

New host records of *Aglaomelissa duckei* and a compilation of host associations of Ericrocidini bees (Hymenoptera: Apidae)

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ABSTRACT. For the first time, confirmed host records are reported for the monotypic Ericrocidini genus *Aglaomelissa* Snelling & Brooks, 1985. *Aglaomelissa duckei* (Friese, 1906) emerged from trap-nests of *Centris* (*Heterocentris*) *analis* (Fabricius, 1804) and *C. (Heterocentris) terminata* Smith, 1874 from two sites in the Brazilian Amazonian region. The parasitism ratio caused by *A. duckei* was high, varying from 80 to 100% of the brood cells in a single trap-nest. Also, a compilation of the known host records for the species of Ericrocidini is presented and host-parasite associations are discussed. Host associations are known for seven of the 11 genera and about 17 of the 42 species of the tribe, involving a total of 34 confirmed or putative host species of Centridini bees. All species of the tribe are known to attack only nests of *Centris* Fabricius, 1804, except *Mesoplia rufipes* (Perty, 1833) that also parasitizes nests of *Epicharis* Klug, 1807. Although the phylogenetic relationships within Ericrocidini and among the subgenera of *Centris* are not well resolved, the current knowledge of the host-parasite associations points to a relatively high degree of specificity and possible coevolution between them.

KEY WORDS. Apoidea; cleptoparasitism; *Centris*; Neotropical; coevolution.

Cleptoparasitic bees are those that invade nests of solitary bees so that their offspring can feed on the provisions stored in the brood cells (WCISLO 1987). The host eggs or early-stage larvae are killed by the parasitic female, which uses its sting or mandibles, or by the cleptoparasitic larva, which is able to kill the host's offspring using strong and well-developed mandibles (ROZEN 2000, ROZEN & GARÓFALO 2001, AUGUSTO & GARÓFALO 2004). In Apinae, many groups of cleptoparasites are either restricted to, or richest and most abundant in, the Neotropical region, as the tribes Osirini, Isepeolini, Rhathymini, Ericrocidini, the subtribe Epeolina (Nomadini s.l.), and the genera *Aglae* Lapeletier & Serville, 1825, *Exaerete* Hoffmannsegg, 1817 (Euglossini), and *Coelioxoides* Cresson, 1878 (Tetrapediini) (KIMSEY 1979, SNELLING & BROOKS 1985, ROIG-ALSINA 1989, 1990, 1991, ROZEN & ROIG-ALSINA 1991, MICHENER 2000, ALVES-DOS-SANTOS *et al.* 2002, ROZEN *et al.* 2006).

Ericrocidini is a tribe with 11 genera (MOURE & MELO 2007) associated, in part, with nests of *Centris* Fabricius, 1804 (Centridini) (WAGENKNECHT 1969, COVILLE *et al.* 1983, ROZEN & BUCHMANN 1990, GAGLIANONE 2001, JESUS & GARÓFALO 2000). One member of this tribe, the monotypic *Aglaomelissa* Snelling & Brooks, 1985, is known from Costa Rica, Colombia, Venezuela, Trinidad, and Pará, in northern Brazil (SNELLING & BROOKS

1985, MICHENER 2000). Its biology is unknown, but ROZEN (1991) collected a female of *Aglaomelissa duckei* (Friese, 1906), together with several females of *Mesoplia rufipes* (Perty, 1833), in a nesting site of *Centris* (*Trachina*) *carrikeri* Cockerell, 1919 in Trinidad. This author also described a first-stage larva from a host cell, and identified it as *A. duckei* based on the presence of an adult female flying over the nesting aggregation and on anatomical differences between it and the first instars of *M. rufipes*, which were found in brood cells of *Epicharis albofasciata* Smith, 1874 (ROZEN 1991: 33). However, this putative host record for *A. duckei* is questionable, because this species is considerably more slender and smaller than *C. carrikeri*, whose body size is more similar to that of *M. rufipes*, its undoubted cleptoparasite (ROZEN 1969: 24). Also, variation in size, morphology and in anatomy of bee larvae is still unclear and further studies about this is needed to help on the identification of the species (J.G. Rozen – American Museum of Natural History, pers. comm.).

