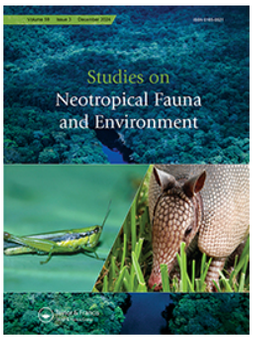

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ORIGINAL ARTICLE

Contribution to the knowledge of the nesting biology of Eumenine wasps (Hymenoptera, Vespidae) in the Brazilian Amazonia

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ABSTRACT

Several recent studies have improved our knowledge on the biodiversity and evolution of Eumeninae wasps, yet many groups lack systematic reviews, and there are still many gaps regarding the nesting biology, with the rather fragmentary information dispersed in the literature. Eumeninae are solitary wasps and important predatory insects regulating arthropod populations and exhibiting remarkable nest-building behaviors. Nesting strategies include using preexisting cavities, making clay pots, or other exposed structures built with plant material, sometimes incorporating chewed leaves, cellulose pulp, or plant resins. Understanding the nesting biology of Eumeninae is important for elucidating the origins of group living and eusociality, as these species range from solitary to primitively social. However, there is a scarcity of information on behavior and nest architecture, hindering a comprehensive understanding of these subjects. In this study, we describe and illustrate for the first time the nest of *Monobia funebris* Gribodo, 1891 (Odynerini), the nest of *Eumenes versicolor* de Saussure, 1852 (Eumenini), and provide additional information on the nesting of *Pachymenes ghilianii* (Spinosa, 1851) (Eumenini) from nests collected in the Brazilian Amazonia. Our observations reveal new facts about nest architecture in Eumeninae and highlight the need for additional efforts to elucidate aspects of the nesting behavior of *M. funebris* and the continued presence of female *P. ghilianii* in the nest after its completion.

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Eumeninae; nests; solitary wasp

Introduction

In recent years there have been contributions to knowledge on the biodiversity and evolution of Eumeninae (Hermes et al. 2014; Grandinete et al. 2015). However, many eumenine groups lack modern systematic reviews and knowledge about nesting biology remains fragmented (Hermes et al. 2015; Abrego et al. 2018).

Eumeninae is an important group among solitary wasps due to their predatory habits, acting as regulators of other arthropod populations (Brock et al. 2021) and the variety of nests building methods of remarkable behavioral complexity (Grandinete et al. 2015). Species may nest in preexisting cavities, clay pots or in exposed structures built with plant material (Hermes et al. 2014) where they may use chewed leaves (Bohart & Stange 1965; Méndez-Abarca et al. 2012) or, in exceptional cases, cellulose pulp (Iwata 1939), or plant resins (Nugroho et al. 2020).

Monobia Saussure, 1852 currently comprises thirty-five described species (Hermes & Carpenter 2012) distributed from northwestern Argentina to the Caribbean islands and semi-arid regions of Mexico and the United States with some species adapted to extreme climatic conditions. However, little is known about the species' nesting biology. Detailed biological data are only available for *M. quadridens* (L.) and *M. angulosa* Saussure, which constructs a series of up to twelve cells, or uses preexisting cavities in wood or clay banks (Rau 1931; Krombein 1967; Camillo et al. 1997). Data on other species are known but in a fragmented manner (Willink 1982; Camillo et al. 1997). *Monobia funebris* which occurs mainly in the humid regions of Brazil, Peru, Colombia, Suriname, and Trinidad (Willink 1982) is an example of such species for which nothing is known about the nesting biology.

Eumenes Latreille, 1802, currently has more than 100 described species globally distributed among two subgenera: *Eumenes* Latreille and *Zeteumetoides* Giordani Soika, 1972 (Grandinete et al. 2018; Qin et al. 2023). The subgenus *Zeteumetoides* includes the species that have the metasomal tergum 1 very long, more than four times longer than wide: *Eumenes filiformis* (de Saussure, 1855) (type species), *E. rufomaculatus* Fox, 1899 and *E. versicolor* de Saussure, 1852 (Grandinete et al. 2018). *Eumenes*

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versicolor is a species with distribution in Brazil, Colombia, French Guiana, and Peru. In Brazil, the species is known to occur in Pará and Roraima (Grandinete et al. 2018). However, until now, no data on the nest architecture of this species has been published.

