Systematics of *Pholidobolus* lizards (Squamata, Gymnophthalmidae) from southern Ecuador, with descriptions of four new species

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Abstract

Four new species of *Pholidobolus* lizards are described from poorly explored areas in the Andes of southern Ecuador based on morphological and genetic evidence. Among other morphological characters, *Pholidobolus samek* sp. nov. and *P. condor* sp. nov. differ from their congeners in having green dorsolateral stripes on head. Males of *P. condor* sp. nov. differ from those of *P. samek* sp. nov. in having reddish flanks and venter. *P. dolichoderes* sp. nov. is distinguished by having a long neck, with more scales between orbit and tympanum, whereas *P. fascinatus* sp. nov. is distinguished by lacking enlarged medial scales on collar and a conspicuous vertebral stripe. In addition, the phylogenetic position of the new species is inferred using DNA sequences of mitochondrial and nuclear genes. The phylogeny supports strongly monophyly of each of the new species and renders *P. macbrydei* paraphyletic and split into six subclades. Available data suggest that the new species have restricted distribution ranges (< 100 km² each), and it is proposed that their classification be as Data Deficient or Critically Endangered species. The results reveal unexpected levels of diversity within *Pholidobolus* in the Andes of southern Ecuador and highlight the importance of improving scientific collections and conservation efforts in this area.

Keywords

Andes, Cordillera del Cóndor, diversity, phylogeny, taxonomy
Introduction

The uplift of the Andes mountains was one of the most influential geological events for the evolution and diversification of the South American biota during the Cenozoic. For example, it created many habitats and microclimates that became important centers of biodiversity and endemism (Pérez-Escobar et al. 2017). Therefore, the evolution of diverse Andean taxa is a complex research topic that has attracted the attention of many scientists (Castoe et al. 2004, Torres-Carvajal et al. 2015, Betancourt et al. 2018, Moravec et al. 2018, Lehr et al. 2019). With more than 250 species, Gymnophthalmidae is one of the most diverse lizard clades in the Neotropics. The uplift of the Andes had a strong influence on the radiation of gymnophthalmid lizards, resulting in high levels of diversity and endemism along the Tropical Andes (Torres-Carvajal et al. 2016; Moravec et al. 2018).

*Pholidobolus* lizards are among the most prominent gymnophthalmids in the northern Andes. They are small (SVL ≤ 60 mm), terrestrial, oviparous, and restricted to the Andes of Colombia, Ecuador, and northern Peru at elevations between 1800 and 4100 m (Hurtado-Gómez et al. 2018; Torres-Carvajal et al. 2014; Venegas et al. 2016). *Pholidobolus* is currently known to include ten species: *P. affinis*, *P. anomalus*, *P. dicrus*, *P. hillisi*, *P. macbrydei*, *P. montium*, *P. paramuno*, *P. prefrontalis*, *P. ulisesi*, and *P. vertebralis*, of which three were described in recent years. Remarkably, *P. anomalus* is the only species in the genus that occurs in southern Peru (Cusco), but its generic identity remains questionable (Torres-Carvajal and Mafla-Endara 2013).

The study of *Pholidobolus* and other gymnophthalmid taxa has been often hampered by the paucity of specimens in collections. For example, the recent description of *P. paramuno* reveals the importance of increased sampling effort in the Paramo ecosystem in the northern Andes of Colombia. Similarly, recent collections in poorly explored areas of the southern Andes of Ecuador yielded new specimens of *Pholidobolus* lizards, which we were unable to assign to any of the currently recognized species. Based on these specimens, here we combine evidence from morphology and DNA sequences to describe four new species of *Pholidobolus* and infer their phylogenetic affinities.

Materials and methods

Genetic data

Total genomic DNA was digested and extracted from liver or muscle tissue using a guanidinium isothiocyanate extraction protocol. Tissue samples were first mixed with Proteinase K and a lysis buffer and digested overnight prior to extraction. DNA samples were quantified using a Nanodrop ND-1000 (NanoDrop Technologies, Inc.), resuspended and diluted to 25 ng/µl in ddH2O prior to amplification.

Using primers and amplification protocols from the literature (Pellegrino et al. 2001; Torres-Carvajal and Mafla-Endara 2013), we obtained 1,493 aligned nucleotides (nt) encompassing three mitochondrial genes, 12S (339 nt), 16S (533 nt), and ND4 (621 nt) from 16 individuals of the four new species herein described, as well as 21 individuals of
Pholidobolus macbrydei. In addition, we obtained 411 nucleotides of the Dynein Axonemal Heavy Chain 3 (DNAH3) nuclear gene from 65 individuals of Anadia rhombifera, Macropholidus annectens, M. huancabambae, M. labiopunctatus, M. ruthveni, Pholidobolus affinis, P. dierus, P. billisi, P. macbrydei, P. montium, P. prefrontalis, P. ulisesi, P. vertebralis, and the four new species. DNAH3 was amplified using the primers DNAH3_f1 (GG-TAAAATGATAGAAGAYTACTG) and DNAH3_r6 (CTKGAGTTRGAHACAAT-KATGCCAT). The amplification protocol consisted of 1 cycle of initial denaturation for 5 min at 95 °C, 40 cycles of denaturation for 35s at 94 °C, annealing for 1 min at 72 °C, and extension for 1 min at 72 °C, as well as a final extension for 10 min at 72 °C (Townsend et al. 2008). Positive PCR products were visualized in agarose electrophoretic gels and treated with ExoSAP-IT to remove unincorporated primers and dNTPs. Cycle sequencing reactions were carried out by Macrogen Inc. GenBank accession numbers of sequences generated in this study are shown in Table 1. After incorporating GenBank sequences, our data matrix for phylogenetic analyses contained 74 taxa and 1904 characters.

Phylogenetic analyses

Data were assembled and aligned in Geneious v5.4.6. (Kearse et al. 2012) under default settings for MAFFT Multiple Alignment (Katoh and Toh 2010). ND4 and DNAH3 sequences were translated into amino acids for confirmation of alignment. The best-fit nucleotide substitution models and partitioning scheme were chosen simultaneously using PartitionFinder v2.1.1 (Lanfear et al. 2012) under the Bayesian Information Criterion (BIC). Genes were combined into a single dataset with four partitions: (i) 1st codon position of ND4 and 12S [GTR + I + G]; (ii) 2nd codon position of ND4, 1st codon and 2nd codon positions of DNAH3 [HKY + I + G]; (iii) 3rd codon position of ND4 [GTR + G]; (iv) 16S and 3rd codon position of DNAH3 [SYM + I + G]. Both maximum likelihood (ML) and Bayesian inference (BI) methods were used to obtain the optimal tree topology of the combined, partitioned dataset using the programs RAxML v.8.2.12 (Stamatakis 2014) and MrBayes v3.2.6 (Ronquist et al. 2012), respectively. The ML analysis was performed under the GTRGAMMA model for all partitions. Nodal support (BS) was assessed with the rapid bootstrapping algorithm under the MRE-based Boot-stopping criterion (252 replicates). For BI analysis, all parameters were unlinked between partitions (except topology and branch lengths), and rate variation (preset ratepr = variable) was invoked. Four independent runs, each with four MCMC chains, were set for ten million generations, sampling every 10,000 generations. All analyses were performed using the CIPRES platform (Miller et al. 2010). Results were analyzed in Tracer 1.6 (Rambaut and Drummond 2007) to assess convergence and effective sample sizes (ESS) for all parameters, based on which the first 10% of trees were removed from each run. The remaining trees were used to calculate posterior probabilities (PP) for each bipartition in a Maximum Clade Credibility Tree. The phylogenetic trees were visualized and edited using FigTree v1.4.2 (Rambaut 2014). In order to address interspecific genetic differentiation, uncorrected genetic distances were calculated in MEGA 7 (Kumar et al. 2016) after removing ambiguous positions for each sequence pair (pairwise deletion option).
| Taxon                   | Voucher | Locality                                      | GenBank number                     | GenSeq Nomenclature |
|------------------------|---------|-----------------------------------------------|------------------------------------|---------------------|
| Anadia rhombifera      | QCAZ 11862 | QCAZ 11862; Ecuador: Cotopaxi: San Francisco de Las Pampas | KU902135 KU902216 KU902291 MN849427 | genseq-4            |
| Macropholidus annectens| QCAZ 11120 | Ecuador: Loja: 15 km E Loja                    | KC894341 KC894355 KC894369 MN849430 | genseq-4            |
|                        | QCAZ 11121 | Ecuador: Loja: 15 km E Loja                    | KC894342 KC894356 KC894370 MN849431 | genseq-4            |
| Macropholidus huancabambae | CORBIDI 10492 | Peru: Piura: Huancabamba: Las Pozas              | KC894343 KC894357 KC894371 MN849428 | genseq-4            |
|                        | CORBIDI 10493 | Peru: Piura: Huancabamba: Las Pozas              | KC894344 KC894358 KC894372 – genseq-4 |
|                        | CORBIDI 10496 | Peru: Piura: Huancabamba: Las Pozas              | KC894345 KC894359 KC894373 MN849429 | genseq-4            |
| Macropholidus labiopunctatus | CORBIDI 12932 | Peru: Piura: Ayabaca                           | KP874774 KP874826 KP874936 MN849432 | genseq-4            |
| Macropholidus ruthveni  | CORBIDI 4281 | Peru: Lambayeque: El Totora                    | KC894354 C894368 C894382 MN849433 | genseq-4            |
| Pholidobolus affinis    | QCAZ 9641 | Ecuador: Cotopaxi: San Miguel de Salcedo, Cutuchi River | KC894348 C894362 C894376 MN849435 | genseq-4            |
|                        | QCAZ 9900 | Ecuador: Chimborazo: Cola                      | KC894349 KC894363 KC894377 – genseq-4 |
| Pholidobolus condor sp. nov. | QCAZ 16788 | Ecuador: Morona-Santiago: el Quimi              | MN724005 MN720239 MN717135 MN849464 | genseq-2            |
|                        | QCAZ 16789 | Ecuador: Morona-Santiago: el Quimi              | MN724006 MN720240 MN717134 MN849465 | genseq-2            |
|                        | QCAZ 16790 | Ecuador: Morona-Santiago: el Quimi              | MN724007 MN720241 MN717136 MN849466 | genseq-2            |
|                        | QCAZ 15844 | Ecuador: Morona-Santiago: el Quimi              | MN723996 MN720230 MN717125 MN849443 | genseq-1            |
| Pholidobolus dicrosp. nov. | QCAZ 5304 | Ecuador: Morona-Santiago: Guarumales            | KP874776 KP874828 KP874938 MN849436 | genseq-4            |
|                        | QCAZ 6936 | Ecuador: Tungurahua: Río Blanco                 | – KP874829 KP874939 MN849437 genseq-4 |
| Pholidobolus dolichoderes sp. nov. | QCAZ 16349 | Ecuador: Cañar: Oña                            | MN724000 MN720234 MN717129 MN849459 | genseq-2            |
|                        | QCAZ 16350 | Ecuador: Cañar: Oña                            | MN724001 MN720235 MN717130 MN849460 | genseq-2            |
|                        | QCAZ 16351 | Ecuador: Cañar: Oña                            | MN724002 MN720236 MN717131 MN849461 | genseq-2            |
|                        | QCAZ 16352 | Ecuador: Cañar: Oña                            | MN724003 MN720237 MN717132 MN849462 | genseq-2            |
|                        | QCAZ 16353 | Ecuador: Cañar: Oña                            | MN724004 MN720238 MN717133 MN849463 | genseq-1            |
| Pholidobolus fascinatus sp. nov. | QCAZ 15118 | Ecuador: El Oro: Chillacocha                    | MN724017 MN720251 MN717146 MN849476 | genseq-2            |
|                        | QCAZ 15120 | Ecuador: El Oro: Chillacocha                    | MN724018 MN720252 MN717147 MN849477 | genseq-1            |
|                        | QCAZ 15122 | Ecuador: El Oro: Chillacocha                    | MN724019 MN720253 – MN849478 genseq-2 |
|                        | QCAZ 15170 | Ecuador: El Oro: Chillacocha                    | MN724020 MN720254 MN717148 MN849479 | genseq-2            |
## Systematics of *Pholidobolus* lizards

### Taxon | Voucher | Locality | GenBank number | GenSeq Nomenclature
--- | --- | --- | --- | ---

**Pholidobolus hillisi**
- **QCAZ 4998** Ecuador: Zamora-Chinchipe: near San Francisco Research Station
  - 12S: KP090167
  - 16S: KP090170
  - ND4: KP090173
  - DNAH3: MN849438
genseq-4

- **QCAZ 4999** Ecuador: Zamora-Chinchipe: near San Francisco Research Station
  - 12S: KP090169
  - 16S: KP090172
  - ND4: KP090175
  - DNAH3: MN849439
genseq-4

- **QCAZ 5000** Ecuador: Zamora-Chinchipe: near San Francisco Research Station
  - 12S: KP090168
  - 16S: KP090171
  - ND4: KP090174
  - DNAH3: MN849440
genseq-4

"*Pholidobolus macbrydei"*
- **KU 218406** Ecuador: Azuay: Cuenca
  - 12S: AY507848
  - 16S: AY507867
  - ND4: AY507866
  - DNAH3: –
genseq-4

- **QCAZ 9914** Ecuador: Azuay: Guabilid
  - 12S: KC894352
  - 16S: KC894366
  - ND4: KC894380
  - DNAH3: MN849441
genseq-4

- **QCAZ 9932** Ecuador: Azuay: 20 km on road Cuenca-El Cajas
  - 12S: KC894353
  - 16S: KC894367
  - ND4: KC894381
  - DNAH3: MN849442
genseq-4

- **QCAZ 9947** Ecuador: Cañar: Cañar
  - 12S: MN724012
  - 16S: MN720246
  - ND4: MN717141
  - DNAH3: MN849474
genseq-4