Here we report confirmed parasitism by *A. duckei* in nests of *Centris* (*Heterocentris*) *analis* (Fabricius, 1804) and *C. (Heterocentris) terminata* Smith, 1874 from two sites in the Brazilian Amazonian region. Also, a compilation of the known host records for species of Ericrocidini is presented and host-parasite associations are discussed.

MATERIAL AND METHODS

Adults of *A. duckei* emerged from nests of *Centris analis* constructed in trap nests made of wood blocks with tunnels drilled in them and tubes made of black cardboard with diameters of 4.8 and 9.7 mm, respectively (see Tab. I). The trap nests were placed in understory sites in the forest reserves of Catuaba and Humaitá (maintained by the Universidade Federal do Acre – UFAC), located near Rio Branco, Acre, Brazil, in 1997-1998. Information on the nests of *Centris terminata* from Manaus, Amazonas, can be found in MORATO *et al.* (1999). Voucher specimens are deposited in the entomological collections of the UFAC, Universidade Federal de Viçosa (UFV), and Universidade Federal do Paraná (DZUP).

Data on host associations for other species of Ericrocini were compiled from literature records and, in a few cases, from personal information provided by colleagues. The names of both hosts and parasites were updated according to current usage (see MOURE *et al.* 2007, MOURE & MELO 2007). Available evidence on parasitism was classified in four categories: A) confirmed host-parasite association, when the parasite was reared from host cells; B) probable association, when the cleptoparasitic female was observed entering the host nest; C) presumed association, when the cleptoparasitic female was collected at the nest site of host species; D) suspected association, when based only on indirect evidence (e.g., cleptoparasite and suspected host having concomitant flight activity).

RESULTS

A summary of the data on nests of *C. analis* and *C. terminata* parasitized by *A. duckei* is presented in table I. The

parasitism ratio caused by *A. duckei* was high, varying from 80 to 100% of the brood cells in a single trap-nest of *C. analis* and 50% of the cells in nests of *C. terminata*. In Humaitá Reserve, four males of *A. duckei* and one male of *C. analis* emerged from a nest that was composed of five cells (nest 27, see table I). Two nests of *C. analis*, both from Catuaba Reserve, were completely parasitized by *A. duckei*. One of them had three cells and three cleptoparasitic females emerged from these cells, while in the second nest, a male of *A. duckei* emerged from the single cell (Tab. I). The parasitic behavior of females of *A. duckei* in the host nests was not studied and remains unknown.

As regards *C. terminata*, MORATO *et al.* (1999) reported an unidentified species of *Mesoplia* Lepeletier, 1841 that emerged from nests of this species. However, restudy of the voucher specimens deposited at UFV by GARM revealed that, in reality, they belong to *A. duckei*. The nests of *C. terminata* were also parasitized by *Mesochora bicolor* Fabricius, 1804 (Tab. I).

Information on known host associations of Ericrocini is presented in table II. Data are available for seven of the 11 genera and about 17 of the 42 species of Ericrocini, involving a total of 34 confirmed or putative host species of Centridini bees.

DISCUSSION

All species of the tribe Ericrocini are known to attack only nests of *Centris* (SNELLING & BROOKS 1985, MICHENER 2000), except *Mesoplia rufipes* that also parasitizes nests of *Epicharis* (ROZEN 1969, HILLER & WITTMANN 1994, GAGLIANONE 2005, ROCHA-FILHO *et al.* 2008). No information is available for the genera *Ctenioschelus* Romand, 1840, *Cyphomelissa* Schrottky, 1902, *Eurytis* Smith, 1854, and *Hopliphora* Lepeletier, 1841. Their putative host associations, however, are discussed below.