Pachymenes de Saussure, 1852, is distributed from Mexico to Argentina, with eighteen described species, fourteen of which are recorded for Brazil (Abrego et al. 2018). Among the species that occur in Brazil, *Pachymenes ghilianii* (Spinola) has a wide distribution in the Neotropics (appendix S1 and S2 of Grandinete et al. 2015). Abrego et al. (2018) present details of the nesting biology of *P. ghilianii*, including the process of building a cell and the moment of emergence of adults, from a nest with four cells, observed in Panama. However, until now, there was no information in the literature about the nesting biology of this species in Brazil.

Information about the nesting biology of eumenine species is of particular interest for elucidating the origins of group living and exploring the mechanisms and selective pressures that have led to eusociality (West-Eberhard 2005). This is so because these species display a range of behaviors, from solitary to primitively social (Hermes et al. 2013). Nonetheless, there is a shortage of records regarding behavior and information related to nest architecture of Eumeninae, leaving many gaps in the understanding of the nesting biology. Observations and records in this field area essential to fill these gaps.

In this study, we describe and illustrate for the first time the nest of *Monobia funebris* Gribodo, 1891 (Odynerini) and the nest of *Eumenes versicolor* de Saussure, 1852 (Eumenini), and then provide additional information on the nesting of *Pachymenes ghilianii* (Spinosa, 1851) (Eumenini) from specimens collected in the Brazilian Amazonia.

Material and methods

All nests described here were collected in active searches for Vespidae nests. Clay nests from which emerged *M. funebris* and the nest of *E. versicolor* were collected on the banks of the 'Tucupi Grande' river, in São Sebastião da Boa Vista, Marajó, Pará (1° 40' 53.5 "S 49° 28' 06.1"W) (Figure 1A). The nest of *M. funebris* consisted of eight cells collected on 24 December 2022, on the roofed deck of an abandoned wooden passenger boat. The nest of *E. versicolor* was collected on

