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The Rediscovery of *Noblella peruviana* after More than 115 Years Helps Resolve the Molecular Phylogeny and Taxonomy of *Noblella* (Amphibia, Anura, Strabomantidae)

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Abstract: We revise the taxonomy of the frog genus *Noblella* on the basis of a molecular phylogeny. Previous studies recognized that *Noblella* is non-monophyletic, with one clade distributed from southeastern Peru to northeastern Bolivia and adjacent areas in Brazil and another clade distributed from northern Peru to Ecuador and southeastern Colombia. The lack of sequences from the type species *Noblella peruviana* prevented the investigation of its phylogenetic position and the status of related taxa. Our rediscovery after more than 115 years allowed for the inclusion of DNA sequences of *Noblella peruviana* obtained from specimens collected at the type locality in southeastern Peru. We inferred a phylogeny based on a concatenated dataset (three mitochondrial and two nuclear loci) using Bayesian and maximum likelihood methods. Our phylogeny corroborated the non-monophyly of *Noblella* and helped resolve the status of related taxa, including *Psychrophrynella bagrecito*, the type species of the genus *Psychrophrynella* (rediscovered after 42 years). We identified a clade containing *N. peruviana*, *P. bagrecito*, and other species of *Noblella* and *Psychrophrynella* distributed in southern Peru. Given that the name *Noblella* predates *Psychrophrynella*, we propose that *Psychrophrynella* should be considered a junior synonym of *Noblella*. The second clade contains species of *Noblella* distributed in Ecuador and northern Peru, including *N. myrmecoides*, which used to be the type species of the genus *Phyllonastes*. Consequently, we propose to reinstate the genus *Phyllonastes* to accommodate all species of *Noblella* distributed in Ecuador, northern Peru, southeastern Colombia, and adjacent areas in Brazil. We present an updated taxonomy including new combinations for 12 species and reinstatements for three species.

Keywords: amphibians; Andes; terrestrial-breeding frogs

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1. Introduction

Terrestrial-breeding frogs (Strabomantidae) living at high elevations in the Andes exhibit morphological traits associated with a predominantly terrestrial lifestyle and cold climate, including a robust body, relatively short limbs and head, absence of digital discs,

and cryptic coloration [1]. The genus *Noblella* Barbour, 1930 [2] currently contains 17 species distributed in the Andes and Amazon region of Colombia, Ecuador, Peru, Bolivia, and adjacent areas in Brazil [3]. Many of these species are morphologically similar to those in closely related genera (e.g., *Psychrophrynella* Hedges, Duellman, and Heinicke, 2008 [4]) distributed in montane habitats. Previous phylogenetic analyses revealed that *Noblella* is non-monophyletic, with a "northern clade" distributed in Ecuador, northern Peru, southeastern Colombia, and adjacent areas in Brazil and a "southern clade" distributed from southeastern Peru to northeastern Bolivia and adjacent areas in Brazil [5–7]. These studies showed that the "northern clade" is closely related to *Bahius bilineatus* (Bokermann, 1975) [8] and *Barycholos* Heyer, 1969 [9], whilst the "southern clade" is closely related to *Microkayla* De la Riva, Chaparro, Castroviejo-Fisher, and Padial, 2017 [10] and the newly described genus *Qosqophryne* Catenazzi, Mamani, Lehr, and von May, 2020 [7].

Over the past few years, it became clear that DNA sequences for *Noblella peruviana* (Noble, 1921) [11], the type species for the genus, were needed to resolve the discrepancy in the distribution of species of *Noblella* [7]. Sequences for *N. peruviana* were not included in previous analyses because no tissues were available for DNA extraction from the old, and presumably formalin-fixed, specimens of the type series. These specimens are the only previously known specimens of *N. peruviana*, which H. H. Keays collected between December 1899 and August 1900 [12] in the Department of Puno. The verbatim location for the original shipment of specimens was Juliaca, in the cold and dry, high-Andean Peruvian Altiplano, certainly not a suitable location for *Noblella* [12]. Instead, the most likely type locality is the vicinity of the Inca Mine of Santo Domingo, in the Cordillera de Carabaya, where, according to Vaurie [13], Keays collected most of the specimens of vertebrates he shipped to the British Museum. Santo Domingo can only be reached by foot, descending the Limbani Valley and crossing the Inambari River, and it is unclear whether Keays collected the specimens at Santo Domingo or along the Limbani trail [12]

Recent studies have highlighted the taxonomic uncertainty surrounding the status of the genus *Psychrophrynella*, which appears to belong to the same lineage containing species of *Noblella* distributed in southern Peru and northern Bolivia [7]. *Psychrophrynella bagrecito* (Lynch, 1986) [14] was designated as the type species of the genus, but its DNA sequences were not included in the phylogeny of Hedges et al. [4] or in subsequent studies [10,15,16]. Similarly to *N. peruviana*, no specimens had been collected since 1974, when K.R. Thomas collected the holotype and some of the paratypes [14]. Additional specimens, also collected in 1974 and assigned as paratypes of *P. bagrecito* [14], belong to a different, undescribed taxon [17]. Thus, a revision of the taxonomy of *Psychrophrynella* has been pending since it was proposed [4].

Here, we examine the phylogenetic relationships among species of *Noblella* and *Psychrophrynella* using DNA sequences obtained from specimens collected during field expeditions in southern Peru. During separate expeditions to the type localities of both type species in 2016 and 2017, we were able to rediscover *N. peruviana* and *P. bagrecito* and obtain genetic sequences. Our analyses include these novel sequences, which are crucial to resolving the taxonomic conundrum of *Noblella*, as well as other previously unsampled species.

2. Materials and Methods

2.1. Field Surveys and Specimen Collection

The putative type locality of *N. peruviana* is the Cordillera de Carabaya, located in Región (Departamento) Puno, southern Peru [12]. Expeditions in 2016 and 2017 to the type locality near the abandoned Inca Mine of Santo Domingo, in the upper reach of a tributary of the Inambari River in the Cordillera de Carabaya, resulted in the rediscovery and collection of voucher specimens and tissues of *N. peruviana* at the type locality and along the Limbani trail in Oconeque near Aquele, in the upper Limbani Valley, at an airline distance of ~26 km from the type locality. Collection at both Santo Domingo and the Limbani trail is important because of the uncertainty regarding the precise location where

Keays collected the holotype in 1899–1900 (see Section 1). The Limbani Valley runs from the opposite side of the Inambari River with respect to the Santo Domingo watershed and is generally drier than the montane forest at the type locality. The type locality of *P. bagrecito* is Marcapata, located in Región (Departamento) Cusco, southern Peru [14]. Expeditions in 2016 and 2017 to Marcapata allowed for the collection of specimens and tissues used in this study.

Research and use of vertebrate animals were approved by the Institutional Animal Care and Use Committees of Southern Illinois University Carbondale (IACUC protocol #16-006), Florida International University (IACUC protocol #18-009), and the University of California (ACUC #R278-0412, #R278-0413, and #R278-0314). The Dirección General Forestal y de Fauna Silvestre, Servicio Nacional Forestal y de Fauna Silvestre (SERFOR), Ministerio de Agricultura y Riego, Peru, issued research and collecting permits (R.D.G. N° 120-2012-AG-DGFFS-DGEFFS, N° 064-2013-AG-DGFFS-DGEFFS, N° 0146-2013-AG-DGFFS-DGEFFS, N° 292-2014-AG-DGFFS-DGEFFS, N° 029-2016-SERFOR-DGGSPFFS, N° 405-2016-SERFOR-DGGSPFFS, and Contrato de Acceso Marco a Recursos Genéticos N° 359-2013-MINAGRI-DGFFS-DGEFFS).

Museum abbreviations are CORBIDI—Centro para Ornitología y Biodiversidad, Lima; CBF—Colección Boliviana de Fauna; KU—Kansas University, Lawrence; LSUMZ—Louisiana Museum of Natural History, Baton Rouge; MNCN—Museo Nacional de Ciencias Naturales, Madrid; MNRJ—Museu Nacional, Rio de Janeiro; MUBI—Museo de Biodiversidad del Perú, Cusco; MUSA—Museo de Historia Natural, Universidad Nacional de San Agustín de Arequipa, Arequipa; MUSM—Museo de Historia Natural de la Universidad de San Marcos, Lima.

2.2. Taxonomic Scope

Our analyses focused on taxa in the subfamily Holoadeninae [4], which includes nine genera [18]: *Bahius*, *Barycholos*, *Bryophryne*, *Euparkerella*, *Holoaden*, *Microkayla*, *Noblella*, *Psychrophrynella*, and *Qosqophryne*. We used sequences from GenBank and newly obtained sequences from previously unsampled species, including *N. lynchi*, *N. peruviana*, *P. bagrecito*, and several undescribed species of *Noblella* and *Psychrophrynella*. Additionally, we included representative species of the genera *Lynchius*, *Oreobates*, *Phrynopus*, and *Pristimantis*, as they are closely related to Holoadeninae [16].

2.3. Laboratory Work

We followed laboratory protocols used in previous studies of terrestrial breeding frogs to extract, amplify, and sequence DNA [4,7,15,19,20]. Primers and thermocycling conditions to amplify DNA via PCR are described in [7,19,20]. We used forward and reverse primers to amplify five loci, including a fragment of the 16S rRNA mitochondrial gene (16S), a fragment of the 12S rRNA mitochondrial gene rRNA gene (12S), the protein-coding mitochondrial gene cytochrome c oxidase subunit I (COI), the nuclear protein-coding gene recombination-activating protein 1 (RAG1), and the tyrosinase precursor (Tyr). We completed the cycle sequencing reactions by using the corresponding PCR primers and the BigDye Terminator 3.1 (Applied Biosystems, Waltham, MA, USA) and obtained sequences by running the purified reaction products in an ABI 3730 Sequence Analyzer (Applied Biosystems). We deposited the newly obtained sequences in GenBank, and we updated the species names associated with four GenBank sequences (Appendix A; Table S1).