Table I. Characteristics and data from the nests of *C. analis* collected at Catuaba and Humaitá reserves, in Acre, and of *C. terminata* at two forest reserves, in Manaus, Brazil. The nests are indicated by their field identification codes.

Nest characteristics	<i>C. terminata</i>		<i>C. analis</i>		
	CL14/1605*	1501b/1606*	1105	1691	27
Nest site	Reserva 1501	Reserva 1501	Reserva Catuaba	Reserva Catuaba	Reserva Humaitá
Location	59°52'W; 2°24'S	59°52'W; 2°24'S	67°37'W; 10°04'S	67°37'W; 10°04'S	67°40'W; 9°45'S
Trap-nest material (mm)	Wood block (25x35x120)	Wood block (25x35x120)	Wood block (25x35x130)	Black cardboard tube (9.5x120)	Black cardboard tube (9.5x120)
Inner diameter (mm)	9.5	9.5	4.8	9.7	9.7
Length (mm)	80	80	80	100	100
Number of cells	3	4	3	1	5
Construction material	Wood fragments + resin	Wood fragments + resin	Wood fragments + resin	Wood fragments + resin	Wood fragments + resin
Length of vestibular cells (mm)	36	22	25	50	15
Species that emerged	<i>A. duckei</i> (1♀) <i>M. bicolor</i> (1♀)	<i>A. duckei</i> (2♀) <i>C. terminata</i> (1♂) <i>M. bicolor</i> (1♀)	<i>A. duckei</i> (3♀)	<i>A. duckei</i> (1♂)	<i>A. duckei</i> (4♂) <i>C. analis</i> (1♀)

* Data from nests of *C. terminata* taken from the study by MORATO *et al.* (1999).

Table II. Known host associations for cleptoparasitic bees of the tribe Ericrocidini.

