

Nesting and Social Behavior of a Wood-Dwelling Neotropical Bee, *Augochlora isthmii* (Schwarz), and Notes on a New Species, *A. alexanderi* Engel (Hymenoptera: Halictidae)

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ABSTRACT: The nesting biology and social behavior are described for *Augochlora* (*Augochlora*) *isthmii* Schwarz at the species' type locality (Barro Colorado Island, Republic of Panamá). Bees nested in a fallen log with wood that was still solid. Nests of *A. isthmii* sometimes contained more than one female, suggesting some form of social behavior, while other females nested alone. Pollen taken from nest cells was almost exclusively (>95%) from a single species of Rubiaceae (nr. *Warszewiczia coccinea*) that is rare on BCI. An occupied nest of a second, related species (*A. alexanderi* Engel, new species) was discovered in a tree branch in southern Colombia, supporting the conclusion that females of the *repandirostris* species-group regularly use wood as a nesting substratum. We provide the first taxonomic descriptions of the male of *A. isthmii* and both sexes of *A. alexanderi*; we also redescribe the female of *A. isthmii*. The evolution of social behavior in the "*Augochlora* group" is briefly considered in light of available information.

KEY WORDS: Apoidea, Halictidae, *Augochlora*, nesting biology, social behavior, taxonomy

Introduction

The bee tribe Augochlorini (Halictidae: Halictinae) is primarily Neotropical, with extensive intra- and inter-specific variation in female behavior, ranging from solitary to social (with or without castes) to parasitic (behavior: Michener, 1990; Wcislo, 1997a, 2000; Danforth and Eickwort, 1997; Yanega, 1997; Packer, 1997; taxonomy: Eickwort, 1969; Engel, 2000). Although ideal for addressing questions regarding social evolution, in practice the behavior of most species (>97%) is unknown or insufficiently studied (Danforth and Eickwort, 1997). Many augochlorines are soil-nesters, and wood-nesting has evolved at least three times in the tribe (Eickwort and Sakagami, 1979; Danforth and Eickwort, 1997; Engel, 2000), an evolutionary change in nest-site preference that entrains a series of environmental changes relevant to understanding other traits such as social behavior.

One of the more species-rich genera is *Augochlora* s. l. with ~130 named species, but information on nesting biology (excluding records of floral visitation) is available for <10% of its species (Moure and Hurd, 1987). Eickwort (1969) recognized three subgenera of *Augochlora*, two of which are behaviorally divergent based on the available data; an extinct subgenus of Miocene age is known from Dominican amber (Engel, 2000). *Augochlora* s. str. are solitary bees that nest in rotting and relatively soft wood or within bromeliads (e.g., Stockhammer, 1966; Sakagami and Moure, 1967; Zillikens *et al.*, 2001); and *A. (Oxystoglossella)* are social and dwell in the soil (e.g., Eickwort and Eickwort, 1972, 1973). Eickwort (1969) recognized a third subgenus, *A. (Mycterochlora)*, that was behaviorally unknown, and is now subsumed within *A. (Augochlora)* (Engel, 2000; Michener, 2000). On the basis of anatomical traits shared with other wood-nesting augochlorine bees (e.g., expanded mandibles and scale-like setae bordering the median

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pseudopygidial slit: Schremmer, 1979), Eickwort (1979) hypothesized that *A. (Mycterochlora)* females nested in wood.

Here we demonstrate that Eickwort correctly identified convergent features for wood-nesting, augochlorine bees. We describe and illustrate the nest structure and contents of *Augochlora (Augochlora) isthmii* Schwarz, previously known only from the holotype from central Panamá (Schwarz, 1934; Michener, 1954), and we document wood-nesting in a related new species in the *repandirostris* species-group (=subgenus *Mycterochlora* sensu Eickwort, 1969) from southern Colombia. We provide taxonomic descriptions of the male and pupa of *A. isthmii* and redescribe the female, and describe both sexes of the Colombian species. We briefly discuss some implications for understanding the evolution of wood-nesting and social behavior within augochlorine bees.

