



A new species of *Ecitonides* Wasmann, 1894 (Coleoptera: Staphylinidae: Paederinae) from Peru and phylogenetic placement of the genus based on molecular data

JOSH JENKINS SHAW^{1*}, MARYZENDER RODRÍGUEZ-MELGAREJO^{2,3}, KEITA MATSUMOTO⁴, SOPHIA WASEL¹ & ROSS PIPER⁵

¹ Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, Copenhagen 2100, Denmark

[✉ josh.shaw@snm.ku.dk](mailto:josh.shaw@snm.ku.dk), [ORCID](https://orcid.org/0000-0001-8585-2226) <https://orcid.org/0000-0001-8585-2226>

² Laboratorio de Entomología, Instituto Argentino de Investigaciones de las Zonas Áridas, (IADIZA-CONICET), Parque Gral. San Martín, s/n, 5500 Mendoza, Argentina

[✉ mmelgarejo@mendoza-conicet.gob.ar](mailto:mmelgarejo@mendoza-conicet.gob.ar), [ORCID](https://orcid.org/0000-0002-3516-4270) <https://orcid.org/0000-0002-3516-4270>

³ Departamento de Entomología, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Jesús María, Lima 14, Perú

⁴ Department of Life Sciences, Natural History Museum, London, SW7 5BD, United Kingdom

[✉ k.matsumoto@nhm.ac.uk](mailto:k.matsumoto@nhm.ac.uk), [ORCID](https://orcid.org/0000-0002-0527-7418) <https://orcid.org/0000-0002-0527-7418>

⁵ Ipswich, Suffolk, UK

[✉ ross_piper@yahoo.com](mailto:ross_piper@yahoo.com)

*Corresponding author: [✉ josh.shaw@snm.ku.dk](mailto:josh.shaw@snm.ku.dk)

Abstract

Ecitonides constanceae sp. nov., a new species of the myrmecophilous genus *Ecitonides* Wasmann, 1894, which is associated with army ants (Hymenoptera: Formicidae: Ecitoninae), is described from Peru. The holotype, which is the only known specimen, was collected at light at Los Amigos Biological Station, Madre de Dios department, Peru. The army ant host species is unknown. The new species is distinguished from congeners and an updated key of the species, as well as a checklist of *Ecitonides* and their associated host ants are provided. Based on the holotype we non-destructively extracted DNA and sequenced two genes which were incorporated into an existing molecular phylogenetic dataset and analysed using Bayesian Inference. *Ecitonides* is recovered as sister to recently described termitophilous genus *Ruptor* Żyła *et al.* 2022 and placed in the so-called ‘Medonina and allied taxa’ clade. Beyond Bayesian Inference phylogenetic analysis and their associated nodal support methods, we also explored the position of the *Ecitonides* within the posterior sample of trees produced in the Bayesian analyses, which further supported its placement.

Resumen

Ecitonides constanceae sp. nov., una nueva especie del género mirmecófilo *Ecitonides* Wasmann, 1894, el cual está asociado con las hormigas legionarias (Hymenoptera: Formicidae: Ecitoninae) es descrita para Perú. El holotipo es el único ejemplar conocido de esta especie y fue recolectado en una trampa de luz en la Estación Biológica Los Amigos, departamento de Madre de Dios, Perú. Se desconoce la especie de hormiga legionaria hospedera de esta especie nueva. La especie nueva es distinguida de sus congéneres y se proporciona una clave actualizada de las especies de *Ecitonides*, así como una lista de verificación de las especies de *Ecitonides* y sus hormigas hospederas asociadas. El ADN fue extraído del holotipo de forma no destructiva y se secuenciaron dos genes que se incorporaron a un conjunto de datos filogenéticos moleculares preexistentes y analizados mediante la metodología de inferencia bayesiana para conocer la posición filogenética de este nuevo taxón. *Ecitonides* se recupera como género hermano de *Ruptor* Żyła *et al.* 2022, género termitófilo recientemente descrito y colocado en el llamado clado ‘Medonina y taxones afines’. Más allá del análisis filogenético de inferencia bayesiana y sus métodos de soporte de nodos asociados, también exploramos la posición de *Ecitonides* dentro del muestreo posterior de árboles producidos en los análisis bayesianos, respaldando aún más su posición filogenética.

