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ORIGINAL RESEARCH ARTICLE

Revision of mimallonid hosts (Lepidoptera: Mimallonidae) of tachinid flies (Diptera: Tachinidae), including a new host record in the Amazon rainforest

Filipe Macedo Gudin[1] · **Paulo Pacheco Junior**[2]

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Abstract

Mimallonid moths, also known as sack-bearer moths, are a small family of Lepidoptera restricted to the New World. Although there have been recent improvements and clarifications in the taxonomy of Mimallonidae species, little is known about their life history and the parasitoids associated with them. Here, we record for the first time the mimallonid species *Psychocampa concolor* Grote and Robinson as the host of the tachinid *Archytas araujoi* Guimarães, in the Amazon rainforest of Macapá, state of Amapá, Brazil. The taxonomy of *A. araujoi* is discussed and notes and illustrations of the immature stages and adults of *P. concolor* are provided. Additionally, we present a revision of mimallonid hosts of Tachinidae in an annotated host catalog, including an overview of the host use and oviposition strategies of their respective parasitoids.

Keywords *Archytas* · Concealed feeding · Neotropical Region · Oviposition strategy · Parasitoid flies · *Psychocampa*

Introduction

Mimallonidae is a small family of New World moths (Lepidoptera), including about 300 species in 41 genera, most of them in the Neotropical Region (St Laurent and Kawahara 2019). Also known as sack-bearer moths, late-instar larvae of Mimallonidae build portable sack-shaped shelters using silk, leaves and frass (St Laurent et al. 2018), and have a well-developed and rugose anal plate on abdominal segment 10, which is used to close the posterior opening of the shelter (St Laurent et al. 2018). The larvae of Mimallonidae typically consume various plants belonging to the order Myrtales (Robinson et al. 2023), and certain species can act as primary or secondary pests in cultivated environments. For example, *Mimallo amilia* (Cramer) has been observed as a pest in *Eucalyptus urophylla* S. T. Blake (Timor white gum), *Myrciaria dubia* (Kunth) McVaugh (camu-camu) and *Psidium guajava* Linnaeus (guava) (Zanuncio et al. 2005). Similarly, *Psychocampa callipius* (Schaus) has been reported as a pest in *Anacardium occidentale* Linnaeus (cashew tree) (Mesquita et al. 2009).

Records of parasitoids in Mimallonidae species are scarce in the literature. Regarding parasitic wasps (Hymenoptera), Janzen and Hallwachs (2009) listed only a few records of parasitism by species of Braconidae and Ichneumonidae in Costa Rica. Aside from these findings, there are no other documented records of parasitic wasps parasitizing Mimallonidae (Noyes 2019). In comparison, tachinid flies (Diptera: Tachinidae) have been more commonly recorded in Mimallonidae, including in economically important species such as *M. amilia* (Guimarães 1977; Arnaud 1978). However, the identification of tachinid species presents significant challenges, especially in the Neotropical Region. This difficulty arises mainly from the absence of identification keys for most tachinid groups and the fact that numerous species are classified in monotypic genera, necessitating comprehensive revision efforts (O'Hara 2013).

Here, we record a new mimallonid host of Tachinidae in the Amazon rainforest: *Psychocampa concolor* Grote and Robinson parasitized by *Archytas araujoi* Guimarães, in Macapá, state of Amapá, Brazil. Illustrations and notes on the immature stages and adults of *P. concolor* are provided, including a comparative diagnosis of *A. araujoi*.

✉ Filipe Macedo Gudin
filipe.gudin@gmail.com

[1] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

[2] Universidade do Estado do Amapá, Macapá, AP, Brazil

Additionally, we provide a revision of mimallonid hosts of tachinid flies in an annotated host catalog, including an overview of the host use and oviposition strategies of their respective parasitoids.

Materials and methods

On 13 February 2020 and 2 April 2021, fourth and fifth instar larvae of *P. concolor* were collected from two embaúba plants, *Cecropia peltate* Linnaeus (Rosales: Urticaceae) (Fig. 1), in Quilombo Lagoa dos Índios, located approximately 8 km from the center of Macapá, state of Amapá, Brazil. The larvae were reared in two plastic boxes (42 × 33 × 28 cm) covered with organza fabric (38 × 52 cm) and fed *ad libitum* with whole leaves of *C. peltate* for one month until the emergence of adults. Some larvae of *P. concolor*, however, had already been parasitized by *A. araujoi* in the field. Photographs of live specimens were taken with a Canon Digital Dslr Eos Rebel T3i camera and a Canon EF 100 mm 1:2.8 macro lens aided by macro twin lite MT-24EX Canon flash, which were stacked with Helicon Focus 6.7.1, edited in Adobe Lightroom Classic 11.5 and Adobe Photoshop 23.3. A sample of adult specimens of *P. concolor* and *A. araujoi* were pinned and deposited in the collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). Specimens of *Psychocampa* were identified by Dr. Ryan St Laurent at the National Museum of Natural History (USNM).

