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Molecular Phylogenetics and Taxonomy of the Andean Genus *Lynchius* Hedges, Duellman, and Heinicke 2008 (Anura: Craugastoridae)

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ABSTRACT: We infer species relationships within *Lynchius*, a frog genus with four species distributed along the paramos and cloud forests of the Andes of northern Peru and southern Ecuador, and assess species diversity in light of comparative analyses of anatomical traits and inferred relationships. Phylogenetic analyses rely on ~7000 base pairs of mtDNA and nuDNA sequences aligned using similarity-alignment and tree-alignment and optimized under maximum likelihood and parsimony criteria. Inferred relationships place *Lynchius* as the sister group of the widespread genus *Oreobates* and this clade as the sister group of the high Andean genus *Phrynopus*. Our analyses corroborate the dissimilar species *Lynchius simmonsii* as part of this clade and place it as the sister group of the remaining species of *Lynchius*. Parsimony and maximum likelihood analyses differ in the internal relationships of *Lynchius* with respect to the placement of *L. flavomaculatus*, *L. nebulanastes*, and *L. parkeri*, but support the existence of two unnamed species. External morphological comparisons provide diagnostic characters for the two new species, which are named and described herein. *Lynchius tabaconas* is sister to *L. flavomaculatus* and occurs at ~2800 m in the cloud forests of Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru. *Lynchius oblitus* occurs in the same area but at a higher elevation (~3300 m) and is sister to a clade formed by *L. flavomaculatus* and *L. tabaconas* in parsimony analyses and to *L. nebulanastes* in maximum likelihood analyses. We provide a new diagnosis for each of the six species and for the genus, as well as some natural history notes.

Key words: Brachycephaloidea; *Lynchius oblitus* sp. nov.; *Lynchius tabaconas* sp. nov.; *Oreobates*; Paramo; *Phrynopus*; Terrarana

THE WET and cold grasslands and elfin forests of the high Andes have been traditionally considered poor in frog diversity. Recent surveys in northern Bolivia and in Peru have nonetheless unraveled unexpected levels of new species of terraranan frogs in different lineages (e.g., De la Riva 2007; Lehr and Catenazzi 2009; Lehr et al. 2012; Chaparro et al. 2015). Albeit these high-elevation lineages have been historically considered part of the genus *Phrynopus* (Lynch 1975), molecular data reveal a contrasting scenario where they have independent origins (Heinicke et al. 2007; Hedges et al. 2008; Padial et al. 2014). According to inferred relationships, species from Bolivia and southern Peru have been placed in the genera *Bryophryne*, *Noblella*, and *Psychrophrynella*, the radiation in the Andes of central Peru retained the name *Phrynopus*, and the genus *Lynchius*—target of this study—was erected to include three species distributed along the paramos and elfin forests of the Cordillera Oriental in southern Ecuador and Cordillera de Huancabamba in northern Peru (Hedges et al. 2008).

Along the Cordillera de Huancabamba in northern Peru and the southern parts of the Cordillera Oriental of Ecuador the western slopes are mostly dry and covered by chaparral-like forest, while the summit and Amazonian versant are moist and covered with dense vegetation. Above ~2000 m elevation on the eastern versant, dense cloud forests and bush-like elfin forests and paramos gradually replace montane forests. *Lynchius flavomaculatus*, the first species

of *Lynchius* discovered, was found in the cloud forests and paramos of a locality 15 km east of Loja (Ecuador; Parker 1938). This locality is now part of the Podocarpus National Park, but this species is currently known to occur farther north and south within Ecuador. *Lynchius nebulanastes* (Cannatella 1984) and *L. parkeri* (Lynch 1975) were found in paramos and cloud forests, even in syntopy, but farther south, along one of the westernmost ridges of the Peruvian Cordillera de Huancabamba. An unnamed species is also known to occur in northern Peru (Lehr 2005; Hedges et al. 2008; Padial et al. 2014) in the paramos and elfin forests of an area intermediate between the southern distribution of *L. nebulanastes* and *L. parkeri* and the northern distribution of *L. flavomaculatus*. A fourth, and morphologically dissimilar species, *L. simmonsii* (Lynch 1974), was recently inferred as the sister group of *Lynchius* and is now considered part of this genus (Padial et al. 2012, 2014). In contrast to the other species of *Lynchius*, *L. simmonsii* occurs at lower elevations (~1800 m) along the cloud forests of the Cordillera del Cóndor, in Ecuador, on the easternmost ridges of the Amazonian versant of the Andes.

Lynchius remains a poorly known Andean clade and, although its phylogenetic relationships and osteology have been studied in some detail (e.g., Lynch 1975; Duellman and Lehr 2009; Padial et al. 2014), several aspects of its systematics and natural history remain scarcely studied. For example, morphological variation within this clade is poorly understood because species were described independently and comparisons were made within a now obsolete phylogenetic framework (e.g., species of *Lynchius* were

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thought to be part of *Phrynopus*, *Ischnocnema*, and *Oreobates*). After the inference of *L. simmonsii* as part of this clade, the patterns of distribution and morphological variation within the clade of *Lynchiuss* changed considerably. Furthermore, the phylogenetic relationships of *Lynchiuss* remain contentious. Molecular phylogenetic analyses have placed *Lynchiuss* as either the sister group of *Phrynopus* (Padial et al. 2009), *Oreobates* (Hedges et al. 2008; Padial et al. 2014), or *Oreobates* and *Phrynopus* (Padial et al. 2012).

In addition to the undescribed species from northern Peru mentioned above, recent fieldwork in this region and in southern Ecuador by some of the authors of this study revealed the existence of another unnamed species of *Lynchiuss* and provided additional material for comparison and more rigorous phylogenetic analyses. Here, we present the results of our analyses of the external morphology of all available specimens and phylogenetic analyses of a matrix composed of mtDNA genes (12S, 16S and intervening genes, cytb) and nuDNA genes (28S c-myc, H3, POMC, Rag, Rho, SIA, and Tyr). Our analyses support the existence of the two aforementioned new species, which are named and described herein. Furthermore, we provide an overview of species diversity, current understanding of morphological variation within species, phylogenetic relationships for the group, and some new natural history notes.

MATERIALS AND METHODS

Morphology

The study of the morphology is based on external qualitative and quantitative traits. Terminology for morphological characters used in the diagnosis and descriptions follows Duellman and Lehr (2009). For morphometrics, the measurements were taken with a digital caliper to the nearest 0.01 mm, but to avoid pseudo-precision, all measurements were rounded to one decimal place. All measurements were taken by the senior author, except for *Lynchiuss simmonsii*. Measurements of the holotype of *L. simmonsii* were taken by J. Padial, while QCAZ vouchers were measured by J. Guayasamin. Abbreviations for measurements are as follows: snout-vent length (SVL); head length (HL; from posterior margin of lower jaw to tip of snout); head width (HW; measured at level of rictus); eye length (EL; measured horizontally); eye-to-nostril distance (EN); internarial distance (IND); eye-to-eye distance (EE; measured at the anterior margins of eyes); tympanic membrane height (TyH); tympanic membrane length (TyL); width of disc of Finger III (F3); width of disc of Finger IV (F4); arm length (FA; from posterior margin of thenar tubercle to elbow); tibia length (TL); thigh length (TH; from vent to knee); foot length (FL; from proximal border of inner metatarsal tubercle to tip of fourth toe); width of disc of Toe IV (T4). Values of interorbital distance and upper eyelid width were not included because of the imprecise landmarks of the structures involved, especially in poorly preserved specimens.

Descriptions of color patterns in life are based on field notes and color digital photographs. Sex and maturity were determined by dissection and direct examination of gonads or by observation of secondary sexual characters. Comparisons of external character states were based both on original

descriptions and examination of museum specimens. Types of all species of *Lynchiuss* were examined.

Specimens collected were photographed alive, euthanized with Lidocaine, fixed in 10% formalin, and preserved in 70% ethanol. Coordinates were obtained by means of a Garmin PSMAP 62sc Handheld Navigator Global Positioning System and further assessments for geographical data and elevation were performed in Google Earth. All geographic coordinates are based on geodetic datum WGS84.

Museum acronyms are those cited by Frost (2016), except that MHNC refers to Museo de Historia Natural de Cusco, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru (MHNCP in Frost 2016). Specimens examined are listed in Appendix I.

Molecular Phylogenetics

Taxon and character sampling.—In order to rigorously test the phylogenetic position and monophyly of *Lynchiuss*, we broadly sampled the holoadenine genera *Oreobates* (22 spp.) and *Phrynopus* (11 spp.), because these are the two genera that have been found most closely related to *Lynchiuss* in all previous phylogenetic analyses (Hedges et al. 2008; Pyron and Wiens 2011; Padial et al. 2012, 2014). We also sampled other genera of Holoadeninae (Padial et al. 2014) by including representative species of *Barycholos* (2 spp.), *Bryophryne* (1 spp.), *Euparkerella* (1 spp.), *Holoaden* (2 spp.), *Hypodactylus* (2 spp.), *Noblella* (3 spp.), and *Psychrophrynella* (3 spp.). Ingroup sampling includes four terminals representing all four nominal species of *Lynchiuss*, plus eight terminals that were not part of any nominal species. *Haddadus binotatus*, a distant Craugastorid of the Craugastorinae (Padial et al. 2014), was used to root the trees.

Our matrix includes legacy (GenBank) and newly produced sequences for 16 genes. Noncoding mtDNA genes include rRNA genes of the heavy strand transcription unit 1 fragment (12S, 16S and the intervening tRNA^{valine}, and tRNA^{leucine} segments). Protein-coding mtDNA genes include cytochrome b (cytb). Nuclear protein-coding genes include two exons of cellular myelocytomatosis (c-myc), histone H3 (HH3), propiomelanocortin A (POMC), recombinase-activating protein 1 (RAG1), rhodopsin (Rhod), seven-in-absentia (SIA), and tyrosinase precursor (Tyr). Noncoding nuclear genes include 28S. Sequences for 12S, 16S, tRNA^{valine}, tRNA^{leucine}, POMC, RAG, and TYR genes were newly produced for this study. Specimen voucher numbers and locality data for sequences produced in this study are listed in Table 1. Accession numbers for all sequences used in this study are listed in Appendix II.

DNA amplification and sequencing.—Genomic DNA was extracted from ethanol-preserved tissues using standard phenol-chloroform extraction protocols. The standard polymerase chain reaction (PCR) amplification protocol was as follows: 95°C/15 s; 35 cycles of 95°C/30 s, 50°C/30 s, 72°C/1 min; and 72°C/10 min. Cycle sequencing reactions were completed using the corresponding PCR primers (Table 2) and BigDye Terminator 3.1 chemistry (Applied Biosciences), with a standard cycle sequencing profile (96°C/3 min; 35 cycles of 96°C/10 s, 50°C/15 s, 60°C/3 min; and 72°C/7 min). PCR products were visualized in agarose gels, and unincorporated primers and dNTPs were removed from PCR products using ExoSap purification (ExoSap-it, GE Health-

TABLE 1.—Sequences of *Lynchius* produced in this study. All voucher specimens are from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru (5°13'45.5"S, 79°17'13.2"W).

	Voucher (MHNC)	DNA collection (MNCN-DNA)	GenBank				
			12S	16S	POMC	RAG	TYR
<i>Lynchius oblitus</i>	8614	48820	KX470776	KX470783	—	KX470792	KX470799
<i>Lynchius oblitus</i>	8652	48806	KX470775	KX470782	—	KX470791	KX470798
<i>Lynchius oblitus</i>	8674	48823	KX470777	KX470784	—	KX470793	KX470800
<i>Lynchius oblitus</i>	8676	48824	KX470778	KX470785	—	KX470794	KX470801
<i>Lynchius oblitus</i>	8677	48825	KX470779	KX470786	—	KX470795	KX470802
<i>Lynchius tabaconas</i>	8637	48795	KX470773	KX470780	KX470787	KX470789	KX470796
<i>Lynchius tabaconas</i>	8650	48804	KX470774	KX470781	KX470788	KX470790	KX470797

care). Double-stranded DNA was sequenced in Macrogen. Raw sequences complementary strands were compared to generate a consensus sequence for each DNA fragment using Geneious v7.0 (Biomatters Ltd., New Zealand).

Phylogenetic Analyses

Parsimony analysis.—Sequences were first aligned in Program MAFFT (see below) and partitioned into fragments of equal length separated by conserved regions with no gaps and few or no nucleotide substitutions. This strategy generated putatively homologous fragments where length variation among DNA sequences was only due to insertions and/or deletions of nucleotides, a requisite for tree-alignment in Program POY (Wheeler et al. 2006). After the removal of gaps implied by MAFFT from sequence fragments, tree-alignment of unaligned sequences was performed under parsimony with equal weights for all classes of transformations using direct optimization (Wheeler 1996; Wheeler et al. 2006) and iterative pass optimization (Wheeler 2003) algorithms in POY 5.1.1 (Varón et al. 2010). Tree searches were first conducted using direct optimization under the command “search,” which implements an algorithm based on random addition sequence Wagner builds, subtree pruning and regrafting, and tree bisection and reconnection (TBR) branch swapping (see Goloboff 1996, 1999), parsimony ratcheting (Nixon 1999), and tree fusing (Goloboff 1999); then, consecutive rounds of searches are done within a specified run-time, storing the shortest trees of each independent run and performing a final round of tree-fusing on the pooled trees. The optimal tree found

during driven searches was swapped using iterative pass optimization (Wheeler 2003). Tree searches were carried out using the American Museum of Natural History's high performance computing cluster ENYO (a cluster of 33 Intel Xeon 3.0GHz dual-core, 128 dual-processors, L2 cache, 64-bit and 1TB shared storage, and 16GB RAM per node). We have observed that POY 4.1.2 or POY 5.1.1 does not always report all equally parsimonious trees when large data sets are analyzed; therefore, the optimal alignment resulting from iterative pass optimization was converted into a data matrix, and driven searches were conducted in Program TNT (Goloboff et al. 2008) until a stable strict consensus was reached at least three times (see below for details of driven searches in TNT). We calculated Goodman–Bremer values (Goodman et al. 1982; Bremer 1988; see Grant and Kluge 2008) for each supported clade in TNT using the optimal tree-alignment matrix and the parameters specified in the bremer.run macro (available with the software package at <http://www.zmuc.dk/public/phylogeny/tnt/>), which begins by searching for trees N steps longer than the optimum (10 random addition sequence Wagner builds and TBR swapping, saving 2 trees/replicate), using inverse constraints for each node of the most parsimonious tree. Swapping of each constrained search was limited to 20 min and constrained searches were repeated three times as specified in the default settings of the bremer.run macro. We also calculated parsimony jackknife frequencies (Farris et al. 1996) for each supported clade by resampling the tree-alignment matrix. We caution that, as in analyses of similarity-alignment matrices, the resulting clade frequencies are conditional on

TABLE 2.—Sequence primers used in this study.