Key words: taxonomy, new species, rove beetle, phylogenetics, systematics

Introduction

Wasmann (1894) described the Neotropical genus *Ecitonides* and the species *E. tuberculosus* based on a single specimen collected from a colony of *Eciton quadriglume* (Haliday, 1836) army ants from Brazil. Later, Wasmann (1900) described two another Brazilian species, *E. brevicornis* and *E. longiceps*. Then, Borgmeier (1932) described *E. spectabilis* from Brazil. After that, Bruch (1933) described *E. verrucosus* from Argentina and later Borgmeier (1959) described another Brazilian species, *E. fraterculus*. Subsequently Seevers (1965) presented a catalogue of *Ecitonides* species and their known hosts, the army ant genera *Labidus* Jurine 1807 and *Nomamyrmex* Borgmeier 1936. Also, he proposed the *Ecitonides* group (*Bolbophites* Fauvel, 1904; *Ecitonides* Wasmann 1894; *Synecitonides* Reichensperger, 1936; *Labidophites* Borgmeier, 1956) may belong to the Echiasteres, following Blackwelder (1944), without any phylogenetic analysis. Several years later, Assing (2012) described *E. volans* from Peru and Makhan (2021) described *E. soesilae* from Suriname. Until now, the genus *Ecitonides* comprises eight valid species distributed in South America (Argentina, Brazil, Paraguay, Peru, and Suriname) (Asenjo *et al.* 2019, Makhan 2021), however, its phylogenetic position inside the subfamily Paederinae is uncertain.

From material collected with light traps in Estación Biológica Los Amigos (Madre de Dios department, 270 m), a remarkable single male specimen was distinguished by its conspicuous habitus. After revising the literature and examining morphological characters, we concluded it is an undescribed species of *Ecitonides*, and here we describe it as *Ecitonides constanceae* **sp. nov.** from Madre de Dios, Peru.

The objective of this paper is to describe a new species, *Ecitonides constanceae* **sp. nov.**, and to explore the phylogenetic placement of the genus based on molecular phylogenetic analyses using two gene fragments and previously generated molecular data for the subfamily Paederinae. Photographs of the habitus and genitalia, a distribution map, and a key to *Ecitonides* species are provided.

Material and methods

Examination of the material

The single male holotype is deposited in the Entomological Collection of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM). It was originally deposited in the collection of the Natural History Museum, London (BMNH) but has since been deaccessioned. The specimen was examined by relaxing in warm water, dissecting the abdomen and its inner contents. Genitalia were placed in a drop of dimethyl hydantoin formaldehyde (DMHF) resin and mounted on a card pinned under the specimen. Habitus photographs were taken with a Canon DSLR camera, Laowa 25mm and 60mm macro lens. All photographs were processed through focus stacking software, Helicon Focus and were later edited using GIMP. The beginning and end of label text are indicated using double quotes (“”) and double slash (/) separates the data on different labels.

Measurements were taken in mm using ImageJ (Schneider *et al.* 2012). The following measurements were taken: Total body length (TL, from apex of head to the tip of the abdomen); head length (HL, from the anterior margin of the frons to the posterior margin of the head); head width (HW, maximum width); pronotum length (PL, from the anterior margin of the pronotum to posterior margin); pronotum width (PW, width at widest point including tubercles); elytral length (EL, from the suture at the apex of the scutellum to the posterior margin of the elytra); length of the aedeagus (LA, from the apex of the ventral process to the base of the aedeagal capsule).

Molecular procedure

The DNA was extracted from the whole abdomen apex, excluding the genital segment and the aedeagus, using the non-destructive Qiagen DNeasy Blood and Tissue kit (Venlo, Netherlands) following the protocol for animal tissue with a prolonged lysis time (12–16 h).

Molecular sequences from two gene fragments cytochrome c oxidase subunit I (COI) and wingless were successfully amplified based on the following primers: COI ‘Pat & Jerry’: C1-J-2183 + L2-N-3014 and wingless: nested PCR using Wg550F + WgABRZ, then Wg578F + WgABR. The two newly generated sequences are available under the following GenBank accession numbers: OQ685081 (COI Pat & Jerry) and OQ686615 (wingless). Details of PCR and sequence alignment can be found in Żyła *et al.* (2022).

Phylogenetic analysis

Two of the resulting sequences (COI ‘Pat & Jerry’ and wingless) were incorporated into the molecular data of Żyła *et al.* (2022), whose goal, like ours, was to explore placement of a usual inquiline taxon. Procedures for alignment and phylogenetic analyses follows Żyła *et al.* (2022) and readers are referred there for particular details. The Bayesian phylogenetic analysis (BI) was carried out using MrBayes v3.2.6 (Ronquist *et al.* 2012) on Computerome (<http://www.computerome.dtu.dk/>). The final dataset/script is available at 10.6084/m9.figshare.24101004. Additional details of the phylogenetic analysis can be found in Żyła *et al.* (2022). We used R/RoguePlots (Klopfstein & Spasojević 2019; R Core Team 2021) to explore phylogenetic placement of *Ecitonides* in all output trees of the Bayesian phylogenetic analysis. The online blog by Mario Coiro (<https://mariocoiro.blog/2020/12/02/how-to-represent-uncertainty-in-phylogenies-rogueplots-to-the-rescue/>) was also useful when implementing RoguePlots. Statistical support for placements of *Ecitonides* was summarized using a majority-rule consensus tree and the post burn-in combined runs from the Bayesian analyses.

Distribution map

The distribution map was created using ggplot2 and several other packages running in R (R Core Team 2021; Wickham 2016).

