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Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae)

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ABSTRACT

A review of bee species used as hosts of mutillid wasps in the Neotropical region is presented. Three new confirmed host records are provided for the mutillid species *Hoplomutilla biplagiata* Mickel, 1939, *Pappognatha limes* Mickel, 1939, and *Tallium aracati* Casal, 1962. Two potential host records are provided for *Euspinolia rufula* Mickel, 1938 and *Lophomutilla inca* Fritz and Pagliano, 1993. Additionally, *Mutilla hoplitiformis* Strand, 1909, is transferred to the genus *Darditilla*. Correlations between host nesting habits and female mutillid morphology are discussed. Lastly, all known confirmed and potential host records in the Neotropical region are compiled.

Introduction

Mutillid wasps (Hymenoptera, Mutillidae), also known as velvet ants, comprise a diverse group of solitary aculeate wasps with over 4200 described species worldwide (Lelej and Brothers, 2008). They occur on all continents except Antarctica, and are most diverse in tropical regions (Brothers, 1975). In the Neotropical region, there are about 1400 described species in two subfamilies, Mutillinae and Sphaeropthalminae (Nonveiller, 1990). A remarkable feature of mutillids is their extreme sexual dimorphism, wherein females are always wingless and males are almost always fully winged and capable of flight.

Most mutillids are solitary parasitoids of solitary hosts (Brothers et al., 2000). The larvae are always ectoparasitoids of host stages which are enclosed in some sort of protective package (i.e. cell, cocoon, puparium, ootheca) and which are not actively feeding (Brothers, 1989). The known host spectrum includes several species of Diptera (e.g. Brothers, 1971; Amini et al., 2014), Coleoptera (Péringuey, 1899; Sergeev and Lelej, 2011), Lepidoptera (Seyrig, 1936), and Blattodea (Mickel, 1974), but velvet ants mainly parasitize other aculeate Hymenoptera, especially bees (the family Apidae *sensu* Melo and Gonçalves, 2005). Despite the size of the family, knowledge of mutillid biology is scanty. The hosts for only 2–3% of velvet ants are known (Brothers, 1989), and complete life history for only a few species has been recorded (e.g. Brothers, 1972, 1978).

Apidae is one of the most diverse families of Hymenoptera, with more than 17,000 bee species in seven subfamilies (Michener, 2007). They occur in virtually all terrestrial habitats and they play a key role in ecosystem function as major pollinators of flowering plants (Waser and Ollerton, 2006). The Neotropical fauna encompasses over 5000 described species (Moure et al., 2007) in five subfamilies: Andreninae, Apinae, Colletinae, Halictinae, and Megachilinae (Melo and Gonçalves, 2005).

The vast majority of bees are solitary ground-nesting or twig-nesting species that provision their larvae with a mixture of pollen and nectar (Michener, 2007). Because of their nesting habits and diversity, bees are known as a major host for mutillid wasps (Brothers, 1989).

Here we present a review of mutillid wasps and their host bees in the Neotropical region based on published records as well as some new findings. A compilation of host records is provided in Table 1.

Material and methods

Data on host associations were compiled from literature records and, in a few cases, from specimens deposited in the entomological collections of the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP) and Utah State University, Logan, Utah, USA (EMUS). The names of the mutillids and the

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Table 1
Known bee host records for mutillid wasps in the Neotropical region.

