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Original Article

Insight into the molecular diversity of *Perreyia flavipes* Konow, 1899 (Hymenoptera, Pergidae), a comparison across its geographic distribution limits in South America

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ABSTRACT. *Perreyia flavipes* Konow, 1899 is one of the fairly known species of the Pergidae family. The larval stage of the species presents a high incidence of intoxication outbreaks in South America with an important economic impact on cattle, sheep, and pig production. Examined specimens were collected from the southern and northern extremes of the species distribution. Southern-limit specimens from Uruguay and Brazil were used to amplify and sequence *COI*, *16S*, and 28S genes, and the same gene sequences were obtained from the Genbank database for the northern limit in Colombia, together with three other species of the Pergidae group. High similarity between Brazilian and Uruguayan samples was found. Colombian haplotypes were highly differentiated from those of the Uruguay-Brazil group. Paired differences between *Perreyia* species were similar to those found between southern and northern comparisons of *P. flavipes*, suggesting the need to deeply understand and describe the incipient differentiation of the species across its wide geographic distribution.

KEYWORDS: 16S, 28S, COI, Genetic divergence, Mitochondrial genes, Nuclear genes, Sawfly

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INTRODUCTION

The sawfly family Pergidae with around 500 species (Smith 1993; Schmidt & Smith 2006; Schmidt et al. 2017), mostly distributed in South America and Australia and with only a few species in New Guinea and North America (Schmidt & Smith 2006), is among the most poorly known groups and is notoriously scarce on phylogenetic studies for species classification or diversity analysis purposes (Schmidt & Walter 2014; Zhang et al. 2025). Among Pergidae species, *Perreyia flavipes* Konow, 1899, a member of the subfamily Perreyiinae, has been reported to occur throughout South America, from Colombia in the north (Schmidt 2012) to Uruguay in the south (Smith 2006). As reported for some other sawfly larvae (Hymenoptera), the larvae are toxic for domestic animals (Dutra 1997, 2003; Soares et al. 2008). A high number of outbreaks occur in Uruguay and, to a lesser extent, in Brazil (Dutra et al. 1997; Soares et al. 2008), with severe losses in cattle (Dutra et al. 1997), sheep (Raymundo et al. 2008), and pigs (Jonck et al 2010). No reported cases exist in Argentina, although the larvae are present.

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Larvae form a compacted black mass of about 100 individuals that moves crawling over the grass and are ingested by grazing animals (Dutra et al. 1997; Soares et al. 2001).

The phylogeny of Pergidae was deeply studied by Schmidt and Walter (2014), focusing on calibration and dating of evolutionary and historical diversification events. Using sequences of three genes, mitochondrial Cytochrome c oxidase I (*COI*) and 16S ribosomal RNA subunit (*16S*), and nuclear 28S ribosomal RNA subunit (*28S*), the authors reconstructed the phylogenetic relationships for some of the Pergidae members. In it, a list of over fifty Pergidae species was sequenced and used for the analyses, including three described species from the genus *Perreyia* (*P. flavipes* Konow, 1899, *P. picea* (Westwood, 1874), and *P. nigriceps* (Westwood, 1874)) as representatives of the Perreyiinae subfamily.

For *P. flavipes* and despite its productive impact and potential control interest, no detailed phylogenetic or geographic diversity studies have been performed. Until now, only a Colombian sample representing the northern limit of its geographic distribution was included in the previously mentioned Pergidae classification study (Schmidt & Walter 2014). For the other three species of Perreyia, all three gene sequences are available at the NCBI-GenBank database. Nonetheless, no comparative analysis of its different populations has been carried out. Due to the vast geographic range and the high number of outbreaks reported in the southern limit of its distribution, the main question of how genetic diversity is organized arises. Thus, the first comparison of northern samples sequences for the three genes (COI, 16S, and 28S), together with southern ones, is the main goal of the present study.