Results

Taxonomy

Ecitonides constanceae sp. nov.

(Figs 1–4)

Type material. Holotype, male, “PERU 270m, Madre de Dios, Estación Biológica Los Amigos, -12.569170, -70.100110” // “21–30.VI.2019 G. Bittencourt leg., General collecting, BMNH(E) 2019-96” // “NHMUK014374061 [QR code]” // “DNA Voucher JJS22-5 NHMD” // “HOLOTYPE *Ecitonides constanceae* sp. nov. Jenkins Shaw *et al.* 2023” [red label] (MUSM).

Diagnosis. The new species is most similar to *E. spectabilis* Borgmeier, due to their similar size, general shape and structure of the head, pronotum and elytra. However, *Ecitonides constanceae* sp. nov. differs from *E. spectabilis* in the position of the eyes (eyes not distinctly interrupting the outline of the head in dorsal view in *E. spectabilis*) and absence of distinct tubercles on the abdominal segments (distinct on abdominal segments III to V of *E. spectabilis*).

Differential diagnosis. *Ecitonides constanceae* sp. nov. differs from *E. verrucosus* Bruch, in the total body length (5.3 mm in *E. verrucosus*) size and shape of the tubercles on the head, pronotum and elytra (smaller and sparser in *E. verrucosus*), the shape of the labrum (bidentate in *E. verrucosus*) and shape of the antennomeres (antennomeres transverses in *E. verrucosus*). From *E. tuberculosus* Wasmann, differs in the total body length (6.3 mm in *E. tuberculosus*) size and shape of the tubercles on the head, pronotum and elytra (smaller and sparser in *E. tuberculosus*). From *E. volans* Assing, differs in the total body length (5.9 mm in *E. volans*), the shape and length of the head (longer and tapering posteriorly in *E. volans*), the shape of the pronotum (widest in posterior third in *E. volans*), shape of the elytra (not sinuate laterally and with elytral suture gaping posteriorly in *E. volans*), shape and structure of the aedeagus. From *E. fraterculus* Borgmeier, in the total body length (5 mm in *E. fraterculus*). From *E. brevicornis* Wasmann, in the size and shape of the tubercles on the head, pronotum and elytra (smaller in *E. brevicornis*), the longer antennae, the position of the eyes (not so visible when viewed from above in *E. brevicornis*), shape of the head (tapering posteriorly in *E. brevicornis*), shape of the pronotum (widest in posterior half in *E. brevicornis*). From *E. soesilae* Makhan, 2021 in the shape of the pronotum, formation of tubercles on the elytra and in the total body length (7.2 mm in *E. soesilae*).



FIGURE 1. *Ectonides constanceae* sp. nov. in dorsal (A) and ventral (B) view. Scale bar: 5.0 mm.

Description. TL = 10.1, HL = 2.16, HW = 1.14, PL = 1.57, PW = 1.51, EL = 1.70, LA = 1.96. Dorsal view as in Fig. 1A. Ventral view as in Fig. 1B.

Head elongate, 1.9 x longer than wide, widest at tubercles protruding from under eyes in dorsal view (Fig. 2A). Head covered in tubercles; dorsal tubercles flattened in lateral view (Fig. 2B). Intervals between tubercles with distinct microsculpture. Lateral margin of head very weakly converging posteriad. Medial area of labrum tridentate (Fig. 2D). Maxillary palpomere (MP) 4 densely setose, aciculate, distinctly thinner and shorter than MP3. Labial palpomere (LP) 3 aciculate, distinctly thinner and shorter than LP2. Eyes kidney-shaped in lateral view (Fig. 2B). Anterior edge of mentum with pair of golden macrosetae. Gular sutures united along length. Antennomeres 1 to 10 elongate (Fig 2E); antennomere 11 slightly transverse, about half the length of antennomere 10. Antennomere 1 distinctly wider than remaining antennomeres and approximately as long as antennomeres 2 to 4 combined. Neck slightly thinner than head, except at point of attachment to head where it is approximately a quarter of width of head.