Mutillidae	Host bee	Subfamily	Parasitism	References
Sphaeropthalminae				
Anomophotopsis				
A. quinteroi Cambra, 2006	*Paroxystoglossa transversa* Moure, 1943	Halictinae	Confirmed	Rocha-Filho and Melo (2011: 2825)
Atillum				
A. albicomum Mickel, 1943	*Caupolicana* sp.	Colletinae	Potential	Fritz (1998: 445)
A. charoneum Mickel, 1943	*Caupolicana* sp.	Colletinae	Potential	Fritz (1998: 445)
A. sumptuosum (Gerstaecker, 1874)[1]	?	Apinae?	Potential	Lynch Arribálzaga (1878: 178)[2]
A. venatrix Mickel, 1943	*Caupolicana* sp.	Colletinae	Potential	Fritz (1998: 445)
Calomutilla				
C. temporalis (Gerstaecker, 1874)[3]	*Pseudaugochlora graminea* (Fabricius, 1804)	Halictinae	Confirmed	Ihering (1904: 466)[4]
Darditilla				
D. hoplitiformis (Strand, 1909) **comb. nov.**[5]	*Ptilothrix plumata* Smith, 1853	Apinae	Potential	Friese (1908: 51)[6], Strand (1909: 233)
Dasymutilla				
D. aequatorialis (André, 1906)[7]	*Melitoma* sp.	Apinae	Confirmed	André (1906: 167)[8]
D. araneoides (Smith, 1862)	*Centris (Centris) flavofasciata* Friese, 1899	Apinae	Potential	Vinson et al. (1987: 260)
D. blattoserica (Kohl, 1882)	*Melitoma* sp.	Apinae	Confirmed	Manley and Pitts (2007: 32)
D. canina (Smith, 1855)	*Melitoma marginella* (Cresson, 1872)	Apinae	Confirmed	Linsley et al. (1980: 22)
D. jalisco Manley, 2003	*Diadasia knabiana* Cockerell, 1917	Apinae	Confirmed	Manley (2003: 682)
D. mirabilis Manley and Pitts, 2007	*Centris* sp.	Apinae	Confirmed	Manley and Pitts (2007: 69)
Dasymutilla sp.	*Centris (Centris) aethiocesta* Snelling, 1984	Apinae	Confirmed	Vinson et al. (1987: 260)[9]
Dasymutilla sp.	*Centris (Centris) flavofasciata* Friese, 1899	Apinae	Potential	Vinson et al. (1987: 260)
Dimorphomutilla				
D. formosa Mickel, 1938[10]	*Corynura (Corynura) chilensis* (Spinola, 1851)	Halictinae	Potential	Janvier (1933)[11]
D. lunulata (Spinola, 1851)[12]	*Alloscirtetica tristrigata* (Spinola, 1851)	Apinae	Potential	Janvier (1933)[13]
Euspinolia				
E. albicoma Mickel, 1938	*Anthophora (Mystacanthophora) incerta* Spinola, 1851	Apinae	Confirmed	Mickel (1938: 66)[14]
E. rufula Mickel, 1938	*Melitoma* sp.	Apinae	Potential	This study
Hoplocrates				
H. specularis (Gerstaecker, 1874)	*Monoeca haemorrhoidalis* (Smith, 1854)	Apinae	Potential	Rocha-Filho and Melo (2011: 2825)
Hoplognathoca				
H. costarricensis Suárez, 1962	*Thygater* sp.	Apinae	Potential	Roubik (1989: 235)
Hoplomutilla				
H. biplagiata Mickel, 1939	*Centris (Paracentris) burgdorfi* Friese, 1900	Apinae	Confirmed	This study