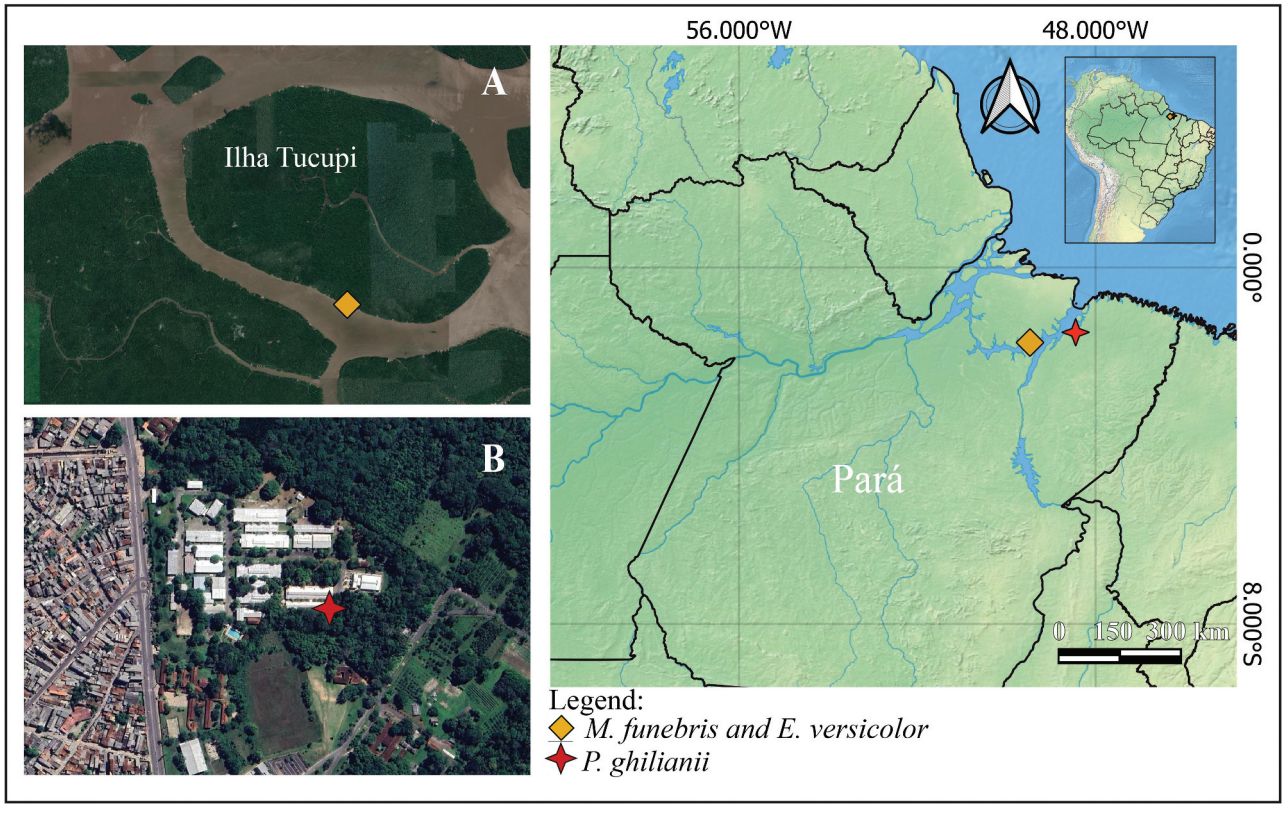

Figure 1. Map and collection locations: A – Google satellite image of the Rio Tucupi Grande, the collection site for *M. funebris* e *E. versicolor*; B – Google satellite image of MPEG Research Campus, Belém, the collection site for *P. ghilianii* (http://eart.google.com).

22 April 2023 and was built in the central vein on the adaxial surface of a dry leaf.

The nest of *Pachymenes ghilianii* was discovered in the late afternoon of 30 May 2023, beneath the roof of one of the buildings closest to the forest on the Campus of Museu Paraense Emílio Goeldi (MPEG) (1° 27'; 06.1" S 48° 26' 38.5" W), Belém, Pará (Figure 1B). The nest was constructed on a deactivated electrical line, situated approximately five meters above the ground. For a duration of 30 minutes, both the nest and the residing female were documented through filming and photography. Collection of the nest and its occupant was conducted only the following morning.

The nests were transported to the laboratory, where they were placed in a transparent plastic pot covered with organza at room temperature, until the adults emerged. One female of each species was pin mounted, and the others were stored in 70% ethanol. All materials were deposited in the Entomological Collection of the MPEG. *Monobia funebris* was identified with the key of Willink (1982), *E. versicolor* with the key of Grandinete et al. (2018), and *P. ghilianii* with the key of Grandinete et al. (2015).

The nests were measured using a millimeter ruler and dissected using scissors and stylets. Wasps' images were taken with a Canon EOS 1000D digital camera with a Macro EF100mm f/2.8 USM lens, and nests images were taken using a Canon EFS 18-55 mm lens. Helicon Focus 8.1.1 Pro software was used to image focus stacking. Adobe Photoshop CS3 was used for photo editing and composing plates.

Results

Description of the nest of Monobia funebris *Gribodo, 1891*

The eight cells were made of clay and laid on the flat deck surface, separated from each other by small distances (ca. 5 mm) (Figure 2A). They had average dimensions of 36.2 mm X 22 mm (length X width). The cells were for the most part oval and had each two larval chambers (Figure 2C), with the opening/

