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Systematics of Amazonian lizards of the genus *Potamites* (Gymnophthalmidae)

Disertación previa a la obtención del título de Licenciado en Ciencias Biológicas

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Certifico que la disertación de Licenciatura en Ciencias Biológicas del candidato Andrés Daniel Zurita Altamirano ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

Omar Torres Carvajal, Ph.D.

Director de la disertación

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A mi familia

Genetic diversity and conservation of Amazonian lizards of the genus *Potamites* (Gymnophthalmidae)

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Abstract

Although recent studies have helped unraveling the evolutionary history of the Neotropical lizard clade Gymnophthalmidae, many questions remain unanswered. Here we focus on assessing the diversity of the genus *Potamites* in Ecuador and Peru. Three mitochondrial and one nuclear marker of 172 individuals from both countries were combined to infer phylogenetic relationships among species of *Potamites* using Bayesian and Maximum likelihood methods. Our results demonstrate that *Potamites* is paraphyletic deriving in the misapplication of the name *Potamites* for the species *P. cochranae* and *P. flavogularis*, which represent a tentative new genus. We also use bPTP species delimitation method to show cryptic diversity within *P. ecpleopus* and *P. strangulatus,* showing 30 unconfirmed candidate species (19 inside *P. ecpleopus* and 11 inside *P. strangulatus*). This could represent an increase in species richness inside each clade of 1900% and 1100% respectively.

Keywords: Gymnophthalmidae, *Potamites*, cryptic diversity, phylogenetics, Neotropics.

Resumen

Aunque algunos estudios recientes han ayudado a clarificarla historia evolutiva del clado de lagartijas neotropicales Gymnophthalmidae quedan muchas preguntas por resolver. En el presente estudio nos centramos en evaluar la diversidad del género *Potamites* en Ecuador y Perú. Se combinaron tres marcadores mitocondriales y uno nuclear de 172 individuos provenientes de ambos países para inferir las relaciones filogenéticas entre las especies de *Potamites* usando métodos de probabilidad bayesiana y máxima verosimilitud. Nuestros resultados demuestran que el taxón *Potamites* es parafilético lo que deriva a la errónea aplicación del nombre *Potamites* en las especies *P. cochranae* y *P. flavogularis* que representan en realidad un nuevo género. También utilizamos bPTP como método de delimitación de especies para demostrar la diversidad críptica dentro de los grupos de *P. ecpleopus* y *P. strangulatus,* mostrando 30 especies candidatas no confirmados (19 dentro de *P. ecpleopus* y 11 dentro de *P. strangulatus*). Esto representaría un aumento de la riqueza de especies dentro de ambos caldos del 1,900% y 1,100% respectivamente.

Palabras clave: Gymnophthalmidae, *Potamites*, diversidad críptica, filogenética, Neotrópico.

Introduction

The lizard clade Gymnophthalmidae consists of 36 genera and 220 species (Uetz and Hošek, 2015). The morphological characteristics of species in this clade are small size, elongated bodies, short limbs and transparent lower eyelids in some groups (Castoe and Doan, 2004). The phylogenetic relationships among its major lineages have not been investigated in detail until recently (Castoe et al., 2004, Doan and Castoe, 2005, Goicochea *et al*. 2012,Lobos, 2013).

Within Gymnophthalmidae, the genus *Potamites* was erected by Doan and Castoe(2005)which comprises 6 species formerly members of the genus *Neusticurus*: *P. apodemus* (Uzzell, 1966), *P. cochranae* (Burtand Burt, 1931), *P. ecpleopus* (Cope, 1876), *P. juruazensis* (Avila-Pires and Vitt, 1998), *P. ocellatus* (Sinitsin, 1930) and *P. strangulatus* (Cope, 1868). The recent description of three species: *P. montanicola* (Chávez and Vásquez, 2012), *P. flavogularis* (Altamirano et al., 2013), and *P. erythrocularis* (Chávez and Catenazzi, 2014), shows that the diversity of this clade was underestimated.

There are four species of *Potamites* in the Amazon region of Ecuador (*P. cochranae*, *P. ecpleopus, P. flavogularis* and *P. strangulatus*; Torres-Carvajal, et al., 2015) and seven speciesin Peru (*P. ecpleopus*, *P. erythrocularis*, *P. flavogularis*, *P. juruazensis*, *P. montanicola, P. ocellatus* and *P. strangulatus;* Chávez and Catenazzi, 2014*)*. Although no molecular systematic studies of this genus have been performed, it is presumed that cryptic species may exist as it has already been shown in other Amazonian taxa, such as

Alopoglossus lizards (Lobos, 2013) and some anurans (Funk et al., 2012; Caminer and Ron, 2014). This study aims to explore species limits in *Potamites* lizards occurring in the Amazon region of Ecuador and Peru.

Methods

Taxon sampling

We sampled all species currently known within the genus *Potamites*, except for *P. erythrocularis* and *P. apodemus*. We obtained and analyzed 137 samples from 54 localities in Ecuador, and 35 samples from 19 localities in Peru (Table 1).

Geographic distribution of seven species currently recognized as *Potamites* is shown in Figures 1 and 2 respectively.

In addition, following previous phylogenetic studies (Pellegrino *et al.,* 2001,Castoe *et al.,*2004, Doan and Castoe, 2005) we used nine species of Cercosaurinae from GenBank as outgroupsand one as ingroup (Table 2), nine of which belong to the clade Cercosaurini (*Cercosaura ocellata, Macropholidus ruthveni, Neusticurus rudis, Petracola ventrimaculatus, Pholidobolus macbrydei, Placosoma glabellum, Potamites ecpleopus* [ingroup], *Proctoporus bolivianus,* and *Riama unicolor*) and one belongs to Bachini *(Bachia flavescens).*

Tissue samples were deposited at Museo de Zoología of Pontificia Universidad Católica del Ecuador (QCAZ), and División de Herpetología, Centro de Ornitología y Biodiversidad, Peru (CORBIDI).

Extraction, PCR and DNA sequencing

DNA was extracted from liver, muscle or tail tissue preserved in ethanol 95% and stored at -80 ° C using a modified guanidine thiocyanate extraction protocol (M. Fujita, unpublished). Tissue samples were mixed with Proteinase K and lysis buffer and digested overnight prior to extraction. DNA extracts were quantified using a Nanodrop® ND-1000 (NanoDrop Technologies, Inc), re-suspended and diluted to 25 ng/ul in ddH_2O.

We amplified 2024 nucleotides (nt) encompassing one nuclear gene, oocyte maturation factor MOS (c-mos, ~391 nt), and three mitochondrial genes: NADH dehydrogenase subunit 4 (ND4, ~681 nt), 12S rRNA (12s, ~390 nt) and 16S rRNA (16s, ~527 nt). Samples were sent to the commercial laboratory Macrogen Inc in Seoul, South Korea for cycle sequencing reactions. Primers and PCR protocols are presented in Table 3.

Model selection and phylogenetic analyses

Sequences were assembled in GeneiousPro 5.4.6 (Drummond *et al.*, 2011) and latter aligned with MAFFT plugin (Katoh *et al.*,2002).Ribosomal (12s and 16s) gene regions with multiple gaps were realigned to minimize indels and optimize nucleotide identities among different individuals. ND4 and C-mos nuclear gene sequences were translated into amino acids in Mesquite v3.00 (Maddison and Maddison, 2011) for confirmation of alignment. Best-fit partitioning schemes and their models of molecular evolution were estimated in PartitionFinder v1.1.1 (Lanfear *et al.*, 2012) under the greedy algorithm and the Bayesian information criterion (Table 4).

For the phylogenetic analyses of the concatenated sequences two approaches were performed, Bayesian Inference (BI) and Maximum-likelihood (ML). BI was carried out in Mr. Bayes v.3.2.1 (Ronquist *et al.*, 2012) with two simultaneous runs for 4×10^7

generations; each replicate used four Monte Carlo Markov Chains, and the temperature parameter was set to 0.7. Trees were sampled every 1,000 generations. Stationarity was confirmed by plotting the lnL per generation and checking all the other parameter values of the model in the program Tracer v.1.6. (Rambaut and Drummond 2009). After confirming that all the analyses reached stationarity at a similar likelihood score and that the topologies were similar, we used a 10% burn-in of the 40,000 trees sampled on each run and the remaining trees where combined to find the posterior probabilities (PP) on a 50% majority-rule consensus tree.

The ML inference was performed in Garli v2.0 (Zwickl, 2006), with 10 replicates for 5×10^6 generations and an intensive search using a stepwise-addition starting tree. The search was programmed to finish 100,000 generations after there were no topology improvements; we used default values for other parameters (Páez and Ron, 2014).Support for individual nodes in the ML tree was assessed with non-parametric bootstrapping (BP) using 200 pseudoreplicates for two independent searches.

Genetic variation

We employed the software Molecular Evolutionary Genetics Analysis (MEGA v6.06; Tamura et al., 2013) to calculate uncorrected “p” genetic distances average values for each mitochondrial gene. Based on the inferred clades, mean in-group and between group distances for 12s, 16s and ND4 were computed as a measure of genetic variation. Table 5 represents the genetic variation average values for *P. cochranae* and *P. flavogularis*. For the remaining *Potamites,* average values for 12s, 16s and ND4 genetic variation are located in Tables 6, 7, 8, respectively).

Species delimitation

To infer the most likely number of species in our data we used the Poisson tree process (bPTP; Zhang et al., 2013) model for species delimitation, using four matrices 12s, 16s, ND4 and a fused matrix of the three mitochondrial markers.

We ran the bPTP analysis for 2×10^6 MCMC generations, with a thinning value of 100 and a burn-in of 25%, excluding outgroups as recommended by Cottontail et al. (2014).Convergence of the MCMC chain was confirmed visually (Zhang et al., 2013).

Results

Phylogenetic trees

BI and ML analyses yielded similar tree topologies; we used the maximum likelihood tree for Figure 3. Both *P. cochranae* and *P. flavogularis* are placed in a different clade (PP=1, BP=100). This tree does not support monophyly of *Potamites* as currently recognized. (Figs. 3 and 4).

Our results show nine different clades within *Potamites sensu stricto*, with *P. strangulatus* (Clades A-F) (PP=0.97, BP=69) as sister to the clade *P. montanicola* + *P. juruazensis* (PP=0.96, BP=71). Together they form the sister clade of *P. ocellatus* (PP=1, BP=100). All these taxa form a clade sister to *P. ecpleopus* (Clades G-I) (PP=0.83). In the Mr. Bayes analysis there is a polytomy consisting in 5 branches: *P. ocellatus clade*, *P montanicola clade*, clades G + H with BP=67, clade I also with BP=67 and one branch going to *P. strangulatus*. Within *Potamites*, all species are strongly supported with high values for one or both analyses, except for *P. ecpleopus* (PP=0.83, BP=67).

The monophyly of *Potamites* excluding *P. cochranae* and *P. flavogularis* is supported (PP=0.96, BP=100).All species of *Potamites sensu stricto, P. montanicola*, *P. ocellatus, P. juruazensis*, *P. strangulatus* and *P. ecpleopus* in Figure 3, form a clade sister to *Proctoporus bolivianus* (PP=0.97, BP=64).Together they form the sister group of the clade (PP=0.99, BP=69) *Cercosaura ocellata* + *Petracola ventrimaculata.* All these taxa form a clade sister to *Macropholidus ruthveni* + *Pholidobolus macbrydei* (PP=1, BP=100). This larger clade is in turn sister to *P. cochranae* and *P. flavogularis* (PP=1, BP=100).

Based on general geographic distribution and branch lengths, we recognize six major subclades within *P. strangulatus* (Clade A (PP=1, BP=100), Clade B (PP=0.78, BP=55), Clade C (PP=0.77, BP=53), Clade D (PP=1, BP=100), Clade E (PP=1, BP=100) and Clade F (PP=1, BP=100) (Figure 5); and three within *P. ecpleopus* (Clade G (PP=0.93, BP=64), Clade H (PP=1, BP=100), Clade I (PP= 0.93, BP=67) (Figure 6).

Geographical distribution of phylogenetic groups of <u>Potamites strangulatus.</u>

Clade A: the individuals forming this clade were retrieved from the Northern part of the Peruvian Amazonian foothills from the Picota and Datem del Marañón provinces at 365-1122 m respectively. This Clade share a location with Clades B and C.

Clade B: corresponds to four specimens collected in Datem del Marañón and Tarapoto provinces 1122m. This Clade share a location with Clades A and C.

Clade C: distributed in Morona Santiago in Ecuador and Tarapoto and Datem del Marañón provinces in Peru at an altitude range of365- 622m. This Clade share a location with Clades A, B and E.

Clade D: presents a distribution in the center of Ecuador, ranging from the Eastern slopes of the Andes in Tungurahua to the east into the Amazon provinces of Pastaza, Napo and Orellana.

Clade E: two individuals from Tarapoto, collected at 771 m. This Clade share a location with Clade C.

Clade F:Southern part of Ecuador in the provinces of Morona Santiago and Zamora Chinchipe and also the northern province of Bagua in the Peruvian Amazon.

Localities of the Clades of *P. strangulatus* in Figure 5.

Geographical distribution of phylogenetic groups of Potamites ecpleopus.

