Revista Brasileira de Entomologia 69(1):e20240081, 2025

SOCIEDADE BRASILEIRA DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

# Drill on drill: adaptive oviposition strategies of *Sycophila* and *Physothorax* wasps on *Ficus citrifolia*

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A R T I C L E I N F O

*Article history:*
Received 11 July 2024
Accepted 12 December 2024
Available online 27 January 2025
Associate Editor: Marcelo Tavares

*Keywords:*
Evolutionary ecology
Insect-plant interaction
Host-parasite interactions
Oviposition behavior
Parasitic wasps

A B S T R A C T

Understanding tri-trophic interactions and the relationship among plants, herbivores, and their natural enemies is fundamental to advancing theoretical and practical ecology. Parasitoidism is among those interactions where tri-trophic levels are usually developed, with hyperparasitism and kleptoparasitism as examples. This study explores the interaction between fig wasps of the genera *Physothorax* Mayr, 1885 and *Sycophila* Walker, 1871 (Hymenoptera: Chalcidoidea) and the gall midge *Ficiomyia brasiliensis* Urso-Guimarães, 2024 (Diptera: Cecidomyiidae) associated with *Ficus citrifolia* Mill. in Ribeirão Preto, Brazil. Through behavioral observations and larval dissections we document the "drill on drill" strategy where *Sycophila* females utilize oviposition holes drilled by *Physothorax* females on the fig surface to access the host gall midge immatures. This behavior suggests a sophisticated adaptation for reducing oviposition time and conserving energy. Additionally, *Sycophila* behavior aligns with kleptoparasitic and hyperparasitic strategies, indicating a complex evolutionary history and ecological interaction. Our findings provide insight into the intricate relationships among non-pollinating fig wasps and their hosts, contributing to the broader understanding of tri-trophic interactions in fig microcosm.

## Introduction

Understanding trophic relationships is crucial for advancing both theoretical and practical ecology. However, tri-trophic interactions (*i.e.*, those involving three trophic levels) remain under-reported in the literature, underscoring the need to reveal and describe these complex relationships to comprehensively understand ecological communities (Tylianakis et al., 2007; Dicke and Baldwin, 2010). These interactions influence species' abundance and distribution, impacting ecosystems' overall structure and function (Estes et al., 2011).

Elucidating trophic relationships is essential for understanding the complex ecology of insect-plant interactions. Tritrophic relationships - encompassing plants, insects, and a third trophic level such as parasitoids - exhibit intricate life histories that shape population dynamics and evolutionary trajectories (Godfray, 1994; Brodeur and Boivin, 2004). Thus, they provide a comprehensive framework for examining the selective forces driving morphological, physiological, and behavioral adaptations in the involved species (Quicke, 1997). Hymenoptera, which constitute nearly 78% of parasitoid species, exhibit a variety of life history strategies, including ecto- and endoparasitism and kleptoparasitism (Eggleton and Belshaw, 1992). Each strategy uniquely impacts host population dynamics (Feener Junior and Brown, 1997; Pennacchio and Strand, 2006; Sharkey, 2007).

The fig-fig wasp system is an excellent model for studying tritrophic interactions. Fig trees (genus *Ficus*) have unique inflorescences (syconium or fig) that harbor a complex microcosm of organisms, from a community of fig wasps (Chalcidoidea, Hymenoptera) to nematodes, mites, and other insects (Pereira et al., 2000; Jauharlina et al., 2012, 2022; Palmieri et al., 2013; Palmieri and Pereira, 2018). Many of these organisms interact with the fig wasps, turning the fig into a minute ecosystem. The fig wasp community encompasses the agaonid pollinating wasps and non-pollinating fig wasps (NPFWs), which exploit fig resources. The pollinating fig wasps enter the fig, pollinate and oviposit, and develop their offspring inside some of the pistillate flowers, while NPFWs exhibit diverse life histories, including gall inducers, kleptoparasites,

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https://doi.org/10.1590/1806-9665-RBENT-2024-0081

and parasitoids of gall inducers, and they usually do this by ovipositing from the external surface of the fig (Borges, 2015).