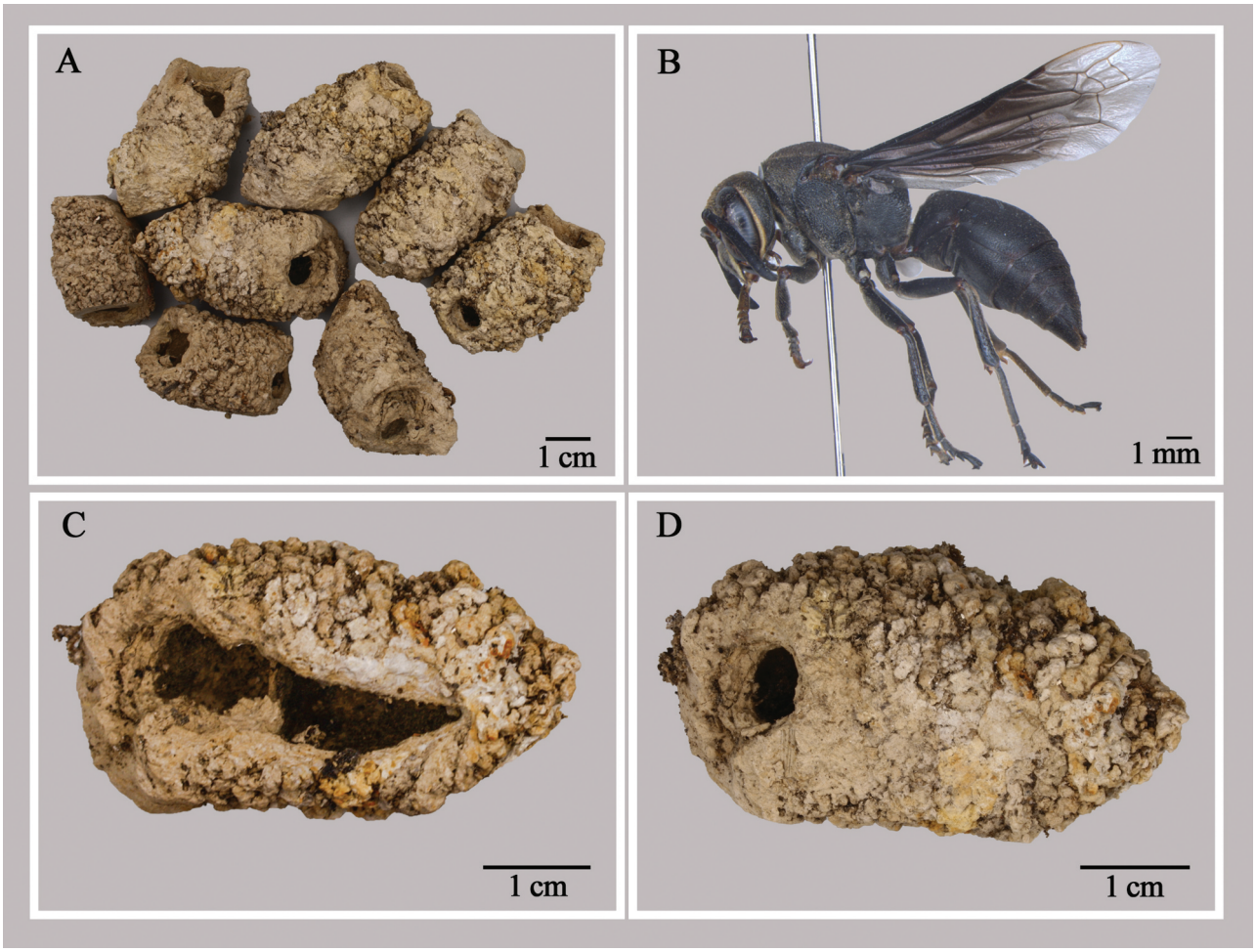

Figure 2. *Monobia funebris* (A–D): A – Nesting cells; B – Habitus lateral of female (MPEG 03056208); C – Cell with longitudinal section, with visualization of the chambers; D – Cell with opening at one end.

closing used by the mother female at one or at both ends (Figure 2A, D).

Externally, the cells had a rough finish and wall thickness measured on average 5.22 mm, being thicker at the opening orifice. Of the eight cells, only two were occupied, and one was dissected. From the dissected cell a larva was obtained which was fixed in alcohol. The other cell was kept in a breeding pot waiting for the emergence of an adult individual, which occurred after 60 days from the collection date (24.ii.2023), with emergence of a female (Figure 2B).

Description of the nest of Eumenes versicolor *de Saussure, 1852*

It was composed of two subspherical cells made of clay and small fragments of plant material, with one cell built on top of the other (Figure 3A, C). Cell measurements are as follows: 1.3 cm in diameter and 1.7 cm in height if the two are added together. While the upper cell is rounded, the lower cell is slightly flattened (Figure 3A, C, D). On the outside, the surface is grayish in color and has a slightly irregular texture. The inside of the nest has a coating of a golden color.