Locus	Primer name and priming region (5'-3')	Source
16S	16Sar: CGCCTGTTTATCAAAAACAT 16Sbr: CCGGTCTGAACTCAGATCACGT	Hillis et al. (1996)
16S	16L19: AATACCTAACGAACCTTAGCGATAGCTGGTT 16H24: TACCTTCGCACGGTTAGKRTACCGCGGCCGT	Hedges et al. (2008)
16S	16S-JMP-F: CATGGTAAGTRTACCGGAAGGTG 16S-JMP-R: ACCAGCTATDACTAAGTTCC	This study
12S-tRNA _{phe}	12S-t-Phe-frog: ATAGCRCTGAARAYGCTRAGATG 12S-frogRa: TCRATTRYAGGACAGGCTCCTCTAG	Wiens et al. (2005)
12S-tRNA _{val}	12S-t-Val-frog: TGTAAGCGARAGGCTTTKGTTAAGCT 12S-frogFa: CAAACTRGATTAGATACCCYACTATG	Wiens et al. (2005)
cmcy	cmcy1U: GAGGACATCTGGAARAARTT cmcy3L: GTCTTCCTCTGTCTRTCTCYTC	Crawford (2003)
POMC	POMC-1: AATGTATYAAAGMMTGCAAGATGGWCCT POMC-2: TAYTGRCCCTTYTTGTGGCRRIT	Wiens et al. (2005)
RAG1	R182: GCCATAACTGCTGGAGCATYAT R270: AGYAGATGTTGCCTGGGTCTTC	Heinicke et al. (2007)
TYR	Tyr1C: GGCAGAGGAWCRTGCCAAGATGT Tyr1G: TGCTGGCGRCTCTCTCCARTCCCA	Bossuyt and Milinkovitch (2000)

this particular alignment and not the data themselves. Given that the tree-alignment matrix is derived from the optimal tree, the resulting clade frequencies are expected to be higher than would be obtained from matrices aligned according to different guide trees (e.g., a UPGMA or neighbor-joining tree, as in MAFFT and Clustal, respectively). We calculated jackknife frequencies from 1000 pseudo-replicates searches using driven searches (see below), gaps treated as fifth state, and removal probability of 0.36 ($\approx e^{-1}$), which purportedly renders jackknife and bootstrap values comparable (Farris et al. 1996).

Maximum likelihood.—Multiple sequence alignments for maximum-likelihood analyses were performed in MAFFT online v7 using the G-INS-i strategy, which is considered appropriate for alignments that consist of large numbers of sequences (Katoh et al. 2005; Katoh and Standley 2013). The G-INS-i strategy performs global alignment with a Fast Fourier Transform approximation progressively on a guide tree (modified UPGMA) followed by iterative edge refinement that evaluates the consistency between the multiple alignment and pairwise alignments. The iterative refinement is repeated until no improvement is observed in the weighted sum-of-pairs score or 1000 cycles are completed (maxiterate = 1000). We applied the default transition:transversion cost ratio of 1:2 but changed the gap opening penalty from 3 times substitutions to 1 time substitutions to avoid penalizing insertions and deletions more than we did in the parsimony analysis.

We used PartitionFinder v1.0.1 (Lanfear et al. 2012) to select the optimal partition scheme and substitution models for our data set under the Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC), and the Corrected Akaike Information Criterion (AIC_c). Compared partition schemes were (1) all data combined; (2) a 2-partition, mtDNA/nuDNA, scheme; (3) by locus (each partition corresponding to individual loci mentioned above); and, (4) by locus and codon position (for protein coding genes).

Adaptive maximum-likelihood tree searches and 1000 bootstrap replicates were performed using random-addition sequence replicates in GARLI v2.0 (Zwickl 2006) through the GARLI Web Server (Bazin et al. 2014). Gaps were treated as missing data (i.e., absence of evidence).

Uncorrected p-distances were estimated in Mega v4.0 (Tamura et al. 2007) for the aligned 16S fragment (1478 bp).

RESULTS

Morphology

The analysis of qualitative morphological characters of 350 specimens (Appendix I) supports the four currently recognized species of *Lynchi*: *L. flavomaculatus*, *L. nebulanastes*, *L. parkeri*, and *L. simmons*; and it further indicates the existence of two new species. A description of the conditions for the different characters for each species is provided in form of a new diagnosis below, and a summary of these is provided in form of a dichotomous key for rapid identification of species. Two new species are diagnosed, described, and named below. The addition of these two species along with the recent addition of *L. simmons* (Padial et al. 2012), further supported by our phylogenetic analyses, renders the current diagnosis of *Lynchi* (Hedges et al.

2008; Duellman and Lehr 2009) incomplete and we therefore provide a new one.

Phylogenetic Analyses

The final data set included 61 terminals. Parsimony tree searches identified an optimal tree of 11,274 steps that was visited 4693 times during 1441 rounds of build + TBR, 31,013 of fusing, and 825 of ratchet. A round of swapping under iterative pass optimization recovered a single tree of 11,222 steps and a tree-alignment of 7959 characters. Additional searches of the tree-alignment in TNT rendered 6 trees of the same length and 55 nodes each (strict consensus shown as Fig. 1A).

The optimal MAFFT similarity-alignment comprises 7145 character columns. The AIC, AIC_c, and BIC in Partition Finder identified the 2-partition (mtDNA/nuDNA) scheme with GTR + I + G substitution model for coding and noncoding mtDNA and TIM + I + G for nuDNA as the most optimal partition scheme (values for the different information criteria: AIC, 109085.32854; AIC_c, 109084.97898; BIC, 110820.623499). Under the selected partition scheme and substitution models, the best maximum likelihood was found once during 10 adaptive searches in GARLI (maximum likelihood score of the optimal tree = -54,289.266; Fig. 1B).

Parsimony and maximum likelihood character optimizations recover a monophyletic *Lynchi* as the sister group of *Oreobates*. These two monophyletic genera form the sister group of *Phrynop*. Within *Lynchi*, parsimony and maximum likelihood recover *L. simmons* as the sister group of the remaining species. Also, both analyses recover one of the new species (*L. tabaconas*) as the sister group of *L. flavomaculatus* (separated by uncorrected p-distances of 6.0%; Table 3). However, the position of *L. nebulanastes* and *L. parkeri* differ between the two analyses. Parsimony recovers *L. oblitus* as the sister group of *L. flavomaculatus* plus *L. tabaconas*, while it is the sister group of *L. parkeri* in maximum likelihood (separated by uncorrected p-distances of 9–10%; Table 3). Regardless of these discrepancies, both analyses support the monophyly of the two new species.

Within *Phrynop*, most relationships are identical between the two analyses, but differ with respect to the position of *P. auriculatus*, *P. heimorum*, and *P. tribulosus*. Several relationships also differ among species of *Oreobates*. *Oreobates ayacucho* is the sister species of *O. lehri*, *O. machiguenga*, and *O. gemcare* in parsimony, while it is sister to *O. lundbergi* and *O. pereger* in maximum likelihood. Also, *O. remotus* is the sister species of *O. berdemenos* in parsimony and of *O. crepitans* in maximum likelihood. *Oreobates heterodactylus* and *O. crepitans* are sister in parsimony, while *O. heterodactylus* is the sister species of *O. berdemenos* in maximum likelihood. Also, while *O. discoi*-*dalis* and *O. barituensis* are sister in parsimony, the latter is sister to *O. ibischi* in maximum likelihood.

Within the rest of outgroups there are differences in the position of *Bryophryne*, *Hypodactylus*, and *Psychrophrynel*-*la*. *Bryophryne* is recovered as the sister group of *Barycholos* and *Noblella* in parsimony, while it is sister to *Euparkerella* and *Holoaden* in maximum likelihood. *Hypodactylus* is recovered as paraphyletic near the root of the tree in maximum likelihood analyses, while it is recovered as the sister group of the clade that includes *Lynchi*, *Oreobates*, and *Phrynop* in parsimony analyses. *Psychrophrynel*-*la*

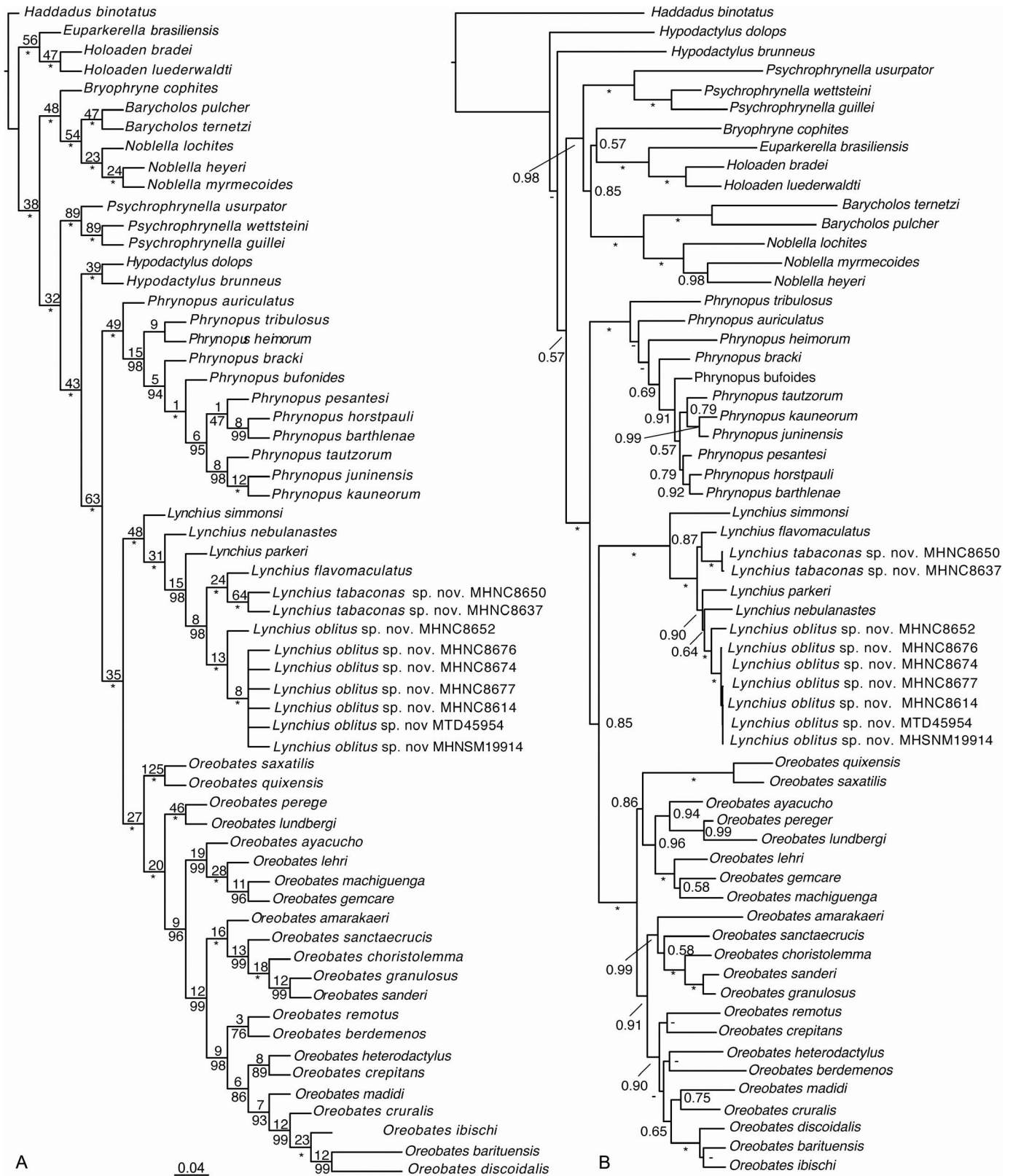


FIG. 1.—Phylogenetic trees resulting from the analysis of data sets of 7959 aligned bp (POY) and 7145 aligned bp (MAFFT) and composed of the mitochondrial genes 12S, 16S, the intervening tRNA^{val}, and tRNA^{leu} segments, a fragment of the coding mtDNA gene cytb, and fragments of the nuclear protein-coding genes c-myc (exons 2 and 3), POMC, RAG1, and Tyr. (A) Maximum parsimony optimal tree of 11,222 transformations depicting the relationships of species of *Lynchiidae* and other genera of Holodeninae. Numbers above ancestral branches indicate Goodman–Bremer values, and those under branches are Jackknife proportions (asterisks represent Jackknife values of 100%). (B) Maximum likelihood optimal tree (log likelihood = –54289.266) and bootstrap node values.

TABLE 3.—Uncorrected pairwise distances (%) for a fragment of the 16S gene compared among species of *Lynchi*.

	1	2	3	4	5	6	7
(1) <i>Lynchi</i> <i>tabaonas</i> MHNC8637							
(2) <i>Lynchi</i> <i>tabaonas</i> MHNC8650	0.1						
(3) <i>Lynchi</i> <i>oblitus</i> MHNC8652	8.4	8.3					
(4) <i>Lynchi</i> <i>oblitus</i> MHNC8614	7.0	7.0	4.8				
(5) <i>Lynchi</i> <i>oblitus</i> MHNC8677	6.9	7.0	4.4	0.6			
(6) <i>Lynchi</i> <i>flavomaculatus</i>	6.2	6.1	7.8	7.0	7.0		
(7) <i>Lynchi</i> <i>nebulanastes</i>	8.5	8.4	8.3	8.6	8.2	8.5	
(8) <i>Lynchi</i> <i>parkeri</i>	10.0	9.9	9.6	9.4	8.9	9.2	10.5

found as the sister group of a clade that includes *Hypodactylus*, *Lynchi*, *Óreobates*, and *Phrynopus* in parsimony, while it is sister to a clade that includes *Barycholos*, *Bryophryne*, *Euparkerella*, *Holoaden*, and *Noblella* in maximum likelihood. It is important to consider, however, that type species of the genera *Noblella* and *Psychrophrynella* have not yet been included in any molecular phylogenetic analysis and, therefore, the monophyly of these two genera remains to be tested.

SYSTEMATIC ACCOUNTS

Lynchi Hedges, Duellman and Heinicke 2008

Diagnosis.—The genus *Lynchi* includes species with the following characteristics: skin on dorsum of head, body, and limbs shagreen with few scattered tubercles, covered with uniform-sized spicule-like warts in *L. simmons*; occipital folds \wedge or V-shaped, when present; middorsal fold present; dorsolateral fold present or absent; venter smooth to areolate; discoidal fold present; tympanic membrane and annulus distinct or indistinct; supratympanic fold and postrictal tubercles present or absent; head as long as wide or slightly longer than wide; snout round to nearly truncate in dorsal view, and rounded or curved anteroventrally in lateral profile; canthus rostralis weakly concave in dorsal view; cranial crests present or absent; upper eyelid with or without small scattered tubercles; dentigerous process of the vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 2–8 teeth; males without nuptial pads, vocal slits present or absent; first finger as long as, shorter than, or longer than second; subarticular tubercles prominent, round or conical; supernumerary tubercles round, smaller than subarticular tubercles; tips of fingers narrowly round; pads, circumferential grooves, lateral fringes, and hand webbing usually absent (present on Fingers I and II in *L. flavomaculatus*); ulnar tubercle absent; palmar tubercle rounded or divided in two subunits; thenar tubercle prominent, elliptical; foot length 42–60% of SVL; Toe III longer than Toe V; tips of toes narrowly rounded, lacking pads and circumferential grooves; toe lateral fringes and webbing absent; inner metatarsal tubercle elongate, prominent; outer metatarsal tubercle round, prominent, slightly smaller than or about the same size as inner; heel and tarsal tubercles absent; frontoparietals with or without exostosis; vomers bearing a broad dentigerous process, widely separated from each other, and bearing a row of teeth. Reproduction by terrestrial eggs and direct-development.

Content.—*Lynchi* *flavomaculatus* (Parker 1938), *L. nebulanastes* (Cannatella 1984), *L. oblitus*, *L. parkeri* (Lynch 1975), *L. simmons* (Lynch 1974), and *L. tabaonas*.

Distribution.—Montane forests, cloud forests, and paramos of the Andes of Peru and Ecuador, along the Cordillera de Huancabamba, Cordillera del Cóndor, and Cordillera Oriental at elevations between 1800 m and 3300 m.

Lynchi *flavomaculatus* (Parker 1938)
(Figs. 2A–B)

Eleutherodactylus *flavomaculatus* Parker 1938

Niceforonia *flavomaculata*: Lynch 1969

Phrynopus *flavomaculatus*: Lynch 1975

Eleutherodactylus *flavomaculatus*: Lehr 2006

“*Eleutherodactylus*” *flavomaculatus*: Heinicke et al. 2007

Lynchi *flavomaculatus*: Hedges et al. 2008

Holotype.—BMNH 1947.2.16.11 (formerly 1935.11.3.16), adult female from 15 km East of Loja City, Ecuador, 3100 m, collected by C. Carrión (Figs. 2A–B).

