ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202401761

BIODIVERSITY AND CONSERVATION | ORIGINAL ARTICLE

Updated phylogeny of *Eragenia* Banks (Hymenoptera: Pompilidae), redescription of the male of *E. aureicornis*, and distribution of the genus in an Amazon-Cerrado transition zone

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ABSTRACT

This study revisits the molecular phylogeny of *Eragenia* by incorporating a specimen of *E. aureicornis*, the type species of the genus, as a new terminal. The new terminal is recovered as the sister species of *E. setosa*, with strong statistical support. The phylogeny sheds light on the evolution of morphological traits in the group, such as the male genital plate. A morphological redescription of the male of *E. aureicornis* is provided, including its first high-resolution images and a detailed description of the genitalia. We present an updated identification key for the male specimens of *Eragenia*. *Eragenia micans* is reported for the first time from the state of Maranhão, Brazil. Despite its continental dimensions and diverse biomes, Brazil harbors only 37.5% of the known *Eragenia* diversity.

KEYWORDS: spider-wasps; taxonomy; Ageniellini; Neotropical region; tropical rainforest; savanna

Filogenia atualizada de *Eragenia* Banks (Hymenoptera: Pompilidae), redescrição do macho de *E. aureicornis* e distribuição do gênero em uma zona de transição Amazônia-Cerrado

RESUMO

Este estudo revisita a filogenia molecular de *Eragenia* ao incorporar um espécime de *E. aureicornis*, a espécie-tipo do gênero, como um novo terminal. O novo terminal é recuperado como espécie-irmã de *E. setosa*, com forte suporte estatístico. A filogenia esclarece a evolução de características morfológicas no grupo, como a placa genital dos machos. É fornecida uma redescrição morfológica do macho de *E. aureicornis*, incluindo suas primeiras imagens em alta resolução e uma descrição detalhada da genitália. Apresentamos uma chave de identificação atualizada para os espécimes machos de *Eragenia*. *Eragenia micans* é registrada pela primeira vez para o estado do Maranhão, Brasil. Apesar de suas dimensões continentais e da diversidade de biomas, o Brasil abriga apenas 37,5% da diversidade conhecida de *Eragenia*.

PALAVRAS-CHAVE: vespas caça-aranhas; taxonomia; Ageniellini; Região Neotropical; floresta tropical úmida; savana

INTRODUCTION

The family Pompilidae is a group of stinging wasps (Hymenoptera: Aculeata) with more than 5,000 known species worldwide (Huber 2017). They are commonly recognized for their remarkable behavior of hunting spiders to feed their immature offspring, a characteristic that has earned them the common designation of spider-wasps (Evans 1953). In the Neotropical region, the diversity of these insects is represented by 946 species within 63 genera (Fernández *et al.* 2022), including 348 species in 38 genera recorded from Brazil (Santos and Waichert 2024).

The family is subdivided into five subfamilies: Ceropalinae, Ctenocerinae, Notocyphinae, Pepsinae, and Pompilinae

CITE AS: Muniz, D.B.; Veloso, R.S.; Waichert, C.; Azevedo, G.G. 2025. Updated phylogeny of *Eragenia* Banks (Hymenoptera: Pompilidae), redescription of the male of *E. aureicornis*, and distribution of the genus in an Amazon-Cerrado transition zone. *Acta Amazonica* 55: e55bc24176.

(Waichert *et al*. 2015b). Within Pepsinae, the tribe Ageniellini comprises 226 species from the Neotropics, distributed among eight genera: *Ageniella* Banks; *Atopagenia* Wasbauer; *Auplopus* Spinola; *Dimorphagenia* Evans; *Eragenia* Banks; *Mystacagenia* Evans; *Phanagenia* Banks; and *Priocnemella* Banks (Fernández *et al*. 2022). This tribe presents a curious and noteworthy case with its cavity-occupying, ground-nesting, and mud-nesting species that can display gregarious or communal behavior through joint nest construction and defense, overlapping generations, and reusing nests (Evans and Shimizu 1996).

The genus *Eragenia* was originally proposed by Banks based on *Eragenia infelix* (Banks) as monotypical (Banks 1946). Later, this species was synonymized with the genus *Priocnemella* Banks by Townes (1957). However, Waichert *et al*. (2015a) conducted a phylogenetic analysis based on molecular characters, recovering and reestablishing *Eragenia* as a monophyletic group formed by 16 species: *Eragenia abdominalis* (Smith); *Eragenia amabilis* (Taschenberg), *Eragenia aureicornis* (Smith); *Eragenia bella* Waichert and Pitts; *Eragenia carinata* Waichert and Pitts; *Eragenia coerulipes* (Smith); *Eragenia congrua* (Fox); *Eragenia dentata* Waichert and Pitts; *Eragenia isolata* (Banks); *Eragenia micans* (Fabricius); *Eragenia oliva* Waichert and Pitts; *Eragenia pseudomicans* Waichert and Pitts; *Eragenia rotunda* Waichert and Pitts; *Eragenia setosa* Waichert and Pitts; *Eragenia tabascoensis* (Cameron); *Eragenia villosa* Waichert and Pitts (Waichert *et al*. 2015a; Fernández *et al*. 2022).

Three species were missing representatives in the molecular phylogeny by Waichert *et al*. (2015a): *E. aureicornis*, *E. carinata*, and *E. rotunda*. *Eragenia aureicornis* was synonymized with *E. infelix* by Waichert *et al*. (2015a), the type species of the genus, which makes it a major taxon to be included in the phylogenetic reconstruction. Male specimens of *E. aureicornis* were not available in the most recent study and the original description is ambiguous, which hindered the formulation of a diagnosis of this species (Waichert *et al.* 2015a).

Eragenia aureicornis was originally described as *Agenia aureicornis* by Frederick Smith in 1873, based on a female specimen from Pará State, Brazil (Smith, 1873). The first description of the male was provided by Banks (1946) as *E. infelix*, based on two males from Iguazu Falls, Argentina. The male description provided by Banks (1946) is outdated, lacking major characters that are currently used to distinguish species, including male genitalia characters. Finally, no images of the male of this species have ever been added to the scientific literature.

Here, we revisit the phylogenetic hypothesis proposed by Waichert *et al*. (2015a) by incorporating a specimen of *E. aureicornis* as a new terminal taxon. We also present a morphological redescription of a male specimen of *E. aureicornis*, including detailed observations of its genitalia, and update the identification key for male specimens provided in the earlier study. On a local scale, we reviewed the distribution records of *Eragenia* in the northern Brazilian state of Maranhão, at the transition between the Amazon and Cerrado biomes, and provide a new species record for the state.

MATERIAL AND METHODS

Specimen collection and species identification

The material reported in here was collected during scientific surveys conducted between 2009 and 2014 in three areas in the Eastern Amazon and Cerrado regions of the state of Maranhão, Brazil. Sítio Aguahy is a private area owned by QUERCEGEN Agronegócios LTDA., located in the municipality of São José de Ribamar, on Upaon-Açu Island, in the metropolitan region of the state capital São Luís. The area encompasses a 6-km^2 remnant of primary Amazon forest and anthropized secondary forest, as well as coastal *restinga* drier and bushier vegetation (Serra *et al*. 2016). *Eragenia* specimens were sampled in secondary forest featuring trails, cassava plantations (*Manihot esculeta* Crantz) (Euphorbiaceae), short trees, and bushes (02°38'53.8"S, 44°08'55.3"W), and in *restinga* (02°38'55"S, 44°07'36.8"W). Parque Agroecológico Buritirana is a private area owned by Instituto Formação, located in the municipality of Peri Mirim (02°38'10.1"S, 44°50'43.9"W) (Martins *et al*. 2017; Araujo *et al*. 2020). Within the Eastern Amazon domain, it covers a 6-km^2 area of secondary forest with a predominance of *Attalea speciosa* Mart. ex Spreng. (Arecaceae) and partially floodable fields (Marinho *et al*. 2018; Araujo *et al*. 2020). Parque Estadual do Mirador is an important conservation unit within the Cerrado domain of Maranhão state (IBGE 2019), covering 5,000 km^2 (ISA 2023) of savanna and dry forest phytophysiognomies and gallery forests, which have been encroached upon by pastures in small farms (Rodrigues and Conceição 2014).