H. conspecta Mickel, 1939	*Eulaema (Eulaema) meriana* (Olivier, 1789)	Apinae	Potential	Cameron and Ramírez (2001: 154)
H. myops myops (Burmeister, 1854)	*Epicharis (Xanthepicharis) bicolor* Smith, 1854	Apinae	Potential	Rocha-Filho et al. (2008: 237)
H. opima Mickel, 1939	*Centris (Melacentris) rufosuffusa* Cockerell, 1935	Apinae	Confirmed	Callan (1977: 131)
H. spinosa (Swederus, 1787)	*Eulaema (Apeulaema) nigrita* Lepeletier, 1841	Apinae	Confirmed	Quintero and Cambra (2001: 300)
H. triumphans Mickel, 1939	*Eufriesea* sp.	Apinae	Confirmed	Lenko (1964: 200)[15]
H. xanthocerata (Smith, 1862)	*Eulaema (Eulaema) meriana* (Olivier, 1789)	Apinae	Confirmed	Roubik (1990: 151)
Hoplomutilla sp.	*Centris (Ptilotopus) derasa* Lepeletier, 1841	Apinae	Potential	Vesey-Fitzgerald (1939: 109)
Hoplomutilla? sp.	*Eulaema (Eulaema) terminata* Smith, 1874	Apinae	Potential	Bennett (1972: 120), Yanega (1994: 465)
Lophomutilla				
L. corupa Casal, 1968	*Dialictus seabrai* (Moure, 1956)	Halictinae	Potential	Bergamaschi et al. (2010: 2604)
L. halicta (Mickel, 1973)	*Augochlorella comis* (Vachal, 1911)[16]	Halictinae	Confirmed	Eickwort and Eickwort (1973: 13), Mickel (1973: 3)
L. inca Fritz and Pagliano, 1993	*Neocorynura* sp.	Halictinae	Potential	This study
Lophomutilla sp.	*Neocorynura muiscae* Smith-Pardo and Gonzalez, 2006	Halictinae	Potential	Gonzalez and Engel (2004: 68), V.H. Gonzalez, pers. comm.
Lophostigma				
L. cincta (du Buysson, 1892)	*Megalopta genalis* Meade-Waldo, 1916	Halictinae	Confirmed	Cambra et al. (2005: 232)
L. cincta (du Buysson, 1892)	*Megalopta amoena* (Spinola, 1853)	Halictinae	Confirmed	Cambra et al. (2005: 232)[17]
Lynchiatilla				
L. parana Cambra, 2012	*Paroxystoglossa spiloptera* Moure, 1960	Halictinae	Potential	Bergamaschi et al. (2012: 63)
Pappognatha				
P. limes Mickel, 1939	*Euglossa (Glossura) ignita* Smith, 1874	Apinae	Confirmed	This study
P. myrmiciformis (Cameron, 1897)	*Euglossa (Glossurella) dodsoni* Moure, 1965	Apinae	Confirmed	Dodson (1966: 619), Yanega (1994: 465)
P. panamensis Quintero and Cambra, 2005	*Euglossa (Euglossa) hemichlora* Cockerell, 1917	Apinae	Confirmed	Cambra et al. (2015: 6)
P. panamensis Quintero and Cambra, 2005	*Euglossa (Glossura) imperialis* Cockerell, 1922	Apinae	Confirmed	Cambra et al. (2015: 6)
P. patruelis (André, 1898)	*Euglossa* sp.	Apinae	Confirmed	Quintero and Cambra (2005: 196), this study
P. speciosa Mickel, 1939	*Euglossa (Glossuropoda) intersecta* Latreille, 1817	Apinae	Confirmed	Dodson (1966: 625)[18], Yanega (1994: 465)