We identified the specimens of *A. araujoi* using keys to the Nearctic and Neotropical species of *Archytas* (Curran 1928; Guimarães 1963a; Ravlin and Stehr 1984), and verified the original descriptions of Brazilian *Archytas* described by Guimarães (1960, 1961a, b, 1963a, b). Photographs of pinned specimens were taken with a Leica MC170 HD digital camera attached to a Leica MZ16 stereomicroscope

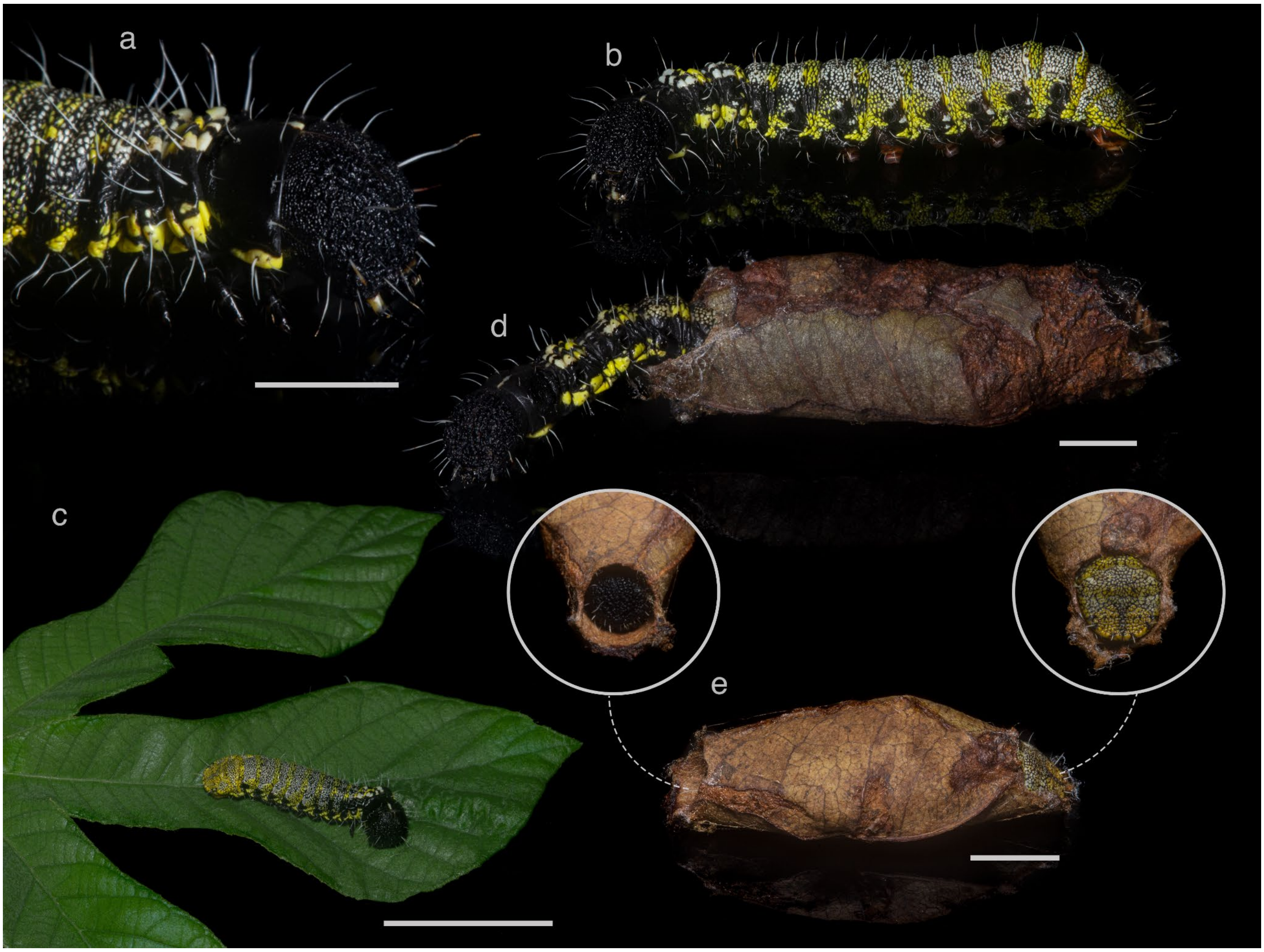


Fig. 1 Immature stages of *Psychocampa concolor* Grote and Robinson. (**a**) Fourth instar, head and thorax in lateral view; (**b**) Fourth instar; lateral habitus; (**c**) Fourth instar, larva on leaf of *Cecropia peltate* Linnaeus; (**d**) Fifth instar; lateral habitus showing the sack-shaped shelter; (**e**) Fifth instar, larva inside its shelter with details of head and anal plate closing the two shelter openings. Scale bars: 0.5 mm (**a**, **b**, **d**) and 1 mm (**c**, **e**)

using the software Leica Application Suite version 4.12.0, stacked with Helicon Focus 6.7.1 and edited in Gimp 2.10. The morphological terminology follows that of Cumming and Wood (2017).