Clade G: Southern Ecuador in Pastaza and Northern Peru, in Loreto, Requena and Picota provinces at 187- 338m.

Clade H:is distributed Sucumbíos and Orellana provinces in the Northeastern part of Ecuador and La Convención province which is located Southeastern in Peru. GenBank sequences of *P. ecpleopus*, which correspond to specimens from Apiacás, Mato Grosso, Brazil are nested within clade H.

Clade I: Sucumbíos, Pastaza, Napo, Morona Santiago, Orellana which represents a wide distribution in the Amazon region in Ecuador and Northern Peru in Datem del Marañón and Condorcanqui. This calde is sympatric with Clades G and H.

Localities of the Clades of *P. ecpleopus* in Figure 6.

Sequence divergence

Ingroup sequence average divergence values of *P. cochranae* and *P. flavogularis* are 0.019 (*P cochranae*) and 0.095 (*P. flavogularis*) for 12s, 0.011 (*P. cochranae*) and 0.015 (*P.*

flavogularis) for 16s, finally 0.014 (*P. cochranae*) and 0.075 (*P. flavogularis*) for ND4. Genetic distances between *P cochranae* and *P. flavogularis* were 0.095 for 12s, 0.054 for 16s, and 0.255 for ND4. Values in Table 5.

Ingroup sequence average divergence values of species of *Potamites sensu stricto* are 0.037 for *P. ocellatus*, 0.034 for *P. montanicola* and 0.039 for *P. juruazensis* for 12s, 0.011 for *P. ocellatus*, 0.030 for *P. montanicola* and 0.016 for *P. juruazensis* for 16s, 0.223 for *P. ocellatus* and 0.149 for *P. montanicola*.

Ingroup sequence average divergence values of the clades of *P. strangulatus* (Clade A - F*)* ranged from 0.003 (Clade F) to 0.038 (Clade C) for 12s, from 0.006 (Clades and D) to 0.041 (Clade A) for 16s and from 0.002 (Clade B) to 0.044 (Clade A) for ND4.

Ingroup sequence average divergence values of the clades of *P. ecpleopus* (Clade H - I*)* ranged from 0.02 (Clade H) to 0.028 (Clade G) for 12s, from 0.016 (Clade G and same value for Clade H) to 0.03 (Clade I) for 16s and from 0.041 (Clade H) to 0.121 (Clade G) for ND4.

Genetic distances between groups average values ranged from 0.026 (Clade G with Clade H) to 0.086 (Clade G with both *P. montanicola* and *P. juruazensis*) for 12s, 0.026 (Clade A and Clade C) to 0.069 (Clade D and Clade I) for 16s, and 0.132 (between *P. ocellatus* and Clade C and same value between Clade D and F) to 0.251 (*P. juruazensis* and Clade E) for ND4.

Values in tables 6, 7 and 8.

Species delimitation

The bPTP analyses yielded a mean of 48 species (range = 38 -58) for the matrix containing all three mitochondrial genes,53 species as the mean result (range = 27 - 78) for the 12s matrix, 60 species as the mean result (range =29 -92) for the 16s matrix and a 39 species as the mean result (range =28 -51) for the ND4 matrix. There is congruency between the mayor features of all bPTP trees and the phylogenetic tree, yet each separate gene depicts differences in the arrangement of the terminal branches. We chose the bPTP tree obtained from the concatenated matrix as it backs the results of the separate gene trees (Tang et al., 2014). Figure 7 is the graphic resolution with the posterior probabilities shown in the bPTP server, illustrating 40 unconfirmed candidate species (within the range 38-58).

Within these results there are 30 unconfirmed candidate species (19 inside *P. ecpleopus* and 11 inside *P. strangulatus*). This could represent an increase in species richness inside each clade of 1900% and 1100% respectively. Table 9 shows the unconfirmed candidate species with the PP values.

Discussion

Our results represent a genetic approach to species delimitation within *Potamites* and can be used as a starting point for an integrative analysis to the same problem. With phenotypic and genotypic evidence, hypotheses of new species are more robust, although cryptic diversity might render most morphological characters useless. Taking into account that we found great diversity it is most probable that we have a complex of species in both *P. strangulatus* and *P. ecpleopus.* Only with an integrative study can we give a number of cryptic species (de Queiroz, 2007). In regards to of cryptic diversity, these are some examples of other Neotropical taxa recently discovered with the help of genetic evidence, such as *Alopoglossus viridiceps* (Torres-Carvajal and Lobos, 2014), *Riama yumborum* (Aguirre-Peñafiel et al., 2014), 3 new species of *Enyalioides* (*E. abisolepis, E. altotambo* and *E. sophiarothschildae*) (Torres-Carvajal et al., 2015) and also *Engystomops* toads (Funk et al., 2012) and *Hypsiboas* frogs (Caminer and Ron, 2014) in the Amazonian basin.

Taxonomy and phylogenetic relationships

The taxonomy of gymnophthalmid lizards has been largely unstable. In recent years, new taxonomic arrangements emerged as phylogenetic studies were published (Castoe et al., 2004, Doan and Castoe, 2005, Goicoechea et al., 2012, Pellegrino et al., 2001, Torres-Carvajal and Mafla-Endara, 2013). Our results indicate that *Potamites* as currently recognized is paraphyletic, with *P. cochranae* and *P. flavogularis* forming a separate clade sister to the clade containing *Macropholidus ruthveni, Pholidobolus macbrydei, Cercosaura ocellata, Petracola ventrimaculatus, Proctoporus bolivianus* and *Potamites sensu stricto* (*P. cochranae*, *P. ecpleopus*, *P. flavogularis*, *P. juruazensis*, *P. montanicola*, *P. ocellatus P. strangulatus*).

Morphological differences between *P. cochranae* and other species of *Potamites* were reported half a century ago by Uzzell (1966), who noted that the tail in this species was not as compressed as other species in the genus (*Neusticurus* at that time). Interestingly, Uzzell went further to suggest that this difference in tail morphology meant that *P. cochranae* was probably not as aquatic as other members in the genus, which has been confirmed by our own field observations.

Variation in <u>Potamites strangulatus</u> (Cope, 1868)

Uzzell (1966) mentioned that the type locality of this species is either between Papallacta and Napo, or along Río Napo, before it joins Río Marañón, in Ecuador or Peru. According to his description, this species occurs in Amazonian lowlands between 100 to 800 m for *P. strangulatus strangulatus*, and between 1300 to 1600 m *P. strangulatus trachodus* although our collection data have shown that the species range goes higher than 800m.

Uzzell (1966) determines some morphological differences between lowlands (<700m) and foothills (>700m) specimens, which does not match the distribution of the clades recovered in this study. Clade D occurs in Eastern Ecuador, from the foothills of the Andes to the lowlands of the Amazon and Clade F is set at the Southern part of Ecuador. Clade F was collected in a range from 738 - 839 m. An important remark is that Clades A, B and C share a common collection place, this place is situated near the valleys of Río Santiago and Río Zamora where *Euspondylus festae* (Peracca, 1897) was described. In the description is written "there may be a population (…) closely related to *N. strangulatus* but differing in having 35 to 38 scales around the mid body region" (p. 303)". *Euspondylus festae*, later *Neusticurus festae,* is a junior synonym of *P. strangulatus* (Uzzell, 1966).It must be taken in consideration that these three clades share this area between the valleys and it is possible that this is actually one or more cryptic species.

Additionally there are differences among central Peru and Ecuadorian specimens in: "not only low scale counts around the mid body region, but also in having tubercles on the body, a common feature of lizards of the genus that the Ecuadorian specimens remarkably do not have" (Uzzell, 1966, p. 307).This specific physical differentiation could be a measurable feature in the clades E and F.

Variation in Potamites ecpleopus (Cope, 1876)

Uzzell (1966) mentioned morphological differences alongside the Northern and Southern specimens and between lowlands and foothills in Colombia, Ecuador and Peru. *P. ecpleopus* is distributed in the Amazon basin and Eastern slopes of the Andes.

The location of the holotype is in Peru; the exact coordinates are unknown but according to Uzzell (1966) it is probably in drainage of Río Huallaga, between Rioja, Moyobamba, Balsapuerto and exit of Huallaga into the Amazon basin.

In the present study we cannot match these differences alongside the clades obtained in the phylogenetic trees. For instance “it is suggested that the large specimens are characteristic of the extreme Southern populations and of those found in the foothills of Ecuador” (p. 292), but clades G and I are both present alongside the north and south and also in the lowlands and foothills.

Uzzell (1966) also described small morphological differences such as small variation of color, scales and snout vent length, among populations of *P. strangulatus* and *P. ecpleopus* from Colombia, Ecuador and Peru. Our results suggest that *Potamites sensu stricto* is more diverse than currently recognized, which could explain the morphological differences reported by Uzzell.

Species delimitation

Zhang et al. (2013) called for caution on datasets where the number of individuals sampled per species is unbalanced because of the tendency to substantially overestimate the number of species. This is the case in our dataset. For instance: Clades of *P. ocellatus*, *P. montanicola* and the Clade E present a sample number of two individuals and in the Clade of *P. juruazensis* the sample number is three individuals; giving a false representation of the heterogeneity within those clades.

Figure 7 illustrates the result of the bPTP analysis, which is similar to the phylogenetic tree (Fig. 5). The 40 unconfirmed candidate species more or less correspond to the clades shown in the phylogenetic tree.

From the 40 unconfirmed candidate species it is notable that only 24 reach the >91 PP criteria for a strong support recommended by Zhang et al. (2013). Candidate species 5 represents a clade within *P. flavogularis*. Candidate species 8, 39 and 40 represent *P. ocellatus*, *P. montanicola* and *P. juruazensis* respectively. Candidate specie 38 represents Clade D (*P. strangulatus*) and candidate species 28 represents Clade E (*P. strangulatus*). Candidate species 15 (*P. ecpleopus*) form a separate species all from the La Convención province. All the other candidate species with high PP are nested within the other clades (A – I) but they do not represent the whole clade as the others mentioned above.

The large number of unconfirmed candidate species reflects high genetic diversity within the clade; nevertheless, we recommend to use it as a basis for further exploration of species limits.

Impact on conservation

The vast genetic diversity within *Potamites* reported in this paper is a great step towards an improved conservation of its species, which are currently not properly assessed due to lack of information (Torres-Carvajal et al., 2014). With each new cryptic species, the distribution range changes and divides the former distribution range, giving more importance to each population because it represents a higher percentage of the whole group (Bickford et al., 2007).

There are some distribution ranges that offer an insight to the vulnerability of candidate cryptic species. For instance Clade B (*P. strangulatus*) is represented by four individuals, two isolated from Tarapoto which are genetically different from the specimens in Clades A and C, also found in the same region, with divergence values of 15.6% with Clade A and 17.2% with Clade C for ND4. It is possible that one of these clades represents the formerly described *Euspondylus festae,* in which case then the range of *P. strangulatus* would be shortened. Clade F contains samples from Southern Ecuador and Northern Peru, forming a clade that is geographically far from the other groups, isolating them from the rest of *P. strangulatus*.

One remarkable result is the distribution of Clade H within *P. ecpleopus,* which geographically comes from two very different and distant locations, one from the Northeastern part of Ecuador and the other from Southern Peru. Possible explanations are that the range of distribution is wider as currently recognized or there is an absence of collected specimens alongside the Northeastern part of Peru, possible Brazil until the Southern part of the Peruvian Amazon. As mentioned above we don't know the conservation status for this species (Torres-Carvajal et al., 2014) and the lack of knowledge about the true diversity and distribution only accentuate the problem, we cannot protect what we do not know about.

The more aware we are about the real range and distribution of each species the more fitting actions can be executed to improve the conservation of species.

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Figure 1. Distribution map of five species currently recognized as *Potamites* based on specimen records deposited at QCAZ and CORBIDI. Locality data are presented in Table 1.

Figure 2. Distribution map of *P. strangulatus* and *P. ecpleopus* illustrating the localities where tissue samples where obtained (included in the phylogeny in this study) and localities where just the specimens where collected without tissue.