The mother female sealed the nest with a circular plug on the sides, and the general appearance of the cell is similar to a jar, as commonly described for this group (Isely 1917). Upon emergence, the adult (Figure 3B) opens a circular hole adjacent to the opening used by the mother female (Figure 3D). The deposition of meconium occurs at the bottom of the cell, opposite to the exit hole.

New information on nest architecture of Pachymenes ghilianii *(Spinosa, 1851)*

The nest of *P. ghilianii* was built on a deactivated electric line, approximately four meters from the ground. The general shape of the nest was ellipsoidal, with a pointed projection at each end (Figure 4A, B). The nest measures 5.3 cm long by 1.7 cm wide and 1.2 cm high. The building material was a mixture of clay and sand, and it was formed by the union of seven cells arranged in parallel, covered by an additional layer of clay and sand.

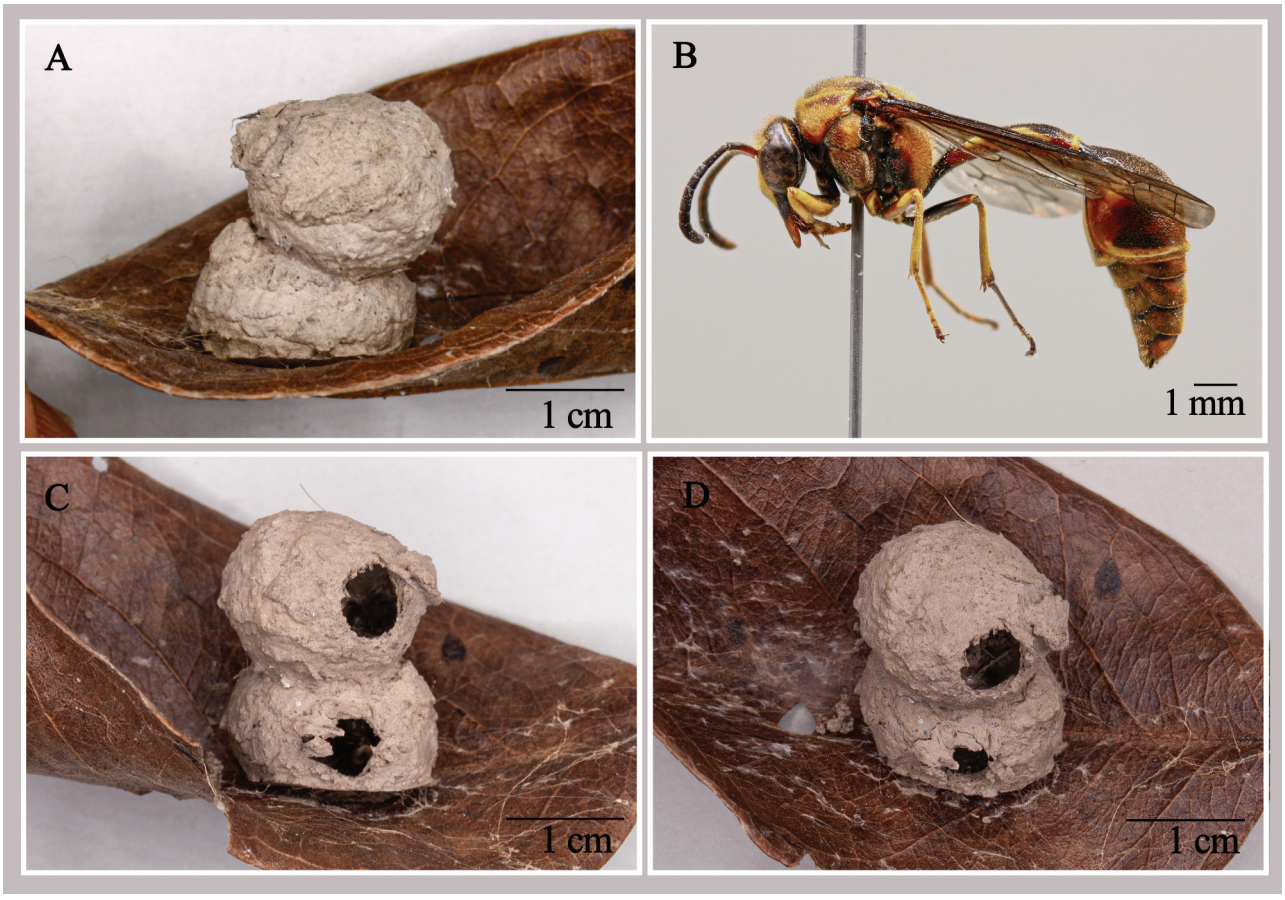

Figure 3. *Eumenes versicolor* (A–D): A - Nesting cells; B – Habitus lateral of female (MPEG 03056209); C – Rounded upper cell and slightly flattened lower cell; D – Circular hole adjacent to the opening used by the mother female.

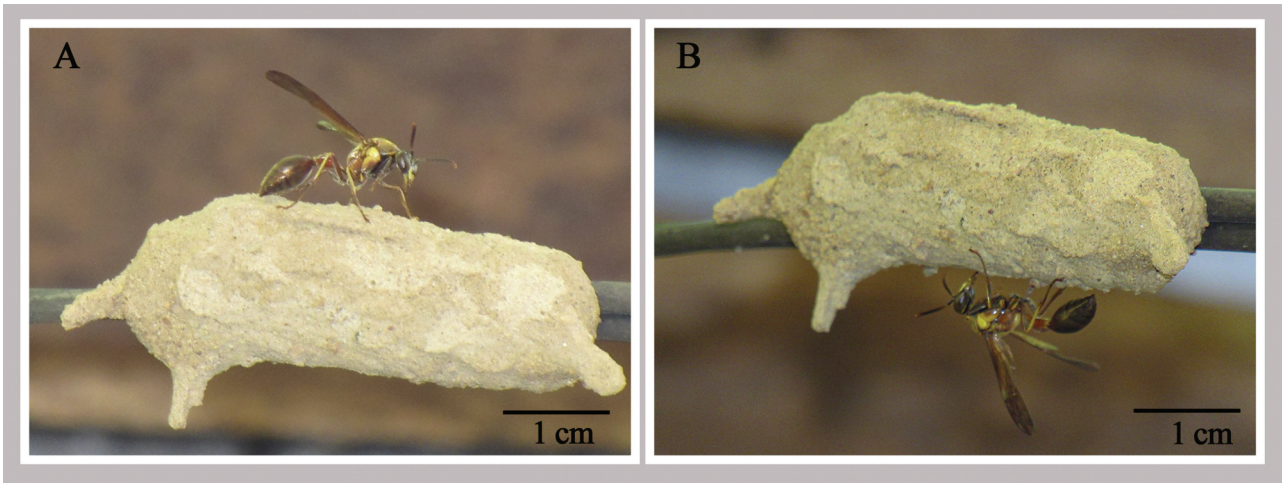

Figure 4. *Pachymenes ghilianii* (MPEG 03056210) (A–B): The nest built on a deactivated electrical line.