The host catalog follows an adapted format presented by Guimarães (1977) and Arnaud (1978). Species are listed alphabetically according to their respective biogeographical regions with valid names accompanied by authorship. Species names of mimallonid hosts are followed by author, year of publication, page number, locality, respective tachinid parasitoid, and notes on the record. When necessary, we included comments and emendations regarding taxonomic nomenclature and reliability of the record in square brackets. To update the host catalog, only published records were considered, excluding dissertations and theses. The original literature was checked to ensure the accuracy of the dates, titles, pagination, names, and localities. The classification of Tachinidae follows O'Hara et al. (2020), and the classification of Mimallonidae follows Laurent and Kawahara (2019).

Results

Record of *Archytas araujoi* in *Psychocampa concolor*

To observe and photograph the life cycle of *P. concolor*, we collected 83 *P. concolor* larvae during the rainy season of the Amazon rainforest in Macapá (December to July): 33 specimens in 2020 and 50 specimens in 2021. Of the total number of collected larvae, 39 were in the fourth instar, without having built shelters (Fig. 1a–c), and 44 were in the fifth instar, with shelters (Fig. 1d–e). The larvae actively fed on the leaves of *C. peltate*, a new host plant record for Mimallonidae (Fig. 1c). Of the 83 larvae, 36 reached the pupal stage 28–31 days after the date of collection (Fig. 2a). Twenty-three adults emerged after 12–13 days (Fig. 2b–c). Some adults copulated after emergence, and the females deposited a row of rectangular yellowish eggs (Fig. 2d). Two males and six females were preserved and pinned.

About 19 days after the caterpillars had pupated, 13 adults of *A. araujoi* (Figs. 3 and 4) emerged directly from the pupae of *P. concolor*: five in 2020 and eight in 2021. We observed that the cuticle of the parasitized pupae of *P. concolor* became fragile and brittle. After opening some of them, a single puparium of *A. araujoi* was found in each pupa (Fig. 3c). Three females (Fig. 3a, b) and one male (Fig. 4) of *A. araujoi* were preserved and pinned.

Notes on characters and distribution of *Psychocampa concolor*

Fourth instar larvae of *P. concolor* (Fig. 1a–b) have cephalic capsule black, pronotum black with a single yellow stripe on lateral margins, mesonotum and metanotum with large laterodorsal black vittae and large white spots on the dorsal surface, spiracles black, legs black, abdominal segments with yellow ground color marked with black network pattern and dorsal bands with white markings, prolegs brownish, and body covered with long and sparse white setae. Fifth instar larvae of *P. concolor* are very similar in shape and color and keep their posterior half hidden inside their shelters (Fig. 1d); however, they differ from fourth instar larvae by having a longer black vittae in the laterodorsal surface of the body, extending to the abdominal segments. When the larva protects itself inside the shelter, the shelter openings are completely sealed by the head and the anal plate (Fig. 1e). The larvae built their shelters by aggregating vegetable fibers of *C. peltate* and frass, using silk to integrate all the elements of the shelter; the caterpillars pupated inside their shelters, forming reddish brown pupae with well-sclerotized extremities that closed both openings of the shelter (Fig. 2a).