Table 1 (*Continued*)

Mutillidae	Host bee	Subfamily	Parasitism	References
Pseudomethoca				
P. hesperus Brothers, 1982	*Halictus (Pachyceble) hesperus* Smith, 1862	Halictinae	Potential	Brothers (1982: 209), Brooks and Roubik (1983: 278)
P. pumila (Burmeister, 1854)	*Dialictus seabrai* (Moure, 1956)	Halictinae	Potential	Bergamaschi et al. (2011: 59)
P. ravula (Cameron, 1894)	*Xenoglossa fulva* Smith, 1854	Apinae	Potential	Linsley et al. (1955: 137)
P. spixi (Diller, 1989)[19]	*Monoeca haemorrhoidalis* (Smith, 1854)	Apinae	Potential	Rocha-Filho and Melo (2011: 2825)
P. spixi (Diller, 1989)[20]	*Monoeca xanthopyga* Harter-Marques, Cunha and Moure, 2001	Apinae	Confirmed	Cunha and Blochtein (2003: 112); Cunha (2004: 36)
P. willei Mickel, 1969	*Dialictus umbripennis* (Ellis, 1913)	Halictinae	Confirmed	Mickel (1969: 526), Wille and Orozco (1970: 215)[21]
P. willei Mickel, 1969	*Halictus (Pachyceble) hesperus* Smith, 1862	Halictinae	Potential	Brothers (1982: 211)[22], Brooks and Roubik (1983: 278)
Pseudomethoca sp.	*Dialictus figueresi* (Wcislo, 1990)	Halictinae	Confirmed	Cambra (1997: 123)[23]
Pseudomethoca sp.	*Augochlora* (*Oxystoglossella*) *nominata* Michener, 1954	Halictinae	Potential	Brothers et al. (2000: 210)
Pseudomethoca sp.[24]	*Augochloropsis iris* (Schrottky, 1902)	Halictinae	Confirmed	Coelho (2002: 185)
Reedomutilla				
R. heraldica (Saussure, 1867)[25]	*Melissoptila dama* (Vachal, 1904)	Apinae	Potential	Jörgensen (1912b: 274)[26]
Sphaeropthalma				
S. (Photopsis) gayi Mickel, 1937[27]	*Neofidelia profuga* Moure and Michener, 1955	Megachilinae	Confirmed	Rozen (1973: 10)
S. (Photopsis) jacala Schuster, 1958	*Centris (Hemisiella) nitida* Smith, 1874	Apinae	Confirmed	Pitts and Parker (2005: 62)
Tallium				
T. aracati Casal, 1962	*Centris (Paracentris) burgdorfi* Friese, 1900	Apinae	Confirmed	This study
Traumatomutilla				
Traumatomutilla sp.	*Diadasina distincta* (Holmberg, 1903)[28]	Apinae	Confirmed	Jörgensen (1912a: 158)
Mutillinae				
Timulla				
T. intermissa Mickel, 1938	*Exomalopsis (Exomalopsis) fulvofasciata* Smith, 1879	Apinae	Potential	Aranda and Graciolli (2013: 2)
T. terminalis (Gerstaecker, 1874)	*Exomalopsis (Exomalopsis) fulvofasciata* Smith, 1879	Apinae	Potential	Aranda and Graciolli (2013: 2)
Unidentified genera				
Mutillidae sp.	*Alepidosceles filitarsis* (Vachal, 1904)[29]	Apinae	Confirmed	Jörgensen (1909: 64)
Mutillidae sp.	*Alloscirtetica tristrigata* (Spinola, 1851)[30]	Apinae	Potential	Ruiz (1940: 309)
Mutillidae sp.	*Chalepogenus caeruleus* (Friese, 1906)[31]	Apinae	Confirmed	Janvier (1926: 240)
Mutillidae sp.	*Exomalopsis* sp.	Apinae	Potential	Ruiz (1940: 322)
Mutillidae sp.	*Augochlora* (*Oxystoglossella*) *morrae* Strand, 1910	Halictinae	Confimed	Michener and Lange (1958: 491)

[1] Cited as *Mutilla sumptuosa*.
[2] *Eucera* sp.
[3] *Ephuta temperalis* [sic].
[4] *Augochlora gramminea* [sic].
[5] *Mutilla hoplitiformis*.
[6] *Mutilla* sp.
[7] *Ephuta aequatorialis*.
[8] *Entechnia taurea*.
[9] *Centris aethectera* [sic].
[10] *Neomotilla attenuata* [corrected by Quintero and Cambra, 2001].
[11] *Halictus chloris*.
[12] *Mutilla lunulata*.
[13] *Tetralonia tristrigata*.
[14] *Podalirius incertus*.
[15] *Euplusia* sp.
[16] *Augochlorella edentata* [Eickwort and Eickwort (1973) reared the mutillid and Mickel (1973) described as *Paramutilla halicta*].
[17] *Megalopta ecuadoria*.
[18] *Euglossa brullei*.
[19] *Pseudomethoca melanocephala*.
[20] *Traumatomutilla* sp. [a misidentification, corrected by Bartholomay et al. (2015a)].
[21] *Lasioglossum (Dialictus) umbripenne*.
[22] *Pseudomethoca transversa*.
[23] *Lasioglossum (Dialictus) figueresi*.
[24] *Sphinctopsis* sp.
[25] *Reedia Claraziana* [sic].
[26] *Epimelissodes dama*.
[27] *Photopsis gayi*.
[28] *Ancyloscelis distinca*.
[29] *Ancyloscelis nigriceps* Friese, 1906.
[30] *Tetralonia tristrigata*.
[31] *Exomalopsis caerulea*.

bees were updated according to Nonveiller (1990) and Moure et al. (2007), respectively.