MATERIAL AND METHODS

We collected specimens from four points in Uruguay and one in Brazil (Fig. 1). Most of the samples were larvae collected by hand on the ground from groups detected on the grass, some of them from grass enclosures associated with reported outbreaks. Some adults were also collected using Malaise traps. All specimens (23 specimens used for the present work) were preserved in 75% EtOH and deposited in our Insect Collection at the CURE. The morphological identity of adult specimens was determined following Neves & Pie (2017) images, where relevant characters were bright orange leg parts and 13-15 antennal articles, which are serrate in females and pectinate in males as described by Smith (1990). Total DNA was extracted from a 2×2 mm homogenized body sample using a slightly modified standard salt-out method from Miller et al. (1988). *COI* gene was PCR-amplified using primers pair LCO1490 (5'GGTCAACAAATCATAAAGATATTGG3') and HCO2198 (5'TAAACTTCAGGGTGACCAAAAAAT CA3') (Folmer et al. 1994), *16S* gene with AHymF (5'TRACTGTRCAAAGGTAGC3') and BHymR (5'TTAATTCAACATCGAGGTC3') (Schulmeister 2003) and *28S* gene with D2F (5'CGGGTTGCTTGAG AGTGCAGC3'), and D2Ra (5'CTCCTTGGTCCGTGTTTC3') (Gillespie et al. 2005). The sequences produced in the present study were combined with previously published sequences of *P. flavipes* (from Colombia), *P. nigriceps,* and *P. picea* retrieved from NCBI (Table 1 for accession details).

Raw sequences for the three genes were edited using Proseq v3.5 (Filatov 2009), aligned using Clustal X (Thompson et al. 1997), and manually examined and adjusted. After editing, sequences for the three genes of twenty-three new individuals of *P. flavipes* were kept for analyses. Based upon current phylogenetic studies, *Decameria vyssus* was chosen as the outgroup taxon (Schmidt & Walter 2014). The final database for phylogenetic and molecular distance analyses consisted of 612, 314, and 363bp for *COI*, *16S*, and *28S*, respectively. Sequences were analyzed for phylogenetic reconstruction individually. Maximum likelihood inference with partition fit was performed with MEGA 11.0.13 software (Tamura et al. 2021) together with the substitution model fit that runs in it (Caspermeyer 2018). Bootstrap (BS) was also used for branch support testing. Bayesian inference was conducted using MrBayes 3.2.6 (Ronquist et al., 2012), with GTR+I+G as the best-fit model for all individuals and concatenated sets. Bayesian analyses were run for 1 million generations with a sample frequency of every 1000 generations, and the first 25% of trees were discarded (*burn-in*) (Ronquist et al 2009). Resulting Bayesian posterior probability (PP) values for each node were used for the topology confidence measure. Also, the genealogical relationships among haplotypes were estimated by using the median-joining method (Bandelt et al. 1999) implemented in Network v10.2.0.0 (Fluxus Technology Ltd. at http://www.Fluxus-engineering.com). Genetic distances between groups were calculated as the mean p-distance (rate of differences by each 100 base pairs of alignment) of haplotypes using MEGA 11.0.13 software (Tamura et al. 2021).

