

**NESTING HABITATS AND RATES OF CELL PARASITISM IN SOME BEE SPECIES OF THE
GENERA *ANCYLOSCELIS*, *CENTRIS* AND *EUGLOSSA* (HYMENOPTERA: APIDAE)
FROM COLOMBIA**

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SUMMARY

We describe a dense nest aggregation of *Ancyloscelis* aff. *apiformis*, two nests of *Centris flavifrons*, and six nests of *Euglossa*. We found a nest of *E. analis* built inside a cavity of a living tree, an aerial nest of *E. cybelia* attached under a leaf of a palm tree and four nests of *E. nigropilosa* associated with timber buildings and abandoned nests of carpenter bees (*Xylocopa* sp.). We report for the first time wasps of the family Eurytomidae (Hymenoptera: Chalcidoidea) and a cuckoo bee, *Coelioxys (Rhinocoelioxys)* sp. (Hymenoptera: Megachilidae), attacking the brood cells of *E. cybelia* and *E. nigropilosa*. We also briefly discuss the variation found in the nest structure of *C. flavifrons*; unlike those nests studied in Costa Rica and northeastern Brazil, the nests in Colombia were shallow (~12 cm) and consisted of a main tunnel with three short branches, each one ending in a single cell. Further data from other localities are needed to detect other variations in the nesting biology and if they are correlated with the morphological variation exhibited by this species or with local differences in parasite pressure.

Key words: Coelioxys, Eurytomidae, nest structure, Neotropic, Xylocopa.

RESUMEN

Describimos una agregación densa de nidos de *Ancyloscelis* aff. *apiformis*, dos nidos de *Centris flavifrons* y seis nidos de *Euglossa*. Encontramos un nido de *E. analis* hecho dentro de una cavidad en un árbol vivo, un nido aéreo de *E. cybelia* pegado al envés de una hoja de palma y cuatro nidos de *E. nigropilosa* asociados a construcciones humanas y nidos abandonados de abejas carpinteras (*Xylocopa* sp.). Registramos por primera vez avispa de la familia Eurytomidae (Hymenoptera: Chalcidoidea) y una abeja parasita, *Coelioxys (Rhinocoelioxys)* sp. (Hymenoptera: Megachilidae), atacando las celdas de cría de *E. cybelia* y *E. nigropilosa*. También discutimos brevemente la variación encontrada en la estructura del nido de *C. flavifrons*; a diferencia de los nidos estudiados en Costa Rica y nororiente del Brasil, los nidos en Colombia fueron superficiales (~12 cm) y consistían de un túnel principal con tres ramificaciones, cada una de ellas terminando en una sola celda. Más datos de otras localidades son necesarios para detectar otras variaciones en la biología de nidificación, y determinar si están relacionadas con la variación morfológica exhibida por esta especie o con diferencias locales en el nivel de parasitismo.

Palabras clave: Coelioxys, Eurytomidae, estructura del nido, Neotrópico, Xylocopa.

INTRODUCTION

The purpose of this paper is to document the nesting habitats and rates of cell parasitism of five bee species of the genera *Ancyloscelis* Latreille, *Centris* Fabricius and *Euglossa* Latreille (Hymenoptera: Apidae) from Colombia (Table 1). Information on behavioral and ecological aspects of bees is valuable to our knowledge of their adaptations to the environment, as well as for a better understanding of their phylogeny and coevolutionary patterns with plants and parasites (Michener 2007). However, biological information is usually limited to some common bee species or species of economical importance; thus, hindering our interpretations of their diversity and evolution.