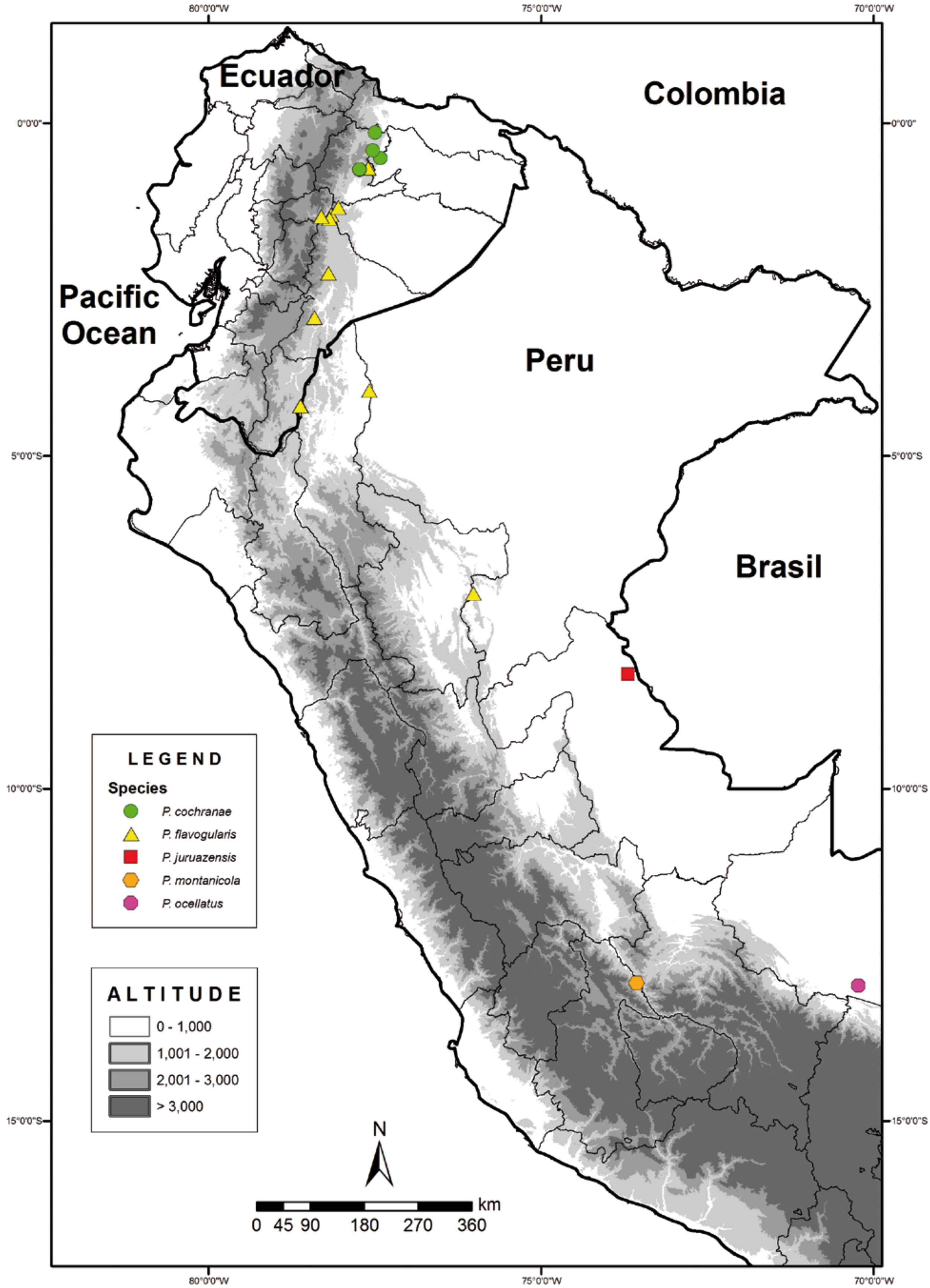
Figure 3. Maximum likelihood tree of 172 terminals for four genes (12S, 16S, ND4, C-mos). Blue color represents posterior probabilities and red color represents maximum likelihood bootstrap. Blue asterisks and red asterisks in the branches represent posterior probabilities (≥0.99) and maximum likelihood bootstrap (>70), respectively. Voucher number, taxon name and collecting locality (province) is shown in each terminal.

Figure 4. Maximum likelihood summarized phylogeny of *Potamites*. Blue color represents posterior probabilities and red color represents maximum likelihood bootstrap. Blue asterisks and red asterisks in the branches represent posterior probabilities (≥0.99) and maximum likelihood bootstrap (>70), respectively.

Figure 5. Distribution map of *P. strangulatus* (Clades A-F) based on specimens deposited at QCAZ and CORBIDI. Clades are presented in Figure 3.

Figure 6. Distribution map of *P. ecpleopus* (Clades G-I) based on specimens deposited at QCAZ and CORBIDI. Clades are presented in Figure3.

Figure 7. Maximum likelihood phylogeny with Bayesian support values based on a concatenated matrix of three mitochondrial genes (12S, 16S, ND4). The blue terminal branches represent unconfirmed candidate species and the red lines show the specimens included in each species. Above the branches are the posterior probabilities support values. Voucher number, taxon name and collecting locality (province) is shown in each terminal.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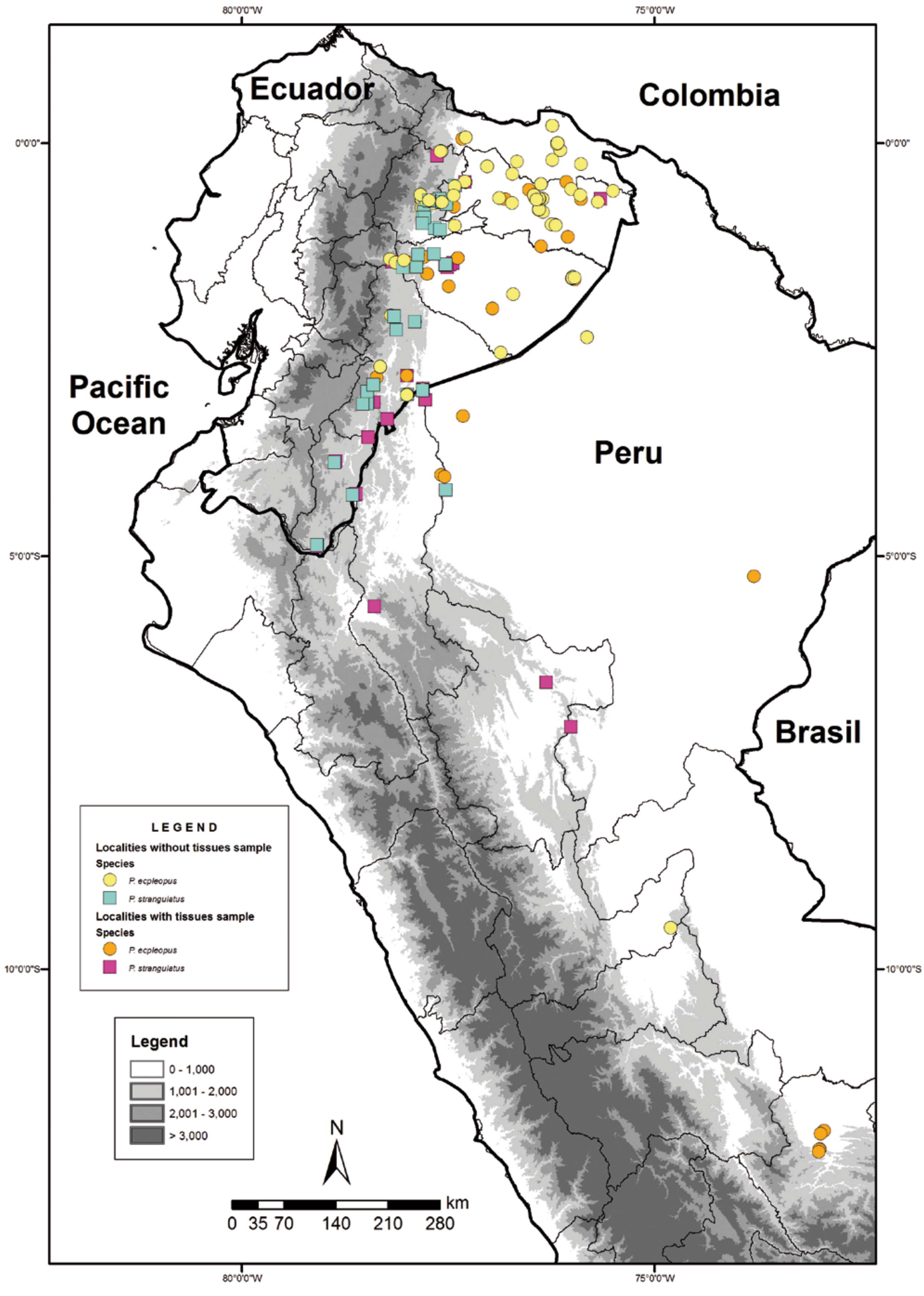
10°0'0"S
15°0'0"S
Ecuador
Colombia
Pacific Ocean
Peru
Brasil
LEGEND
Species
P. cochranae
P. flavogularis
P. juruazensis
P. montanicola
P. ocellatus
ALTITUDE
0 - 1,000
1,001 - 2,000
2,001 - 3,000
> 3,000
N
km
0 45 90 180 270 360

Figure 1.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Ecuador
Colombia
Pacific Ocean
Peru
Brasil
LEGEND
Localities without tissues sample
Species
P. ecpleopus
P. stranguIatus
Localities with tissues sample
Species
P. ecpleopus
P. stranguIatus
Legend
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0 35 70 140 210 280
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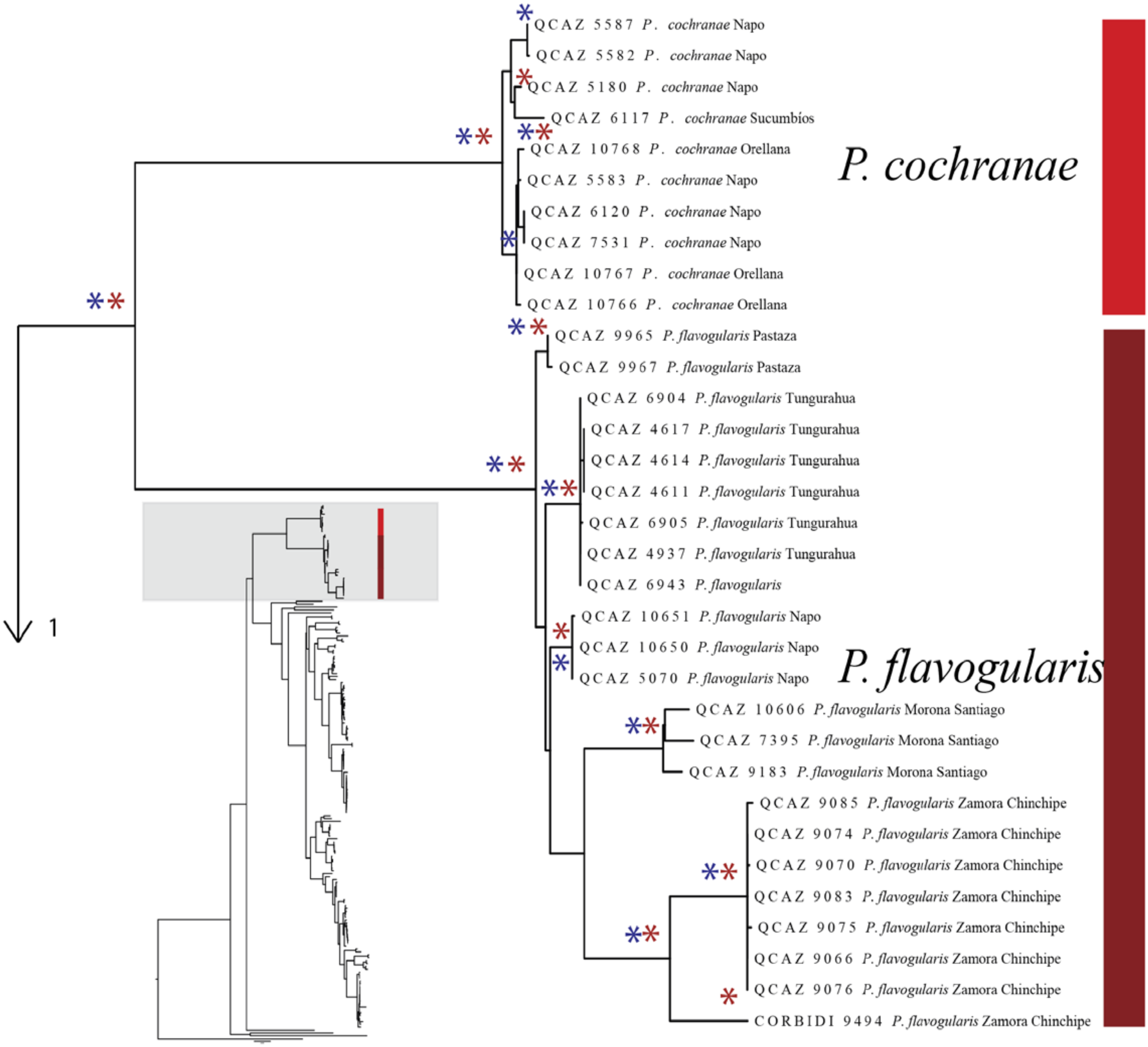
Figure 2.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QCAZ 10768 P. cochranae Orellana
QCAZ 5583 P. cochranae Napo
QCAZ 6120 P. cochranae Napo
QCAZ 7531 P. cochranae Napo
QCAZ 10767 P. cochranae Orellana
QCAZ 10766 P. cochranae Orellana
P. cochranae
QCAZ 9965 P. flavogularis Pastaza
QCAZ 9967 P. flavogularis Pastaza
QCAZ 6904 P. flavogularis Tungurahua
QCAZ 4617 P. flavogularis Tungurahua
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QCAZ 4611 P. flavogularis Tungurahua
QCAZ 6905 P. flavogularis Tungurahua
QCAZ 4937 P. flavogularis Tungurahua
QCAZ 6943 P. flavogularis
QCAZ 10651 P. flavogularis Napo
QCAZ 10650 P. flavogularis Napo
QCAZ 5070 P. flavogularis Napo
P. flavogularis
QCAZ 10606 P. flavogularis Morona Santiago
QCAZ 7395 P. flavogularis Morona Santiago
QCAZ 9183 P. flavogularis Morona Santiago
QCAZ 9085 P. flavogularis Zamora Chinchipe
QCAZ 9074 P. flavogularis Zamora Chinchipe
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QCAZ 9083 P. flavogularis Zamora Chinchipe
QCAZ 9075 P. flavogularis Zamora Chinchipe
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CORBIDI 9494 P. flavogularis Zamora Chinchipe
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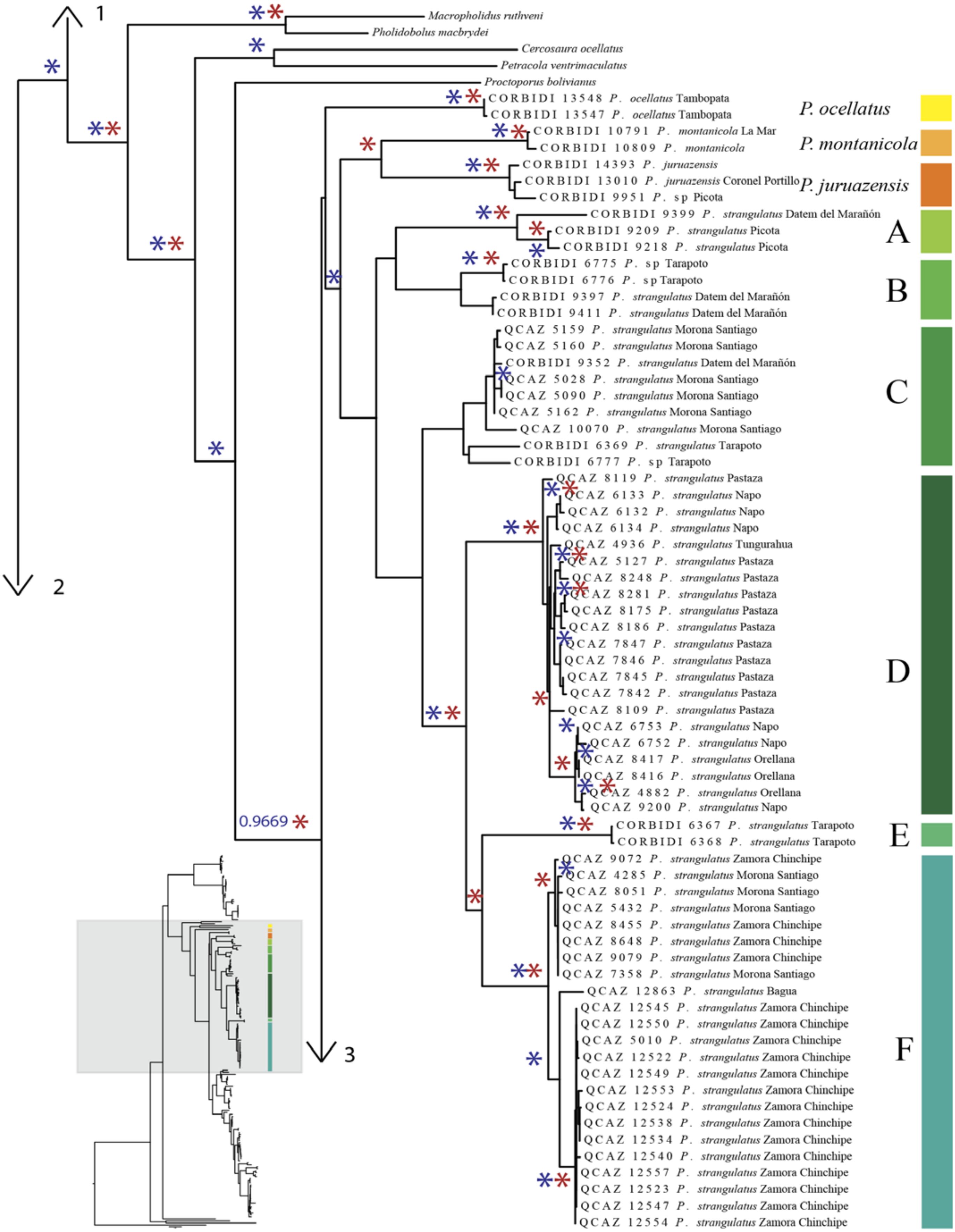
Figure 3.



