

Collection of Pollen Grains by *Centris (Hemisiella) tarsata* Smith (Apidae: Centridini): Is *C. tarsata* an Oligolectic or Polylectic Species?

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Lia Gonçalves, Cláudia Inês da Silva, and Maria Luisa Tunes Buschini (2012) Collection of pollen grains by *Centris (Hemisiella) tarsata* Smith (Apidae: Centridini): Is *C. tarsata* an oligolectic or polylectic species? *Zoological Studies* 51(2): 195-203. Among pollinator species, bees play a prominent role in maintaining biodiversity because they are responsible, on average, for 80% of angiosperm pollination in tropical regions. The species richness of the bee genus *Centris* is high in South America. In Brazil, these bees occur in many types of ecosystems. *Centris tarsata* is an endemic species occurring only in Brazil. No previous studies considered interactions between plants and this bee species in southern Brazil, where it is the most abundant trap-nesting bee. Accordingly, the goals of this study were to investigate plants used by this species for its larval food supply and determine if this bee is polylectic or oligolectic in this region. This work was conducted in the Parque Municipal das Araucárias, Guarapuava (PR), southern Brazil, from Mar. 2002 to Dec. 2003. Samples of pollen were collected from nests of these bees and from flowering plants in grassland and swamp areas where the nests were built. All of the samples were treated with acetolysis to obtain permanent slides. The family Solanaceae was visited most often (71%). *Solanum americanum* Mill. (28.6%) and *Sol. variable* Mart. (42.4%) were the primary pollen sources for *C. tarsata* in the study area. We found that although *C. tarsata* visited 20 species of plants, it preferred *Solanum* species with poricidal anthers and pollen grains with high protein levels. This selective behavior by females of *C. tarsata* indicates that these bees are oligolectic in their larval provisioning in this region of southern Brazil. <http://zoolstud.sinica.edu.tw/Journals/51.2/195.pdf>

Key words: *Centris (Hemisiella) tarsata*, *Solanum variable*, *Solanum americanum*, Provision of pollen grains.

Bees of the family Apidae can fly long distances in tropical forests in search of preferred plant species, thus promoting cross-pollination (Frankie et al. 1983, Roubik 1993). The plant-pollinator relationship is symbiotic and establishes a beneficial relationship between 2 species with different levels of dependency (Boucher et al. 1982, Del-Claro 2004). According to Faegri and Van der Pijl (1979) and Proctor et al. (1996), plant-pollinator interactions are considered to result from natural selection, which produces a wide variety of adaptations in plants, allows the transfer of pollen

grains, and increases gene flow within a species.

Among pollinator species, bees play an important role in maintaining biodiversity. On average, they are responsible for 80% of angiosperm pollination in tropical regions (Kevan and Baker 1983, Bawa 1990). The higher efficiency of bees as pollinators results from their high numbers compared to other pollinators and from their superior adaptations to complex floral structures. For example, their bodies and mouthparts are adapted to collect and transport resources, such as nectar and pollen, respectively (Kevan and Baker

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1983, Michener 2000).

Some bee species belonging to the tribes Tapnotaspidini and Centridini exhibit reproductive cycles and nesting activities that are synchronized with the flowering periods of certain species of plants (Rocha-Filho et al. 2008, Aguiar and Melo 2009, Bezerra et al. 2009, Gaglianone et al. 2011). These bees visit flowers to obtain oil, pollen, nectar, and resin (resources needed to build parts of their nests) to feed the larvae and maintain adults and their reproductive activities (Vogel 1974, Buchmann 1987, Roubik 1989, Vinson et al. 1996). Some studies showed the importance of these bees as pollinators of various species of Neotropical plants (Frankie et al. 1976, Gottsberger et al. 1988, Freitas 1997), including those producing oil, such as species of the Malpighiaceae (Rêgo and Albuquerque 1989, Freitas et al. 1999) and Scrophulariaceae (Vogel and Machado 1991).

The genus *Centris* is typically tropical, and its species belong to 12 subgenera. The species richness of *Centris* is high in South America. In Brazil, these bees are found in various ecosystems, such as dunes and sandbanks (Silva and Martins 1999, Silva et al. 2001, Viana and Alves-dos-Santos 2002), caatinga (Martins 1994, Zanella 2000, Aguiar and Almeida 2002, Aguiar et al. 2003), grasslands, and savannas (Silveira and Campos 1995, Albuquerque and Mendonça 1996).

Centris tarsata has only been recorded from Brazil. The distribution of *C. tarsata* in Brazil is based on Aguiar and Garófalo (2004), information from specimens deposited in entomological collections (J.M.F. Camargo, pers. commun.), samples of females and/or males collected on flowers (Camargo and Mazucato 1984, Vogel and Machado 1991, Martins 1994, Silveira and Campos 1995, Albuquerque and Mendonça 1996, Freitas 1997, Schindwein 1998, Zanella 2000), and the location of nests (Chandler et al. 1985, Camilo et al. 1995, Silva et al. 2001, Viana et al. 2001, Aguiar and Martins 2002). This information indicates that *C. tarsata* occurs in the states of PA, MA, PI, CE, PB, PE, BA, MG, SP, PR, RS, MS, MT, and GO.