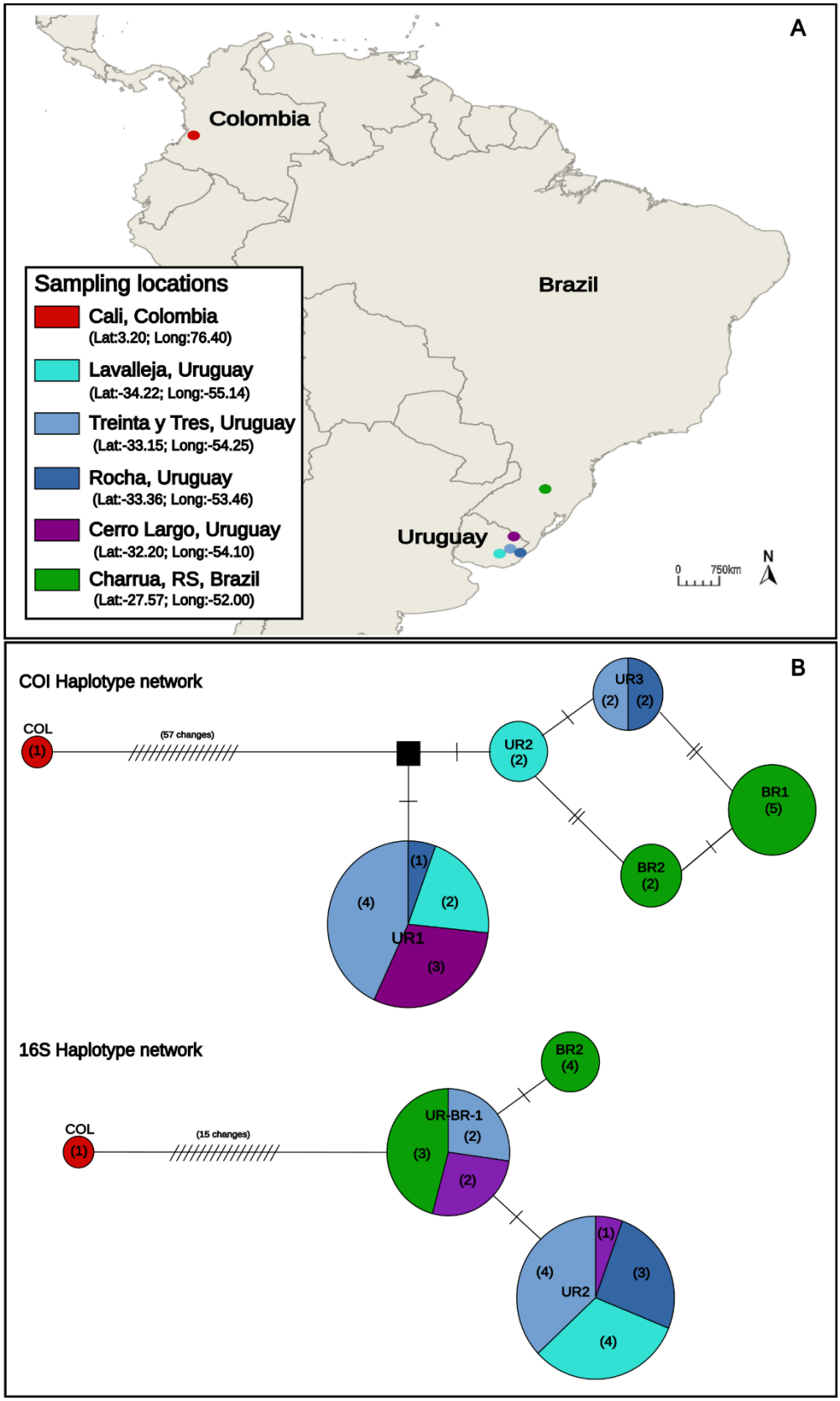

Figure 1. **A.** Sampling localities used for the analyses, from Uruguay and Brazil (individuals collected and sequenced), and the locality from Colombia (downloaded from the BOLD database). **B.** Median-joining analysis from Network v10.2.0.0 for *COI* and *16S* genes. Circles are haplotypes, size is related to abundance, abundance values for haplotypes in each locality are between brackets. The number of differences between haplotypes is marked with lines in each branch. The black square is an ancestral unsampled projected haplotype. Code used for *P. flavipes* haplotypes is UR for Uruguayan, BR for Brazilian, UR-BR for shared haplotypes, and COL for Colombian ones.

Table 1. Genbank accession codes for all sequences used. Those generated in this article and those downloaded from the online database.