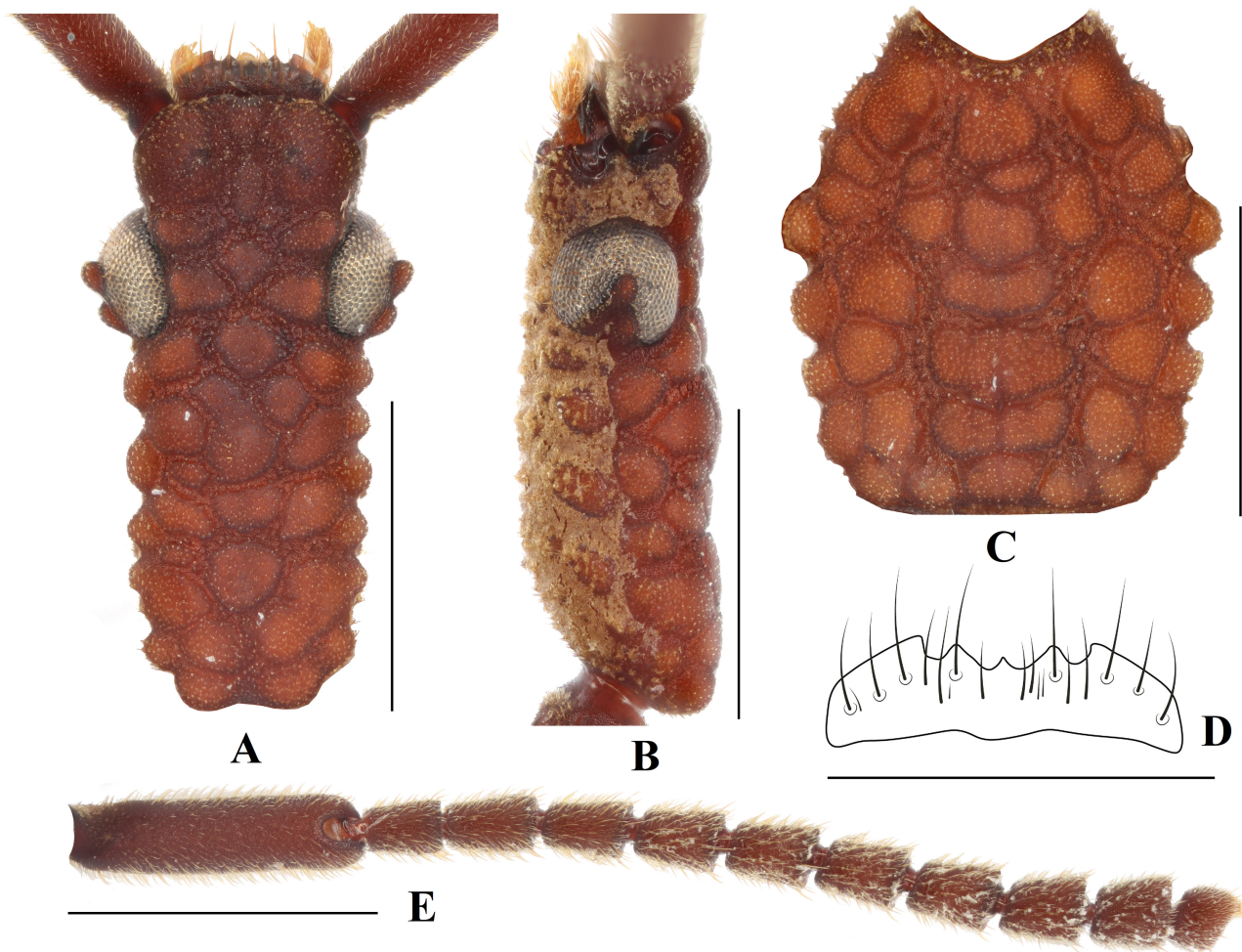


FIGURE 2. Morphological details of *Ectonides constanceae* sp. nov. A. Close up of head in dorsal view. B. Close up of head in lateral view. C. Close up of pronotum. D. Drawing of labrum. E. Antenna. Scale bars: A–C, E = 1.0 mm; D = 0.5 mm.

Pronotum as long as wide (Fig. 2C), widest just in front of middle. Entire dorsal surface covered in large tubercles, which are more or less symmetrical either side. Intervals between tubercles with distinct microsculpture. In lateral view, middle area of pronotum distinctly elevated compared to sides. Prothorax ventrally; division into basisternum and furcasternum not obvious due to extensive tubercles and setae. Presumed furcasternum acutely pointed. Protibiae with distinct indentation on inner margin. Protarsomeres 1 to 4 transverse, equal in length; protarsomere 5 elongate, approximately equal to combined length of protarsomeres 1 to 4. Claws large, almost as long as protarsomere 5. Mesoscutellum rounded apically, with distinct microsculpture. Elytra widest in posterior quarter, lateral margins somewhat sinuate. Tubercles of each elytron arrange in five rows. Hind wings apparently well developed. Mesoventral process acutely produced. Meso- and metatarsi very similar to protarsi.

Abdominal segments III to VII each with two pairs of paratergites, the outer paratergite very thin from segment IV. Tergites III to VI with distinct tubercles and surface granulation. Tergite VII and VIII without tubercles. Segments IX to X with tufts of long black/golden setae.

Male. Sternite VIII emarginate (Fig. 3A). Aedeagus long and rather slender, with rounded apex (Fig. 3B), curved in lateral view (Fig. 3C), without parameres.

Female. Unknown.



FIGURE 3. *Ecitonides constanceae* sp. nov. A. Male sternite VIII. B. Aedeagus in dorsal view. C. Aedeagus in lateral view. Scale bar: 1.0 mm.

