is facing an uncertain future.

The increasing descriptions of new species within the Ecuadorian territory have a practical application in the conservation of biodiversity. By highlighting the presence of new vertebrates with restricted distributions in the Andes, the visualization of this unique biodiversity is indisputable.

ACKNOWLEDGEMENTS

We conducted this research under research permits and agreement for genetic resources access (MAE-DNB-CM-2018-0106, 019-2018-IC-FAU-DNB/MAE) issued by Ministerio del Ambiente del Ecuador. We carried out this study following the guidelines for treatment and management of live amphibians and reptiles in field and laboratory investigations (Beaupre et al., 2004), recommended by the American Society of Ichthyologists and Herpetologists, the Herpetologists' League and the Society for the Study of Amphibians and Reptiles.

This study was developed as part of "Proyecto Descubre Napo", an initiative of Universidad San Francisco de Quito in association with Wildlife Conservation Society, and funded by the Gordon and Betty Moore Foundation, as part of the project "WCS Consolidating Conservation of Critical Landscapes (mosaics) in the Andes". We express our gratitude to the following people for their support: Ana Nicole Acosta-Vásconez, Susana Cárdenas, Mariela Domínguez, Jonathan Guillemot, Andrés León-Reyes, Emilia Peñaherrera, Carolina Proaño, Robert P. Reynolds, Alejandra Robledo, Ana Sevilla, Rebecca Zug. Work at Los Cedros Biological Reserve was developed as part of project "Muestreo de Grupos Ecológicos Clave", research program "Evaluación biológica rápida del corredor norte de la Reserva de Mashpi", a joint initiative of Fundación Futuro and Universidad San Francisco de Quito USFQ (Instituto ECOLAP, Museo de Zoología, Instituto iBIOTROP). This research was supported by Universidad San Francisco de Quito USFQ through research funds for the Museo de Zoología & Laboratorio de Zoología Terrestre, Instituto de Diversidad Biológica y Tropical iBIOTROP granted to DFCH; USFQ Collaboration Grants and COCIBA Grants (project HUBI ID 34, 39, 48, 1057, 7703, 12268, 13524) granted to DFCH and CRP; and Collaboration Grants and COCIBA Grants (project HUBI ID 5521, 5467, 5447, 11164, 16871) granted by USFQ to JMG. Work by DFCH was supported by Programa "Becas de Excelencia", Secretaría de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT), Ecuador; the Smithsonian Women's Committee, the 2002 Research Training Program, National Museum of Natural History, Smithsonian Institution; María Elena Heredia and Laura Heredia. We thank the Inédita Program from the Ecuadorian Science Agency SENESCYT (Respuestas a la Crisis de Biodiversidad: La Descripción de Especies como Herramienta de Conservación; INEDITA PIC-20-INE-USFQ-001) that funded the molecular component of this study. We are grateful for the comments of Edgar Lehr and an anonymous reviewer to improve the manuscript.

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APPENDIX I

Examined specimens.

*Noblella lochites***.** Ecuador, Napo: ZSFQ 346, Archidona, Reserva Narupa, 1176 m; ZSFQ 347, Reserva Narupa, 1152 m; ZSFQ 348, Reserva Narupa, 1167 m; Zamora Chinchipe: ZSFQ 1119, Yantzaza, Concesión La Zarza, 1385 m; ZSFQ 1124, Concesión La Zarza, 1357 m; ZSFQ 1186, ZSFQ 1187, ZSFQ 1188, Yantzaza, Río Blanco, 1654 m; ZSFQ 1188, Río Blanco, 1830 m.

Noblella cf. *lochites*. Ecuador, Zamora Chinchipe: ZSFQ 3262 – 326, Yantzaza, Estación Experimental El Padmi UNL, 775 m. Noblella myrmecoides: Ecuador, Napo: ZSFQ 670, Mera, Parque Nacional Llanganates, 1325 m; ZSFQ 671, Parque Nacional Llanganates, 1352 m; ZSFQ 672, Parque Nacional Llanganates, 1327 m.

Noblella cf. *myrmecoides*. Ecuador, Tungurahua: ZSFQ 1341, Río Negro, Reserva Río Zuñag, 1269 m.

Noblella coloma. Ecuador: Pichincha: QCAZ 7277, 7412, 8701, 11614, 26307, 32702, Reserva Ecológica Río Guajalito; 1800–2000 m.

Noblella heyeri. Ecuador, Loja: QCAZ 31470, 31471, 31473, Loja–Zamora road; 2385 m, QCAZ 22501, Zamora-Huaico; 2000 m.

Noblella worleyae. Ecuador, Imbabura: ZSFQ 345, 550, 551, 552, 2502, 2503, 2504, Reserva Manduriacu, 1184–1597 m.