Parasitism was classified into two categories: (A) confirmed, when the mutillid was reared from host bee cells; and (B) potential, when the mutillid was observed entering or attempting to enter the bee nest, or found within the bee nest, or walking on nest entrances and surroundings, or when potential host cells found inside the bee nest contained mutillid cocoons or empty brownish papery cocoons, presumed to belong to mutillids. We do not consider as a valid potential host record some cases in literature in which a mutillid was only observed in the vicinity of nesting sites of bees.

Results

A summary of all potential and confirmed known records of bees as hosts of mutillid wasps in the Neotropical region is presented in Table 1. Data on confirmed parasitism are available for 29 species in 12 genera, only in the subfamily Sphaeropthalminae, and involve a total of 34 cases of parasitism of bees, including three cases where the mutillids were not identified (Table 1). Their host bees belong to the subfamilies Apinae (24 cases), Halictinae (nine cases) and Megachilinae (one case). The mutillid genera with the most records as a parasitoid are *Dasymutilla* Ashmead, with six species, *Hoplomutilla* Ashmead and *Pappognatha* Mickel, both with five species, and *Pseudomethoca* Ashmead, with four species. Orchid bees (Apinae, Euglossini) are the group of bees with the most records as hosts of mutillid wasps, with nine cases. Further, *Euglossa* Latreille is the genus of bees with the most records as hosts of Mutillidae, with six cases (see Table 1).

Three new confirmed host records, as well as two potential host records, are presented here, with voucher specimens deposited at DZUP and EMUS collections. *Hoplomutilla biplagiata* Mickel, 1939 and *Tallium aracati* Casal, 1962 emerged from the nests of *Centris (Paracentris) burgdorfi* Friese, 1900 (bee specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP) collection and in DZUP) in Natal, Rio Grande do Norte, Brazil (DZUP), and the third record was made based on a specimen of *Pappognatha limes* Mickel, 1939 bearing a label on the pin indicating that *Euglossa (Glossura) ignita* Smith, 1874 was its host in Iquitos, Peru (DZUP). Additionally, a potential host record is based on a pinned female specimen of *Lophomutilla inca* Fritz and Pagliano, 1993, which bears a label noting that it was taken from a nest of *Neocorynura* sp. in Tunja, Colombia (EMUS). Lastly, an additional potential host record is based on two pinned female specimens of *Euspinolia rufula* Mickel, 1938 collected near Sayán, Peru (EMUS); one specimen bears a label stating, "dead in nests of *Melitoma*", while the second specimen bears a label stating, "in nest of *Melitoma*".

Strand (1909) described *Mutilla hoplitiformis* from San Bernardino, Paraguay based on a single female that was found inside the nest of the bee *Ptilothrix plumata* Smith, 1853 (here considered as a potential host). This species has not been treated since its description (Strand, 1909) and was still in the genus *Mutilla* Linnaeus until this paper (Nonveiller, 1990). The type of *M. hoplitiformis* is deposited in the Museum für Naturkunde, Berlin, Germany (ZMB), and was examined by DRL. Based on its granulate pygidium (see Luz and Williams, 2014), it is clear that this species belong to the genus *Darditilla* Casal. Therefore, it is hereby transferred to *Darditilla*, in the new combination *Darditilla hoplitiformis* (Strand, 1909) **comb. nov.**

Discussion

Based on the available data, Apidae appear to be the primary hosts for mutillid wasps in the Neotropical region. Nevertheless, there are several cases of other hymenopterans as confirmed hosts of Mutillidae in the neotropics, such as apoid wasps of the families Crabronidae (e.g. Quintero and Cambra, 2001; Bartholomay et al., 2015b) and Sphecidae (e.g. Morato, 1994; Fritz, 1998), and spider wasps of the family Pompilidae (e.g. Zanette et al., 2004).