The studied bee species are widely distributed in the Neotropical region and have interesting relationships with native plants, but little has been published about their nesting biology. For example, the nests of *Ancyloscelis*, a genus containing about 30 species, are only known for *A. apiformis* (under the name of *A. armata* Smith) and *A. panamensis* Michener 1954 (Torchio 1974, Michener 1954, 1974; Rozen 1984). Some species are oligolectic on *Ipomoea* Linnaeus (Convolvulaceae) or Pontederiaceae and some have long tongues with hooked hairs for pulling pollen out of the flowers (Michener 2007). For *Centris* and *Euglossa*, with more than 100 species each, the nesting biology is roughly known for about 20 % of the species (e.g., Ramírez et al. 2002, Cameron 2004, Michener 2007). *Centris* is well known among bee and plant biologists for collecting floral oils from several plant families, including Malpighiaceae and Krameriaceae. Most species nest in the ground, although those of the subgenera *Hemisiella*, *Heterocentris* and *Xanthemisia* nest in preexisting cavities (e.g., Lima & Gaglianone 2003, Michener 2007). *Euglossa* bees are commonly known as orchid bees because of their amazing behavioral and morphological adaptations with Orchidaceae. These bees are intensively collected in many Neotropical areas using synthetic chemical baits, but the nesting biology of the majority of the species remains to be studied. Some *Euglossa* species also nest in preexisting cavities, whereas others build exposed nests (aerial nests); the latter nests, enclosed within a spherical resin envelope (involucrum), are attached to twigs, stems and the underside of leaves. Like *Centris*, the nesting substrate in *Euglossa* commonly differs among

subgenera or species groups (e.g., Cameron 2004, Roubik & Hanson 2004).

We describe a dense nest aggregation of *Ancyloscelis* aff. *apiformis*, the nest of a ground nesting *Centris* and cavity and aerial nests of three species of *Euglossa*. We report for the first time wasps of the family Eurytomidae (Hymenoptera: Chalcidoidea) and a cuckoo bee, *Coelioxys* (*Rhinocoelioxys*) sp. (Hymenoptera: Megachilidae), attacking the brood cells of *E. cybelia* and *E. nigropilosa*. We also briefly discuss the variation found in the nest structure of *Centris flavifrons*.

MATERIAL AND METHODS

We found the nests on the dates and locations indicated in Table 1. We excavated the nests of *Ancyloscelis* and *Centris* using a geological pick and a pocketknife. We collected and transported the *Euglossa* nests to the laboratory at night when all bees were presumably inside the nest, except for the nest of *E. cybelia* collected during the daytime. Once the adults were removed, we kept the nests for about four weeks in the dark inside Ziplock plastic bags containing moistened cotton. We collected and killed all bees and parasites that emerged during this period in 75 % ethanol. Cells that remained sealed after four weeks were opened and their contents examined.

We measured nest features with a caliper, except for the cell entrance which was measured under an Olympus SZ60 stereomicroscope with an ocular micrometer. Maximum nest depth was measured from the nest entrance to the bottom of the deepest cell. Voucher specimens of bees, parasites and nest structures are deposited in the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva (Boyacá) and the first author's personal collection.

RESULTS

Ancyloscelis aff. *apiformis*

Nest architecture. We found a dense aggregation (~ 143 nests/m²) of this species in a shaded, dry vertical bank, on one side of a pavement road. Females and males were seen entering and leaving this aggregation at the time it was found. We extracted two blocks (~ 400 cm², 15–20 cm thick) from the nest site and dissected it in the laboratory. Nest entrances were circular in cross section (\bar{x} = 3.2 mm ± 0.1, n = 6) and lacked turrets. Because of the high nest density and

presumably long-term occupation of the nest site, as judged by the number of old cells found (see below), it was difficult to accurately trace the complete structure of an individual nest. However, our observations suggested that nests probably consisted of a short main tunnel (length, ~ 2–4 cm; diameter, $\bar{x} = 3.3 \text{ mm} \pm 0.07$, $n = 5$) ending in one or a few short linear series of ovoid cells. When cells were found in a series, they were separated by a space of 2.5 mm from each other. Cells were found at different angles with respect to the vertical bank, ranging from perpendicular to nearly parallel to it. Cell dimensions were as follows: diameter, $\bar{x} = 4.9 \text{ mm} \pm 0.7$, $n = 7$; length, $\bar{x} = 7.5 \text{ mm} \pm 0.5$, $n = 5$; cell cap diameter, $\bar{x} = 3.3 \text{ mm} \pm 0.1$, $n = 5$; cell cap thickness, $\bar{x} = 1.1 \text{ mm} \pm 0.2$, $n = 7$; emergence