The complex interaction among the NPFW is well illustrated by Compton et al. (2009), where *Apocrypta* Coquerel, 1855 and *Sycoryctes* Mayr, 1885 (Pteromalidae) females probe the figs to oviposit, while *Watshamiella* Wiebes, 1981 females actively orbit them. After the initial oviposition of the former species, the *Watshamiella* (Pteromalidae) female swiftly introduces its ovipositor into the hole drilled by these preceding species, showing a sophisticated strategy for accessing host larvae. This oviposition behavior is known as the "drill on drill" strategy and represents an intriguing example of adaptive behavior in parasitoid communities. This strategy involves a secondary parasitoid exploiting the oviposition hole created by a primary parasitoid, thus facilitating its egg-laying process (Quicke, 1997).

We report a similar interaction among insects associated with the Neotropical fig tree *Ficus citrifolia* Mill., section *Americanae*, involving two unrelated parasitoid species belonging to the genera *Physothorax* Mayr, 1885 (Torymidae) and *Sycophila* Walker, 1871 (Eurytomidae). Our study shows that these parasitoids target a third party in the fig-wasp interaction, the gall midge *Ficiomyia brasiliensis* Urso-Guimarães, 2024 (Cecidomyiidae) (Urso-Guimarães et al., 2024), and their interaction indicates a convergent evolution of this oviposition behavior within other NPFWs, suggesting high selective pressure on the oviposition strategies of these wasps.

## Materials and methods

### *Study area and species*

The study was conducted on the campus of the University of São Paulo in Ribeirão Preto, Brazil (21°10′S, 47°49′W), encompassing natural vegetation areas and gardens. We investigated *Physothorax* and *Sycophila* wasps, parasitoids of the gall midge *F. brasiliensis* associated with *F. citrifolia* Mill. *Ficus citrifolia* is a hemiepiphytic species in the *Americanae* section, widely distributed in the neotropics, from Florida to northern Argentina (Berg and Villavicencio, 2004).

### *Behavioral observation*

The oviposition behavior of female *Physothorax* and *Sycophila* was observed several times in 2012 on figs of *F. citrifolia* trees. Additionally, from June to August 2018, two *F. citrifolia* trees were monitored every two days between 13:00 and 14:00 hours throughout the development of their figs. Monitoring began at the onset of fig development (from the abscission of the bracts surrounding the figs) and continued until the dispersal of the wasp offspring. We recorded all NPFW species that probed the figs during the monitored period, focusing specifically on the behavior of females of *Physothorax* and *Sycophila* species. The observed wasps were collected using an entomological aspirator for further morphospecies identification. Field photographs were taken with a Canon EOS Rebel T6 camera and a Canon EF-S 60mm f/2.8 Macro lens.

### *Larval Biology*

Protuberances on the surface of the fig appeared a few days after the pollination phase. Dissection of the figs revealed that the protuberances corresponded to galls induced by *F. brasiliensis*. We also observed females of *Physothorax* and *Sycophila* inserting their ovipositors near these protuberances, suggesting the wasps were depositing their eggs in these galls.

Based on the observations described above, we sampled two fig trees, collecting approximately 10 figs per tree at each of four developmental stages, resulting in a total of around 40 figs per tree and 80 figs overall. The development stages of the galls in these figs corresponded roughly to 20, 30, 40, and 50 days after the start of monitoring, covering the development of the insects from the phase when the galls were perceivable by the protuberances to the emergence of the adult gall midges.

The sampled figs were preserved in 70% ethanol for subsequent gall dissection. Each fig was cut open to collect the *F. brasiliensis* galls under a dissecting stereoscope. All available cecidomyiid galls were sampled, totaling 339 *F. brasiliensis* galls. Each gall was transferred to a petri dish containing a layer of 70% ethanol and meticulously dissected under a 20X magnification stereomicroscope to avoid damaging the immature stages. The gall contents were sorted (*i.e.*, insect species and developmental stage). The parasitoid species was identified only in galls containing pupa or adult individuals, as the *Physothorax* and *Sycophila* larvae are morphologically similar. The immature insects were photographed with a digital camera under a Leica M16 stereomicroscope.