2.4. Molecular Phylogenetic Analyses

Our analyses included sequences from 153 specimens. We used Geneious R6, version 6.1.8 [21], to align the sequences using the Geneious multiple alignment program for nucleotide (consensus) sequences. We used PartitionFinder, version 1.1.1 [22], to select the appropriate models of nucleotide evolution, and we used the Bayesian information criterion (BIC) to determine the best partitioning schemes and substitution models. Our analyses included two outgroup taxa, *Niceforonia philippi* and *Niceforonia brunnea*. It is worth noting that sequences of *N. philippi* downloaded from GenBank were listed as *N. dolops*, which is a junior synonym of *N. philippi* [23]. The best partitioning scheme

included six subsets (BIC value: 59,247.168). The first partition subset included both the 12S and 16S sequences and the best fitting substitution model was GTR + I + G. The remaining five subsets were partitioned according to codon positions as follows (substitution model in parenthesis): one set including the 1st codon position of COI (SYM + I + G), one set including the 2nd codon position of COI (F81 + I), one set including the 3rd codon position of COI (GTR + G), one set including the 1st and 2nd codon position of RAG1 and the 1st and 2nd codon position of Tyr (GTR + I + G), and one set including the 3rd codon position of both RAG1 and Tyr (K80 + G).

We used Bayesian and Maximum Likelihood (ML) methods to infer a phylogeny of the study species. A 2546-bp concatenated alignment, including the five loci, was used in both analyses. First, we used MrBayes, version 3.2.0 [24], to perform an MCMC Bayesian analysis consisting of two simultaneous runs of 10 million generations, and we set the sampling rate to be once every 1000 generations. Each run had three heated chains and one "cold" chain, and the burn-in was set to discard the first 25% of samples from the cold chain. At the end of the MCMC run, the average standard deviation of split frequencies was 0.004046.

Following the completion of the analysis, we used Tracer 1.6 [25] to verify convergence. Subsequently, we used FigTree (http://tree.bio.ed.ac.uk/software/figtree/; URL accessed on 15 January 2024) to visualize the majority-rule consensus tree and the posterior probability values to assess node support. We used IQ-TREE [26] to perform the ML analysis on the concatenated dataset. We ran the analysis using the default setting (ultrafast bootstrap method, 10,000 bootstrap alignments) and the partitioning scheme and substitution models determined by PartitionFinder. Then, we used FigTree to visualize the ML consensus tree.

3. Results

3.1. Molecular Phylogenetic Analysis

Both Bayesian and maximum likelihood analyses showed that *Noblella* is non-monophyletic, with a clade distributed in southern Peru and another clade distributed in Ecuador and northern Peru (Figures 1 and S1). The first clade contains *Noblella peruviana*, *Psychrophrynella bagrecito*, and other species of *Noblella* and *Psychrophrynella* distributed in southern Peru; in turn, this clade is sister to the clade formed by *Microkayla* and *Qosqophryne*. The second clade contains species of *Noblella* distributed in Ecuador and northern Peru, including *N. myrmecoides*, which was previously placed in the genus *Phyllonastes* [27] (Figures 1 and S1).

3.2. Taxonomy

In this section, we present an updated taxonomy of *Noblella* consistent with the molecular phylogeny results. Given that the name *Noblella* predates *Psychrophrynella*, we propose that *Psychrophrynella* should be considered a junior synonym of *Noblella*. Additionally, we propose to reinstate the genus *Phyllonastes* to accommodate all species of *Noblella* distributed in Ecuador, northern Peru, southeastern Colombia, and adjacent areas in Brazil. In addition to the updated list of species included under each genus, new combinations and reinstatements are included below.

***Noblella* Barbour**

Noblella Barbour, 1930: 81 [2]. Type species *Sminthillus peruvianus* Noble, 1921: 1 [11], by original designation.

Phyllonastes Heyer, 1977: 151 [27]. Type species *Euparkella myrmecoides* Mynch, 1976, by original designation.

Content: Twelve species currently recognized in the genus (this paper): *N. bagrecito*, *N. carrascoicola*, *N. chirihampatu*, *N. glauca*, *N. losamigos*, *N. madreselva*, *N. peruviana*, *N. pygmaea*, *N. ritarasquinae*, *N. thiuni*, *N. usurpator*, and *N. vilcabambensis*.

(Note: No sequences available for *N. carrascoicola* and *N. ritarasquinae*. Proposed inclusion in the genus is based on similarities in morphology and geographic distribution.)

***Noblella bagrecito* new combination (Lynch, 1986)**

Phrynopus bagrecito Lynch, 1986 [14]

Psychrophrynella bagrecito—Hedges, Duellman, and Heinicke, 2008: 103 [4].

Psychrophrynella bagrecito—Duellman and Lehr, 2009: 260 [1].

Holotype. KU 196512, adult female, from Río Marcapata below Marcapata, about 2740 m a.s.l., Provincia Quispicanchis, Región (Departamento) Cusco, Perú.

Additional specimens. Paratopotypes KU 196512–26 and LSUMZ 32150–64. Four males CORBIDI 17482, 17483, 17525, MUBI 19040, one female CORBIDI 17527, and one juvenile CORBIDI 17526 from Cachihua (13.58975 S, 70.95609 W), near Marcapata, 2688 m a.s.l., Provincia Quispicanchis, Región (Departamento) Cusco, Perú; and one male CORBIDI 17528 and one juvenile MUBI 19041 from Limacpunko (13.55277 S, 70.90308 W), 2280 m a.s.l., Provincia Quispicanchis, Región (Departamento) Cusco, Perú, all collected on 9 August 2017 by A. Catenazzi and A. Ttito (Figure 2).

Genus reallocation. We assign *Psychrophrynella bagrecito* to the genus *Noblella* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Noblella peruviana*, the type species of the genus *Noblella*.

Remarks. Four paratypes (KU 196527–28 and LSUMZ 32167–68) from Huyro between Huayopata and Quillabamba [14] belong to a distinct, undescribed species, as confirmed by DNA sequences (unpublished data). All additional localities reported by Duellman and Lehr [1] (p. 319) also refer to other species of *Noblella*. Therefore, the known distribution of *N. bagrecito* is restricted to the Marcapata Valley from 2280–2740 m a.s.l.