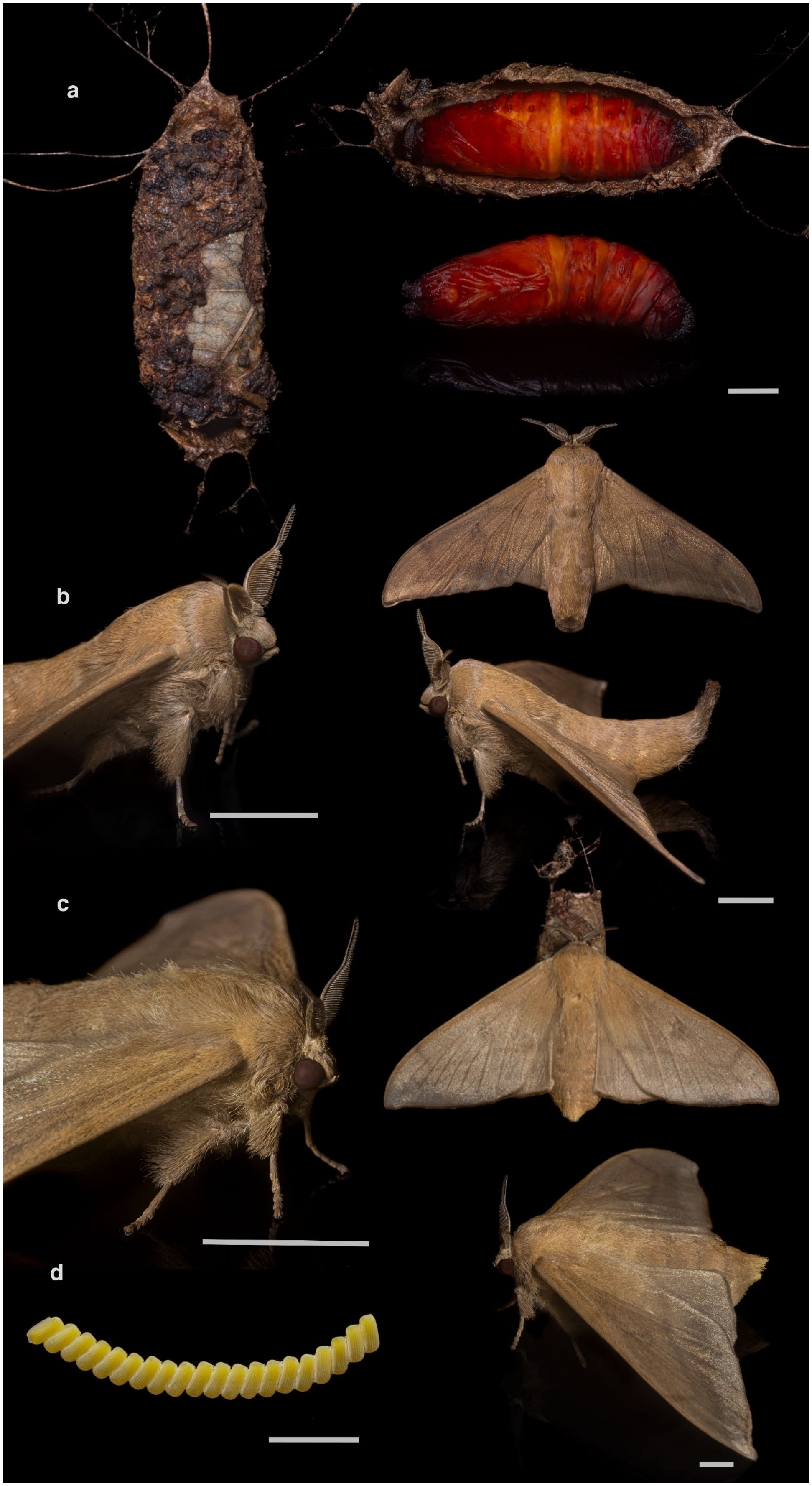
Adults of *P. concolor* have uniform coloration, without clear maculation on their wings. Males are smaller and darker than females, having body and wings dark brown, forewings narrow and elongate with distal margin straight, and apex of abdomen with an erect tuft of scales covering the genitalia (Fig. 2b). Females have body and wings grayish light brown, forewings wide and slightly falcate, with rounded distal margin (Fig. 2c). Additional characters of the male and female genitalia of *P. concolor* can be verified in St Laurent and Kawahara (2019: 78, 85).

The holotype male of *P. concolor* was described from the state of Pará, Brazil (St Laurent and Kawahara 2019), and this species was also recorded in the state of Maranhão (Herbin and Mielke 2014). This is the first record of *P. concolor* in the state of Amapá, suggesting that this species is distributed in the northern part of the Amazon rainforest.

Diagnosis and distribution of *Archytas araujoi*

Specimens of *A. araujoi* can be distinguished from the remaining *Archytas* species by having a first aristomere long and subequal to the length of the second aristomere, parafacial covered with black setulae, head and anterior part of thorax with yellow pruinosity, scutum with four narrow vittae, pleural thoracic sclerites covered with black setulae, tegula and basicosta brownish-yellow, wings slightly infuscate, calypteres dark brown, legs black, and abdomen entirely shining black or dark brown bearing a pair of

Fig. 2 Pupa and adults of *Psychocampa concolor* Grote and Robinson. (**a**) Pupa, inside and outside the shelter; (**b**) Male, lateral and dorsal habiti; (**c**) Female, lateral and dorsal habiti; (**d**) Eggs. Scale bars: 0.5 mm