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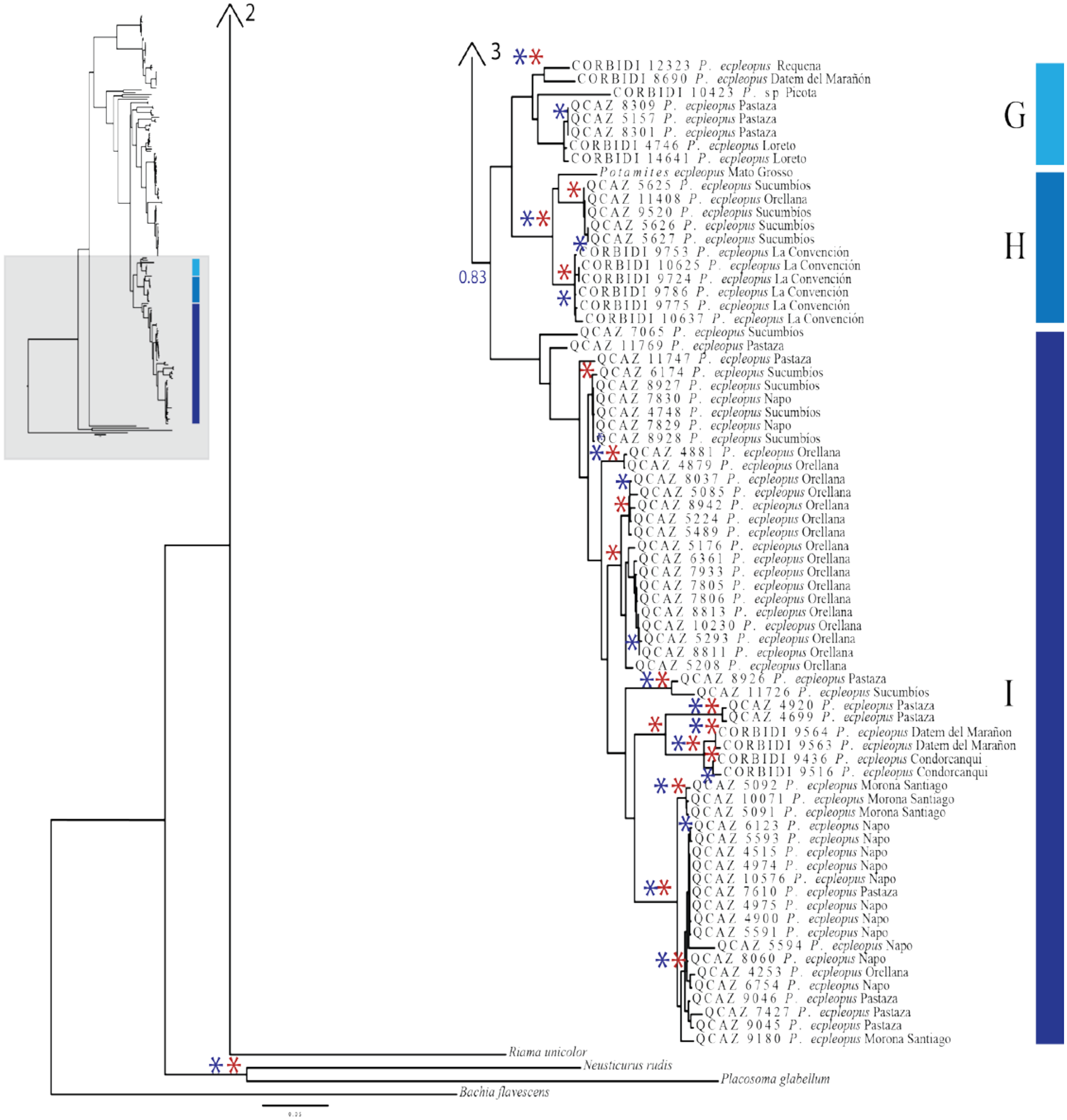

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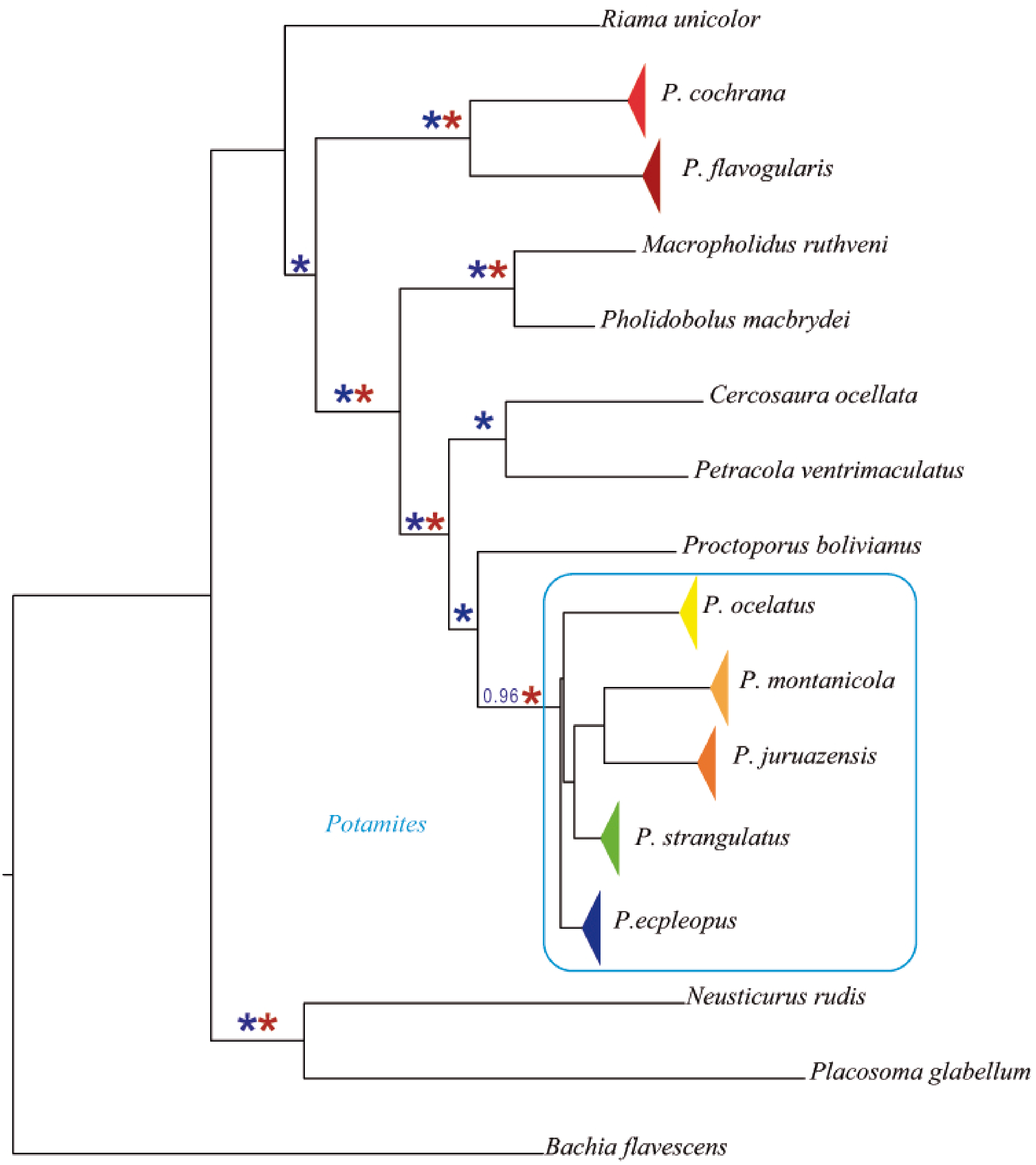
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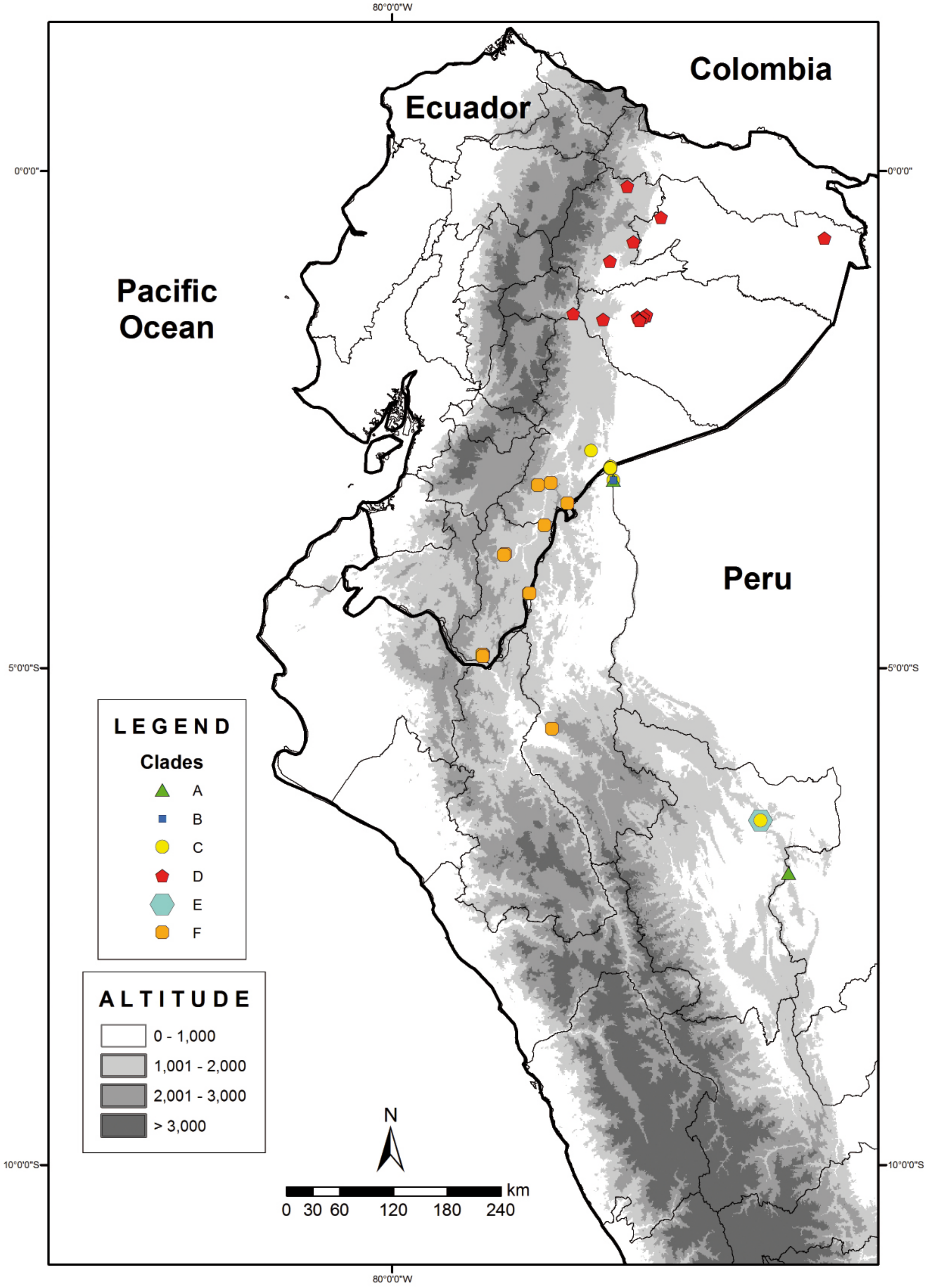
Proctoporus bolivianus
P. ocelatus
P. montanicola
P. juruazensis
P. strangulatus
P.ecpleopus
0.96
Potamites
Neusticurus rudis
Placosoma glabellum
Bachia flavescens