Distribution and natural history. The type locality, Los Amigos Biological Station, is situated 100 km west of Puerto Maldonado in Madre de Dios department in southeastern Peru (Figs. 4 A, B, C), near the confluence of Madre de Dios and Los Amigos rivers. This locality is placed in a tropical humid forest at 270 m.a.s.l. The holotype was collected at an MV light sheet (Fig. 4C).

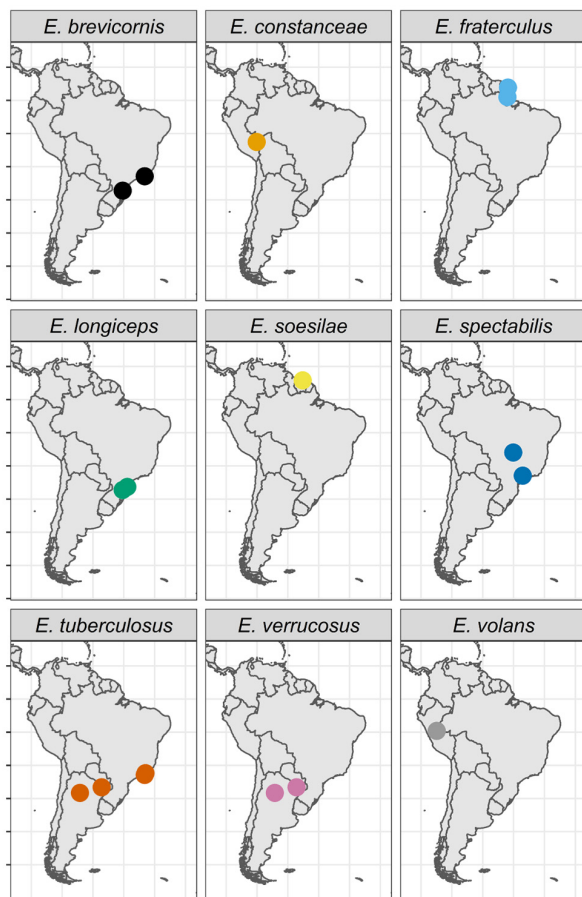
Etymology. The species is name after the daughter of author Ross Piper. This specific epithet is a noun in genitive case.

Key to species of *Ecitonides*

1	Head 2 times longer than wide	2
-	Head more than 2 times longer than wide	8
2 (1)	Sternites III-VI with large elongated tubercles	<i>E. soesilae</i> (Makhan 2021:24, fig. 2)
-	Sternites III-VI without large elongated tubercles	3
3 (2)	Antennae longer than the head	4
-	Antennae not longer than the head	7

- 4 (3) Head oblong. Elytron with 5 rows of tubercles 5
 - Head increasing the width toward the posterior margin. Elytron with 4 rows of tubercles. Body length 5 mm
 *E. verrucosus* (fig.1 in Bruch, 1933:13).
- 5 (4) Antennae about 1.4x as long as head. Elytra 0.8x as long as pronotum. Body length 6 mm.
 *E. volans* (fig.1 in Assing, 2012: 403)
 - Antennae about 2x as long as head. Elytra 1.3 x as long as pronotum 6
- 6 (5) Abdominal segments III–V with distinct tubercles. Body length 10 mm *E. spectabilis* (fig. 1 in Borgmeier, 1932: 398)
 - Abdominal segments III–V without distinct tubercles. Body length 10 mm *E. constanceae* **sp. nov.** (Figs. 1–3)
- 7 (3) Antennomeres 7–10 strongly transverse. Tubercles present in tergites III–VI. Body length 5 mm. *E. fraterculus*
 - Antennomeres 7–10 not transverse. Tubercles present only in tergite III. Body length 7 mm
 *E. brevicornis* (fig. 3 in Borgmeier, 1949: plate V)
- 8 (1) Head 3 times as long as wide. Body length 6 mm *E. tuberculosus* (fig. 10 in Bruch 1933: 16)
 - Head 4 times as long as wide. Body length 7 mm *E. longiceps* (fig. 15 in Wasmann 1900: plate 14)

A



B



C



FIGURE 4. A. Distribution maps of all species of *Ecitonides*. B. Surrounding habitat of *E. constanceae* **sp. nov.** C. Light sheet at which the *E. constanceae* **sp. nov.** was collected.

Phylogenetic placement

The Bayesian analysis reached convergence with an Average standard deviation of split frequencies of 0.003 after 10 million generations. All Effective Sample Sizes (ESS) were greater than 200 for all parameters. Average PSRF (Potential Scale Reduction Factor) was 1.000 with a maximum value of 1.002. Convergence was also visually checked