Species	Genbank accession number	Reference
***Perreyia flavipes* (UR-BR)**		
COI	URU(PX481269-71)/ BRA(PX481272-73)/	Current study
16S	URU(PX591199)/ BRA(PX591200)/ UR-BR(PX591201)	Current study
28S	UR-BR(PX591216)	Current study
***Perreyia flavipes* (COL)**		
COI	KC567865.1	Schmidt and Walter (2014)
16S	KF318499.1	Schmidt and Walter (2014)
28S	KF445043.1	Schmidt and Walter (2014)
Perreyia picea		
COI	KC567867.1	Schmidt and Walter (2014)
16S	KF318496.1	Schmidt and Walter (2014)
28S	KF445039.1	Schmidt and Walter (2014)
Perreyia nigriceps		
COI	KC567866.1	Schmidt and Walter (2014)
16S	KF318503.1	Schmidt and Walter (2014)
28S	KF445047.1	Schmidt and Walter (2014)
***Decameria vyssus* (outgroup)**		
COI	KC567840.1	Schmidt and Walter (2014)
16S	KF318476.1	Schmidt and Walter (2014)
28S	KF445021.1	Schmidt and Walter (2014)

RESULTS

For the twenty-three sample dataset that was generated, including Uruguayan and Brazilian samples, 5 haplotypes were found for *COI* (3 exclusive to Uruguayan samples, 2 exclusive to Brazilian and none shared), 3 haplotypes for *16S* (1 exclusive to Uruguayan samples, 1 exclusive to Brazilian and 1 shared), and no variations were found for *28S* gene sequences, with 1 haplotype shared by all samples (See supplementary material for haplotypes alignments, Figs S1, S2, S3). Distances between groups, represented as the p-distance (differences by each 100bp) (Table 2) showed the *COI* gene with the highest values of diversity (0.075–0.138), followed by *16S* (0.050–0.109) with similar values, and finally the *28S* (0.006–0.045) with the lower ones.

Both methods (Maximum Likelihood, Bayesian) used for phylogenetic inferences resulted in similar, but not identical topologies for each gene individually and the concatenated analyses; therefore, here we present the resulting phylogenetic trees for concatenated sequences analyses for description (Fig. 2) (See both ML and Bayes trees for each gene at Suppl., Fig. S4 for *16S*, S5 for *COI*, and Fig. S6 for *28S*). Monophyly of Uruguayan-Brazilian (UR-BR) *P. flavipes* samples was always retrieved and highly supported (BS = 98%; *PP = 0.99*) (Fig. 2), with the same values for *COI* and *16S*, and not needed for *28S*, as only one haplotype was found for all samples. The Genbank Colombian (COL) sample of *P. flavipes* was found to be the closest to the UR-BR group (BS = 65%; *PP = 0.71*) in concatenated sequences based phylogenies, and also for the *16S* (both methods, BS = 96%; *PP = 0.76*) and the *COI* (Bayes, *PP = 0.54*). As previously reported by Schmidt et al. (2014), *P. picea* was retrieved as the sister taxon to the UR-BR/COL clade only for ML method with low support (BS = 54%) and for *16S* gene with both methods and moderate support (BS = 73%; *PP = 0.68*). Alternatively, the Bayesian method found the clade *P. picea/P. Nigriceps* as sister to UR-BR/COL but with low support (*PP = 0.39*). Moreover, the *COI* (Bayes) retrieved *P. nigriceps* as closer to UR-BR/COL clade (*PP = 0.87*), *COI* (ML) retrieved *P. nigriceps* closer than COL sequence to UR-BR (BS = 47%), and for the *28S* (both methods) *P. picea* was found closer to UR-BR than COL sample but with low support (BS = 42%; *PP = 0.33*), and *P. nigriceps* as sister to them with moderate support (BS = 57%; *PP = 0.50*).