Diagnosis.—A large *Lynchi* (adult females SVL = 34.6–44.2 mm, $n = 31$; adult males SVL = 24.0–35.2 mm, $n = 27$) characterized as follows: (1) skin on dorsum of head, body, and limbs shagreen, with few scattered tubercles that are more abundant posteriorly; occipital folds absent; middorsal fold complete or incomplete when present; dorsolateral folds absent; venter smooth to weakly areolate; groin smooth; discoidal and thoracic folds present; (2) tympanic membrane and annulus distinct, its diameter 42–53% of eye diameter; supratympanic fold low; postrictal tubercles present; (3) head as long as wide or slightly longer than wide (HW/HL = 0.9–1.0); snout round in dorsal and lateral views; canthus rostralis weakly concave in dorsal view; loreal region concave, sloping gradually toward the lips; lips not flared; (4) cranial crests present; upper eyelid covered by small scattered tubercles; (5) dentigerous process of vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 5–6 teeth; (6) males with vocal slits on each side of the tongue and no nuptial pads; (7) fingers long and slender, first finger as long as second; subarticular tubercles prominent, round; supernumerary tubercles round, smaller than subarticular tubercles; tips of fingers narrowly round; pads present in Fingers I and II; circumferential grooves, lateral fringes, and hand webbing absent; (8) ulnar tubercle absent; (9) palmar tubercle divided in two subunits, the inner subunit much larger than the outer; thenar tubercle prominent, elliptical; (10) foot length ~50% of SVL, lateral fringes and webbing absent; Toe III longer than Toe V; Toe III usually reaching the distal border of second subarticular tubercle of Toe IV, Toe V reaching the proximal border of second subarticular tubercle of Toe IV; subarticular tubercles prominent, round; supernumerary tubercles absent; tips of

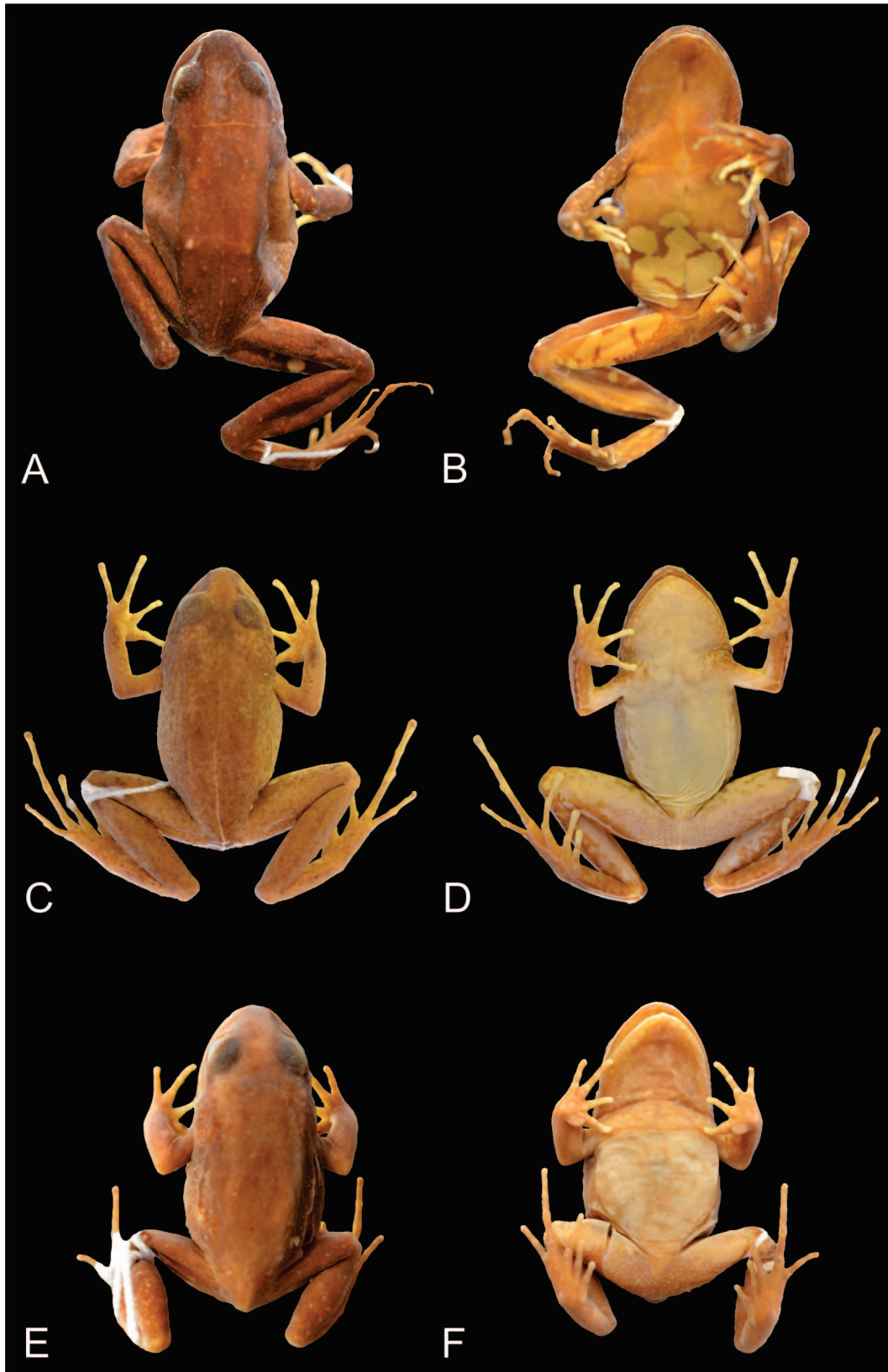


FIG. 2.—Adult female holotype of *Lynchius flavomaculatus* (BMNH 1947.2.16.11, SVL = 39.4 mm; A–B), adult female holotype of *L. nebulanastes* (KU 181407, SVL = 35.0 mm; C–D), and adult male holotype of *L. parkeri* (KU 135278, SVL 22.2 mm; E–F). A color version of this figure is available online.

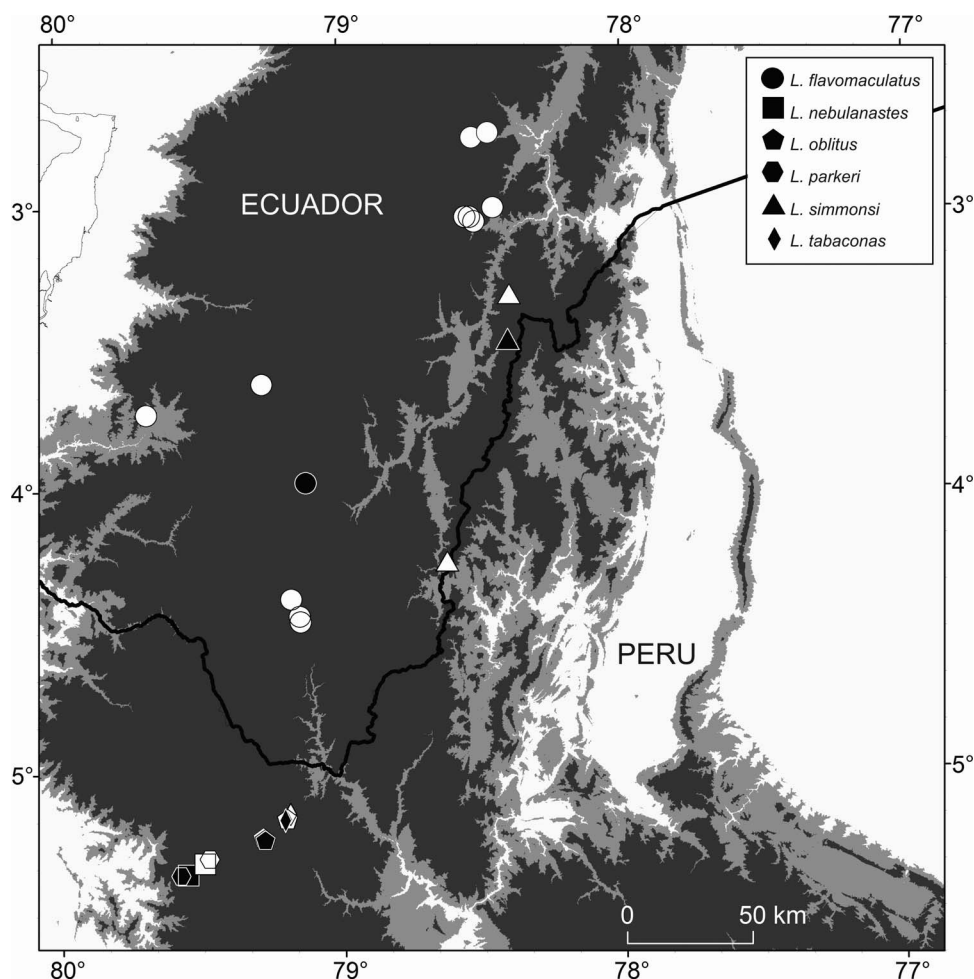


FIG. 3.—Geographic distribution of six species of *Lynchius*. Solid symbols represent the type locality of each species. Area above 500 m in light gray and area above 1000 m in dark gray.

toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal tubercle elongate, prominent; outer metatarsal tubercle slightly smaller, round, prominent; subarticular tubercles round, prominent; supernumerary tubercles absent; (12) heel and tarsal tubercles absent; (13) in life, dorsum mottled dark yellow and reddish brown with indistinct yellow bars on limbs, head, and upper lips; dark brown transversal bars on limbs; flanks yellow with brown spots; venter grayish brown, belly with conspicuous yellow blotches, also present on ventral surfaces of limbs; yellow blotches on groin and anterior surfaces of thighs; Fingers I and II yellow dorsally and ventrally; iris pale green with black reticulations; in preservative, dorsum dark brown with a light brown spotted pattern; indistinct cream bars on limbs and upper lips; interorbital bar light brown, when present; some specimens with a cream middorsal stripe extending to posterior surface of thigh; throat and belly brown; belly with conspicuous cream blotches (yellow in life), in some specimens coalescing completely, turning belly uniformly cream; cream blotches on groin and ventral surface of limbs; Fingers I and II white.

Distribution and ecology.—*Lynchius flavomaculatus* is known to occur in paramos at 2215–3100 m on the Cordillera Occidental in southeastern Ecuador (provinces of Loja,

Zamora-Chinchipe, and Morona-Santiago; Fig. 3). Lehr (2006) recorded one specimen from the Río Blanco Basin (3100 m) in Province of Huancabamba, Department of Piura, Peru. This species is terrestrial, occurring in grasslands of the Paramo ecoregion (Lynch 1975; Duellman and Lehr 2009). Females produce large unpigmented eggs, suggesting that they undergo direct development without larval phase (Lynch 1969).

Remarks.—Parker (1938) provided an accurate description of the holotype and also described the intraspecific variation, especially regarding coloration. He described the skin as smooth in ventral and dorsal surfaces, although our observations indicate otherwise (see diagnoses). Lynch (1969) noted that males lack nuptial pads, while Lehr (2006) mentioned the presence of nuptial pads in males. Our re-examination of specimens (including KU19737, the specimen in fig. 6, Lehr 2006:339) failed to find nuptial pads. Lynch (1975) provided a brief description of the cranial osteology (only four characters) and a drawing of the skull in dorsal view. Duellman and Lehr (2009) list the discoidal fold as absent and eyelid as lacking tubercles, but our examination of specimens (listed in Appendix I) indicates otherwise. They also provide a picture of a live specimen from the type locality (their fig. 71, 2009:87).

Lynchiuss nebulanastes (Cannatella 1984)
(Figs. 2C–D)

Phrynopus nebulanastes Cannatella 1984

Eleutherodactylus nebulanastes: Lehr 2005

“Eleutherodactylus” nebulanastes: Heinicke et al. 2007

Lynchiuss nebulanastes: Hedges et al. 2008

Holotype.—KU 181407, adult female from El Tambo, 31.5 km East of Conchaque, 2700 m, Departamento Piura, Peru (Figs. 2C–D), collected by T.J. Berger, D.C. Cannatella, and W.E. Duellman on 27 February 1979 (fig. 72 in Duellman and Lehr 2009).

Diagnosis.—A moderately large species of *Lynchiuss* (adult females SVL = 34.5–40.7 mm, $n = 10$; adult males SVL = 27.0–35.8 mm, $n = 10$) characterized as follows: (1) skin on dorsum of head, body, and limbs shagreen, with scattered tubercles, more abundant posteriorly; shanks bearing abundant small tubercles, in some specimens larger and wart-like; occipital folds absent; middorsal fold from the end of head to cloacal region; lateral folds present; dorsolateral fold long and discontinuous; venter and groin smooth; discoidal and thoracic folds present; (2) tympanic membrane and annulus indistinct; supratympanic fold low, extending behind the tympanic region; postrictal tubercles present, in a row; (3) head as long as wide or slightly longer than wide (HW/HL = 0.9–1.0); snout short, round in dorsal and lateral views; canthus rostralis weakly concave in dorsal view; (4) cranial crests absent; upper eyelid covered by small scattered tubercles; (5) dentigerous process of vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 3–5 teeth; (6) males lacking vocal slits and nuptial pads; (7) fingers long and slender, first finger as long as second; subarticular tubercles prominent, round; supernumerary tubercles large, round, smaller than subarticular tubercles; tips of fingers narrowly round; pads, circumferential grooves, lateral fringes, and hand webbing absent; (8) ulnar tubercle absent; (9) palmar tubercle divided in two subunits, inner subunit much larger than outer; thenar tubercle prominent, elliptical; (10) foot length 50–60% of SVL, lateral fringes and foot webbing absent; Toe III longer than Toe V; Toe III usually reaching distal margin of second subarticular tubercle of Toe IV, Toe V reaching middle of second subarticular tubercle of Toe IV; subarticular tubercles prominent, round; supernumerary tubercles absent; tips of toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal tubercle elongate, prominent; outer metatarsal tubercle smaller, round, prominent; subarticular tubercles round, prominent; supernumerary tubercles absent; (12) heel and tarsal tubercles absent; (13) in life, dorsum brown, reddish brown or dark green; some specimens with cream middorsal stripe extending to posterior surface of thigh and shank, sometimes reaching plantar surface; flanks cream with black mottling; limbs light brown; canthus rostralis dark brown to black; light brown bar parallel to upper lip; venter greenish yellow with brown or gray mottling; ventral surfaces of limbs and spots on groin and thighs bright yellow; iris dull bronze; in preservative, dorsum brown with black and pale spots; canthus rostralis dark brown; belly cream; throat light brown to pale.

Distribution and ecology.—*Lynchiuss nebulanastes* occurs in humid forests from 2779 m to 2820 m elevation on the western slopes of the Cordillera de Huancabamba (Fig. 3). According to Cannatella (1984), specimens were found under rocks in disturbed elfin forests, and the male advertisement call sounds like a “tick–tick–tick.”