hole, $\bar{x} = 2.2 \text{ mm} \pm 0.2$, $n = 6$. The cell cap was convex and rough on the inside and concave and smoother on the outside. There were several cells containing male and female pupae and many old empty cells in the nest block; there were no newly constructed cells or cells being provisioned. Feces were arranged irregularly from the bottom to almost cell entrance in the inner cell wall. The cocoon that covered the cell was translucent and whitish. In addition to the numerous *Ancyloscelis* cells in the nest block, we found five old, empty and larger cells of an unknown bee. It is likely that those cells belong to *Melitoma* Lepeletier & Serville (Apidae, Emphorini), a bee frequently recorded associated with nest aggregations of *Ancyloscelis* (Torchio 1974, Michener 1954, 1974).

Table 1. Bee species studied in Colombia. Habitat: D = dry forest; R = secondary tropical rain forest. * = The exact number of nests was difficult to determine because of the high nest density and presumably long-term occupation of the nest site (see text for explanation).

Species	Location	Habitat	# of nests	Date	Associated organisms
Centridini					
<i>Centris flavifrons</i> (Fabricius 1775)	Tolima: Cunday (4°00'5.5''N, 74°74'4.4''W), 780 m	D	2	Dec 2004	Not found
Euglossini					
<i>Euglossa analis</i> Westwood 1840	Caquetá: Km 28 N of Florencia (1°42.702'N, 75°42.876'W), 1327 m	R	1	Jul 2006	Not found
<i>Euglossa cybelia</i> Moure 1968	Norte del Santander: Toledo, Parque Natural Tamá (7°7'N, 72°13'W), 1100 m	R	1	Sep 1999	Eurytomidae (Hymenoptera: Chalcidoidea)
<i>Euglossa nigropilosa</i> Moure 1965	Caquetá: Km 28 N of Florencia (1°42.702'N, 75°42.876'W), 1327 m	R	4	Jul 2006	<i>Coelioxys</i> (<i>Rhinocoelioxys</i>) sp. (Megachilidae)
Emphorini					
<i>Ancyloscelis</i> aff. <i>apiformis</i> (Fabricius 1775)	Cundinamarca: Girardot (4°14'19''N, 74°44'9.5''W), 326 m	D	~ 11*	Dec 2004	Bee fly (Diptera: Bombyliidae)

Associated organisms. An unidentified bee fly (Diptera: Bombyliidae) emerged from one of the cells in the nest block.

Centris flavifrons

Nest architecture. The two nests of this species were located in an open, sandy, flat ground and were separated by a distance of 60 cm. Nest entrances were circular (14.8–16.0 mm in diameter) and had an irregular tumulus approximately 9 cm in length and 4 cm in width, which was sparsely covered by grasses (Figure 1). The nests were shallow (~ 12 cm) and consisted of a main unlined tunnel (length, 20–22 cm diameter,

$\bar{x} = 1.3 \text{ cm} \pm 0.2$, $n = 6$) that branched into three short tunnels (length, $\bar{x} = 6.7 \text{ cm} \pm 0.2$, $n = 6$), each one ending in a single, nearly vertically oriented cell (Figure 2). From the nest entrance, the main tunnel descended at a 45° angle for 10–12 cm and then horizontally for an additional 10 cm before it branched off.