Table 2. Matrix of p-distances between sampling locations and Perreyia species. Uruguay and Brazil haplotypes (UR-BR), the Colombian haplotype (COL).

p-distance COI/16S/28S	UR-BR	COL	*P. picea*	*P. nigriceps*
UR-BR	--			
COL	0.097/0.050/0.006	--		
P. picea	0.099/0.078/0.011	0.138/0.093/0.017	--	
P. nigriceps	0.075/0.091/0.034	0.114/0.109/0.037	0.110/0.102/0.045	--

The internal relationships for *P. flavipes* showed the monophyly of Brazilian haplotypes with high support (BS = 76%; *PP = 0.99*) and also with the *COI* gene (BS = 68%; *PP = 0.99*). The Uruguayan samples were retrieved as a polyphyletic group for all genes and methods, with some haplotypes grouped closer to those from Brazil, and always basal to them. The *16S* Bayesian phylogenetic tree retrieved an exception to that, but low supported (*PP = 0.31*) with the Brazilian BR2 haplotype basal to Uruguayan (UR2) and shared haplotype (UR-BR1) clade. Two clades were found for concatenated (Fig. 2) and *COI* analyses (Fig. S5) for *P. flavipes,* with all Uruguayan sampling localities represented in both clades.

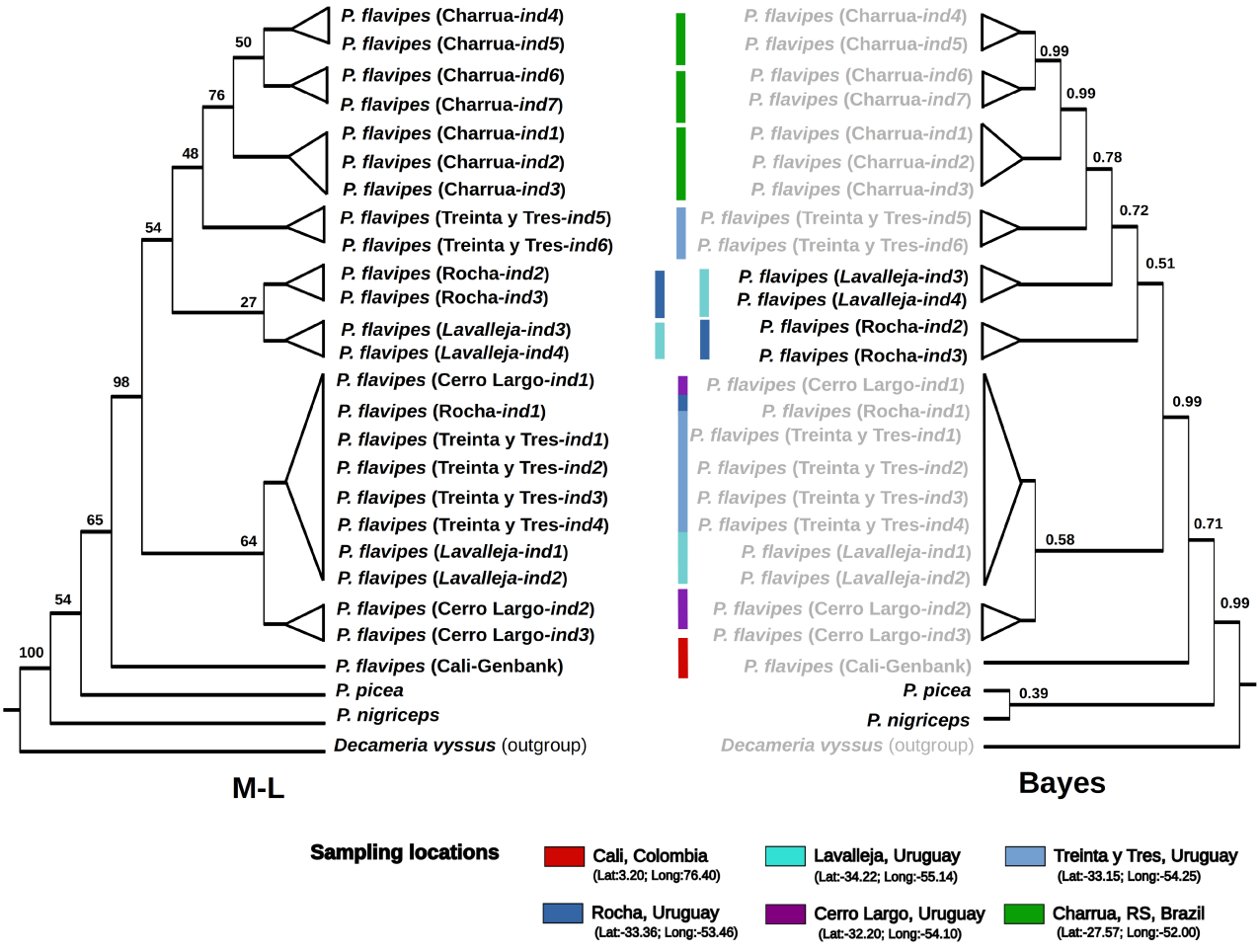

Figure 2. Phylogenetic trees for Perreyia species and *P. flavipes* haplotypes based on concatenated sequences from *COI*, *16S,* and *28S* genes. For Maximum likelihood (left, M-L) and Bayesian (right, Bayes) trees, bootstrap values and Bayesian posterior probability are shown at each node, respectively. Conserved relationships between methods presented in gray color, and changes are in black in the Bayes tree. Central lines color-coded the geographical distribution of the individuals sampled. Terminal triangles are collapsed clades of identical haplotypes.

DISCUSSION

Molecular tools to disentangle phylogenetic relationships among populations are a first step in the study of the diversification process of species (Templeton 1998; Barraclough & Nee 2001; Coyne & Orr 2004; Morlon et al. 2024). In this work, three genes, with a total of 1.289 base pairs edited and aligned, were used for the first study of the intraspecific diversity of a South American Perreyiinae member. The closest group to *Perreyia flavipes* is supported by some genes and methods. Exceptions to this as that found for the *28S, which* suggested *P. picea* closer to UR-BR than the Colombian *P. flavipes* sample, or that found for the maximum likelihood-based *COI* with *P. nigriceps* as a sister taxon to UR-BR, or the concatenated Bayesian tree that grouped *P. nigriceps* and *P. picea* as a clade sister to all *P. flavipes*. However, all exceptions to *P. picea* as a closer taxon