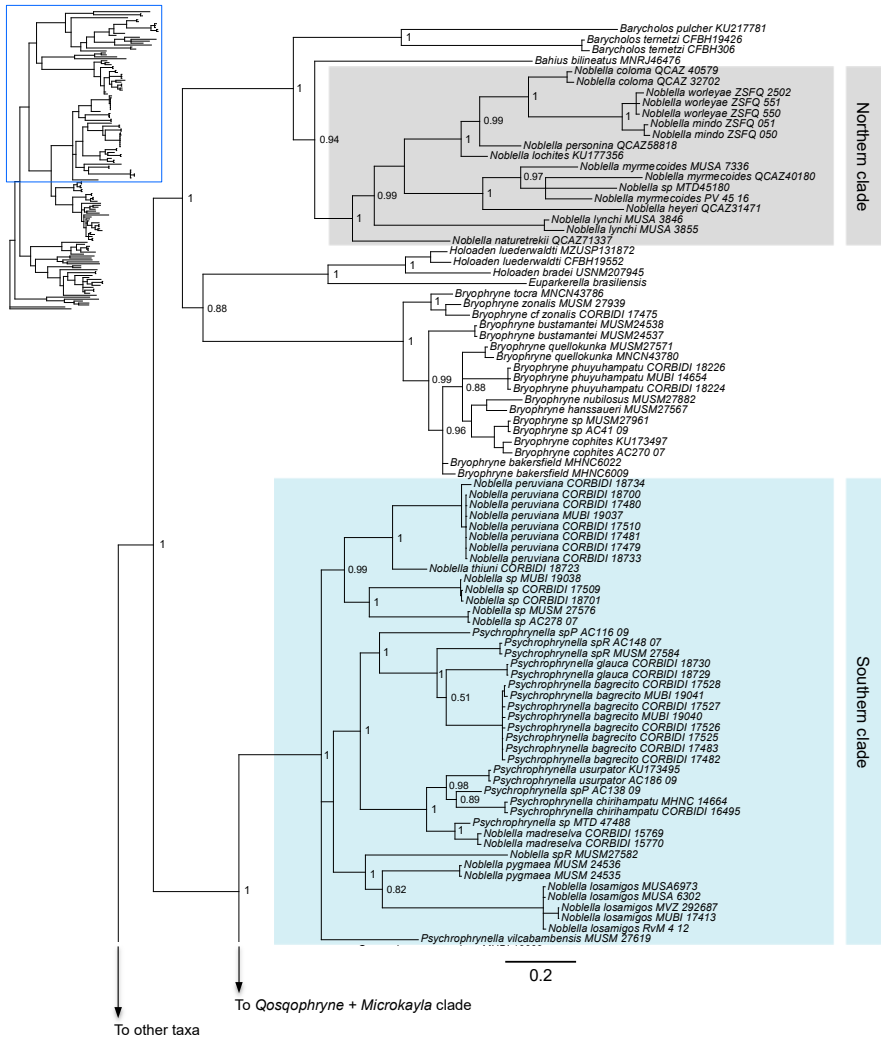

Figure 1. *Cont.*

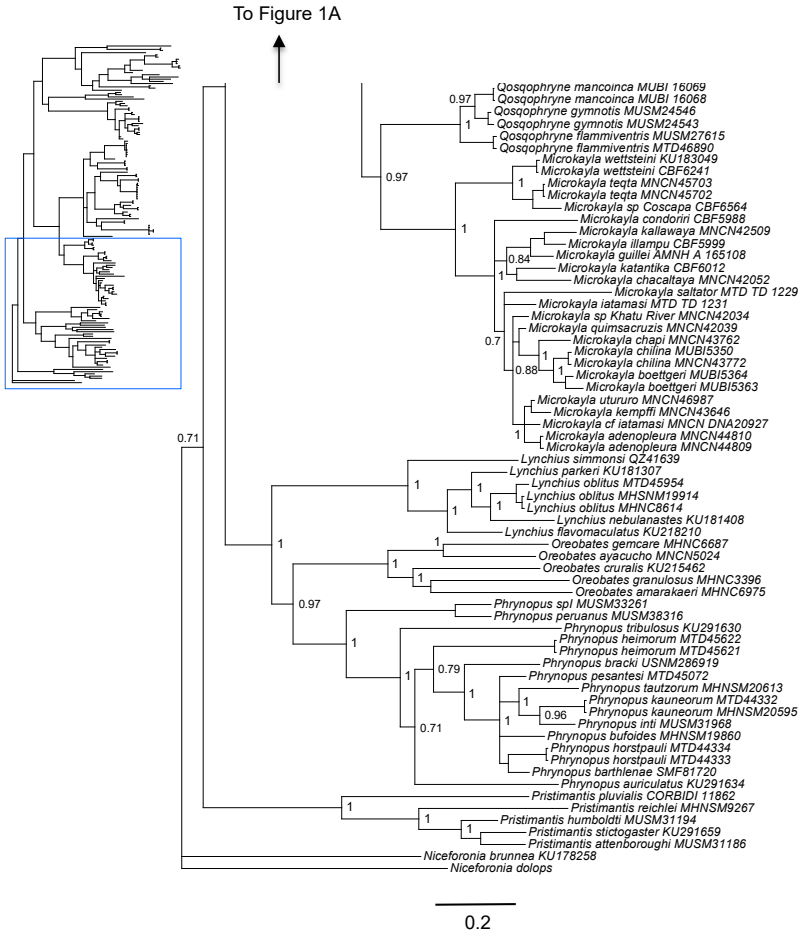

Figure 1. (**Top**): Consensus Bayesian phylogeny based on a 2546-bp concatenated dataset (fragments of genes 16S, 12S, COI, RAG1, and Tyr) analyzed in MrBayes. Posterior probability values are indicated at each node. The area in gray indicates a clade with species distributed in northern Peru and Ecuador ("northern clade"), and the area in light blue indicates a clade with species distributed in southern Peru ("southern clade" containing the type species *Noblella peruviana*). Consensus Bayesian phylogeny based on a 2546-bp concatenated dataset (fragments of genes 16S, 12S, COI, RAG1, and Tyr) analyzed in MrBayes. Posterior probability values are indicated at each node. (**Bottom**): Part of the consensus Bayesian phylogeny showing closely related clades *Qosqophryne* and *Microkayla*, and more distantly related clades including *Lynchius*, *Oreobates*, and *Phrynopus*.

Noblella chirihampatu new combination (Catenazzi and Ttito, 2016)

Psychrophrynella chirihampatu Catenazzi and Ttito 2016 [28]

Holotype. CORBIDI 16495, an adult male from Área de Conservación Privada (ACP) Ukumari Llaqta, 2730 m, Comunidad Campesina de Japu, Distrito Paucartambo, Provincia Paucartambo, Región Cusco, Perú.

Additional specimens. Ten paratopotypes: five adult males, CORBIDI 16496 and 16497 and MHNC 14658, 14664, and 14666, and five adult females, CORBIDI 16498–16499, 16696, and MHNC 14661–14662, collected at the type locality. Sixteen paratypes: all from ACP Ukumari Llakta: nine adult males, CORBIDI 16505–16509 and MHNC 14656 and 14670–14672, and one adult female, CORBIDI 16504, collected near Tambo, 3160 m; two adult males, CORBIDI 16503 and MHNC 14667, and four adult females, CORBIDI 16501–2 and MHNC 14668–69, collected at the Playa campsite, 2780 m [28].

Genus reallocation. We assign *Psychrophrynella chirihampatu* to the genus *Noblella* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Noblella peruviana*, the type species of the genus *Noblella*.

***Noblella glauca* new combination (Catenazzi and Ttito, 2018)**
Psychrophrynella glauca Catenazzi and Ttito 2018 [29]
Holotype. CORBIDI 18729, an adult female from 13.67603 S, 70.46588 W (WGS84), 2225 m, near Thiuni, Distrito Ollachea, Provincia Carabaya, Región (Departamento) Puno, Peru, collected by A. Catenazzi and A. Ttito on 14 August 2017 [29].
Additional specimens. Three paratopotypes, one adult male, CORBIDI 18730, one adult female, MUBI 16322, and one juvenile, MUBI 16323, were collected with the holotype [29].
Genus reallocation. We assign *Psychrophrynella glauca* to the genus *Noblella* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Noblella peruviana*, the type species of the genus *Noblella*.

***Noblella peruviana* (Noble, 1921)**
Sminthillus peruvianus Noble, 1921 [11]
Noblella peruviana—Barbour, 1930 [2], Griffiths, 1959 [30], De la Riva, Chaparro, and Padial, 2008 [12]
Eleutherodactylus peruvianus—Lynch, 1971 [31]
Phrynopus peruvianus—Lynch, 1975 [32] (Based on misidentifications, in reference to *Noblella usurpator*.)
Holotype. Holotype: AMNH 14526, "near Juliaca, Departamento Puno, Peru", most likely in error, collected by H. H. Keays, date not known.
Paratopotypes. AMNH 14527–28, UMMZ 56621; AMNH 88061 (cleared and stained).
Newly referred specimens. Eight specimens: two females, CORBIDI 17510, CORBIDI 18700; one male, MUBI 10937, and one juvenile, CORBIDI 17480, collected at the type locality, along the trail from Santo Domingo to Punto 1 (13.83210 S, 69.63710 W), 1955 m, on 7 June 2016 by A. Catenazzi, A. Ttito, and J. C. Jahuanchi; and three males CORBIDI 18733, CORBIDI 17479, CORBIDI 17481 from the type locality, collected on 24 on July 2017 by A. Catenazzi, A. Ttito, I. Diaz, and J. C. Jahuanchi; and one male, CORBIDI 18734, from Oconeque, near Aquele, Limbani Valley (14.05853 S, 69.71528 W), 1982 m, collected on 4 August 2017 by A. Catenazzi, I. Diaz, A. Ttito and J. C. Jahuanchi (Figure 3).
Generic placement. This is the type species of the genus.
Remarks. Referred specimen CORBIDI 18734 is the first record outside of the type locality. The known distribution range of *N. peruviana* spans ~30 km by airline and includes localities from the upper Limbani Valley to Santo Domingo in the Cordillera de Carabaya.

***Noblella usurpator* new combination (De la Riva, Chaparro, and Padial, 2008)**
Phrynopus peruvianus (part) Lynch, 1975 [32] (p. 36).
"Phrynopus" peruvianus—Hedges, Duellman, and Heinicke, 2008 [4] (p. 103).
Psychrophrynella usurpator—De la Riva, Chaparro, and Padial 2008 [12] (p. 44).
Psychrophrynella usurpator—Duellman and Lehr, 2009 [1] (p. 261).
Holotype. KU 138939, adult female, from the north slope of Abra Acjanacu, 3400 m a.s.l., 29 km NNE Paucartambo, Región (Departamento) Cusco, Perú.
Genus reallocation. We assign *Psychrophrynella usurpator* to the genus *Noblella* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Noblella peruviana*, the type species of the genus *Noblella*.

***Noblella vilcabambensis* new combination (Condori, Acevedo-Rincón, Mamani, Delgado C., and Chaparro, 2020)**
Psychrophrynella vilcabambensis—Condori, Acevedo-Rincón, Mamani, Delgado C., and Chaparro 2020 [33] (p. 129).
Holotype. MUBI 13485, adult male, from Challcha, 3707 m a.s.l., Distrito Vilcabamba, Provincia La Convención, Región (Departamento) Cusco, Perú.
Genus reallocation. We assign *Psychrophrynella vilcabambensis* to the genus *Noblella* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Noblella peruviana*, the type species of the genus *Noblella*.

***Phyllonastes* Heyer**
Phyllonastes Heyer, 1977 [27] (p. 151). Type species *Euparkerella myrmecoides* Lynch, 1976 [34] (p. 50), by original designation.
Content: Ten species currently recognized in the genus (this paper): *P. coloma*, *P. duellmani*, *P. heyeri*, *P. lochites*, *P. lynchi*, *P. mindo*, *P. myrmecoides*, *P. naturetrekii*, *P. personina*, and *P. worleyae*.
(Note: No sequences available for *P. duellmani*. Proposed inclusion in *Phyllonastes* is based on similarities in morphology and geographic distribution.)