Cleptoparasites	Hosts	Type of evidence	References
<i>A. excellens</i> Schrottky, 1902	<i>C. (Ptilotopus) scopipes</i> Friese, 1899	Confirmed ^A	GAGLIANONE (2001)
	<i>C. (Ptilotopus) sponsa</i> Smith, 1854	Confirmed	PICKEL (1928)
<i>A. palmatus</i> (Olivier, 1879)	<i>C. (Ptilotopus) derasa</i> Lepeletier, 1841	Confirmed	ROZEN (1969) ¹
	<i>C. (Ptilotopus) nobilis</i> Westwood, 1840	Suspected ^D	DUCKE (1902, 1903) ¹³
	<i>C. (Ptilotopus) sp.</i> ⁹	Confirmed	SILVESTRI (1903)
<i>A. duckei</i> (Friese, 1906)	<i>C. (Heterocentris) analis</i> (Fabricius, 1804)	Confirmed	This study
	<i>C. (Heterocentris) terminata</i> Smith, 1874	Confirmed	MORATO <i>et al.</i> (1999) ⁸
	<i>C. (Trachina) carrikeri</i> Cockerell, 1919	Confirmed *	ROZEN (1991)
<i>E. gayi</i> Spinola, 1951	<i>C. (Paracentris) nigerrima</i> (Spinola, 1851)	Suspected	HERBST (1917) ¹⁴ , WAGENKNECHT (1969) ²
	<i>C. (Penthemisia) chilensis</i> (Spinola, 1851)	Suspected	HERBST (1917) ¹⁴ , WAGENKNECHT (1969) ²
	<i>C. (Wagenknechtia) cineraria</i> Smith, 1854	Suspected	WAGENKNECHT (1969) ²
	<i>C. (Wagenknechtia) rhodophthalma</i> Pérez, 1911	Suspected	WAGENKNECHT (1969) ²
<i>E. lendianum</i> (Friese, 1910)	<i>C. (Paracentris) nigerrima</i>	Suspected	WAGENKNECHT (1969) ³
	<i>C. (Wagenknechtia) cineraria</i>	Suspected	WAGENKNECHT (1969) ³
	<i>C. (Wagenknechtia) orellanai</i> Ruiz, 1940	Suspected	WAGENKNECHT (1969) ³
	<i>C. (Wagenknechtia) rhodophthalma</i>	Suspected	WAGENKNECHT (1969) ³ , CHIAPPA <i>et al.</i> (2000) ¹²
<i>E. wagenknechti</i> (Ruiz, 1938)	<i>C. (Penthemisia) chilensis</i>	Suspected	WAGENKNECHT (1969) ⁴
	<i>C. (Wagenknechtia) rhodophthalma</i>	Suspected	WAGENKNECHT (1969) ⁴
<i>E. lata</i> (Cresson, 1878)	<i>C. (Paracentris) caesalpiniae</i> Cockerell, 1897	Confirmed	ROZEN & BUCHMANN (1990)
<i>Ericrocis</i> sp.	<i>C. (Paracentris) cf. atripes</i> Mocsáry, 1899	Confirmed	ROZEN (1991)
<i>M. bicolor</i> (Fabricius, 1804)	<i>C. (Hemisiella) dichrotricha</i> (Moure, 1945)	Confirmed	MORATO <i>et al.</i> (1999)
	<i>C. (Hemisiella) nitida</i> Smith, 1874	Presumed ^C	SNELLING & BROOKS (1985)
	<i>C. (Hemisiella) tarsata</i> Smith, 1874	Confirmed	COCKERELL (1912), AGUIAR & MARTINS (2002), AGUIAR & GARÓFALO (2004), AGUIAR <i>et al.</i> (2005)
	<i>C. (Hemisiella) trigonoides</i> Lepeletier, 1841	Confirmed	PACKER (1977)
	<i>C. (Heterocentris) analis</i>	Confirmed	JESUS & GARÓFALO (2000)
	<i>C. (Heterocentris) terminata</i>	Confirmed	MORATO <i>et al.</i> (1999)
<i>M. asteria</i> (Smith, 1854)	<i>C. (Centris) pulchra</i> Moure <i>et al.</i> , 2003	Confirmed	M.C. Ramos pers. comm.
	<i>E. (Epicharis) bicolor</i> Smith, 1854	Presumed	ROCHA-FILHO <i>et al.</i> (2008)
	<i>E. (Epicharis) nigrita</i> (Friese, 1900)	Presumed	GAGLIANONE (2005)
<i>M. jenseni</i> (Friese, 1906)	<i>C. (Paracentris) sp.</i> ¹⁰	Suspected	WAGENKNECHT (1969)
	<i>C. (Wagenknechtia) muralis</i> Burmeister, 1876	Confirmed	F. Vivallo, pers. comm.
<i>M. alboguttata</i> (Ducke, 1905)	<i>C. (Centris) aenea</i> Lepeletier, 1841	Probable ^B	MOURE (1967) ⁵
<i>M. bifrons</i> (Fabricius, 1804)	<i>C. (Centris) caxiensis</i> Ducke, 1907	Confirmed	M.C. Ramos, pers. comm.
<i>M. decorata</i> (Smith, 1854)	<i>C. (Centris) flavofasciata</i> Friese, 1900	Presumed	VINSON <i>et al.</i> (1987)
<i>M. dugesi</i> (Cockerell, 1917)	<i>C. (Paracentris) anomala</i> Snelling, 1966	Suspected	SNELLING (1984)
<i>M. cf. friesei</i> (Ducke, 1902)	<i>C. (Paracentris) sp.</i>	Confirmed	ROZEN (2000)
<i>M. aff. pilicrus</i> (Friese, 1902)	<i>C. (Centris) decolorata</i> Lepeletier, 1841	Presumed	RAW (1984) ⁶
	<i>C. (Centris) fasciata</i> Smith, 1854	Presumed	RAW (1984) ⁶

Continue

Table II. Continued.

