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Paracyphononyx scapulatus (Hymenoptera, Pompilidae), a koinobiont ectoparasitoid of *Trochosa* sp. (Araneae, Lycosidae)

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Abstract

The genus *Paracyphononyx* Gribodo, 1884 (Pompilidae) contains species that act as koinobiont parasitoids of cursorial spiders. Here, we record a new parasitism interaction involving the pompilid wasp *Paracyphononyx scapulatus* (Bréthes) and the hunter spider *Trochosa* sp. (Lycosidae), and we describe how the wasp develops on the spider. This study contributes new information about the interaction between koinobiont ectoparasitoid wasps and spiders, which probably arose independently in different groups of wasps.

Keywords

Atlantic forest, Lycosidae, Hunter spider, Larval development, Parasitoid wasp

Introduction

The Pompilidae family contains about 5000 known wasp species worldwide. In the Neotropical region (Central and South America), around 1000 species have been described, belonging to 60 genera and five subfamilies (Pitts et al. 2006). In North America, 282 species have been documented in detail, belonging to 40 genera (Goulet and Huber 1993). In South America, this family has been studied in Brazil, Argentina, Uruguay, Paraguay, and Chile (Banks 1946, 1947, Bradley 1944) and, recent studies are being conducted in Colombia (Fernández 1995, 2000). Fernández (2000) reported 50 genera belonging to four subfamilies in South America; however, most of these genera require detailed taxonomic revision.

All species of Pompilidae use spiders as a food source for larval development, leading to their common name of “Spider Wasps” (Brothers and Finnermore 1993, Brothers 1995). Many species of this wasp family are idiobiont ectoparasitoids of cursorial spiders, building their nests in pre-existing holes in the soil or burrows dug by the wasps (Martins 1991). However, some koinobiont ectoparasitoids, belonging to the genus *Paracyphononyx* Gribodo, 1884 (Pompilidae), allow the host to resume activities after paralyzing it and laying a single egg on the spider’s abdomen (Grout and Brothers 1982, Conley 1985, El-Hennawy 1996).

Paracyphononyx has been recorded in the tropics and warmer temperate regions throughout the world (Evans 1966), with nine species recorded in Brazil (Fernández 2000). Only three species of *Paracyphononyx* are known to use spiders as hosts, notably those belonging to the Lycosidae. These interactions were recorded in the Afrotropical region for *P. africanus* (Radoskowski, 1881), *P. funereus* (Lepeletier, 1845) in the Nearctic, and *P. ruficrus* (Klug, 1834) in the Palearctic.

The Lycosidae is distributed worldwide, containing small species (4–10 mm body length) that roam freely among stones or low vegetation, and larger species (10–20 mm body length) that typically dig burrows (Foelix 2011). Besides the records of Lycosidae used by Pompilidae as hosts, recent studies have presented data of a lycosid parasitized by an acrocerid fly (koinobiont endoparasitoid; Toft et al. 2012) and egg sacs parasitized by wasps of the families Ichneumonidae and Platygasteridae (Cobb and Cobb 2004, Bowden and Buddle 2012). The lycosid genus *Trochosa* comprises small to medium sized spiders (5.8–13.0 mm body length) which are often found at the edge of woods and in woodland habitats (Dreyer and Brady 2008). They usually are nocturnal in the adult stage (Workman 1978).

Here, we record the occurrence of a new parasitic interaction involving *Paracyphononyx scapulatus* (Bréthes) and the hunter spider *Trochosa* sp. (Lycosidae), with a description of wasp development.

Methods

At 11:30 on July 3, 2014, we found a lycosid spider (*Trochosa* sp.) with a *Paracyphononyx scapulatus* egg on its abdomen (Fig. 1A) in a fragment of Atlantic Forest in the

municipally of Iracema do Oeste, Paraná, Brazil (24°29'11"S, 53°21'14"W). We collected the spider alive, and placed it in a plastic container (12 × 12 × 10 cm). We fed the spider with *Musca domestica* Linnaeus, 1758 (Muscidae) and kept the individual at natural conditions of temperature (21 °C) and photoperiod (13 h of light and 11 h of darkness). We then observed the behavior of the spider as the parasitoid developed from a larva to an adult wasp. In parallel, we photographed the spider daily, to obtain a time-series of the development of the parasitoid. We recorded the period of each developmental stage, cocoon construction, and adult wasp emergence. We measured the length and width of the larva throughout its development by analyzing the photographs using the software ImageJ (National Institute of Health).

