

Research Article

***Pseudacteon* Parasitoids of *Azteca instabilis* Ants in Southern Mexico (Diptera: Phoridae; Hymenoptera: Formicidae)**

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Received 31 August 2011; Revised 27 December 2011; Accepted 10 January 2012

Academic Editor: Jean Paul Lachaud

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Three new species of the genus *Pseudacteon* are described, all from Chiapas, Mexico, and all of which are parasitoids of the ant *Azteca instabilis*. Sternite 6 of *Pseudacteon dorymyrmecis* Borgmeier is illustrated for the first time, and *P. confusus* Disney is synonymized with this species. The natural history of the *Azteca-Pseudacteon* interaction is described.

1. Introduction

The species of the phorid fly genus *Pseudacteon* Coquillett have been under intense scrutiny lately because of their potential to control invasive species of fire ants (*Solenopsis invicta* and *S. saevissima* in North America; *S. geminata* elsewhere) [1–3]. Other lesser-studied species of *Pseudacteon*, many of them undescribed, attack different hosts, including species of *Crematogaster*, *Lasius*, *Liometopum*, *Nylanderia*, *Pseudolasius*, and other small ants.

In a series of papers [4–7], a new host record, with *Azteca instabilis* Fr. Smith, has been documented from southern Mexico. Below, the so-far-known species of *Pseudacteon* associated with these ants are described, their identification clarified, and natural history summarized.

2. Materials and Methods

Specimens were collected into 70% alcohol and dried using hexamethyldisilazane [8]. They were deposited in the following collections:

CEET: El Colegio de la Frontera Sur, Colección de Insectos Asociados a Plantas Cultivadas en la Frontera Sur, Tapachula, Chiapas, Mexico,

LACM: Natural History Museum of Los Angeles County, California, USA,

MCZC: Museum of Comparative Zoology, Harvard University, Massachusetts, USA,

MUCR: Universidade de Costa Rica, San Jose, Costa Rica,

USNM: Smithsonian Institution, Washington, DC, USA.

3. Systematics

Pseudacteon Coquillett [9]; full synonymy in Borgmeier, 1968 [10]; type species. *Pseudacteon crawfordi* Coquillett, original designation.

Note on gender: the word *Actaeon* is a Greek name for a (male) hunter; thus, the name *Pseudacteon* means “false Actaeon” and is masculine in gender.

Pseudacteon laciniosus new species (see Figures 1(a) and 2(a)).

Diagnosis. The last general key to adults of *Pseudacteon* is that of Borgmeier [11]. This new species keys to couplet 10, where a user is given the alternatives of “ovipositor lanceolate” versus “ovipositor subcylindrical, tapering at apex.” Since the protruding stylet could fool users into accepting the first alternative, these flies could key out to either *P. dorymyrmecis* Borgmeier in the first lead or *P. onyx*