The *Eragenia* specimens were sampled using entomological nets (at Sítio Aguahy and Parque Estadual do Mirador) and Malaise traps (at Parque Agroecológico Buritirana). All collected specimens were mounted on entomological pins and dehydrated before being integrated into the entomological collection of the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL-UFMA) at the Department of Biology (DEBIO) of Universidade Federal do Maranhão (UFMA), where they were consulted by us for this study. Two specimens were donated to the entomological collection of the Zoology Department (DZUB) at Universidade de Brasília (UnB), Distrito Federal, Brazil.

The labels of the specimens examined were transcribed as follows: a backslash (\ ) indicates different lines on the same label, while single quotation marks (' ') indicate different labels on the same specimen.

Species were identified using taxonomic keys provided by the literature on Pompilidae (Banks 1946, 1947; Townes

1957; Evans 1973; Brothers and Finnamore 1993; Wahis and Rojas 2003), and the key to the species of *Eragenia* by Waichert *et al*. (2015a).

Images and map generation

All images of the specimens were captured using a ZEISS AxioCam ERc 5s video camera coupled to a ZEISS SteREO Discovery.V8 stereomicroscope, controlled by the AxionVision software (AxioVs40x64 V 4.9.1.0) from ZEISS Group. Image stacks were combined with Zerene Stacker Version 1.04 (Zerene Society, LLC), and all post-editing was done using the GNU Image Manipulation Program (GIMP 2.10.34) software.

Images of the male genitalia were captured using a Leica S9i stereomicroscope with an integrated 10 MP camera. The genitalia was dissected after the specimen was softened in 90% ethanol for 15 minutes. A potassium hydroxide solution (KOH 10%) was used to remove muscles. The extracted genitalia was left in the KOH solution until removal was complete. Then, the genitalia was placed in acetic acid for 10 minutes to neutralize the KOH, and transferred to a tube filled with glycerin.

The distribution map of the records was generated using QGIS 3.30.2 's-Hertogenbosch' software (QGIS Development Team). All cartographic information was obtained from Instituto Brasileiro de Geografia e Estatística (IBGE) (https://www.ibge.gov.br/geociencias/downloads-geociencias.html), Terrabrasilis (http://terrabrasilis.dpi.inpe.br/downloads/) and Google Earth (Google LLC) (https://earth.google.com), in addition to data provided by the Global Positioning System (GPS) device (Garmin GPSmap 60CSx) from the Laboratório de Ecologia e Sistemática de Insetos Polinizadores e Predadores (LESPP), at the Department of Biology (DEBIO) of Universidade Federal do Maranhão (UFMA). Post-edits to the distribution map were performed using the GNU Image Manipulation Program (GIMP 2.10.34) software. For locality records without specific GPS coordinates, we used reference coordinates for the respective municipality.

Taxonomic morphometrics

The width of the first flagellomere was measured from the transverse median line of the segment. The width of the clypeus (WC) was measured from the perpendicular median line, and its length (LC) from the transverse median line. The lower interocular distance (LID) was measured between the inner margins of the eyes directly above the upper margin of the clypeus; the median interocular distance (MID) as the widest portion of head between the median points of the eyes (frontal view); and the upper interocular distance (UID) between the upper tips of the eyes in frontal view. The transfacial distance (TFD) was measured between the median point of the lower margin of the clypeus to the upper tip of the head in frontal view; and the facial distance (FD) from the widest portion of the head in frontal view. The post-ocellar line (POL) was measured between the inner margins of the posterior ocelli; and the ocello-ocular line (OOL) between the lateral margin of the right posterior ocellus and the upper tip of the eye.

In the forewing, the lengths of the first radial sector (1Rs) and second radial sector (2Rs) cells were measured as follows: (1) from the distance between the bases of the radial sector (Rs) and second radial-medial (2r-m) veins, and (2) from the distance between the bases of the radial sector (Rs) and third radial-medial (3r-m) veins. The widths of the first radial sector (1Rs) and second radial sector (2Rs) cells were measured as follows: (1) from the junction of the radial-radial sector (r-rs) and radial sector (rs) veins to the diametrically opposite point on the medial (M) vein, and (2) from the junction between the third radial-medial (3r-m) and radial sector (Rs) veins to the diametrically opposite point on the medial (M) vein. To measure the length of the third radial sector (3Rs) cell, we used the distance between the base of the third radial-medial (3r-m) and the tip of the medial (M) vein.

The terminology used here followed Harris (1979) for integument sculpturing and Goulet and Huber (1993) for body segmentation and wing venation, with some adaptations: all the extension of the forewing below the anal (A) vein was regarded as "anal cell" (Comstock-Needham 1898), and the second radial 1 (2R1) was regarded as the "marginal cell" (Gauld and Bolton 1988). All morphometric measurements of the head were conducted according to Evans (1949).

Phylogenetic analysis

We reconstructed a maximum likelihood phylogenetic gene tree for the species of *Eragenia* using the Genbank sequences amplified and sequenced by Waichert *et al*. (2015a) (accession numbers KM594322 to KM594360 and KM660591 to KM660592), adding the sequence of a female specimen identified in here as *E. aureicornis* (GenBank accession number PV077271 and SisGen registration A68F39D).

We amplified the mitochondrial marker cytochrome c oxidase I (COI) using the primers designed by Folmer *et al*. (1994). The PCR protocol was performed in a 47µL reaction mix with 3 µL of template DNA, using GoTaq® Hot Start Polymerase (PROMEGA), and an annealing temperature of 46°C. The extraction was conducted with the Genomic DNA from Tissue kit following the manufacturer's protocol (Macherey-Nagel GmbH & Co. KG. 2017). The PCR amplicon was purified using 1 µL of ExoSAP for every 10 µL of PCR product and thermocycled at 37°C and 80°C for 15 minutes. The sequencing reaction was carried out at Núcleo de Genética Aplicada à Conservação da Biodiversidade (NGACB) at Universidade Federal do Espírito Santo. The PCR amplified a fragment of 650 bp, which was trimmed, cleaned, and aligned with the dataset using Geneious Prime

2020.0.2 (https://www.geneious.com). The final matrix was combined with the dataset of long-wavelength rhodopsin (LWLh) downloaded from GenBank, using Geneious Prime 2020.0.2.

We inferred a maximum likelihood (ML) analysis using the IQ-TREE software (Nguyen *et al*. 2015) on the IQ-TREE web server (http://iqtree.cibiv.univie.ac.at) (Trifinopoulos *et al*. 2016). The dataset was partitioned by gene and by codon for COI. The model of evolution was estimated during the analyses using ModelFinder (Kalyaanamoorthy *et al*. 2017). The best-fit model of evolution, determined using BIC, was as follows: TIM+F+G4, HKY+F+I, K3Pu+F+I+G4 for the COI partitions, and K2P+G4 for LWRh gene. To access node support, we conducted 1000 replicated of ultrafast bootstrap (UFBoot) (Minh *et al*. 2013) and Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al*. 2010).