Figure 4.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Colombia
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Pacific Ocean
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Figure 5.

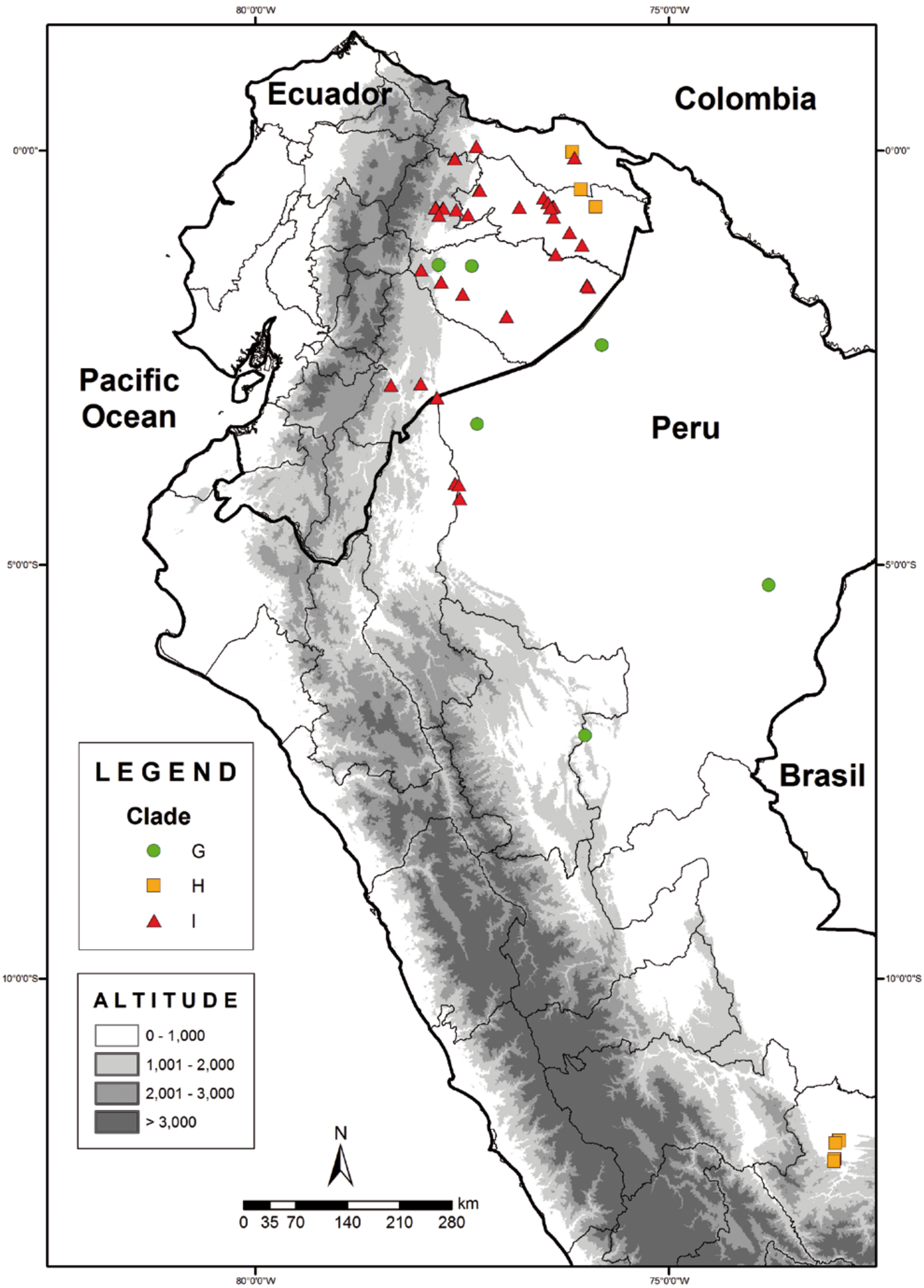
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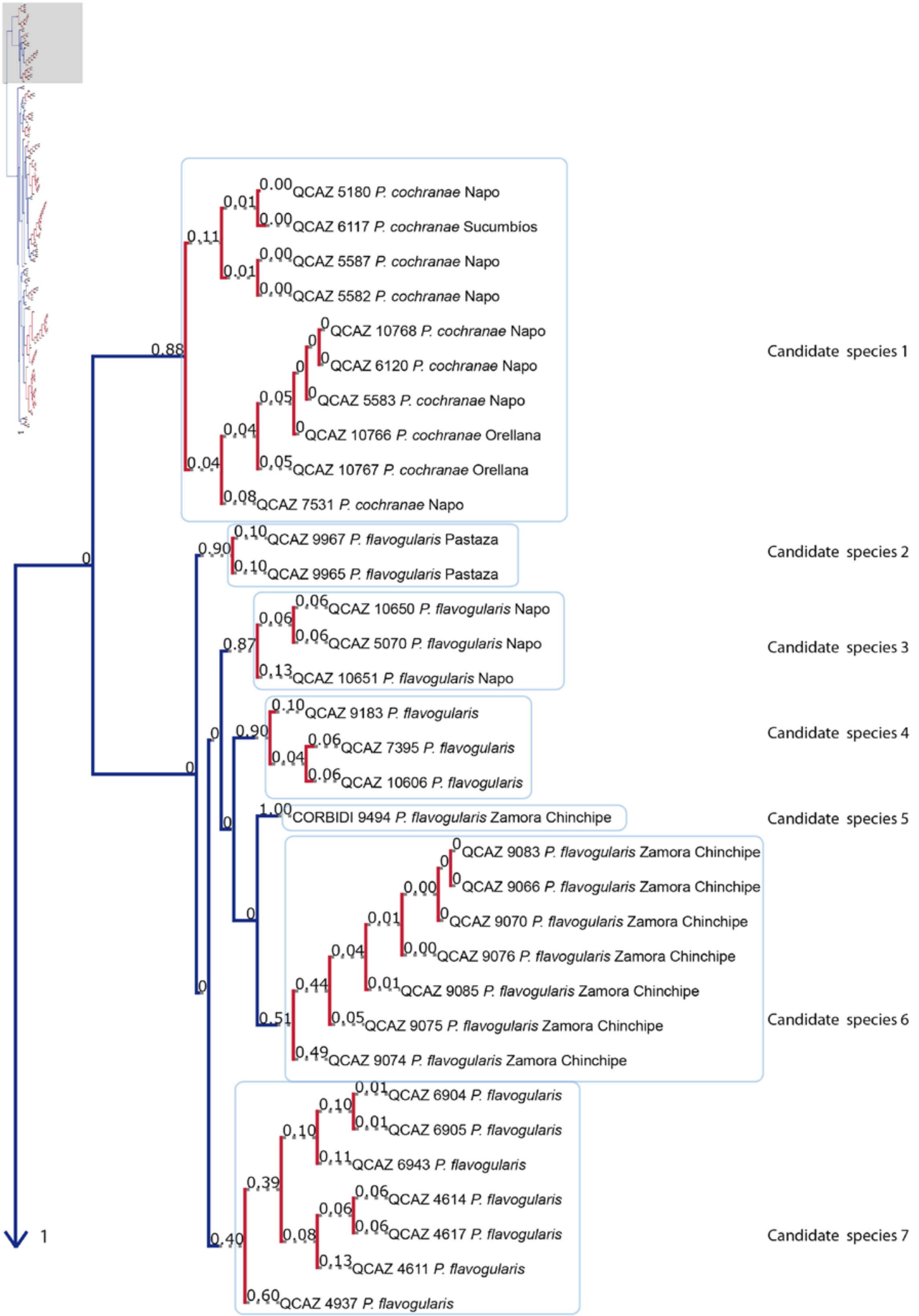
Figure 6.



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QCAZ 10768 P. cochranae Napo
QCAZ 6120 P. cochranae Napo
QCAZ 5583 P. cochranae Napo
QCAZ 10766 P. cochranae Orellana
QCAZ 10767 P. cochranae Orellana
QCAZ 7531 P. cochranae Napo
Candidate species 1
QCAZ 9967 P. flavogularis Pastaza
QCAZ 9965 P. flavogularis Pastaza
Candidate species 2
QCAZ 10650 P. flavogularis Napo
QCAZ 5070 P. flavogularis Napo
QCAZ 10651 P. flavogularis Napo
Candidate species 3
QCAZ 9183 P. flavogularis
QCAZ 7395 P. flavogularis
QCAZ 10606 P. flavogularis
Candidate species 4
CORBIDI 9494 P. flavogularis Zamora Chinchipe
Candidate species 5
QCAZ 9083 P. flavogularis Zamora Chinchipe
QCAZ 9066 P. flavogularis Zamora Chinchipe
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QCAZ 9076 P. flavogularis Zamora Chinchipe
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Candidate species 6
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QCAZ 6905 P. flavogularis
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QCAZ 4937 P. flavogularis
Candidate species 7
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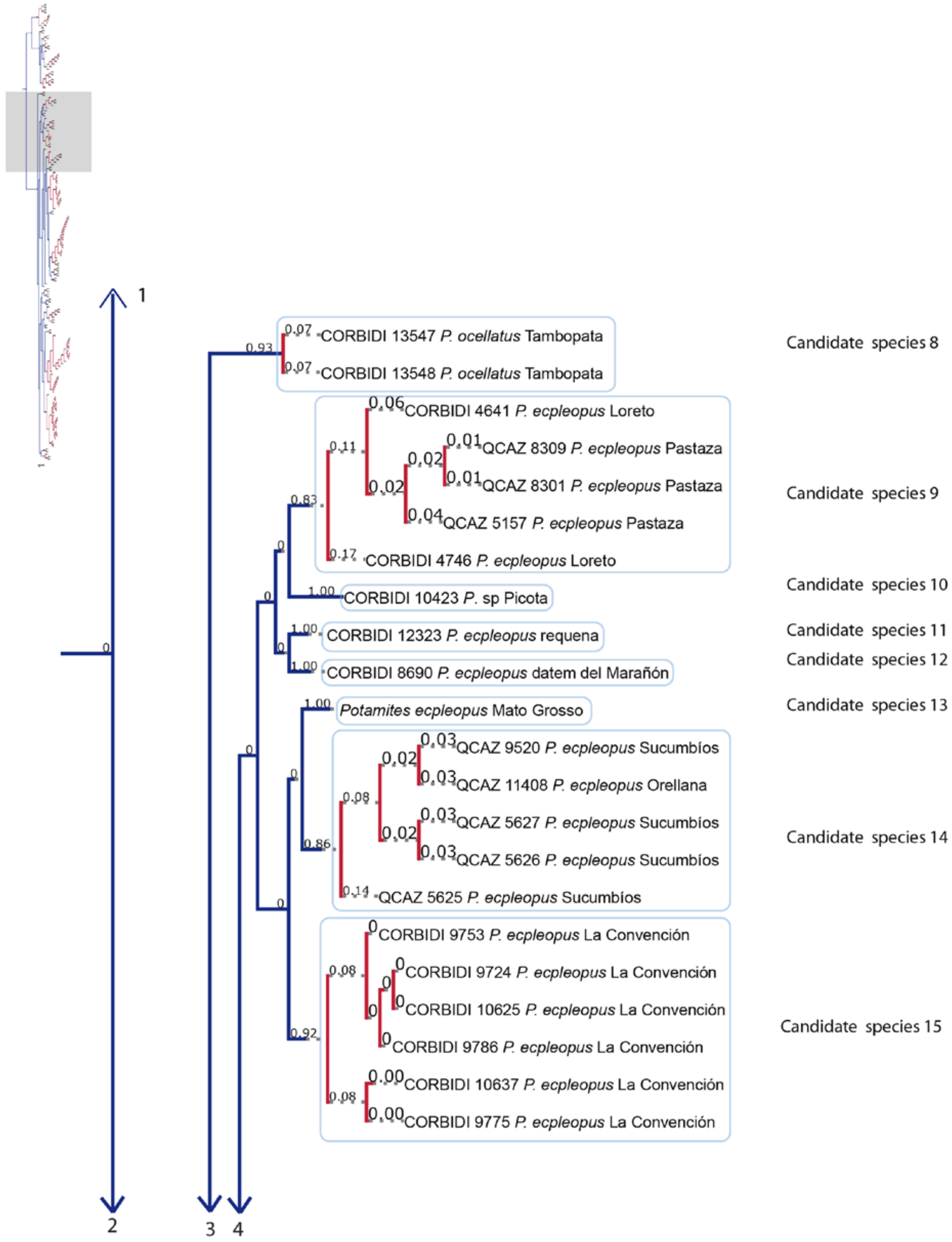
Figure 7.