- **QCAZ 10051** Ecuador: Cañar: Río Gualllicanga, quebrada Juncal
  - 12S: MN724014
  - 16S: MN720248
  - ND4: MN717143
  - DNAH3: MN849472
genseq-4

- **QCAZ 10052** Ecuador: Cañar: Río Gualllicanga, quebrada Juncal
  - 12S: MN724015
  - 16S: MN720249
  - ND4: MN717144
  - DNAH3: MN849473
genseq-4

- **QCAZ 10050** Ecuador: Cañar: A 1000 m de la Panamericana Juncal
  - 12S: MN724013
  - 16S: MN720247
  - ND4: MN717142
  - DNAH3: MN849471
genseq-4

- **QCAZ 15811** Ecuador: Cañar: Mazar
  - 12S: MN724021
  - 16S: MN720255
  - ND4: MN717149
  - DNAH3: MN849480
genseq-4

- **QCAZ 15812** Ecuador: Cañar: Mazar
  - 12S: MN724022
  - 16S: MN720256
  - ND4: MN717150
  - DNAH3: MN849481
genseq-4

- **QCAZ 15813** Ecuador: Cañar: Mazar
  - 12S: MN724023
  - 16S: MN720257
  - ND4: MN717151
  - DNAH3: MN849482
genseq-4

- **QCAZ 15814** Ecuador: Cañar: Mazar
  - 12S: MN724024
  - 16S: MN720258
  - ND4: MN717152
  - DNAH3: –
genseq-4

- **QCAZ 15815** Ecuador: Cañar: Mazar
  - 12S: MN724025
  - 16S: MN520259
  - ND4: MN717153
  - DNAH3: –
genseq-4

- **QCAZ 15816** Ecuador: Cañar: Mazar
  - 12S: MN724026
  - 16S: MN720260
  - ND4: MN717154
  - DNAH3: MN849483
genseq-4

- **QCAZ 15817** Ecuador: Cañar: Mazar
  - 12S: MN724027
  - 16S: MN720261
  - ND4: MN717155
  - DNAH3: MN849484
genseq-4

- **QCAZ 15818** Ecuador: Cañar: Mazar
  - 12S: MN724028
  - 16S: MN720262
  - ND4: MN717156
  - DNAH3: MN849485
genseq-4

- **QCAZ 15819** Ecuador: Cañar: Mazar
  - 12S: MN724029
  - 16S: MN720263
  - ND4: MN717157
  - DNAH3: MN849486
genseq-4

- **QCAZ 15820** Ecuador: Cañar: Mazar
  - 12S: MN724030
  - 16S: MN720264
  - ND4: MN717158
  - DNAH3: MN849487
genseq-4

- **QCAZ 15823** Ecuador: Cañar: Mazar
  - 12S: MN724031
  - 16S: MN720265
  - ND4: MN717159
  - DNAH3: MN849488
genseq-4

- **QCAZ 15824** Ecuador: Cañar: Mazar
  - 12S: MN724032
  - 16S: MN720266
  - ND4: MN717160
  - DNAH3: MN849489
genseq-4

- **QCAZ 6945** Ecuador: Loja: Jimbura
  - 12S: MN724008
  - 16S: MN720242
  - ND4: MN717137
  - DNAH3: MN849467
genseq-4

- **QCAZ 6946** Ecuador: Loja: Jimbura
  - 12S: MN724009
  - 16S: MN720243
  - ND4: MN717138
  - DNAH3: MN849468
genseq-4
| Taxon                           | Voucher   | Locality                           | GenBank number | GenSeq | Nomenclature |
|--------------------------------|-----------|------------------------------------|----------------|--------|--------------|
|                                |           |                                    |                |        |              |
|                                |           |                                    |    12S        |  16S   | ND4          | DNAH3        |
| **"Pholidobolus macbrydei"**   | QCAZ 10054| Ecuador: Loja: Colambo Yacuri Forest| MN724016       | MN720250| MN717145     | MN849475     |
|                                | QCAZ 7894 | Ecuador: El Oro: Guanazán          | MN724011       | MN720245| MN717140     | MN849470     |
|                                | QCAZ 7891 | Ecuador: El Oro: Guanazán          | MN724010       | MN720244| MN717139     | MN849469     |
| **Pholidobolus montium**       | QCAZ 4051 | Ecuador: Pichincha: Quito          | KC894346       | KC894360| KC894374     | MN849443     |
|                                | QCAZ 9044 | Ecuador: Pichincha: Tababela       | KC894347       | KC894361| KC894375     | MN849444     |
| **Pholidobolus paramuno**      | MHUAR 12451| Colombia: Antoquia                | MK215018       | MK215032| MK215046     | –             |
|                                | MHUAR 12480| Colombia: Antoquia                | MK215019       | MK215033| MK215047     | –             |
|                                | MHUAR 12481| Colombia: Antoquia                | MK215020       | MK215034| MK215048     | –             |
| **Pholidobolus prefrontalis**  | QCAZ 9908 | Ecuador: Chimborazo: Alausí        | KC894350       | KC894364| KC894378     | –             |
|                                | QCAZ 9951 | Ecuador: Chimborazo: Tixán         | KC894351       | KC894365| KC894379     | MN849448     |
| **Pholidobolus samek sp. nov.**| QCAZ 14954| Ecuador: Zamora Chinchipe: Cerro Plateado| MN723997  | MN720231| MN717126     | MN849445     |
|                                | QCAZ 14955| Ecuador: Zamora Chinchipe: Cerro Plateado| MN723998  | MN720332| MN717127     | MN849446     |
|                                | QCAZ 14956| Ecuador: Zamora Chinchipe: Cerro Plateado| MN723999  | MN720233| MN717128     | MN849447     |
| **Pholidobolus ulisesi**       | CORBIDI 12735| Peru: Cajamarca: Jaen: Huamantanga Forest| KP874787  | KP874839| KP874948     | MN849449     |
|                                | CORBIDI 12737| Peru: Cajamarca: Jaen: Huamantanga Forest| KP874788  | KP874840| KP874949     | –             |
|                                | CORBIDI 1679| Peru: Chota: La Granja             | KP874786      | KP874838| KP874947     | MN849450     |
| **Pholidobolus vertebralis**   | QCAZ 10667| Ecuador: Pichincha: Santa Lucía de Nanegal| KP874784  | KP874836| KP874946     | MN849455     |
|                                | QCAZ 10750| Ecuador: Pichincha: Santa Lucía de Nanegal| KP874785  | KP874837| KP874947     | MN849458     |
|                                | QCAZ 5057 | Ecuador: Carchi: Chilma Bajo       | KP874778      | KP874830| KP874940     | MN849451     |
|                                | QCAZ 8687 | Ecuador: Carchi: Chilma Bajo       | KP874779      | KP874831| KP874941     | MN849452     |
|                                | QCAZ 8688 | Ecuador: Carchi: Chilma Bajo       | KP874780      | KP874832| KP874942     | MN849453     |
|                                | QCAZ 8689 | Ecuador: Carchi: Chilma Bajo       | KP874781      | KP874833| KP874943     | MN849454     |
|                                | QCAZ 8717 | Ecuador: Carchi: next to Chilma Bajo| KP874782      | KP874834| KP874944     | MN849456     |
|                                | QCAZ 8724 | Ecuador: Carchi: next to Chilma Bajo| KP874783      | KP874835| KP874945     | MN849457     |
Specimens and morphological data

We examined 98 specimens of *Pholidobolus macbrydei* (Appendix I) and 41 of the new species described herein (see corresponding type series). All specimens are deposited in the herpetological collection at Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (**QCAZ**). The following measurements were taken with a digital caliper (to the nearest 0.1 mm):

| Abbreviation | Description |
|--------------|-------------|
| AGD          | axilla-groin distance; |
| HL           | head length; |
| HW           | head width; |
| ShL          | shank length; |
| SVL          | and snout-vent length. |

Tail length (**TL**) was measured with a ruler. Sex was determined by dissection or by noting the presence of everted hemipenes. We followed the terminology of Montanucci (1973) and Kizirian (1996) for morphological characters.

Because the new species are similar in morphology to *Pholidobolus macbrydei*, we assessed the degree of differentiation among them with a Principal Components Analysis (PCA) in R (R Core Team 2018). The PCA was based on 16 quantitative morphological characters: (1) number of supraoculars (**NSO**), (2) number of scales along margin of upper jaw (**SUI**), (3) number of scales along margin of lower jaw (**SLJ**), (4) number of gular and jaw scales (**SGJ**), (5) number of ventrals (**SGV**), (6) number of dorsals (**DEL**), (7) number of temporals (**NTS**), (8) number of scales around body (**SAB**), (9) number of scales around tail (**SAT**), (10) number of supradigital scales of third finger (**SF3**), (11) number of supradigital scales of fifth finger (**SF5**), (12) number of supradigital scales of third toe (**ST3**), (13) number of supradigital scales of fourth toe (**ST4**), (14) number of supradigital scales of fifth toe (**ST5**), (15) lower eyelid scales (**LES**), and (16) collar scales (i.e., posterior transverse row of gulars; **SGC**) (Peters 1964, Montanucci 1973).

Hemipenes were prepared following the procedures described by Manzani and Abe (1988), as modified by Pesantes (1994) and Zaher (1999). Organs were everted after immersion in a potassium hydroxide solution, the retractor muscles were manually separated, and the everted organs filled with blue-stained petroleum jelly. Hemipenes were then immersed in an alcoholic solution of Alizarin Red for 24 hours in order to stain eventual calcified structures (e.g., spines or spicules), in an adaptation proposed by Nunes et al. (2012) on the procedures described by Uzzell (1973) and Harvey and Embert (2008). The terminology of hemipenial structures follows previous literature (Dowling and Savage 1960; Hurtado-Gómez et al. 2018; Nunes et al. 2012; Sánchez-Pacheco et al. 2017; Savage 1997; Venegas et al. 2016).

**Systematics**

The taxonomic conclusions of this study are based on the observation of morphological features and color pattern, as well as inferred phylogenetic relationships.
consider this information as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998; 2007).

The new species share with all known species of *Pholidobolus* the presence of a ventrolateral fold between fore and hind limbs and the absence of a single transparent palpebral disc (Montanucci 1973).

**Results**

**Phylogenetic relationships and genetic distances**

Tree topologies under ML and BI approaches were generally similar; here we describe the maximum clade credibility tree (Fig. 1). Our hypothesis supports the monophyly of *Pholidobolus* (BS= 60, PP = 0.99) and is congruent with previous molecular phylogenies in that *P. ulisesi* and *P. hillisi* form a clade (BS = 62, PP = 0.92) sister to all other congeners (Torres-Carvajal et al. 2015, 2016; Hurtado-Gómez et al. 2018). Following branching order, the strongly supported species pair *P. affinis, P. montium* is sister to all remaining species, which form a clade where (*P. prefrontalis* (*P. paramuno, P. dicrus, P. vertebralis*)) is sister to a subclade containing the new species described in this paper and a paraphyletic *P. macbrydei*. Hereafter we refer to the latter subclade as the “*P. macbrydei*” species complex.

The “*P. macbrydei*” species complex (BS = 81, PP = 1) is divided into two allopatric and strongly supported clades (Fig. 1) that include four new species described below and a paraphyletic “*P. macbrydei*” divided in six subclades (Clades A–F). A southeastern clade (BS = 99, PP = 1) contains *P. condor* sp. nov. as sister to (*P. samek* sp. nov., “*P. macbrydei*” Clade A [Loja province]). The ML tree recovered *P. condor* as sister to “*P. macbrydei*” Clade A with low support (BS = 58). A northwestern clade (BS = 85, PP = 0.96) is composed of “*P. macbrydei*” Clade B from Cañar province as sister to a clade that includes all remaining samples, in which *P. fascinatus* sp. nov. is nested along with “*P. macbrydei*” Clades C, D, and E (Azuy and Cañar provinces) in a strongly supported subclade (BS = 71, PP = 1) sister to the maximally supported (*P. dolichoderes, “*P. macbrydei*” Clade F [El Oro province]). All new species are strongly supported as monophyletic (BS ≥ 98, PP = 1).