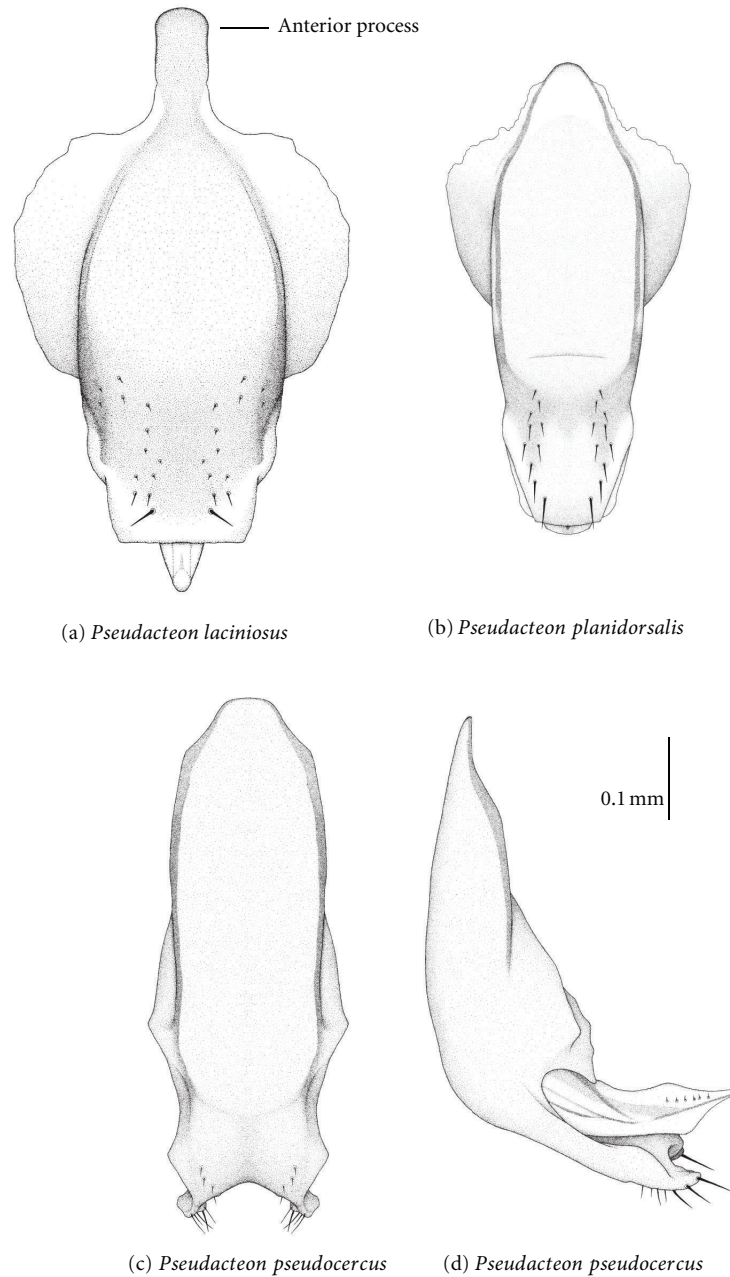


FIGURE 1: *Pseudacteon* species, female oviscapes, dorsal and right lateral (Figure 1(d)).

Steyskal in the second. Both of these species are markedly smaller than *P. laciniosus*, and both have narrower oviscapes. Further, based on examination of the holotype specimen, sternite 6 of *P. dorymyrmecis* has a long pair of medial setae originating basally on the segment (see Figure 2(b)). The oviscape of *P. onyx* was illustrated by Borgmeier [12] and is much more ventrally curved than that of *P. laciniosus*. Finally, unlike both of the other species, *P. laciniosus* has a dark brown body that strongly contrasts with its yellowish legs.

Disney (in [13]) described a new species, *Pseudacteon confusus*, that also keys to *P. dorymyrmex*. We examined a

paratype female of *P. confusus*, comparing it to the holotype female of *P. dorymyrmex*, and conclude the two are the same species. Therefore, *P. confusus* is a junior subjective synonym of *P. dorymyrmex* (new synonymy).

Description. (Female) Body length 1.2–1.5 mm (mean = 1.3). Frons dark brown, with 2-4-4-4 setae and one pair of proclinate supraantennal setae. Flagellomere 1 dark brown, rounded, flat; length of arista about two times that of flagellomere 1. Palpus light brown, setulae thick. Thorax dark brown. Scutellum with two pairs of large setae, anterior