In parallel, we dissected galls in advanced stages of development induced by fig wasps. We observed other species of *Physothorax* and *Sycophila* associated with galls from *Idarnes dimorphicus* Farache & Rasplus, 2017 (*incertus* group) and an unidentified species of *Idarnes* Walker, 1843 (*flavicollis* group). We did not show and discuss these data due to the low parasitoid infestation in these *Idarnes* galls and incomplete data on their biology.

## Results

### *Behavioral observations*

The oviposition period of *Physothorax* sp. and *Sycophila* sp. females lasts about 10 days, starting approximately 20 days after the onset of fig development. This period corresponded to the interfloral stage, during which the seeds and larvae of the gall-inducing species were developing. *Physothorax* and *Sycophila* females exhibited distinct behaviors while probing the figs. Oviposition by *Physothorax* lasted approximately 3-6 minutes (Figure 1A). *Sycophila* females actively searched and localized *Physothorax* and kept a few millimeters distance from it (Figure 1B). Once the *Physothorax* female detached its ovipositor, the *Sycophila* female antennated the probing spot for 5-8 seconds before inserting its ovipositor through the puncture (Figure 1C). *Sycophila* oviposition lasted 2-3 minutes. In some cases, *Physothorax* females showed a host-guarding reaction to the presence of *Sycophila* females, detaching their ovipositor and lunging at the *Sycophila* female. Occasionally, the *Physothorax* female resumed oviposition after temporarily driving away the competitor. When multiple *Sycophila* females foraged the same fig, they aggressively competed for access to the oviposition spot, engaging in a series of thrusts lasting 5-10 seconds until one dispersed. No damage to the wasps was observed. The remaining female then resumed antennation and oviposition in the spot drilled by the *Physothorax* female.

### *Larval biology*

The gall formed by *F. brasiliensis* is a pocket-like swelling, approximately 3 mm in length and 1.7 mm in width. These galls are larger than those produced by fig wasps. Unlike most fig wasp galls, they develop from the fig wall and extend toward the fig lumen. On average, there are 8.9 ± 6.4 galls per fig (mean ± standard deviation, n = 38 figs). Individuals of *Physothorax* sp., *Sycophila* sp., and an unidentified species