In the Neotropical region, the cases of confirmed parasitism of bees by mutillid wasps occur only in the subfamily Sphaeropthalminae. The other subfamily of Mutillidae present in the neotropics, Mutillinae, has been implicated only as a potential parasite of one bee species (Aranda and Graciolli, 2013; see Table 1). Otherwise, it is known to parasitize members of the families Crabronidae (e.g. Callan, 1942; Quintero and Cambra, 1996b) and Pompilidae (e.g. Zanette et al., 2004; Loyola and Martins, 2006).

The degree of host specificity remains poorly known in Mutillidae. Some species seem to be more situation-specific rather than host-specific, and this could be a general characteristic of the entire family (Brothers, 1989). Despite this situation, Krombein (1972), Quintero and Cambra (1996a), and Williams et al. (2011) have revealed a link between female morphology and host preference in Mutillidae. According to Quintero and Cambra (1996a, referencing Naumann, 1991), species with a well-defined pygidial plate bound by lateral carinae in the female typically parasitize ground-nesting hosts, while females with an undefined pygidium parasitize arboreal or twig-nesting hosts. A well-developed pygidial plate is also found in females of bee species nesting in the ground, while those nesting in other substrates have a vestigial plate or lack it entirely (Michener, 2007). Bees use the pygidial plate to smooth out the walls of their underground brood cells and to pack soil when closing the lateral tunnels (Batra, 1984). Brothers (1972) noted that females of the mutillid *Pseudomethoca frigida* (Smith, 1855), after ovipositing on an immature ground-nesting sweat bee, *Dialictus zephyrus* (Smith, 1853), used their [defined] pygidium to tamp down soil particles used to seal the host cell.

Additionally, according to Krombein (1972) and Williams et al. (2011), mutillid species that parasitize ground-nesting hosts usually have a well-developed foretarsal rake on the external margin of the foretarsus, and the mid- and hindtarsi have apical spines on the outer margin that are longer than the spines on the inner margin. Conversely, mutillid species that parasitize arboreal or twig-nesting hosts lack a foretarsal rake, and the apical spines on the inner and outer margins of the mid- and hindtarsi are similar in length. Unlike bees, which do not have well-developed tarsal rakes, mutillid females probably behave like other aculeate wasps that build underground nests and use their tarsal rakes to push the soil backwards under the body when excavating the ground in search of host brood cells to parasitize.

Although the available host information is sparse, there seems to be a non-random association between some genera of Mutillidae and some genera of Apidae that they parasitize; further, female mutillid morphology and nesting habits of the host appear to be correlated. We discuss some known cases below.

Dasymutilla Ashmead is a genus of mutillid wasps with over 200 described species that are distributed throughout North America, Central America, and northern South America (Pilgrim et al., 2009). Females of this genus have a well-defined pygidial plate and foretarsal rake, and six different species are known to parasitize ground-nesting bees of the subfamily Apinae in the neotropics (see Table 1). This evidence corroborates the assertions made by Krombein (1972), Quintero and Cambra (1996a), and Williams et al. (2011). In addition to parasitizing ground-nesting *Centris* bees, four species of *Dasymutilla* are known to parasitize Emphorini bees of the genera *Melitoma* Lepeletier and Serville and *Diadasia* Patton in the neotropics. Nests of emphorine bees are shallow and often built in aggregations in banks or in flat ground; the nest entrances are frequently surrounded by mud turrets (Michener, 2007). Species of *Dasymutilla* are known to parasitize numerous ground-nesting bee

genera in the Nearctic region, including species of *Melitoma* and *Diadasia* (Bartholomay et al., 2015a).