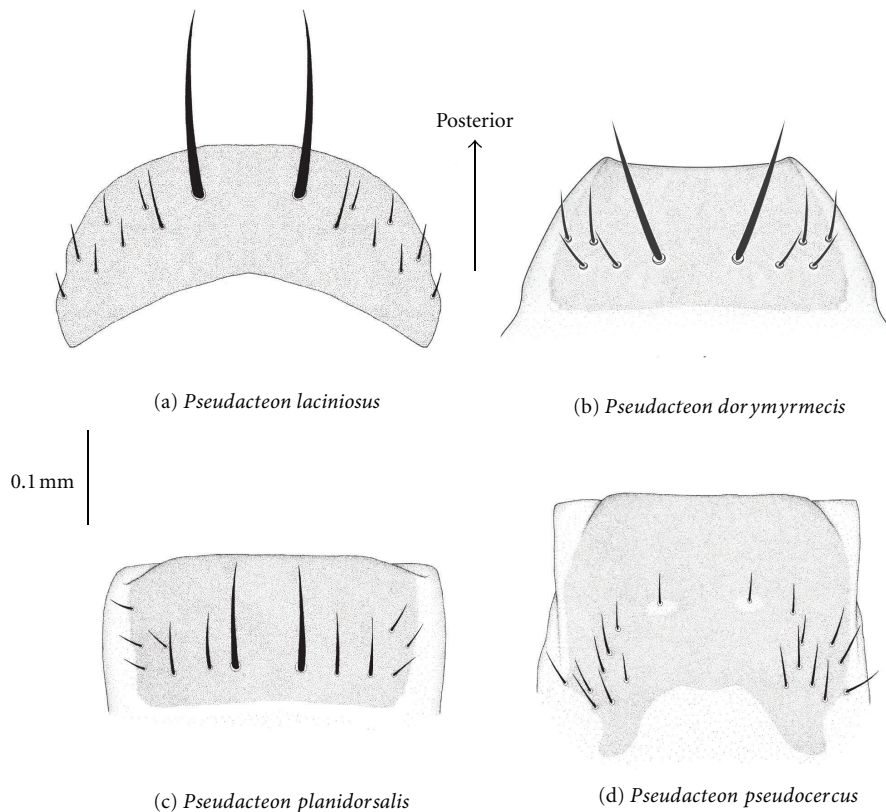


FIGURE 2: *Pseudacteon* species, venter of segment six.

pair 0.8 length of posterior pair. Legs yellowish brown, except forecoxa lighter, mid- and hind coxae darker brown. Wing with mean costal length 0.36 wing length, range 0.35–0.37. Halter yellow. Abdominal tergites dark brown, ventral abdominal membrane dark gray. Tergite 6 with large posterior emargination and lateral pair of setae. Sternite 6 with one large (0.18 mm) pair of slightly divergent setae; more lateral pair much smaller (0.06 mm), but larger to subequal in size to median pair on one or both sides in some specimens; with scattered setulae (see Figure 2(a)). Oviscape (Figure 1(a)) with narrow anterior process, convex dorsally, with large lateral flanges anteriorly, terminating bluntly, although preserved specimens often with stylet protruding, making oviscapes appear pointed. Minute setae on dorsal surface of oviscape arranged in laterally concave lines, with larger, divergent, apical pair.

Holotype. ♀, Mexico: Chiapas: Finca Irlanda, 15°11' N, 92°20' W, July 2010, S. Philpott, over *Azteca instabilis* (barcode LACM ENT 139561) (CEET).

Paratypes. 16♀, same data as holotype (CEET, LACM, MCZC, USNM).

Etymology. The specific epithet is from a Latin word for “fringed,” referring to the enlarged lateral margin of the oviscape.

Pseudacteon planidorsalis new species (see Figures 1(b) and 2(c))

Diagnosis. The species is similar to *Pseudacteon dorymyrmecis*, but differs in the presence of longer setae flanking the relatively shorter medial pair on sternite six.