In the savanna area of Uberlândia (Minas Gerais State, Brazil), *C. tarsata* was recorded as one of the principal pollinators of West Indian cherry *Malpighia emarginata* DC (Malpighiaceae) (Vilhena and Augusto 2007). This bee is solitary and tends to nest in preexisting cavities. Its nests can be built in trap-nests (Silva et al. 2001, Aguiar and Garófalo 2004, Buschini and Wolff

2006). In southern Brazil, *C. tarsata* is the most abundant bee species (Buschini 2006). It prefers open habitats and shows greater nesting activity during the hot season, especially in Dec. and Jan. (Buschini and Wolff 2006).

Several studies were conducted in Brazil to identify sources of pollen used by different species of bees and to understand the degree of association between bees and the plants that they visit. Through an analysis of pollen grains, it is possible to identify the main floral resources used by bees. This information allows the assessment of resource availability in the field and the identification of times of resource scarcity (Salgado-Labouriau 1961, Ortiz 1994, Bastos et al. 2003).

An analysis of the pollen spectrum of *C. tarsata* based on samples from nests in the northeastern micro-region of Bahia State, Brazil indicated the presence of 17 pollen types from 7 plant families. These samples, representing an assemblage of 5-11 pollen types, identified plants used by the bees to feed their offspring (Dórea et al. 2009). In Maranhão State, also in northeastern Brazil, pollen analyses of *C. tarsata* showed relatively high quantities of pollen grains from *Banisteriopsis* sp. (Malpighiaceae) and *Cassia* sp. (Caesalpinaceae).

Centris tarsata is endemic to Brazil. No previous studies of the interactions of plants with this bee species have been conducted in southern Brazil, where it is the most abundant trap-nesting bee. The goals of this study were to investigate the plants that constitute the larval food supply for *C. tarsata* and determine whether this bee has a polylectic or an oligolectic tendency in this region.

MATERIALS AND METHODS

This study was carried out in the Parque Municipal das Araucárias, located in the municipality of Guarapuava, Paraná State, southern Brazil (25°21'06"S, 51°28'08"W). The area of the park is approximately 104 ha. The vegetation is composed of mixed ombrophilous forest (42.75%), gallery forest (10.09%), fields (6.8%), swamps (7.13%), and altered areas (33.23%). The grasslands are physiologically characterized by areas of low grasses and no bushes. Species of the families Cyperaceae, Leguminosae, Verbenaceae, Compositae, and Umbelliferae are the principal plants in this habitat. The grasslands are surrounded by Araucaria

forests, dominated by *Araucaria angustifolia* (Coniferae: Araucariaceae). The swamps are located in the lowest-elevation regions of the park and are primarily composed of grasses and members of the Compositae (Buschini and Fajardo 2010). According to the Köppen classification, the climate is humid mesothermic, with no dry season and mild summers because of the elevation. The winter is moderate, with the frequent occurrence of frost. The annual mean temperature is approximately 16°C.

In this study, pollen grains were removed from provisioned cells of 11 nests of *C. tarsata* from a total of 128 trap-nests installed in the swamp and grassland areas. *Centris tarsata* has a seasonal pattern of nesting activity from Nov. to May (Buschini and Wolff 2006), so the pollen grains used in this study were collected from Mar. 2002 to Dec. 2003. Pollen collected from the nests was preserved on permanent slides with the acetolysis method (Erdtman 1960). Five pollen grain slides were made for each nest to produce a total of 55 slides. Pollen grains were also collected from flowering plants from May 2006 to Apr. 2007. Pollen was collected throughout the area in which nests were built. The pollen was removed from the flowers and/or buttons of each plant to obtain 2 slides per plant. All pollen grain slides from both nests and plants were examined using light microscopy to identify plants used by the bee. The pollen was quantified by consecutively counting 300 pollen grains per slide. Total numbers of pollen grains counted were 1500 grains per nest and 16,500 grains in all. Subsequently, we determined the percentages of occurrence of each species and botanical family in *C. tarsata* nests according to the classification of Barth (1970) and Louveaux et al. (1970 1978). Thus, pollen types were classified as dominant (> 45% of total grain on the slides), accessory (15%-45%), important isolates (3%-14%), and occasional isolates (< 3%).

RESULTS

We collected 99 flowering plant species in the study area during the activity period of *C. tarsata*. Overall, 20 pollen types from 17 plant families were collected by this bee (Fig. 1, Table 1).

The family Solanaceae was visited most often (71%). *Solanum americanum* Mill. (28.6%) and *Sol. variable* Mart. (42.4%) were the primary pollen sources for *C. tarsata* in the study area. The 2nd most frequently visited family was the

Phytolaccaceae. *Phytollaca dioica* L. supplied 15.4% of the pollen in the samples. The family Malpighiaceae represented 4.5% of the pollen in the samples, whereas the families Lauraceae (3.2%), Myrthaceae (2.8%), Melastomataceae (1.01%), Lythraceae (0.9%), Campanulaceae (0.4%), Convolvulaceae (0.2%), Caesalpiniaceae (0.16%), Asteraceae (0.1%), Amaranthaceae (0.08%), and Polygalaceae (0.07%) occurred at low percentages. *Erythroxyllum deciduum* A. St. Hil. (0.03%), of the family Erythroxilaceae, and another species not yet identified (Undetermined-1) (0.01%) appeared in more than 1 sample but at low occurrence percentages. Although the pollen types of *Styrax leprosum* Hook and Arn. (0.09%) and another unidentified species (Undetermined-2) (0.04%) were recorded in only 1 sample, their percentages were higher than those of *Ery. deciduum* and Undetermined-1.