showed low statistical support in contrast to the moderate to high values supporting it. Such kind of discrepancies between methods have been widely reported in phylogenetic relationships studies (see Giacomelli et al., 2024, for a review of cases), also with Hymenoptera examples (Klopfstein et al., 2010; Tao et al., 2026). Nevertheless, only three species of *Perreyia* were included for sequence analyses, from at least twelve previously reported species in nature (Smith 2006). In this sense, a wider taxonomic sampling, a broader set of genes, and extension of bases sequenced would be useful to increase the number of *Perreyia* species analyzed and to clarify the ingroup fragile relationships and their evolution.

Highly similar sequences were found for Uruguayan and Brazilian *P. flavipes* samples. Although more extensive geographic sampling is needed, the southern distribution of the species showed predominant shared haplotypes for each of the three genes. On the other hand, database-available sequences of *P. flavipes* from the northern extreme of the species distribution were consistently divergent. As shown by pairwise sequence distances, mean divergence between *P. flavipes* from Colombia and UR-BR was around 10 bp for *COI*, 5 bp for *16S,* and 0.6 bp for *28S* per 100 bp compared. These results are highly comparable to those found between pairs of sequences of established different species inside the *Perreyia* group, for mitochondrial *COI* and *16S* genes (11% and 10%, respectively), and to those found for Perreyiinae subfamily species (17% *COI*, 12% *16S*, data not shown). For the nuclear *28S* gene, the distance between *Perreyia* species *P. nigriceps* and *P. picea* was of 4%, higher than that found for UR-BR and COL samples; however, the mean distance of *P. picea* to UR-BR samples was a closer 1%. This lower rate of divergence could be underestimated due to selection pressure, as *28S* is a coding region of the genome. Previous incongruence between nuclear and mitochondrial genes, including *28S*, has been reported in other Hymenoptera studies (e.g., Budrys et al. 2023) and particularly for Pergidae, *28S* has been reported to have a lower family-level resolution (Malagón-Aldana et al. 2022). At the geographic level, network analysis of haplotypes showed a high presence of variants exclusive to each sampling location, suggesting that the inclusion of new locations along species distribution should be a priority for further understanding of its diversity distribution, as discussed for other taxa in South America (Turchetto-Zolet et al. 2012).