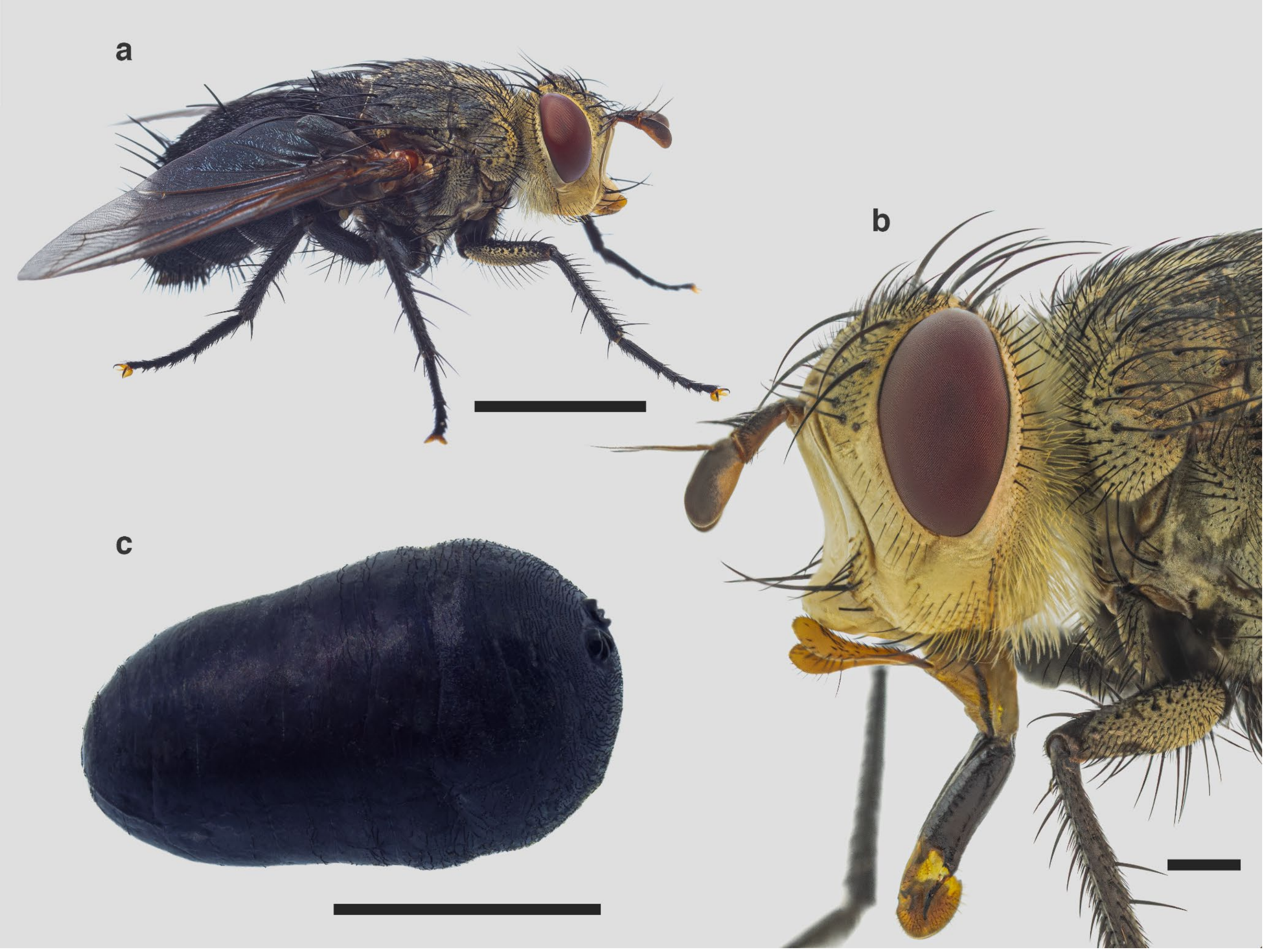


Fig. 3 Adult female and puparium of *Archytas araujoi* Guimarães. (**a**) Female, lateral habitus; (**b**) Female, head in lateral view; (**c**) Puparium in lateral view. Scale bars: 1 mm (**b**) and 5 mm (**a**, **c**)

marginal setae on tergite 3 (Figs. 3 and 4). Males differ from females in that they lack proclinate orbital setae, and show first flagellomere with anterior margin convex and syncercus concave with apex long and obtuse (Fig. 4). A comprehensive comparison of the main characters of the related *Archytas* species is provided in the Discussion section.

Archytas araujoi was described from the state of Pará (Guimarães 1963b). This is the first record of this species in the state of Amapá, suggesting that it may have a distribution similar to that of *P. concolor*. However, better knowledge on the distribution of both species is required to confirm this statement.

Annotated catalog of mimallonid hosts of Tachinidae

Currently, there are at least eleven Tachinidae species within seven genera in the New World recorded as parasitoids of at least seven species of Mimallonidae (Table 1). In some records, the host species are classified as Lacosomidae, a previous classification of mimallonid species. Based on the literature records, only late-instar caterpillars of Mimallonidae are attacked by these species of tachinids, which emerge in the fifth instar or pupa. An annotated host catalog of mimallonid hosts of Tachinidae is provided below.

Nearctic region

Cicinnus melsheimeri (Harris)

Schaffner and Griswold (1934: 102, 111, record from Manchester, Hartford County, Connecticut, United States of America, parasitoid as *Chrysotachina alcedo* (Loew)).

St Laurent et al. (2017: 181, record from Tompkins County, New York, United States of America, parasitoid as unidentified Tachinidae).