Results and discussion

The *Paracyphononyx scapulatus* egg (1.4 mm length and 0.8 mm width) was deposited on the anterior-dorsal region of the abdomen of a juvenile *Trochosa* sp. (abdomen: 9 mm length and 6 mm width; cephalotorax: 7 mm length and 5.8 mm width; Fig. 1A), and hatched after seven days. The host remained active (resting during the day and walking at night), while the attached larva gradually fed on the spider's hemolymph in the abdomen. This result indicates that *P. scapulatus* is a koinobiont parasitoid, like other species of *Paracyphononyx* for which the biology is known (Grout and Brothers 1982, Conley 1985, El-Hennawy 1996). Conley (1985) documented *P. funereus* (Lepeletier 1845) as a koinobiont parasitoid of the spider *Geolycosa rafaellana* (Chamberlin, 1928), causing high mortality to adult females during the winter. Grout and Brothers (1982) observed *P. africanus* paralyzing its lycosine host temporarily, depositing a single egg transversely on the concave anterodorsal surface of the spider abdomen, and then abandoning the host, which subsequently recovered normal activity. El-Hennawy (1996) recorded the wasp *P. ruficrus* manipulating the behavior of a lycosid spider, inducing the host to construct a silken cocoon around itself.

The larval development of *Paracyphononyx scapulatus* includes five instars, evidenced by marked increase in size of the larva between each stage (Fig. 1B–F), doubling its length between the fourth and fifth instars (Fig. 2). The fifth instar larva killed the spider in the morning, 20 days after the egg hatched. The spider body was then completely consumed over the next two days. On the second day, the larva spun in different locations on the ground of the plastic container looking for suitable substrate to construct a cocoon (Fig. 1G). The larva located a suitable site on the afternoon of the second day (16:00), and required about 16 hours to construct the cocoon (cocoon: 16 mm length and 6 mm width). We observed the presence of meconium after six days in the portion of the cocoon that was fixed onto the substrate (Fig. 1H, arrow). An adult female wasp (15 mm length) emerged 32 days after cocoon construction, cutting its apical region (Fig. 1I–J). Fifty-four days was required for the development period from the egg hatching to adult emergence. This period is higher than that observed by El-Hennawy (1996) for the congeneric wasp *P. ruficrus*, which had a 30-day total development period.