Uncorrected *p*-genetic distances for 16S, 12S, and ND4 are presented in Tables 2, 3, and 4, respectively. Distance values among all recognized species of *Pholidobolus*, the four new species described in this paper, and the six “*P. macbrydei*” clades range between 1 (e.g., *P. condor* sp. nov. vs. *P. samek* sp. nov., Clade C vs. Clade D)—10% (e.g., *P. paramuno* vs. *P. dicrus*) for 12S (average = 5% ± 0.01 SD); 1 (*P. dolichoderes* sp. nov. vs. Clade F)—6% (e.g., *P. dicrus* vs. *P. ulisesi*) for 16S (average = 4% ± 0.01 SD); and 4 (*P. dolichoderes* sp. nov. vs. Clade F)—19% (e.g., *P. dicrus* vs. *P. vertebralis*) for ND4 (average = 14% ± 0.03 SD). Maximum distance values within the “*P. macbrydei*” complex are 5% (Clade A vs. Clade F) for 12S, 4% (*P. condor* sp. nov. vs. Clade F) for 16S, and 14% (Clade A vs. Clade F) for ND4. The genetic distances for the nuclear gene NDH3 are generally low (0–3%, average = 1% ± 0.01 SD).
Systematics of *Pholidobolus* lizards

Figure 1. Phylogeny of *Pholidobolus*. Maximum clade credibility tree derived from a partitioned analysis of 1904 bp of mitochondrial and nuclear DNA. Bayesian posterior probabilities are shown above branches and bootstrap values (RAxML analysis) below branches; values ≤ 0.5 and 50, respectively, are not shown. For clarity, outgroup taxa and values on short branches are not shown. Species outside the "*P. macbrydei*" complex are in grey; new species described in this paper are in color matching the distribution records of the map in Figure 7. The species name followed by voucher number and province ("*P. macbrydei*" complex only) are provided for each terminal. Photographs from top to bottom: *P. dolichoderes* sp. nov. holotype, *P. fascinatus* sp. nov. holotype, "*P. macbrydei*" (Clade B) QCAZ 15824, *P. samek* sp. nov. holotype, *P. condor* sp. nov. holotype.
Table 2. Pairwise genetic distances (uncorrected $p$) of 16S DNA sequences among species and clades of *Pholidobolus* included in this study. This analysis involved 66 nucleotide sequences and 533 positions.

| Taxon                                      | 1  | 2      | 3      | 4      | 5      | 6      | 7      | 8      | 9      | 10     | 11     | 12     | 13     | 14     | 15     | 16     | 17     |
|--------------------------------------------|----|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| *Pholidobolus condor* sp. nov.             |    |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |
| *Pholidobolus samek* sp. nov.              | 0.03 |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |
| *Pholidobolus dolichoderes* sp. nov.       | 0.04 | 0.03   |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |
| *Pholidobolus fascinatus* sp. nov.         | 0.03 | 0.03   | 0.03   |        |        |        |        |        |        |        |        |        |        |        |        |        |        |
| Clade A                                    | 0.03 | 0.02   | 0.04   | 0.03   |        |        |        |        |        |        |        |        |        |        |        |        |        |
| Clade B                                    | 0.03 | 0.03   | 0.03   | 0.03   | 0.02   |        |        |        |        |        |        |        |        |        |        |        |        |
| Clade C                                    | 0.02 | 0.02   | 0.03   | 0.02   | 0.03   | 0.03   |        |        |        |        |        |        |        |        |        |        |        |
| Clade D                                    | 0.03 | 0.02   | 0.03   | 0.03   | 0.03   | 0.03   | 0.02   |        |        |        |        |        |        |        |        |        |        |
| Clade E                                    | 0.03 | 0.03   | 0.04   | 0.02   | 0.04   | 0.03   | 0.02   | 0.03   | 0.03   |        |        |        |        |        |        |        |        |
| Clade F                                    | 0.04 | 0.03   | 0.01   | 0.04   | 0.04   | 0.02   | 0.03   | 0.03   | 0.03   | 0.04   | 0.04   | 0.04   | 0.03   | 0.03   | 0.03   | 0.04   |
| *Pholidobolus affinis*                     | 0.04 | 0.03   | 0.03   | 0.03   | 0.04   | 0.03   | 0.03   | 0.02   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   |
| *Pholidobolus dicrus*                      | 0.04 | 0.04   | 0.04   | 0.04   | 0.04   | 0.04   | 0.04   | 0.03   | 0.05   | 0.04   | 0.05   | 0.04   | 0.05   | 0.04   | 0.05   | 0.05   |
| *Pholidobolus hillisi*                     | 0.05 | 0.05   | 0.05   | 0.05   | 0.04   | 0.04   | 0.04   | 0.03   | 0.05   | 0.04   | 0.04   | 0.04   | 0.05   | 0.04   | 0.04   | 0.05   |
| *Pholidobolus montium*                     | 0.03 | 0.02   | 0.03   | 0.03   | 0.02   | 0.02   | 0.02   | 0.04   | 0.03   | 0.04   | 0.03   | 0.04   | 0.04   | 0.04   | 0.04   | 0.04   |
| *Pholidobolus paramuno*                    | 0.04 | 0.04   | 0.04   | 0.03   | 0.04   | 0.03   | 0.03   | 0.04   | 0.04   | 0.04   | 0.03   | 0.04   | 0.04   | 0.04   | 0.03   | 0.03   |
| *Pholidobolus prefrontalis*                | 0.03 | 0.03   | 0.03   | 0.03   | 0.02   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   | 0.03   |
| *Pholidobolus ulisesi*                     | 0.05 | 0.05   | 0.05   | 0.05   | 0.05   | 0.06   | 0.06   | 0.05   | 0.05   | 0.06   | 0.04   | 0.05   | 0.05   | 0.05   | 0.05   | 0.05   |
| *Pholidobolus vertebralis*                 | 0.05 | 0.04   | 0.04   | 0.04   | 0.05   | 0.04   | 0.04   | 0.05   | 0.05   | 0.05   | 0.05   | 0.04   | 0.04   | 0.04   | 0.04   | 0.04   | 0.06  |
Table 3. Pairwise genetic distances (uncorrected $p$) of 12S DNA sequences among species and clades of *Pholidobolus* included in this study. This analysis involved 65 nucleotide sequences and 339 positions.

| Taxon                              | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|------------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| *Pholidobolus condor* sp. nov.     |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| *Pholidobolus samek* sp. nov.     | 0.01 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| *Pholidobolus dolichoderes* sp. nov. | 0.04 | 0.04 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| *Pholidobolus fascinatus* sp. nov. | 0.03 | 0.03 | 0.03 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| Clade A                           | 0.03 | 0.03 | 0.05 | 0.04 |    |    |    |    |    |    |    |    |    |    |    |    |    |
| Clade B                           | 0.03 | 0.03 | 0.04 | 0.03 | 0.03 |    |    |    |    |    |    |    |    |    |    |    |    |
| Clade C                           | 0.02 | 0.02 | 0.02 | 0.02 | 0.03 | 0.03 |    |    |    |    |    |    |    |    |    |    |    |
| Clade D                           | 0.02 | 0.02 | 0.03 | 0.02 | 0.04 | 0.03 | 0.01 |    |    |    |    |    |    |    |    |    |    |
| Clade E                           | 0.02 | 0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.01 | 0.01 |    |    |    |    |    |    |    |    |    |
| Clade F                           | 0.04 | 0.04 | 0.01 | 0.04 | 0.05 | 0.04 | 0.03 | 0.03 | 0.03 |    |    |    |    |    |    |    |    |
| *Pholidobolus affinis*             | 0.05 | 0.04 | 0.06 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.06 |    |    |    |    |    |    |    |
| *Pholidobolus dicrois*             | 0.07 | 0.07 | 0.08 | 0.07 | 0.07 | 0.07 | 0.08 | 0.07 | 0.08 | 0.08 | 0.08 |    |    |    |    |    |    |
| *Pholidobolus hillisi*             | 0.05 | 0.04 | 0.05 | 0.05 | 0.06 | 0.05 | 0.04 | 0.04 | 0.05 | 0.05 | 0.06 | 0.08 |    |    |    |    |    |
| *Pholidobolus montium*             | 0.03 | 0.04 | 0.05 | 0.05 | 0.06 | 0.04 | 0.04 | 0.04 | 0.05 | 0.02 | 0.07 | 0.05 |    |    |    |    |    |
| *Pholidobolus paramuno*            | 0.06 | 0.06 | 0.07 | 0.07 | 0.07 | 0.06 | 0.06 | 0.06 | 0.07 | 0.10 | 0.07 | 0.06 |    |    |    |    |    |
| *Pholidobolus prefrontalis*        | 0.02 | 0.02 | 0.04 | 0.04 | 0.03 | 0.02 | 0.03 | 0.03 | 0.05 | 0.03 | 0.04 | 0.02 | 0.06 |    |    |    |    |
| *Pholidobolus ulisesi*             | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.03 | 0.04 | 0.04 | 0.04 | 0.07 | 0.04 | 0.04 | 0.06 | 0.03 |    |    |    |
| *Pholidobolus vertebralis*         | 0.08 | 0.08 | 0.09 | 0.08 | 0.07 | 0.08 | 0.08 | 0.08 | 0.09 | 0.08 | 0.06 | 0.10 | 0.08 | 0.10 | 0.06 | 0.08 |    |
Table 4. Pairwise genetic distances (uncorrected $p$) of ND4 DNA sequences among species and clades of *Pholidobolus* included in this study. This analysis involved 64 nucleotide sequences and 621 positions.

| Taxon                     | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    |
|---------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| *Pholidobolus condor* sp. nov. | 0.08  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| *Pholidobolus samek* sp. nov. | 0.13  | 0.12  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| *Pholidobolus dolichoderes* sp. nov. | 0.09  | 0.10  | 0.09  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| *Pholidobolus fascinatus* sp. nov. | 0.09  | 0.10  | 0.13  | 0.11  |       |       |       |       |       |       |       |       |       |       |       |       |       |
| Clade A                   | 0.12  | 0.11  | 0.10  | 0.09  | 0.13  | 0.11  |       |       |       |       |       |       |       |       |       |       |       |
| Clade B                   | 0.11  | 0.10  | 0.10  | 0.09  | 0.11  | 0.10  | 0.09  | 0.10  | 0.09  |       |       |       |       |       |       |       |       |
| Clade C                   | 0.10  | 0.10  | 0.09  | 0.10  | 0.11  | 0.12  | 0.11  | 0.12  | 0.12  | 0.11  |       |       |       |       |       |       |       |
| Clade D                   | 0.10  | 0.09  | 0.10  | 0.09  | 0.10  | 0.11  | 0.10  | 0.11  | 0.11  | 0.09  | 0.11  |       |       |       |       |       |       |
| Clade E                   | 0.10  | 0.11  | 0.10  | 0.09  | 0.10  | 0.11  | 0.10  | 0.11  | 0.11  | 0.11  |       |       |       |       |       |       |       |
| Clade F                   | 0.12  | 0.12  | 0.12  | 0.12  | 0.11  | 0.12  | 0.11  | 0.12  | 0.12  | 0.12  | 0.10  | 0.10  | 0.09  | 0.10  | 0.10  | 0.09  |       |
| *Pholidobolus affinis*     | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  |
| *Pholidobolus dicros*      | 0.14  | 0.15  | 0.15  | 0.15  | 0.15  | 0.15  | 0.15  | 0.15  | 0.15  | 0.15  | 0.16  | 0.16  | 0.16  | 0.16  | 0.16  | 0.16  | 0.16  |
| *Pholidobolus hillisi*     | 0.13  | 0.14  | 0.15  | 0.16  | 0.17  | 0.18  | 0.19  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  |
| *Pholidobolus montium*     | 0.13  | 0.14  | 0.15  | 0.16  | 0.17  | 0.18  | 0.19  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  |
| *Pholidobolus paramuno*    | 0.14  | 0.14  | 0.15  | 0.16  | 0.17  | 0.18  | 0.19  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  |
| *Pholidobolus prefrontalis*| 0.14  | 0.15  | 0.16  | 0.17  | 0.18  | 0.19  | 0.20  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  | 0.18  |
| *Pholidobolus vertebralis* | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  | 0.17  |
Morphological comparisons among species

Two components with eigenvalues > 1.0 were extracted from the PCA (Table 5). These components accounted for 50.7% of the total variation. The highest loadings corresponded to supratympanic temporals (NTS) and number of scales along margin of upper jaw (SUJ) for PC I, and number of scales around the tail (SAT) and number of scales around the body (SAB) for PC II (Table 5). In general, there is wide overlap in morphological space among species of the “P. macbrydei” complex (Fig. 2).

Comparative hemipenial morphology

Hemipenes of holotypes of the four new species described herein are approximately 4–5 mm and 5–7 subcaudal scales long. The organs are fully everted in specimens of P. fascinatus, P. condor, and P. samek and partially everted in P. dolichoderes; the hemipenes of the holotype of P. fascinatus and P. condor are fully expanded, whereas the organs of P. dolichoderes and P. samek are partially expanded (Fig. 3). All hemipenes have two small lobes detached from the hemipenial body when the organ is fully everted. The hemipenis of P. condor presents a distinctive capitular groove originating at the median hemipenial body and extending toward the lobes. The lobes of P. fascinatus, P. condor, and P. samek present folds on their tips, which are not visible in P. dolichoderes due to the partial eversion. The hemipenial body is

Table 5. Character loadings, eigenvalues, and percentage of variance explained by Principal Components (PC) I and II. The analysis was based on 16 morphological characters of specimens of “Pholidobolus macbrydei”, Pholidobolus samek sp. nov., Pholidobolus condor sp. nov., Pholidobolus dolichoderes sp. nov. and P. fascinatus sp. nov. Highest loadings are in bold.

| Variable | PC I | PCA | PC II |
|----------|------|-----|-------|
| NSO      | 0.13 | -0.11 |     |
| SUJ      | **0.32** | -0.15 |     |
| SLJ      | 0.30 | -0.10 |     |
| SGJ      | 0.29 | -0.07 |     |
| SGV      | 0.31 | 0.25  |     |
| DEL      | 0.30 | 0.33  |     |
| NTS      | **0.32** | -0.20 |     |
| SAB      | 0.26 | **0.39** |       |
| SAT      | 0.18 | **0.55** |     |
| SF3      | 0.18 | -0.11 |     |
| SF5      | 0.22 | -0.31 |     |
| ST3      | 0.24 | 0.04  |     |
| ST4      | 0.20 | -0.12 |     |
| ST5      | 0.29 | -0.02 |     |
| LES      | -0.05 | 0.20  |     |
| SGC      | -0.22 | 0.35  |     |
| Eigenvalue | 6.51 | 1.60  | 9.99 |
| %        | 40.69 | 9.99  |     |
cylindrical in *P. dolichoderes* and *P. condor,* whereas in *P. samek* and *P. fascinatus* the body is conical, with the basis distinctly thinner than the rest of the body. The sulcus spermaticus is broad in *P. fascinatus, P. dolichoderes,* and *P. samek,* narrower in *P. condor;* in *P. fascinatus* and *P. condor,* the sulcus spermaticus is deeper than in *P. dolichoderes* and *P. samek.* The sulcus originates medially at the base of the organ and extends in a straight line throughout the body towards the lobes in all species. However, unlike *P. dolichoderes* and *P. condor,* the sulcus originates between thick lips in *P. samek* and *P. fascinatus.* In all species, the sulcus spermaticus bifurcates at the lobular crotch, with each branch extending along the medial face of each lobe.

The sides and borders of the sulcate and asulcate faces are ornamented with a series of roughly equidistant and chevron-shaped flounces, with the chevron vertices aligned medially on each side and directed proximally. All flounces bear calcified comb-like series of spicules, distinctively stained in red with Alizarin. The number of flounces extending along the hemipenial body varies slightly among species: 21 in *P. condor* and *P. samek* and 22 in *P. dolichoderes* and *P. fascinatus.* The base of the asulcate face bears three medial flounces in *P. condor, P. dolichoderes,* and *P. samek,* and four in *P. fascinatus.* All species have a conspicuous unevenness forming a bulge along the margins of the asulcate face.