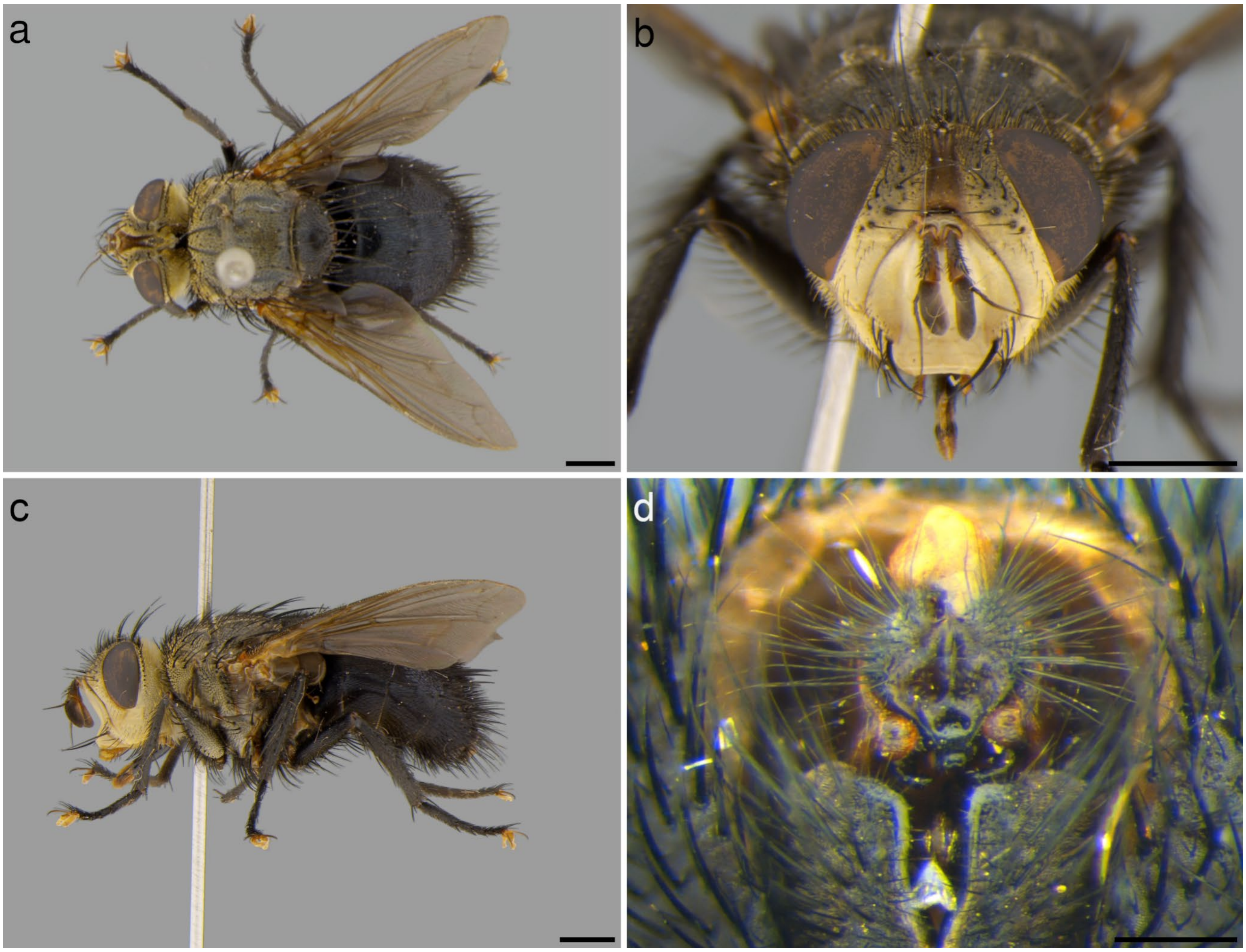


Fig. 4 Adult male of *Archytas araujoi* Guimarães. (**a**) Dorsal habitus; (**b**) Head in frontal view; (**c**) Lateral habitus; (**d**) Detail of syncercus and surstyli. Scale bars: 0.5 mm (**d**) and 2 mm (**a**–**c**)

Table 1 List of mimallonid hosts and their respective tachinid parasitoids according to biogeographical region. Tachinidae species with question marks refer to unreliable records as discussed in the host catalog. Details about the records, localities, and respective references can be found in the host catalog in the main text

Mimallonid hosts	Tachinidae species
Nearctic Region	
Cicinnus melsheimeri	*Chrysotachina alcedo*
Lacosoma arizonicum	*Lespesia* sp.
Neotropical Region	
Cicinnus packardii	*Belvosia leucopyga* *Belvosia weyenberghiana*
Lacosoma maldera	*Houghia romeroae*
Mimallo amilia	*Houghia* sp. *Houghia tropica* (?) *Nepocarcelia* sp. (?)
Mimallo sp.	*Houghia punctiger*
Psychocampa concolor	*Archytas araujoi*
Trogoptera salvita	*Houghia blancoi*
Unidentified species	*Chrysotachina* sp. *Hyphantrophaga virilis* *Sphaerina* sp.

Lacosoma arizonicum Dyar

St Laurent et al. (2017: 181, record from Arizona, United States of America [Cochise County or Pima County, origin not specified], parasitoid as unidentified *Lespesia* Robineau-Desvoidy).

Neotropical region

Cicinnus packardii (Grote)

Lima (1936: 280, record from Brazil (Rio de Janeiro, Rio Grande do Sul or São Paulo, origin not specified), parasitoid as *Belvosia leucopyga* Wulp).

Lima (1948: 24 [inaccurate reference in (Guimarães 1977)], record from Brazil [origin not specified], as *Perophora packardi* [misspelling], parasitoid as *Belvosiopsis weyenberghiana* Wulp [=*Belvosia weyenberghiana*]).

Lacosoma maldera Schaus

Fleming et al. (2014: 81, record from Area de Conservación Guanacaste, Guanacaste, Costa Rica, parasitoid as *Houghia romeroae* Fleming and Wood).

Mimallo amilia (Cramer)

Lima (1950: 247, record from Brazil [origin not specified], parasitoid as unidentified Tachinidae, probably *Tapajohougia* [misspelling, *Tapajohoughia* Townsend (=*Houghia* Coquillett)]).