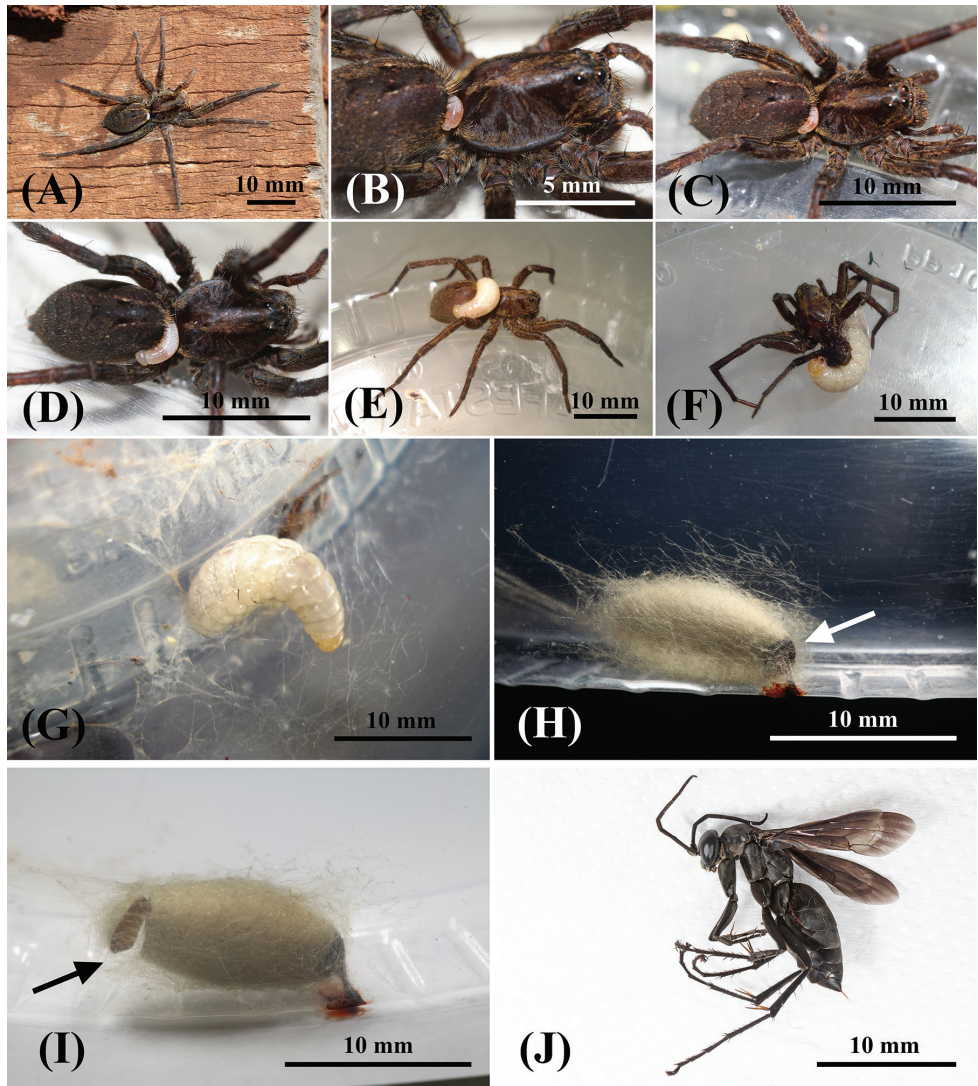


Figure 1. Juvenile *Trochosa* sp. spider parasitized by the wasp *Paracyphononyx scapulatus* and containing on its abdomen: **A** the egg of the wasp; the **B** first **C** second **D** third, and **E** fourth instar larva of the wasp **F** the fifth instar larva of the wasp starting the consume the spider abdomen **G** the fifth instar larva constructing the cocoon **H** the cocoon containing the meconium (arrow) **I** the cocoon after adult wasp emergence (arrow indicates the location where the wasp emerged) **J** the adult female wasp. Photography: Hebert da Silva Souza (**A–D**), Eduardo Messas Junior (**E–G**), and Yuri Fanchini Messas (**H–J**).

To date, all observations involving *Paracyphononyx* as the koinobiont ectoparasitoid (Grout and Brothers 1982, Conley 1985, El-Hennawy 1996), including the present study, have shown that this wasp genus only uses spiders belonging to the Lycosidae as hosts. This observation indicates the existence of host-parasitoid specificity.

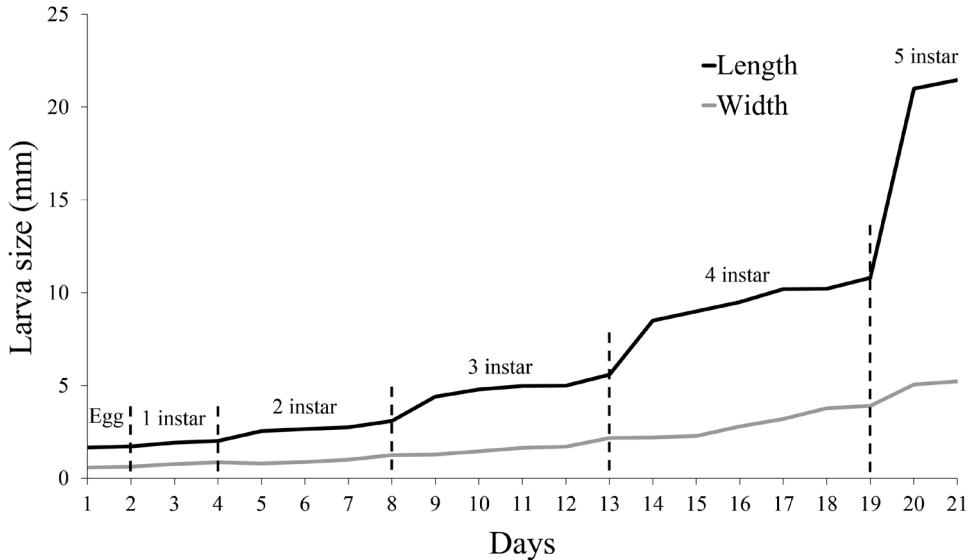


Figure 2. Size of *Paracyphononyx scapulatus* larva on the abdomen of the *Trochosa* sp. (length and width) during their development.