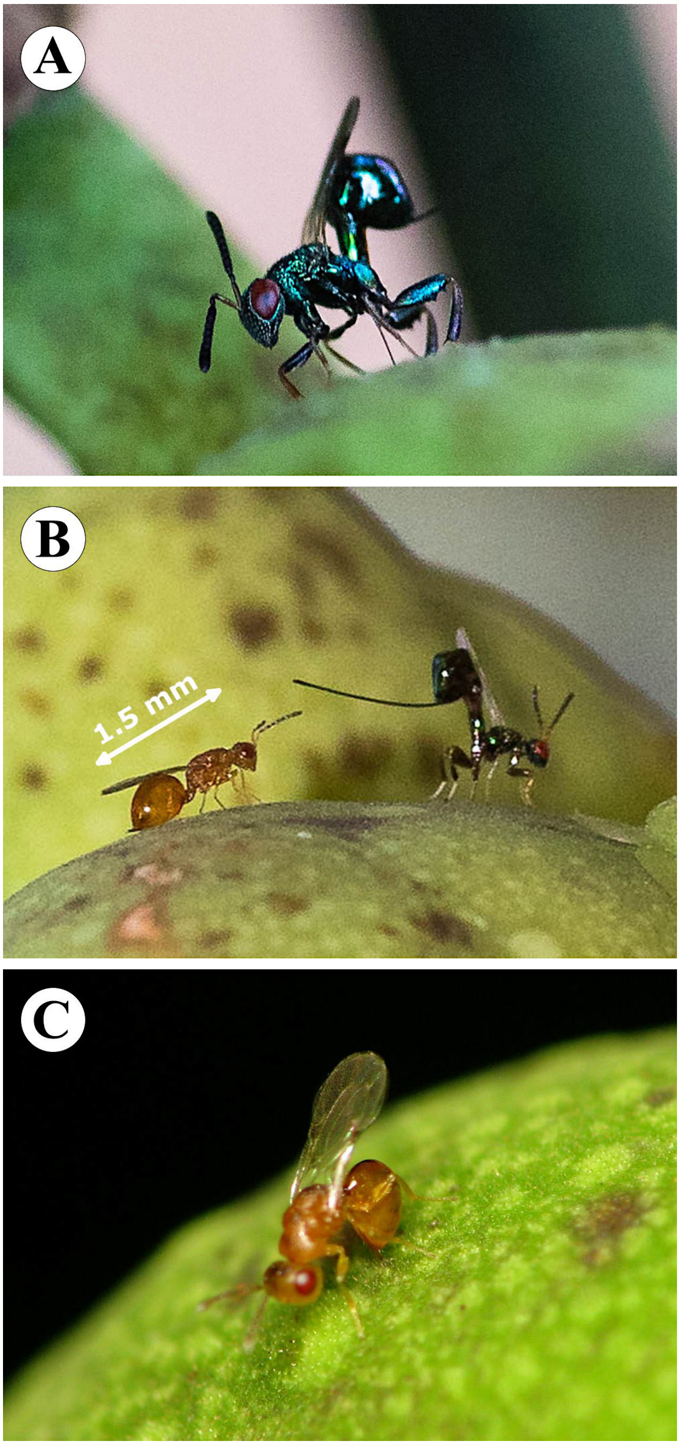


**Figure 1** Drill on drill strategy involving *Physothorax* and *Sycophila* wasps in figs of *Ficus citrifolia*. A. *Physothorax* sp. female probing the fig. B. A *Sycophila* sp. female close to an ovipositing *Physothorax* sp. female. C. A *Sycophila* sp. female probing the fig through the hole drilled by *Physothorax*. Image B shows the approximate body size of the *Sycophila* sp. female.

of platygastrid parasitized the galls collected from the studied trees. Platygastridae sp. is probably a polyembryonic-gregarious parasitoid (Gordh et al., 1999), occurring 21.9 ± 8.3 individuals per gall (mean ± standard deviation, n = 11 galls). The Playsgastridae results are presented solely for reporting purposes, and as they do not relate to the primary objective of this study they will not be discussed further. Galls from tree 1 exhibited a higher parasitism rate (44.7%) than tree 2 (9.5%). In both samples, *Physothorax* sp. was the most frequent parasitoid (Table 1).

**Table 1**
Rate of parasitism in galls of *Ficiomya brasiliensis* dissected in *Ficus citrifolia* figs. The indeterminate category includes *Ficiomya* galls containing wasp larvae whose species could not be identified.

| Gall content | Number | Percentage |
|---|---|---|
| | Tree 1 | |
| *Ficiomyia brasiliensis* | 141 | 55.3 |
| *Physothorax* sp. | 72 | 28.2 |
| *Sycophila* sp. | 18 | 7.1 |
| Platygastridae sp. | 11 | 4.3 |
| Indeterminate | 13 | 5.1 |
| Total | 255 | 100 |
| | Tree 2 | |
| *Ficiomyia brasiliensis* | 76 | 90.5 |
| *Physothorax* sp. | 3 | 3.6 |
| *Sycophila* sp. | 0 | 0 |
| Platygastridae sp | 2 | 2.4 |
| Indeterminate | 3 | 3.6 |
| Total | 84 | 100 |

Dissection of galls at various developmental stages revealed that *Physothorax* sp. and *Sycophila* sp. are ectoparasitoids. The eggs of both species are deposited on the pupa of *F. brasiliensis* approximately 30 days after the initial fig development (Figure 2A), and their larva attaches to the abdominal region of the pupa (Figure 2B). It was impossible to recognize the wasp species at this developmental stage as their larva are morphologically similar.

In figs of about 40 days into development, we observed advanced-stage *Physothorax* larva and *Sycophila* prepupa (Figure 2C-D). We only observed a single immature in each dissected gall and did not find immatures of both species together in the same gall. The advanced-stage larva and pupa of *Sycophila* were often associated with remnants of the host. The host remnants exhibited a characteristic globular appearance, with only the larval mouthparts identifiable. This type of remnant was not observed with advanced-stage larvae or pupae of *Physothorax*.