***Phyllonastes coloma* new combination (Guayasamin and Terán-Valdez, 2009)**
Noblella coloma Guayasamin and Terán-Valdez, 2009 [35] (p. 48).
Holotype. QCAZ 26307, from Reserva Florística Río Guajalito (0°14′ S, 78°49′ W), 1800–2000 m a.s.l., 3 km NW from Km 59 on the old road from Quito to Santo Domingo, Provincia Pichincha, Ecuador.
Genus reallocation. We assign *Noblella coloma* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes duellmani* reinstatement (Lehr, Aguilar, and Lundberg, 2004)**
Phyllonastes duellmani Lehr, Aguilar, and Lundberg, 2004 [36] (p. 214).
Noblella duellmani—De la Riva, Chaparro, and Padial, 2008 [12] (p. 68).
Holotype. KU 196529, from Cillapata (approximately 1.5 km north-northeast of Auquimarca), approximately 10°43′52″ S, 75°42′48″ W, 2900 m a.s.l., Distrito Paucartambo, Provincia Pasco, Departamento Pasco, Peru.
Genus reallocation. We reinstate *Noblella duellmani* to the genus *Phyllonastes* based on morphological similarity and relative geographic proximity to other species that belong to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes heyeri* reinstatement (Lynch, 1986)**
Phyllonastes heyeri Lynch, 1986 [14] (p. 426).
Noblella heyeri—De la Riva, Chaparro, and Padial, 2008 [12] (p. 68).
Noblella heyeri—Duellman and Lehr, 2009 [1] (p. 92).
Holotype. KU 196529, 33 km SW Huancabamba, Región (Departamento) Piura, Perú, 3100 m a.s.l.
Genus reallocation. We reinstate *Noblella heyeri* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes lochites* new combination (Lynch, 1976)**
Euparkerella lochites Lynch, 1976 [34] (p. 49).
Phyllonastes lochites—Heyer, 1977 [27] (p. 152).
Phyllonastes lochites—Lynch, 1986 [24] (p. 426).
Noblella lochites—De la Riva, Chaparro, and Padial, 2008 [12] (p. 68).
Holotype. KU 147070, from Río Piuntza, on the northern end of the Cordillera del Condor, Morona-Santiago Province, Ecuador, 1550 m a.s.l. (approximately 3°15′ S, 78°20′ W).
Genus reallocation. We assign *Noblella lochites* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes lynchi* reinstatement (Duellman, 1991)**
Phyllonastes lynchi Duellman, 1991 [37] (p. 10).
Noblella lynchi—De la Riva, Chaparro, and Padial, 2008 [12] (p. 68).
Noblella lynchi—Duellman and Lehr, 2009 [1] (p. 93).
Holotype. KU 196529, from 33 km SW Huancabamba, Región (Departamento) Piura, Perú, 3100 m a.s.l.

Genus reallocation. We reinstate *Noblella heyeri* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes mindo* new combination (Reyes-Puig, Guayasamin, Koch, Brito-Zapata, Hollanders, Costales, and Cisneros-Heredia, 2021)**
Noblella mindo Reyes-Puig, Guayasamin, Koch, Brito-Zapata, Hollanders, Costales, and Cisneros-Heredia, 2021 [38] (p. 66).
Holotype. ZSFQ 050, from El Cinto, 11 Km E from Mindo town, Mindo (0.09022° S, 78.818581° W), 1673 m a.s.l., province of Pichincha, Ecuador.
Genus reallocation. We assign *Noblella mindo* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes myrmecoides* new combination (Lynch, 1976)**
Euparkerella myrmecoides Lynch, 1976 [34] (p. 50).
Phyllonastes myrmecoides—Heyer, 1977 [27] (p. 152).
Noblella myrmecoides—De la Riva, Chaparro, and Padial, 2008 [12] (p. 68).
Holotype. TCWC 41532, from Mishana (2 1/2 h by speedboat up the Río Nanay from the Navy dock 5 km NNE Iquitos), Departamento Loreto, Perú.
Additional specimens. Two adult males from Manseriche, Datem del Marañon, Loreto (MUSA 7332, SVL 11.4 mm; MUSA 7333) (Figure S2).
Genus reallocation. We assign *Noblella myrmecoides* to the genus *Phyllonastes* based on molecular phylogenetic analyses and because it is the type species of the genus *Phyllonastes*.
Remarks. Many specimens of small Holoadeninae from the lowlands of southern Peru and Bolivia have been identified as *Noblella myrmecoides*, most likely in error (e.g., see recent checklist of amphibians of Madidi National Park in [39]). Several of these specimens were reassigned to *Noblella losamigos* [40], but it is unclear whether additional species of *Noblella* might be concealed under the former identification of *Noblella myrmecoides*.

***Phyllonastes naturetrekii* new combination (Reyes-Puig, Reyes-Puig, Ron, Ortega, Guayasamin, Goodrum, Recalde, Vieira, Koch, and Yánez-Muñoz, 2019)**
Noblella naturetrekii Reyes-Puig, Reyes-Puig, Ron, Ortega, Guayasamin, Goodrum, Recalde, Vieira, Koch, and Yánez-Muñoz, 2019 [5] (p. 6).
Holotype. DHMECN 13390, from Bosque Protector Cerro Candelaria (1.428722° S, -78.30421° W), 2000 m a.s.l., Naturetrek Reserve, Río Verde, Cantón Baños, Tungurahua Province, Ecuador.
Genus reallocation. We assign *Noblella naturetrekii* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes personina* new combination (Harvey, Almendáriz C., Brito-M., and Batallas-Revelo, 2013)**
Noblella personina Harvey, Almendáriz C., Brito-M., and Batallas-Revelo, 2013 [41] (p. 3).
Holotype. EPN 14324, from the forest at the Sardinayacu Lake Complex (2°03′48.4″ S, 78°14′11.3″ W), 1916 m a.s.l., Cantón Morona, Parroquia Sinaí, Morona Santiago, Ecuador.
Genus reallocation. We assign *Noblella personina* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

***Phyllonastes worleyae* new combination (Reyes-Puig, Maynard, Trageser, Vieira, Hamilton, Lynch, Culebras, Kohn, Brito-M., and Guayasamin, 2020)**
Noblella worleyae Reyes-Puig, Maynard, Trageser, Vieira, Hamilton, Lynch, Culebras, Kohn, Brito-M., and Guayasamin, 2020 [42] (p. 164).
Holotype. ZSFQ 551, from Río Manduriacu Reserve (0.312057° N, 78.854330° W), 1184 m a.s.l., Cantón Cotacachi, Imbabura Province, Ecuador.
Genus reallocation. We assign *Noblella worleyae* to the genus *Phyllonastes* based on molecular phylogenetic analyses that indicate that it belongs to a reciprocally monophyletic clade that includes *Phyllonastes myrmecoides*, the type species of the genus *Phyllonastes*.

DNA sequences: Incertae sedis

The list included below represents DNA sequences that differ considerably from sequences from closely related species (in the same genus), likely derived from errors in assigning the tissue source or locality applied to the tissue source when uploading sequences to GenBank). We recommend not using these sequences of dubious origin. If used in the future, results should be interpreted with caution.

MF186541. *Bryophryne tocra* RAG1 sequence. This sequence is very similar to RAG sequences from several species of *Phrynopus* rather than other *Bryophryne*.

MF186583. *Bryophryne tocra* Tyr sequences. This sequence is very similar to Tyr sequences from several species of *Phrynopus* rather than other *Bryophryne*.