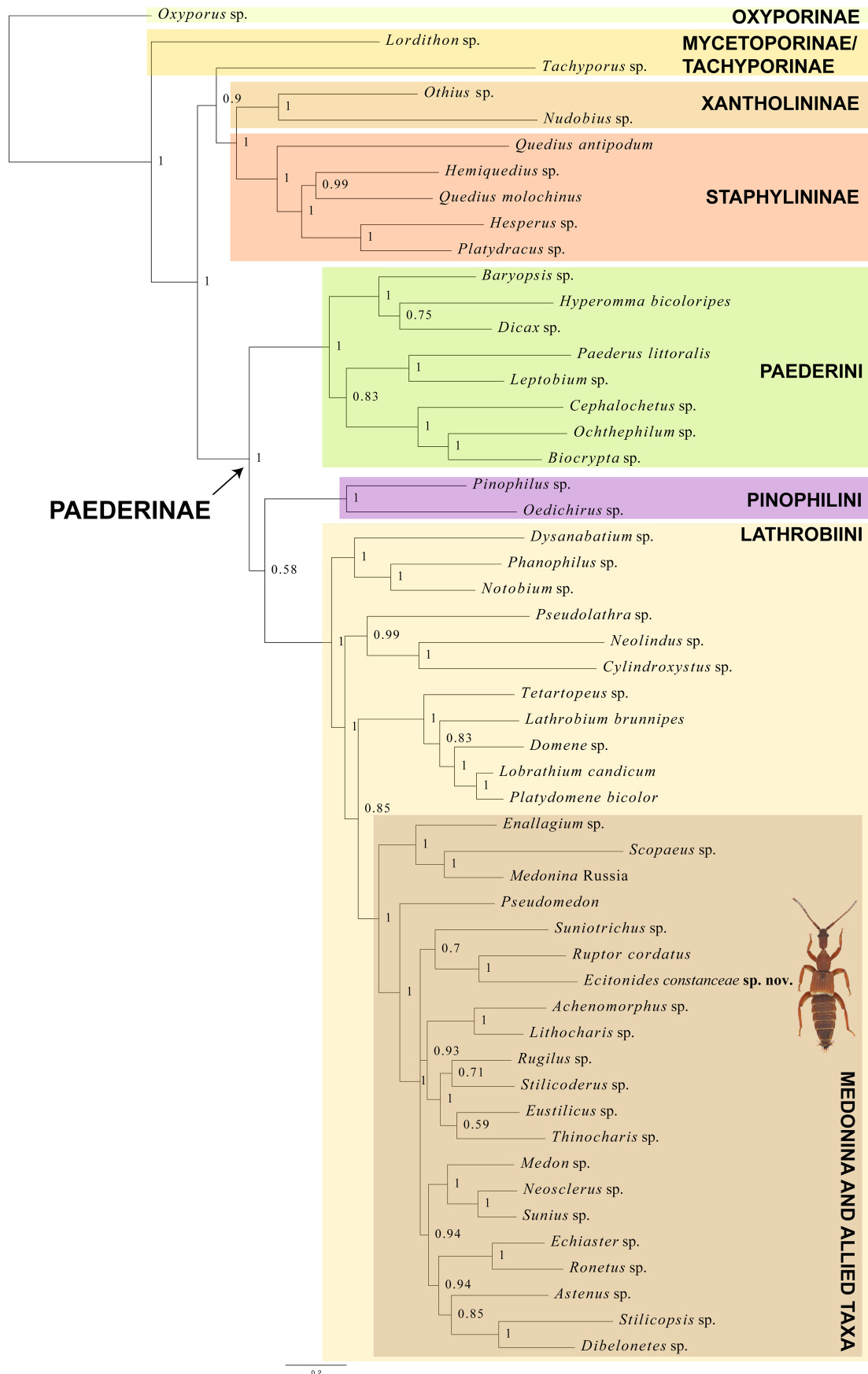


FIGURE 5. 50% majority rule consensus tree from the Bayesian phylogenetic analysis of molecular data. Posterior probabilities are given at the respective nodes.