About 50 days after the initial fig development, the parasitized galls contained only the *Physothorax* and *Sycophila* pupae, indicating that the immature *F. brasiliensis* was consumed entirely at this stage (Figure 2E-F).

## Discussion

The fig (syconium) harbors a complex community of chalcid wasps, including gallers, parasitoids, kleptoparasites, and potentially hyperparasitoids. The precise ecological relationships among these wasps remain largely unclear, and their interactions outside the fig are poorly understood. Various wasp species often interact on the fig surface during specific developmental phases. Besides this rich community of wasps, other organisms interact with the wasps and the plant, using the fig as a resource (Pereira et al., 2000; Palmieri and Pereira, 2018). Among these organisms, gall midges belonging to the genus *Ficiomyia* were reported to develop from pocket-shaped galls, which are outgrowths inside the fig cavity (Roskam and Nadel, 1990). It remains unclear what specific plant tissues are involved in the galling process, but it is suggested that the galls might originate from the parenchyma of the fig wall or underdeveloped flowers (Roskam and Nadel, 1990).

Hedberg et al. (2024) report a species of *Physothorax* as a parasitoid of an unidentified *Ficiomyia* gall midge in *Ficus citrifolia* figs in Panama, without providing further details on the wasp's oviposition behavior. Further studies are necessary to determine if the insects found in Brazil and Panama belong to the same species. Here, we show that females of *Sycophila* sp. use the holes previously drilled in the fig wall