Gonçalves and Gonçalves (1973: 12, record from Rio de Janeiro, Rio de Janeiro, Brazil, parasitoid as unidentified *Nepocarcelia* Townsend [**Note**: this Neotropical genus includes only two species, which have not been studied since their descriptions. Townsend (1936), however, compared *Nepocarcelia* to *Macrohoughia* Townsend, junior synonym of *Houghia* Coquillett. Therefore, it is probable that this record is based on misidentified specimens that actually belong to *Houghia*]).

Guimarães (1977: 76, repetition of record from Lima (1950), parasitoid as *Tapajohoughia tropica* Townsend [=*Houghia tropica*. **Note**: As *Tapajohoughia tropica* is the sole species of the genus, Guimarães probably assumed that the record from Lima (1950) referred to this species. However, there is no evidence that the original record referred to this particular species; thus identification is unreliable]).

Mimallo sp.

Guimarães (1977: 68, record from São Paulo, Brazil, parasitoid as *Petrargyrops punctiger* Townsend [=*Houghia punctiger*]).

Psychocampa concolor Grote and Robinson

Gudin and Pacheco-Junior, present record from Macapá, Amapá, Brazil, parasitoid as *Archytas araujoi* Guimarães.

Trogoptera salvita Schaus

Fleming et al. (2014: 40, record from Area de Conservación Guanacaste, Guanacaste, Costa Rica, parasitoid as *Houghia blancoi* Fleming and Wood).

Unidentified Mimallonidae

Stireman et al. (2017: 15 [see Supporting Information within citation, table S2], record from Yanayacu Biological Station & Center for Creative Studies, Quijos Valley, Napo, Ecuador, parasitoids as unidentified *Chrysotachina* Brauer and Bergenstamm and *Sphaerina* Wulp).

Fleming et al. (2019: 273, record from Area de Conservación Guanacaste, Guanacaste, Costa Rica, parasitoid as *Hyphantrophaga virilis* (Aldrich and Webber)).

Discussion

Considerations on the biology of *Psychocampa concolor* and *Archytas araujoi*

The fact that caterpillars of *P. concolor* feed on *C. peltate* confirms the patterns found by St Laurent et al. (2021), who showed that members of the tribe Psychocampini are mostly associated with non-Myrtales host plants. Species of *Psychocampa* Grote and Robinson are usually recorded in Malpighiales and Sapindales (St Laurent et al. 2021), whereas this is the first time that a species of this genus has been recorded in Rosales. Although we did not observe the behavior of *A. araujoi*, it is known that *Archytas* females lay incubated membranous eggs with well-developed first instar larvae on the buds, leaves, and stems of the host's food plant (Allen 1926; Hughes 1975). The larvae then wait for the host to pass through and attach themselves to the host's body. Therefore, it is highly probable that *A. araujoi* uses the same oviposition strategy when attacking the larvae of *P. concolor*.

Taxonomy of *Archytas araujoi* and related species

Archytas Jaennicke is the largest genus of New World Tachinini, including 99 valid species (O'Hara et al. 2020). The taxonomy of *Archytas* species is complex and challenging, because adults are very similar in external features and most diagnostic characters are based on details of the male terminalia (Guimarães 1960, 1961a, b, 1963a, b). The genus is classified in two subgenera: *Archytas* and *Nemochaeta* Wulp (Ravlin and Stehr 1984; O'Hara and Wood 2004). However, most Neotropical species are not currently assigned to any subgenus. The specimens of *Archytas* reared from *P. concolor* fit the description of the subgenus *Nemochaeta* provided by Ravlin and Stehr (1984), with the first aristomere long and subequal to the length of the second aristomere and the parafacial covered with black setulae (Figs. 3b and 4b).

In the key to the Nearctic *Archytas* (Ravlin and Stehr 1984), our specimens run to *A.* (*Nemochaeta*) *metallicus* (Robineau-Desvoidy), which is the single Nearctic species of *Archytas* with calypteres dark brown. In the key to *Archytas* species of Curran (1928), they run to Curran's inaccurate concept of *A. pilosa* Drury, which actually refers to *A.* (*Nemochaeta*) *metallicus* (Sabrosky and Arnaud 1965; O'Hara and Wood 2004), having calypteres dark brown and proepisternum covered with black setulae. Thompson (1963) also provided a key to the *Archytas* species of Trinidad, but the characters used in the couplets did not fit our specimens. Guimarães (1963a) revised the Neotropical species of *Archytas* of the "*dissimilis* group", i.e., species that share similar characters with *A.* (*Nemochaeta*) *dissimilis* (Wulp), type species of the subgenus *Nemochaeta*; in his key, the specimens run to *A. goncalvesi* Guimarães due to the shape of the apex of male syncercus. *Archytas goncalvesi*, however, have calypteres white and males with an abdomen brownish-yellow laterally and a dorsal black vitta.