Remarks.—Cannatella (1984) provided an accurate description of this species, but our diagnosis (based on specimens listed in Appendix I) includes several characters that differ from the original description in some respects (Cannatella’s observations in parenthesis): dorsal skin shagreen with scattered tubercles (skin of dorsum smooth); palmar tubercle divided (not bifid); and snout round (subacuminate in dorsal view and sloping in lateral profile). According to the original description, *L. nebulanastes* has tympanic annulus, columella, and cavum tympanum, its tympanum is concealed by the skin, and males lack vocal sacs (Cannatella 1984). The original description also includes a picture of the holotype and a male paratype, a drawing of dorsal and ventral view of the cranium, and a brief description of cranial osteology, including the description of the frontoparietal as not rugose. Although the drawings show the nasals without contact (state observed by us after examination of the same specimen, KU 181416), Cannatella (1984) described the nasals as having median contact. Lehr (2005) noted that circumferential grooves were present on fingers and toes, as well as lateral fringes, but our observations contradict those character states. Duellman and Lehr (2009) report the discoidal fold as absent and eyelid as lacking tubercles, but our examination of specimens reveals both structures to be present. They also provide a picture of a live specimen from the type locality (their fig. 72, 2009:89).

Lynchiuss oblitus sp. nov.
(Figs. 4, 5)

Phrynopus sp. n. 1: Lehr et al. 2005

Phrynopus parkeri: Lehr 2006 [misidentification].

Lynchiuss sp.: Hedges et al. 2008

Lynchiuss sp.: Padial et al. 2014

Holotype.—MHNC 8674, an adult female from Quebrada del Vino, 22 km West from San Ignacio, inside of National Sanctuary of Tabaconas-Namballe (NSTN), District Namballe, Province San Ignacio, Department of Cajamarca, Peru, 3270 m (5°14′15.10″S, 79°16′48.65″W; Figs. 4, 5), collected by A. Pari and K. Pino, on 26 October 2009.

Paratypes.—Five adult males: MHNC 8614 from Laguna Victoria (NSTN), District Tabaconas, Province San Ignacio, Department of Cajamarca, Peru, 3297 m (5°13′45.25″S, 79°17′13.57″W), collected by J. Delgado, on 5 October 2009; MHNC 8652 from Quebrada del Vino, 22 km West from San Ignacio (NSTN), District Namballe, Province San Ignacio, Department of Cajamarca, Peru, 2950 m (5°09′53.31″S, 79°12′4.56″W), collected by J.C. Chaparro, on 18 October 2009; MHNC 8676 from Quebrada del Vino, 22 km West from San Ignacio (NSTN), District Namballe, Province San Ignacio, Department of Cajamarca, Peru, 3270 m (5°14′15.10″S, 79°16′48.65″W), collected by A. Pari and K. Pino, on 7 October 2009; MHNSM 19914 and MTD 45954 from Lagunas Arrebiatadas (NSTN), Province San Ignacio,



FIG. 4.—Adult female holotype of *Lynchius oblitus* (MHNC 8674, SVL = 25.5 mm) from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru, 3300 m (5°13'45.5"S, 79°17'13.2"W). A color version of this figure is available online.

Department of Cajamarca, Peru. Three adult females: MHNC 8601 (Fig. 6) from Laguna Victoria (NSTN), District Tabaconas, Province San Ignacio, Department of Cajamarca, Peru, 3291 m (5°14'15.10"S, 79°16'48.65"W), collected by J. Delgado, on 4 October 2009; MHNC 8675 and MHNC 8677 from Quebrada del Vino, 22 km West from San Ignacio (NSTN), District Namballe, Province San Ignacio, Department of Cajamarca, Peru, 3291 m (5°14'15.10"S, 79°16'48.65"W), collected by A. Pari and K. Pino, on 7 October 2009.

Referred specimens.—Six specimens: MHNC 8598–8599, MHNC 8602, MHNC 8606, MHNC 8625–8626 from the same locality and data as paratype MHNC 8614. Four specimens: MHNC 8672–8673, MHNC 8689–8690 from Quebrada del Vino, 22 km West from San Ignacio (NSTN), District Namballe, Province San Ignacio, Department of Cajamarca, Peru, 2950 m (5°9'53.31"S, 79°12'4.56"W), collected by J.C. Chaparro, on 17 October 2009.

Diagnosis.—A small *Lynchius* (SVL of adult females 24.5–28.4 mm, $n = 4$; adult male 21.7 mm; see Table 4), characterized as follows: (1) skin on dorsum of head, body, and limbs shagreen, with few scattered tubercles; occipital folds V-shaped; middorsal fold present; middorsum bearing folds < >-shaped or w-shaped; dorsolateral folds long and discontinuous; venter smooth; groin smooth; discoidal and

thoracic folds present; (2) tympanic membrane and annulus distinct, its diameter 45–56% of eye diameter; supratympanic fold poorly defined; posttricial tubercles absent; (3) head as long as wide or slightly longer than wide (HW/HL = 1.0); snout broadly rounded in dorsal view and curved anteroventrally in lateral profile; canthus rostralis weakly concave in dorsal view; (4) cranial crests present; upper eyelid without tubercles; (5) dentigerous process of vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 2–3 teeth; (6) males lacking vocal slits and nuptial pads; (7) hands with short fingers, first finger as long as or shorter than second; subarticular tubercles prominent, round; supernumerary tubercles present; tips of fingers narrowly round; pads, circumferential grooves, lateral fringes, and hand webbing absent; (8) ulnar tubercle absent; (9) palmar tubercle divided in two subunits, inner subunit much larger than outer; thenar tubercle prominent, elliptical; (10) foot length ~45% of SVL; lateral fringes and toe webbing absent; Toe III longer than Toe V; Toe III usually reaching middle of second subarticular tubercle of Toe IV, Toe V reaching proximal border of second subarticular tubercle of Toe IV; subarticular tubercles low, round; supernumerary tubercles absent; tips of toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal tubercle elongate, prominent;

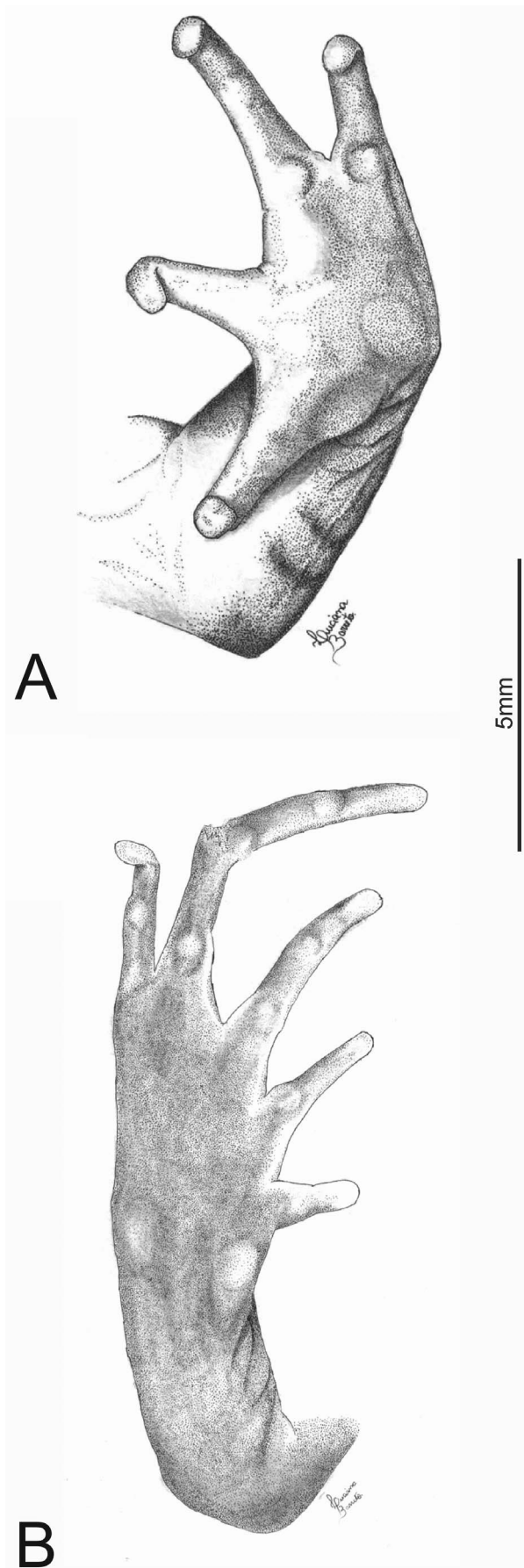


FIG. 5.—*Lynchius oblitus* sp. nov. Ventral views of left hand (A) and right foot (B) of holotype (MHNC 8674).

outer metatarsal tubercle round, about the same size as inner; subarticular tubercles round, low; supernumerary tubercles absent; (12) heel and tarsal tubercles absent; (13) in preservative, dorsal surfaces brown; light brown $< >$ -shaped or w-shaped occipital mark; canthus rostralis dark brown, a dark brown stripe posterior to eyes; hind limbs brown with dark brown bars; throat cream with brown mottling or uniformly cream; belly and ventral surfaces of limbs cream with dark brown blotches. Coloration in life (based on MHNC 8601) follows the same pattern observed in specimens in preservative. However, in life the cream areas are yellowish, dorsal surfaces are light brown to orange, and dorsal marks are cream and surrounded by dark brown. Iris greenish brown with dark brown reticulations.

Comparisons.—The new species differs from *Lynchius flavomaculatus* (characters of this and other species in parentheses) by its small size, with SVL < 29 mm in females and < 21.7 mm in male (females SVL = 34.6–44.2 mm; males SVL = 24.0–35.2 mm) and by bearing occipital folds and folds on middorsum (absent). *Lynchius oblitus* can be distinguished from *L. nebulanastes* and *L. parkeri* by having a distinct tympanum (indistinct), cranial crests (absent), yellow mottling on venter (absent), and by bearing occipital folds and folds on middorsum (absent). From *L. simmonsii*, it differs by its small size, with SVL < 29 mm in females and < 21.7 mm in male (females SVL = 35.0–40.1 mm; male SVL = 28.3 mm), rounded plantar tubercles (conical), skin on dorsum shagreen with scattered tubercles (dorsum covered with uniform-sized spicule-like warts), occipital and dorsolateral folds (absent), folds on middorsum (absent), lateral fringes on fingers and toes absent (present), and yellow mottling on venter (venter brown). *Lynchius oblitus* differs from *L. tabaconas* by having occipital folds, folds on middorsum, and cranial crests (absent).

Description of holotype.—Head as long as wide (HW/HL = 1.0); snout rounded in dorsal view and curved anteroventrally in lateral profile; nostrils not protuberant, oriented laterally; canthus rostralis weakly concave in dorsal view, round in frontal profile; loreal region concave; lips not flared; upper eyelid with few small granules; cranial crests present. Supratympanic fold weakly distinct; tympanic membrane and annulus distinct; tympanic membrane nearly round, its length more than half of eye length; postrectal tubercles absent. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae small, round, separated by a distance equal to six times the diameter of choana; dentigerous process of the vomers prominent, oblique, situated posteromedial to choanae (posterior margin at level of choanae), their width approximately two times diameter of choanae, bearing 2 or 3 vomerine teeth. Skin of dorsal surfaces shagreen, with few scattered tubercles on dorsum; ventral surfaces smooth; thighs coarsely areolate posteriorly in ventral view; occipital fold V-shaped; middorsum bearing folds $< >$ -shaped; dorsolateral folds present, complete; discoidal fold poorly defined; thoracic fold present. Ulnar tubercle absent; palmar tubercle completely divided in two subunits, inner subunit much larger than outer; thenar tubercle prominent, elliptical; subarticular tubercles round, larger than supernumerary tubercles; finger tips narrowly rounded; pads weakly present, circumferential grooves absent; fingers lacking lateral fringes and webbing; relative length of fingers: I $<$ II $<$ III $>$ IV. Foot length 45% of SVL; heel and tarsus lacking tubercles or

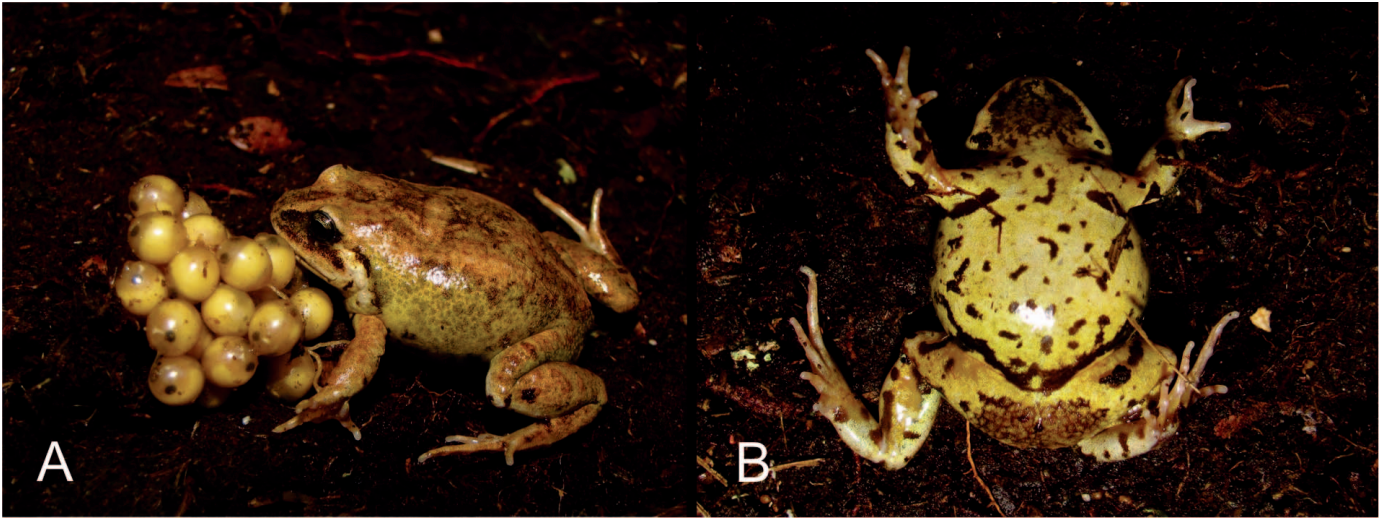


FIG. 6.—Adult female paratype of *Lynchius oblitus* (MHNC 8601) from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru, 3300 m (5°13′45.5″S, 79°17′13.2″W). Dorsal (A) and ventral (B) views. Photo: Nature Consulting SAC. A color version of this figure is available online.

folks; inner metatarsal tubercle oval, prominent, larger than outer metatarsal tubercle; outer metatarsal tubercle round; toes lacking lateral fringes and webbing; toe tips narrowly rounded; pads and circumferential grooves absent; relative length of toes: I < II < III > V < IV; Toe V reaching proximal margin of second subarticular tubercle of Toe IV, and Toe III reaching its middle. In preservative, dorsal surfaces brown, a cream <->-shaped occipital mark; head as dorsum, canthus rostralis dark brown, almost black; dark brown stripes posterior to eye. Hind limbs brown with dark brown bars; forelimbs light brown with dark brown spots. Throat and belly brown with cream mottling; ventral surfaces of limbs dark brown with cream blotches that run together on thighs and forelimbs.

Variation.—The only male examined (MTD 45954) has a brown venter with few cream dots, cream mottling posterior to eyes, and hind limbs brown without bars. For variation in measurements, see Table 4.

Etymology.—The specific epithet *oblitus*, a Latin verb in the past participle form meaning forgotten, neglected, refers to the fact that this species has been known to exist for >10

yr, but was not named and described until now. We wish to highlight the fact that an increasing number of species are being labeled as candidate species while their formal descriptions are neglected or postponed, hampering the incorporation of these species into empirical analyses of species diversity, evolution, and conservation.

Distribution and ecology.—This species is known from the type locality, which belongs to sector Namballe, in Tabaconas-Namballe National Sanctuary, and an area between 2800 m to 3297 m in sector Tabaconas, within the ecotone of paramo (above 3100 m) and dwarf forest or montane evergreen forest (below 3100 m; Fig. 3) in the northern Andes. Specimens were observed walking on the leaf litter during the night in montane cloud forests and paramo. They were captured by hand or pitfall traps. Females lay eggs under leaf litter and inside of plant roots and the eggs undergo direct development. *Lynchius oblitus* occurs in sympatry with *Gastrotheca monticola* and *Pristimantis bellator* in sector Tabaconas and with *G. monticola*, *P. bustamante*, *P. schultei*, and *L. tabaconas* in sector Namballe.