Materials and Methods

One part of this study was conducted between 9–25 April 2000, which is near the end of the dry season, on Barro Colorado Island (BCI), Republic of Panamá (9°09'N, 79°51'W; for description of BCI, see Rau, 1933; Leigh, 1999). Nest descriptions follow Sakagami and Michener (1962) and Eickwort and Sakagami (1979). Nest entrances were marked with stakes inserted into the wood. One or two days before we excavated nests, we captured adults as they were leaving the nests using conical traps made of wire and netting placed over the entrances; other females were aspirated directly from nests. Immediately prior to excavation, we used a syringe to inject into the tunnel a slurry of plaster-of-Paris and water, which was allowed to harden. We then used wood chisels and a hammer to carefully excavate nests. Adults and immatures were fixed in Kahle's solution for later dissection and examination, and pollen was transferred to a plastic tray for later identification. Adult bees and nest features were measured in the field using dial calipers; cell, nest tunnel, and nest entrance samples were collected, and then later examined and measured under a Wild® M10 stereomicroscope with an ocular micrometer. Mean values are given with standard errors.

Voucher specimens of *A. isthmii* (adults, larvae, and nest structures) are deposited in the Smithsonian Tropical Research Institute Dry Reference Collection, Balboa, Panamá (STRI); duplicates of the adults are deposited in the Museo de Invertebrados "Graham Fairchild," Universidad de Panamá, República de Panamá (MIUP), and the Natural History Museum, University of Kansas (SEMC). Voucher specimens of *A. alexanderi* are the type specimens, and are deposited as given in the descriptions; nest structures are in the Laboratorio de Investigaciones en Abejas, Universidad Nacional de Colombia, Santafé de Bogotá, Colombia.

In the descriptions, morphological terminology is based on Engel (2001) and terminology for surface sculpturing follows Harris (1979), while the format generally follows that used elsewhere for halictid bees. The abbreviations F, OD, S, and T are used for flagellomere, ocellar diameter (based on the median ocellus), metasomal sternum, and metasomal tergum, respectively.

Nesting Behavior and Natural History

Nest Site Localities

Augochlora (Augochlora) isthmii Schwarz

Eight nests of *A. isthmii* were discovered in a fallen avocado tree trunk [*Persea americana* (Lauraceae): length, 3.1 m; diameter, 35 cm], located on a 45° sloping bank

beside the stairs from the Visitor's Center to the Dining Hall on BCI. The bank was partly covered by small trees, herbaceous vegetation, and ferns. The log was relatively solid, such that wood was removed only with a wood chisel and hammer blows. The surface of the log was peppered with a large number of small holes (~ 5 mm diameter) that were presumably made by other wood-boring insects. Nests were situated on the top and sides of the log, forming a sparse aggregation of 5.4 nests/m², with a minimum nearest-neighbor distance of 9.4 cm ($\bar{x} = 15.3 \pm 3.4$ cm, $n = 8$).

Augochlora (Augochlora) alexanderi Engel

A single nest of *A. alexanderi* (Fig. 2) was discovered during the rainy season (3 July 2000) in secondary forest in Montañita, Departamento del Caquetá, Colombia, at ~ 500 m elevation. The nest was within a solid broken branch having a diameter of ~ 2.1 cm, length of 104 cm, and was found parallel to the surface at 117 cm above the soil.

Nest Architecture

Augochlora (Augochlora) isthmii Schwarz

Females started new nests in holes made by other wood-boring insects. Nest entrances were circular with a diameter from 3.1 to 4.1 mm ($\bar{x} = 3.4 \pm 0.4$ mm, $n = 5$), and were flush with the surface of the log. Active nests were usually easy to locate because wood particles accumulated below an entrance. Below the constricted nest entrance the tunnel widened, from 5–8 mm in diameter ($\bar{x} = 6.4 \pm 1.1$ mm, $n = 10$), and total tunnel length varied from 75 mm to 90 mm in length ($\bar{x} = 86 \pm 6.5$ mm, $n = 5$), extending into the center of the log. Most tunnels were unbranched, although one nest had short branches (15–20 mm) that were sealed off with wood fibers. Tunnel walls were partly or wholly lined with comminuted wood.