Description. (*Female*) Body length 1.1–1.4 mm (mean = 1.3). Frons dark brown, with 2-4-4-4 setae and one pair of proclinate supra-antennal setae. Flagellomere 1 dark brown, rounded, flat; length of arista about two times that of flagellomere 1. Palpus yellow, setulae thick. Thorax brown. Scutellum with two pairs of large setae, anterior pair 0.47–0.60 length of posterior pair. Legs yellowish brown, except forecoxa lighter. Wing with mean costal length 0.38 wing length, range 0.37–0.39. Halter yellow. Abdominal tergites dark brown, ventral abdominal membrane dark gray. Tergite 6 with large posterior emargination and lateral pair of setae. Sternite 6 with one large (0.09 mm) pair of large setae and smaller lateral setae in basal transverse row; smaller lateral setae scattered more posteriorly (see Figure 2(c)). Oviscape (Figure 1(b)) lacking narrow anterior process, flat dorsally, with large lateral flanges anteriorly, terminating in rounded point (which is difficult to see in Figure 1(b) because the oviscape is downturned apically). Minute setae on dorsal surface of oviscape arranged in laterally convex lines, with slightly larger apical pair.

Holotype. ♀, Mexico: Chiapas: Finca Belen, 15°15' N, 92°23' W, 8.ii.2003, S. Philpott, over *Azteca instabilis* (barcode LACM ENT 294148) (CEET).

Paratypes. 3♀, same data as holotype (LACM).

Etymology. The specific epithet is from a Latin word for “flat backed,” referring to the surface of the oviscapae.

Pseudacteon pseudocercus new species (see Figures 1(c), 1(d) and 2(d))

Diagnosis. This species can be recognized by the strongly downturned, lightly sclerotized oviscapae with the pair of cercuslike apical processes. Other species of *Pseudacteon* with a bilobed oviscapae have the structure strongly sclerotized and dark brown in color.

Description. (Female) Body length 1.2 mm. Frons dark brown, with 2-4-4-4 setae and one pair of proclinate supra-antennal setae. Flagellomere 1 dark brown, rounded, flat; length of arista about two times that of flagellomere 1. Palpus light brown, setulae small, thin. Thorax brown. Scutellum with two pairs of large setae, anterior pair 0.47–0.60 length of posterior pair. Legs yellowish brown, except forecoxa lighter. Wing with costa 0.40 wing length. Halter yellow. Abdominal tergites brown, ventral abdominal membrane gray. Tergite 6 with large posterior emargination, pair of lateral setae near midline, and longer, thicker seta more laterally. Sternite 6 anteriorly emarginate, with scattered small setae (see Figure 2(d)). Oviscapae (see Figures 1(c) and 1(d)) without narrow anterior process, convex dorsally, apically downturned with pair of cercuslike lobes.

Holotype. ♀, MEXICO: Chiapas: Finca Belen, 15°15' N, 92°23' W, 8.ii.2003, S. Philpott, over *Azteca instabilis* (barcode LACM ENT 294147) (CEET). No other specimens preserved.

Etymology. The specific epithet is from Latin words for “false circus,” referring to the apex of the oviscapae.

4. Natural History

Little is known about the life cycle of *P. lacinosus*, *P. planidorsalis*, and *P. pseudocercus*, as the three species are only known from adults. Further, most natural history information available treats the flies as a genus, rather than as individual species, so more work will be necessary to distinguish between them. Adults have been observed in a range of shaded coffee plantations varying in canopy cover from ~25 to 100% in the Soconusco region of Chiapas, Mexico. Specifically, *P. lacinosus*, *P. planidorsalis*, and *P. pseudocercus* have been observed in Finca Irlanda, Tapachula municipality (15°11' N, 92°20' W), between 800–1100 m elevation, Finca Hamburgo, Tapachula municipality, between 800 to 1100 m elevation (15°10' N, 92°19' W), and in Finca Belen, Huixtla municipality, between 800 to 1200 m elevation (15°15' N, 92°23' W). The shade coffee habitats from which the phorids have been seen range from shaded monocultures with relatively low levels of canopy cover, tree

diversity, and density to rustic coffee plantations with a high diversity and density of shade trees and nearly 100% canopy cover [14]. Preliminary work indicates that the relative abundance of the three species in a range of coffee agroecosystems is similar, even as canopy conditions change [15].