Cleptoparasites	Hosts	Type of evidence	References
<i>M. regalis</i> (Smith, 1854)	<i>C. (Centris) flavofasciata</i>	Confirmed	VINSON <i>et al.</i> (1987)
<i>M. rufipes</i> (Perty, 1833)	<i>C. (Centris) aenea</i>	Probable	AGUIAR & GAGLIANONE (2003), L.M. Lacerda, pers. comm.
	<i>C. (Centris) flavofasciata</i>	Presumed	VINSON <i>et al.</i> (1987)
	<i>C. (Centris) varia</i> (Erichson, 1848)	Confirmed	COVILLE <i>et al.</i> (1983) ¹¹
	<i>C. (Trachina) carrikeri</i>	Confirmed	ROZEN (1969)
	<i>E. (Anepicharis) dejeanii</i> Lepeletier, 1841	Confirmed	HILLER & WITTMANN (1994) ⁷
	<i>E. (Epicharis) bicolor</i>	Confirmed	ROCHA-FILHO <i>et al.</i> (2008)
	<i>E. (Epicharis) nigrita</i>	Confirmed	GAGLIANONE (2005)
<i>Mesoplia</i> sp.	<i>E. (Epicharoides) albofasciata</i> Smith, 1874	Confirmed	ROZEN (1969)
	<i>C. (Centris) aethiocesta</i> Snelling, 1984	Probable	VINSON & FRANKIE (1988)
<i>Mesoplia</i> sp.	<i>C. (Centris) flavifrons</i> (Fabricius, 1775)	Probable	VINSON & FRANKIE (1988)
<i>Mesoplia</i> sp.	<i>C. (Centris) flavifrons</i>	Probable	RÊGO <i>et al.</i> (2006)

*Questionable host association (see text for details).

¹ Cited as *A. splendidus urichi*, ² *M. gayi*, ³ *M. lendlianum*, ⁴ *M. wagenknechtii*, ⁵ *M. albopunctata*, ⁶ *M. azurea*, ⁷ '*M. spinipes*' nomen nudum, ⁸ *Mesoplia* sp., ⁹ *C. thoracica* [an misidentification of a *C. (Ptilotopus)*, since *C. thoracica* belongs to the subgenus *Melacentris*, which is not known to nest in termite nests], ¹⁰ *C. austrani* [a misidentification, since *C. austrani* does not occur in Chile (F. Vivallo, pers. comm.)], ¹¹ *C. segregata*, ¹² *M. landlianum* [sic], ¹³ *A. splendidus*, ¹⁴ *M. gayi*.

^A Confirmed host-parasite association: when the parasite was reared from host cells; ^B probable association: when the cleptoparasitic female was observed entering the host nest; ^C presumed association: when the cleptoparasitic female was collected at the nest site of host species; ^D suspected association: when based only on indirect evidence (e.g., parasite and suspected host having concomitant flight activity).

Although the available information is still fragmentary, there seems to be a non-random association between the genera of Ericrocidini and the subgenera of *Centris* that they parasitize. *Ericrocis* Cresson, 1887, a genus restricted to northern Mexico and southern USA and recovered as sister-group to the remaining genera of the tribe by SNELLING & BROOKS (1985), parasitizes species of the soil-nesting subgenus *Centris* (*Paracentris*) Cameron, 1903 (ROZEN & BUCHMANN 1990, ROZEN 1991).