Cells of *A. isthmii* were spaced at varying intervals along the main burrow, and radiated in all directions (Fig. 1), but tended to be concentrated near the end of the tunnel, possibly because the wood in the rotting interior of the log was softer than nearer the surface, though we did not quantify substrate hardness. Each cell was connected directly to the main tunnel without a lateral tunnel (sessile). Cells were constructed within excavated cavities (but not within chambers), and cells could be removed intact. Cell walls were made of fine wood particles pressed together; the thin walls were irregular on the outer surfaces, but were smooth and shiny on the entire inner surface that was lined with a hydrophobic compound, presumably Dufour's glands secretions as in other bees (refs. in Cane, 1983; Wcislo and Cane, 1996). The cells were similar in overall appearance to other halictine bees, being slightly flattened on the bottom surface with a rounded oval upper surface; 12–15 mm in length ($\bar{x} = 13.9 \pm 1.1$ mm, $n = 6$), 5–7.1 mm in width ($\bar{x} = 6.3 \pm 0.6$ mm, $n = 6$), and 4.5–5.4 mm in cell entrance diameter ($\bar{x} = 4.8 + 0.37$ mm, $n = 5$). We found only one cell with a complete pollen mass, which measured 3.7 mm long, 4.0 mm wide, and 4.1 mm high; the mass had a dough-like consistency. Cells were closed with a plug of pressed wood fibers, from 1.6 to 2 mm wide ($\bar{x} = 1.8 \pm 0.06$ mm, $n = 7$), that was smooth on the surface facing the tunnel; the interior surface of the plug had a slight concentric depression, similar to that seen in the cell plug of ground-nesting augochlorine bees (see Sakagami and Michener, 1962). Defecated feces were in the position usual for halictine bees, on the upper rear wall of the cell. Sometimes feces could be distinguished as individual flattened bands (~ 0.2 mm wide) but usually the boundaries were smeared. The number of cells per nest ranged from 5 to 17 ($\bar{x} = 9 \pm 4.9$ cells per nest, $n = 7$). Cell contents of singleton nests ranged from an egg with a pollen mass to pigmented pupae,

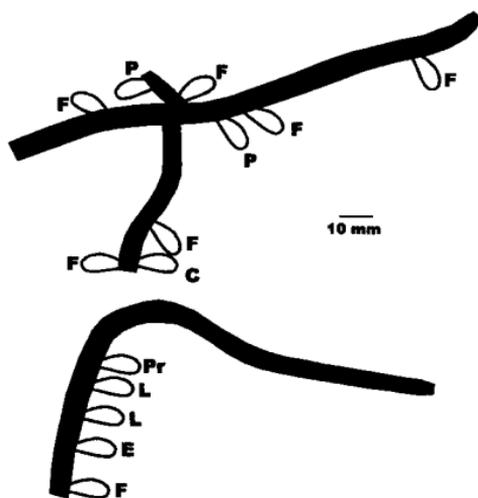


Fig. 1. Schematic illustrations of nests of *Augochlora (Augochlora) isthmii* Schwarz within a fallen log. E = egg; L = larva feeding on pollen; Pr = post-feeding, pre-defecating larva; P = pupa; C = callow adult within cell; F = old cell filled with wood shavings.

while contents of multi-female nests ranged from the egg stage to callow adults within cells. The egg was positioned on top of the pollen mass. In one case the deepest cells in a nest were the oldest, and cells were progressively younger toward the surface (Fig. 1, bottom), but we do not know whether this is typical or coincidental.

Augochlora (Augochlora) alexanderi Engel

The nest of *A. alexanderi* had a constricted entrance hole (diameter = 3.6 mm) on the underside of the stick, located about 85 mm from the end of the stick (Fig. 2). The tunnel diameter enlarged gradually from the entrance (4.4 mm) to the end (5.2 mm), and was 56 mm long. Inside the entrance the tunnel was almost perpendicular to the surface of the stick for 11 mm and then curved sharply to follow the long axis of the stick. Inner tunnel walls were partly lined with comminuted wood. We found two old cells with feces and one with a pigmented male pupa. Cells were constructed within cavities, and not excavated; approximate length was 8.8 mm ($n = 1$) with a diameter of ~ 4.3 mm ($n = 2$), and were radially distributed and attached directly to the main burrow without lateral tunnels (Fig. 2). There were openings along the tunnel wall, some of which had their inner walls partly lined, suggestive of very old cells or tunnel branches, but most such cavities had irregular, unlined inner walls; it was not clear if these holes were cells under construction or not.