Within the shade coffee habitats, females of *P. lacinosus*, *P. planidorsalis*, and *P. pseudocercus* have only been observed when hovering over or ovipositing in the host ant species, *A. instabilis*, or flying out of leaf litter collected from the ground or on tree trunks and branches near to *A. instabilis* nests. Males of the three species have not been collected or identified. As a group, the flies are attracted to the host ant by an alarm pheromone (1-acetyl-2-methylcyclopentane) released from the dorsal section of the ant gaster, but they do not attempt to oviposit without ant movement [16]. Work is underway to determine whether visual and similar chemical cues are used by each species in host location and host selection processes. Once a female fly locates host individuals, it will remain in the area for up to several minutes, closely hovering over and following moving ant individuals. Individual flies have been observed to attempt to oviposit at least a dozen times before disappearing from view; actual oviposition has not yet been quantified. Several individuals of the three species (up to 8–10) have been observed simultaneously around the same *A. instabilis* nest.

Phorids strongly modify the behavior of the *A. instabilis* ants and thereby indirectly affect other insects in coffee agroecosystems. *Azteca instabilis* is an aggressive, canopy-dominant ant that has important impacts on many members of the coffee insect food web [17]. In the presence of *Pseudacteon* flies, *A. instabilis* ant foraging is reduced (by about 50%) for up to 90 min. after the first appearance of the phorid [4]. Once the *Pseudacteon* arrives near an *A. instabilis* nest, the ants will either (1) run back to their nest, or to hiding places under tree bark or (2) remain motionless with their heads tilted back [17]. This reduction in ant activity allows other species of ants to gain access to food resources [3, 5] and reduces the predatory effects of ants on lepidopteran larvae [4] and the coffee berry borer (*Hypothenemus hampei* Ferrari) [18]. Furthermore, *A. instabilis* normally prevent adults of the coccinellid beetle *Azya orbiger* Mulsant from feeding on scale insects (*Coccus viridis* Green), a keystone mutualist of the ant. When the *A. instabilis* are under attack by the phorids, *A. orbiger* greatly increase their feeding rates [19] and oviposition rates (Hsieh and Perfecto, unpublished data). The host ant, *A. instabilis*, is patchily distributed within coffee agroecosystems, and one force maintaining this distribution and relative abundance of colonies within sample areas may be attacks from the phorid flies [7]. Thus the *Pseudacteon* flies, through their influence on the activity and distribution of this keystone species, likely have widespread impacts on the coffee insect food web. This result contrasts with conclusions of studies with *Pseudacteon tricuspis* Borgmeier and *P. curvatus* Borgmeier and fire ants (*S. invicta*). At least some studies have concluded that phorids attacking *S. invicta* do not have long-term impacts on the ants or associated arthropods (e.g., [20]).

Phorids that attack *A. instabilis* do not lower population sizes, similar to findings with *P. tricuspis* and *P. curvatus*, but likely impact coffee food webs due to their role in maintaining a similar number of colonies and reducing ant behavior.

Field evidence and observations suggest that *P. lacinosus*, *P. planidorsalis*, and *P. pseudocercus* adults probably live near their host, in leaf litter on the ground. Data suggest that the fly population is likely distributed in a density dependent manner, as number of attacks on *A. instabilis* individuals are more frequent and more numerous where *A. instabilis* densities are greater [6, 7]. Likewise, field evidence indicates that *Pseudacteon* adults are usually located within the leaf litter on the ground because time to first oviposition attempt on *A. instabilis* adults placed on the ground is much less than for ants placed at 1.5 m above ground [6]. However, more rapid arrival on the ground could mean that the phorids primarily search for hosts at ground level.

5. Key to Females of *Pseudacteon* Attacking *Azteca* in Southern Mexico

This key is intended for ant ecologists who need to identify phorid parasitoids from known ant hosts. A new general key to New World *Pseudacteon* is needed, as researchers currently must use a combination of Borgmeier [11], Porter and Pesquero [21], Plowes et al. [1], the key below, and reference to species not covered in the previously listed keys [22–26].