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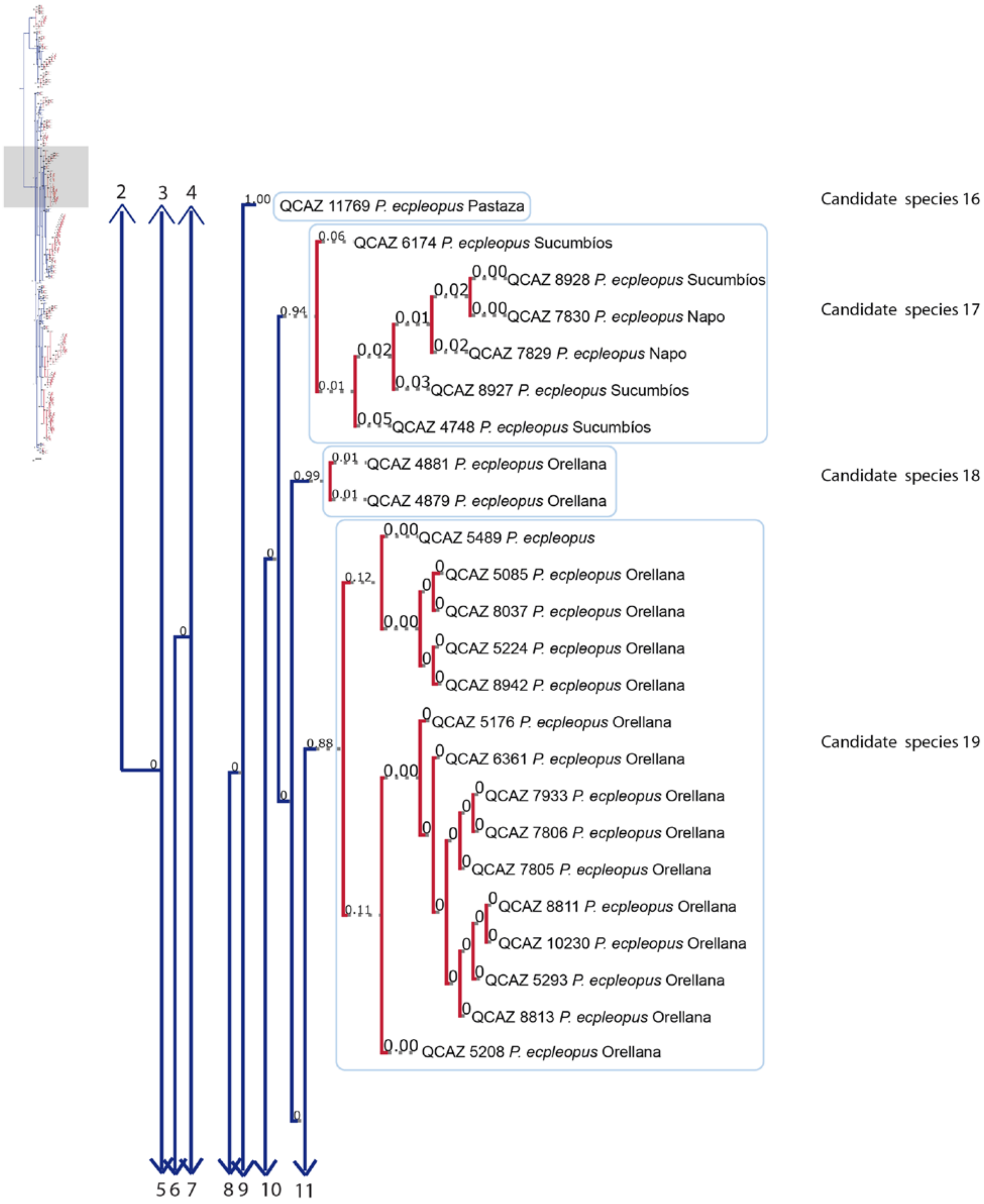

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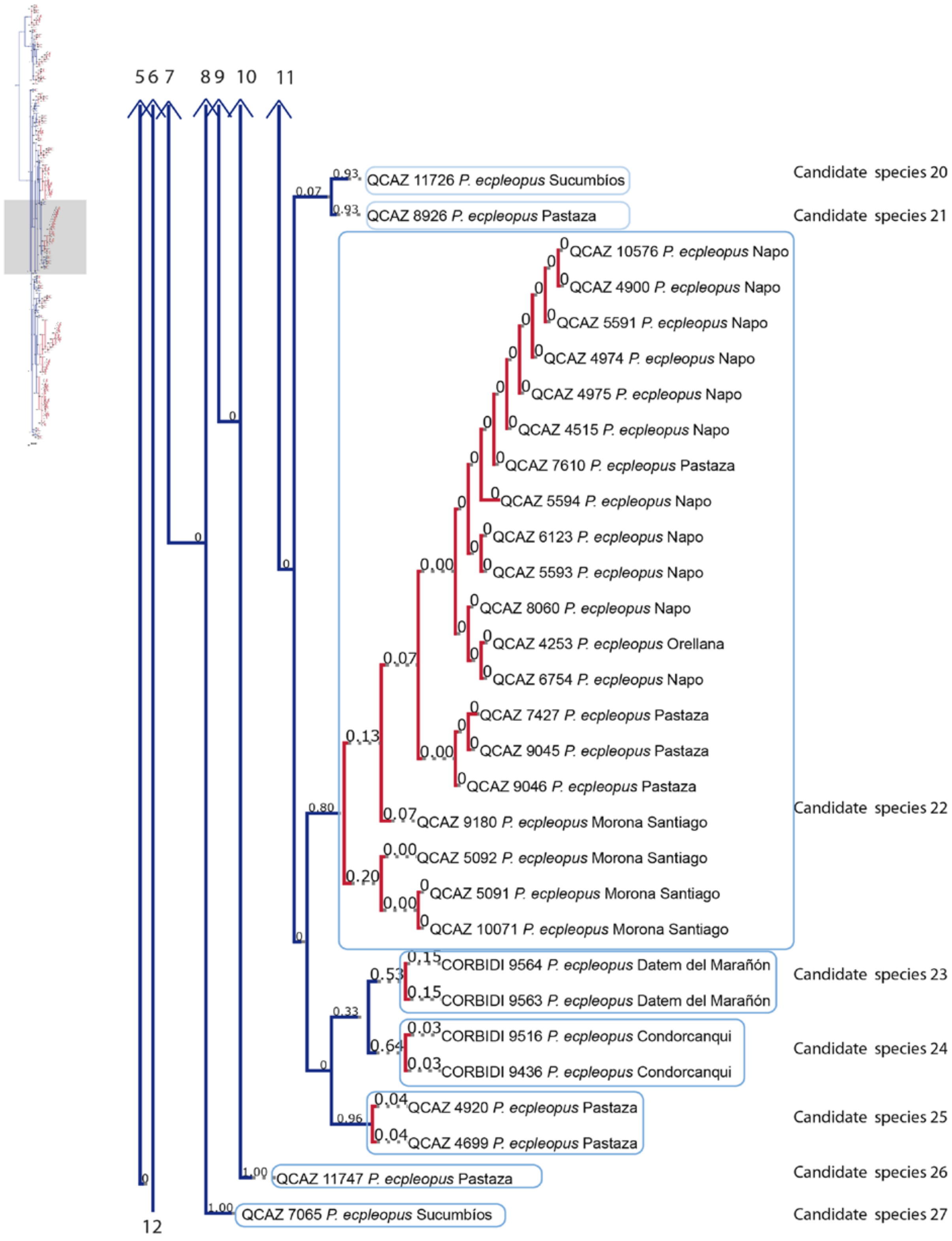

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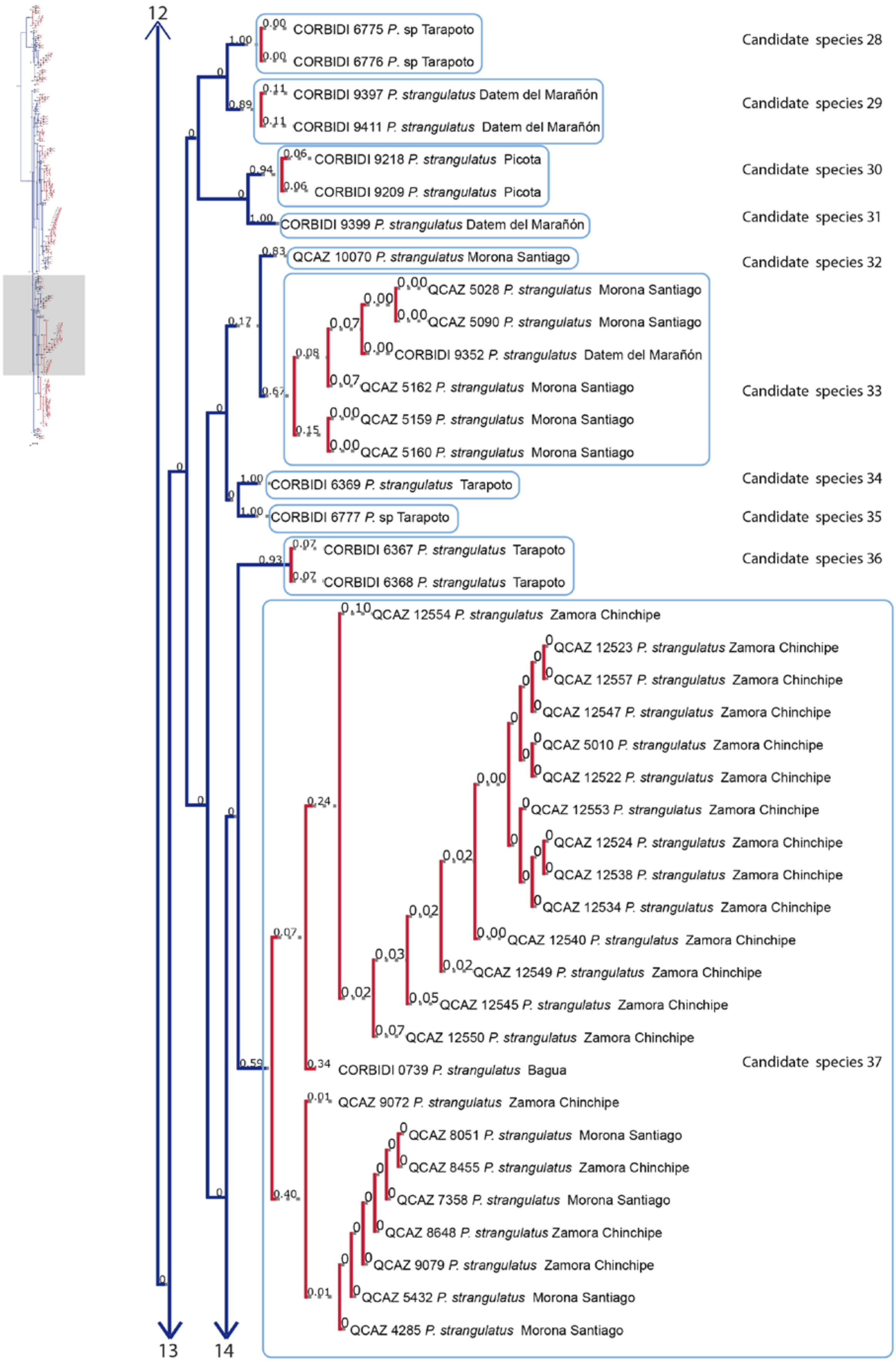