![Principal components analysis of 16 morphological variables and 140 specimens of the “Pholidobolus macbrydei” species complex. See Table 5 for character loadings on each component.](image)
Figure 3. Comparative hemipenial morphology of *Pholidobolus*. Sulcate (left), lateral (center) and asulcate (right) views of: A *Pholidobolus samek* sp. nov. (QCAZ 14955) B *Pholidobolus condor* sp. nov. (QCAZ 15844) C *Pholidobolus dolichoderes* sp. nov. (QCAZ 16353) D *Pholidobolus fascinatus* sp. nov. (QCAZ 15120). Scale bar: 1 mm.
Systematic accounts

**Pholidobolus samek** sp. nov.
http://zoobank.org/431C8AD2-3164-4051-B7DC-1459C4949F51
Figures 4–6
Proposed standard English name: Green-striped cuilanes
Proposed standard Spanish name: Cuilanes de franjas verdes

**Holotype.** QCAZ 14955 (Figs 4, 5), adult male, Ecuador, Provincia Zamora-Chinchipe, Cerro Plateado Biological Reserve, Cerro Plateado plateau, 4.6159S, 78.7870W, WGS84, 2844 m, 23 September 2016, collected by Diego Almeida, Eloy Nusirquia, Fernando Ayala, Javier Pinto, Alex Achig and Malki Bustos.

**Paratypes (6).** Ecuador: Provincia Zamora-Chinchipe: QCAZ 14954 (adult female), same data as holotype; QCAZ 14956 (adult female), Cerro Plateado Biological Reserve, 4.6050S, 78.8167W, WGS84, 2320 m, 28 September 2016; QCAZ 14969–70, 14976–77(hatchlings) Cerro Plateado Biological Reserve, 4.6179S, 78.7838W, WGS84, 2873 m, 24 September 2016, same collectors as holotype.

**Diagnosis.** *Pholidobolus samek* is unique among its congeners, except *P. condor* sp. nov., in having green dorsolateral stripes on the head. However, adult males of *P. samek* differ from those of *P. condor* sp. nov. in having brighter dorsolateral head stripes and lacking a reddish venter. In addition, *P. affinis*, *P. prefrontalis*, *P. macbrydei*, *P. dolichoderes* sp. nov., and *P. montium* differ from *P. samek* (character states of *P. samek* in parentheses) in having a loreal scale frequently in contact with the supralabials (loreal scale not in contact with supralabials), and dorsal scales finely wrinkled (slightly keeled). *Pholidobolus ulisesi* and *P. hillisi* differ from *P. samek* in having a diagonal white bar along the rictal region (white rictal bar absent). *Pholidobolus samek* can be distinguished from *P. dicrus* by lacking a bifurcating vertebral stripe at midbody. *Pholidobolus affinis*, *P. prefrontalis*, *P. dicrus*, *P. hillisi*, and *P. vertebralis* further differ from *P. samek* in having well defined prefrontal scales (if present, prefrontal scales poorly differentiated). Additionally, *P. samek* has fewer dorsal scales (27–29) than *P. affinis* (45–55), *P. montium* (35–50), *P. prefrontalis* (37–46), *P. macbrydei* (31–43), *P. fascinatus* sp. nov. (32–37), and *P. dolichoderes* sp. nov. (35–40). *Pholidobolus samek* can be further distinguished from *P. fascinatus* by having widened medial scales on collar, and from *P. dolichoderes* sp. nov. by having fewer temporals (4–5 and 7–9, respectively), fewer ventrals (19–21 and 25–27), and fewer gulars (15–18 and 22–23).

**Characterization.** (1) Two (rarely three) supraoculars, anteriormost slightly larger than posterior one; (2) prefrontals present or absent; (3) femoral pores absent in both sexes; (4) four to five opaque lower eyelid scales; (5) scales on dorsal surface of neck striated, becoming slightly keeled from forelimbs to tail; (6) two or three rows of lateral granules at midbody; (7) 27–29 dorsal scales between occipital and posterior margin of hindlimb; (8) lateral body fold present; (9) keeled ventrolateral scales on each side absent; (10) dorsum grayish brown with a distinct golden gray middorsal stripe, slender at midbody, becoming pale gray towards tail; (11) labial stripe white or orange;
(12) flanks of body dark brown; (13) conical hemipenial body, with sulcus spermaticus originating between thick lips.

**Description of holotype.** Adult male (QCAZ 14955) (Figs 4, 5); SVL 46.7 mm; TL 80.9 mm; dorsal and lateral head scales juxtaposed, finely wrinkled; rostral hexagonal, 2.06 times as wide as high; frontonasal irregularly quadrangular, wider than long, laterally in contact with nasal, loreal and first superciliary, slightly bigger than frontal; prefrontal scales absent; frontal longer than wide, in contact with one supraocular on the left side, and two on the right side; frontoparietals pentagonal, longer than wide, slightly wider posteriorly, each in contact laterally with supraocular II; interparietal roughly heptagonal; parietals slightly bigger than interparietal, hexagonal, and positioned anterolaterally to interparietal, each in contact anteriorly with supraocular II (and supraocular III on right side) and dorsalmost postocular; postparietals three, medial scale smaller than laterals; seven supralabials, fourth one longest and below center of eye; six infralabials, fourth one shortest and below center of eye; temporals enlarged, irregularly hexagonal, juxtaposed, smooth; two large supratemporal scales, smooth; nasal slightly divided, irregularly pentagonal, longer than high, in contact with rostral anteriorly, first and second supralabials ventrally, frontonasal dorsally, loreal postero-dorsally and frenocular posteroventrally; nostril on ventral aspect of nasal, directed lateroposteriorly; loreal rectangular, wider dorsally; frenocular higher than long, in contact with nasal, separating loreal from supralabials; two supraocuclar on left side, three on right side (posteriormost much smaller), with the first one being the largest; four elongate superciliaries, first one enlarged, in contact with loreal; palpebral disc divided into four enlarged, pigmented scales; suboculars three (on the left side the medial subocular is fragmented), elongated and homogeneous in size; two postoculare, the dorsalmost wider than the other; ear opening vertically oval, without denticulate margins; tympanum recessed into a shallow auditory meatus; mental semicircular, wider than long; posttemporal pentagonal, slightly wider than long, followed posteriorly by three pairs of genials, the anterior two in contact medially and the posterior one separated by postgenials; all genials in contact with infralabials; gulars imbricate, smooth, posteriorly widened in two longitudinal rows; posteriormost row of gulars (collar) with six scales, the medial two widened.

Nuchal scales similar in size to dorsals, except for the anteriormost that are widened; scales on sides of neck small and granular; dorsal scales hexagonal, elongate, imbricate, arranged in transverse rows; scales on dorsal surface of neck striated, becoming progressively keeled from forelimbs to tail; number of dorsal scales between occipital and posterior margin of hindlimbs 27; dorsal scale rows in a transverse line at midbody 26; one longitudinal row of smooth, enlarged ventrolateral scales on each side; dorsals separated from ventrals by two rows of small scales at level of 13th row of ventrals; lateral body fold between fore and hindlimbs present; ventrals smooth, wider than long, arranged in 20 transverse rows between collar fold and preanals; six ventral scales in a transverse row at midbody; subcaudals smooth; axillary region with granular scales; scales on dorsal surface of forelimb striated, imbricate; scales on ventral surface of forelimb granular; two thick, smooth thenar scales; supradigits (left/right)
Figure 4. Holotype of *Pholidobolus samek* sp. nov. (QCAZ 14955) in dorsal (A), ventral (B), and lateral (C) views. Male, SVL = 46.7 mm. (A, B): preserved specimen; (C): live specimen. Photographs by Darwin Nuñez and Valeria Chasihuisa.
Figure 5. Head of holotype of *Pholidobolus samek* sp. nov. (QCAZ 14955) in lateral (A), dorsal (B), and ventral (C) views. Photographs by Valeria Chasiluisa. Scale bar: 5 mm.
3/3 on finger I, 6/7 on II, 8/8 on III, 9/9 on IV, 6/6 on V; supradigits 3/4 on toe I, 6/6 on II, 10/9 on III, 11/12 on IV, 7/7 on V; subdigital lamellae of fingers I and II single, paired on III (except the four distalmost), paired at base on IV, on finger V all single; subdigital lamellae 5/5 on finger I, 11/12 on II, 15/16 on III, 17/16 on IV, 9/10 on V; subdigital lamellae on toes I and II single, on toe III, IV and V all paired, except for the three distalmost subdigitals; subdigital lamellae 6/6 on toe I, 11/10 on II, 16/15 on III, 21/21 on IV, 14/14 on V; groin region with small, imbricate scales; scales on dorsal surface of hindlimbs smooth and imbricate; scales on ventral surface of hindlimbs smooth; scales on posterior surface of hindlimbs granular; femoral pores absent; preanal pores absent; cloacal plate paired, bordered by four scales anteriorly, of which the two medialmost are enlarged.

Additional measurements (mm) and proportions of the holotype: HL 11.4; HW 7.4; ShL 7.0; AGD 23.9; TL/SVL 1.5; HL/SVL 0.2; HW/SVL 0.2; ShL/SVL 0.1; AGD/SVL 0.5.

Color of holotype in life. Dorsal background from head to base of tail grayish brown, with a golden light brown vertebral stripe extending from occiput to tail; bright green dorsolateral stripes on head; cream white longitudinal stripe extending from first supralabial to shoulder; sides of neck, flanks and limbs dark brown; reddish brown narrow stripe extending from tympanum to arm insertion; ventrolateral region of body grayish brown; throat cream; chest, belly and base of tail cream orange (Figs 4C, 6B).

Color of holotype in preservative. Dorsal background uniformly grayish brown, with a golden–gray vertebral stripe extending from occiput to tail; vertebral stripe wider anteriorly, becoming slightly slender at most posterior part of body; dorsal and lateral surfaces of head brown (rostral, frontonasal, frontal, frontoparietals, and supraoculars); bluish white longitudinal stripe extending from first supralabial to shoulder and fading on flanks; ventrolateral aspect of neck dark brown with a dorsolateral light brown stripe extending posteriorly along flanks to hindlimbs; forelimbs with scattered ocelli (black with white center); flanks grayish brown with two dorsolateral stripes on each side, the dorsal one dark brown and the most ventral one brown diffuse with dark brown spots; tail brown dorsally; ventral surface of head gray, chest and venter dark gray, ventral surface of tail slightly gray, with scattered dark brown marks.

Variations. Measurements and scale counts of *Pholidobolus samek* are presented in Table 6. Supralabials 8/7 (left/right) and temporals five in specimen QCAZ 14956; small and separated prefrontals on both sides in QCAZ 14954 and one prefrontal on right side in QCAZ 14956; little intrusive scales between parietal and postparietal in QCAZ 14954; frontal hexagonal in QCAZ 14954; roughly decagonal interparietal in QCAZ 14954. Usually two scales on posterior cloacal plate, four in QCAZ 14954 and 14956. Male is larger (SVL 46.7 mm, \(N = 1\)) than females (maximum SVL 45.4 mm, \(N = 2\)). Hatchlings (QCAZ 14969, 14970, 14976) with eight or seven (QCAZ 14976) posterior gular (collar) scales. Unlike the male holotype, females have an orange-brown longitudinal stripe extending from third supralabial to shoulder and fading on the flanks (Fig. 6).

Distribution and natural history. *Pholidobolus samek* inhabits cloud forests in Cordillera del Cóndor, southeastern Ecuador at elevations between 2324–2844 m (Fig. 7). The new species is known only from Zamora-Chinchipe province, on the
sandstone plateaus of Cerro Plateado Biological Reserve. The ground at the type locality is covered with mosses, roots, and bromeliads. Such ground cover is locally known as bamba. All specimens were found active at 11h30–17h00 under stones or terrestrial bromeliads (Fig. 8). Four eggs, collected under flat stones on 24-09-2016, were incubated in sphagnum and perlite in captivity for two months approximately. They were
Table 6. Summary of morphological characters and measurements (mm) of *Pholidobolus samek* sp. nov., *P. condor* sp. nov., *P. dolichoderes* sp. nov., and *P. fascinatus* sp. nov. Range (first line) and mean ± standard deviation (second line) are presented.

| Character                          | *P. samek* sp. nov. N = 7 (adults = 3) | *P. condor* sp. nov. N = 4 (adults = 1) | *P. dolichoderes* sp. nov. N = 5 (adults = 3) | *P. fascinatus* sp. nov. N = 27 (adults = 4) |
|-----------------------------------|----------------------------------------|----------------------------------------|-----------------------------------------------|-----------------------------------------------|
| Scales along margin of upper jaw  | 7–10 (9.14 ± 1.07)                     | 8–9 (8.75 ± 0.5)                      | 9–11 (10.2 ± 0.84)                           | 7–10 (8.36 ± 0.91)                           |
| Scales along margin of lower jaw  | 8–9 (8.25 ± 0.5)                       | 5–10 (7.14 ± 2.67)                    | 10–11 (10.2 ± 0.45)                          | 4–10 (7.4 ± 1.58)                            |
| Gulars                            | 15–18 (16.71 ± 1.11)                   | 14–16 (15 ± 0.82)                     | 22–23 (22.8 ± 0.48)                          | 14–17 (15.72 ± 0.89)                         |
| Ventral in transverse row at midbody | 19–21 (20 ± 0.82)                   | 18–20 (19 ± 1.15)                     | 25–27 (25.8 ± 0.84)                          | 21–25 (22.96 ± 1.21)                         |
| Dorsals from occiput to base of tail | 27–29 (27.71 ± 0.76)                | 26–30 (27.75 ± 1.71)                  | 35–40 (36.8 ± 2.05)                          | 32–37 (34.64 ± 1.19)                         |
| Temporals                         | 4–5 (4.14 ± 0.38)                      | 4–5 (4.25 ± 0.5)                      | 7–9 (8 ± 0.70)                               | 3–5 (3.44 ± 0.65)                            |
| Scales around midbody             | 25–32 (27.71 ± 2.75)                   | 27–30 (28 ± 1.41)                     | 31–33 (32.2 ± 0.84)                          | 28–34 (30.96 ± 1.79)                         |
| Scales around tail                | 14–16 (15 ± 0.81)                      | 14–20 (17.86 ± 2.73)                  | 18–19 (18.6 ± 0.55)                          | 18–22 (20.32 ± 1.18)                         |
| Lower eyelid scales               | 4–5 (4.14 ± 0.38)                      | 5                                     | 4–6 (4.8 ± 0.84)                             | 4–6 (5.04 ± 0.61)                            |
| Gular (collar) scales             | 6–8 (7.14 ± 0.9)                       | 6–9 (7.75 ± 1.26)                     | 6–8 (6.4 ± 0.89)                             | 9–12 (10.28 ± 0.73)                          |
| Head length in adults             | 9.9–11.4 (10.76 ± 0.77)                | 11                                    | 9.7–10.6 (10.05 ± 0.46)                      | 8.9–12.3 (10.22 ± 1.80)                      |
| Head width in adults              | 6.5–7.4 (6.93 ± 0.48)                  | 6.6                                    | 6.2–6.3 (6.26 ± 0.05)                        | 6.6–9.2 (7.58 ± 1.45)                        |
| SVL in adults                     | 41.6–49.3 (45.89 ± 3.89)               | 42.7                                   | 41.1–50.6 (45.75 ± 4.74)                     | 42.6–52.5 (47.3 ± 4.98)                      |

14.0–14.1 mm long, 8.0–8.5 mm wide, and weighted 0.4 g on average. Hatchlings (QCAZ 14969–70, 14976–77) weighted 0.3 g and were 24.7 mm in SVL on average.