- (1) Apex of oviscapae with lobelike processes (Figures 1(d) and 2(a)); venter of segment 6 with short setae only (Figure 2(d)).....*P. pseudocercus* new species
 - Apex of oviscapae without lobe-like processes (Figures 1(a) and 1(c); venter of segment 6 with some long setae.....2
- (2) Oviscapae anteriorly with narrow process, dorsally domelike, with small setulae scattered posteriorly, but longer pair near apex; apex of oviscapae truncate (Figure 1(a)); enlarged ventral setae of segment 6 placed posterior to midpoint of sternite, much longer than other ventral setae (see Figure 2(b)).....*P. lacinosus* new species
 - Oviscapae anteriorly with broad apex; dorsally flattened on apical third (except for downturned tip); small setulae in laterally convex rows; apex of oviscapae pointed; enlarged ventral setae of segment 6 placed anterior to midpoint of sternite, only slightly longer than those directly lateral (see Figure 2(d)).....
*P. planidorsalis* new species

Acknowledgments

The authors thank Brian Koehler and Inna Strazhnik for expertly rendering the illustrations and Vladimir Berezovskiy and Giar-Ann Kung for technical assistance. Dr. R.H.L. Disney kindly loaned them a paratype specimen of *P. confusus* for comparison, and Dr. Carlos Lamas loaned them the holotype of *P. dorymyrmecis*. This research was supported

by NSF Grant DEB-1025922 to B. Brown and P. Smith, DEB-1020096 to S. Philpott, and DEB-0349388 to I. Perfecto and J. Vandermeer.

References

- [1] R. M. Plowes, E. G. Lebrun, B. V. Brown, and L. E. Gilbert, "A Review of *Pseudacteon* (diptera: Phoridae) that parasitize ants of the *Solenopsis geminata* complex (hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, vol. 102, no. 6, pp. 937–958, 2009.
- [2] S. D. Porter and L. E. Gilbert, "Assessing host specificity and field release potential of fire ant decapitating flies (Phoridae: *Pseudacteon*)," in *Assessing Host Ranges for Parasitoids and Predators Used for Classical Biological Control: A Guide to Best Practice*, R. G. van Driesche and R. Reardon, Eds., pp. 152–176, USDA Forest Service, Morgantown, WV, USA, 2004.
- [3] D. H. Feener Jr. and B. V. Brown, "Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae)," *Annals of the Entomological Society of America*, vol. 85, no. 1, pp. 80–84, 1992.
- [4] S. M. Philpott, J. Maldonado, J. Vandermeer, and I. Perfecto, "Taking trophic cascades up a level: behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems," *Oikos*, vol. 105, no. 1, pp. 141–147, 2004.
- [5] S. M. Philpott, "Trait-mediated effects of parasitic phorid flies (Diptera: Phoridae) on ant (Hymenoptera: Formicidae) competition and resource access in coffee agro-ecosystems," *Environmental Entomology*, vol. 34, no. 5, pp. 1089–1094, 2005.
- [6] S. M. Philpott, I. Perfecto, J. Vandermeer, and S. Uno, "Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid," *Environmental Entomology*, vol. 38, no. 3, pp. 790–796, 2009.
- [7] J. Vandermeer, I. Perfecto, and S. M. Philpott, "Clusters of ant colonies and robust criticality in a tropical agroecosystem," *Nature*, vol. 451, no. 7177, pp. 457–459, 2008.
- [8] B. V. Brown, "A further chemical alternative to critical-point-drying for preparing small (or large) flies," *Fly Times*, vol. 11, p. 10, 1993.
- [9] D. W. Coquillett, "A new phorid genus with horny ovipositor," *The Canadian Entomologist*, vol. 39, no. 6, pp. 207–208, 1907.
- [10] T. Borgmeier, "A catalogue of the Phoridae of the World (Diptera, Phoridae)," *Studia Entomologica*, vol. 11, no. 1–4, pp. 1–367, 1968.
- [11] T. Borgmeier, "New or little-known phorid flies, mainly of the Neotropical Region," *Studia Entomologica*, vol. 12, no. 1–4, pp. 33–132, 1969.
- [12] T. Borgmeier, "Revision of the North American phorid flies—part I. The Phorinae, Aenigmatiinae and Metopininae, except *Megaselia* (Diptera, Phoridae)," *Studia Entomologica*, vol. 6, no. 1–4, pp. 1–256, 1963.
- [13] R. H. L. Disney, L. Elizalde, and P. J. Folgarait, "New species and new records of scuttle flies (diptera: Phoridae) that parasitize leaf-cutter and army ants (hymenoptera: Formicidae)," *Sociobiology*, vol. 54, no. 2, pp. 601–631, 2009.
- [14] P. Moguel and V. M. Toledo, "Biodiversity conservation in traditional coffee systems of Mexico," *Conservation Biology*, vol. 13, no. 1, pp. 11–21, 1999.