Pollen Utilization

Augochlora (Augochlora) isthmii Schwarz

Pollen grains from 17 plant species belonging to 14 families were found within *A. isthmii* cells (Table 1). In all cases the vast majority (95–100%) of pollen within each cell was from a single species of Rubiaceae related to the wild poinsettia, *Warszewiczia* nr. *coccinea*; *Vismia* sp. (Clusiaceae) accounted for 2–5% of the pollen in 4 of 11 cell samples. The remaining species were present in trace amounts (<1% of the total per cell)

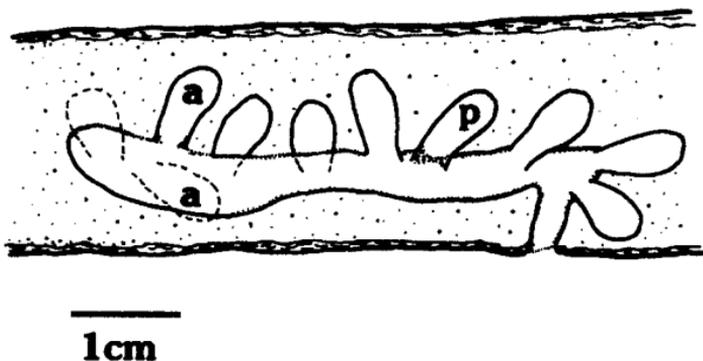


Fig. 2. Schematic illustrations of a nest of *Augochlora (Augochlora) alexanderi* Engel within a stick. P = pupa; a = old cell filled with wood shavings.

and may be contaminants or were gathered incidentally during nectar visits. In Panamá, *W. nr. coccinea* is a characteristic subcanopy tree of tropical wet and moist forest (Croat, 1978), as are its congeners elsewhere in the Neotropics (Gentry, 1993). On BCI, which has a strong dry season (Windsor, 1990), *W. nr. coccinea* is rare and usually seen only along the island's shore (Croat, 1978), where presumably it has access to the lake via the water table; it has never been recorded in four complete censuses of all plant stems >1 cm diameter on a 50 ha plot at a slightly higher and drier site elsewhere on BCI (Condit *et al.*, 1996). *Warszewiczia nr. coccinea* lacks the appearance of a "bee plant": it has a reddish calyx and conspicuous, elongate bright red bracts, with small yellow flowers and orange pollen; it blooms during the late dry season to the middle of the wet season in Panamá, especially in July and August but also sporadically at other times of the year (Croat, 1978).

Augochlora (Augochlora) alexanderi Engel

Identification of fecal pollen from one cell of *A. alexanderi* revealed *Clusia nr. melchiori* Gleason (Clusiaceae) and *Vismia nr. macrophylla* Kunth (Clusiaceae).

Female Behavior

Augochlora (Augochlora) isthmii Schwarz

Females were actively excavating within nests, as inferred from the tailings of wood dust piled below the nest entrances, and were actively collecting pollen when the site was discovered. The eight nests contained from 1–5 ($\bar{x} = 2.4 \pm 0.87$) adult females. Three nests had a single female, each of which was mated and had well-developed ovaries (Group A of Michener and Wille, 1961). Each singleton had some wear-and-tear on the wings and mandibles (class 2 or 3 of Michener and Wille, 1961), suggesting these females were already active in the field. Three multi-female nests had 5, 4, and 4 females, respectively. Pooled across nests, mated females had greater wing wear than did unmated females (mean wing wear index of 3.4 and 1.6 for mated and unmated females, respectively; indices follow Michener and Wille, 1961). In one nest the two mated females were larger than the unmated ones; in another nest some mated females were larger than unmated ones, while others were smaller than unmated ones; and in the third nest all females were mated, but small sample sizes preclude statistical analyses. The following observations, though brief, indicate that these multi-female nests are functioning colonies,

Table 1. List of plant species from which *Augochlora (Augochlora) isthmii* Schwarz collected pollen near the end of the dry season in central Panamá. $N = 11$ cells sampled; * = pollen grains comprised <1% of total grains in a cell for all samples.

Amaranthaceae	* <i>Cyathula prostrata</i> Blume
Anacardiaceae	* <i>Spondias mombin</i> L.
Apocynaceae	* <i>Lacmellea panamensis</i> Markgraf
Asteraceae	*aff. <i>Calea</i> sp.
	* <i>Vernonia</i> sp.
Clusiaceae	<i>Vismia</i> sp.
Convolvulaceae	* <i>Maripa panamensis</i> Hemsley
Euphorbiaceae	* <i>Hyeronima laxiflora</i> Muell. Arg.
Euphorbiaceae	* <i>Sapium</i> sp.?
Gramineae	*aff. <i>Paspalum</i> sp.
Malpighiaceae	* <i>Hiraea quapara</i> Morton
Phytolaccaceae	* <i>Microtea</i> sp.?
Rubiaceae	aff. <i>Warszewiczia coccinea</i> (Vahl) Klotzsch
	*aff. <i>Genipa americana</i> L.
Sapindaceae	* <i>Serjania</i> sp.
Solanaceae	* <i>Solanum</i> sp.
Tiliaceae	*aff. <i>Heliocarpus popayanensis</i> H.B. & K.