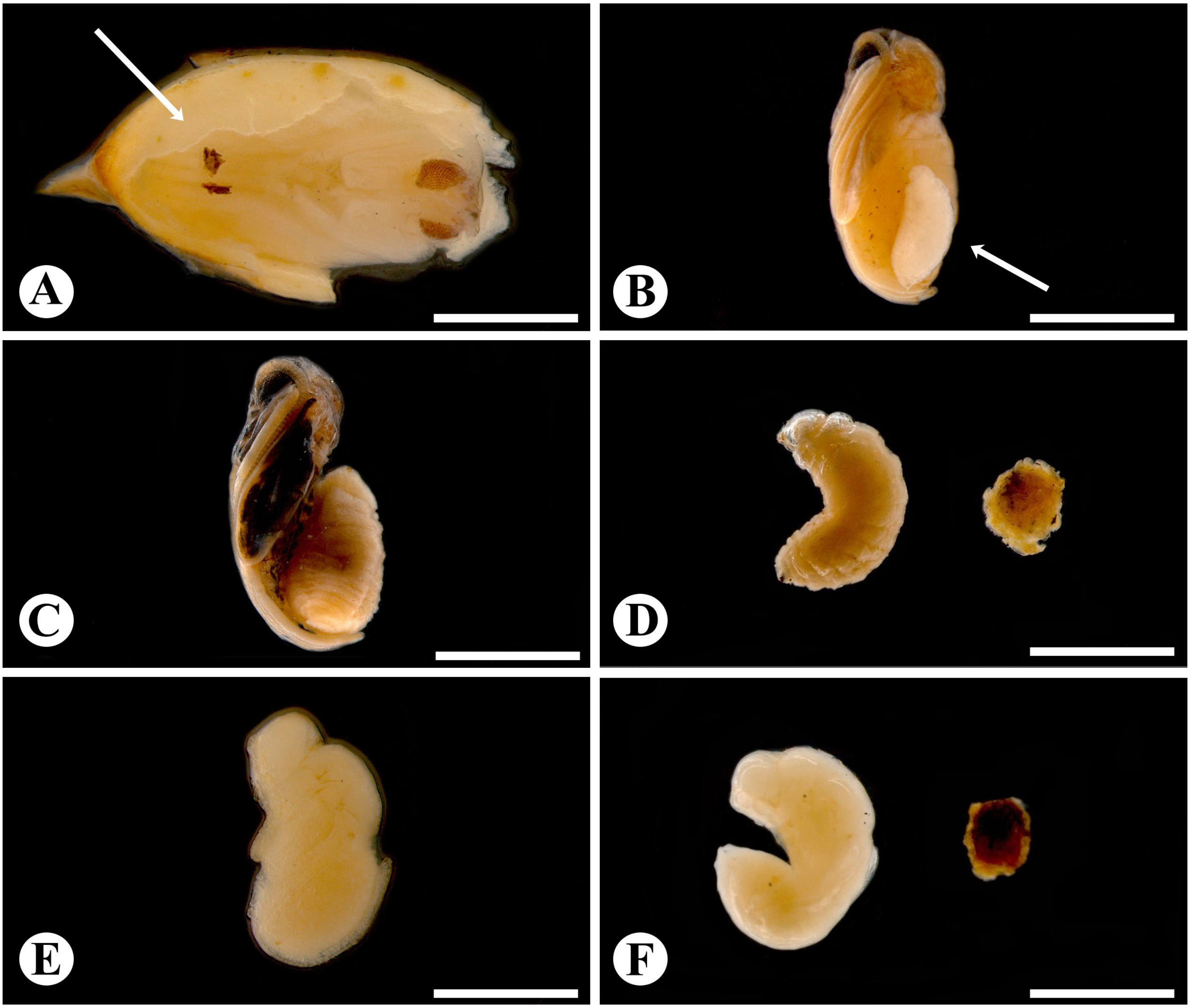


**Figure 2** Immature development of the *Ficiomyia brasiliensis* parasitoids. A. *F. brasiliensis* pupa with a parasitoid egg (damaged during the gall dissection) on its abdominal region (arrow). B. *Physothorax* sp. or *Sycophila* sp. larva (arrow) on the host pupa. C. Advanced-stage *Physothorax* sp. larva on the host pupa. D. *Sycophila* prepupa and the host remnants. E. *Physothorax* sp. pupa. F. *Sycophila* sp. pupa and the host remnants. Scale bars = 1 mm.

by *Physothorax* sp. females. This "drill on drill" strategy highlights the intricate interaction between these parasitoid species, suggesting they share an evolutionary history. The oviposition behavior of *Sycophila* involves a series of steps with a repertoire of behaviors. These behaviors are (1) the recognition of the primary parasitoid, (2) the interpretation of when it finishes oviposition, (3) the search and identification of the drilled oviposition hole and (4) the reaction to rival wasps.

The "drill on drill" strategy is reported in different hymenopteran families, pointing out that this strategy has evolved independently several times in parasitoids. In Eurytomidae, *Eurytoma monemae* Ruschka, 1918 uses the drill made by the primary parasitoid *Praestochrysis shanghaiensis* (Smith, 1874) (Chrysididae) in the cocoon of the oriental moth, *Monema flavescens* Walker, 1855 (Lepidoptera: Limacodidae) (Clausen, 1940); *E. waachtlii* Mayr, 1878 and *E. pini* Bugbee, 1958 use the drills of *Scambus* Hartig, 1838 spp. (Ichneumonidae) to parasitize *Pissodes validirostris* Gyllenhal, 1835 (Coleoptera: Curculionidae) and *Rhyacionia buoliana* (Denis & Schiffermüller, 1775) (Lepidoptera: Tortricidae) larvae, respectively (Arthur, 1961; Roques, 1976). The sirex woodwasp (Siricidae) is parasitized by the ichneumonid *Rhyssa persuasoria* (Linnaeus, 1758), and a secondary parasitoid, *Rhyssella approximator* (Fabricius, 1793) (Ichneumonidae), makes use of the hole drilled by the former to probe the wood (Couturier, 1949). This oviposition behavior has been reported for pteromalid species associated with Afrotropical fig trees, where *Watshamiella* species use the hole drilled by *Apocrypta* and *Sycoryctes* to probe the fig (Compton et al., 2009).