Later, Guimarães (1963b) described two species of *Archytas* from the Amazon rainforest of the state of Pará, Brazil, that fit the description of the subgenus *Nemochaeta*: *A. araujoi* and *A. pearsoni* Guimarães. Our specimens share the same characters of *A. araujoi*, including the shape of the apex of the male syncercus (Fig. 4d). Guimarães, however, adopted a very restricted concept of species delimitation based mainly on slight differences in the shape of the male syncercus and surstyli. Therefore, our specimens also share some characters present in the description of *A. pearsoni*, such as the first flagellomere of males with anterior margin convex and head with a more marked yellow pruinosity (Fig. 4b–c); males of this species, however, have a syncercus with apex short and blunt. Adopting a wider variance of intraspecific characters, our series of specimens suggests that both species may be synonymous. However, this question cannot be solved at the moment, pending revision of the type material and taxonomy of Neotropical species of *Archytas*.

Oviposition strategies of tachinids parasitoids of Mimallonidae

There are at least three oviposition strategies in tachinids parasitoids of Mimallonidae: indirect oviposition with ovoviviparous species that lay incubated membranous eggs with well-developed first instar larvae on the host's path (e.g., in *Archytas* and *Chrysotachina* Brauer and Bergenstamm) (Allen 1926; Nunez and Couri 2002); direct oviposition with oviparous species that lay incubated membranous eggs directly on the host's cuticle (e.g., in *Lespesia* Robineau-Desvoidy) (Etchegaray and Nishida 1975; Cardoza et al. 1997); and indirect oviposition with oviparous species that lay incubated microtype eggs on the leaves of the host plant, which are subsequently ingested by the host (e.g., in *Belvosia* Robineau-Desvoidy, *Houghia* Coquillett and *Hyphantrophaga* Townsend) (Aldrich 1928; Fleming et al. 2014, 2019). The oviposition strategy of *Sphaerina* species remains unknown (Wood 1985).

St Laurent et al. (2017) raised an interesting question regarding the possibility of having tachinids specialized on lepidopteran hosts that show concealed feeding habits, such as Mimallonidae. When studying the trophic dynamics of a tropical tachinid-caterpillar community, Stireman et al. (2017) observed that concealed feeding caterpillars experienced fewer attacks from tachinids in comparison to more exposed hosts. However, tachinids that were reared from concealed feeding caterpillars were more likely to exhibit indirect oviposition strategies. The records described in the host catalog above confirm this pattern, as most Tachinidae species that parasitize Mimallonidae show indirect oviposition strategies as well.

However, it is not possible to trace any species or genus exclusively adapted to exploit only mimallonid hosts. *Archytas* species are also parasitoids of several species in the families Erebidae, Geometridae, Lasiocampidae, Megalopygidae, Noctuidae, Notodontidae, and Psychidae (Guimarães 1977; Arnaud 1978). *Belvosia* species have been frequently reared from Saturniidae, but also attack species of Erebidae, Hesperiidae, Limacodidae, Megalopygidae, Noctuidae, Notodontidae, Nymphalidae, and Sphingidae (Guimarães 1977; Arnaud 1978; Silva et al. 2023). *Chrysotachina* species also attack Hesperiidae (O'Hara 2002). *Houghia* species have been frequently reared from Hesperiidae, but also attack species of Dalceridae, Elachistidae, Erebidae, Geometridae, Noctuidae, Notodontidae, Nymphalidae, Riodinidae, Saturniidae, and Sphingidae (Guimarães 1977; Fleming et al. 2014). *Hyphantrophaga* species have been reared from at least 29 families of Lepidoptera

(Arnaud 1978; Fleming et al. 2019). *Lespesia* species also parasitize a wide range of hosts including the orders Coleoptera, Lepidoptera and Hymenoptera (Guimarães 1977; Arnaud 1978; Ordaz-Silva et al. 2013). Lastly, *Sphaerina* species have been reared mostly from Crambidae and Hesperiidae, but also from Notodontidae (Wood and Zumbado 2010).

Such host diversity within each genus, particularly among those that include species employing indirect oviposition strategies, aligns with hypotheses proposing that most tachinids may not necessarily be generalists but can instead have broad host ranges (Eggleton and Gaston 1992; Stireman et al. 2017). However, recent efforts relying on molecular markers to delimit species and clarify tachinid-host associations have suggested that the apparent host diversity within Tachinidae species may be misleading, due to the existence of numerous cryptic species (Smith et al. 2007; Fleming et al. 2014, 2019).

Conclusions

Archytas araujoi is the first species of the genus recorded in Mimallonidae. The distribution of both species, *A. araujoi* and *P. concolor*, was extended to the northern part of the Amazon rainforest, and the immature stages of *P. concolor* were recorded here for the first time. Although parasitism records in Mimallonidae by tachinids are scarce, mimallonid moths are attacked by at least eleven species of Tachinidae, most of them exhibiting indirect oviposition strategies that are suitable to exploit concealed feeding hosts.

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Author contributions FMG identified the parasitoid species, described and discussed the taxonomy of the specimens, and wrote the first draft. PPJ collected the data, photographed the specimens, and edited the images. Both authors contributed to the conception and design of the study, and approved the final manuscript.

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Declarations

Competing interests The authors declare no conflict of interest.

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