A female was in place and so remained during the entire observation period. It performed movements around the nest, touching it with her abdomen. All cells were closed, and at one end it was possible to observe that the material was still humid. We so can infer that the female had completed construction not long before. The collection of this *P.ghilianii* nest only took place the day after the observation (01.vi 2023), around 9 am and the female was still in place. We estimate that she spent at least seventeen hours on the nest, from the moment of first observation until when she was finally collected.

In the laboratory, the first emergence was a male and occurred the day after collection (02.vi.2023). The second emergence was a female and happened on 03.vi.2023. The third and fourth emergencies occurred in the period 08–12.vi.2023, a male and a female. The fifth emergence occurred on 13.vi.2023, a female, and a further male emerged on 14.vi.2023. One male individual died before emerging. The primary sex-ratio (females/males) was 0.75.

Discussion

Species of Eumeninae may be classified into three types regarding nesting biology: (I) burrowers that excavates nests in the soil, (II) renters that occupy and modify preexisting, and (III) builders that construct their entire nest (Iwata 1976; Cowan 1991). However, due to the observed behavioral and nests architecture plasticity in some species (Evans & Matthews 1974; Krombein 1979; Hermes et al. 2015), it becomes unfeasible to use this trait as a character in the natural classification of the subfamily (Hermes et al. 2013).