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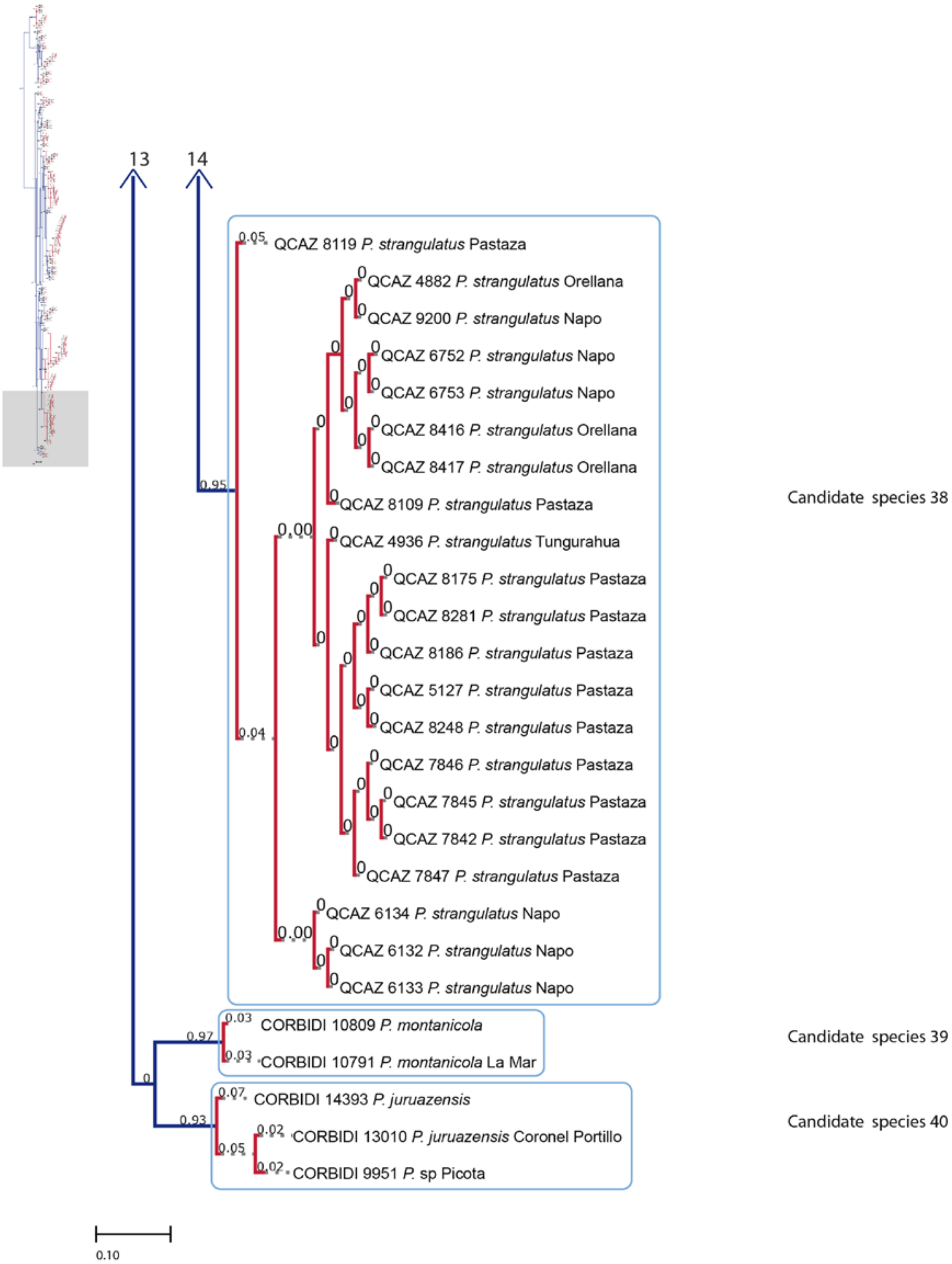

Figure 7. Continued

Table 1. List of specimen vouchers, collecting localities, and GenBank accession numbers of DNA sequences generated in this study. Localities and voucher/field numbers are given for the species used in this study. Acronyms QCAZR=Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador; CORBIDI= Centro de Ornitología y Biodiversidad.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR4253	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR4285	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR4515	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR4611	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR4614	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR4617	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR4699	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR4748	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR4879	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR4881	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR4882	*Potamites strangulatus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR4900	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR4920	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR4936	*Potamites strangulatus*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR4937	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR4974	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR4975	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5010	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR5028	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5070	*Potamites flavogularis*	Ecuador	Napo	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR5085	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5090	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5091	*Potamites ecpleopus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5092	*Potamites ecpleopus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5127	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR5157	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR5159	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5160	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5162	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5176	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5180	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5208	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5224	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5293	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5432	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR5489	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR5582	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5583	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5587	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5591	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR5593	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR5625	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR5626	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR5627	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR6117	*Potamites cochranae*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR6120	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6123	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6132	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6133	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6134	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6174	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR6361	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR6752	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6753	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6754	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR6904	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR6905	*Potamites flavogularis*	Ecuador	Tungurahua	Pending	Pending	Pending	Pending
QCAZR7065	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR7358	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR7395	*Potamites flavogularis*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR7427	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR7531	*Potamites cochranae*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR7610	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR7805	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR7806	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR7829	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR7830	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR7842	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR7845	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR7846	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR7847	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR7933	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR8037	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR8051	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR8060	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR8109	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8119	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8175	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8186	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8248	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8281	*Potamites strangulatus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8301	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8309	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR8416	*Potamites strangulatus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR8417	*Potamites strangulatus*	Ecuador	Orellana	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR8455	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR8648	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR8811	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR8813	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR8926	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR8927	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR8928	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR8942	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR9045	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR9046	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR9066	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9070	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9072	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9074	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9075	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9076	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9079	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9083	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9085	*Potamites flavogularis*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR9180	*Potamites ecpleopus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR9183	*Potamites flavogularis*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR9200	*Potamites strangulatus*	Ecuador	Napo	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR9520	*Potamites ecpleopus*	Ecuador	Sucumbíos	Pending	Pending	Pending	Pending
QCAZR9965	*Potamites flavogularis*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR9967	*Potamites flavogularis*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR10070	*Potamites strangulatus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR10071	*Potamites ecpleopus*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR10230	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR10576	*Potamites ecpleopus*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR10606	*Potamites flavogularis*	Ecuador	Morona Santiago	Pending	Pending	Pending	Pending
QCAZR10650	*Potamites flavogularis*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR10651	*Potamites flavogularis*	Ecuador	Napo	Pending	Pending	Pending	Pending
QCAZR10766	*Potamites cochranae*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR10767	*Potamites cochranae*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR10768	*Potamites cochranae*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR11408	*Potamites ecpleopus*	Ecuador	Orellana	Pending	Pending	Pending	Pending
QCAZR11726	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR11747	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR11769	*Potamites ecpleopus*	Ecuador	Pastaza	Pending	Pending	Pending	Pending
QCAZR12522	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12523	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12524	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12534	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12538	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
QCAZR12540	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12545	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12547	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12549	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12550	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12553	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12554	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
QCAZR12557	*Potamites strangulatus*	Ecuador	Zamora Chinchipe	Pending	Pending	Pending	Pending
CORBIDI4641	*Potamites ecpleopus*	Perú	Loreto	Pending	Pending	Pending	Pending
CORBIDI4746	*Potamites ecpleopus*	Perú	Loreto	Pending	Pending	Pending	Pending
CORBIDI12323	*Potamites ecpleopus*	Perú	Requena	Pending	Pending	Pending	Pending
CORBIDI10625	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending
CORBIDI10637	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending
CORBIDI8690	*Potamites ecpleopus*	Perú	Datem	Pending	Pending	Pending	Pending
CORBIDI9436	*Potamites ecpleopus*	Perú	Condorcanqui	Pending	Pending	Pending	Pending
CORBIDI9516	*Potamites ecpleopus*	Perú	Condorcanqui	Pending	Pending	Pending	Pending
CORBIDI9563	*Potamites ecpleopus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9564	*Potamites ecpleopus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9724	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending
CORBIDI9753	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending
CORBIDI9775	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending
CORBIDI9786	*Potamites ecpleopus*	Perú	La Convención	Pending	Pending	Pending	Pending

Table 1. Continued.

Voucher	Species	Country	Province	12S	16S	ND4	CMOS
CORBIDI9494	*Potamites flavogularis*	Perú	Condorcanqui	Pending	Pending	Pending	Pending
CORBIDI13010	*Potamites juruazensis*	Perú	Coronel Portillo	Pending	Pending	Pending	Pending
CORBIDI10791	*Potamites montanicola*	Perú	La Mar	Pending	Pending	Pending	Pending
CORBIDI10809	*Potamites montanicola*	Perú		Pending	Pending	Pending	Pending
CORBIDI13547	*Potamites ocellatus*	Perú	Tambopata	Pending	Pending	Pending	Pending
CORBIDI13548	*Potamites ocellatus*	Perú	Tambopata	Pending	Pending	Pending	Pending
CORBIDI10423	*Potamites* sp.	Perú	Picota	Pending	Pending	Pending	Pending
CORBIDI6775	*Potamites* sp.	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI6776	*Potamites* sp.	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI6777	*Potamites* sp.	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI9951	*Potamites* sp.	Perú	Picota	Pending	Pending	Pending	Pending
CORBIDI6367	*Potamites strangulatus*	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI6368	*Potamites strangulatus*	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI6369	*Potamites strangulatus*	Perú	Tarapoto	Pending	Pending	Pending	Pending
CORBIDI9209	*Potamites strangulatus*	Perú	Picota	Pending	Pending	Pending	Pending
CORBIDI9218	*Potamites strangulatus*	Perú	Picota	Pending	Pending	Pending	Pending
CORBIDI9352	*Potamites strangulatus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9397	*Potamites strangulatus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9399	*Potamites strangulatus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9411	*Potamites strangulatus*	Perú	Datem del Marañón	Pending	Pending	Pending	Pending
CORBIDI9523	*Potamites strangulatus*	Perú	Bagua	Pending	Pending	Pending	Pending

Table 2. GenBank accession numbers and voucher of DNA sequences of outgroups used for phylogenetic analysis. Museum acronyms: CBF-Colección Boliviana de Fauna, Herpetology, La Paz, Bolivia; CORBIDI- Centro de Ornitología y Biodiversidad Lima, Peru; KU- University of Kansas, Museum of Natural History, Division of Herpetology, USA;LSUMZ-Louisiana State University, Museum of Natural Science, Louisiana, USA.

Voucher	Species	12S	16S	ND4	CMOS
KU219838	*Petracola ventrimaculatus*	AY507863	AY507883	AY507894	AY507910
CORBIDI 4281	*Macropholidus ruthveni*	KC894354	KC894368	KC894382	
KU218406	*Pholidobolus macbrydei*	AY507848	AY507867	AY507886	AY507896
KU217211	*Riama unicolor*	AY507862	AY507880	AY507893	AY507907
CBF3438	*Proctoporus bolivianus*	JX435941	JX435995	JX436070	JX436041
LSUMZ H12977	*Bachia flavescens*	AF420705	AF420753	AF420869	AF420859
MRT 977406	*Cercosaura ocellata*	AF420677	AF420731	AF420883	AF420834
LG 940	*Placosoma glabellum*	AF420674	AF420742	AF420907	AF420833
MRT 926008	*Neusticurus rudis*	AF420689	AF420709	AF420905	
MRT 0472	*Potamites ecpleopus*	AF420656	AF420748	AF420890	AF420829

Table 3. Protocols for amplification of mitochondrial genes and nuclear gene by the Polymerase chain reaction (PCR).