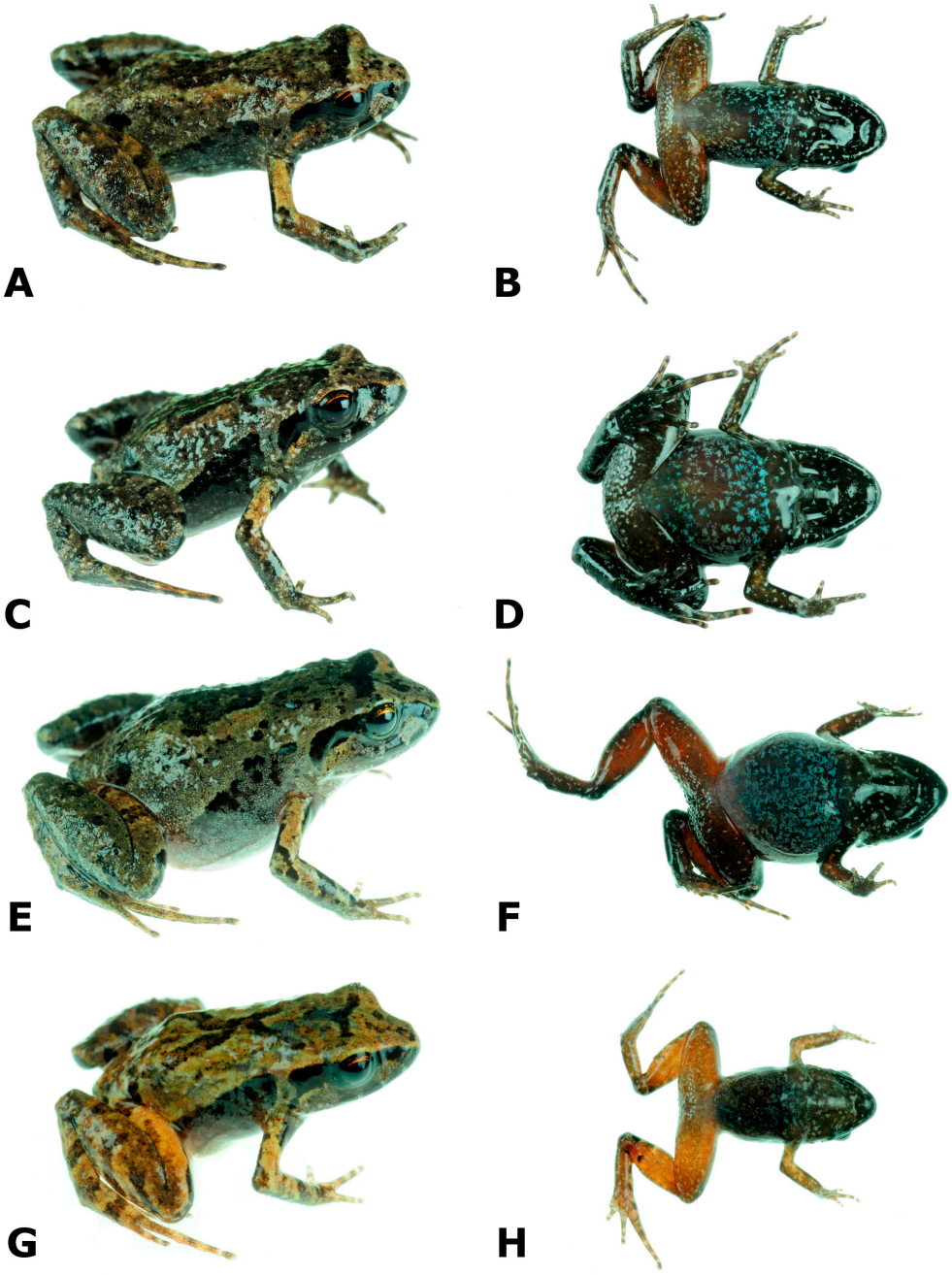

Figure 2. *Noblella bagrecito*, adult specimens collected at the type locality (**A**–**F**) and at the nearby locality of Limacpunko (**G**,**H**). Snout-vent length (SVL) is given in mm. (**A**,**B**) male (CORBIDI 17482, SVL = 17.5 mm); (**C**,**D**) male (CORBIDI 17483, SVL = 12.5 mm); (**E**,**F**) female (CORBIDI 15727, SVL = 21.5 mm); (**G**,**H**) male (CORBIDI 15728, SVL = 12.5 mm).

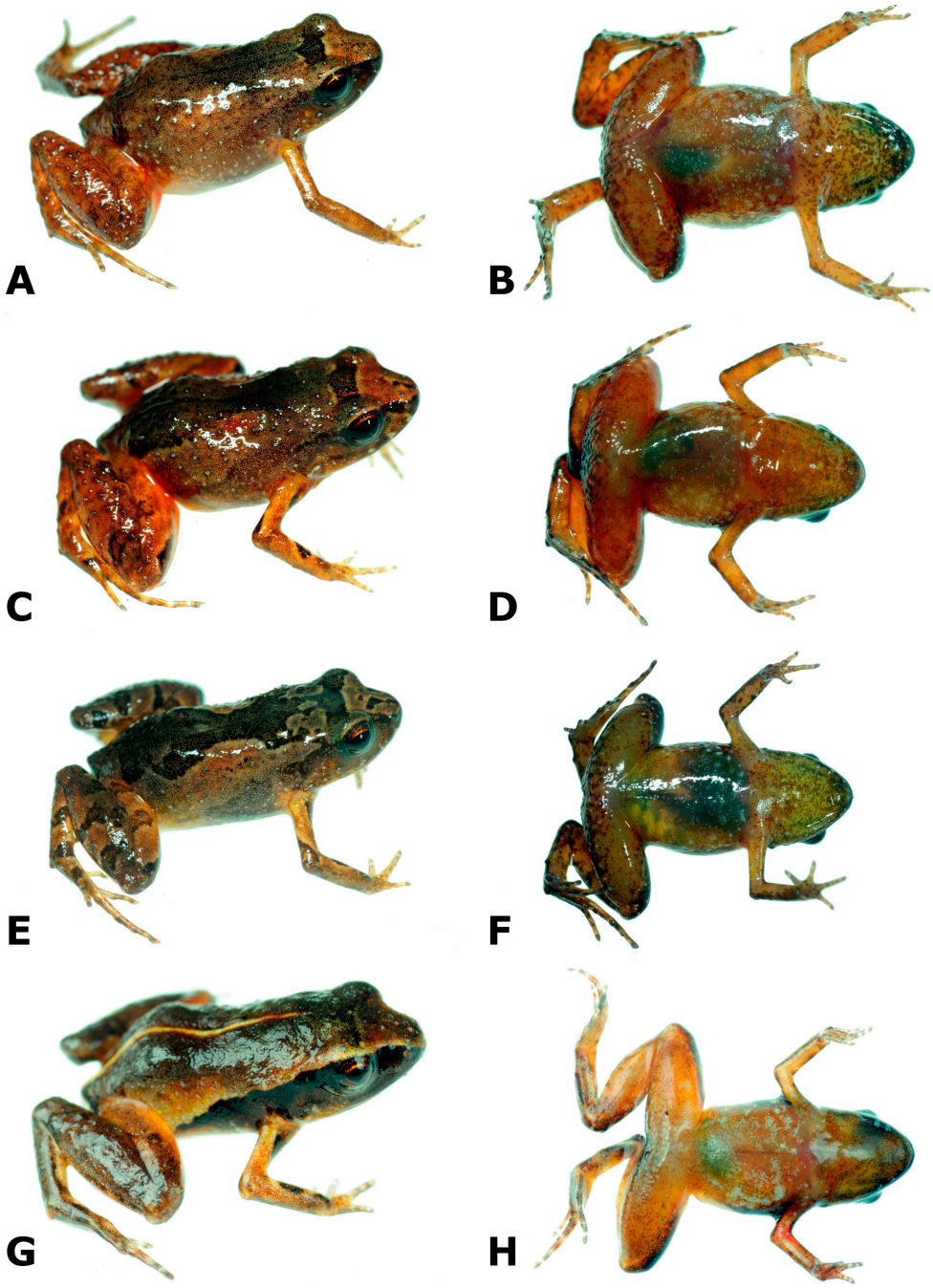

Figure 3. *Noblella peruviana*, adult specimens collected at the type locality (**A**–**F**) and at Oconeque, Aquele, Limbani, Puno (**G**,**H**). Snout-vent length (SVL) is given in mm. (**A**,**B**) female (CORBIDI 17510, SVL = 17.8 mm); (**C**,**D**) male (MUBI 19037, SVL = 13.3 mm); (**E**,**F**) female (CORBIDI 18700, SVL = 16.7 mm); (**G**,**H**) male (CORBIDI 18734, SVL = 11.0 mm).

4. Discussion

Our study helps resolve the taxonomy and systematics of the genus *Noblella*, and it is the first to include DNA sequences from the type species (*N. peruviana*) in a phylogenetic analysis. As previously suggested [7,40], any taxonomic decision on the status of the "northern clade" of *Noblella* depended on the resolution of the "southern clade" as the latter is geographically closer to the type locality of *N. peruviana* (Figure 4). The non-monophyly of *Noblella* was recognized in previous studies, yet the lack of molecular data from the type species prevented clarifying the taxonomic status of members of both clades. Our study

also clarifies the status of *Psychrophrynella*, which is here considered to be a junior synonym of *Noblella*.

Crucial to our findings was the rediscovery of the two type species, *N. peruviana* and *N. bagrecito*, and the inclusion (for the first time) of their DNA sequences in a phylogenetic analysis. We rediscovered *N. peruviana* 116–117 years after it was last collected and *N. bagrecito* 42 years after it was last collected, exemplifying the necessity of fieldwork when searching for 'lost' and missing species. A variety of reasons may explain amphibian rediscoveries [43], including hypothesized recoveries following disease-driven declines [44], but our rediscoveries espouse a trend common to many tropical, small, and endemic species of rediscovered amphibians [45]. Specifically, both *N. peruviana* and *N. bagrecito* are minute, inconspicuous inhabitants of the leaf litter or terrestrial moss layer and only known from their type localities, which in the case of *N. peruviana* is quite remote. These characteristics help explain the lack of observations during several decades.