Cells resembled those of other ground nesting *Centris* bees (e.g., Lima & Gaglianone 2003), being urn-shaped, with a rough outer surface made of sand particles and a shiny, dark brown smooth inner surface, including the cell closure. Cell caps were surrounded by a short lip (~ 1 mm high) formed by the cell walls and had a hollow (2.0–

2.5 mm in diameter) central projection about 3.4 mm high. Cells were constructed at different depths ranging from 4.0 to 9.0 cm ($\bar{x} = 6.7 \pm 0.7$, $n = 6$). Cells were on average 1.4 cm in diameter (± 0.6 , $n = 6$) and 2.5 cm in length (± 0.7 , $n = 4$). Two of the three cells found on each nest had pollen and an egg; the remaining cells were open and had been provisioned. Eggs were cylindrical in cross section and slightly curved, about 6 mm in length. Brood provisions were dry, compact and occupied about one third of the cell length.

Euglossa analis

Nest architecture. The nest was found within a cavity of a living tree, 2 m above ground, in a secondary tropical rain forest. The diameter of the tree trunk at the level of the nest entrance ranged from 4.2–6.9 cm. The nest entrance was circular (6 mm) and made of a dark resin. The ovoid resin cells (dimensions: length, 11.5 mm; diameter, 9.5 mm; cell entrance diameter, 6.4 mm; wall thickness, 0.5–1 mm) were attached directly to the inner walls of the nest cavity. The nest had 12 cells in total, three of which were open, empty and old. Four cells were arranged in a column below the entrance level and were separated from each other by spaces ranging from 1.0–5.8 mm. The remainder cells were irregularly clustered in front and above the nest entrance. There were no resin walls or involucrem delimiting the nest area inside the cavity. A single adult female was in the nest. Three females emerged during the first week, followed by six males that emerged irregularly during the subsequent weeks.

Euglossa cybelia

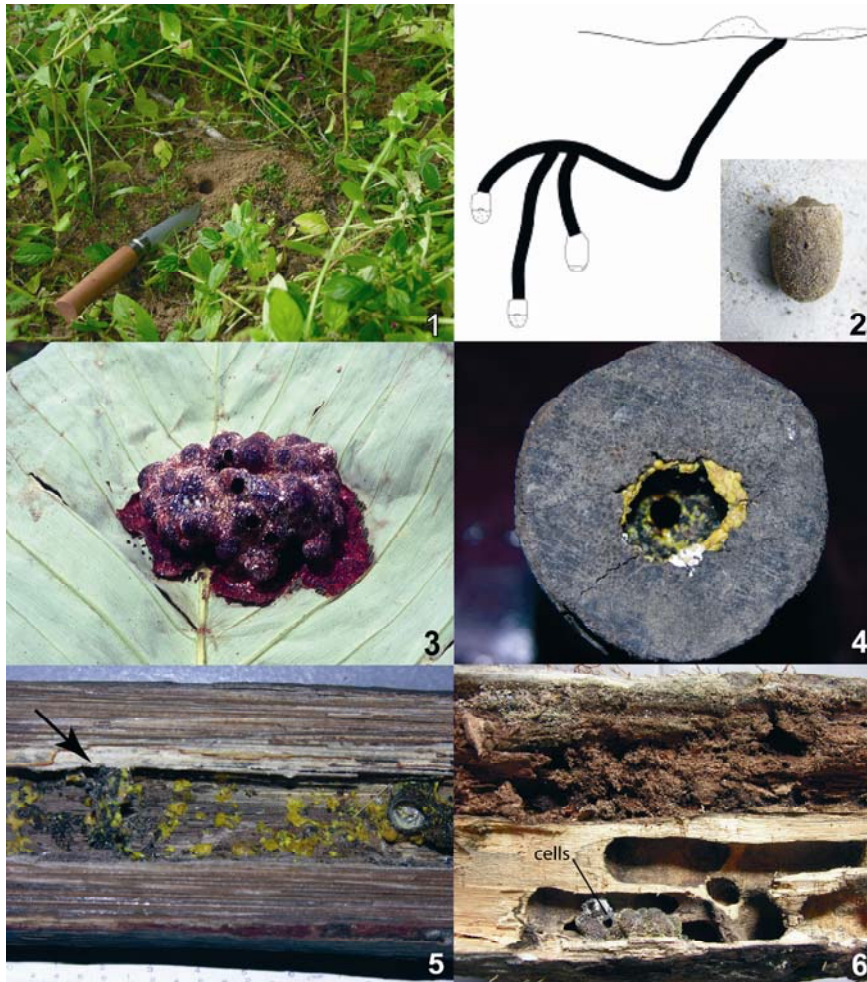
Nest architecture. This nest was found under a leaf of a palm tree (Arecaceae). The nest lacked the involucrem frequently found in other aerial nests of *Euglossa* and there were no adults at the moment it was found (Figure 3). The nest was attached to the leaf by a peduncle (3 cm x 2 cm) and the irregular cell cluster was approximately 7 cm x 5 cm across. There were 55 cells in total, 21 of them open, empty and old. The ovoid cells (dimensions: length, $\bar{x} = 15.0 \text{ mm} \pm 0.5$; diameter, $\bar{x} = 10.0 \text{ mm} \pm 0.5$; wall thickness, $\bar{x} = 1.2 \text{ mm} \pm 0.2$, $n = 15$) were predominantly made of resin, with pieces of bark and leaves. In the laboratory, 16 bees emerged (eight of each sex) during the following week.