RESULTS

Species identification and distribution

In total, six specimens of *Eragenia* wasps were sampled from the study areas, which were confidently assigned to three species: *E. aureicornis* (one female, Figure 1; and three males, Figure 2), *E. congrua* (one male, Figure 3), and *E. micans* (one male, Figure 4). The specimens of *E. aureicornis* were sampled in Sítio Aguahy (one female) and Parque Estadual do Mirador (three males). The *E. congrua* specimen was collected in Parque Agroecológico Buritirana, and the *E. micans* specimen was collected in Sítio Aguahy (Table 1; Figure 5).

Phylogenetic analysis

Figure 2. Male of *Eragenia aureicornis* (LEACOL-26509). **A** – lateral habitus; **B** – dorsal habitus; **C** – forewing; **D** – hindwing; **E** – head (frontal view); **F** – genitalia in frontal view (left rotated); **G** – genitalia in lateral view (left rotated).

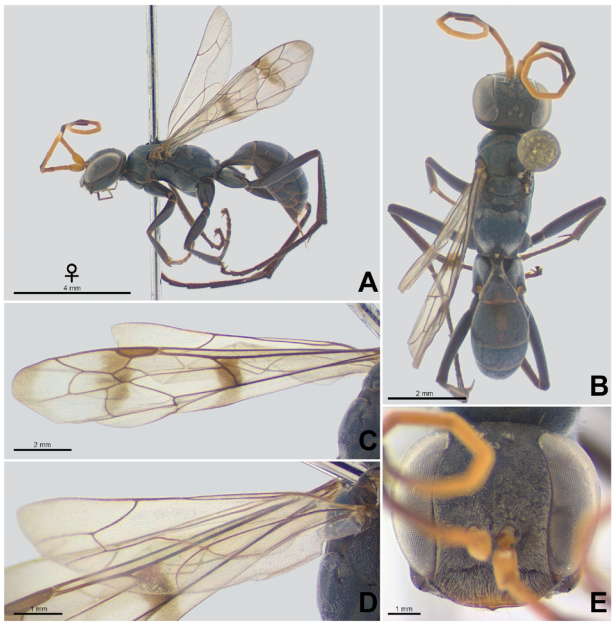

Figure 1. Female of *Eragenia aureicornis* (LEACOL-26510). **A** – lateral habitus; **B** – dorsal habitus; **C** – forewing; **D** – hindwing; **E** – head (frontal view).

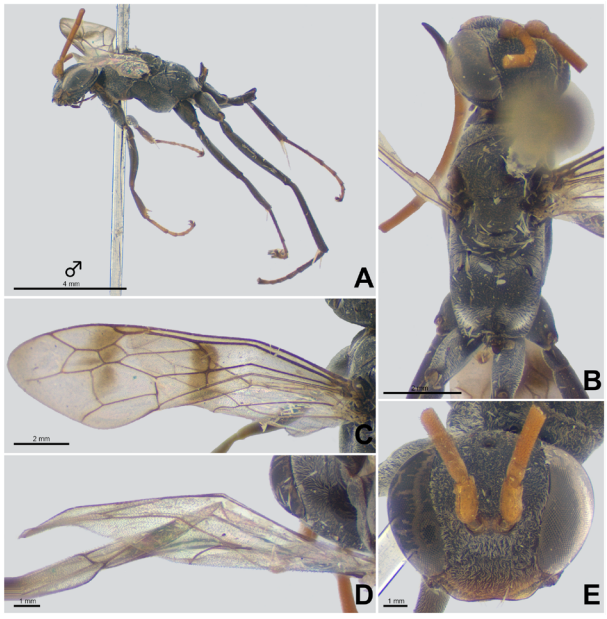

Figure 3. Male of *Eragenia congrua* (LEACOL-26511). **A** – lateral habitus; **B** – dorsal habitus; **C** – forewing; **D** – hindwing; **E** – head (frontal view).

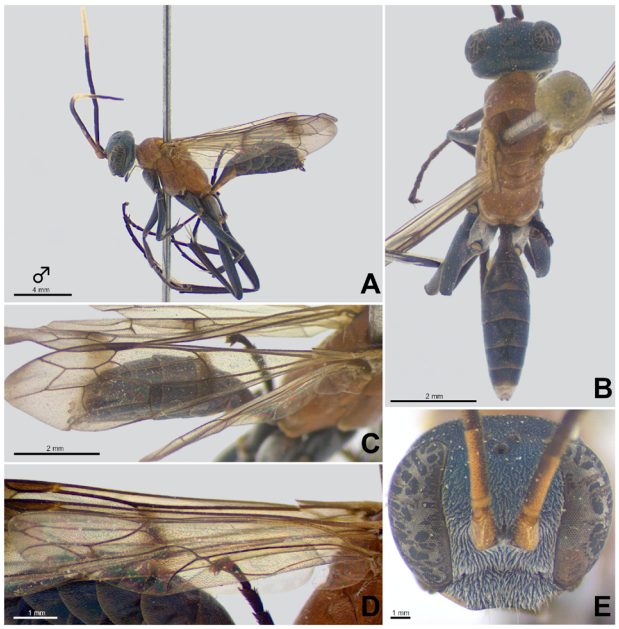

Figure 4. Male of *Eragenia micans* (LEACOL-26512). **A** – lateral habitus; **B** – dorsal habitus; **C** – forewing; **D** – hindwing; **E** – Head (frontal view).

The COI topology was congruent with the phylogeny reconstructed by Waichert *et al.* (2015a) and the topology obtained from the combined dataset. Herein, we focus on discussing the results from the combined data analysis. *Eragenia aureicornis* nested with *E. setosa* in the analyses with strong statistical support (UFBoot% = 99.9, SH-aLRT = 100) (Figure 6). The phylogenetic relationship of the clade (*E. aureicornis* + *E. setosa*) remains uncertain. In the ML analysis, this clade branches off from a larger clade containing species such as *E. abdominalis, E. congrua, E. coerulipes, E. pseudomicans, E. amabilis,* and *E. villosa,* albeit with low statistical support (UFBoot% = 73.3, SH-aLRT = 57) (Figure 6).

Eragenia aureicornis (Smith, 1873)

Agenia aureicornis Smith, 1873: [Holotype: ♀, BRAZIL, Pará (BMNH)].

Ageniella delila Banks, 1944: [Holotype: ♀, GUYANA, Katarbo (MZC)]. Synonymized by Waichert *et al.* (2015a).

Ageniella bequaertii Banks, 1945: [Holotype: ♀, COLOMBIA, Boyacá (MZC)]. Synonymized by Waichert *et al.* (2015a).

Table 1. Occurrence records of *Eragenia* Banks in Maranhão state, Brazil. Coordinates are for the municipality.