- [15] K. Reese and S. M. Philpott, "Differences in relative abundance of three *Pseudacteon* phorid fly species in coffee farms differing in shade management," in preparation.
- [16] K. A. Mathis, S. M. Philpott, and R. F. Moreira, "Parasite lost: chemical and visual cues used by *Pseudacteon* in search of *Azteca instabilis*," *Journal of Insect Behavior*, vol. 24, no. 3, pp. 186–199, 2011.
- [17] J. Vandermeer, I. Perfecto, and S. Philpott, "Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service," *BioScience*, vol. 60, no. 7, pp. 527–537, 2010.
- [18] G. L. Pardee and S. M. Philpott, "Cascading indirect effects in a coffee agroecosystem: effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat," *Environmental Entomology*, vol. 40, no. 3, pp. 581–588, 2011.
- [19] H. Liere and A. Larsen, "Cascading trait-mediation: disruption of a trait-mediated mutualism by parasite-induced behavioral modification," *Oikos*, vol. 119, no. 9, pp. 1394–1400, 2010.
- [20] L. W. Morrison and S. D. Porter, "Testing for population-level impacts of introduced *Pseudacteon tricuspis* flies, phorid parasitoids of *Solenopsis invicta* fire ants," *Biological Control*, vol. 33, no. 1, pp. 9–19, 2005.
- [21] S. D. Porter and M. A. Pesquero, "Illustrated key to *Pseudacteon* decapitating flies (Diptera: Phoridae) that attack *Solenopsis saevissima* complex fire ants in South America," *Florida Entomologist*, vol. 84, no. 4, pp. 691–699, 2001.
- [22] B. V. Brown, S. A. Schneider, and J. S. Lapolla, "A new North American species of *Pseudacteon* (Diptera: Phoridae), parasitic on *Nylanderia arenivaga* (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, vol. 104, no. 1, pp. 37–38, 2011.
- [23] R. H. L. Disney, "Three new species of scuttle-fly (Diptera: Phoridae) that parasitize ants (Hymenoptera: Formicidae) in North America," *Journal of Zoology*, vol. 197, no. 4, pp. 473–481, 1982.
- [24] L. A. Calcaterra, "*Pseudacteon calderensis*, a new fly species (Diptera: Phoridae) attacking the fire ant *Solenopsis interrupta* (Hymenoptera: Formicidae) in northwestern Argentina," *Annals of the Entomological Society of America*, vol. 100, no. 4, pp. 470–473, 2007.
- [25] B. V. Brown, P. Folgarait, and L. Gilbert, "A new species of *Pseudacteon* attacking *Solenopsis* fire ants (Hymenoptera: Formicidae) in Argentina," *Sociobiology*, vol. 41, no. 3, pp. 685–688, 2003.
- [26] M. R. Mattos and M. R. Orr, "Two new *Pseudacteon* species (Diptera: Phoridae), parasitoids of ants of the genus *Linepithema* (Hymenoptera: Formicidae) in Brazil," *Studia Dipterologica*, vol. 9, no. 1, pp. 283–288, 2002.



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