The frequencies of occurrence of pollen types in the 11 samples analyzed showed that *Sol. americanum* and *Sol. variable* (100%) were the most consistent, followed by *Janusia guaranitica* and *Cinnamomum amoenum* (Ness and Mart.) Kosterm (60%), *Gomphrena elegans* Mart., and *Ipomoea grandifolia* Lam. (40%). The 14 other pollen types occurred in 10%-30% of samples: *Phytollaca dioica*, *Vernonia* sp. Schreb, *Senna multijuga* (Rich.) H. S., *Cuphea* sp. P. Browne (30%), *Ery. deciduum*, *Janusia* sp. A. Juss, *Tibouchina cerastifolia* Cong, and Undetermined-1 (20%), and *Baccharis* sp. L., *Lobelia* sp. Pohl, *Ipomoea purpurea* (L.) Roth, *Campomanesia adamantium* O. Berg, *Polygala* sp. L., *Sty. leprosum* Hook. and Arn, and Undetermined-2 (10%).

DISCUSSION

Although *C. tarsata* used 20 types of pollen grains, pollen of *Sol. americanum*, *Sol. variable*, and *Phy. dioica* were most common in the larval diet. The importance of the family Solanaceae as a source of pollen for *C. tarsata* was also reported by Aguiar et al. (2003) and Dórea et al. (2009) in the Caatinga, xerophytic vegetation predominant in semi-arid northeastern Brazil. According to Buchmann (1983), the presence of poricidal anthers in flowers of the Solanaceae establishes a close relationship with females of *Centris*. In this plant-pollinator relationship, pollination by vibration (buzz-pollination) is an effective method of extracting pollen from these plants (Buchmann