Municipality	Site	Coordinates	Biome	Recorded species
Governador Edison Lobão	Bananal	05°39'17.7"S, 47°23'33.6"W	Cerrado	*E. congrua* (1♂, MPEG-HYM11090914)*
Peri Mirim	Parque Agroecológico Buritirana	02°38'10.1"S, 44°50'43.9"W	Amazon	*E. congrua* (1♂, LEACOL-26511)
Mirador	Parque Estadual do Mirador	06°43'50"S, 44°58'59"W	Cerrado	*E. aureicornis* (1♂, LEACOL-26509; 2♂, DZUB)
Governador Edison Lobão	Ribeirãozinho	05°44'41.2"S, 47°21'46.1"W	Cerrado	*E. aureicornis* (1♀, MPEG-HYM11091900)*; *E. isolata* (1♂, MPEG-HYM11091900)*
São José de Ribamar	Sítio Aguahy	02°38'55"S, 44°07'36.8"W	Amazon	*E. aureicornis* (1♀, LEACOL-26510); *E. micans* (1♂, LEACOL-26512)

* = previously recorded in the supplementary material of Waichert *et al.* (2015a). At the time of sampling in 1989, both Bananal and Ribeirãozinho were settlements within the boundaries of the municipality of Imperatriz. However, they are now part of the municipality of Governador Edison Lobão, established in 1994 (MARANHÃO 1994).

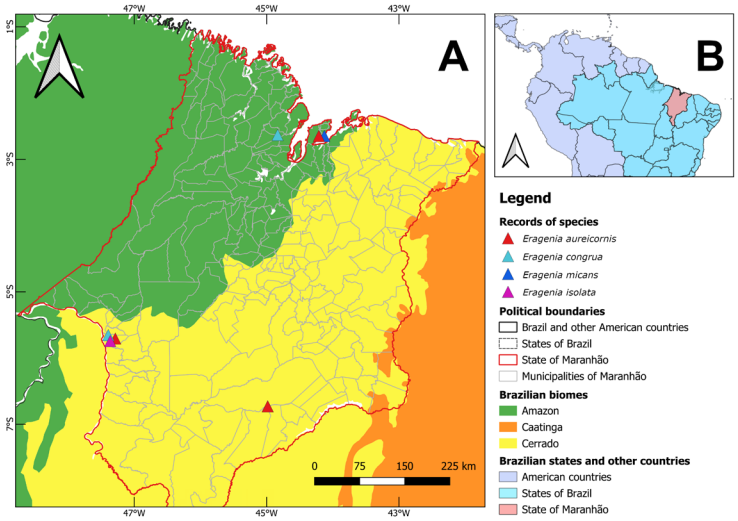

Figure 5. A – Locality records of *Eragenia* Banks in the state of Maranhão, Brazil; **B** – The insept shows the location of the state of Maranhão in Brazil.

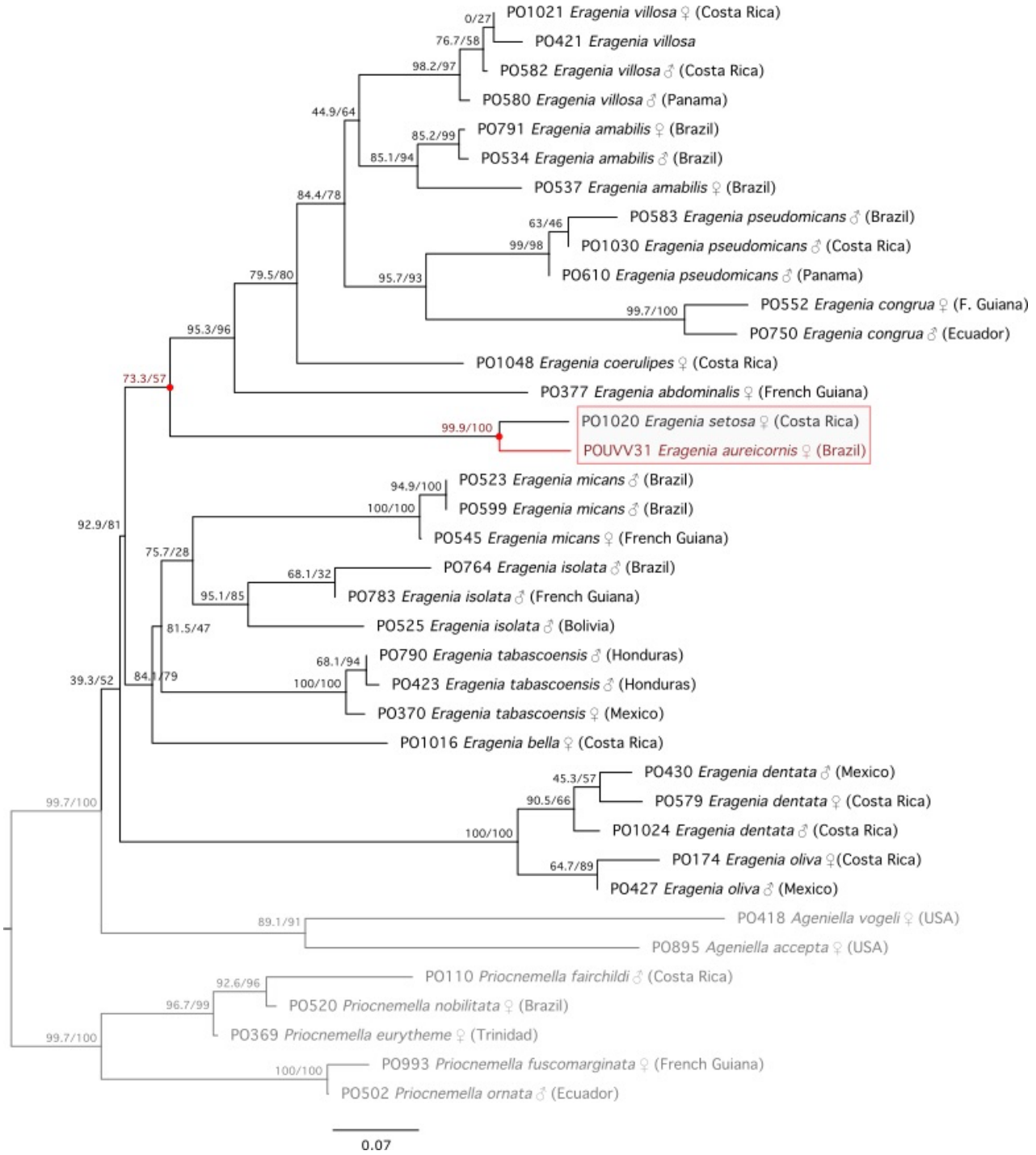

Figure 6. Phylogenetic relationships among species of *Eragenia* Banks inferred from maximum likelihood (ML) analyses based on combined dataset (COI + LWLh). Values on the side of nodes of branches indicate ultrafast bootstrap (UFBoot%) and Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT), respectively. The name in dark red indicates the inserted *E. aureicornis* sequence as a new terminal.

Eragenia infelix Banks, 1946: [Holotype: ♀, ARGENTINA, Iguazu Falls (CUIC)]. Synonymized by Waichert *et al*. (2015a).

Eragenia infelix Banks, 1946: [Paratype: ♂, ARGENTINA, Iguazu Falls (CUIC)].

Diagnosis. Integument in females black with blue reflections, except for greenish-blue reflections in the mesonotum, in males black in the head and mesosoma, brownish in metasoma; antennae brown dorsally and yellowish

ventrally, with segments 7-12 entirely yellowish in females, at least first three segments entirely yellowish in males; clypeus flat with the apical margin sinuate and a median apical tooth in females, trapezoidal convex with the apical margin slightly arcuate and pubescent in males; fore- and hindwings hyaline in both sexes, forewing with two dark bands: one partially covering the radial (R), first radial (1R1), first medial (1M) (almost imperceptible), first cubital (1Cu), second cubital (2Cu) and anal (A) cells, and the other partially covering the second radial 1 (2R1), first radial sector (1Rs), second radial sector (2Rs), second medial (2M) and third medial (3M) (almost inconspicuous) cells; in the studied specimens, in the female, the 1Rs cell is 3× longer than wider and the 2Rs cell is about 3× 1Rs total length, while in the male, the 1Rs cell is 1.42× longer than wider and the 2Rs cell is about 2.06× 1Rs total length.