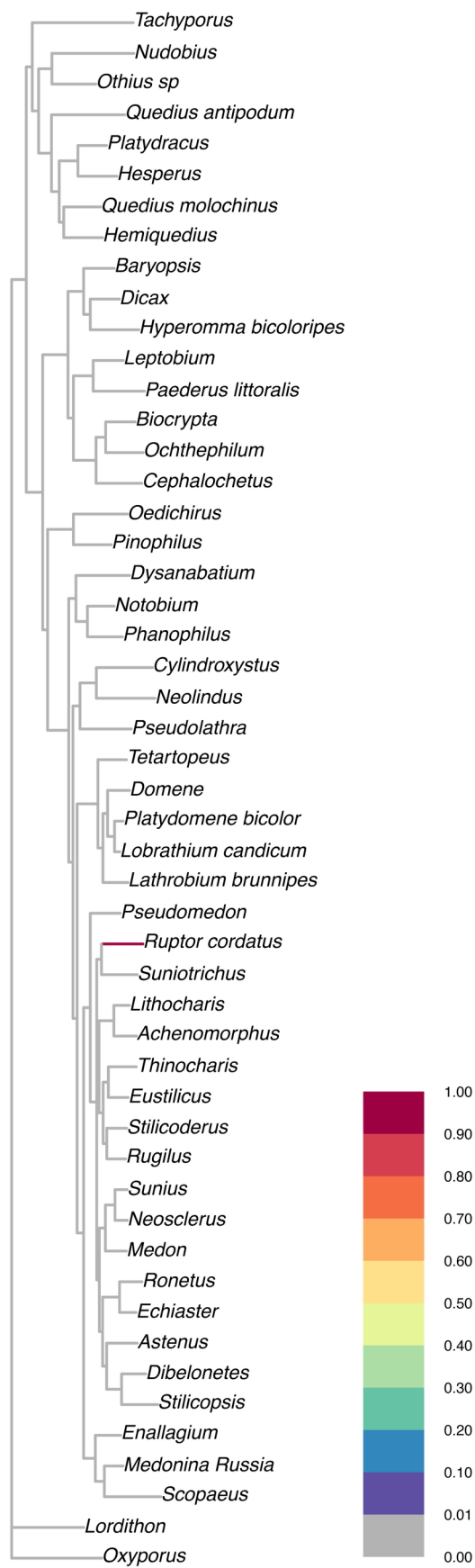


FIGURE 6. RoguePlots showing support for the placement of the *Ecitonides constanceae* **sp. nov.** Colour key represents the percentage of trees that *Ecitonides constanceae* was sister to a particular taxon.

using Tracer v1.7.2 (Rambaut *et al.* 2018). The 50% majority rule consensus tree with posterior probabilities at the respective nodes is shown in Fig. 5. Overall topology is the same as in Żyła *et al.* (2022), however the most notable difference is a change in the position of *Ruptor cordatus*. In Żyła *et al.* (2022) *Ruptor cordatus* was recovered in a rather isolated position, however in our analysis (Fig. 5) it is recovered sister to *Ecitonides* with strong support (PP = 1). The analysis of the posterior sample of trees using RoguePlots (Klopfstein & Spasojević 2019) shows that the highest probability (99%) was for *Ecitonides constanceae* to be sister to *Ruptor cordatus* (Fig. 6).

Discussion

With the description here of *Ecitonides constanceae* **sp. nov.**, the genus now contains nine described species occurring across five South American countries. The country with the greatest species richness of *Ecitonides* species is Brazil with five species, followed by Argentina with two species and Peru, now with two species. Species of *Ecitonides* are known from four army ant host species (Table 1). Unfortunately host data is not available for *E. volans*, *E. constanceae* and *E. soesilae* but it is notable that both *E. volans* and *E. constanceae* were collected at light.

TABLE 1. Updated checklist of the species of *Ecitonides* (based on Assing, 2012).

Species	Distribution also see Fig. 4	Host
<i>brevicornis</i> Wasmann, 1900	Brazil	<i>Labidus praedator</i> (Smith, 1858)
<i>constanceae</i> sp. nov.	Peru	unknown
<i>fraterculus</i> Borgmeier, 1959	Brazil	<i>Labidus praedator</i> (Smith, 1858)
<i>longiceps</i> Wasmann, 1900	Brazil	<i>Labidus coecus</i> (Latreille, 1802)
<i>spectabilis</i> Borgmeier, 1932	Brazil	<i>Nomamyrmex esenbeckii crassicornis</i> (Smith, 1855) <i>Nomamyrmex hartigii</i> (Westwood, 1842)
<i>tuberculosis</i> Wasmann, 1894 = <i>fiebrigi</i> Wasmann, 1909	Brazil, Argentina, Paraguay	<i>Eciton quadriglume</i> (Haliday, 1836) record in Wasmann 1894: 212 <i>Labidus praedator</i> (Smith, 1858)
<i>verrucosus</i> Bruch, 1933	Argentina	<i>Labidus coecus</i> (Latreille, 1802)
<i>volans</i> Assing, 2012	Peru	unknown
<i>soesilae</i> Makhan, 2021	Suriname	unknown

Assing (2012) reported the personal communication of Alfred Newton who suggested that *Ecitonides* may be closely related to the genus *Echiaster* of the subtribe Echiasterina (tribe Lathrobiini), however Assing (2012) expressed doubts about this based the morphology of the mouthparts, the antennae, and the male sexual characters. Assing (2012) instead suggested that *Ecitonides* may in fact belong to the subtribe Cryptobiina (tribe Paederini). Even though we were only able to include two genes from *Ecitonides* in the phylogenetic analysis, its placement within the ‘Medonina and allied taxa’ clade of the tribe Lathrobiini is well supported using Bayesian phylogenetic inference of molecular data (Fig. 5) and within the posterior sample of trees produced in the same analysis based on RoguePlots (Fig. 6). Like other members of this clade, *Ecitonides* has small and acicular apical maxillary palpomere and the presence of apical ctenidium on the one side of metatibia only. The recovery of *Ecitonides* and *Ruptor* as sister genera is in some ways surprising. Their external morphology and host preferences are extremely different, with *Ecitonides* associated with army ants (Hymenoptera: Formicidae) (Table 1) and *Ruptor* associated with *Labiotermes labralis* (Holmgren, 1906) (Blatodea: Termitidae) (Żyła *et al.* 2022).