Koinobiont ectoparasitoids of the genus group *Polysphincta* (Hymenoptera: Ichneumonidae, Pimplinae) exhibit high parasitoid-host specificity, using only one species or groups of spider species that share common characteristics as hosts (Matsumoto and Konishi 2007, Sobczak et al. 2009, Gonzaga and Sobczak 2011, Takasuka and Matsumoto 2011, Eberhard 2013, Sobczak et al. 2014). Furthermore, parasitic wasps tend to select intermediate-sized hosts that have sufficient biomass for larval development, but do not represent a threat to the wasp during the attack (Gonzaga and Sobczak 2011). Few records exist of parasitism by *Paracyphononyx*; consequently, knowledge about the ecology and natural history of this genus remain limited. Therefore, we encourage future studies to elucidate the type of host selection used by this group of wasps.

Paracyphononyx scapulatus attacked the *Trochosa* sp. during winter, which is also when Conley (1985) recorded 50–60% mortality of adult *Geolycosa rafaellana* females caused by *P. funereus*. The same author observed that the parasitism rates were not strongly related to reduced-density populations of *G. rafaellana*, indicating that *P. funereus* selectively forages in areas with higher spider density (Conley 1985). Thus, there may be a phenological adjustment between *P. scapulatus* and *Trochosa* sp., the period of wasp attacks coincides with the period when the number of juvenile spiders is at its peak, which provide sufficient biomass for adequate larval development.

We did not observe any behavioral modification by the larva on the parasitized *Trochosa* sp. After killing the spider, the *Paracyphononyx scapulatus* larva started cocoon construction much faster than that observed for *P. ruficrus* by El-Hennawy (1996). However, in the previous study the *Lycosa* host spun a silken chamber, clos-

ing itself and the *P. ruficrus* wasp larva inside. Then, the wasp larva continued to feed on the spider inside the silken shelter, killing the host and building its cocoon. Similar behavior was observed by Day (1981) for *Pompilus cinereus* (Fabricius). Most known behavioral manipulation interactions induced by parasitoid wasps target web building spiders, with behavior modification tending to include the construction of modified webs which may exhibit a tridimensional tangle structure, absence of sticky spirals, central hub and stabilimentum, reduced number of radial lines and refuges that protect the cocoon and increase parasitoid survival (Eberhard 2013, Korenko et al. 2015). Data about the behavioral manipulation of pompilid hosts remains limited. In this study, having the spider caged in a featureless container did not allow us to test if the parasite tried to manipulate the spider behavior (e.g. induce it to hide itself and consequently hide the wasp cocoon). Thus, new records and more conclusive studies are necessary to understand the behavioral modification induced by Pompilidae species.

Many Pompilidae species hunt wandering spiders on the ground; consequently, immobilized spiders are exposed to predators, such as ants. Thus, these wasp species may dig burrows or use pre-existing holes to hide the paralyzed spider with its egg. In comparison, the type of koinobiont parasitism adopted by *Paracyphononyx scapulatus* (i.e., allowing the spider to continue normal activity), may be an alternative strategy to prevent the exposure hosts to predation. According to Korenko et al. (2011), most interactions between koinobiont parasitic wasps and spiders are host-specific, with the life histories of both wasp and spider being tightly coupled. Therefore, we would expect *P. scapulatus* to kill the host during the day at the end of the larval development under natural conditions, which is when the spider is typically resting in a refuge.

The genus-group *Polysphincta* is well-known to contain exclusively koinobiont ectoparasitoids of spiders (Gauld and Dubois 2006). Yet, knowledge about the host-parasite interactions of Pompilidae family have been summarized in a few studies that provide limited and brief information. Further investigations detailing these interactions may provide a promising path towards understanding the evolution of koinobiont ectoparasitism, which probably arose independently in different groups of wasps.

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