Associated organisms. After bee emergence, a total of 45 unidentified wasps of the family Eurytomidae (Hymenoptera: Chalcidoidea) emerged from the remainder cells ($\bar{x} = 2.5$ adult wasps per cell, $n = 18$ cells) during the subsequent four weeks. Thus, 53 % of the sealed cells of this nest were parasitized.

Euglossa nigropilosa

Nest architecture. Except for a nest that was inside a dead, dry hollow trunk of a palm tree (Figures 4, 5), all nests were found inside the tunnels of old, empty, abandoned nests of carpenter bees (Figure 6) [*Xylocopa* (*Neoxylocopa*) sp. (Apidae, Xylocopini)]. All nests were associated with timber buildings, except nest # 4 that was found in an open grazing pasture. Nests were found at different heights, ranging from 40 cm ($n = 4$) to 2 m above the ground. Each nest had three, four, five and six adult bee females. Bees used the nest entrance of the old *Xylocopa* nests (23–25 mm in diameter as in the tunnels) to build their entrance with a bright yellow resin, except for nest # 4 that did not have one. The nest entrance was rounded (6.5–7.6 mm in diameter) and was closed with resin at sunset. The cells were clustered and distributed in small groups inside the tunnels of the *Xylocopa* nests (Figure 6) and were separated by divisions (4–5 mm thick) made of resin as in the nest entrance. On average, cells of *E. nigropilosa* were spread out along a section of 12.7 cm (± 2.2 , $n = 3$ nests) of the *Xylocopa* tunnels. The shape and arrangement of the cells were as described for *E. analis* but with the following dimensions: length, $\bar{x} = 14.4 \text{ mm} \pm 1.6$; diameter, $\bar{x} = 8.8 \text{ mm} \pm 0.7$; wall thickness, $\bar{x} = 1.25 \text{ mm} \pm 0.2$, $n = 6$. On average, each nest had 9 sealed cells (± 1.7 , $n = 27$), 2.3 old, empty cells (± 2.5 , $n = 7$) and 3.3 (± 2.9 , $n = 10$) cells under construction.

Associated organisms. We found a cuckoo bee, *Coelioxys* (*Rhinocoelioxys*) sp. (Megachilidae), had parasitized four cells (14.8 %) out of a total of 27 examined cells pooled across nests. All parasitized cells belonged to nest #4, which also had six sealed cells, three old and empty cells and two cells under construction. The six sealed cells contained four male and two female colored bee pupae. Thus, the percentage of brood parasitism in nest # 4 was 40 %.