Remarks.—Specimens MTD 45954 and MHSNM 19914 were first identified as “*Phrynopus* sp. 1” by Lehr et al. (2005). Subsequently, Lehr (2006) considered them males of *Lynchius parkeri* and reported them as the first record of this species for the Departamento of Cajamarca, Peru. Hedges et al. (2008) and Padial et al. (2014) referred to MTD 45954 as “*Lynchius* sp.”; they did not find it nested with *L. parkeri*, but as the sister group of a clade formed by *L. flavomaculatus*, *L. parkeri*, and *L. nebulanastes*. We consider MHSNM 19914 as part of *L. oblitus* based on phylogenetic analyses, and MTD 45954 to be *L. oblitus* based on both phylogenetic analyses and external morphology.

Lynchius parkeri (Lynch 1975)
(Figs. 2E–F)

Phrynopus parkeri Lynch 1975
Lynchius parkeri: Hedges et al. 2008

Holotype.—KU 135278, adult male from the summit of the cordillera between Canchaque and Huancabamba,

TABLE 4.—Morphometrics of *Lynchius oblitus* (in mm).

	Females				Male MTD 45954
	MHNC 8674	MHNC 8601	MHNC 8675	MHNC 8677	
Snout–vent length	25.5	28.4	24.5	28.3	21.7
Head length	9.8	10.7	9.5	10.7	8.4
Head width	9.6	10.8	9.7	10.7	8.1
Eye length	2.8	3.1	2.6	2.8	2.5
Eye-to-nostril distance	2.5	2.7	2.2	2.4	2.0
Internarial distance	2.4	2.5	2.2	2.4	2.3
Eye-to-eye distance	4.2	4.2	3.8	4.3	3.8
Tympanic membrane height	1.6	1.8	1.9	1.5	1.5
Tympanic membrane length	1.6	1.7	1.5	1.2	1.6
Width of disc of Finger III	0.4	0.5	0.4	0.5	0.4
Width of disc of Finger IV	0.4	0.4	0.5	0.5	0.4
Arm length	6.2	6.1	5.3	6.3	5.3
Tibia length	10.1	10.8	9.8	10.6	6.2
Thigh length	10.1	11.5	9.4	11.5	9.7
Foot length	11.5	11.7	10.9	11.6	10.4
Width of disc of Toe IV	0.4	0.4	0.4	0.5	0.4

Departamento of Piura, Peru, 3100 m (Figs. 2E–F), collected by Thomas H. and P.R. Fritts on 11 May 1970.

Diagnosis.—A small *Lynchius* (adult females SVL = 24.9–34.5 mm, $n = 40$; adult males SVL = 21.1–28.3 mm, $n = 35$) characterized as follows: (1) skin on dorsum of head, body, and limbs shagreen, with few scattered tubercles; shank with transversal folds; occipital folds Λ -shaped, when present; middorsal and dorsolateral folds long and discontinuous; when present; venter smooth to weakly areolate; discoidal and thoracic folds present; (2) tympanic membrane and annulus indistinct; supratympanic fold poorly defined; postrictal tubercles present, forming a low row; (3) head as long as wide or slightly longer than wide (HW/HL 0.9–1.0); snout round in dorsal and lateral views; canthus rostralis weakly concave in dorsal view; (4) cranial crests absent; upper eyelid tubercles absent; (5) dentigerous process of vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 2–4 teeth; (6) males lacking vocal slits and nuptial pads; (7) hands with long and slender fingers, first finger as long as or shorter than second; subarticular tubercles prominent, round; supernumerary tubercles round, smaller than subarticular tubercles; tips of fingers narrowly round; pads, circumferential grooves, lateral fringes, and hand webbing absent; (8) ulnar tubercle absent; (9) palmar tubercle completely divided in two subunits, inner subunit much larger than outer; thenar tubercle prominent, elliptical; (10) foot length 42–51% of SVL, lateral fringes and webbing absent; Toe III longer than Toe V; Toe III usually reaching distal margin of second subarticular tubercle of Toe IV, Toe V reaching middle of second subarticular tubercle of Toe IV; subarticular tubercles prominent, round; supernumerary tubercles present; tips of toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal tubercle elongate, prominent; outer metatarsal tubercle round, prominent, about the same size as inner; subarticular tubercles round, prominent; supernumerary tubercles usually absent; (12) heel and tarsal tubercles absent; (13) in life, dorsum coloration gray, reddish or grayish brown, or dark brown; flanks dark brown with metallic green mottling; posterior surfaces of thighs dark brown to black with yellow spots and blotches; venter dark gray to black with large yellow blotches on belly in males, yellow with brown reticulations on belly in females; canthus rostralis dark brown; cream labial stripe present; iris dark brown; in preservative, dorsum light brown to grayish brown; dorsum usually lighter than flanks; some specimens with two cream dorsal bars on middorsum; light brown bar parallel to upper lip; belly cream mottled with brown; throat light brown; some specimens with a middorsal stripe extending to posterior surface of thigh and shank, sometimes reaching plantar surface.

Distribution and ecology.—*Lynchius parkeri* is known at elevations from 2700 m to 3100 m on the Cordillera de Huancabamba in Peru (Fig. 3). It occurs in cloud forests and paramos, where it has been found under rocks and within low vegetation. The advertisement call is a soft chirp (Duellman and Lehr 2009).

Remarks.—Lynch (1975) provides an accurate description of this species, but our diagnosis includes a larger number of characters and differs from the original description in that we report dorsal skin texture as shagreen. Also, according to the original description, *Lynchius parkeri* has a

tympanum concealed by skin. Lynch (1975) described males as having vocal slits and subgular vocal sac, whereas Cannatella (1984) failed to find vocal slits. Our observations also failed to find vocal slits. Lehr (2006) noted that males have nuptial pads, but we observed that both males and females have some rugosity on the dorsal surface of Finger I that does not constitute glandular tissue (observation based on specimens listed in Appendix I). Lynch (1975) presented a brief description of cranial osteology and a drawing of the skull in dorsal view. He considered the frontoparietals lacking rugosities, and they are shown as smooth on the drawing (Lynch 1975:26, his fig. 10). However, Cannatella (1984) found the frontoparietals to be rugose, an observation that agrees with our examination of the skull of two specimens (KU 135306 and KU 181824; Fig. 7).

Lynchius simmonsii (Lynch 1974)
(Fig. 8)

Ischnocnema simmonsii Lynch 1974

Oreobates simmonsii: Caramaschi and Canedo 2006

Lynchius simmonsii: Padial et al. 2012

Holotype.—KU 147068, young female from Río Piuntza, Cordillera del Cóndor, Provincia Morona-Santiago, Ecuador, 1830 m, collected by J.E. Simmons and B. MacBryde on 4 January 1972.

Diagnosis.—A moderately large *Lynchius* (adult females SVL = 35.0–40.1 mm, $n = 3$; adult male SVL = 28.3 mm; Table 5) characterized as follows: (1) skin on dorsum of head, body, and limbs covered with uniformly sized spicule-like warts, which are larger in males than in females; warts on flanks slightly flatter than those of dorsum; occipital folds absent; middorsal fold present on head of females and along head and body of males; dorsolateral folds absent; venter areolate, discoidal fold present; (2) tympanic membrane and annulus distinct, its length 54–57% of eye length; supratympanic fold low, covering upper-posterior margin of tympanic annulus; postrictal tubercles present; (3) head large, as wide as long; snout short, round to nearly truncate in dorsal view and rounded in lateral view; canthus rostralis weakly concave in dorsal view; loreal region concave; lips not flared; (4) cranial crests absent; upper eyelid covered by same spicule-like warts as in dorsum; (5) dentigerous process of vomers large, situated posteromedial to choanae, each process bearing 4–8 teeth; (6) males with small vocal slits and no nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, conical; supernumerary tubercles large, prominent, round to conical, smaller than subarticular tubercles; skin on palmar surface covered by small, round warts; tips of fingers narrowly rounded, lacking pads and circumferential grooves; fingers with keel-like lateral fringes; (8) ulnar tubercles absent; (9) palmar tubercle prominent, bifid distally, with inner subunit larger than outer; thenar tubercle prominent, elliptical; (10) foot length 45–49% of SVL, lateral fringes present, webbing absent; Toe III longer than Toe V; Toe III usually reaching midpoint of second subarticular tubercle of Toe IV, Toe V reaching or nearly reaching proximal border of second subarticular tubercle of Toe IV; subarticular tubercles prominent, conical; supernumerary tubercles present; tips of toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal

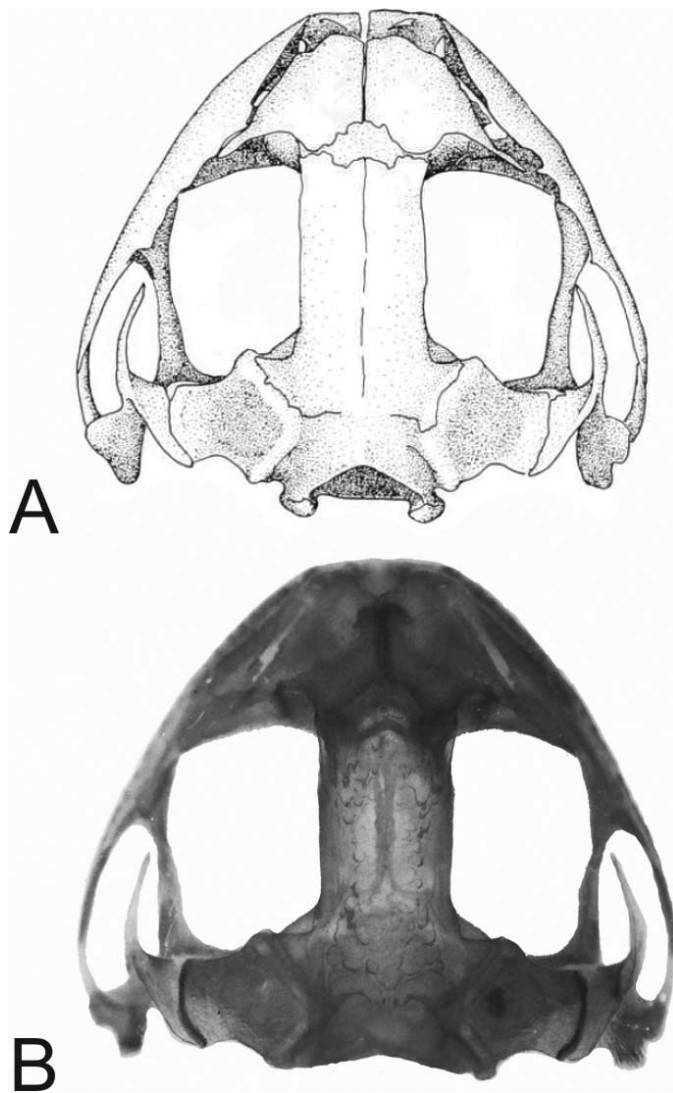


FIG. 7.—Skull of *Lynchius parkeri*. (A) KU 135306 in dorsal view (modified from Lynch, 1975:26, his fig. 10) and (B) a picture of the same skull; note ornamentation in frontoparietals.

tubercle elongate, prominent; outer metatarsal tubercle smaller, round, prominent; subarticular tubercles prominent, conical; supernumerary tubercles smaller than subarticular tubercles; (12) heel and tarsal tubercles absent; (13) in life, dorsum brownish black to black, with or without dark brown marks (interorbital bar, occipital and sacral blotches); venter brown with small cream flecks; iris black with minute light blue spots and an orange circumciliary ring; in preservative, dorsal coloration dark brown to black with or without diffuse brown areas (interocular bar, dorsal blotches), face with two or three diffuse labial bars and with or without small white spots; throat, chest, and belly pale brown to brown with small cream flecks.

Variation.—The specimens revised herein differ in some aspects from those described by Lynch (1974). Lynch (1974) mentioned a short sagittal interocular ridge; the trait is present in all females, but the only male known (QCAZ 41640) has a middorsal ridge that extends along the head and body. Low discoidal and supratympanic folds are evident in all examined specimens (reported as absent by Lynch 1974).

Finally, most specimens have a black dorsal coloration without evident dorsal marks. In the holotype description, Lynch (1974) mentioned that the dorsum is brownish black with diffuse brown areas (interocular bar, blotches on back) in preservative; this description is accurate for one of the newly collected specimens (QCAZ 30828), but the other three specimens have an almost solid black dorsum (Fig. 8).

Distribution and ecology.—*Lynchius simmonsii* was only known from the type locality. Here we report two additional populations along the Cordillera del Cóndor (Provincia Zamora-Chinchipe, Ecuador): Cóndor Mirador (03°18'25"S, 78°23'36"W, 1850 m), and Alto Miazí (04°15'23.6"S, 78°37'20.8"W, 1300 m; Fig. 3). This species probably occurs in adjacent Peru.

Remarks.—*Lynchius simmonsii* was first described by Lynch (1974) based on two specimens, a juvenile female (KU 147068, holotype) and an unsexed juvenile from the same locality (KU 147069). No other information on *L. simmonsii* had been reported ever since. The diagnosis provided herein is based on the type material, three adult females (QCAZ 30828, 30829, 41639), and one adult male (QCAZ 41640) from Cordillera del Cóndor.

Lynchius tabaconas sp. nov.
(Figs. 9, 10, 11)

Holotype.—MHNC 8637, an adult female from Quebrada del Vino (NSTN), District Tabaconas, Province San Ignacio, Department of Cajamarca, Peru, 2745 m (5°09'53.31"S, 79°12'4.56"W), collected by J.C. Chaparro, on 16 October 2009 (Figs. 9, 10, 11A–B).

Paratype.—MHNC 8650, an adult male, from Quebrada del Vino (NSTN), District Tabaconas, Province San Ignacio, Department of Cajamarca, Peru, 3115 m (5°10'9.65"S, 79°12'26.89"W), collected by J.C. Chaparro, on 17 October 2009 (Fig. 11C–D).

Referred specimen.—MHNC 8649 from the same locality as the holotype.

Diagnosis.—A small *Lynchius* (adult female SVL = 28.5 mm; adult male SVL = 18.6 mm), characterized as follows: (1) skin on dorsum of head, body, and limbs shagreen, with few scattered tubercles; occipital folds absent; middorsal fold complete; dorsolateral folds present, complete; venter smooth; posterior ventral region of thighs coarsely areolate; groin smooth; discoidal fold present posteriorly, weak; thoracic fold absent; (2) tympanic membrane and annulus distinct, its diameter 48–58% of eye diameter; supra-tympanic fold poorly defined; postrictal tubercles present; (3) head slightly longer than wide (HW/HL = 0.9–1.0); snout broadly rounded in dorsal view, short and rounded in lateral profile; canthus rostralis weakly concave in dorsal view; (4) cranial crests absent; upper eyelid bearing few minute tubercles; (5) dentigerous process of vomers prominent, slightly oblique, situated posteromedial to choanae, each process bearing 5 or 6 teeth; (6) males lacking vocal slits and nuptial pads; (7) hands with slender fingers, first finger longer than second; subarticular tubercles prominent, round; supernumerary tubercles round, smaller than subarticular tubercles; tips of fingers narrowly round; pads, circumferential grooves, lateral fringes, and hand webbing absent; (8) ulnar tubercle absent; (9) palmar tubercle undivided, rounded; thenar tubercle prominent, elliptical; (10) foot



FIG. 8.—Adult female of *Lynchius simmonsii* from Alto Miazzi, 1300 m (04°15′23.6″S, 78°37′20.8″W), Zamora-Chinchipe, Ecuador (QCAZ 41639, SVL = 40.1 mm). Dorsal (A) and ventral (C) views; ventral view of left hand (B). Photos: Santiago R. Ron. A color version of this figure is available online.