Redescription of the male. Body length: 8.59 mm; forewing length: 5.38 mm; maximum forewing width: 2.27 mm. **Coloration** (Figure 2a,b). Head entirely black, except malar space dark yellowish; mandible with basal third black, second and apical thirds dark yellowish, apex of outer tooth reddish; palpi light brownish; at least first three antennal segments entirely yellowish. Mesosoma entirely black, except for propleura dark yellowish; metasoma dark brownish; all coxae black; all trochanters dark brownish; all femur dark brownish, except for apex of profemur light yellowish; protibia light yellowish (including tibial spur), mesotibia and metatibia dark brownish (tibial spurs of both whitish); protarsus light yellowish, except for apex of fifth tarsomere and arolium dark brownish, claws dark yellowish, mesotarsus light brownish, except for fourth and fifth tarsomeres (including claws and arolium) dark brownish, and metatarsus dark brownish; forewing with two dark bands: one partially covering the radial (R), first radial (1R1), first medial (1M) (almost imperceptible), first cubital (1Cu), second cubital (2Cu) and anal (A) cells, and the other also partially covering the second radial 1 (2R1), first radial sector (1Rs), second radial sector (2Rs), second medial (2M) and third medial (3M) (almost imperceptible) cells. Metasoma dark brownish. **Head** (Figure 2e) wide; TFD 0.68× FD; MID 1.81× FD; punctuation conspicuous in the frons. Pubescence in clypeus, paraocular space and occiput. Ocelli in a short triangle; lateral ocelli closer to each other than to compound eyes; POL 0.83× OOL. Mandible almost equally broad through its length, two sharpened apical teeth, basal-most larger. Clypeus trapezoid, convex, apical margin slightly arcuate; WC 2.58× LC. Length of first flagellomere 4.09× its width; ratio of the three first antennal segments approximately 8:3:11; length of the first flagellomere 0.65× UID. **Mesosoma** (Figure 2a-d). Punctated and pubescent areas sparse, the latter more conspicuous along the propodeal declivity. Pronotum not elongated, declivity very accentuated, width 3.5× its length; collar short, almost absent. Punctures on propodeum conspicuous; propodeal disc covered by a conspicuous pubescence of long white setae; declivity not abrupt (flat appearance). Forewing long (length 0.85× body length), maximum width 0.27× its length; length of marginal cell 2.05× the distance from end to wing apex; third radial sector (3Rs) cell 0.69× longer than second radial sector (2Rs) cell; second radial sector (2Rs) long, length 2× its width; second medial-cubital (2m-cu) vein slightly curvy near middle point, meeting second radial sector (2Rs) cell 0.30× the distance from base to apex of cell. Coxae with a central punctate area on dorsal side, surrounded by an appressed pubescence that extends covering the ventral side; trochanters of fore and mid leg smooth, with some pubescence, trochanter of hind leg slightly punctate through a central stripe on dorsal side, but covered by white pubescence surrounding it and covering ventral side; fore- and mesofemur smooth, metafemur slightly punctate. Ratio of length of tibial spurs approximately 3:7:8. **Metasoma** (Figure 2a,b) slightly pilose, covered by inconspicuous and appressed white pubescence; 0.98× as long as mesosoma. **Genitalia** (Figure 2f,g). Parapenial lobe split; lobes finger-like, curved, length 0.33× total genitalia length; apical lobe rounded, curved; width wider on apex and relatively constrained along length. Digitus wide, width 0.55× distance from apex to base of digitus; dorsal lobe convex, apex scooped, transversal carina apically delimitating, distal margin slightly rounded, ventral margin angulated, prolonged inward; length 0.4× paramere length; setae inconspicuous; ventral lobe leveled, short, punctate, setae inconspicuous. Aedeagus lanceolate, almost as long as parapenial lobe, apex semi-angulate. Paramere long, length 0.6× total genitalia length; base wider in half of length, sharp sclerotized expansions on 0.4 and 0.6 of paramere length from the base; apex rounded in lateral view, sword-like in ventral view; setae thin, long. Subgenital plate with base short, setose, trilobed; median lobe expanded; base wide; apex lanceolate, rounded.

Distribution. Argentina (Misiones province), Bolivia (Beni department), Brazil (Amapá, Amazonas, Bahia, Espírito Santo, Maranhão, Mato Grosso, Pará, Rondônia, and Tocantins states), Colombia (Boyacá department), Costa Rica (Guanacaste province), Ecuador (Esmeraldas, Napo, and Sucumbíos provinces), French Guiana (Awala-Yalimapo, Kourou, and Sinnamary communes), Guyana (Cuyuni-Mazaruni region), Peru (Cuzco and Madre de Dios departments) and Trinidad (Arima borough).

Examined material. BRAZIL: Maranhão: 'Brasil, Maranhão, Prq. \ Est. do Mirador, 29.xi.2009, \ 6.7305°S 44.9830°W, \ D. Muniz, G. Azevedo & \ C. Maia, B. ativa' 'LEACOL-26509' (1♂, LEACOL); 'Brasil, Maranhão, S. J. \ de Ribamar, S. Aguahy, \ 2011, 2.6486°S \ 44.1268°W, B. Ferreira \ & T. Silva, Malaise' 'LEACOL-26510' (1♀, LEACOL); 'Brasil, Maranhão, Prq. \ Est. do Mirador, 29.xi.2009, \ 6.7305°S 44.9830°W, \ D. Muniz, G. Azevedo & \ C. Maia, B. ativa' (1♂, DZUB); 'Brasil, Maranhão, Prq. \ Est. do Mirador, 29.xi.2009, \ 6.7305°S 44.9830°W \ D.

Muniz, G. Azevedo & \ C. Maia, B. ativa' (1♂, DZUB); 'BR: AM, Novo Airão, \ IG.MT, 2º49'00"S \ 60º55'08"W, 7-9.xii.2013, \ JAR CAMARA CHICO \ Malaise trap' 'POUVV31' (1♀, DZUB).

Behavioral biology. Unknown.

Observations (Figures 1, 2). Male coloration is highly divergent from the female's: the male is black (head and mesosoma) and dark brownish (metasoma), while the female is almost entirely covered in metallic blue. Sexual dimorphism was also observed in the forewing venation of the studied specimens (Figures 1c 2c). In females (1) the 1Rs cell is 3× longer than wider (1.42× longer than wider in the male); (2) the 2Rs cell is about 3× 1Rs total length (2.06× 1Rs total length in the male); (3) the second medial-cubital (2m-cu) vein meets the second radial sector (2Rs) cell 0.28× the distance from the base to the apex of the cell in the female (meets the second radial sector (2Rs) cell 0.30× the distance from the base to the apex of the cell in the male); (4) the first medial-cubital (1m-cu) vein meets the first radial sector (1Rs) cell 0.67× the distance from the base to the apex of the cell (meets the first radial sector (1Rs) cell 0.41× the distance from the base to the apex of the cell in the male); (5) the length of the marginal cell 1.35× the distance from its end to the wing apex (2.05× the distance from its end to the wing apex in the male). Both sexes share a convex downward curve in their mesopleuron, although in the male it appears more pronounced than in the female. The same pattern is observed in the male of *Eragenia congrua*, its second radial sector (2Rs) and the third radial sector (3Rs) cells are narrower than in the male of *E. aureicornis*. The male genitalia of *E. aureicornis* is very similar to that of the male of *E. bella*, both species sharing two projections in the paramere. They differ by the lack of two teeth at the distal-apical margin of the basal ring in *E. aureicornis*, which are present in *E. bella*; and the aedeagus differ by having an angular apex in *E. aureicornis* and being rounded in *E. bella*. The male of *E. bella* shows green metallic reflection, whereas this characteristic is absent in *E. aureicornis*.