**Conservation status.** *Pholidobolus samek* is only known from Cordillera del Cóndor. The population size for this species is unknown, but our sampling suggests low abundances. Because of the small known distribution, as well as habitat destruction through mining activities nearby (Van Teijlingen 2016), we suggest assigning *P. samek* to the Critically Endangered category under criteria B1a, b(iii); C1; D, according to IUCN (2012) guidelines.

**Etymology.** The specific epithet *samek* means green in the Shuar language, in allusion to the green dorsolateral head stripes distinguishing the new species from other congeners. The type locality of *Pholidobolus samek* lies within territory of Shuar indigenous people, who inhabit the Amazonian rainforest in Ecuador and Peru.

**Remarks.** *Pholidobolus samek* sp. nov. is very similar morphologically and genetically to *P. condor* sp. nov. These species can be easily distinguished from each other by coloration in adult males, although we recognize that our sample size is small (*N* = 7 and 4, respectively) and includes only one adult male per species. However,
further evidence supports recognition of *P. samek* and *P. condor* as different species. First, they are reciprocally monophyletic and they are not sister taxa, with *P. samek* being sister to “*P. macbrydei*” Clade A (Fig. 1), which is very different in color patterns from either *P. samek* or *P. condor* (V. Parra and O. Torres-Carvajal, personal observation). Second, unlike the 12S gene (the less variable gene in this study), genetic distances between *P. samek* and *P. condor* for 16S and ND4 are not the lowest (Tables 2 and 4, respectively) within *Pholidobolus*. For example, the 16S distance between *P. samek* and *P. condor* (3%) is the same as the distance between the well-recognized species *P. paramuno* and *P. affinis*. In addition, genetic exchange among *P. samek*, *P. condor* and Clade A is very unlikely as they are isolated from each other on mountain tops above 2000 m (Fig. 7).

**Pholidobolus condor** sp. nov.

http://zoobank.org/BB38EC4E-634D-4728-BA30-412913E7D0E0

Figures 9, 10

Proposed standard English name: Condor cuilanes
Proposed standard Spanish name: Cuilanes del Cóndor
Figure 8. Habitat of *Pholidobolus samek* sp. nov. **A** Vegetation around type locality, Cerro Plateado Biological Reserve, Ecuador **B** habitat where holotype was found. Photographs by Álvaro Pérez.
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Holotype. QCAZ 15844 (Figs 9, 10), adult male, Ecuador, Provincia Morona Santiago, buffer zone of El Quimi Biological Reserve, plateau on the eastern side of El Quimi river valley, 3.51892S, 78.3690W, WGS84, 2209 m, 11 July 2017, collected by Diego Almeida, Darwin Núñez, Eloy Nusirquia, Alex Achig and Ricardo Gavilanes.

Paratypes (3). Ecuador: Provincia Morona Santiago: QCAZ 16790 (hatchling), El Quimi Biological Reserve, base camp towards old heliport (high zone), 3.51894S, 78.36897W, WGS84, 2226 m, 17 April 2018; QCAZ 16788–89 (hatchlings), El Quimi Biological Reserve, near base camp, 3.5182S, 78.3913W, WGS84, 1994 m, 12 April 2018, collected by Diego Almeida, Darwin Núñez, Eloy Nusirquia, Alex Achig and María del Mar Moretta.

Diagnosis. Pholidobolus condor is unique among its congeners, except P. samek sp. nov., in having green dorsolateral stripes on the head. However, adult males of P. condor differ from those of P. samek sp. nov. in having lighter dorsolateral head stripes, and reddish flanks and venter. In addition, P. ulisesi, P. dicrus, P. hillisi, and P. vertebralis differ from P. condor (character states of P. condor in parentheses) in having a conspicuous light vertebral stripe (light vertebral stripe absent). Pholidobolus affinis, P. prefrontalis, P. dicrus, P. hillisi, and P. vertebralis further differ from P. condor in having prefrontal scales (prefrontal scales absent). Additionally, P. condor sp. nov. has fewer dorsal scales (26–30) than P. affinis (45–55), P. montium (35–50), P. prefrontalis (37–46), P. macbrydei (31–43), and P. dolichoderes sp. nov. (35–40). Pholidobolus condor can be further distinguished from P. fascinatus sp. nov. by having widened medial scales on collar, and from P. dolichoderes sp. nov. by having fewer temporals (7–9 and 4–5, respectively), fewer ventrals (18–20 and 25–27), and fewer gulars (14–16 and 22–23).

Characterization. (1) Two (rarely three) supraoculars, anteriormost larger than posterior one; (2) prefrontals absent; (3) femoral pores absent; (4) four opaque lower eyelid scales; (5) scales on dorsal surface of neck striated or smooth, progressively striated from forelimbs to tail; (6) two rows of lateral granules at midbody; (7) 27–31 dorsal scales between occipital and posterior margin of hindlimb; (8) lateral body fold present; (9) keeled ventrolateral scales on each side absent; (10) dorsum dark brown with a narrow, pale brown stripe; (11) labial stripe white; (12) flanks of body dark brown or gray; (13) hemipenial body cylindrical with distinctive capitular groove.

Description of holotype. Adult male (QCAZ 15844) (Figs 9, 10); SVL 42.7 mm; TL 74.8 mm; dorsal and lateral head scales juxtaposed, finely wrinkled; rostral hexagonal, 1.67 times as wide as high; frontonasal quadrangular, slightly bigger than frontal, laterally in contact with nasal, loreal and first superciliary; prefrontal scales absent; frontal pentagonal, longer than wide, wider anteriorly, in contact with first superciliary and supraocular; frontoparietals hexagonal, longer than wide, slightly wider in the middle, each in contact laterally with supraocular II; interparietal octagonal, with a short medial suture posteriorly, lateral borders nearly parallel to each other; parietals larger than interparietal, hexagonal and positioned anterolaterally to interparietal, each in contact laterally with supraocular II and dorsalmost postocular; postparietals three, medial scale smaller than lateral ones; eight supralabials, fourth one longest and below center of eye; six infralabials, fourth one below center of eye; temporals enlarged, irregularly hexagonal, smooth; two
Figure 9. Holotype of *Pholidobolus condor* sp. nov. (QCAZ 15844) in dorsal (A), ventral (B), and lateral (C) views. Male, SVL = 42.7 mm. Preserved specimen (A); live specimen (B, C). Photographs by Malki Bustos.
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Figure 10. Head of holotype of *Pholidobolus condor* sp. nov. (QCAZ 15844) in lateral (A), dorsal (B), and ventral (C) views. Photographs by Valeria Chasiluisa. Scale bar: 5 mm.
large and smooth supratemporals; nasal shield slightly divided above nostril, irregularly pentagonal, longer than high, in contact with rostral anteriorly, first and second supralabials ventrally, frontonasal dorsally, loreal posteriorly and frenocular posteriorly; nostril on ventral aspect of nasal, directed laterally; loreal quadrangular, slightly wider dorsally, not in contact with supralabials; frenocular higher than long, in contact with nasal; nasal separating loreal from supralabials; two supraoculars, anterior most one the widest; four elongate superciliaries, anterior most enlarged, in contact with loreal; palpebral disc divided into five pigmented scales; four suboculars, anterior most three elongated and homogeneous in size, posterior most widest; two postoculars, the dorsal most wider than the other; ear opening vertically oval, without denticulate margins; tympanum recessed into a shallow auditory meatus; mental wider than long; postmental pentagonal, slightly wider than long, followed posteriorly by three pairs of genials, the anterior two pairs in contact medially and the third pair separated by postgenials; all genials in contact with infralabials; gulars imbricate, smooth, widened in two longitudinal rows; posterior row of gulars (collar) with nine scales, the medial three slightly widened.

Nuchal scales slightly smaller than dorsals, except for the anterior most that are widened; scales on sides of neck small and granular; dorsal scales elongate, imbricate, arranged in transverse rows; scales on dorsal surface of neck striated, becoming progressively keeled from forelimbs to tail; dorsal scales between occipital and posterior margin of hindlimbs 27; dorsal scale rows in a transverse line at midbody 27; one longitudinal row of smooth, enlarged ventrolateral scales on each side; dorsals separated from ventrals by two rows of small scales at the level of 13th row of ventrals; lateral body fold between fore and hindlimbs present; ventrals smooth, wider than long, arranged in 20 transverse rows between collar fold and preanals; six ventral scales in a transverse row at midbody; subcaudals smooth; axillary region with granular scales; scales on dorsal surface of forelimb striated, imbricate; scales on ventral surface of forelimb granular; two thick, smooth thenar scales; supradigitals (left/right) 3/3 on finger I, 6/6 on II, 8/8 on III, 9/9 on IV, 6/6 on V; supradigitals 3/3 on toe I, 6/6 on II, 9/9 on III, 12/12 on IV, 7/7 on V; subdigital lamellae of finger I, II, III, and V single, on finger IV few scales in the middle paired; subdigital lamellae 6/6 on finger I, 11/11 on II, 15/15 on III, 17/16 on IV, 10/10 on V; subdigital lamellae on toes I and II single, on toes III, IV and V paired, except for two or three distalmost subdigitals; subdigital lamellae 7/6 on toe I, 12/12 on II, 15/16 on III, 22/22 on IV, 12/12 on V; groin region with small, juxtaposed scales; scales on dorsal surface of hindlimbs striated and imbricate; scales on ventral surface of hindlimbs smooth; scales on posterior surface of hindlimbs granular; femoral pores absent; preanal pores absent; cloacal plate paired, bordered by four scales anteriorly, of which the two medial most are enlarged.

Additional measurements (mm) and proportions of the holotype: HL 11.0; HW 6.6; ShL 5.8; AGD 20.4; TL/SVL 1.7; HL/SVL 0.3; HW/SVL 0.2; ShL/SVL 0.1; AGD/SVL 0.5.

Color of holotype in life. Dorsal background from head to base of tail dark brown, with a golden brown vertebral stripe extending from occiput to tail; greenish cream dorsolateral stripes on head, becoming light brown on posterior part of body; white longitudinal stripe extending from first supralabial to shoulder; sides of neck, flanks
and limbs dark brown; chocolate brown narrow stripe extending from tympanum to arm insertion; ventrolateral region of body grayish brown; throat reddish cream; chest, belly, base of tail and lateral region of tail bright orange, with brown marks in some scales; ventral surface of hind limbs with orange diffuse marks (Fig. 9B,C).

**Color of holotype in preservative.** Dorsal background uniformly dark brown with a grayish brown middorsal stripe extending from occiput onto tail; dorsolateral stripe distinct, pale gray, extending from snout to near base of tail; head brown dorsally (rostral, frontonasal, frontal, frontoparietals and supraoculars) and dark brown laterally; white longitudinal stripe extending from first supralabial to forelimb; lateral aspect of neck dark brown with a dorsolateral light brown stripe extending posteriorly along flanks to hindlimbs; flanks grayish brown; tail dark brown dorsally and bronze laterally; ventral surface of head gray, with dirty cream genials and scattered black marks; chest, belly and ventral surface of tail light gray with light red spots; ventral surface of limbs dark gray (Fig. 9A).

**Variations.** Measurements and scale counts of *Pholidobolus condor* are presented in Table 6. Supraoculars three on left side in specimen QCAZ 16789; supralabials six in QCAZ 16789 and 16790, and seven in QCAZ 16788; two quadrangular frontonasals in QCAZ 16788; transverse rows of ventral scales between collar fold and preanals 18 in QCAZ 16788 and 19 in QCAZ 16790. Hatchlings with eight (QCAZ 16788–89) or six (QCAZ 16790) posterior gular (collar) scales. Unlike the adult male, hatchlings lack reddish color on tail.

**Distribution and natural history.** *Pholidobolus condor* occurs in Cordillera del Cóndor in southeastern Ecuador at elevations between 1994–2226 m. The new species is known from El Quimi Biological Reserve in Morona Santiago province (Fig. 7). The holotype was found active at 21h14 at the base of a bromeliad on a sandstone plateau of shrub vegetation (Fig. 11).