Using already drilled holes likely confers selective advantages by conserving energy that would otherwise be expended on drilling and, more crucially, by substantially reducing oviposition time (Couturier, 1949; Compton et al., 2009). In our observations of NPFWs, *Sycophila* females oviposited approximately twice as fast as *Physothorax* females. For the Afrotropical *Watshamiella* species, the oviposition time is about five times shorter than that of primary parasitoids (Compton et al., 2009). Females of NPFWs are especially vulnerable to predation during oviposition (Bronstein, 1988; Pereira et al., 2000; Ranganathan and

Borges, 2009; Bain et al., 2014). Therefore, the duration of exposure to predators during oviposition is likely under intense selective pressure.

The structure of the ovipositor in Hymenoptera is complex and closely associated with the species' life history and the resources they exploit (Quicke et al., 1994). The ovipositor structure of parasitoids has also served as bioinspiration for the development of medical instruments, such as steerable needles for precision surgery (Scali et al., 2017), drill rasps for creating cavities in thigh bones (Nakajima and Schwarz, 2014), and drill bits designed to perforate extraterrestrial surfaces, addressing challenges such as low gravity on Mars or the Moon and the low mass of probes carrying these drilling devices (Gouache et al., 2010; Alkalla et al., 2019). In fig wasps, the morphology of the ovipositor appears to evolve rapidly within lineages. Species with different life histories, such as gall inducers and kleptoparasites/parasitoids, are reported within the same genus (Ghara and Borges, 2010; Elias et al., 2012). The ovipositor morphology of these species typically corresponds to their specific life histories, reflecting the ecological niches they occupy and the resources they exploit (Ghara et al., 2011; Elias et al., 2018). Thus, the "drill on drill" behavior observed in the studied *Sycophila* species and other wasp species is unlikely to represent an evolutionary solution to physical constraints on their ovipositor structure. Comparative data on the ovipositor morphology of primary and secondary fig wasp parasitoids are unavailable. Suppose future studies may reveal morphological differences correlated with oviposition behavior. These differences would likely be adaptations to the "drill on drill" behavior (a consequence) rather than the cause selected for this reproductive behavior.

Determining the life history of *Sycophila* sp. is not a trivial task. In some aspects, it resembles kleptoparasitism, which occurs when one species (the perpetrator) exploits various types of resources from another species (the victim), including food, inanimate objects, domicile, parental care, mating partners, and information (Nishimura, 2010). According to this broad definition, the *Sycophila* female exploits the information and drilling service the *Physothorax* female provides. Additionally, its larva develops at the expense of the host, who is initially parasitized by the *Physothorax* larva. As the *Sycophila* larva often outcompetes the *Physothorax* larva, this interaction also relates to hyperparasitism, which occurs when a secondary insect parasitoid develops at the expense of a primary parasitoid. Sullivan and Völkl (1999) define "indirect" hyperparasitoids as those that attack the primary parasitoid's host, thereby only indirectly attacking the parasitoid itself. In this aspect, *Sycophila* sp. can be considered an indirect hyperparasitoid. This dual aspect of *Sycophila's* life history, incorporating both kleptoparasitic and hyperparasitic strategies, highlights the complexity of parasitoid-host interactions and underscores the adaptive versatility of these wasps in exploiting available ecological niches.

Janšta et al. (2018) speculate that Torymidae wasps may have originated as parasitoids of gall wasps (Cynipidae) or gall midges (Cecidomyiidae). However, a comprehensive phylogenetic analysis of the *Physothorax* genus is needed to determine whether it initially diversified as parasitoids of Cecidomyiidae before associating with galling fig wasps, or vice-versa. Therefore, the specialized relationships between species of *Sycophila*, *Physothorax*, and their potential hosts can help elucidate how associations between NPFWs evolved. Understanding these enhances our comprehension of ecological interactions and evolutionary dynamics in multitrophic insect-plant interactions.

**Acknowledgments**

The authors thank the Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, for providing the infrastructure necessary to carry out this research.

**Funding**

Levi O. Barros and Rodrigo A. S. Pereira were supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant # 142322/2020-2, 303986/2023-9). Sergio Jansen-González and Rodrigo A. S. Pereira were supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (grant # 2009/10273-9, 2022/11911-3). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

**Conflicts of interest**

The authors declare no conflicts of interest.

**Author contribution statement**

LOB, SJG, RASP contributed equally to all stages of the preparation of this manuscript.

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