Some eumenine species exhibit the behavior of constructing multiple adjacent cells (Buyanjargal & Abasheev 2015). The *Monobia funebris* nest described here might be such a case of cells aggregation, but we do not have the essential information on the number of females involved in construction of the cells. In a species of the related eumenine genus *Montezumia* Saussure, 1852, Lopes and Noll (2018) observed a relatively large aggregate of (19–22) cells of *M. brethesi* Bertoni 1918 that were effectively constructed by multiple females, and the authors suggested the possibility of communal nesting and interpreted it as single nest.

There are few studies that provide comprehensive analyzes and long-term observations on the biology of *Monobia* species, and the most complete ones are the studies by Krombein (1967) and Camillo et al. (1997) that provide information on the nesting biology of *Monobia quadridens* and *Monobia angulosa*, respectively, from trap nests. These studies describe cell walls with thicknesses that can reach up to 10 mm, and with even thicker closures. In general, the nesting cells of *M. funebris* are thick, large, and coarse. The documented maturation time for individuals of *Monobia* species has varied from 26 to 160 days (Rau & Rau 1918; Frost 1944; Krombein 1967; Camillo et al. 1997). However, the data that most closely approximates the presently observed time between nest collection and the emergence of *M. funebris* is the one recorded by Frost (1944) for *Monobia* sp., with a duration between 52–56 days.

The nest of *E. versicolor* described here is formed by two grouped cells. In general, *Eumenes* species build nests with isolated or grouped cells on various substrates such as flat surfaces of rocks and logs, or concave surfaces, or linear substrates like grass and shrub stems (Iwata 1964; Fateryga & Matushkina

2010). The emergence of an adult *E. versicolor* does not occur through the same opening used by the nesting female, the brood exit hole being on the sides of the cell. This behavior was observed in the species *E. fraternus* Say, 1824, which also builds nests with isolated cells or in groups of two to five globular cells (Isely 1917).

The nest of *P. ghilianii* is a cluster of cells, with an extra mud layer surrounding the nest, so that cell division is not visible. This type of additional layer has been reported before for the Neotropical species *Brachymenes dyscherus* Saussure, 1852 (Camillo 1999) and *Hypodynerus andeus* (Packard, 1869) (Méndez-Abarca et al. 2012). This extra layer may increase protection against potential enemies (Hunt 2007; Hermes et al. 2013). The nest of *P. ghilianii* described by Abrego et al. (2018), collected in Panama, did not have an additional layer covering the cells, and it is worth noting that it was collected after the female had already provisioned and sealed the fourth cell. However, in the case here reported, since we did not observe the entire building process of the nest, we lack the information on when the female added this extra layer.

The observed nesting female of *P. ghilianii*, by remaining in the nest after provisioning, may be considered as demonstrating some level of prolonged parental care, to which can be added that the first individual of the offspring, a male, emerged the day after the observation, so it is very likely that the female met her son. Further studies are required to better understand this behavior, as it can provide us with information to understand the evolution of behavior in Eumeninae.

In the observed nest of *P. ghilianii*, the first four emergences occurred in the following sequence: first, a male emerged, the next day a female, then the second male, followed by the second female. In *Eumenes punctaticlypeus kostylevi* Kurzenko, and in some species of the genus *Delta* de Saussure, it has been observed that eggs giving rise to males are laid before those giving rise to females (Fateryga & Matushkina 2010 and references). This phenomenon was termed proterandry by Jayakar (1963) and ensures the maturation of males before females. While this mechanism is likely peculiar to many solitary wasp species that construct aerial nests (Fateryga & Matushkina 2010), it is not what we observed in *P. ghilianii* in which the emergences that could be observed in the lab formed a male/female alternating series.

The information on Eumenine nesting biology remains fragmented and dispersed in the literature. Our observations show new facts of nest architecture in Eumeninae and highlight the need for additional efforts to elucidate aspects of the nesting behavior of *M. funebris*, and the continued presence of female *P. ghilianii* in the nest after its completion.

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Disclosure statement

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