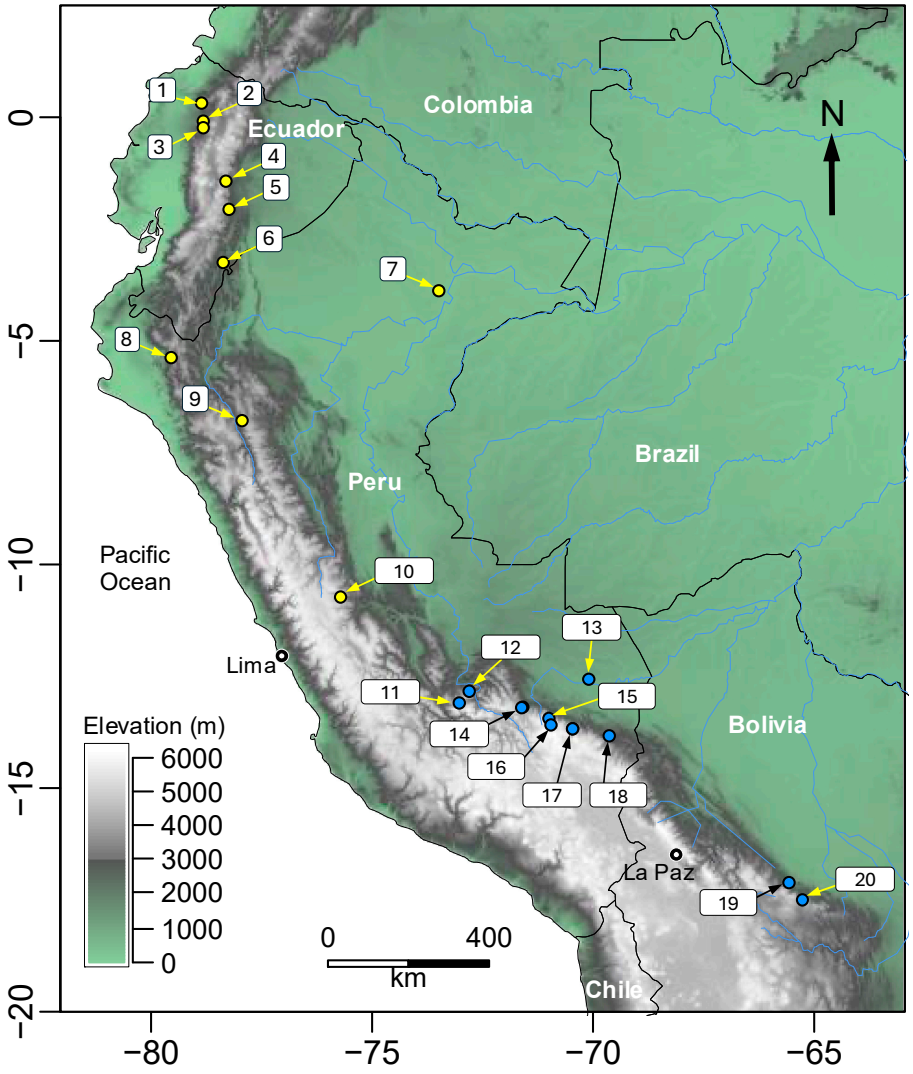

Figure 4. Map of northwestern South America showing the location of the type localities of species in the genera *Phyllonastes* (yellow dots) and *Noblella* (blue dots). (1 = *Phyllonastes worleyae*, 2 = *Phyllonastes mindo*, 3 = *Phyllonastes coloma*, 4 = *Phyllonastes naturetrekii*, 5 = *Phyllonastes personina*, 6 = *Phyllonastes lochites*, 7 = *Phyllonastes myrmecoides*, 8 = *Phyllonastes heyeri*, 9 = *Phyllonastes lynchi*, 10 = *Phyllonastes duellmani*, 11 = *Noblella vilcabambensis*, 12 = *Noblella madreselva*, 13 = *Noblella losamigos*, 14 = *Noblella pygmaea* and *Noblella usurpator*, 15 = *Noblella chirihampatu*, 16 = *Noblella bagrecito*, 17 = *Noblella glauca* and *Noblella thiuni*, 18 = *Noblella peruviana*, 19 = *Noblella ritarasquinae*, 20 = *Noblella carrascoicola*.

According to several authors [4,12,35,37], the genus *Noblella* can be recognized by a combination of morphological characters, including a differentiated tympanic membrane (except in *N. madreselva* [46]); head narrower than body; cranial crests absent; dentigerous processes of vomers absent; Finger I shorter than, or equal in length to, Finger II; Toe III shorter than Toe V; tips of at least Toes III–IV pointed; subarticular tubercles not protruding; conspicuous tarsal tubercle; dark inguinal spots; small body size (SVL < 22 mm). However, some characters are ambiguous (e.g., terminal discs on fingers and toes not expanded or slightly expanded; discs and circumferential grooves present distally; terminal phalanges narrowly T-shaped). Moreover, most of these characters are present in species of *Phyllonastes*.

Further research on osteological, morphological, and life-history traits will help elucidate true synapomorphies in each genus. For example, only some species of *Noblella* (*N. chirihampatu*, *N. bagrecito,* and *N. usurpator*) bear a tarsal tubercle, varying in size and shape from large, elongate, and oblique (*N. usurpator*; [12]) to small and sickle-shaped (*N. bagrecito*; [12]). In contrast, members of *Microkayla* lack a tarsal tubercle [10]. Osteological studies will likely reveal important diagnostic and evolutionary informative traits in the future, and we recommend the use of computed tomography to examine osteological features in specimens of these minute and fragile frogs. Additional fieldwork is also needed to characterize the advertisement calls of *Noblella* species. For example, preliminary analyses suggest that the advertisement call of *N. pygmaea* has 6–8 notes, whereas the call of *N. usurpator* typically has 20–30 notes (A. Catenazzi, personal observation); the call of *N. glauca* has 26 notes [29]. Similar bioacoustic data from other localities will allow us to determine key differences between co-occurring species.

In light of our results, the geographic distribution of *Phyllonastes myrmecoides* needs to be updated. The currently available map includes a large region of lowland and montane forests in five countries [47]. However, it is likely that *P. myrmecoides* is restricted to a smaller region in northern Peru and Ecuador.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16100613/s1, Figure S1: Maximum likelihood (ML) phylogeny based on a 2546-bp concatenated dataset (fragments of genes 16S, 12S, COI, RAG1, and Tyr); Figure S2: Photographs of live specimens of (A) *Phyllonastes myrmecoides* (B) *Phyllonastes* cf. *lynchi*; (C) *Noblella usurpator*; (D) *Noblella losamigos*; Table S1: GenBank accession numbers for the taxa sampled in this study.

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Appendix A

Note about species names associated with GenBank sequences. GenBank sequence with accession number EF493714 represents *Noblella usurpator*. This sequence was originally published as *Phrynopus peruvianus* on GenBank (Hedges et al. [4]). Some researchers erroneously used it as representative of *Noblella peruviana* in their analysis (e.g., EF493714. *Noblella peruviana* 12S and 16S sequences). De la Riva et al. [17] confirmed that it belongs to *Noblella usurpator*.

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Supplementary files

Table S1. Genbank accession numbers for the taxa sampled in this study. Museum collection abbreviations: CORBIDI – Centro para Ornitología y Biodiversidad, Lima; CBF – Colección Boliviana de Fauna; KU – Kansas University, Lawrence; LSUMZ – Louisiana Museum of Natural History, Baton Rouge; MNCN – Museo Nacional de Ciencias Naturales, Madrid; MNRJ – Museu Nacional, Rio de Janeiro; MUBI – Museo de Biodiversidad del Perú, Cusco; MUSA – Museo de Historia Natural, Universidad Nacional de San Agustín de Arequipa, Arequipa; MUSM – Museo de Historia Natural de la Universidad de San Marcos, Lima. Field collection abbreviations: AC – Alessandro Catenazzi Field Series; CFBHT – Celio F. B. Haddad Field Series; RvM – Rudolf von May Field Series. Genbank accession numbers of the new sequences are highlighted in bold font.

Taxon	**Voucher_Nbr**	**16S**	**12S**	**COI**	**RAG1**	**Tyr**
Bahius bilineatus	MNRJ46476	JX267324	JX267393	–	JX267556	JX267691
Barycholos pulcher	KU217781	EU186709	–	–	–	EU186765
Barycholos ternetzi	CFBH19426	JX267466	–	–	JX267543	JX267680
Barycholos ternetzi	CFBH306	DQ283094	–	–	–	DQ282921
Bryophryne bakersfield	MHNC6009	KT276288	KT276284	–	KT276278	–
Bryophryne bakersfield	MHNC6022	KT276287	KT276281	–	KT276276	–
Bryophryne bustamantei	MUSM24537	MT437052	–	–	MT431911	–
Bryophryne bustamantei	MUSM24538	CMT437053	–	–	MT431912	–
Bryophryne cf. zonalis	CORBIDI_17475	MT437054	–	MT435518	–	–
Bryophryne cophites	AC270_07	KY652641	–	KY672976	KY672961	KY681062
Bryophryne cophites	KU173497	EF493537	EF493537	–	EF493423	EF493508
Bryophryne hanssaueri	MUSM27567	KY652642	–	KY672977	KY681084	KY681063
Bryophryne nubilosus	MUSM27882	KY652643	–	KY672978	KY681085	KY681064
Bryophryne phuyuhampatu	CORBIDI 18224	MF419254	–	–	–	–
Bryophryne phuyuhampatu	CORBIDI_18226	MF419256	–	–	–	–
Bryophryne phuyuhampatu	MUBI 14654	MF419259	–	–	–	–
Bryophryne quellokunka	MNCN43780	MF186387	MF186309	–	MF186526	–
Bryophryne quellokunka	MUSM27571	MT437061	–	–	–	–
Bryophryne sp	AC41_09	MT437063	–	–	MT431917	–
Bryophryne sp	MUSM27961	MT437062	–	–	MT431916	–
Bryophryne tocra	MNCN43786	MF186396	–	–	–	–
Bryophryne zonalis	MUSM27939	MT437064	–	–	**PQ374242**	–
Euparkerella brasiliensis	na	JX267468	JX267390	–	JX267545	JX267682
Holoaden bradei	USNM207945	EF493366	EF493378	–	EF493449	EU186779
Holoaden luederwaldti	CFBH19552	JX267470	–	–	JX267549	–