Updated key to male *Eragenia* Banks (modified from Waichert *et al*. 2015a)

(males of *E. carinata*, *E. coerulipes*, and *E. setosa* unknown)

1. Head, mesosoma, and metasoma reddish-orange; southern USA to Ecuador (see Figure 4i in Waichert *et al*. 2015a)..... .....***Eragenia tabascoensis*** (Cameron)

1'. Head, mesosoma, and metasoma of other colour combinations; if metasoma is red, then head and mesosoma area of a different color.....**2**

2. Head and mesosoma black; metasoma reddish-orange; legs with bluish or purplish reflections (see Figure 4f,k in Waichert *et al*. 2015a).....**3**

2'. Head, mesosoma, and metasoma of different color combinations; if metasoma is reddish-orange, then leg integument without bluish reflections.....**4**

3. Small species, 4.5-6.5 mm; subgenital plate triangular, not constricted medially, with a bifid carina that is expanded in lateral view; forewing with cell 3Rs small, less than 2× as long as 2Rs; Costa Rica, Panama, Trinidad and northern South America (see Figures 4k, 8e in Waichert *et al*. 2015a)..... .....***Eragenia isolata*** (Banks)

3'. Medium to large species, 8-10 mm; subgenital plate constricted medially, without expansion seen in lateral view; forewing with cell 3Rs long, angulate, more than 2× as long as 2Rs; Brazil and Peru (see Figures 4f, 8a in Waichert *et al*. 2015a).....***Eragenia abdominalis*** (Smith)

4. Mesosoma red, or partially red; metasoma with bluish metallic reflections; legs with bluish-purple reflections (see Figure 5 in Waichert *et al*. 2015a).....**5**

4'. Mesosoma black (sometimes with strong green or blue reflections); metasoma black with or without golden pubescence, or brownish. If the metasoma has bluish reflections, the mesosoma is never red.....**7**

5. Head with blue metallic reflections (Figure 4e); apical margin of clypeus convex (Figure 4e); subgenital plate wide throughout; paramere short, with two lateral expansion (see Figure 10f in Waichert *et al*. 2015a); Costa Rica to southern Brazil; (Figure 4) .....***Eragenia micans*** (Fabricius)

5'. Head without blue metallic reflections (sometimes with faint blue metallic reflections); apical margin of clypeus almost straight; subgenital plate constricted medially (see Figure 10e in Waichert *et al*. 2015a); paramere long, lanceolate, without lateral expansions.....**6**

6. Mesosoma entirely red; forewing translucent with two dark bands; forewing with cell 3Rs 1.7× as long as 2Rs, both cells almost the same height (see Figure 8j in Waichert *et al*. 2015a); Honduras to Panama ....***Eragenia pseudomicans*** Waichert and Pitts

6'. Mesosoma not entirely red; forewing faint or strongly yellowish with one or two dark bands; forewing with cell 3Rs 2.2× as long as 2Rs, 3Rs distally extended (see Figure 8b in Waichert *et al*. 2015a); Trinidad and northern South America .....***Eragenia amabilis*** (Taschenberg)

7. Subgenital plate never strongly constricted medially (see Figure 10h,k,m in Waichert *et al*. 2015a).....**8**

7'. Subgenital plate strongly constricted medially (see Figure 10b,c in Waichert *et al*. 2015a).....**11**

8. Integument black without olive green reflections or golden pubescence covering mesosoma and/or metasoma (Figure 2a,b); Costa Rica, Trinidad and South America to Argentina; (Figure 2).....***Eragenia aureicornis*** (Smith)

8'. Integument black with olive green reflections and golden pubescence covering mesosoma and/or metasoma.....**9**

9. Clypeus invaginated medially; aedeagus sword-like (see Figure 9j,v in Waichert *et al*. 2015a); Mexico to Costa Rica .....***Eragenia dentata*** Waichert and Pitts

9'. Clypeus centrally flat; aedeagus tongue-like (see Figure 9c,e in Waichert *et al*. 2015a).....**10**

10. Length of the parapenial lobes 0.6× the total genitalia length, width of the apical lobe constant along length; digitus arched, length 0.6× the paramere length; paramere apex lanceolate; Mexico to Costa Rica..... .....***Eragenia oliva*** Waichert and Pitts

10'. Length of the parapenial lobes 0.4× the total genitalia length, apical lobe thicker on apex and base; digitus truncate; length 0.4× the paramere length; paramere apex rounded; Guatemala to Panama.....***Eragenia bella*** Waichert and Pitts

11. Integument black with bluish reflections; subgenital plate without lateral expansions along the constricted median portion; Nicaragua to Panama. ....***Eragenia villosa*** Waichert and Pitts

11'. Integument black without bluish reflections (Figure 3a,b); subgenital plate with lateral expansions along the constricted median portion; northern South America (Figure 3). ....***Eragenia congrua*** (Fox)

DISCUSSION

The strong statistical support for the phylogenetic relation of *E. aureicornis* with *E. setosa* corroborates the proposal to resurrect *Eragenia* as a valid genus, as the type species is nested within the *Eragenia* clade proposed by Waichert *et al*. (2015a). *Eragenia setosa* has been reported from Costa Rica, but its males remain unknown. The wing venation pattern is similar between both species, with short and squared 2Rs, but *E. setosa* can be distinguished from *E. aureicornis* by the integument, which is covered with scale-like golden pubescence and long setae, features that are absent in *E. aureicornis.* The genetic proximity between the specimens suggests that the species require closer examination.

Eragenia has most species with restricted distribution, yet *E. aureicornis* is widely distributed in Meso and South America (Fernandez *et al*. 2022), and it is possible that more than one lineage is currently recognized as *E. aureicornis.* Only four species of *Eragenia* (*E. aureicornis, E. isolata*, *E. micans*, and *E. tabascoensis*) have a wide distribution from Mesoamerica and South America. *Eragenia tabascoensis* is the only of these species recorded in the southern part of North America. The majority, nine species (*E. bella*, *E. carinata*, *E. coerulipes*, *E. dentata*, *E. oliva*, *E. pseudomicans*, *E. rotunda*, *E. setosa*, and *E. villosa*), are restricted to Mesoamerica, whereas three species (*E. abdominalis*, *E. amabilis*, and *E. congrua*) are restricted to South America. *Eragenia aureicornis*, *E. amabilis*, and *E. micans* are the only species of the genus recorded in the southern portion of South America. Cryptic species and color pattern convergence have been discussed in *Eragenia* by Waichert *et al*. (2015a).

In the phylogenetic analysis by Waichert *et al*. (2015a), *E. setosa* is related to the clade formed by *E. setosa* + *E. micans* + *E. tabascoensis* + *E. bella* + *E. isolata*. With the inclusion of *E. aureicornis* in the molecular phylogeny, *E. setosa* becomes related to a clade formed by *E. aureicornis* + *E. setosa* + *E. abdominalis* + *E. congrua* + *E. coerulipes* + *E. pseudomicans* + *E. amabilis* + *E. villosa*. However, the low statistical support in both the clade recovered by Waichert *et al*. (2015), with five species, and the clade recovered in this study, with eight species, hinders a more in-depth discussion on the relationship of the species in the genus.