Several eggs were found within a bromeliad, suggesting that females of *P. condor* lay their eggs in communal nests. Four eggs that were found on the ground at the base of bromeliads and under a trunk were incubated in sphagnum and perlite in captivity for approximately three months. On average, hatchlings weighted 0.4 g and were 23.7 mm in SVL.

**Conservation status.** *Pholidobolus condor* is only known from Cordillera del Cóndor in southeastern Ecuador. This area is currently threatened by mining activities (Ron et al. 2018; Valencia et al. 2017; Van Teijlingen 2016). Habitat destruction and fragmentation is evident at a distance of ~11 km from the collection sites (Mazabanda et al. 2018). Because of the small known distribution and habitat disturbance, we suggest assigning *P. condor* to the Critically Endangered category under criteria B1a, b(iii); C1; D, according to IUCN (2012) guidelines.

**Etymology.** The specific epithet *condor* refers to Cordillera del Cóndor, where the new species was discovered. The Cordillera del Cóndor is an eastern outlier of the main Andean chain, where a significant number of species have been discovered in the last decade (Brito et al. 2017; Huamantupa-Chuquimaco and Neill 2018; Ron et al. 2018; Torres-Carvajal et al. 2009; Valencia et al. 2017).

**Remarks.** See remarks on *Pholidobolus samek* sp. nov. above.
Figure 11. Habitat of *Pholidobolus condor* sp. nov. at El Quimi Biological Reserve, Ecuador. Photographs by Álvaro Pérez.

*Pholidobolus dolichoderes* sp. nov.
http://zoobank.org/95D82201-D761-40F4-8395-4AAC38F24563
Figures 12–14
Proposed standard English name: Long-necked cuilanes
Proposed standard Spanish name: Cuilanes de cuello largo

**Holotype.** QCAZ 16353 (Figs 12, 13), adult male, Ecuador, Provincia Azuay, San Felipe de Oña, 3.4292S, 79.2364W, WGS84, 2672 m, 16 March 2018, collected by Diego Almeida, Darwin Núñez, Eloy Nusirquia, Alex Achig and Katherine Nicolalde.

**Paratypes (4).** Ecuador: Provincia Azuay: QCAZ 16349, 16352 (adult females), San Felipe de Oña, Susudel-Poetate road, 3.4322S, 79.2369W, WGS84, 2506 m, 16 March 2018; QCAZ 16350–51 (juveniles), San Felipe de Oña, 3.4275S, 79.2339W, WGS84, 2675 m, 16 March 2018, same collectors as holotype.

**Diagnosis.** *Pholidobolus dolichoderes* is unique among its congeners in having a long neck with granular scales between the posterior corner of the orbit and the anterior edge of the tympanum, as well as an inconspicuous ventrolateral fold between fore and hindlimbs. In addition, *P. ulisesi, P. dicrus, P. hillisi, and P. vertebralis* differ from *P. dolichoderes* in having a conspicuous light vertebral stripe. The new species further differs from *P. affinis* in lacking ocelli on flanks, and from *P. condor* sp. nov., *P. macbrydei*, and *P. montium* in having prefrontal scales. *Pholidobolus dolichoderes* has more dorsals
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(35–40) and ventrals (25–27) than *P. samek* sp. nov. (27–29 and 19–21, respectively) and *P. condor* sp. nov. (26–30 and 18–20), and, unlike *P. fascinatus* sp. nov., it has widened medial scales on collar. In addition, *P. dolichoderes* has more temporals (7–9) and gulars (22–23) than *P. samek* sp. nov. (4–5 and 15–18, respectively), *P. condor* sp. nov. (4–5 and 14–16), and *P. fascinatus* sp. nov. (3–5 and 14–17).

**Figure 12.** Holotype of *Pholidobolus dolichoderes* sp. nov. (QCAZ 16353) in life in dorsal (A), ventral (B), and lateral (C) views. Male, SVL = 41.1 mm. Photographs by Gustavo Pazmiño.
Figure 13. Head of holotype of *Pholidobolus dolichoderes* sp. nov. (QCAZ 16353) in lateral (A), dorsal (B), and ventral (C) views. Photographs by Valeria Chasiluisa. Scale bar: 5 mm.
Characterization. (1) Three supraoculares, anteriormost larger than posterior ones; (2) prefrontals present; (3) femoral pores present in both sexes; (4) four to six opaque lower eyelid scales; (5) scales on dorsal surface of neck smooth, becoming slightly keeled from forelimbs to tail; (6) two or three rows of lateral granules at midbody; (7) 35–20 dorsal scales between occipital and posterior margin of hindlimb; (8) lateral body fold present but inconspicuous; (9) keeled ventrolateral scales on each side absent; (10) dorsum dark brown with a diffuse pale brown vertebral stripe that becomes grayish brown towards tail; (11) labial stripe white; (12) flanks of body gray brown; (13) white stripe along forelimb present; (14) hemipenial body cylindrical, with sulcus spermaticus originating between thick lips.

Description of holotype. Adult male (QCAZ 16353) (Figs 12, 13); SVL 41.1 mm; TL 96.3 mm; dorsal and lateral head scales imbricated, smooth; rostral hexagonal, 1.75 times as wide as high; frontonasal heptagonal, slightly wider than long, laterally in contact with nasal, similar in size to frontal; prefrontals present, in wide contact medially, and in contact with loreal and first superciliary laterally; frontal hexagonal, longer than wide, wider anteriorly, in contact with first and second supraoculares; frontoparietals hexagonal, longer than wide, slightly wider posteriorly, each in contact with second and third supraoculares, parietals and interparietal; interparietal heptagonal, lateral borders nearly parallel to each other; parietals wider than interparietal, heptagonal, and positioned anterolaterally to interparietal, each in contact with third supraocular and dorsalmost postocular; postparietals three, medial scale smaller than lateral ones; seven supralabials, fourth one the longest and below center of eye; five infralabials, fourth one below center of eye; temporals small, irregularly, smooth; supratemporal scales not well differentiated, smooth; nasal shield divided above the nostril, longer than high, in contact with rostral anteriorly, first and second supralabials ventrally, frontonasal dorsally, loreal posteriorly; loreal pentagonal, slightly wider dorsally, in contact with second and third supralabials; frenocular longer than high, in contact with loreal; three supraoculares, with the first one being the widest; four elongate superciliaries, anteriormost one enlarged, in contact with loreal; palpebral disc oval, pigmented, divided into four scales; four suboculars, two elongated and similar in size, the anteriormost and posteriormost larger than the others; three postoculares, dorsalmost wider than the others; ear opening vertically oval, without denticulate margins; tympanum recessed into a shallow auditory meatus; mental wider than long; postmental pentagonal, slightly wider than long, followed posteriorly by three pairs of genials, the anterior two pairs in contact medially and the third pair separated by postgenials; all genials in contact with infralabials; gulars imbricate, smooth, widened in two longitudinal rows; gular fold complete, posterior row of gulars (collar) with six scales, the medial two distinctly widened.

Nuchal scales slightly smaller than dorsals, except for the anteriormost that are widened; scales on sides of neck small and granular; dorsal scales elongate, juxtaposed, arranged in transverse rows; scales on dorsal surface of neck striated, becoming slightly keeled from forelimbs to tail; dorsal scales between occipital and posterior margin of hindlimbs 35; dorsal scale rows in a transverse line at midbody 32; one longitudinal row of smooth, enlarged ventrolateral scales on each side; dorsals separated from ven-
trals by three rows of granular scales at level of 13th row of ventrals; lateral body fold between fore and hindlimbs poorly defined; ventrals smooth, arranged in 26 transverse rows between collar fold and preanals; six ventral scales in a transverse row at midbody; subcaudals smooth; axillary region with granular scales; scales on dorsal surface of forelimb smooth, imbricate; scales on ventral surface of forelimb granular; two thick, smooth thenar scales; supradigitals (left/right) 3/0 on finger I, 7/7 on II, 9/8 on III, 10/10 on IV, 5/5 on V; supradigitals 4/4 on toe I, 7/7 on II, 11/11 on III, 12/11 on IV, 9/8 on V; subdigital lamellae of fingers I and II mostly single, III and IV paired proximally, on finger V all single; subdigital lamellae 5 on left finger I (right finger missing), 10/10 on II, 14/14 on III, 14/14 on IV, 9/9 on V; subdigital lamellae on toe I single, on toe II paired at the middle, on toe III and IV paired along proximal half, and on toe V paired proximally; subdigital lamellae 5/5 on toe I, 10/10 on II, 14/14 on III, 18/19 on IV, 11/11 on V; groin region with small, imbricate scales; scales on dorsal surface of hindlimbs striated and imbricate; scales on ventral surface of hindlimbs smooth; scales on posterior surface of hindlimbs granular; femoral pores present, three on left leg and five on right leg; preanal pores absent; cloacal plate paired, bordered by four scales anteriorly, of which the two medialmost are enlarged.

Additional measurements (mm) and proportions of the holotype: HL 9.8; HW 6.2; ShL 5.4; AGD 20.7; TL/SVL 2.4; HL/SVL 0.2; HW/SVL 0.1; ShL/SVL 0.1; AGD/SVL 0.5.

Color of holotype in life. Dorsal background of head dark brown; diffuse pale brown vertebral stripe that becomes grayish brown towards tail; creamy white dorsolateral stripes on head extending posteriorly and fading away at midbody; white longitudinal stripe extending from first supralabial to shoulder; sides of neck brown; flanks grayish brown with diffuse dark brown marks; limbs brown; ventrolateral region of body grayish brown; throat and chest cream; belly grayish cream; base of tail gray with dark little spots (Figs 12, 14B).

Color of holotype in preservative. Dorsal background uniformly brown with a diffuse light brown vertebral stripe extending from occiput onto tail, but fading at posterior end of body; dorsal and ventral surface of head brown; flanks light brown, with scattered dark brown spots; head and neck with two distinct white longitudinal stripes, the ventral one extending from first supralabial to forelimb, and the dorsal one from canthus rostralis to scapular region, posterior to which if fades into a light brown stripe; lateral aspect of neck dark brown; tail grayish brown; gular, chest and venter regions pale gray; ventral surface of tail and limbs gray.

Variations. Measurements and scutellation data of Pholidobolus dolichoderes are presented in Table 6. Superciliaries 4/5 (left/right) in specimen QCAZ 16350; palpebral disc divided into 5/6 scales in QCAZ 16352 and 3/5 in QCAZ 16351; frontonasal pentagonal in QCAZ 16349–52; prefrontals pentagonal in QCAZ 16349, 16350 and 16352; two rows of lateral granules at midbody in QCAZ 16439, 16350 and 16351. Usually six gular (collar) scales, eight in QCAZ 16349. Male is smaller (SVL 41.1 mm, N = 1) than females (maximum SVL 48.1 mm, N = 2).
Adult females differ from holotype in having a grayish brown vertebral stripe, fading away posteriorly, and grayish brown flanks (Fig. 14). Juvenile QCAZ 16350 differs from holotype in having grayish brown flanks, without scattered dark brown spots; juvenile QCAZ 16351 is unique in having white spots on flanks and over forelimbs.

**Distribution and natural history.** *Pholidobolus dolichoderes* is known to occur between 2506–2675 m in San Felipe de Oña, southwestern Azuay province (Fig. 7). This area is composed of many different landscapes including small valleys, desert areas and wet paramo. Most specimens were found active at day (10h26–15h30), mostly on the ground or near spiny ground bromeliads known as achupallas (*Puya* sp.).

**Conservation status.** *Pholidobolus dolichoderes* is only known from unprotected localities around Oña. The population size of this species is unknown, but our sampling suggests low abundances. Because of the small known distribution and lack of additional data, we suggest assigning *P. dolichoderes* to the Data Deficient category according to IUCN (2012) guidelines.

**Etymology.** The specific epithet *dolichoderes* derives from the Greek words *dolikhós*, meaning long, and *derê*, meaning neck, in allusion to the distinctively long neck of this species.
Pholidobolus fascinatus sp. nov.

http://zoobank.org/C5EC3F40-41DF-4A7D-A3AA-C2C8A6EF81C1

Figures 15–17

Proposed standard English name: Haunted cuilanes
Proposed standard Spanish name: Cuilanes encantados

Holotype. QCAZ 15120 (Figs 15, 16), adult male, Ecuador, Provincia El Oro, Lake Chillacocha, 3.4984S, 79.6188W, WGS84, 3382 m, 20 November 2016, collected by Diego Almeida, Darwin Núñez, Eloy Nusirquia, Santiago Guamán and Guadalupe Calle.

Paratypes (26). Ecuador: Provincia El Oro: QCAZ 15122 (adult male), QCAZ 15121 (adult female), QCAZ 15169–73, 15177–78, 15180, 15193, 15221, 15243–44, 15396–15405 (juveniles), same data as holotype; QCAZ 15118 (adult female), Lake Chillacocha, 3.4986S, 79.6187W, WGS84, 3348 m, 17 November 2016, same collectors as holotype.

Diagnosis. Pholidobolus fascinatus is unique among its congeners in lacking widened medial scales on collar (posterior row of gulars). In addition, P. fascinatus differs from P. affinis, P. prefrontalis, P. macbrydei, P. dolichoderes sp. nov., and P. montium in having a loreal scale frequently in contact with the supralabials (loreal scale, if present, not in contact with supralabials in the other species). Pholidobolus ulisesi, P. dicrus, P. hillisi, P. paramuno, and P. vertebralis differ from P. fascinatus in having a conspicuous light vertebral stripe. Pholidobolus samek sp. nov. and P. condor sp. nov. differ from P. fascinatus in having bright green dorsolateral stripes on the head. In addition, P. fascinatus has more dorsals (32–37) and ventrals (21–25) than P. samek sp. nov. (27–29 and 19–21, respectively) and P. condor sp. nov. (26–30 and 18–20); and it has fewer temporals (3–5) and gulars (14–17) than P. dolichoderes sp. nov. (7–9 and 22–23, respectively).