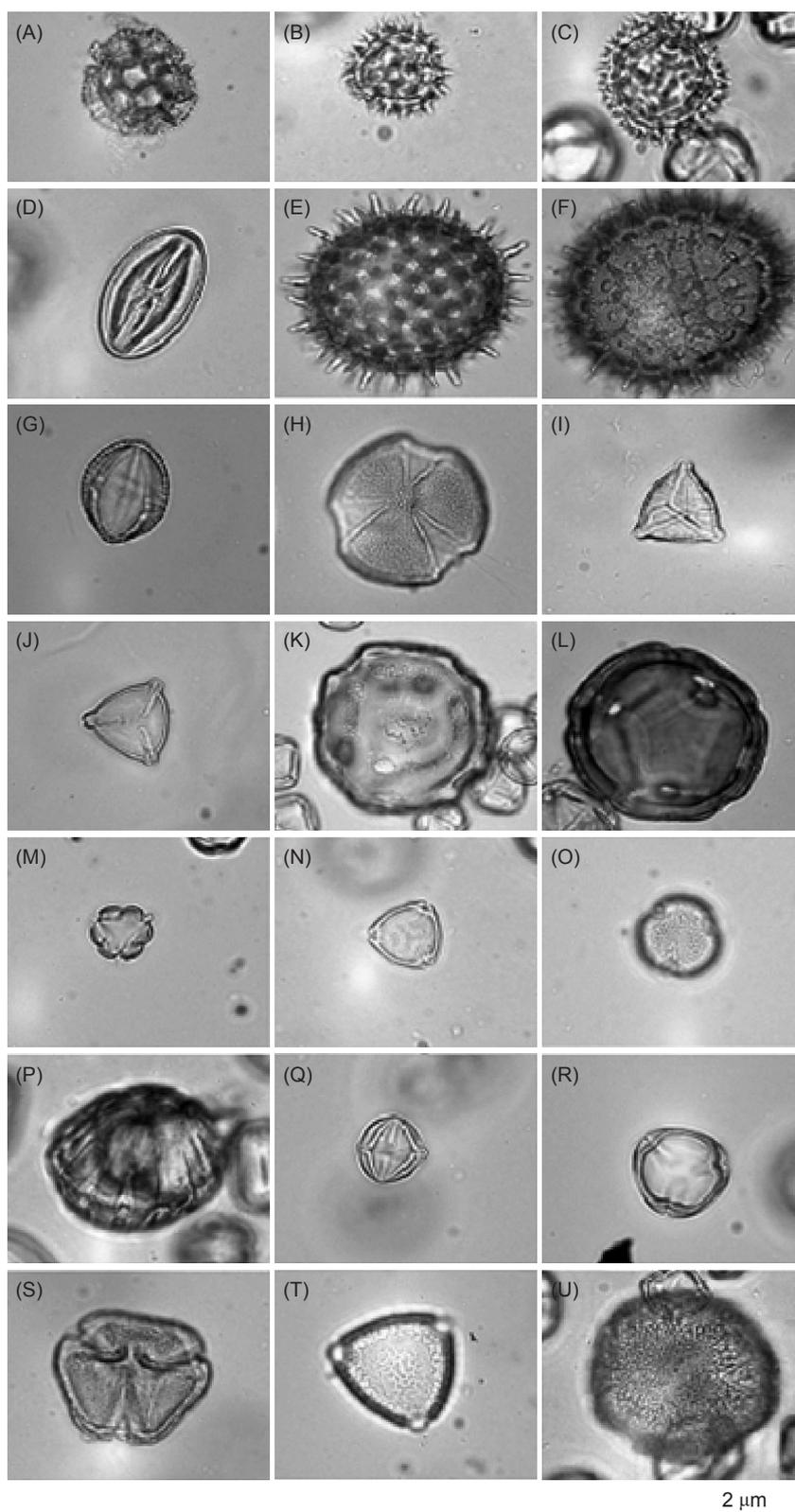


Fig. 1. Pollen grains found in nests of *Centris tarsata*. (A) *Gomphrena elegans*, (B) *Baccharis* sp., (C) *Vernonia* sp., (D) *Lobelia* sp., (E) *Ipomoea grandifolia*, (F) *I. purpurea*, (G) *Erythroxylum deciduum*, (H) *Senna multijuga*, (I) *Cinnamomum amoenum*, (J) *Cuphea* sp., (K) *Janusia guaranitica*, (L) *Janusia* sp., (M) *Tibouchina cerastifolia*, (N) *Campomanesia adamantium*, (O) *Phytolacca dioica*, (P) *Polygala* sp., (Q) *Solanum americanum*, (R) *Sol. variable*, (S) *Styrax leprosum*, (T) Undetermined-1, (U) Undetermined-2.

1983). The collection of pollen by vibration also occurs on flowers of the Melastomataceae (Buchmann and Hurley 1978) and Caesalpiniaceae (Moure and Castro 2001). This method of pollination is associated with small pollen grains, as in *Solanum* species. These grains have a high amount of protein, which is important for larval development (Roulston et al. 2000).

Studies in different Brazilian biomes also highlighted the importance of the families Solanaceae (Dórea et al. 2009), Malpighiaceae, Caesalpiniaceae, and Myrtaceae (Mendes and

Rego 2007) as sources of pollen for *C. tarsata*. Aguiar et al. (2003), in Itatim (BA), northeastern Brazil, recorded the presence of pollen of the Caesalpiniaceae in the diet of *C. tarsata* offspring. *Senna* Mill. was also found to represent a frequent source of pollen and nectar for this bee. Plants of this genus are also associated with a mechanism of pollination by vibration (Santos et al. 2004, Anacleto and Marchini 2005, Andena et al. 2005). Moreover, Aguiar et al. (2003) stated that solitary bees, such as species of *Centris*, are more likely to act as generalists during foraging for nectar than

Table 1. Occurrence of pollen grain types in nests of *Centris tarsata*: pollen accessory (PA), pollen important isolate (PII), pollen occasional isolate (POI)

Pollen type	Resources available	Life form	Local occurrence	Month of collection	Percent occurrence on slides	Classification of pollen types
Amaranthaceae						
<i>Gomphrena elegans</i> Mart.	-	Herb	Swamp	Mar.	0.08%	POI
Asteraceae						
<i>Baccharis</i> sp. L.	Pollen, nectar	Shrub	Grassland	Feb., Mar.	0.04%	POI
<i>Vernonia</i> sp. Schreb.	Pollen, nectar	Tree	Forest	Oct.	0.06%	POI
Campanulaceae						
<i>Lobelia</i> sp. Pohl.		Herb	Swamp	Feb.	0.4%	POI
Convolvulaceae						
<i>Ipomoea grandifolia</i> Lam.	Pollen	Liana	Swamp	Mar.	0.13%	POI
<i>Ipomoea purpúrea</i> (L.) Roth.	Pollen	Liana	Swamp	Mar.	0.07%	POI
Erythroxilaceae						
<i>Erythroxylum deciduum</i> A. St. Hil.	Pollen, nectar	Shrub	Grassland	Sept.	0.03%	POI
Caesalpiniaceae						
<i>Senna multijuga</i> (Rich.) H. S.	Pollen, nectar	Tree	Grassland	Feb.	0.16%	POI
Lauraceae						
<i>Cinnamomum amoenum</i> (Nees) Kosterm.	Pollen	Tree	Forest	Oct.	3.2%	PII
Lythraceae						
<i>Cuphea</i> sp. P. Browne.	Pollen, nectar	Herb	Swamp	Apr.	0.9%	POI
Malpighiaceae						
<i>Janusia guaranitica</i> (A. St.-Hil.) A. Juss.	Pollen, oil	Herb	Grassland	Dec.	3.2%	PII
<i>Janusia</i> sp. A. Juss.	Pollen, oil	-	-	-	1.3%	POI
Melastomataceae						
<i>Tibouchina cerastifolia</i> Cong.	Pollen, oil	Herb	Grassland	Jan., Feb.	1.01%	POI
Myrtaceae						
<i>Campomanesia adamantium</i> O. Berg.	Pollen	Tree	Grassland	Oct.	2.8%	POI
Phytolaccaceae						
<i>Phytolacca dioica</i> L.	Pollen	Tree	Grassland, forest	Oct.	15.4%	PA
Polygalaceae						
<i>Polygala</i> sp. L.	Pollen, nectar	-	-	-	0.07%	POI
Solanaceae						
<i>Solanum americanum</i> Mill.	Pollen	Herb	Grassland, swamp	Mar.	28.6%	PA
<i>Solanum variabile</i> Mart.	Pollen	Tree	Grassland	Nov.	42.4%	PA
Styracaceae						
<i>Styrax leprosum</i> Hook. and Arn.	Pollen, nectar	Tree	Forest	Oct.	0.09%	POI
Undetermined-1	-	-	-	-	0.04%	POI
Undetermined-2	-	-	-	-	0.01%	POI

during foraging for pollen and oil. Those authors also stated that the exploitation of resources from the families Caesalpiniaceae and Malpighiaceae is frequently found in different biomes.