In conclusion, the characterization of the molecular diversity of *P. flavipes* between southern and northern individuals suggests great differentiation comparable to that found at the interspecies level. *P. flavipes* is a species with a high toxicity level and a significant economic impact reported for the southern region of South America, and this work highlights the need for a deeper sampling and the relevance of understanding the poorly studied speciation and diversification processes for this group in the region, as well as the association between environmental and genetic differences.

AUTHOR'S CONTRIBUTION

The authors confirm their contribution to the paper as follows: M. Feijoo: conceptualization, investigation, sampling, laboratory work, data analysis, direction, supervision and writing of the manuscript; J. Escalona: sampling, laboratory work, review and editing of the manuscript; A.C. Corro: laboratory work, review and editing of the manuscript; M.P. Soares: sampling, review and editing of the manuscript; F. Dutra: sampling, review and editing of the manuscript. The authors read and approved the final version of the manuscript presented.

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AVAILABILITY OF DATA AND MATERIAL

The sequence's accession links are detailed in the "Materials and Methods" section. The specimens listed in this study are deposited in the DSAyPC collection and are available from the curator upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

GENERATIVE AI STATEMENT

We declare that generative AI tools were not used in the preparation of this manuscript, neither for content generation nor data analyses.

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نگرشی بر تنوع مولکولی *Perreyia flavipes* Konow, 1899 (Hymenoptera, Pergidae)، مقایسه‌ای در مرزهای انتشار جغرافیایی آن در آمریکای جنوبی

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چکیـده: زنبور *Perreyia flavipes* Konow, 1899 یکی از گونه‌های نسبتاً شناخته شده خانواده Pergidae است. مرحلهٔ لاروی این گونه دارای شیوع بالای ایجاد مسمومیت در جنوب آمریکای جنوبی است که تأثیر اقتصادی مهمی بر تولید دام، گوسفند و خوک دارد. نمونه‌های بررسی شده از دامنه‌های جنوبی و شمالی منطقهٔ انتشار این گونه جمع‌آوری شده‌اند. نمونه‌های مربوط به حد جنوبی از اروگوئه و برزیل برای تکثیر و توالی‌یابی ژن‌های COI، 16S و 28S استفاده شدند و توالی‌های همان ژن‌ها از پایگاه داده Genbank برای حد شمالی در کلمبیا به همراه سه گونه دیگر از گروه Pergidae به دست آمد. شباهت بالایی بین نمونه‌های برزیلی و اروگوئه‌ای یافت شد. هاپلوتیپ‌های کلمبیایی به شدت با گروه اروگوئه–برزیل تفاوت داشتند. تفاوت‌های بین گونه‌های جنس *Perreyia* مشابه آنچه در مقایسه مناطق جنوبی و شمالی *P. flavipes* مشاهده شد، نشان میدهد که برای توصیف تمایز نوظهور این گونه در گستره وسیع توزیع جغرافیایی آن، به مطالعات بیشتر و درک عمیق‌تر نیاز است.

واژگـان کلیدی: 16S، 28S، COI، واگرایی ژنتیکی، ژن‌های میتوکندریایی، ژن‌های هسته‌ای، زنبورهای تخمریز اره‌ای