FIG. 9.—Adult female holotype of *Lynchius tabaconas* (MHNC 8637, SVL = 28.5 mm) from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru, 2745 m (5°09'46.7"S, 79°17'13.2"W). A color version of this figure is available online.

length ~45% of SVL; lateral fringes and foot webbing absent; Toe III longer than Toe V; Toe III usually reaching middle of second subarticular tubercle of Toe IV, Toe V reaching proximal border of second subarticular tubercle of Toe IV; subarticular tubercles low, round; supernumerary tubercles absent; tips of toes narrowly rounded, lacking pads and circumferential grooves; (11) inner metatarsal tubercle elongate; outer metatarsal tubercle round, about the same size as inner; subarticular tubercles round, low; supernumerary tubercles absent; (12) heel and tarsal tubercles absent; (13) in life, dorsum of head, body, and limbs dark green with reddish-brown tubercles; canthus rostralis slightly darker than dorsum; middorsal stripe and dorsal surface of forelimbs reddish brown; males with transversal black bars on flanks, hind limbs, and groin; throat grayish brown with white and yellow mottling; belly grayish brown, female with dense yellow blotches and male with white and yellow mottling; ventral surfaces of limbs grayish brown with yellow blotches; yellow blotches also present on axillary region and groin; iris cooper or cooper with greenish border. In preservative, dorsum and dorsal surfaces of limbs grayish brown; middorsal stripe cream; flanks light brown with lighter spots; throat light brown with cream mottling; belly grayish brown, with yellow blotches and mottling cream.

Comparisons.—*Lynchius tabaconas* differs from *L. flavomaculatus* (characters of this and other species in parentheses) by its small size, with SVL = 28.5 mm in female and 18.6 mm in male (females SVL = 34.6–44.2 mm; males

SVL = 24.0–35.2 mm) and by lacking cranial crests (present). From *L. nebulanastes* and *L. parkeri* it differs by having the tympanum distinct (indistinct), lacking supernumerary tubercles (present), and having yellow blotches and/or mottling on venter (absent). *Lynchius tabaconas* differs from *L. simmonsii* by its small size, with SVL = 28.5 mm in female and 18.6 mm in male (females SVL = 35.0–40.1 mm; male SVL = 28.3 mm), having rounded plantar tubercles (conical), skin on dorsum shagreen with scattered tubercles (dorsum covered with uniform-sized spicule-like warts), dorsolateral folds (absent), lateral fringes on fingers and toes absent (present), and yellow blotches and/or mottling on venter (absent). It differs from *L. oblitus* by lacking occipital folds, folds on middorsum, and cranial crests (present).

Description of holotype.—Head as long as wide (HW/HL = 1.0); snout rounded in dorsal view and in lateral profile; nostrils slightly protuberant, oriented laterally; canthus rostralis weakly concave in dorsal view, round in frontal profile; loreal region concave; lips not flared; upper eyelid with few small tubercles; cranial crests absent. Supratympanic fold indistinct; tympanic membrane and annulus weakly distinct; tympanic membrane nearly round, its length less than half of eye length; two small postriectorial tubercles. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae small, round, separated by distance equal to six times the diameter of choana; dentigerous process of vomers prominent, oblique, situated posteromedial to choanae

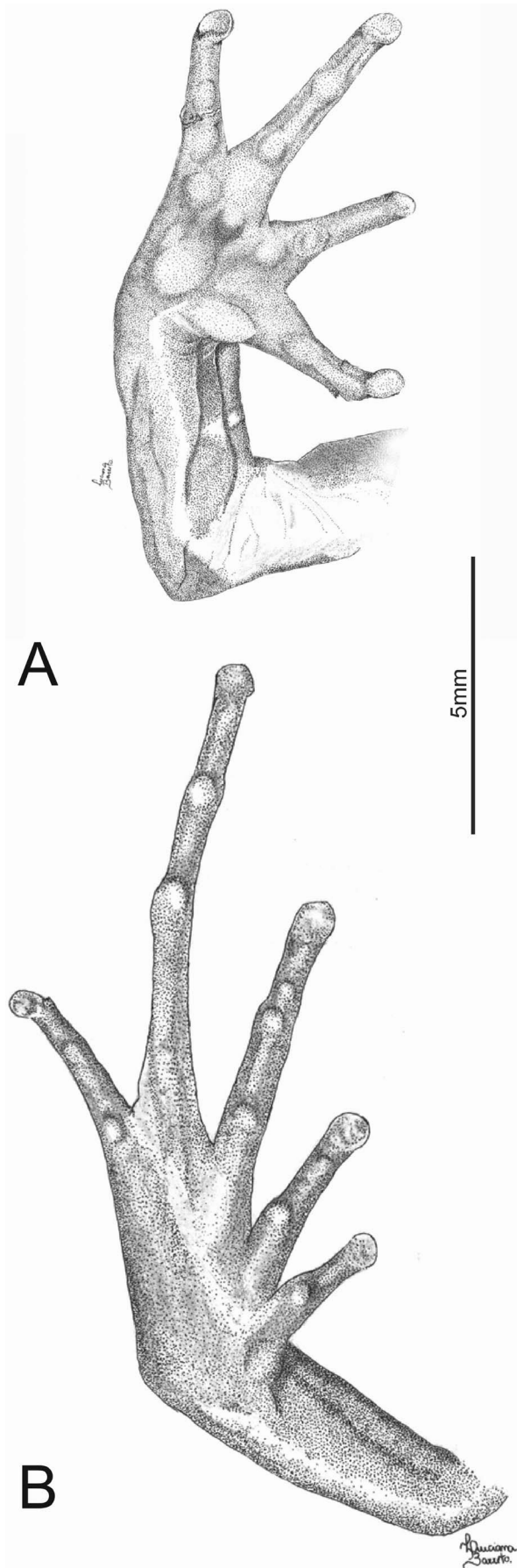


FIG. 10.—*Lynchius tabaconas* sp. nov. Ventral views of right hand (A) and right foot (B) of holotype (MHNC 8637).

TABLE 5.—Morphometrics of *Lynchius simmonsii* (in mm).

	Females				Male
	KU 147068	QCAZ 30828	QCAZ 30829	QCAZ 41639	QCAZ 41640
Snout-vent length	25.2	36.0	35.0	40.1	28.3
Head length	11.1	13.7	14.2	16.5	11.8
Head width	10.1	13.8	13.8	16.5	11.6
Eye length	3.8	4.7	4.4	5.0	4.1
Eye-to-nostril distance	2.3	—	—	—	—
Internarial distance	2.2	—	—	—	—
Eye-to-eye distance	3.7	—	—	—	—
Tympanic membrane height	2.2	—	—	—	—
Tympanic membrane length	1.9	2.6	2.5	2.7	2.3
Width of disc of Finger III	6.7	—	—	—	—
Width of disc of Finger IV	13.9	17.1	16.9	19.5	14.2
Arm length	13.8	—	—	—	—
Tibia length	14.6	—	—	—	—
Thigh length	14.4	17.5	16.9	18.7	12.6

(posterior margin at level of choanae), their width about three times the diameter of choanae, bearing 5 or 6 vomerine teeth. Ulnar tubercle absent; palmar tubercle undivided, rounded; thenar tubercle prominent, elliptical; subarticular tubercles round, prominent, larger than supernumerary tubercles; finger tips narrowly rounded; pads and circumferential grooves absent; fingers lacking lateral fringes and webbing; relative length of fingers: $I > II < III > IV$. Toes slender (foot length 46% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle oval, prominent, about the same size as outer metatarsal tubercle; outer metatarsal tubercle round, low; toes lacking lateral fringes and webbing; toe tips narrowly rounded; pads and circumferential grooves absent; relative length of toes: $I < II < III > V < IV$; Toe V reaching proximal margin of second subarticular tubercle of Toe IV, and Toe III reaching its middle. Skin of dorsum and limbs shagreen with scattered tubercles; ventral surfaces smooth; thighs coarsely areolate posteriorly in ventral view; occipital fold absent; dorsolateral folds present, complete; discoidal fold present; no thoracic fold. In life, dorsum and dorsal surfaces of limbs dark green; a reddish-brown middorsal stripe extending along posterior surface of thigh and shank, here becoming lighter, and reaching plantar surface; head as dorsum, canthus rostralis slightly darker. Throat grayish brown with yellow spots; belly gray with dense yellow blotches; ventral surfaces of limbs grayish brown with yellow blotches; yellow blotches also present on axillary region and groin. In preservative, dorsum and dorsal surfaces of limbs grayish brown; middorsal stripe cream; flanks light brown with lighter spots; throat light brown, belly grayish brown with cream blotches and spots.

Measurements (in mm, data for female holotype followed by male paratype in parentheses).—SVL 28.5 (18.6), HL 10.8 (6.8), HW 10.4 (6.4), EL 3.2 (2.0), EN 3.0 (2.0), IND 2.4 (1.7), EE 4.4 (3.2), TyH 1.8 (1.4), TyL 1.5 (1.2), F3 0.5 (0.3), F4 0.4 (0.3), FA 6.1 (4.4), TB 12.3 (8.6), TH 12.5 (8.5), FL 13.2 (8.3), T4 0.5 (0.4).

Variation.—Based only on a single female and a single male, females are larger than males. In life, the male had dark ventral surfaces mottled with yellow and white and black bars on the flanks, groin, and hind limbs (absent in the female).

Etymology.—The specific epithet “tabaconas” is a noun that refers to the area of the type locality, Tabaconas-

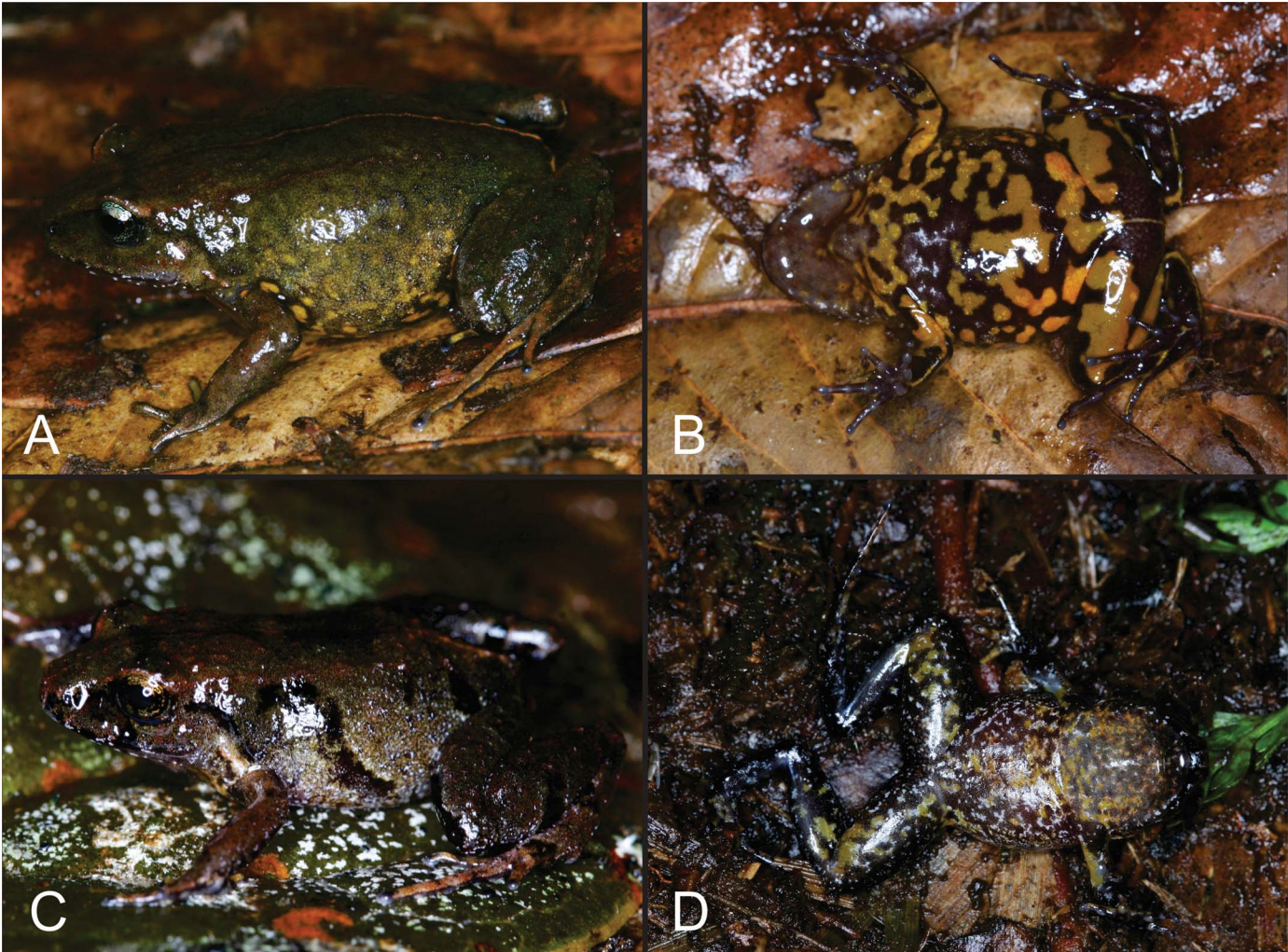


FIG. 11.—Adult female holotype of *Lynchius tabaconas* (MHNC 8637, SVL = 28.5 mm; A–B) and adult male paratype of *Lynchius tabaconas* (MHNC 8650, SVL = 18.6 mm; C–D) from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru, 2745 m (5°09′46.7″S, 79°17′13.2″W). A color version of this figure is available online.

Namballe National Sanctuary, which was established in 1988 to protect the biodiversity and the role of the paramo ecosystem in the Cordillera de Huacabamba.

Distribution and ecology.—This species is only known from the type locality in the sector of Namballe inside Tabaconas-Namballe National Sanctuary, in an area between 2960 m and 3115 m, within the ecotone between the dwarf forest or montane evergreen forest (above 2700 m) and paramo (above 3100 m; Fig. 3) from northern Andes. Specimens were found on the ground of forests and captured through pitfall traps in the paramo. The new species occurs in sympatry with *Gastrotheca monticola*, *Pristimantis bustamante*, *P. schultei*, and *Lynchius oblitus*. See more details about vegetation in Chaparro et al. (2012).

KEY TO SPECIES OF *LYNCHIUS*

- 1. Skin of dorsum covered with uniformly sized spicule-like warts; palmar and plantar tubercles conical *L. simmonsii*
Skin of dorsum shagreen, with scattered tubercles; palmar and plantar tubercles rounded 2
- 2. Tympanic membrane and annulus distinct (i.e., not differentiated from surrounding skin)..... 3

- Tympanic membrane and annulus indistinct, tympanum concealed by skin..... 5
- 3. Occipital folds V-shaped; middorsum bearing <>-shaped or w-shaped folds..... *L. oblitus*
Occipital folds absent; middorsum lacking folds 4
- 4. Large (adult females SVL = 34.6–44.2 mm; adult males SVL = 24.0–35.2 mm); cranial crests present; males with vocal slits.....*L. flavomaculatus*
Small (adult female SVL = 28.5 mm; adult male SVL = 18.6 mm); cranial crests absent; males lacking vocal slits*L. tabaconas*
- 5. Legs long (TB/SVL, TH/SVL, and FL/SVL = 0.5–0.6); upper eyelid covered by small scattered tubercles; frontoparietals not rugose *L. nebulanastes*
Legs short (TB/SVL, TH/SVL, and FL/SVL = 0.4–0.5); upper eyelid not covered by small scattered tubercles; frontoparietals rugose *L. parkeri*

DISCUSSION

The clade containing *Lynchius*, *Oreobates*, and *Phrynos* constitutes a morphologically and ecologically diverse group of frogs with a broad distribution in South America.