Gen and primers	Sequences (5' – 3')	PCR Protocol
12S		
12Sa[a];12Sb[a]	**F:** CTGGGATTAGATACCCCACTA **R:** TGAGGAGGGTGACGGGCGGT	((94.00 °C - 03:00 min, 1 cycle)/ (92.00 °C - 30 seg, 56.00 °C - 30 seg, 72.00 °C - 01:50 min, 33 cycles)/(72.00 °C - 10:00 min, 1 cycle)/ (4.00 °C))
16S		
16SF.0[b]; 16SR.0[b]	**F:** CTGTTTACCAAAAACATMRCCTYTA **R:** TAGATAGAAACCGACCTGGATT	((96.00 °C - 03:00 min, 1 cycle)/ (95.00 °C - 30 seg, 51.00 °C - 01:00 min, 72.00 °C - 01:00 min, 40 cycles)/(72.00 °C - 10:00 min, 1 cycle)/ (4.00 °C))
16SL[c]; 16SH[c]	**F:** CGCCTGTTTAACAAAAACAT **R:** CCGGTCTGAACTCAGATCACGT	
ND4		
ND4F[d]; ND4R[d]	**F:** CACCTATGACTACCAAAAGCTCATGT **R:** CATTACTTTTACTTGGATTTGCACCA	((96.00 °C - 03:00 min, 1 cycle)/ (95.00 °C - 30 seg, 52.00 °C - 01:00 min, 72.00 °C - 01:00 min, 40 cycles)/(72.00 °C - 10:00 min, 1 cycle)/ (4.00 °C))
ND412931L[e]; ND4R[d]	**F:** CTACCAAAAGCTCATGTAGAAGC **R:** CATTACTTTTACTTGGATTTGCACCA	
ND4[d]; Leu[d]	**F:** CACCTATGACTACCAAAAGCTCATGTAGAAGC **R:** CATTACTTTTACTTGGATTTGCACCA	
c-mos		
G73[f]; G74[f]	**F:** GCGGTAAAGCAGGTGAAGAAA **R:** TGAGCATCCAAAGTCTCCAATC	((96.00 °C - 03:00 min, 1 cycle)/ (95.00 °C - 25 seg, 56.00 °C - 01:00 min, 72.00 °C - 01:00 min, 35 cycles)/(72.00 °C - 10:00 min, 1 cycle)/ (4.00 °C))

Primers references: [a] Harris et al.(1998); [b] primers designed by A. S. Whiting; [c] Pellegrino et al. (2001), [d]Arevalo et al. (1994); [e]Blair et al. (2009), [f]Saint et al., (1998).

Table 4. PartitionFinder v1.1.1 best-fit partition scheme and evolution models used for ML and BI.

Partition	Best Model	Components
1	GTR+I+G	12S, 16s
2	GTR+I+G	ND4 first position
3	HKY+I+G	ND4 second position
4	GTR+G	ND4 third position
5	HKY+G	CMOS first position, CMOS second position
6	HKY+G	CMOS third position

Table 5.Genetic divergence average values matrices for the mitochondrial DNA 12s, 16s and ND4 of *P. cochranae and P. flavogularis.*

12s	*P. cochranae*	*P. flavogularis*
P. cochranae	0.019	
P. flavogularis	0.095	0.095

16s	*P. cochranae*	*P. flavogularis*
P. cochranae	0.011	
P. flavogularis	0.054	0.015

ND4	*P. cochranae*	*P. flavogularis*
P. cochranae	0.014	
P. flavogularis	0.255	0.075

Table 6.Genetic divergence average values matrix for the mitochondrial DNA 12s of *Potamites sensu stricto* species, bold font. Standard Error in italic font.

	12s	*P. ocellatus*	*P. montanicola*	*P. juruazensis*	Clade A	Clade B	Clade C	Clade D	Clade E	Clade F	Clade G	Clade H	Clade I
	P. ocellatus	**0.037**	*0.01*	*0.01*	*0.013*	*0.008*	*0.008*	*0.011*	*0.01*	*0.011*	*0.005*	*0.006*	*0.008*
	P. montanicola	**0.081**	**0.034**	*0.009*	*0.01*	*0.009*	*0.009*	*0.012*	*0.012*	*0.011*	*0.011*	*0.011*	*0.01*
	P. juruazensis	**0.078**	**0.067**	**0.039**	*0.011*	*0.007*	*0.008*	*0.012*	*0.01*	*0.01*	*0.011*	*0.01*	*0.009*
Clade A	*P. strangulatus*	**0.08**	**0.059**	**0.062**	**0.004**	*0.011*	*0.01*	*0.015*	*0.013*	*0.013*	*0.013*	*0.013*	*0.012*
Clade B	*P. strangulatus*	**0.068**	**0.073**	**0.059**	**0.069**	**0.037**	*0.001*	*0.008*	*0.006*	*0.005*	*0.009*	*0.007*	*0.007*
Clade C	*P. strangulatus*	**0.071**	**0.073**	**0.065**	**0.064**	**0.037**	**0.038**	*0.008*	*0.008*	*0.005*	*0.009*	*0.009*	*0.007*
Clade D	*P. strangulatus*	**0.069**	**0.074**	**0.065**	**0.069**	**0.045**	**0.044**	**0.007**	*0.012*	*0.01*	*0.012*	*0.012*	*0.01*
Clade E	*P. strangulatus*	**0.06**	**0.069**	**0.053**	**0.054**	**0.037**	**0.046**	**0.043**	**0**	*0.01*	*0.011*	*0.01*	*0.01*
Clade F	*P. strangulatus*	**0.065**	**0.066**	**0.052**	**0.053**	**0.034**	**0.036**	**0.03**	**0.026**	**0.003**	*0.011*	*0.011*	*0.011*
Clade G	*P. ecpleopus*	**0.051**	**0.086**	**0.086**	**0.074**	**0.07**	**0.07**	**0.066**	**0.06**	**0.064**	**0.028**	*0.004*	*0.009*
Clade H	*P. ecpleopus*	**0.051**	**0.081**	**0.069**	**0.071**	**0.059**	**0.066**	**0.061**	**0.046**	**0.051**	**0.035**	**0.02**	*0.009*
Clade I	*P. ecpleopus*	**0.062**	**0.067**	**0.061**	**0.064**	**0.053**	**0.058**	**0.049**	**0.044**	**0.051**	**0.063**	**0.057**	**0.021**

Table 7.Genetic divergence average values matrix for the mitochondrial DNA 16s of *Potamites sensu stricto* species, bold font. Standard Error in italic font.

	16s	*P. ocellatus*	*P. montanicola*	*P. juruazensis*	Clade A	Clade B	Clade C	Clade D	Clade E	Clade F	Clade G	Clade H	Clade I
	P. ocellatus	**0.011**	*0.006*	*0.008*	*0.006*	*0.007*	*0.007*	*0.01*	*0.011*	*0.009*	*0.008*	*0.008*	*0.007*
	P. montanicola	**0.042**	**0.03**	*0.005*	*0.006*	*0.006*	*0.006*	*0.007*	*0.009*	*0.008*	*0.007*	*0.005*	*0.006*
	P. juruazensis	**0.041**	**0.042**	**0.016**	*0.004*	*0.005*	*0.006*	*0.009*	*0.01*	*0.009*	*0.007*	*0.005*	*0.006*
Clade A	*P. strangulatus*	**0.043**	**0.05**	**0.033**	**0.041**	*0.002*	*0.002*	*0.007*	*0.006*	*0.007*	*0.006*	*0.006*	*0.005*
Clade B	*P. strangulatus*	**0.051**	**0.055**	**0.038**	**0.032**	**0.031**	*0.001*	*0.008*	*0.007*	*0.008*	*0.007*	*0.006*	*0.006*
Clade C	*P. strangulatus*	**0.049**	**0.056**	**0.037**	**0.026**	**0.027**	**0.022**	*0.008*	*0.007*	*0.007*	*0.007*	*0.007*	*0.006*
Clade D	*P. strangulatus*	**0.054**	**0.052**	**0.053**	**0.044**	**0.051**	**0.048**	**0.006**	*0.01*	*0.009*	*0.009*	*0.009*	*0.009*
Clade E	*P. strangulatus*	**0.062**	**0.061**	**0.05**	**0.036**	**0.045**	**0.039**	**0.046**	**0**	*0.008*	*0.009*	*0.01*	*0.009*
Clade F	*P. strangulatus*	**0.05**	**0.06**	**0.052**	**0.044**	**0.058**	**0.049**	**0.047**	**0.035**	**0.006**	*0.009*	*0.01*	*0.008*
Clade G	*P. ecpleopus*	**0.052**	**0.049**	**0.04**	**0.045**	**0.053**	**0.05**	**0.053**	**0.053**	**0.055**	**0.016**	*0.005*	*0.007*
Clade H	*P. ecpleopus*	**0.047**	**0.038**	**0.033**	**0.044**	**0.051**	**0.049**	**0.058**	**0.055**	**0.062**	**0.035**	**0.016**	*0.007*
Clade I	*P. ecpleopus*	**0.053**	**0.062**	**0.043**	**0.051**	**0.06**	**0.058**	**0.069**	**0.065**	**0.062**	**0.058**	**0.057**	**0.03**

Table 8.Genetic divergence average values matrix for the mitochondrial DNA ND4 of *Potamites sensu stricto* species, bold font. Standard Error in italic font.

	ND4	*P. ocellatus*	*P. montanicola*	*P. juruazensis*	Clade A	Clade B	Clade C	Clade D	Clade E	Clade F	Clade G	Clade H	Clade I
	P. ocellatus	**0.223**	*0.008*	*0.012*	*0.011*	*0.011*	*0.005*	*0.01*	*0.013*	*0.009*	*0.008*	*0.009*	*0.008*
	P. montanicola	**0.196**	**0.149**	*0.014*	*0.011*	*0.012*	*0.012*	*0.012*	*0.015*	*0.012*	*0.005*	*0.011*	*0.009*
	P. juruazensis	**0.204**	**0.206**	**n/c**	*0.016*	*0.018*	*0.018*	*0.018*	*0.019*	*0.017*	*0.013*	*0.015*	*0.014*
Clade A	*P. strangulatus*	**0.215**	**0.209**	**0.201**	**0.044**	*0.014*	*0.015*	*0.016*	*0.018*	*0.015*	*0.012*	*0.015*	*0.012*
Clade B	*P. strangulatus*	**0.182**	**0.188**	**0.194**	**0.156**	**0.002**	*0.017*	*0.017*	*0.019*	*0.016*	*0.012*	*0.015*	*0.011*
Clade C	*P. strangulatus*	**0.132**	**0.201**	**0.203**	**0.198**	**0.172**	**0.015**	*0.013*	*0.017*	*0.013*	*0.012*	*0.015*	*0.013*
Clade D	*P. strangulatus*	**0.172**	**0.198**	**0.208**	**0.202**	**0.193**	**0.135**	**0.017**	*0.018*	*0.013*	*0.012*	*0.015*	*0.012*
Clade E	*P. strangulatus*	**0.206**	**0.248**	**0.251**	**0.22**	**0.229**	**0.182**	**0.197**	**0**	*0.016*	*0.015*	*0.018*	*0.014*
Clade F	*P. strangulatus*	**0.167**	**0.225**	**0.237**	**0.215**	**0.181**	**0.142**	**0.132**	**0.175**	**0.04**	*0.012*	*0.015*	*0.012*
Clade G	*P. ecpleopus*	**0.183**	**0.166**	**0.184**	**0.197**	**0.176**	**0.18**	**0.191**	**0.239**	**0.206**	**0.121**	*0.009*	*0.007*
Clade H	*P. ecpleopus*	**0.19**	**0.195**	**0.192**	**0.208**	**0.175**	**0.196**	**0.199**	**0.257**	**0.197**	**0.149**	**0.041**	*0.012*
Clade I	*P. ecpleopus*	**0.197**	**0.196**	**0.19**	**0.185**	**0.144**	**0.187**	**0.193**	**0.211**	**0.205**	**0.171**	**0.192**	**0.088**

Table 9. bPTP server result of the unconfirmed candidate species with high posterior probabilities(≥0.91).

Unconfirmed candidate species	PP
5	1
8	0.97
10	1
11	1
12	1
13	1
15	0.92
16	1
17	0.94
18	0.99
20	0.93
21	0.93
25	0.96
26	1
27	1
28	1
30	0.94
31	1
34	1
35	1
36	0.93
38	0.95
39	0.97
40	0.93

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Genus *Pachygnatha* Sundevall, 1823

Pachygnatha atromarginata sp. n. (Figs 100-111)

Holotype. m, CAMEROON, Mount Koupé, 1600 m, rain forest, 8 February 1983, Bosmans & Bosselaers (sweep net), (MRAC).

Paratypes. Same data as for holotype, 4 mm 8ff W (MRAC).

Other material. Mount Koupé, 1300 m, rain forest, 1f, 31 January 1983 (pitfall trap); 1f, 2 February 1983 (sweep net) (MRAC Mount Koupé, 900 m, rain forest, 1 m (subadult) 2ff, 31 January 1983 (pitfall trap), Bosmans & Bosselaers (all MRAC).

Etymology. The name refers to the dark, reticulated marginal zone of the carapace.

Diagnosis. This species can be distinguished by the shape of the paracymbium (Fig. 103) and the vulvar morphology (Fig. 111) in the female.

Description

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Genus *Phyllodoce* Lamarck, 1818

Phyllodoce citrina Malmgren, 1865: Fig. 2.

Phyllodore citrina Malmgren, 1865: 95-96, pl. XIII, fig. 24.

Phyllodoce badia Malmgren, 1867: 22, pl. II, fig. 6.

Anaitides citrina Bergström 1914: 140-141, fig. 41; Eliason 1962a: 18; Hartmann-Schröder 1971: 105-107, fig. 33D-F; Uschakov 1972: 136-137, pl. V, figs 5, 6.

Material examined. Phyllodoce citrina: 3 syntypes from Spitsbergen (SMNH type collection 2419 and 2420); 1 syntype from Spitsbergen (BMNH 1865.9.23.3); about 30 specimens from Wales, Shetland, western Norway, Spitsbergen, and Greenland (SMNH, MZB); about 10 specimens from the Arctic, Bering Sea and the Sea of Okhotsk (ZIL). *Phyllodoce badia*: several syntypes (at least 4 specimens and some fragments) from Bohuslän, Sweden (SMNH type collection 2423).

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