Holoaden luederwaldti	MZUSP131872	EU186710	EU186728	–	EU186747	EU186768
Lynchius flavomaculatus	KU218210	EU186667	EU186667	–	EU186745	EU186766
Lynchius nebulanastes	KU181408	EU186704	EU186704	–	–	–
Lynchius oblitus	MHNC8614	KX470783	KX470776	–	KX470792	KX470799
Lynchius oblitus	MHSNM19914	AM039640	AM039708	–	–	–
Lynchius oblitus	MTD45954	AM039639	AM039707	–	–	–
Lynchius parkeri	KU181307	EU186705	EU186705	–	–	–
Lynchius simmonsi	QZ41639	JF810004	JF809940	–	JF809915	JF809894
Microkayla adenopleura	MNCN44809	MF186339	–	–	–	–
Microkayla adenopleura	MNCN44810	MF186340	MF186283	–	MF186537	MF186565
Microkayla boettgeri	MUBI5363	MF186353	MF186294	–	–	MF186559
Microkayla boettgeri	MUBI5364	MF186354	–	–	–	–
Microkayla cf. iatamasi	MNCN-DNA 20927	MF186365	–	–	–	–
Microkayla chacaltaya	MNCN42052	MF186357	–	–	MF186532	–
Microkayla chapi	MNCN43762	MF186417	MF186328	–	MF186540	MF186562
Microkayla chilina	MNCN43772	MF186414	MF186327	MF186457	MF186539	MF186561
Microkayla chilina	MUBI5350	MF186411	–	–	–	–
Microkayla condoriri	CBF5988	MF186358	–	–	–	–
Microkayla guillei	AMNH A165108	AY843720	AY843720	–	–	DQ282995
Microkayla iatamasi	MTD_TD_1231	AM039644	AM039712	–	–	–
Microkayla illampu	CBF5999	MF186373	–	–	–	–
Microkayla kallawaya	MNCN42509	MF186379	–	–	–	–
Microkayla katantika	CBF6012	MF186380	–	MF186453	–	–
Microkayla kempffi	MNCN43646	MF186384	–	–	–	–
Microkayla quimsacruzis	MNCN42039	MF186407	–	–	–	–
Microkayla saltator	MTD_TD_1229	AM039642	AM039710	–	–	–
Microkayla sp. Coscapa	CBF6564	MF186399	–	–	–	–
Microkayla sp. Khatu River	MNCN 42034	MF186409	–	–	–	–
Microkayla teqta	MNCN 45702	MF186400	MF186318	–	–	MF186552
Microkayla teqta	MNCN 45703	MF186401	MF186319	–	–	MF186557
Microkayla utururo	MNCN 46987	MF186433	–	–	–	–
Microkayla wettsteini	CBF 6241	MF186434	MF186338	–	MF186531	MF186551
Microkayla wettsteini	KU 183049	EU186696	EU186696	–	EU186755	EU186776
Niceforonia brunnea	KU 178258	EF493357	EF493357	–	EF493422	EF493484

Niceforonia dolops	na	EF493394	EF493394	–	EF493414	EF493483
Noblella coloma	QCAZ 32702	MT710931	–	–	–	–
Noblella coloma	QCAZ 40579	MT710932	–	–	–	–
Noblella heyeri	QCAZ 31471	JX267541	JX267463	–	–	–
Noblella lochites	KU 177356	EU186699	EU186699	–	EU186756	EU186777
Noblella losamigos	MUBI 17413	MN056358	–	MN356098	–	–
Noblella losamigos	MUSA 6302	MN100040	–	–	**PQ374244**	–
Noblella losamigos	MUSA 6973	KY652644	–	–	KY672962	KY681065
Noblella losamigos	MVZ 292687	MN366392	–	MN356099	–	–
Noblella losamigos	RvM 4_12	**PQ362290**	–	–	–	–
Noblella lynchi	MUSA 3846	**PQ362307**	–	–	**PQ374257**	–
Noblella lynchi	MUSA 3855	**PQ362308**	–	–	**PQ374258**	–
Noblella madreselva	CORBIDI 15769	MN064565	–	–	MN355547	–
Noblella madreselva	CORBIDI 15770	MN056356	–	–	–	–
Noblella mindo	ZSFQ 050	OM200087	–	–	–	–
Noblella mindo	ZSFQ 051	OM200088	–	–	–	–
Noblella myrmecoides	CORBIDI PV45	MN056357	–	–	–	–
Noblella myrmecoides	MUSA 7336	**PQ362309**	–	–	**PQ374259**	–
Noblella myrmecoides	QCAZ 40180	JX267542	JX267464	–	–	–
Noblella naturetrekii	QCAZ 71337	MK838462	MK838467	–	–	–
Noblella personina	QCAZ 58818	MK838465	MK838468	–	MN068028	–
Noblella peruviana	CORBIDI 17479	**PQ362291**	–	–	–	–
Noblella peruviana	CORBIDI 17480	**PQ362292**	–	**PQ359786**	**PQ374245**	–
Noblella peruviana	CORBIDI 17481	**PQ362293**	–	**PQ359787**	–	–
Noblella peruviana	CORBIDI 17510	**PQ362294**	–	**PQ359788**	**PQ374246**	–
Noblella peruviana	CORBIDI 18700	**PQ362295**	–	**PQ359789**	**PQ374247**	**PQ374260**
Noblella peruviana	CORBIDI 18733	**PQ362296**	–	**PQ359790**	–	–
Noblella peruviana	CORBIDI 18734	**PQ362297**	–	**PQ359791**	–	–
Noblella peruviana	MUBI 19037	**PQ362298**	–	**PQ359792**	**PQ374248**	–
Noblella pygmaea	MUSM 24535	**PQ362299**	–	–	**PQ374249**	–
Noblella pygmaea	MUSM 24536	KY652645	–	KY672979	KY681086	KY681066
Noblella sp.	AC278_07	**PQ362300**	–	–	**PQ374250**	**PQ374261**
Noblella sp.	CORBIDI 17509	**PQ362301**	–	–	**PQ374251**	**PQ374262**
Noblella sp.	CORBIDI 18701	**PQ362302**	–	**PQ359793**	**PQ374252**	**PQ374263**
Noblella sp.	MTD 45180	AM039646	AM039714	–	–	–

Noblella sp.	MUBI 19038	**PQ362303**	–	**PQ359794**	**PQ374253**	–
Noblella sp.	MUSM 27576	**PQ362304**	–	–	**PQ374254**	**PQ374264**
Noblella sp. R	MUSM 27582	KY652646	–	KY672980	KY681087	KY681067
Noblella thiuni	CORBIDI 18723	MK072732	–	**PQ359795**	–	–
Noblella worleyae	ZSFQ 2502	MT710933	–	–	–	–
Noblella worleyae	ZSFQ 550	MT710934	–	–	–	–
Noblella worleyae	ZSFQ 551	MT710935	–	–	–	–
Oreobates amarakaeri	MHNC 6975	JF809996	JF809934	–	JF809913	JF809891
Oreobates ayacucho	MNCN IDlR 5024	JF809970	JF809933	–	JF809912	JF809890
Oreobates cruralis	KU 215462	EU186666	EU186666	–	EU186743	EU186764
Oreobates gemcare	MHNC 6687	JF809960	JF809930	–	JF809909	–
Oreobates granulosus	MHNC 3396	EU368897	JF809929	–	JF809908	JF809887
Phrynopus auriculatus	KU 291634	EF493708	EF493708	–	–	–
Phrynopus barthlenae	SMF 81720	AM039653	AM039721	–	–	–
Phrynopus bracki	USNM 286919	EF493709	EF493709	–	EF493421	–
Phrynopus bufoides	MHNSM 19860	AM039645	AM039713	–	–	–
Phrynopus heimorum	MTD 45621	AM039635	AM039703	MF186462	MF186545	MF186580
Phrynopus heimorum	MTD 45622	AM039636	AM039704	–	–	–
Phrynopus horstpauli	MTD 44333	AM039651	AM039719	–	–	–
Phrynopus horstpauli	MTD 44334	AM039647	AM039715	–	–	–
Phrynopus inti	MUSM 31968	MF651902	MF651909	–	MF651917	–
Phrynopus kauneorum	MHNSM 20595	AM039655	AM039723	–	–	–
Phrynopus kauneorum	MTD 44332	AM039650	AM039718	–	–	–
Phrynopus peruanus	MUSM 38316	MG896582	MG896605	MG896615	MG896626	MG896631
Phrynopus pesantesi	MTD 45072	AM039656	AM039724	–	–	–
Phrynopus spI	MUSM 33261	MG896589	MG896606	–	MG896629	–
Phrynopus tautzorum	MHNSM 20613	AM039652	AM039720	–	–	–
Phrynopus tribulosus	KU 291630	EU186725	EU186707	–	–	–
Pristimantis attenboroughi	MUSM 31186	KY594752	–	KY962779	KY962759	–
Pristimantis humboldti	MUSM 31194	KY962798	–	KY962791	KY962775	–
Pristimantis pluvialis	CORBIDI 11862	KX155577	–	–	KY962769	–
Pristimantis reichlei	MHNSM 9267	EF493707	EF493707	–	EF493436	–
Pristimantis stictogaster	KU 291659	EF493704	EF493704	–	EF493445	–
Psychrophrynella bagrecito	CORBIDI 17482	**PQ362282**	–	–	–	–