Characterization. (1) Two (rarely three) supraoculars, anteriormost larger than posterior one; (2) prefrontals present or absent; (3) femoral pores absent in both sexes; (4) four to six opaque lower eyelid scales; (5) scales on dorsal surface of neck smooth, becoming striated from forelimbs to tail; (6) one row of lateral granules at midbody; (7) 32–37 dorsal scales between occipital and posterior margin of hindlimb; (8) lateral body fold present; (9) dorsum brown with a diffused chocolate brown middorsal stripe that fades away towards tail; (11) labial stripe white or cream; (12) flanks of body brown; (13) conical hemipenial body, with sulcus spermaticus originating between distinctly thick lips; (14) 22 flounces extending along hemipenial body.

Description of holotype. Adult male (QCAZ 15120) (Figs 15, 16); SVL 52.5 mm; TL 37.6 mm; dorsal and lateral head scales juxtaposed, finely wrinkled; rostral hexagonal, 2.27 times as wide as high; frонтonasal hexagonal, wider than long, in contact with nasal laterally, slightly larger than frontal; prefrontal scales irregularly pentagonal; frontal heptagonal, longer than wide, slightly wider anteriorly, in contact with prefrontals and frонтonasal anteriorly, two supraoculars laterally, and frонтoparietals posteriorly; frонтoparietals pentagonal, longer than wide, slightly wider posteriorly, each in contact laterally with supraocular II; interparietal heptagonal, lateral borders nearly
parallel to each other; parietals hexagonal, each in contact laterally with supraocular II and dorsalmost postocular; postparietals four, with medial scales less than half the size of lateral ones; eight supralabials, fourth one the longest and below center of eye; eight infralabials, third and fourth one below center of eye; temporals enlarged, irregularly hexagonal, juxtaposed, smooth; two large, smooth supratemporal scales; nasal divided, irregularly pentagonal, longer than high, in contact with rostral anteriorly, first and second supralabials ventrally, frontonasal dorsally, loreal posterodorsally and frenocular posterventrally; nostril in center of nasal, directed lateroposteriorly; loreal rectangular, wider ventrally; frenocular longer than high, higher anteriorly, in contact with nasal, separating loreal from supralabials; two supraoculars, homogeneous in size; four superciliaries, anteriormost enlarged and in contact with loreal; palpebral disc divided into five pigmented scales; suboculars elongated, four on right side and three on left side; two postoculads, dorsalmost wider than the other; ear opening vertically oval, without denticulate margins; tympanum recessed into a shallow auditory meatus; mental semicircular, longer than wide; postmental pentagonal, slightly longer than wide, followed posteriorly by three pairs of genials, the anterior two in contact medially and the posterior one separated by postgenials; all genials in contact with infralabials; gulars imbricate, smooth, widened in two longitudinal rows; posterior row of gulars (collar) with 11 scales that are similar in size.

Nuchal scales similar in size to dorsals, except for the anteriormost that are widened; scales on sides of neck small and slightly granular; dorsal scales hexagonal, elongate, imbricate, arranged in transverse rows; scales on dorsal surface of neck smooth, becoming progressively striated from forelimbs to tail; dorsal scales between occipital and posterior margin of hindlimbs 33; dorsal scale rows in a transverse line at midbody 25; dorsals separated from ventrals by one row of small scales at level of 13th row of ventrals; lateral body fold between fore and hindlimbs present; ventrals smooth, wider than long, arranged in 25 transverse rows between collar fold and preanals; six ventral scales in a transverse row at midbody; subcaudals smooth; axillary region with granular scales; scales on dorsal surface of forelimb striated, imbricate; scales on ventral surface of forelimb granular; two thick, smooth thenar scales; supradigitals (left/right) 3/3 on finger I, 7/6 on II, 8/8 on III, 10/10 on IV, 5/5 on V; supradigitals 3/3 on toe I, 6/6 on II, 8/9 on III, 11/11 on IV, 8/8 on V; subdigital lamellae of finger I single, on finger II all paired, except by the three distalmost, on finger III (proximal half) paired, on finger IV slightly paired at the middle, on finger V all single in right finger and three paired in left finger; subdigital lamellae 5/5 on finger I, 9/9 on II, 13/13 on III, 14/15 on IV, 9/9 on V; subdigital lamellae on toes I and II paired proximally and single distally, on toes III, IV and V paired, except for the three to five distalmost subdigitals; subdigital lamellae 5/5 on toe I, 10/10 on II, 14/13 on III, 18/18 on IV, 11/12 on V; groin region with small, imbricate scales; scales on dorsal surface of hindlimbs smooth and imbricate; scales on ventral surface of hindlimbs smooth; scales on posterior surface of hindlimbs granular; femoral pores absent; preanal pores absent; cloacal plate paired, bordered anteriorly by two enlarged scales.
Additional measurements (mm) and proportions of the holotype: HL 12.3; HW 9.2; ShL 6.7; AGD 26.5; TL/SVL 0.7; HL/SVL 0.2; HW/SVL 0.2; ShL/SVL 0.1; AGD/SVL 0.5.

**Color in life of the holotype.** Dorsal background from head to base of tail brown, with a diffuse chocolate-brown middorsal stripe that fades away towards tail; light brown dorsolateral stripes on head extending posteriorly and fading away at midbody; white longitudinal stripe extending from third supralabial to shoulder; sides of neck, flanks, and limbs brown; reddish brown narrow stripe extending from tympanum to arm insertion; ventrolateral region of body grayish brown; throat and chest gray; belly background gray with conspicuous orange marks; tail orange anteriorly and laterally (Figs 15, 17A).
Figure 16. Head of holotype of *Pholidobolus fascinatus* sp. nov. (QCAZ 15120) in lateral (A), dorsal (B), and ventral (C) views. Photographs by Valeria Chasiluisa. Scale bar: 5 mm.
**Color in preservative of the holotype.** Dorsal background uniformly brown with a cream brown vertebral stripe extending from head onto tail; vertebral stripe slender anteriorly, becoming slightly wider posteriorly; head light brown with black dots dorsally (rostral, frontonasal, frontal, frontoparietals and supraoculars) and brown laterally; cream longitudinal stripe extending from third supralabial to shoulder; ventrolateral aspect of neck brown; forelimbs with scattered black dots; flanks brown; tail brown dorsally; ventral surface of head light gray, chest and venter dark gray, ventral surface of tail slightly brown, with scattered dark brown marks.

**Variations.** Measurements and scale counts of *Pholidobolus fascinatus* are presented in Table 6. Supralabials 9/9 (left/right) in specimens QCAZ 15118 and 15122, and supraoculurs 3/3 in QCAZ 15118; loreal scale absent in QCAZ 15118; prefrontals absent in QCAZ 15122 and 15173; little intrusive scales between postparietal and frontoparietals in QCAZ 15118, 15121 and 15122; frontonasal quadrangular in QCAZ 15122; frontonal nonagonal and pentagonal in QCAZ 15118 and 15173, respectively; interparietal hexagonal in QCAZ 15122; parietal pentagonal in QCAZ 15170. Four posterior cloacal scales in QCAZ 15118. Males are slightly smaller (SVL 47.6 mm, *N* = 2) than female (maximum SVL 48.2 mm, *N* = 2). Adult male QCAZ 15122 differs from holotype in having sides of tail and chest dark brown without gray spots. Adult female QCAZ 15118 differs from holotype in having a light gray chest, a dark gray ventral surface of tail, dark brown sides of tail, and in lacking orange or red brown color on sides of neck (Fig. 17).

**Distribution and natural history.** *Pholidobolus fascinatus* inhabits wet paramo in the western slopes of the Andes of southern Ecuador (Fig. 7). The new species is known only from El Oro province, at 3348–3382 m. All specimens were found active at 14h00–17h00 mostly under stones.

We found 41 eggs (17 as fragmented eggshells) in a communal nest next to male QCAZ 15120. We incubated the 24 unhatched eggs in soil and perlite in captivity. They were 11.9–13.2 mm long, 5.5–9.2 mm wide, and weighted 0.5 g on average. Hatchlings (*N* = 20) weighted 0.4 g and were 26.2 mm in SVL on average.

**Conservation status.** *Pholidobolus fascinatus* is only known from localities around Lake Chillacocha. The population size for this species is unknown, but our sampling suggests average abundances. Because of the small known distribution and lack of additional data, we suggest assigning *P. fascinatus* to the Data Deficient category, according to IUCN (2012) guidelines.

**Etymology.** The species epithet *fascinatus* is a Latin word meaning enchanted, in allusion to Lake Chillacocha, also known as the Enchanted Lake. According to local belief, this lake is enchanted and has healing powers.

**Discussion**

The systematics of *Pholidobolus* and its sister taxon *Macropholidus* have been controversial partly because morphological evidence has been misinterpreted. Nonetheless, the recent use of molecular phylogenies has reshaped the systematics and taxonomy.
of this clade (Torres-Carvajal and Mafla-Endara 2013; Torres-Carvajal et al. 2015). In addition, recent collections in poorly explored areas along the Andes of Colombia, Ecuador, and Peru have led to the discovery and description of new species (Hurtado-Gómez et al. 2018; Torres-Carvajal et al. 2014; Venegas et al. 2016). In this paper we use morphological and molecular evidence to describe four new species of *Pholidobolus*, all except *P. dolichoderes* sp. nov. from remote highlands, based mostly on recent collections in southern Ecuador. Unexpectedly, allocating the new species described herein within the phylogenetic tree of *Pholidobolus* rendered *P. macbrydei* paraphyletic, suggesting that populations currently assigned to this taxon represent multiple species, some of which (e.g., Clades A and F) match the evolutionary significant units identified by Mafla-Endara (2011). Nonetheless, we refrain from describing any of these putative species (Clades A–F) in this paper as we believe that further sampling and analysis are necessary. According to our PCA results, three of the four new species are morphologically different from other “*Pholidobolus macbrydei*” (Fig. 2). Components I and II in the PCA, however, explain less than 50% of the variation within the “*P. macbrydei*” clade (Table 5). Thus, it is necessary to study additional morphological characters and increase sample size to better elucidate morphological differences.

**Figure 17.** Color variation in live specimens of *Pholidobolus fascinatus* sp. nov. A male holotype (QCAZ 15120, SVL = 52.5 mm) B male paratype (QCAZ 15122, SVL = 42.6 mm) C female paratype (QCAZ 15118, SVL = 46.7 mm).
Mafla-Endara (2011) also suggested hybridization between *P. macbrydei* from Cañar province and *P. prefrontalis* based on both the relatively great variation in morphology within the Cañar populations, and their morphological similarity to *P. prefrontalis*. Nevertheless, our nuclear phylogenetic tree does not suggest hybridization between *P. macbrydei* and *P. prefrontalis* (Appendix II).

Current evidence prevents us from assigning the name *P. macbrydei* to any of the recovered clades. However, we suspect that *P. macbrydei* belongs or is more closely related to Clades C, D, and E for two reasons (Fig. 1). First, adult males in these clades match closely the description of *P. macbrydei* (Montanucci 1973). Second, Clades C, D, and E lie nearby the type locality of *P. macbrydei*. It is noteworthy that Clade B also lies near the type locality of *P. macbrydei* (Fig. 7), although males in Clade B lack the red lateral stripes characteristic of *P. macbrydei*. DNA samples from the type locality should help clarify the taxonomy of this group.

The Cordillera del Cóndor is a sub-Andean mountain chain geologically similar to the Tepuis of the Guiana region. It is composed of marine and continental sediments (Neill 2005). This area is presently threatened by mining activities, despite discovery of a significant number of new species in the last ten years (Brito et al. 2017; Huamantupa-Chuquimaco and Neill 2018; Mashburn et al. 2020; Ron et al. 2018; Torres-Carvajal et al. 2009; Valencia et al. 2017) suggesting that Cordillera del Cóndor is a diversity hotspot. Our discovery of *P. samek* and *P. condor* further supports this idea. Therefore, we strongly advise authorities to improve conservation efforts for Cordillera del Cóndor.

The discovery of four new species and a paraphyletic *P. macbrydei* reveals high levels of unexpected diversity within *Pholidobolus* from southern Ecuador. This study supports the idea that Andean herpetofauna in this region is more diverse in species numbers than previously thought (Sánchez-Pacheco et al. 2012), especially for poorly explored areas like Cordillera del Cóndor. Collections in this area are usually scarce due to complex logistics. However, we recommend more intensive sampling efforts. Future studies should include larger samples and other types of evidence (e.g., genomic data, environmental variables) that might prove useful for species delimitation within *Pholidobolus* and other vertebrate taxa.

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References

Betancourt R, Reyes-Puig C, Lobos SE, Yáñez-Muñoz MH, Torres-Carvajal O (2018) Systemática de los saurios Anadia Gray, 1845 (Squamata: Gymnophthalmidae) de Ecuador: límite de especies, distribución geográfica y descripción de una especie nueva. Neotropical Biodiversity 4: 83–102. https://doi.org/10.1080/23766808.2018.1487694

Brito JM, Tinoco N, Chávez D, Moreno-Cárdenas P, Batallas D, Ojala-Barbour R (2017) New species of arboreal rat of the genus Rhipidomys (Cricetidae, Sigmodontinae) from Sangay National Park, Ecuador. Neotropical Biodiversity 3:1, 65–79. https://doi.org/10.1080/23766808.2017.1292755

Castoe TA, Doan TM, Parkinson CL (2004) Data partitions and complex models in Bayesian analysis: The phylogeny of gymnophthalmid lizards. Systematic Biology 53: 448–469. https://doi.org/10.1080/10635150490445797

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

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

Dowling HG, Savage JM (1960) A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica 45: 17–28.