Figures 1–2. Nest entrance, schematic illustration of a nest and detailed view of an urn-shaped cell of *Centris flavifrons*, respectively (see text for measurements).

Figure 3. Aerial nest of *Euglossa cybelia* under a leaf of a palm tree. The nest lacked the involucrem frequently found in other *Euglossa* aerial nests.

Figures 4–6. Nest entrance and inner views of *E. nigropilosa* nests inside a dead, dry hollow trunk of a palm tree and tunnels of abandoned carpenter bee nests [*Xylocopa* (*Neoxylocopa*) sp. (Apidae, Xylocopini)]. The arrow in Figure 5 points at the resin-made entrance shown in Figure 4 (see text for measurements).

DISCUSSION

Our brief observations on the nests of *A. aff. apiformis* from Colombia are similar to those of Torchio (1974), Michener (1954, 1974) and Rozen (1984); that is, nests are built in dense aggregations, in vertical, deep shaded banks and frequently associated with nests of *Melitoma* bees. However, given that only two of the 30 species of *Ancyloscelis* have been studied, it would not be surprising to find these bees nesting in other

conditions. Many aspects of the natural history of these bees remain to be discovered.

Centris flavifrons sensu Snelling (1984) is a morphologically highly variable species (especially in body size and color) widely distributed in Central and South America, whose “forms” sometimes are recognized as separate species or subspecies. Despite its wide distribution, the nests of *C. flavifrons* have only been studied in Costa Rica (CR) (Vinson & Frankie 1988) and northeastern Brazil (Rego et al.

2006). In CR, nests were located in the sides of small depressions or holes and had six to ten blind side tunnels scattered along the main tunnel. In Brazil, nests were found on flat ground and did not have blind tunnels; in both cases, nests had a single brood cell and were considerably deep (over 25 cm). The two nests in Colombia were also found on flat ground and did not have blind tunnels, but were shallower (~12 cm) than those from CR and Brazil, consisting of a main tunnel with three short branches, each one ending in a single cell (Figure 2). On each nest, cells had been provisioned or had pollen and an egg, suggesting that they were built around the same time, likely by the same female.

Nests of *C. flavifrons* in CR were frequently attacked by cleptoparasitic bees of the genus *Mesoplia* Lepeletier (Apidae, Ericrocidini). Thus, Vinson & Frankie (1988) suggested that the widely dispersed nesting sites and nests with long, deep tunnels having many blind side branches, might be adaptations to environments with heavy parasite pressure; however, the influence of other ecological variables cannot be ruled out. Further data from other localities across the distribution range of *C. flavifrons* are needed to detect other variations in the nesting biology and if they are correlated with the morphological variation exhibited by this species or with local differences in parasite pressure.

Except for the lack of an involucrem in the nest of *E. cybelia*, the nest architecture of the observed aerial and cavity nests of *Euglossa* is similar to that of previous records (e.g., Otero 1996 for *E. nigropilosa*) or other species of the genus (Roubik

& Hanson 2004 and references therein). Given that aerial nests frequently have involucrem, its absence in the nest of *E. cybelia*, as well as of adult females, suggests that the nest might have been disturbed. Hymenopterans, such as the cuckoo bees in the genus *Coelioxys* Latreille and small parasitoid wasps of the families Eulophidae, Eurytomidae and Torymidae (Chalcidoidea), have been frequently recorded parasitizing brood provisions of *Euglossa* (Ramírez et al. 2002, Roubik & Hanson 2004), albeit not from the species we studied. Eurytomidae wasps were previously known from nests of *E. hemichlora* Cockerell 1917 (Roubik & Hanson 2004) and *Monodontomerus argentinus* Brèthes (Hymenoptera: Torymidae) was the only known parasite to attack nests of *E. nigropilosa* (Otero 1996, 2001).

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