In Salinas (MG), southeastern Brazil, Guimarães (2006) found that the family Myrtaceae was visited by several species of *Centris*. Similar results were obtained in the São Francisco Valley of Brazil by Siqueira et al. (2005), who reported a high frequency of *Centris* and *Xylocopa* visitation to flowers of this family. Pollen is the primary resource provided by this family for bees, which are probably its most efficient pollinators (Gressler et al. 2006). In these plants, pollination also occurs by vibration, although the anthers exhibit longitudinal dehiscence and are not poricidal (Proença 1992).

Although the percentage of pollen from plants of the family Malpighiaceae in the diet of *C. tarsata* in Guarapuava was low (4.5%), this finding does not mean that these plants have little importance as resource suppliers for these bees. According to Anderson (1979), Vogel (1990), and Ramalho and Silva (2002), a close relationship between bees of the tribe Centridini and plants of this family can be interpreted as a product of a long evolutionary history of interactions between the 2 groups. This history could even explain the high reproductive success of these plants in the Americas. The plants provide both oil and pollen to feed the larvae of these bees. They bloom almost year-round, but the flowers are more highly abundant during the warm and rainy period (Silberbauer-Gottsberger and Gottsberger 1988). In the Brazilian savanna (i.e., the cerrado), the nesting and foraging activities of the Centridini are generally more frequent during the period of peak flowering of the Malpighiaceae (Rocha-Filho et al. 2008). The Centridini is considered to be key pollinators of this plant family (Michener 2000, Machado 2002 2004, Machado et al. 2002, Alves dos Santos et al. 2007). The system of oil production in these plants and collection of the oil by the bees require a series of morphological adaptations in both groups and behavioral adaptations by the bees (Simpson and Neff 1977). The oil, the primary resource that attracts the bees to the plants, is secreted by glands called elaiophores (Vogel 1974, Simpson and Neff 1981) and is included in the diet of larval bees.

In the Malpighiaceae, pollen grain sizes usually range from medium to large. Pollen of *Janusia* occurred in small quantities in bee nests, but these quantities were considerably higher than

those found for *Sol. americanum*, *Sol. variabile*, and *Phy. dioica*. According to Severson and Parry (1981), measurements of a pollen sample should be representative of the mass of pollen by including the average number of grains counted and should also reflect the estimated volumetric contribution of the grain type. Thus, the degree of importance of 1 type of pollen grain should not be based solely on its percentage but should also include both its numeric and volumetric representation in the sample.

The sporadic presence of pollen of the Melastomataceae in nests of *C. tarsata* in Guarapuava may reflect the tendency of the bees to seek the oil of these plants to build their nests. When collecting the oil, they place their ventral abdomen and thorax on the stigma and anthers of the flowers. This behavior facilitates the transfer of pollen to the stigma (Gimenes and Lobão 2006) and also results in the transport of small amounts of pollen from the plants to the bees' nests. In studies in Camaçari (BA), northeastern Brazil, Oliveira-Rebouças and Gimenes (2004) observed that medium- and large-sized species of *Centris* were highly efficient at collecting pollen from flowers of the Melastomataceae. In the study region, the use of pollen of the Convolvulaceae (e.g., *Ipomoea*) by *Centris* may be related to the morphology of the pollen grains. These grains are large-sized, are porate and colpate with a perforated exine, and are spiculated and hairy. The spine characteristic of this genus assists in the attachment of pollen grains to the hair of bees, thereby optimizing the transport process (Machado and Melhem 1987, Sengupta 1972, Leite et al. 2005).

The occurrence of pollen from the Phytolaccaceae, Lauraceae, and Styracaceae in the diet of *C. tarsata* may be related to the bees' search for resources in plants located in transitional areas between the grassland and Araucaria forest. These areas are close to sites where the bees nest. Frankie et al. (1983) also observed many species of *Centris* foraging in the canopy of mass-flowering tree species.

Although *C. tarsata* was found to visit 20 species of plants, it preferred *Solanum* species with poricidal anthers and pollen grains with high amounts of protein. This selective behavior by females of *C. tarsata* indicates that this bee is oligolectic in its larval provisioning in this region of southern Brazil. Because *C. tarsata* occurs in areas of natural grasslands and collects pollen from plants in transition zones between these areas and

Araucaria forest, these bees undoubtedly promote the pollination of various plant species in these areas that are currently suffering from severe exploitation and fragmentation in southern Brazil. Further studies should be conducted to investigate the ability of these bees to explore different grassland fragments in this region and transport pollen grains between them, thereby increasing the genetic variability of the region's plants.