Hoplomutilla Ashmead is a Neotropical genus with more than 90 described species (Mickel, 1939a; Schuster, 1951) that includes some of the largest species of mutillid wasps in the neotropics. Females usually have a well-defined pygidium and are known to parasitize large apine oil-collecting bees of the tribes Centridini (*Centris* Fabricius) and Epicharitini (*Epicharis* Klug), as well as large orchid bees (the genera *Eufriesea* Cockerell and *Eulaema* Lepeletier in the tribe Euglossini). Most species of Centridini and all Epicharitini bees build underground nests in banks or in flat ground (Michener, 2007), while orchid bees of the genera *Eufriesea* and *Eulaema* construct their nests in cavities in banks, tree trunks, logs, etc. (Dressler, 1982; Michener, 2007). Surprisingly, female morphology (i.e. form of foretarsus and pygidium, outlined above) is indicative of host preference for only some members of *Hoplomutilla*, such as *H. biplagiata* Mickel, 1939 parasitizing the ground-nesting *Centris* (*Paracentris*) *burgdorfi* Friese, 1900 (this study) and *H. xanthocerata* (Smith, 1862) parasitizing *Eulaema* (*Eulaema*) *meriana* (Olivier, 1789) in a rotten log 1.5 m above the ground (Roubik, 1990). Mutillid females in the former case have well developed pygidium and foretarsal rake, while in the latter case the females have an undefined pygidium and lack a foretarsal rake, a pattern consistent with the nesting habits of their bee hosts. On the other hand, there are two unusual records, one confirmed and one potential, involving *Hoplomutilla* species with a foretarsal rake and defined pygidium parasitizing the orchid bee genera *Eufriesea* and *Eulaema*, which nest above-ground (Cameron and Ramírez, 2001; Quintero and Cambra, 2001; see Table 1). These latter records are noteworthy considering the otherwise consistent relationship between morphology and host choice for the other records reviewed in this study.

The most remarkable and specific case of association between mutillid wasps and bees appears to occur between the genera *Pappognatha* Mickel and orchid bees of the genus *Euglossa* Latreille. *Pappognatha* is a Neotropical mutillid genus with 15 described species (Quintero and Cambra, 2005) that possess a unique characteristic for the New World mutillids, wherein both sexes have the mandibles clothed with dense, short setae (Mickel, 1939b). Females have an undefined pygidium and do not possess a foretarsal rake. In addition to these morphological traits, *Pappognatha* is the only known mutillid genus that has an arboreal habit as a general characteristic (Yanega, 1994). Their unique confirmed hosts are orchid bees of the genus *Euglossa*, with six reported cases, including the new one presented here. Many species of *Euglossa* build aerial resin nests (Dressler, 1982; Michener, 2007), which suggests host-specificity for *Pappognatha* species. On the other hand, species of *Pappognatha* are also able to parasitize non-aerial nests of *Euglossa* built in cavities close to the ground surface, as observed for *P. patruelis* by GARM (unpubl. obs.; reported by Quintero and Cambra (2005) from specimen label data). A female of *P. patruelis* was found inside a nest of an unidentified species of *Euglossa* built in a small cavity of a rotten log lying in the ground of a forest site in Minas Gerais, Brazil. The mutillid female was inside the cavity with her head near the entrance orifice in the resin wall made by the *Euglossa* female. The female and the brood cells were collected, but no adults emerged from the nest in the following weeks. Upon dissection of the nest, two dead mutillid imagoes (one female and one male) were found within their respective cells, as well as additional dead mutillid pupae. No immatures of the host bee were present, indicating that all cells had been successfully parasitized by the *Pappognatha* female. Based on this single observation, the behavior of the female *Pappognatha* suggested that she was guarding the parasitized host nest. Regarding the peculiar mandibles of *Pappognatha*, their dense cover of pubescence might be an adaptation to prevent resin from sticking to them as they chew through the host cell walls.

According to Brothers (1989), fewer than 4% of mutillid species have any biological traits studied. More than 25 years since Brothers' observation, most aspects of the biology of Mutillidae remain unclear and have been little studied. Detailed studies on host-parasitoid relations and behavior of mutillid wasps are still lacking and virtually missing worldwide.

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