Unfortunately, we were unable to successfully amplify any other ‘house-keeping’ genes commonly used in Paederinae and Staphylininae molecular phylogenetics. This was likely due to poor preservation of the specimen, which was collected in 70% ethanol and kept at room temperature for some time. Despite this, the results of our phylogenetic analysis including exploring the target taxon as a potential ‘rogue’ due to missing data, clearly provide a reliable insight into its phylogenetic placement. With the recent discovery of *Ruptor* (Żyła *et al.* 2022), it is very likely that undiscovered lineages of termitophilous and myrmecophilous Paederinae exist in the Neotropical region. We hope our contribution here will stimulate further taxonomic and evolutionary work on these poorly known beetle groups.

Acknowledgments

Thanks to Don Stenhouse for providing some relevant literature. MRM acknowledges the Latin American Doctoral Fellowship granted by the National Scientific and Technical Research Council of Argentina (CONICET). Thanks to David Wilcockson, Aberystwyth University, the Amazon Conservation Association and the staff of the Los Amigos Biological Station. Thanks to Karen Siu Ting for help with the permits.

References

- Asenjo, A., Irmeler, U., Klimaszewski, J., Chandler, D.S., Fierros-López, H.E. & Vieira, J.S. (2019) Staphylinidae (Insecta: Coleoptera) in Latin America: synopsis, annotated catalog, diversity and distribution. *Zootaxa*, 4621 (1), 1–406.
<https://doi.org/10.11646/zootaxa.4621.1.1>
- Assing, V. (2012) A new species of the myrmecophilous genus *Ecitonides* from Peru (Coleoptera: Staphylinidae: Paederinae). *Linzer Biologische Beiträge*, 44, 401–408.
- Blackwelder, R.E. (1944) Checklist of the Coleopterous Insects of Mexico, Central America The West Indies, and South America. Part 1. *Bulletin of the United States National Museum*, 185, i–xii + 1–188.
<https://doi.org/10.5479/si.03629236.185.i>
- Borgmeier, T. (1932) Dois novos coleópteros ecitófilos do Brasil (Staphylinidae). *Revista de Entomologia*, 2, 397–401.
- Borgmeier, T. (1959) Notá previa sôbre alguns coleópteros ecitófilos da família Staphylinidae. *Boletim do Museu Nacional nova série Zoologia*, 214, 1–15.
- Bruch, C. (1933) Coleópteros mirmecófilos de Misiones (Staph. Pselaph. Hister.). *Revista de Entomologia*, 3, 12–37.
- Klopfstein, S. & Spasojevic, T. (2019) Illustrating phylogenetic placement of fossils using RoguePlots: An example from ichneumonid parasitoid wasps (Hymenoptera, Ichneumonidae) and an extensive morphological matrix. *PLoS One*, 14 (4), e0212942.
<https://doi.org/10.1371/journal.pone.0212942>
- Makhan, D. (2021) *Ecitonides soesilae* sp. nov. a new myrmecophilous species of Suriname (Coleoptera: Staphylinidae: Paederinae). *University of Sindh Journal of Animal Sciences*, 5, 21–25.
- Rambaut A., Drummond A.J., Xie, D., Baele G. & Suchard M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67, 901–904.
<https://doi.org/10.1093/sysbio/syy032>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from: <https://www.R-project.org/> (accessed 4 September 2023)
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Seevers, C.H. (1965) The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). *Fieldiana: Zoology*, 47, 139–351.
<https://doi.org/10.5962/bhl.title.3063>
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675.
<https://doi.org/10.1038/nmeth.2089>
- Wasmann, E. (1894) *Kritisches Verzeichniss der myrmekophilen und termitophilen Arthropoden. Mit Angabe der Lebensweise und mit Beschreibung neuer Arten*. Felix L. Dames, Berlin, xiii + 231 pp.
<https://doi.org/10.5962/bhl.title.122977>
- Wasmann, E. (1900) Neue Dorylinengäste aus dem neotropischen und dem äthiopischen Faunengebiet (114. Beiträge zur Kenntnis der Myrmekophilen und Termitophilen). *Zoologische Jahrbücher*, Abteilung für Systematik, Geographie und Biologie der Tiere, 14, 215–289.
<https://doi.org/10.5962/bhl.part.11529>
- Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, New York. ISBN 978-3-319-24277-4. Available from: <https://ggplot2.tidyverse.org> (accessed 4 September 2023)
- Żyła, D., Bogri, A., Hansen, A.K., Jenkins Shaw, J., Kypke, J. & Solodovnikov, A. (2022) A New Termitophilous Genus of Paederinae Rove Beetles (Coleoptera, Staphylinidae) from the Neotropics and Its Phylogenetic Position. *Neotropical Entomology*, 51, 282–291.
<https://doi.org/10.1007/s13744-022-00946-x>