The monophyly of these genera, as well as intergeneric relationships within the clade ((*Lynchi* + *Oreobates*) *Phrynopus*), is corroborated by our parsimony and maximum likelihood analyses under two different strategies of alignment. Thus, variation in sampled gene sequences across loci with different evolutionary histories and rates of change (i.e., coding and noncoding mtDNA and nuDNA genes) provides consistent and strong (resilient to assumptions) evidence for the single and unique origin of this clade and its monophyletic genera. However, several internal relationships as well as the position of several outgroup taxa differ among analyses. Whether these differences are determined by the different assumptions of methods, or whether these assumptions are sensitive to evidence (taxon and character sampling), is a matter to be decided by future analyses with increasing character and taxon sampling. However, the latter hypothesis has received support from recent studies, reporting increasingly congruent relationships between maximum likelihood and parsimony analyses (under tree-alignment) when additional taxa and characters were sampled (e.g., Padial et al. 2014; Castroviejo-Fisher et al. 2015).

The phylogenetic framework provided by our analyses, which include all taxa described for *Lynchi*, almost all *Oreobates*, and almost half of *Phrynopus* species, constitutes a good starting point for testing different scenarios of diversification and character evolution in the Neotropics. Although it is not the goal of the present study to test biogeographic hypotheses or the variety of evolutionary hypotheses that can be proposed based on observed patterns of morphological variation and geographical distribution in light of phylogeny, we provide below an overview of patterns and outline several possible scenarios that could be subjects of future studies.

First of all, the molecular perspective on the affinities of *Lynchi*, *Oreobates*, and *Phrynopus* provided by this study is considerably different from the scenario constructed on the basis of external morphology and osteology and involves a more complex biogeographic history and a new interpretation of morphological variation. For example, all but the two new species of *Lynchi* and *L. simmons* were considered part of the genus *Phrynopus* as defined by Lynch (1975) because of their overall similarity—knob-shaped phalanges, chubby bodies, short extremities, inconspicuous plantar tubercles, and narrow heads. Also, *L. simmons* was until very recently considered part of *Oreobates* and was initially described as an *Ischnocnema* (Lynch 1974) when *Ischnocnema* was considered a broadly distributed genus that included most species of what is now *Oreobates* (see Caramaschi and Canedo 2006). Furthermore, with the transfer of *P. ayacucho* Lehr 2007 and *P. pereger* Lynch 1975 to *Oreobates*, and the transfer of *O. simmons* (Lynch 1974) to *Lynchi*, putative morphological synapomorphies for the three genera have vanished, such as the presence of conical plantar tubercles (as proposed for *Oreobates*; Padial et al. 2007) or the knobbed versus t-shaped terminal phalanges (as proposed for *Phrynopus*; Lynch 1975; Trueb and Lehr 2008). Also, Trueb and Lehr (2008) described a number of characters purportedly distinguishing *Lynchi*, *Oreobates*, and *Phrynopus* that turned out to vary within genera, such as lack of dentigerous processes of the vomers in *Phrynopus*, presence of cranial

crests in *Lynchi*, and extraordinarily large medial and lateral processes of the premaxillae in *Lynchi* and *Phrynopus* in comparison to *Oreobates*. They also pointed out multiple differences in composite characters (e.g., the relative length of the cultriform process with respect to the orbit, or the relative length of fingers) that still need to be reduced to independent transformation series to be tested as synapomorphies (Grant and Kluge 2004). A comprehensive analysis of the external and internal anatomy of *Lynchi*, *Oreobates*, and *Phrynopus* and the phylogenetic analysis of resulting characters is still needed to reach an adequate understanding of the origin of morphological variation in these clades. Fortunately, ongoing studies of the internal anatomy of terraranan frogs (e.g., Taboada et al. 2013) is leading to the discovery of synapomorphies at different levels, and increasing taxon and character sampling will probably lead to further discoveries and a better picture of morphological character variation across clades.

Lynchi and *Phrynopus* have relatively small and ecologically restricted distributions in the high Andes and, as mentioned above, most species in these two clades possess a number of external and osteological similarities (see Lynch 1975; Trueb and Lehr 2008). All species of *Lynchi* and *Phrynopus* are Andean and terrestrial, but while *L. simmons*—the sister species of the rests of *Lynchi*—occurs in montane forest below 2000 m, all other *Lynchi* and *Phrynopus* inhabit cloud and elfin forests above 2200 m. The high Andean species in both *Lynchi* and *Phrynopus* are overall short-legged, have rounded bodies, narrow heads, short extremities, short digits with knobbed, rather than t-shaped, terminal phalanges that lack expanded toepads. These similarities among high-altitude species led Lynch (1975) and subsequent authors to deduce a single origin for these similar traits, but our analyses support instead that *Phrynopus* and *Lynchi* are not closely related and, hence, that similar traits evolved independently as the result of independent histories, perhaps connected to adaptation to similar environments.

The genus *Oreobates* has a broader diversity in anatomical traits and distribution that encompasses a diverse number of South American ecoregions. Only two species of *Oreobates* (*O. ayacucho* and *O. pereger*) occur in the high Andean humid grasslands (i.e., wet puna ecoregion, as this habitat is named in southern and central Peru; Olson et al. 2001), while most other species occur in montane forests of the eastern slopes of the Andes between 1000 m and 3000 m elevation. There are, nonetheless, several species inhabiting warmer environments such as the Amazon lowlands (e.g., *O. cruralis* and *O. quixensis*), the Cerrado (*O. crepitans* and *O. heterodactylus*; Padial et al. 2012), and the dry Atlantic forests of eastern Brazil (*O. remotus*; Teixeira et al. 2012). Also, several species have colonized the highly seasonal inter-Andean dry valleys (e.g., *O. ibischi*, Reichle et al. 2001; *O. berdemenos*; Pereyra et al. 2014), and the Yungas of northern Argentina (*O. barituensis*; Vaira and Ferrari 2008). Interestingly, the two terrestrial species from the high Andean grasslands (*O. ayacucho* and *O. pereger*) resemble *Lynchi* and *Phrynopus* and were indeed considered part of *Phrynopus* (Lynch 1975). As such, the independent evolution of similar traits in *O. ayacucho* and *O. pereger* further support the hypothesis that adaptation to high-altitude environments of the Andes led to similar transformations

of traits in *Lynchi*us, *Oreobates*, and *Phrynop*us. This pattern is further supported by the similar morphologies of other high Andean genera (such as *Bryophry*ne, *Niceforonia*, and *Psychrophry*nella) that were also formerly considered part of *Phrynop*us.

Traits of species inhabiting other environments also support the idea that convergent evolution is behind several recurrent patterns of morphological variation. For example, species from more xeric habitats such as Cerrado (*Oreobates crepitans*, *O. heterodactylus*) or the inter-Andean dry valleys (*O. ibischi*, *O. discoidalis*), which often perch on low vegetation, and are slender and have long extremities with T-shaped terminal phalanges and large discs on fingers and toes, were formerly associated with more arboreal genera such as *Eleutherodactylus* (Lynch 1989; Lynch and Duellman 1997) and *Pristimantis* (Hedges et al. 2008). Molecular phylogenetic analyses indicate instead that similarity is the result of independent evolutionary histories (e.g., Hedges et al. 2008; Canedo and Haddad 2012; Padial et al. 2014). Likewise, the similarity between species of *Oreobates* from montane forests and the Amazon lowlands to *Lynchi*us *simmons*i and some species of *Ischnocnema* (i.e., tuberculate skins, long extremities and large heads, conical plantar tubercles, lack of expanded finger and toe discs) also suggests the possibility of convergent evolution as the result of adaptation to the conditions of the forest floor of tropical forests. These are nonetheless hypotheses deduced from raw observation of patterns in light of the relationships inferred in this study and that obviously require further testing.

Inferred relationships and distribution patterns also point out obvious biogeographical connections. For example, the relationships of *Oreobates* support an Atlantic Forest–Andean connection through the Cerrado and/or Amazonia, as indicated by the close relationship among *O. remotus*, *O. crepitans*, and *O. heterodactylus* (dry Atlantic Forest and Cerrado species), with Amazonian (*O. cruralis*) and Andean species (*O. berdemenos*, *O. discoidalis*, *O. ibischi*, and *O. madidi*). This biogeographic connection is also supported by the distribution and relationships of *Barycholos*, with one species in the Cerrado and one in the Pacific versant of the Andes, and has recently been supported for marsupial frogs (Teixeira et al. 2012; Blackburn and Duellman 2013; Castroviejo-Fisher et al. 2015). Also, it seems that species diversity of the clade formed by *Lynchi*us, *Oreobates*, and *Phrynop*us is concentrated in the Andes. The position of some lowland–montane forest taxa such as *O. quixensis* and *O. saxatilis* in *Oreobates* as a sister group that is sister to the rest of the species in the genus (Padial et al. 2012) and of the montane species *L. simmons*i as the sister group of the remaining species of *Lynchi*us indicates a montane forest origin of the high Andean anurans; this is a quite reasonable hypothesis that will nevertheless need to be tested.

At last, it is worth pointing out again that phylogenetic, anatomical, and biogeographical patterns discussed above confront the problem of underestimated species numbers. Three candidate species of *Oreobates* reported by Padial et al. (2012) remain to be named—one from the dry inter-Andean valleys of central Bolivia, one from the Yungas of Cochabamba (Bolivia), and one from montane forests in southern Peru. Four other species of *Oreobates* have been recently discovered in Peru—one in the montane forests of

eastern Loreto, one in the mountain forest of central Cusco, one from dry forest from eastern Apurímac, and one from inter-Andean dry forests in central Peru; all those species remain to be named (J.C. Chaparro, personal communication). The pace of species discovery in recent years also provides a glimpse of the rapidly growing understanding of species diversity with the exploration of new areas and the study of available collections. As many as 17 species of *Phrynop*us have been discovered during the past 10 yr and ongoing surveys in central Peru are revealing further new species (E. Lehr, personal observation). Twelve species of *Oreobates* have been named during the same period (see Padial et al. 2012 and references therein) and many areas of the Andes and the Amazon suitable for the existence of species in this group remain to be surveyed. *Lynchi*us has received far less attention than these latter two groups and, yet, surveys in a relatively small area revealed two nonsister species segregated altitudinally (the ones described herein), indicating that more species could await discovery in the many areas of the Cordillera de Huancabamba, Cordillera Oriental, and Cordillera del Cóndor. Overall, field surveys and taxonomic work are still largely insufficient at this time and for a region that extends for thousands of kilometers along the Andes and the adjacent lowlands; this fact precludes access to accurate data that are needed for rigorous empirical analyses of biodiversity patterns and evolutionary history.

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LITERATURE CITED

- Bazinnet, A.L., D.J. Zwickl, and M.P. Cummings. 2014. A gateway for phylogenetic analysis powered by grid computing featuring GARLI 2.0. *Systematic Biology* 63:812–818. DOI: <http://dx.doi.org/10.1093/sysbio/syu031>
- Blackburn, D.C., and W.E. Duellman. 2013. Brazilian marsupial frogs are

- diphyletic (Anura: Hemiphractidae: *Gastrotheca*). Molecular Phylogenetics and Evolution 68:709–714.
- Bossuyt, F., and M.C. Milinkovitch. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. Proceedings of the National Academy of Science of the United States of America 97:6585–6590.
- Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803. DOI: <http://dx.doi.org/10.2307/2408870>
- Canedo, C., and C.F. Haddad. 2012. Phylogenetic relationships within anuran clade Terrarana, with emphasis on the placement of Brazilian Atlantic rainforest frogs genus *Ischnocnema* (Anura: Brachycephalidae). Molecular Phylogenetics and Evolution 65:610–620.
- Cannatella, D.C. 1984. Two new species of the leptodactylid frog genus *Phrynopis*, with comments on the phylogeny of the genus. Occasional Papers of the Museum of Natural History, The University of Kansas 113:1–16.
- Caramaschi, U., and C. Canedo. 2006. Reassessment of the taxonomic status of the genera *Ischnocnema* Reinhard and Lütken, 1862 and *Oreobates* Jiménez-de-la-Espada, 1872, with notes on the synonymy of *Leiuperus verrucosus* Reinhardt and Lütken, 1862 (Anura: Leptodactylidae). Zootaxa 1116:43–54. DOI: <http://dx.doi.org/10.1206/3752.2>
- Castroviejo-Fisher, S., J.M. Padial, I. De la Riva, J.P. Pombal, Jr., H.R. da Silva, F.J.M. Rojas-Runjaic, E. Medina-Méndez, and D.R. Frost. 2015. Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development. Zootaxa 4004:1–75. DOI: <http://dx.doi.org/10.11646/zootaxa.4004.1.1>
- Chaparro, J.C., A.P. Motta, R.C. Gutiérrez, and J.M. Padial. 2012. A new species of *Pristimantis* (Anura: Strabomantidae) from Andean cloud forests of northern Peru. Zootaxa 3192:39–48.
- Chaparro, J.C., J.M. Padial, R.C. Gutiérrez, and I. De la Riva. 2015. A new species of Andean frog of the genus *Bryophryne* from southern Peru (Anura: Craugastoridae) and its phylogenetic position, with notes on the diversity of the genus. Zootaxa 3994:94–108. DOI: <http://dx.doi.org/10.11646/zootaxa.3994.1.4>
- Crawford, A.J. 2003. Relative rates of nucleotide substitution in frogs. Journal of Molecular Evolution 57:636–641.
- De la Riva, I. 2007. Bolivian frogs of the genus *Phrynopis*, with the description of twelve new species (Anura: Brachycephalidae). Herpetological Monographs 21:241–277. DOI: <http://dx.doi.org/10.1655/07-011.1>
- Duellman, W.E., and E. Lehr. 2009. Terrestrial Breeding Frogs (Strabomantidae) in Peru. Natur und Tier-Verlag, Germany.
- Farris, J.S., V.A. Albert, M. Källersjö, D. Lipscomb, and A.G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12:99–124.
- Frost, D.R. 2016. Amphibian species of the world: An online reference. American Museum of Natural History, USA. Available at <http://research.amnh.org/herpetology/amphibia/index.html>. Archived by WebCite at <http://www.webcitation.org/6j9N1ccW5> on 20 July 2016.
- Goloboff, P.A. 1996. Methods for faster parsimony analysis. Cladistics 12:199–220.
- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. Cladistics 15:415–428.
- Goloboff, P.J., S. Farris, and K. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.
- Goodman, M., M.L. Weiss, and J. Czelusniak. 1982. Molecular evolution above the species level, branching patterns, rates, and mechanisms. Systematic Zoology 31:376–399.
- Grant, T., and A.G. Kluge. 2004. Transformation series as an ideographic character concept. Cladistics 20:23–31.
- Grant, T., and A.G. Kluge. 2008. Credit where credit is due: The Goodman–Bremer support metric. Molecular Phylogenetics and Evolution 49:405–406.
- Hedges, S.B., W.E. Duellman, and M.P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. Zootaxa 1737:1–182.
- Heinicke, M.P., W.E. Duellman, and S.B. Hedges. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. Proceedings of the National Academy of Science of the United States of America 104:10092–10097.
- Hillis, D.M., C. Moritz, and B.K. Mable (eds.). 1996. Molecular Systematics. Sinauer Associates, USA.
- Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software Version 7: Improvements in performance and usability. Molecular Biology and Evolution 30:772–780.
- Katoh, K., K. Kuma, H. Toh, and T. Miyata. 2005. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30:3059–3066.
- Lanfear, R., B. Calcott, S.Y. Ho, and S. Guindon. 2012. PartitionFinder, combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29:1695–1701. DOI: <http://dx.doi.org/10.1093/molbev/mss020>
- Lehr, E. 2005. A new species of the *Eleutherodactylus nigrovittatus* group (Anura: Leptodactylidae) from Andean Peru. Herpetologica 61:199–208.
- Lehr, E. 2006. Taxonomic status of some species of Peruvian *Phrynopis* (Anura: Leptodactylidae), with the description of a new species from the Andes of southern Peru. Herpetologica 62:331–347.
- Lehr, E., and A. Catenazzi. 2009. Three new species of *Bryophryne* (Anura: Strabomantidae) from the region of Cusco, Peru. South American Journal of Herpetology 4:125–138.
- Lehr, E., A. Müller, and G. Fritzsche. 2005. Analysis of Andes frogs (*Phrynopis*, Leptodactylidae, Anura) phylogeny based on 12S and 16S mitochondrial rDNA sequences. Zoologica Scripta 34:593–603.
- Lehr, E., J. Moravec, and J.C. Cusi. 2012. Two new species of *Phrynopis* (Anura, Strabomantidae) from high elevations in the Yanachaga-Chemillén National park in Peru (Departamento de Pasco). ZooKeys 235:51–71.
- Lynch, J.D. 1969. Taxonomic notes on Ecuadorian frogs (Leptodactylidae: *Eleutherodactylus*). Herpetologica 25:262–274.
- Lynch, J.D. 1974. A new species of leptodactylid frog *Ischnocnema* from the Cordillera del Condor in Ecuador. Journal of Herpetology 8:85–87.
- Lynch, J.D. 1975. A review of the Andean leptodactylid frog genus *Phrynopis*. Occasional Papers of the Museum of Natural History, The University of Kansas 35:1–51.
- Lynch, J.D. 1989. Intrageneric relationships of mainland *Eleutherodactylus* Leptodactylidae I. A review of the frogs assigned to the *Eleutherodactylus discoidalis* species group. Milwaukee Public Museum Contributions in Biology and Geology 79:1–25.
- Lynch, J.D., and W.E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: Systematics, ecology and biogeography. University of Kansas Natural History Museum Special Publications 23:1–236.
- Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15:407–414.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, ..., K.R. Kassem. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51:933–938.
- Padial, J.M., S. Castroviejo-Fisher, J. Köhler, E. Domic, and I. De la Riva. 2007. Systematics of the *Eleutherodactylus fraudator* species group (Anura, Brachycephalidae). Herpetological Monographs 21:214–241.
- Padial, J.M., S. Castroviejo-Fisher, and I. De la Riva. 2009. The phylogenetic relationships of *Yunganastes* revisited (Anura: Terrarana). Molecular Phylogenetics and Evolution 52:911–915.
- Padial, J.M., J.C. Chaparro, S. Castroviejo-Fisher, J.M. Guayasamín, E. Lehr, A.J. Delgado, M. Vaira, M. Teixeira, Jr., R. Aguayo, and I. De la Riva. 2012. A revision of species diversity in the Neotropical genus *Oreobates* (Anura: Strabomantidae), with the description of three new species from the Amazonian slopes of the Andes, and the proposal of candidate species. American Museum Novitates 3752:1–55.
- Padial, J.M., T. Grant, and D.R. Frost. 2014. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. Zootaxa 3825:1–132. DOI: <http://dx.doi.org/10.11646/zootaxa.3825.1.1>
- Parker, H.W. 1938. The vertical distribution of some reptiles and amphibians in southern Ecuador. Annals and Magazine of Natural History 2:438–450.
- Pereyra, M.O., D. Cardozo, J.L. Baldo, and D. Baldo. 2014. Description and phylogenetic position of a new species of *Oreobates* (Anura: Craugastoridae) from northwestern Argentina. Herpetologica 70:211–227.
- Pyron, R.A., and J.J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61:543–583.
- Reichle, S., S. Lötters, and I. De la Riva. 2001. A new species of the *discoidalis* group of *Eleutherodactylus* (Anura, Leptodactylidae) from Inner-Andean dry valleys of Bolivia. Journal of Herpetology 35:21–26.
- Taboada, C., T. Grant, J.D. Lynch, and J. Faivovich. 2013. New morphological synapomorphies for the New World direct-developing frogs (Amphibia: Anura: Terrarana). Herpetologica 69:342–357.
- Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular

- Evolutionary Genetics Analysis (MEGA) software Version 4.0. Molecular Biology and Evolution 24:1596–1599.
- Teixeira, M., Jr., R.C. Amaro, R.S. Recoder, M.A. Sena, and M.T. Rodrigues. 2012. A relict new species of *Oreobates* (Anura, Strabomantidae) from the seasonally dry tropical forests of Minas Gerais, Brazil, and its implication to the biogeography of the genus and that of South American dry forests. *Zootaxa* 3158:37–52.
- Trueb, L., and E. Lehr. 2008. A new species of *Phrynopus* (Anura, Strabomantidae) from Peru, with comments on the osteology of the genus. *Phyllomedusa* 7:11–24.
- Vaira, M., and L. Ferrari. 2008. A new species of *Oreobates* (Anura: Strabomantidae) from the Andes of northern Argentina. *Zootaxa* 1908:41–40.
- Varón, A., L.S. Vinh, and W.C. Wheeler. 2010. POY Version 4: Phylogenetic analysis using dynamic homologies. *Cladistics* 26:72–85.
- Wheeler, W.C. 1996. Optimization alignment, the end of multiple sequence alignment in phylogenetics? *Cladistics* 12:1–10.
- Wheeler, W.C. 2003. Implied alignment, a synapomorphy-based multiple sequence alignment method and its use in cladogram search. *Cladistics* 19:261–268.
- Wheeler, W.C., C.P. Arango, T. Grant, D. Janies, A. Varón, L. Aagesen, J. Faivovich, C. D'Haese, W.L. Smith, and G. Giribet. 2006. Dynamic Homology and Phylogenetic Systematics: A Unified Approach Using POY. American Museum of Natural History, USA.
- Wiens, J.J., J.W. Fetzner, C.L. Parkinson, and T.W. Reeder. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology* 54:719–748.
- Zwickl, D.J. 2006. Genetic Algorithm Approaches for the Phylogenetic Analysis of Large Biological Sequence Datasets Under the Maximum Likelihood Criterion. Ph.D. dissertation, University of Texas, USA.

APPENDIX I

Specimens Examined

- Lynchiuss flavomaculatus*.—ECUADOR: Loja: 13–14 km E Loja, 2850 m, KU 119721–24; 8–9 km N San Lucas, 3000 m, KU 119737–42, 121354; 10 km S Saraguro, KU 142201–02; 19.4 km S Yangana, KU 218210. Morona-Santiago: FMNH 197838, 197846, USNM 98929–30, 195393–424, 260788; 28 km SW Plan de Milagro, KU 202654–55. Zamora-Chinchi: 15 km E Loja, 2700 m, BMNH 1947.2.16.11 (holotype), 1947.2.16.12–14 (paratypes); KU 119716–20, 119725–36, 119743 (cleared and stained), 141474–77, 142198–200, 165955–67, 166294 (cleared and stained), 202656.
- Lynchiuss nebulanastes*.—PERU: Piura: El Tambo, 31.5 km E Chanchaque, 2770 m, KU 181407 (holotype), 181392–406, 181408–14 (paratype), 181415–16 (cleared and stained), 181841, 219806–819.
- Lynchiuss oblitus*.—PERU: Cajamarca: Santuario Nacional Tabaconas-Namballe: MHNC 8598, 8599, 8601, 8602, 8606, 8614, 8625, 8626, 8652, 8672, 8673, 8674, 8675, 8676, 8677, 8689, 8690, MTD 45954.
- Lynchiuss parkeri*.—PERU: Piura: FLMNH 34092–108; Cordillera between Chanchaque (=Chanchaque) and Huancabamba, KU 135278 (holotype), 135279–311 (paratypes), 135306 (cleared and stained); El Tambo, 31.5 km E Chanchaque, 2770 m, KU 181288–91, 181393, 219820; 25 km SW Huancabamba, KU 181292–356, 181823, 181824 (cleared and stained), 181825–27, 181828 (cleared and stained), 181829, 196581–91, LSU 32172–32239.
- Lynchiuss simmonsii*.—ECUADOR: Morona-Santiago: Río Piuntza, Cordillera del Cóndor, 1830 m, KU 147068 (holotype), 147069 (paratype); Zamora-Chinchi: Cordillera del Cóndor, Cóndor Mirador, 1850 m, QCAZ 30829–30; Miaz Alto, 1300 m, QCAZ 41639–40.
- Lynchiuss tabaconas*.—PERU: Cajamarca: Santuario Nacional Tabaconas-Namballe, MHNC 8637, 8649, 8650.

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APPENDIX II
GenBank accession numbers for loci and terminals of species sampled in this study.

	12S	16S	RAG	TYR
<i>Barycholos pulcher</i>	EU186727	EU186709	EU186744	EU186765
<i>Barycholos ternetzi</i>	—	DQ283094	—	JX267680
<i>Bryophryne cophites</i>	EF493537	EF493537	EF493423	EF493508
<i>Euparkerella brasiliensis</i>	JX267390	JX267468	JX267545	JX267682
<i>Haddadus binotatus</i>	EF493361	EF493361	EF493397	DQ282918
<i>Holoaden bradei</i>	EF493378	EF493366	EF493449	EU186779
<i>Holoaden luederwaldti</i>	EU186728	EU186710	JX267549	EU186768
<i>Hypodactylus brunneus</i>	EF493357	EF493357	EF493422	EF493484
<i>Hypodactylus dolops</i>	EF493394	EF493394	EF493414	EF493483
<i>Lynchiuss flavomaculatus</i>	EU186667	EU186667	EU186745	EU186766
<i>Lynchiuss nebulanastes</i>	EU186704	EU186704	—	—
<i>Lynchiuss parkeri</i>	EU186667	EU186705	—	—
<i>Lynchiuss simmonsii</i>	JF809940	JF810004	JF809915	JF809894
<i>Noblella heyeri</i>	JX267463	JX267541	—	—
<i>Noblella lochites</i>	EU186699	EU186699	EU186756	EU186777
<i>Noblella myrmecoides</i>	JX267464	JX267542	—	—
<i>Oreobates amarakaeri</i>	JF809934	JF809996	JF809913	JF809891
<i>Oreobates ayacucho</i>	JF809933	JF809970	JF809912	JF809890
<i>Oreobates barituensis</i>	JF809935	JF809999	JF809914	JF809892
<i>Oreobates berdemenos</i>	KJ125511	KJ125507	—	—
<i>Oreobates choristolemma</i>	JF809921	FJ539067	JF809900	JF809881
<i>Oreobates crepitans</i>	—	KJ125510	—	—
<i>Oreobates cruralis</i>	EU186666	EU186666	EU186743	EU186764
<i>Oreobates discoidalis</i>	JF809925	FJ539068	JF809904	JF809884
<i>Oreobates gemcare</i>	JF809930	JF809960	JF809909	—
<i>Oreobates granulatus</i>	JF809929	EU368897	JF809908	JF809887
<i>Oreobates heterodactylus</i>	JF809923	EU192296	JF809902	JF809882
<i>Oreobates ibischi</i>	FJ438817	FJ438806	—	—
<i>Oreobates lehri</i>	JF809927	JF809957	JF809906	—
<i>Oreobates lundbergi</i>	JF809928	JF809958	JF809907	JF809886
<i>Oreobates machiguenga</i>	JF809932	JF809969	JF809911	JF809889
<i>Oreobates madidi</i>	JF809922	FJ539070	JF809901	—
<i>Oreobates pereger</i>	JF809926	JF809958	JF809905	JF809885
<i>Oreobates quixensis</i>	EF493828	EF493662	—	JF809893
<i>Oreobates remotus</i>	—	JN688275	—	—
<i>Oreobates sanctaerucis</i>	JF809924	JF809951	JF809903	JF809883
<i>Oreobates sanderi</i>	—	EU368904	—	—
<i>Oreobates saxatilis</i>	JF809931	EU186708	JF809910	JF809888
<i>Phrynopus auriculatus</i>	EF493708	EF493708	—	—
<i>Phrynopus barthlenae</i>	AM039721	AM039649	—	—
<i>Phrynopus bracki</i>	EF493709	EF493709	EF493421	EF493507
<i>Phrynopus bufoides</i>	AM039713	AM039645	—	—
<i>Phrynopus heimorum</i>	AM039704	AM039636	—	—
<i>Phrynopus horstpauli</i>	AM039715	AM039651	—	—
<i>Phrynopus juninensis</i>	AM039725	AM039657	—	—
<i>Phrynopus kauneorum</i>	AM039718	AM039650	—	—
<i>Phrynopus pesantesi</i>	AM039724	AM039656	—	—
<i>Phrynopus tautzorum</i>	AM039720	AM039652	—	—
<i>Phrynopus tribulosus</i>	EU186725	EU186707	—	—
<i>Psychrophrynella guillei</i>	AY843720	AY843720	—	DQ282995
<i>Psychrophrynella usurpator</i>	EF493714	EF493714	EU186762	EU186780
<i>Psychrophrynella wettsteini</i>	EU186696	EU186696	EU186755	EU186776

	28S	CYTB	HH3	POMC
<i>Barycholos ternetzi</i>	DQ283496	JX298401	DQ284144	JX298136
<i>Haddadus binotatus</i>	DQ283493	GQ345198	DQ284142	GQ345259
<i>Holoaden bradei</i>	—	JX298403	—	JX298138
<i>Hypodactylus brunneus</i>	GQ345138	GQ345203	GQ345218	GQ345264
<i>Lynchiuss nebulanastes</i>	—	—	—	AY819154
<i>Oreobates berdemenos</i>	—	KJ125511	—	—
<i>Oreobates crepitans</i>	—	KJ125512	—	—
<i>Oreobates cruralis</i>	—	EU368881	—	—
<i>Oreobates discoidalis</i>	—	EU368883	—	—
<i>Oreobates heterodactylus</i>	—	EU368885	—	—
<i>Oreobates madidi</i>	—	EU368887	—	—
<i>Oreobates quixensis</i>	—	EU368889	—	AY819093
<i>Oreobates remotus</i>	—	JN688276	—	—
<i>Oreobates sanderi</i>	—	EU368891	—	—
<i>Oreobates saxatilis</i>	—	—	DQ284091	—
<i>Phrynopus bracki</i>	GQ345137	GQ345202	GQ345217	GQ345263

APPENDIX II
Continued.

	28S	CYTb	HH3	POMC
<i>Psychrophrynella guillei</i>	AY844323	—	DQ284371	—
<i>Psychrophrynella usurpator</i>	—	GQ345205	—	—
<i>Psychrophrynella wettsteini</i>	GQ345139	—	GQ345219	GQ345266
	CMYC-EX2	CMYC-EX3	RHO	SIA
<i>Barycholos ternetzi</i>	—	—	DQ283810	—
<i>Haddadus binotatus</i>	GQ345147	GQ345165	DQ283807	GQ345309
<i>Hypodactylus brunneus</i>	GQ345151	—	—	GQ345315
<i>Hypodactylus dolops</i>	—	—	GQ345304	—
<i>Lynchiuss nebulanastes</i>	AY819320	—	—	—
<i>Oreobates ibischi</i>	AY211288	AY211288	—	—
<i>Oreobates quixensis</i>	AY819178	AY819257	—	—
<i>Oreobates saxatilis</i>	—	—	DQ283788	DQ282661
<i>Phrynopus bracki</i>	GQ345150	GQ345168	GQ345303	GQ345314
<i>Psychrophrynella wettsteini</i>	GQ345153	—	—	GQ345316