Mesonychium Lepeletier & Serville, 1825 and *Epiclopus* Spinola, 1851 are closely related (SNELLING & BROOKS 1985). The first genus is widespread, ranging from Venezuela and Brazil, in the north, to central Chile and Argentina, whereas the latter is restricted to Chile and western Argentina (MICHENER 2000, MOURE & MELO 2007). The available host records indicate that these two genera are mainly associated with *C. (Paracentris)* and *C. (Wagenknechtia)* Moure, 1950, with *Mesonychium* also attacking *C. (Centris)*. The records of females of *M. asteria* Smith, 1854 flying over nests of *Epicharis nigrita* (Friese, 1900) (GAGLIANONE 2005) and of *Epicharis bicolor* Smith, 1854 (ROCHA-FILHO *et al.* 2008) constitute only indirect evidence, and cannot be taken as confirming the association with *Epicharis*.

Acanthopus Klug, 1807 and its allies (*Cyphomelissa*, *Eurytis*, and *Hopliphora*) contain the largest species of Ericrocidini bees (MICHENER 2000). Host records are known only for *Acanthopus* and all of them are species of *Centris* (*Ptilotopus*) Klug, 1810,

whose nests are excavated in arboreal and/or epigeous mud termite nests (DUCKE 1903, SILVESTRI 1903, PICKEL 1928, ROZEN 1969, GAGLIANONE 2001). Judged by their relatively large body size and geographic distribution, the remaining three genera in this group are likely to be associated with the subgenera *Centris* (*Aphemisia*) Ayala, 2002, *C. (Melacentris)* Moure, 1996, and perhaps *C. (Trachina)* Klug, 1807.

Mesoplia is the richest genus within Ericrocidini, with at least 21 species (ROCHA-FILHO & MELO, unpub. data). Moreover, it exhibits the largest range among the tribe's genera, its distribution extending from southern United States (Arizona) to northern Argentina, including the Antilles (SNELLING & BROOKS 1985). Regarding its host association, there are more known records for *Mesoplia* than for any other Ericrocidini genus (see references in table II). *Mesoplia* attacks mostly species of *C. (Centris)*, with three known exceptions, two of them involving species of *C. (Paracentris)*. The third exception involves attacks to nests of *Epicharis* by *Mesoplia rufipes*, an association confirmed by several studies (ROZEN 1969, HILLER & WITTMANN 1994, GAGLIANONE 2005, ROCHA-FILHO *et al.* 2008) and involving at least three subgenera and five species of *Epicharis*. Use of *Epicharis* as hosts by *M. rufipes* is undoubtedly a derived feature within Ericrocidini.

According to SNELLING & BROOKS (1985), *Mesocheira* Lepeletier & Serville, 1825, *Ctenioschelus*, and *Aglaomelissa* form a clade supported by several unique synapomorphies. Except

for the two species of *Ctenioschelus*, the other two genera contain each a single species. *Mesocheira bicolor* is known to parasitize only species of *Centris* (*Hemisiella*) Moure, 1945 and *C. (Heterocentris)* Cockerell, 1899. Species in both subgenera are mason bees and nest in preexisting cavities, the females bringing soil particles (*C. (Hemisiella)*) or using wood chips (*C. (Heterocentris)*) to build the cell walls (SNELLING & BROOKS 1985, MORATO *et al.* 1999, JESUS & GARÓFALO 2000, AGUIAR & GARÓFALO 2004). Likewise, the confirmed host of *A. duckei* also belongs to *C. (Heterocentris)*. Despite the lack of host records for *Ctenioschelus*, based on its geographic distribution, body size and close relationship to *Aglaomelissa* and *Mesocheira*, this genus is likely to attack species of *C. (Xanthemisia)* Moure, 1945, a subgenus also known to nest in wood cavities (VINSON *et al.* 1993, F.A. Silveira – Universidade Federal de Minas Gerais, pers. comm.).

Many aspects of the biology of Ericrocidini bees remain unclear and have been poorly studied. Detailed studies of the behavior of females and first instar larvae are still lacking. Although the phylogenetic relationships within Ericrocidini and among the subgenera of *Centris* are not well resolved, the current knowledge on host-parasite associations points to a relatively high degree of specificity and possible coevolution between them.

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