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REFERENCES

- Aguiar AJC, CF Martins. 2002. Abelhas e vespas solitárias em ninhos-armadilha na Reserva Biológica Guaribas (Mamanguape, Paraíba, Brasil). *Rev. Bras. Zool.* **19**: 101-116.
- Aguiar AJC, GAR Melo. 2009. Notes on oil sources for the bee genus *Caenonomada* (Hymenoptera, Apidae, Tapinotaspidini). *Rev. Bras. Entomol.* **53**: 154-156.
- Aguiar CML, GF Almeida. 2002. Atividade diária de coleta de óleo por espécies de *Centris* (Hymenoptera: Apidae) em *Mcvaughia bahiana* W.R. Anderson (Malpighiaceae) na caatinga. *Acta Biol. Leop.* **24**: 131-140.
- Aguiar CML, CA Garófalo. 2004. Nesting biology of *Centris (Hemisiella) tarsata* Smith (Hymenoptera, Apidae, Centridini). *Rev. Bras. Zool.* **21**: 477-486.
- Aguiar CML, FCV Zanella, CF Martins, CAL Carvalho. 2003. Plantas visitadas por *Centris* spp. (Hymenoptera: Apidae) na caatinga para obtenção de recursos florais. *Neotrop. Entomol.* **32**: 247-259.
- Albuquerque PMC, JAC Mendonça. 1996. Anthophoridae (Hymenoptera, Apoidea) e Flora associada em uma formação de cerrado no município de Barreirinhas, Ma, Brasil. *Acta Amazôn.* **26**: 45-54.
- Alves-dos-Santos I, IC Machado, MC Gaglione. 2007. História natural das abelhas coletoras de óleo. *Oecol. Bras.* **11**: 242-255.
- Anacleto DA, LC Marchini. 2005. Análise faunística de abelhas (Hymenoptera, Apoidea) coletadas cerrado do Estado de São Paulo. *Acta Sci. Biol. Sci.* **27**: 277-284.
- Andena SR, LR Bego, MR Mechi. 2005. A Comunidade de abelhas (Hymenoptera, Apoidea) de uma área de cerrado (Corumbataí, SP) e suas visitas às flores. *Rev. Bras. Zool. Zool. Zool.* **7**: 55-91.
- Anderson WR. 1979. Floral conservatism in Neotropical Malpighiaceae. *Biotropica* **11**: 219-223.
- Barth OM. 1970. Análise microscópica de algumas amostras de mel. Pólen dominante. *Anais Acad. Bras. Ciênc.* **42**: 351-366.
- Bastos EMAF, VM Silveira, AEE Soares. 2003. Pollen spectrum of honey produced in cerrado areas of Minas Gerais State (Brazil). *Braz. J. Biol.* **63**: 599-615.
- Bawa KS. 1990. Plant-pollinator interactions in tropical rain forests. *Ann. Rev. Ecol. Syst.* **21**: 399-422.
- Bezerra ES, AV Lopes, IC Machado. 2009. Biologia reprodutiva de *Byrsonima gardnerana* A. Juss. (Malpighiaceae) e interações com abelhas *Centris* (Centridini) no Nordeste do Brasil. *Rev. Bras. Bot.* **32**: 95-108.
- Boucher DH, S James, KH Keeler. 1982. The ecology of mutualism. *Ann. Rev. Ecol. Syst.* **13**: 315-347.
- Buchmann SL. 1983. Buzz pollination in angiosperms. In CE Jones, RJ Little, eds. *Handbook of experimental pollination biology*. New York: Scientific and Academic Editions, pp. 73-113.
- Buchmann SL. 1987. The ecology of oil flowers and their bees. *Ann. Rev. Ecol. Syst.* **18**: 343-369.
- Buchmann SL, JP Hurley. 1978. A biophysical model for buzz pollination in angiosperms. *J. Theor. Biol.* **72**: 639-657.
- Buschini MLT. 2006. Species diversity and community structure in trap-nesting bees in southern Brazil. *Apidologie* **37**: 58-66.
- Buschini MLT, S Fajardo. 2010. Biology of the solitary wasp *Trypoxylon (Trypargilum) agamemnon* Richards 1934 (Hymenoptera: Crabronidae) in trap-nests. *Acta Zool. Stockh.* **91**: 426-432.
- Buschini MLT, LL Wolff. 2006. Biologia de nidificação de *Centris (Hemisiella) tarsata* Smith no Sul do Brasil (Hymenoptera, Apidae, Centridini). *Braz. J. Biol.* **66**: 1091-1101.
- Camargo JMF, M Mazucato. 1984. Inventário da apifauna e flora apícola de Ribeirão Preto, SP - Brasil. *Dusenya* **14**: 55-87.
- Camillo E, CA Garófalo, JC Serrano, G Muccillo. 1995. Diversidade e abundância sazonal de abelhas e vespas solitárias em ninhos-armadilha (Hymenoptera, Apocrita, Aculeata). *Rev. Bras. Entomol.* **39**: 459-470.
- Chandler L, JAF Barrigosi, EBS Diaz. 1985. The first definitive host record for *Leucospis cayennensis* Westwood (Hymenoptera: Leucospidae). *Rev. Ceres* **32**: 170-174.
- Del-Claro K. 2004. Multitrophic relationships, conditional mutualisms, and the study of interaction biodiversity in tropical savannas. *Neotrop. Entomol.* **33**: 665-672.
- Dórea MC, FAR Santos, LCL Lima, LER Figueroa. 2009. Análise Polínica do Resíduo Pós-Emergência de Ninhos de *Centris tarsata* Smith (Hymenoptera: Apidae, Centridini). *Neotrop. Entomol.* **38**: 197-202.
- Erdtman G. 1960. The acetolized method. A revised description. *Svensk Bot. Tidskrift* **54**: 561-564.
- Faegri K, L Van der Pijl. 1979. *The principles of pollination ecology*. 3rd ed. Oxford: Pergamon Press, 244 pp.
- Frankie GW, PA Opler, KS Bawa. 1976. Foraging behaviour of solitary bees: implications for outcrossing of a Neotropical forest tree species. *J. Ecol.* **64**: 1049-1057.
- Frankie GW, SB Vinson, PA Opler. 1983. *Centris aethyctera* and *Centris fuscata* in the lowland dry forest of Costa Rica (Hymenoptera: Anthophoridae). In DH Janzen, ed. *Costa Rica Natural History*. Chicago, Univ. Press, pp. 707-708.
- Freitas BM. 1997. Number and distribution of cashew (*Anacardium occidentale*) pollen grains on the bodies of its pollinators, *Apis mellifera* and *Centris tarsata*. *J. Apicult. Res.* **36**: 15-22.
- Freitas BM, JE Alves, GF Brandão, ZB Araujo. 1999. Pollination requirements of West Indian cherry (*Malpighia emarginata*) and its putative pollinators, *Centris* bees. *J. Agric. Sci.* **133**: 303-311.
- Gaglianone MC, AJC Aguiar, F Vivallo, I Alves-dos-Santos. 2011. Checklist das Abelhas Coletoras de Óleos do