Harvey MB, Embert D (2008) Review of Bolivian Dipsas (Serpentes: Colubridae), with comments on other South American species. Herpetological Monographs 22: 54–105. https://doi.org/10.1655/07-023.1

Huamantupa-Chuquimaco I, Neill D (2018) Vochysia condorensis (Vochysiaceae), a new species from the Cordillera del Cóndor, Ecuador. Phytotaxa 340(1): 79–85. https://doi.org/10.11646/phytotaxa.340.1.6

Hurtado-Gómez J, Arredondo J, Nunes PMS, Daza JM (2018) A New Species of Pholidobolus (Squamata: Gymnophthalmidae) from the Paramo Ecosystem in the Northern Andes of Colombia. South American Journal of Herpetology 13(3): 271–286. https://doi.org/10.2994/SAJH-D-15-00014.1

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Switzerland and Cambridge, UK, iv + 32 pp.

Katoh K, Toh H (2010) Parallelization of the MAFFT multiple sequence alignment program. Bioinformatics 26: 1899–1900. https://doi.org/10.1093/bioinformatics/btq224

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kizirian DA (1996) A review of Ecuadorian Proctoporus (Squamata: Gymnophthalmidae) with descriptions of nine new species. Herpetological Monographs 10: 85–155. https://doi.org/10.2307/1466981

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular biology and evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054
Lanfear R, Calcott B, Ho SYW, Guindon S (2012) Partition-Finder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Lehr E, Moravec J, Šmíd J, Lundberg M, Köhler G, Catenazzi A (2019) A new genus and species of arboreal lizard (Gymnophthalmidae: Cercosaurinae) from the eastern andes of Peru. Salamandra 55: 1–13.

Mafla-Endara P (2011) Filogeografía de las lagartijas andinas del género Pholidobolus (Squamata: Gymnophthalmidae) en Ecuador. Disertación previa a la obtención del título de Licenciada en Ciencias Biológicas. Pontificia Universidad Católica del Ecuador.

Manzani PR, Abe AS (1988) Sobre dos novos métodos de preparo do hemipênis de serpentes. Memorias do Instituto Butantan 50: 15–20.

Mashburn B, Pérez Á, Persson C, Zapata N, Cevallos D, Muchhala N (2020) Burmeistera quimiensis (Lobelioideae, Campanulaceae): A new species from the Cordillera del Cóndor range in southeast Ecuador. Phytotaxa 433: 67–74. https://doi.org/10.11646/phytotaxa.433.1

Mazabanda C, Kemper R, Thieme A, Hettler B, Finer M (2018) Impacts of Mining Project “Mirador” in the Ecuadorian Amazon. Monitoring Andean Amazon Project (MAAP). https://maaproject.org/mirador-ecuador

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, 1–8. https://doi.org/10.1145/2016741.2016785

Montanucci RR (1973) Systematics and evolution of the Andean lizard genus Pholidobolus (Sauria: Teiidae). Miscellaneous Publication. Museum of Natural History, University of Kansas 59: 1–52.

Moravec J, Šmíd J, Štundl J, Lehr E (2018) Systematics of Neotropical microteiid lizards (Gymnophthalmidae, Cercosaurinae), with the description of a new genus and species from the Andean montane forests. ZooKeys 774: 105–139. https://doi.org/10.3897/zook.eys.774.25332

Neill DA (2005) Cordillera del Cóndor: Botanical treasures between the Andes and the Amazon. Plant Talk 41: 17–21.

Nunes PMS, Fouquet A, Curcio FF, Kok PJR, Rodrigues MT (2012) Cryptic species in Iphisa elegans Gray, 1851 (Squamata: Gymnophthalmidae) revealed by hemipenial morphology and molecular data. Zoological Journal of the Linnean Society 166: 361–376. https://doi.org/10.1111/j.1096-3642.2012.00846.x

Pellegrino KCM, Rodrigues MT, Yonenaga-Yassuda Y, Sites JW (2001) A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. Biological Journal of the Linnean Society 74: 315–338. https://doi.org/10.1006/bijl.2001.0580

Pérez-Escobar O, Gottschling M, Chomicki G, Condamine F, Klitgård B, Pansarin E, Gerlach G (2017) Andean Mountain Building Did Not Preclude Dispersal of Lowland Epiphytic Orchids in the Neotropics. Scientific Reports 7: 4919. https://doi.org/10.1038/s41598-017-04261-z

Pesantes OS (1994) A Method for preparing the hemipenis of preserved snakes. Journal of Herpetology 28: 93–95. https://doi.org/10.2307/1564686
Systematics of Pholidobolus lizards

Peters AJ (1964) Dictionary of Herpetology. Hafner Publishing Company, New York, 392 pp.
R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org
Rambaut A (2014) FigTree version 1.4.2. http://tree.bio.ed.ac.uk/software/figtree/
Rambaut A, Drummond A (2007) Tracer v1.4. http://beast.bio.ed.ac.uk/Tracer
Ron SR, Caminer MA, Varela-Jaramillo A, Almeida-Reinoso D (2018) A new treefrog from Cordillera del Cóndor with comments on the biogeographic affinity between Cordillera del Cóndor and the Guianan Tepuis (Anura, Hylidae, Hyloscirtus). ZooKeys 809: 97–124. https://doi.org/10.3897/zookeys.809.25207
Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Høhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029
Sánchez-Pacheco SJ, Aguirre-Peñafl V, Torres-Carvajal O (2012) Lizards of the genus Riama (Squamata: Gymnophthalmidae): the diversity in southern Ecuador revisited. South American Journal of Herpetology 7: 259–275. https://doi.org/10.2994/057.007.0308
Sánchez-Pacheco SJ, Torres-Carvajal O, Aguirre-Peñafl V, Nunes PMS, Verrastro L, Rivas GA, Rodrigues MT, Grant T, Murphy RW (2017) Phylogeny of Riama (Squamata: Gymnophthalmidae), impact of phenotypic evidence on molecular datasets, and the origin of the Sierra Nevada de Santa Marta endemic fauna. Cladistics 34: 260–291. https://doi.org/10.1111/cla.12203
Savage JM (1997) On terminology for the description of the hemipenis of squamate reptiles. Herpetological Journal 7: 23–25.
Stamatakis A (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033
Torres-Carvajal O, de Queiroz K, Etheridge R (2009) A new species of iguanid lizard (Hopllocercinae, Enyalioides) from southern Ecuador with a key to eastern Ecuadorian Enyaloides. Zookeys 27: 59–71. https://doi.org/10.3897/zookeys.27.273
Torres-Carvajal O, Lobos SE, Venegas PJ (2015) Phylogeny of Neotropical Cercosaura (Squamata: Gymnophthalmidae) lizards. Molecular Phylogenetics and Evolution 93: 281–288. https://doi.org/10.1016/j.ympev.2015.07.025
Torres-Carvajal O, Lobos SE, Venegas PJ, Chávez G, Aguirre-Peñafl V, Zurita D, Echevarría LY (2016) Phylogeny and biogeography of the most diverse clade of South American gymnophthalmid lizards (Squamata, Gymnophthalmidae, Cercosaurinae). Molecular Phylogenetics and Evolution 99: 63–75. https://doi.org/10.1016/j.ympev.2016.03.006
Torres-Carvajal O, Mafla-Endara P (2013) Evolutionary history of Andean Pholidobolus and Macropholidus (Squamata: Gymnophthalmidae) lizards. Molecular Phylogenetics and Evolution 68: 212–217. https://doi.org/10.1016/j.ympev.2013.03.013
Torres-Carvajal O, Venegas PJ, Lobos SE, Mafla-Endara P, Nunes PMS (2014) A new species of Pholidobolus (Squamata: Gymnophthalmidae) from the Andes of southern Ecuador. Amphibian & Reptile Conservation 8: 76–88.
Townsend TM, Alegre RE, Kelley ST, Wiens JJ, Reeder TW (2008) Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from
squamate reptiles. Molecular Phylogenetics and Evolution 47: 129–142. https://doi.org/10.1016/j.ympev.2008.01.008

Uzzell T (1973) A revision of the genus Prionodactylus with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). Postilla 159: 1–67. https://doi.org/10.5962/bhl.part.11535

Valencia JH, Dueñas MR, Székely P, Batallas D, Pulluquitín F, Ron SR (2017) A new species of direct-developing frog of the genus *Pristimantis* (Anura: Terrarana: Craugastoridae) from Cordillera del Cóndor, Ecuador, with comments on threats to the anuran fauna in the region. Zootaxa 4353: 447–466. https://doi.org/10.11646/zootaxa.4353.3.3

Van Teijlingen K (2016) The ‘will to improve’ at the mining frontier: Neo-extractivism, development and governmentality in the Ecuadorian Amazon. Extractive Industries and Society 3: 902–911. https://doi.org/10.1016/j.exis.2016.10.009

Venegas PJ, Echeverría LY, Lobos SE, Nunes PMS, Torres-Carvajal O (2016) A new species of Andean microteiid lizard (Gymnophthalmidae: Cercosaurinae: *Pholidobolus*) from Peru, with comments on *P. vertebralis*. Amphibian & Reptile Conservation 10(1): 21–33.

Zaher H (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. Bulletin of the American Museum of Natural History 240: 1–168. http://hdl.handle.net/2246/1646

### Appendix I

Additional specimens examined of *Pholidobolus machrydei*. ECUADOR: **Provincia Azuay**: Cuenca-Azogues, 2.895222S, 78.958222W, 2486 m, QCAZ 6985; Cuenca-Chaucha, 2.861209S, 79.37869W, 2943 m, QCAZ 9668; Cuenca-Cochapamba, 2.797120S, 79.41562W, 3548 m, QCAZ 10133–10135; Cuenca-El Cajas, 2.77744S, 79.17001W, 3508 m, QCAZ 9932, 9936; 2.74105S, 79.23479W, 4092 m, QCAZ 8010; 2.776299S, 79.23743W, 4068 m, QCAZ 8011; 3.04155S, 79.21567W, 3766 m, QCAZ 8897, 8899–903, 8906; Cuenca-Mazan Forest, 2.87522S, 79.12923W, 3189 m, QCAZ 8008, 8013; Cutchil, 3.13999S, 78.81300W, 2900 m, QCAZ 823; Guablidi, 2.77488S, 78.69758W, 2453 m, QCAZ 9915, 9919–9920; Gualaceo, 2.909767S, 78.73436W, 2625 m, QCAZ 10875; Gualaceo-Limón; 2.948S, 78.71200W, 3110 m, QCAZ 819–20, 822; 2.964S, 78.70199W, 3140 m, QCAZ 825; Patacocha hill, 3.121109S, 79.065W, 3340 m, QCAZ 6144; Pucara, 3.21367S, 79.46739W, QCAZ 11038; Quinoas river, 3.087267S, 79.27762W, 3200 m, QCAZ 1564, 1566; Sigsig, 2.99900S, 78.80700W, 2890 m, QCAZ 1537; 3.129500S, 78.80400W, 2969 m, QCAZ 5605–5606, 5608; Sigsig-Gualacuiza, 3.106087S, 78.79558W, 2935 m, QCAZ 8646–8647; Tarqui, 3.0158805, 79.04447W, 2680 m, QCAZ 8512. **Provincia Cañar**: Cajas National Park, 2.70654S, 79.22765W, 3651 m, QCAZ 8946; Cañar, 2.560760S, 78.93077W, QCAZ 9947; Gualicanga river, 2.473189S, 78.97289W, 3048 m, QCAZ 10051–53; Gualaceo, 2.882159S, 78.77536W, 2298 m, QCAZ 9606; Juncal, 2.432109S, 78.90223W,
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3960 m, QCAZ 10048; 2.473189S, 78.97289W, 3048 m, QCAZ 10050; Mazar, 2.54508S, 78.70078W, 2839 m, QCAZ 15811–13; 2.54649S, 78.69826W, 2924 m, QCAZ 15814–16; 2.57138S, 78.746W, 3442 m, QCAZ 15817–15823; 2.5708S, 78.74586W, 3451 m, QCAZ 15824; 2.545804S, 78.69611W, 2842 m, QCAZ 10970. **Provincia Chimborazo:** Frutatían lake, 2.21584S, 78.50136W, 3700 m, QCAZ 9217–9218; Magdalena lake, 2.187416S, 78.50686W, 3556 m, QCAZ 9214; Ozogoche, 2.368733S, 78.68871W, 4040 m, QCAZ 6006; Riobamba-Melán, 1.875020S, 78.54773W, 3564 m, QCAZ 9626–9628; Riobamba-Timbo, 1.929219S, 78.53718W, 3408 m, QCAZ 9616–9620; Shulata, 2.339309S, 78.84322W, 3228 m, QCAZ 5597–5598. **Provincia El Oro:** Guanazán, 3.440034S, 79.48695W, 2638 m, QCAZ 7894. **Provincia Loja:** Fierro Hurco, 3.710421S, 79.30498W, 3439 m, QCAZ 6949–6950; Jimbura-Jimbura lake, 4.708868S, 79.44657W, 3036 m, QCAZ 6947–6948; Jimbura- path to Jimbura lake, 4.709469S, 79.43558W, 3348 m, QCAZ 10054–10055, 10057–10062; Jimbura-Lagunillos, 4.628244S, 79.46353W, 3450 m, QCAZ 6146–6147; 4.817000S, 79.36199W, 3600 m, QCAZ 3785; San Lucas, 3.731853S, 79.26059W, 2470 m, QCAZ 2861; Saraguro, 3.62025S, 79.23581W, 3100 m, QCAZ 3606; 3.679457S, 79.23769W, 3190 m, QCAZ 3673–3674; Tarqui, QCAZ 5545. **Provincia Morona Santiago:** Sangay National Park, 1.960939S, 78.43198W, 3345 m, QCAZ 9612. **Provincia Tungurahua:** Patate-El Corral, 1.2725S, 78.46805W, 3468 m, QCAZ 9995–9996. **Provincia Zamora Chinchipe:** Podocarpus National Park, 4.484149S, 79.14875W, 1800 m, QCAZ 3743.
Phylogeny of *Pholidobolus*. ML phylogram derived from the analysis of 411 bp of nuclear DNA. Bootstrap values are shown above branches and Bayesian posterior probabilities below branches (≤ 50% not shown). Asterisks indicate maximum values. The outgroup taxon (*Anadia rhombifera*) is not shown. Species names followed by voucher numbers are shown.