and not pre-reproductive assemblages sensu Michener (1990). First, we observed females actively nesting (e.g., collecting pollen, nest construction) indicating that bees were reproductively active when we discovered the nests. Second, degree of wing wear and mandibular wear varied among nest-mate females, suggesting that not all females were from the same pre-reproductive cohort. Third, some females within the multi-female nests had well-developed ovaries, while others did not. Finally, the brood sex ratio was 2:1 female to male ($n = 22$ pupae) pooled over nests, but we did not measure investment ratios. Among nests, however, the bees might be splitting sex ratios (female: male): two nests had a male-biased sex ratio (1:3 each); one nest had a slightly female biased ratio (2:1), and the other was extremely female biased (11:0).

Augochlora (Augochlora) alexanderi Engel

The nest of *A. alexanderi* contained one adult female and two adult males. One male escaped. The female's mandibles and wings were unworn, suggesting that she was a newly emerged adult; we did not dissect this female. As inferred from cell contents, this nest was probably an old or inactive nest with a pre-reproductive assemblage of adults, and so nothing about female social behavior can be deduced.

Systematics

Augochlora (Augochlora) isthmii Schwarz

(Fig. 3)

Augochlora fulgidana isthmii Schwarz, 1934:3. Michener, 1954:66.

Augochlora (Mycterochlora) isthmii (Schwarz); Moure and Hurd, 1987:276.

DIAGNOSIS: Female *A. isthmii* can be distinguished from other Mesoamerican *Augochlora* by the characters of the *repandirostris* species-group (e.g., apical margin of clypeus procurved, male genitalic structures) as well as by the strong and closely punctate head and mesoscutum with copper-red highlights, and black metasoma with metallic green reflections. Schwarz (1934) superficially described this species, based on a single female

half of its posterior length. Distal hamuli arranged 2-1-2 along anterior margin of hind wing.

Clypeus with strong punctures separated by less than a puncture width, integument between punctures smooth; supraclypeal area closely punctuate as on remainder of face, punctures smaller than clypeus, progressively closer and smaller toward supraocular and ocellar areas; small impunctate areas just above antennal sockets; vertex and gena granulate to colliculate, postgena with sparse faint punctures. Pronotum faintly imbricate; anterior area of mesoscutum colliculate, punctures larger and more widely separated by 2-4 times puncture width on central disc, integument between punctures smooth; scutellum with minute punctures separated by 2-3 times puncture width, integument between punctures smooth; metanotum finely colliculate. Preepisternum and hypoepimeron strong and closely punctuate, larger punctures on the former. Mesepisternum with coarse punctures separated by 1-2 times puncture width, integument smooth. Metepisternum mostly with punctures smaller than previous areas separated by 1-2 times puncture width, finely punctuate on the lower half. Lateral and posterior surfaces of propodeum colliculate as metanotum; basal area of propodeum with strong striae radiating from basal margin, integument between striae smooth and shining. Tegula with strong and dense punctures anteriorly, smooth and shiny on disc area. Metasomal terga finely strigulate, with minute punctures, sparse on T1 and coarser and deeper on T5; marginal areas on T1-T4 impunctate. Sterna imbricate.

Head predominantly metallic green with copper-red highlights, except apical margin of clypeus, labrum, mandibles, scape and pedicel black; apex of labral distal process and mandible reddish brown; flagellum dark brown. Mesoscutum with metallic copper-red highlights as head, remainder of thorax brilliant metallic green with weak copper highlights. Tegula and legs dark brown, except distal tarsal segments amber. Metasoma black with metallic green highlights lateral on T1-2 and just above along of the posterior marginal area on T3-4. Wings slightly dusky; veins and pterostigma dark brown.