- Estado de São Paulo, Brasil. *Biot. Neotrop.*, **11**: 1-10. (Online Edição em Inglês)
- Gimenes M, CS Lobão. 2006. A polinização de *Krameria bahiana* B.B. Simpson (Krameriaceae) por abelhas (Apidae) na restinga, BA. *Neotrop. Entomol.* **35**: 440-445.
- Gottsberger G, JMF Camargo, I Silberbauer-Gottsberger. 1988. A bee-pollinated tropical community: the beach dune vegetation of Ilha de São Luís, Maranhão. *Braz. Bot. Jahrb. Syst.* **109**: 469-500.
- Gressler E, MA Pizo, L Patrícia, C Morellato. 2006. Polinização e dispersão de sementes em Myrtaceae do Brasil. *Rev. Bras. Bot.* **29**: 509-530.
- Guimarães RA. 2006. Abelhas (Hymenoptera: Apoidea) visitantes das flores da goiaba (*Psidium guajava* L.), laranja (*Citrus sinensis* L.) e tangerina (*Citrus reticulata* B.) em pomares comerciais em Salinas - MG. Vitória da Conquista, BA: Univ. Estadual do Sudoeste da Bahia.
- Kevan PG, HG Baker. 1983. Insects as flower visitors and pollinators. *Ann. Rev. Entomol.* **28**: 407-453.
- Leite KRB, R Simão-Bianchini, FAR Santos. 2005. Morfologia polínica do gênero *Merremia* Dennst. (Convolvulaceae) ocorrentes no Estado da Bahia, Brasil. *Acta Bot. Bras.* **19**: 313-321.
- Louveaux J, A Maurizio, G Vorwohl. 1970. Methods of melissopalynology. *Bee World* **51**: 25-138.
- Louveaux J, A Maurizio, G Vorwohl. 1978. Methods of melissopalynology. *Bee World* **59**: 139-157.
- Machado IC. 2002. Flores de óleo e abelhas coletoras de óleo floral: conceitos, distribuição e revisão. Ribeirão Preto, SP, BR.: Anais do V Encontro Sobre Abelhas, pp. 129-135.
- Machado IC. 2004. Oil-collecting bees and related plants: a review of the studies in the last twenty years and case histories of plants occurring in NE Brazil. In BM Freitas, JOP Pereira, eds. *Solitary bees. Conservation, rearing and management for pollination*. Fortaleza, CE, BR: Imprensa Univ., pp. 255-281.
- Machado IC, TS Melhem. 1987. Morfologia polínica de *Ipomoea hederifolia* L. e *I. quamoclit* L. (Convolvulaceae). *Hoehnea* **14**: 25-30.
- Machado IC, S Vogel, AV Lopes. 2002. Pollination of *Angelonia cornigera* Hook. (Scrophulariaceae) by long-legged oil-collecting bees in NE Brazil. *Plant. Biol.* **4**: 352-359.
- Martins CF. 1994. Comunidade de abelhas (Hym., Apoidea) da caatinga e do cerrado com elementos de campo rupestre do Estado da Bahia, Brasil. *Rev. Nord. Biol.* **9**: 225-257.
- Mendes FN, MMC Rêgo. 2007. Nidificação de *Centris (Hemisiella) tarsata* Smith (Hymenoptera, Apidae, Centridini) em ninhos-armadilha no Nordeste do Maranhão, Brasil. *Rev. Bras. Entomol.* **51**: 382-388.
- Michener CD. 2000. *The bees of the World*. Baltimore, MD: Johns Hopkins Univ. Press, 913 pp.
- Moure JS, MS Castro. 2001. Uma nova espécie de *Centris Fabricius* (Hymenoptera, Apoidea, Anthophoridae) do Nordeste do Brasil. *Rev. Bras. Zool.* **18**: 329-333.
- Oliveira-Rebouças P, M Gimenes. 2004. Abelhas (Apoidea) Visitantes de Flores de *Comolia ovalifolia* DC Triana (Melastomataceae) em uma Área de Restinga na Bahia. *Neotrop. Entomol.* **33**: 315-320.
- Ortiz PL. 1994. The Cistaceae as food resources for honey bees in SW Spain. *J. Apic. Res.* **33**: 136-144.
- Proctor M, P Yeo, A Lack. 1996. *The natural history of pollination*. London: Harper Collins Publishers, 496 pp.
- Proença CEB. 1992. Buzz pollination older and more widespread than we think? *J. Trop. Ecol.* **8**: 115-120.
- Ramalho M, M Silva. 2002. Flora oleífera e sua guilda de abelhas em uma comunidade de restinga tropical. *Rev. Univ. Estadual Feira Santana Bras.* **2**: 34-43.
- Rêgo MMC, PMC Albuquerque. 1989. Comportamento das abelhas visitantes de murici, *Byrsonima crassifolia* (L.). Kunth, Malpighiaceae. *Bol. Mus. Para. Emílio Goeldi. Sér. Zool.* **5**: 179-193.
- Rocha-Filho LC, CI Silva, MC Gaglianone, SC Augusto. 2008. Nesting behavior and natural enemies of *Epicharis (Epicharis) bicolor* Smith, 1854 (Hymenoptera: Apidae). *Trop. Zool.* **21**: 227-242.
- Roubik DW. 1989. *Ecology and natural history of tropical bees*. Cambridge Tropical Biology Series. New York: Cambridge Univ. Press, 514 pp.
- Roubik DW. 1993. Tropical pollinators in the canopy and understory - field data and theory for stratum preferences. *J. Insect Behav.* **6**: 659-673.
- Roulston TH, JH Cane, SL Buchmann. 2000. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecol. Monogr.* **70**: 617-643.
- Salgado-Labouriau ML. 1961. Pollen grains of plants of the "Cerrado" I. *Ann. Acad. Bras. Cienc.* **33**: 119-130.
- Santos FM, CAL Carvalho, RF Silva. 2004. Diversidade de abelhas (Hymenoptera: Apoidea) em uma área de transição Cerrado-Amazônia. *Acta Amazon.* **34**: 319-328.
- Schindwein C. 1998. Frequent oligolecty characterizing a diverse bee-plant community in a xerophytic bushland of subtropical Brazil. *Stud. Neotrop. Fauna E* **33**: 46-59.
- Sengupta S. 1972. On the pollen morphology of Convolvulaceae with special reference to taxonomy. *Rev. Palaeobot. Palynol.* **13**: 157-212.
- Severson DW, JE Parry. 1981. A chronology of pollen collection by honeybees. *J. Apic. Res.* **20**: 97-103.
- Silberbauer-Gottsberger I, G Gottsberger. 1988. A polinização de plantas do cerrado. *Rev. Bras. Biol.* **48**: 651-663.
- Silva FO, BF Viana, EL Neves. 2001. Biologia e Arquitetura de ninhos de *Centris (Hemisiella) tarsata* Smith (Hymenoptera: Apidae: Centridini). *Neotrop. Entomol.* **30**: 541-545.
- Silva MCM, C Martins. 1999. Flora apícola e relações tróficas de abelhas (Hymenoptera: Apoidea) em uma área de duna (praia de Interlagos, Cabedelo - PB, Brasil). *Principia* **7**: 40-51.
- Silveira FA, MJO Campos. 1995. A mellissofauna de Corumbataí (SP) e Paraopeba (MG) e uma análise da biogeografia das abelhas do cerrado brasileiro (Hymenoptera, Apoidea). *Rev. Bras. Entomol.* **39**: 371-401.
- Simpson BB, JL Neff. 1977. *Krameria*, free-fatty acids and oil-collecting bees. *Nature* **267**: 150-151.
- Simpson BB, JL Neff. 1981. Floral rewards: alternatives to pollen and nectar. *Ann. MO Bot. Gard.* **68**: 301-322.
- Siqueira KMM, CF Martin, C Schindwein, LHP Kill. 2005. Polinizadores efetivos da goiaba (*Psidium guajava*) em área irrigada do submédio do vale do São Francisco. *Ann. Enc. Zool. Nord.* **15**: 260.
- Viana BF, I Alves-dos-Santos. 2002. Bee diversity of the coastal sand dunes of Brazil. In PG Kevan, VL Imperatriz-Fonseca, eds. *Pollinating bees: the conservation link between agriculture and nature*. Brasília, BR: Ministério