The actual geographic distribution of the species of *Eragenia* remains unclear, as the genus is rare, with few specimens represented in collections. The few species with wide distributions exhibit large spatial gaps in their geographical records, and several species with seemingly restricted distributions, such as those in Mesoamerica, may have a much broader range than is currently known. Also, the molecular data available are limited to specific locations within the range of more widely distributed species, making it difficult to achieve a broader understanding of intraspecific genetic variation within the genus. Six species of *Eragenia* are known to occur in Brazil: *E. amabilis*, *E. abdominalis*, *E. aureicornis*, *E. congrua*, *E. isolata*, and *E. micans* (Santos and Waichert 2024).

Our study confirms the presence of two species of *Eragenia* in the state of Maranhão (*E. aureicornis* and *E. congrua*) and adds *E. micans* as a new record for the state. Thus, considering previous records reported by Waichert *et al*. (2015a), the transitional zone in Maranhão now accounts for 67% of the Brazilian diversity of *Eragenia* (Waichert *et al*. 2015a; Fernández *et al*. 2022).

Eragenia congrua is restricted to South America, known from Brazil, Colombia, Ecuador, French Guiana, Peru, and Venezuela (Waichert *et al*. 2015a; Fernández *et al*. 2022). In Brazil, it has been recorded in the states of Amazonas, Bahia, Maranhão, Mato Grosso, Pará, and Rondônia (Waichert *et al*. 2015a; Santos and Waichert 2024), in the Amazon, Cerrado, and Atlantic Forest biomes. We provide the first record of this species for the eastern border of the Amazon in Maranhão. Additionally, the previous record (1989) of this species from the Bananal settlement (municipality of Governador Edison Lobão) remains the only record for the Cerrado biome (Waichert *et al*. 2015a).

Eragenia isolata is widely distributed in Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Trinidad, and Venezuela (Waichert *et al*. 2015a; Fernández *et al*. 2022). In Brazil, it has been reported in Amazonas, Distrito Federal,

Maranhão, Pará, and Rondônia (Santos and Waichert 2024), in the Amazon and Cerrado biomes. The only record of *E. isolata* in Maranhão is from the Ribeirãozinho settlement (municipality of Governador Edison Lobão) in 1989, being the second record for the species in the Brazilian Cerrado biome, following a record from central Brazil, both reported in the supplementary material of Waichert *et al*. (2015a).

Within the Neotropical Region, *E. micans* is widely distributed in Bolivia, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Trinidad, Peru, and Venezuela (Santos and Waichert 2024). In Brazil, it was previously recorded in Amazonas, Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso do Sul, Minas Gerais, Pará, Rio de Janeiro, Rondônia, Santa Catarina, São Paulo, and Rio Grande do Sul (Waichert *et al*. 2015a; Santos and Waichert 2024), in the Amazon, Cerrado, Atlantic Forest, Pantanal, and Pampa biomes. Our study provides the first record of this species for the state of Maranhão, establishing its easternmost record in the Amazon biome.

In Maranhão, a number of scientific studies focused on Aculeata, yet few groups have been studied extensively. The most recent studies have focused on bees (Hymenoptera: Apidae) (Rêgo and Albuquerque 2012; Ferreira *et al*. 2020), Vespidae wasps (Silva *et al*. 2011; Somavilla *et al*. 2014; Hermes and Lopes 2018), and ants (Prado *et al*. 2019), without reference to any other lineage of Aculeata. Our review of collection material revealed that records for Pompilidae are rare and based on inventories conducted a long time apart. Given the high extinction rate associated with human activities (Otto 2018; INPE 2024), we emphasize the need for more fauna inventories for a better understanding of the geographic distribution of Pompilidae in Neotropical ecosystems.

CONCLUSIONS

Our study corroborates the revalidation of *Eragenia*, placing the type species of the genus, *E. aureicornis*, within the *Eragenia* clade as proposed by Waichert *et al*. (2015a). The inclusion of *E. aureicornis* in the genus phylogeny alters the relationship of *E. setosa* with the other species. Although we included most of the species in the genus, our phylogenetic hypothesis does not show a well-supported structure with internal nodes. Our findings advance the taxonomic understanding of the genus, particularly *E. aureicornis*, by providing a comprehensive redescription of the male, including a detailed description of the genitalia, which enabled the insertion of this species in the updated identification key for males of *Eragenia*. In addition, we present the first record of *E. micans* for the Brazilian state of Maranhão, which is now the easternmost record of this species for the Amazon biome. Our study also contributes to the expansion of biogeographic knowledge about the pompilid fauna in the Neotropical Region.

ACKNOWLEDGMENTS

We would like to thank Instituto Formação for granting permission to collect in Parque Agroecológico Buritirana, the Maranhão State Secretariat for the Environment (SEMA) for the collection permit in Parque Estadual do Mirador, and QUERCEGEN Agronegócios LTDA for allowing specimen collection at Sítio Aguahy. We are also grateful to Eduardo Fernando dos Santos for the preliminary identification of the Pompilidae specimens, Thayrine Luane Martins Sardinha for collecting specimens in Peri Mirim, and the anonymous reviewers for their valuable suggestions that improved the manuscript.

REFERENCES

Araujo, E.C.; Martins, L.P.; Duarte, M.; Azevedo, G.G. 2020. Temporal distribution of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in the eastern extreme of the Amazon region. *Acta Amazonica* 50: 12-23.

Banks, N. 1944. The Psammocharidae (Hymenoptera) Taken at Kartabo and Other Localities in British Guiana. *Zoologica: scientific contributions of the New York Zoological Society* 29: 97-112.

Banks, N. 1945. The Psammocharidae (spider-wasps) of northern South America, Part 2. *Boletin de Entomologia Venezolana* 4: 81-126.

Banks, N. 1946. Studies of South American Psammocharidae, Part I. *Bulletin of the Museum of Comparative Zoology* 96: 311-525.

Banks, N. 1947. Studies of South American Psammocharidae, Part II. *Bulletin of the Museum of Comparative Zoology* 99: 311-525.

Brothers, D.J.; Finnamore, A.T. 1993. Superfamily Vespoidea. In: Goulet, H.; Huber, J.T. (Eds.). *Hymenoptera of the World: An Identification Guide to Families*. Research Branch, Agriculture Canada, Ottawa, p.161-278.

Comstock, J.H.; Needham, J.G. 1898. The wings of insects: Chapter III (continued): IX. The venation of the wings of Hymenoptera. *The American Naturalist* 32: 413-424.

Evans, H.E. 1949. A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae), Part I. *Transactions of the American Entomological Society* 75: 133-270.

Evans, H.E. 1953. Comparative ethology and the systematics of spider wasps. *Systematic Zoology* 2: 155-172.

Evans, H.E. 1973. Studies on Neotropical Pompilidae (Hymenoptera). IX. The genera of Auplopodini. *Psyche: A Journal of Entomology* 80: 212-226.

Evans, H.E.; Shimizu, A. 1996. The evolution of nesting building and communal nesting in Ageniellini (Insecta: Hymenoptera: Pompilidae). *Journal of Natural History* 30: 1633-1648.

Fernández, F.; Rodriguez, J.; Waichert, C.; Decker, B.; Pitts, J.P. 2022. Twenty two years later: An updated checklist of Neotropical spider wasps (Hymenoptera: Pompilidae). *Zootaxa* 5116: 451-503.