Psychrophrynella bagrecito	CORBIDI 17483	**PQ362283**	–	**PQ359796**	–	–
Psychrophrynella bagrecito	CORBIDI 17525	**PQ362284**	–	**PQ359797**	–	–
Psychrophrynella bagrecito	CORBIDI 17526	**PQ362285**	–	–	–	–
Psychrophrynella bagrecito	CORBIDI 17527	**PQ362286**	–	–	–	–
Psychrophrynella bagrecito	CORBIDI 17528	**PQ362287**	–	**PQ359798**	–	–
Psychrophrynella bagrecito	MUBI 19040	**PQ362288**	–	–	–	–
Psychrophrynella bagrecito	MUBI 19041	**PQ362289**	–	–	–	–
Psychrophrynella chirihampatu	CORBIDI 16495	KU884559	–	–	–	–
Psychrophrynella chirihampatu	MHNC 14664	KU884560	–	**PQ359799**	**PQ374243**	–
Psychrophrynella glauca	CORBIDI 18729	MG837565	–	**PQ359800**	–	–
Psychrophrynella glauca	CORBIDI 18730	MG837566	–	**PQ359801**	–	–
Psychrophrynella sp.	MTD 47488	MT437066	–	–	–	–
Psychrophrynella sp. P	AC116_09	KY652660	–	KY672992	KY681089	KY681081
Psychrophrynella sp. P	AC138_09	**PQ362305**	–	–	**PQ374255**	–
Psychrophrynella sp. R	AC148_07	KY652661	–	KY672993	KY681090	KY681082
Psychrophrynella sp. R	MUSM 27584	**PQ362306**	–	–	**PQ374256**	–
Psychrophrynella usurpator	AC186_09	KY652662	–	KY672994	KY672975	KY681083
Psychrophrynella usurpator	KU173495	EF493714	EF493714	–	EU186762	EU186780
Psychrophrynella vilcabambensis	MUSM 27619	MT437065	–	–	–	–
Qosqophryne flammiventris	MTD 46890	MT437055	–	–	–	–
Qosqophryne flammiventris	MUSM 27615	MT437056	–	–	MT431913	–
Qosqophryne gymnotis	MUSM 24543	MT437058	–	–	MT431915	–
Qosqophryne gymnotis	MUSM 24546	MT437057	–	–	MT431914	–
Qosqophryne mancoinca	MUBI 16068	MT437059	–	MT435519	–	–
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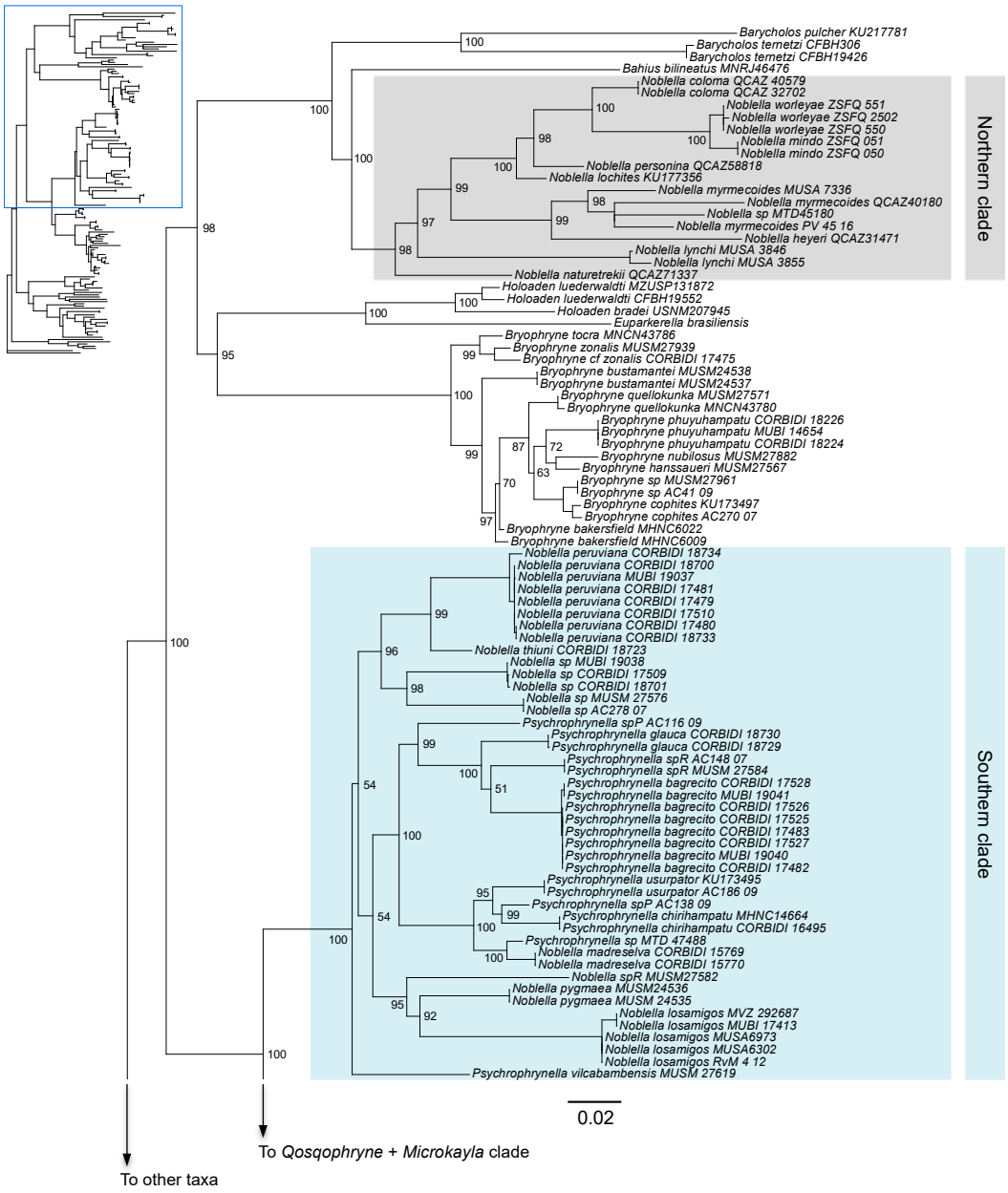
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Noblella worleyae ZSFQ 551
Noblella worleyae ZSFQ 2502
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Noblella mindo ZSFQ 051
Noblella mindo ZSFQ 050
Noblella personina QCAZ58818
Noblella lochites KU177356
Noblella myrmecoides MUSA 7336
Noblella myrmecoides QCAZ40180
Noblella sp MTD45180
Noblella myrmecoides PV 45 16
Noblella heyeri QCAZ31471
Noblella lynchi MUSA 3846
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Bryophryne tocra MNCN43786
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Bryophryne sp AC41 09
Bryophryne cophites KU173497
Bryophryne cophites AC270 07
Bryophryne bakersfield MHNC6022
Bryophryne bakersfield MHNC6009
Noblella peruviana CORBIDI 18734
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Noblella sp MUBI 19038
Noblella sp CORBIDI 17509
Noblella sp CORBIDI 18701
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Psychrophrynella spP AC116 09
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Psychrophrynella glauca CORBIDI 18729
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Psychrophrynella sp MTD 47488
Noblella madreselva CORBIDI 15769
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Noblella spR MUSM27582
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Noblella losamigos MVZ 292687
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Noblella losamigos MUSA6302
Noblella losamigos RvM 4 12
Psychrophrynella vilcabambensis MUSM 27619
Northern clade
Southern clade
0.02
To other taxa
To Qosqophryne + Microkayla clade

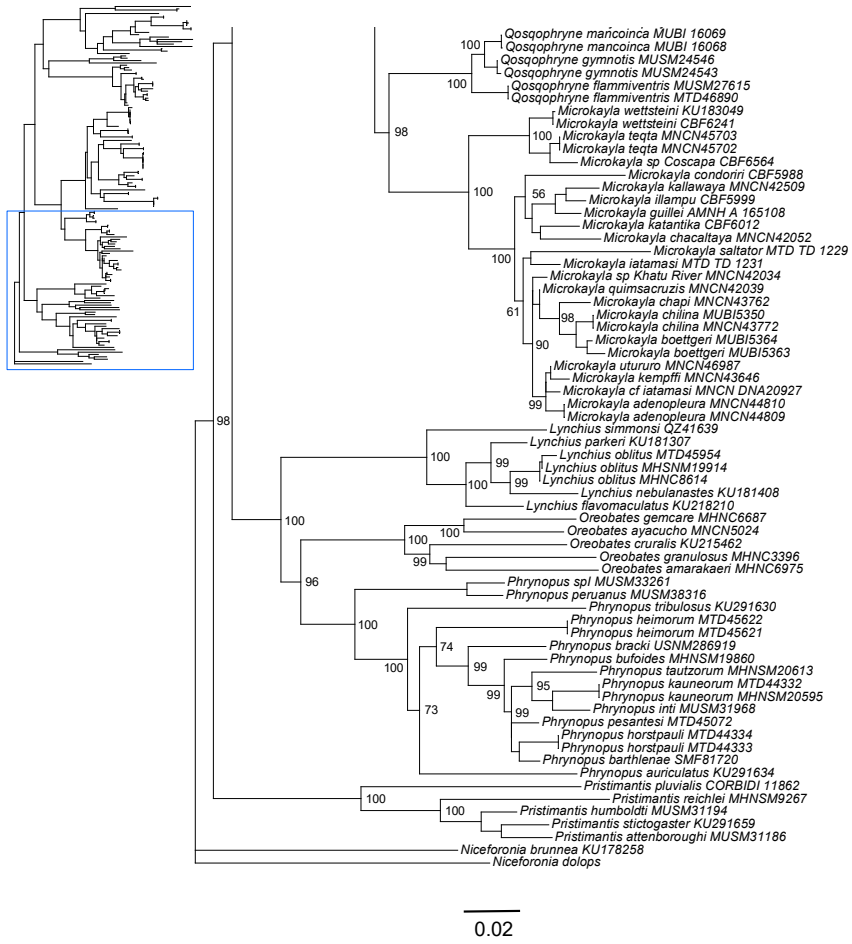

Figure S1. Top: Maximum likelihood (ML) phylogeny based on a 2546-bp concatenated dataset (fragments of genes 16S, 12S, COI, RAG1, and Tyr). ML values are indicated at each node. The area in gray indicates a clade with species distributed in northern Peru and Ecuador ("northern clade"), and the area in light blue indicates a clade with species distributed in southern Peru ("southern clade" containing the type species *Noblella peruviana*). Bottom: Part of the consensus Bayesian phylogeny showing closely related clades *Qosqophryne* and *Microkayla*, and more distantly related clades including *Lynchius*, *Oreobates*, and *Phrynopus*.

Figure S2. Photographs of live specimens of (A) *Phyllonastes myrmecoides*, Datem del Marañon, Loreto (adult male, MUSA 7333); (B) *Phyllonastes cf. lynchi*, Bongara, Amazonas (adult female, MUSA 3857); (C) *Noblella usurpator*, Paucartambo, Cusco (adult female, RvM 41.13); (D) *Noblella losamigos*, Manu, Madre de Dios (adult male, MUSM 37357, paratype).