- do Meio Ambiente, pp. 135-153.
- Viana BF, FO Silva, AMP Kleinert. 2001. Diversidade e sazonalidade de abelhas solitárias (Hymenoptera: Apoidea) em dunas litorâneas no nordeste do Brasil. Neotrop. Entomol. **30**: 245-251.
- Vilhena AMGF, SC Augusto. 2007. Polinizadores da aceroleira *Malpighia emarginata* DC (Malpighiaceae) em área de Cerrado no Triângulo Mineiro. Biosci. J. **23**: 14-23.
- Vinson SB, GW Frankie, HJ Williams. 1996. Chemical ecology of bees of the genus *Centris* (Hymenoptera: Apidae). Fla. Entomol. **79**: 109-129.
- Vogel S. 1974. Ölblumen und ölsammelnde Bienen. Trop. Subtrop. Pflanz. **7**: 285-369.
- Vogel S. 1990. History of the Malpighiaceae in the light of pollination ecology. Memoir. NY Bot. Gard. **55**: 130-142.
- Vogel S, ICS Machado. 1991. Pollination of four sympatric species of *Angelonia* (Scrophulariaceae) by oil-collecting bees in NE, Brasil. Plant. Syst. Evol. **178**: 153-178.
- Zanella FCV. 2000. The bees of the Caatinga (Hymenoptera, Apoidea, Apiformes): a species list and comparative notes regarding their distribution. Apidologie **31**: 579-592.