Ferreira, L.A.C.; Martins, D.C.; Rêgo, M.M.C.; Albuquerque, P.M.C. 2020. Três décadas da Coleção do Laboratório de Estudos sobre Abelha da Universidade Federal do Maranhão (LEACOL). In: Souza, A.O.; Oliveira, J.O.; Nunes, A.S.A.; Moraes, C.A.A.; Reis, J.A.; Cavalcante, K.S.B.; Matos, L.R.; Maristela, S.; Nascimento, S.M.V.; Campelo, T.N.S. (Eds.). *Maranhão de Multiplicidades: Científico, Consciente e Cultural*. FAPEMA, São Luís. p.181-208.

Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. 1994. DNA primers for amplification of cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294-299.

Gauld, I.; Bolton, B. 1988. *The Hymenoptera*. Oxford University Press, Oxford, 332p.

Goulet, H.; Huber, J.T. 1993. *Hymenoptera of the World: An identification guide to families*. 1st Research Branch, Agriculture Canada, Ottawa, 681p.

Guindon, S.; Dufayard, J.F.; Lefort, V.; Anisimova, M.; Hordijk, W.; Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307-321.

Harris, R.A. 1979. A glossary of surface sculpturing. *Occasional Papers of the Bureau of Entomology of the California Department of Agriculture* 28: 1-31.

Hermes, M.G.; Lopes, R.B. 2018. A new species of *Zethus* Fabricius (Hymenoptera, Vespidae, Zethinae) from Northeast Brazil, with notes on morphology and distributional records of *Z. alessandroi* Lopes. *Zootaxa* 4462: 245-250.

Huber, J.T. 2017. Biodiversity of Hymenoptera. In: Foottit, R.G.; Adler, P.H. *Insect Biodiversity: Science and Society*. Wiley-Blackwell, Oxford, p.419-461.

IBGE. 2019. Instituto Brasileiro de Geografia e Estatística. Biomas e Sistema Costeiro-Marinho do Brasil. (https://biblioteca.ibge.gov.br/index.php/biblioteca-catalogo?view=detalhes&id=2101676). Accessed on 28 Jul 2022.

INPE. 2024. PRODES (Program for Deforestation Monitoring) Instituto Nacional de Pesquisas Espaciais. (https://data.inpe.br/bigweb/biomasbr/notas-tecnicas/estimativa-de-desmatamento-na-amazonia-legal-para/). Accessed on 05 Feb 2025.

ISA. 2023. Unidades de Conservação no Brasil. *PES de Mirador*. Instituto Socioambiental (https://uc.socioambiental.org/pt-br/arp/763). Accessed on 18 Jan 2023.

Kalyaanamoorthy, S.; Minh, B.Q.; Wong, T.K.; Von Haeseler, A.; Jermiin, L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587-589.

Macherey-Nagel GmbH & Co. KG. 2017. Genomic DNA from tissue — User manual NucleoSpin® Tissue. (https://www.bioke.com/blobs/manuals/MN/UM_gDNATissue_2017.pdf). Accessed on 07 Mar 2024.

Maranhão. 1994. Lei n. 6.194 de 10 de novembro de 1994. Cria o município de Governador Edison Lobão e dá outras providências. (https://transparencia.governadoredisonlobao.ma.gov.br/transparencia/viewUrl/2). Accessed on 14 Nov 2023.

Marinho, D.; Muniz, D.B.; Azevedo, G.G. 2018. Nesting biology of three *Megachile* (Hymenoptera: Megachilidae) species from Eastern Amazon, Brazil. *Revista Brasileira de Entomologia* 62: 97-106.

Martins, L.P.; Araujo Junior, E.D.C.; Martins, A.R.P.; Colins, M.S.; Almeida, G.C.F.; Azevedo, G.G. 2017. Butterflies of Amazon and Cerrado remnants of Maranhão, Northeast Brazil. *Biota Neotropica* 17: e20170335.

Minh, B.Q.; Nguyen, M.A.T.; Von Haeseler, A. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30: 1188-1195.

Nguyen, L.T.; Schmidt, H.A.; Von Haeseler, A.; Minh, B.Q. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268-274.

Otto, S.P. 2018. Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B* 285: 20182047.

Prado, L.P.; Feitosa, R.M.; Triana, S.P.; Gutiérrez, J.A.M.; Rousseau, G.X.; Silva, R.A.;*et al*. 2019. An overview of the ant fauna (Hymenoptera: Formicidae) of the Maranhão state, Brazil. *Papéis Avulsos de Zoologia* 59: e20195938.

Rêgo, M.M.C.; Albuquerque, P.M.C. 2012. Biodiversidade de abelhas em Zonas de Transição no Maranhão. *Documentos (Embrapa Semiárido)* 249: 36-57.

Rodrigues, M.S.; Conceição, G.M. 2014. Diversidade florística das diferentes fisionomias de Cerrado do Parque Estadual do Mirador, Maranhão, Brasil. *Brazilian Geographical Journal* 5: 139-156.

Santos, E.F.; Waichert, C. 2024. Pompilidae. Catálogo Taxonômico da Fauna do Brasil, PNUD. (http://fauna.jbrj.gov.br/fauna/faunadobrasil/157346). Accessed on 01 Feb 2024.

Serra, F.C.V.; Lima, P.B.; Almeida Júnior, E.B. 2016. Species richness in restinga vegetation on the eastern Maranhão state, Northeastern Brazil. *Acta Amazonica* 46: 271-280.

Silva, S.S.; Azevedo, G.G.; Silveira, O.T. 2011. Social wasps of two Cerrado localities in the northeast of the Maranhão state, Brazil (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Entomologia* 55: 597-602.

Smith, F. 1873. Descriptions of new species of fossorial Hymenoptera in the collection of the British Museum. *Annals and Magazine of Natural History* 4: 1-30.

Somavilla, A.; Marques, D.W.A.; Barbosa, E.A.S.; Pinto Júnior, J.S.; Oliveira, M.L. 2014. Vespas sociais (Vespidae: Polistinae) em uma área de floresta ombrófila densa Amazônica no Estado do Maranhão, Brasil. *EntomoBrasilis* 7: 183-187.

Townes, H. 1957. Nearctic wasps of the subfamilies Pepsinae and Ceropalinae. *Bulletin of the United States National Museum* 209: 1-307.

Trifinopoulos, J.; Nguyen, L.T.; Von Haeseler, A.; Minh, B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: 232-235.

Wahis, R.; Rojas, F. 2003. Los pompílidos de Chile (Hymenoptera: Pompilidae). *Revista Chilena de Entomologia* 29: 89-103.

Waichert, C.; Von Dohlen, C.D.; Pitts, J.P. 2015a. Resurrection, revision and molecular phylogenetics of *Eragenia* Banks with implications for Ageniellini systematics (Hymenoptera: Pompilidae). *Systematic Entomology* 40: 291-489.

Waichert, C.; Rodriguez, J.; Wasbauer, M.S.; Von Dohlen, C.D.; Pitts, J.P. 2015b. Molecular phylogeny and systematics of spider wasps (Hymenoptera: Pompilidae): redefining subfamily boundaries and the origin of the family. *Zoological Journal of the Linnean Society* 175: 271-287.

RECEIVED: 17/05/2024
ACCEPTED: 04/03/2025
ASSOCIATE EDITOR: Ana Lucia Tourinho
DATA AVAILABILITY: The data that support the findings of this study are available in Genbank and LEACOL-UFMA with the GenBank accession number PV077271, and the corresponding catalog numbers listed as LEACOL-26509, LEACOL-26510, LEACOL-26511, and LEACOL-26512.