Pubescence predominately yellowish on head and thorax. Long erect hairs minutely branched on paraocular areas and front, which are projecting on a whitish pubescence of short adpressed hairs. Scattered and shorter on clypeus; supraclypeal area glabrous. Short semierect simple hairs on the outer surface of antennal scape and pedicel. Gena densely covered with semierect and short white hairs finely branched, long and sparse on postgena. Erect hairs on mesoscutum fuscous, shorter than those on scutellum and metanotum; longest on scutellum. Propodeal area densely covered by a fine adpressed whitish branched hairs; erect hairs in remaining areas of thorax mainly yellowish. Legs with fuscous to dark fuscous pubescence. Metatibial scopa with thick apically branched hairs along anterior margin, otherwise simple or branched from apical half. Erect yellowish branched hairs on base and sides of T1. Long black bristles on T2-T6, more dense and longer on sides of each terga, and progressively increasing in length and density toward end of metasoma. T2-T4 densely covered with adpressed short golden hairs; pseudopygidial area of T5 with scale-like setae bordering median slit. Sterna with long erect fuscous hairs.

Male. As described for the female, except as follows ($N = 3$ bees for all measurements). Body length, 7.0. Forewing length from apex of costal sclerite to tip of wing, 4.8. Head wider than long (1.8: 1.7). Clypeus unmodified, 1.4 times as broad as long (0.7: 0.5). Scape twice as long as wide (0.4: 0.2); pedicel as long as $F1 + F2$; $F2$ shorter than $F3$; $F8-F11$ slightly crenulated; flagellum reaching axilla. Ocellular distance 0.3; distance between lateral ocelli 0.3; distance from median ocellus to lateral ocellus 0.08. Gena as wide as width of compound eye in profile. Intertegular distance 2.0. Clypeus metallic

green; mandibles and labrum yellow. Legs dark brown, except the tarsi of all legs yellowish. Metasoma black, except T7 which is yellowish with the apical margin carinate, with metallic green highlights on the sides and bordering the posterior marginal area on T1–T3. Wings hyaline. Punctuation denser and coarser on scutellum, metanotum, propodeal areas and metasomal terga than female. Pubescence yellowish and much less dense than female. Supraclypeal area covered with long hairs like those on paraocellar areas. Terga more densely covered by small, adpressed and golden hairs than female. Sterna with shorter yellowish hairs than female. Genitalia and associated sterna as in Fig. 3.

Pupa. Male and female pupae agree closely with the description for *A. nominata* (Eickwort and Eickwort, 1972), differing by the presence of a small tubercle on the base of outer surface of scape, tubercles in front of eye-notches are lower, virtually absent, with number of tubercles on metasomal terga as follows: T1 with 3 rounded tubercles (larger in the male) close to median line and two small tubercles widely separated; T2 with 9 to 12 tubercles progressively pointed per side, smaller than on T1; T3 with all tubercles pointed except the first one, 9 to 11 per side; 7–9, 6–7, and 4–5 tubercles per side on T4, T5, and T6, respectively; and 2 tubercles per side on T7 (male).

HOLOTYPE: Female, PANAMÁ: Barro Colorado Island, 11 December 1930, H. F. Schwarz. Specimen in the American Museum of Natural History, New York.

ADDITIONAL MATERIAL: Six females, three males; PANAMÁ: Barro Colorado Island, 9–25 April 2000, V. H. Gonzalez and W. T. Wcislo (STRI, MIUP, SEMC).

COMMENTS: In comparison with the type specimen of *A. isthmii*, the mesoscutal punctures of Schwarz's holotype are very slightly more widely separated than those on our specimens. Callow specimens examined differed in the metallic green thorax (excepting mesoscutum) and whitish pubescence. One male specimen had yellowish spots on the inner surface of all tibiae, and the basal and apical margins of the outer surface.

Augochlora (Augochlora) alexanderi Engel, new species
(Figs. 4, 5a–c)

DIAGNOSIS: This species belongs to the *repandirostris* species-group (=subgenus *Mycterochlora* sensu Eickwort, 1969). The labral apex is slightly extended and procurved and the apical margin of the male T7 is carinate. In addition, like its related congeners [e.g., *A. repandirostris* (Vachal), *A. pachytes* (Vachal), and *A. isthmii*], *A. alexanderi* has the strong lateral extensions dorsally on the penis valve posteriorly joined by a V-shaped ridge (Fig. 5). The species can be differentiated by its genitalic structure (Fig. 5) which is most similar to *A. repandirostris*. In *A. alexanderi* the ventral spines on the ventral gonostylar process are reduced in number and size relative to the stout series formed in *A. repandirostris* (Fig. 5c, d), the setae laterally bordering the gonostylus are absent, and the distance between the ventral gonobasal arms is greater relative to the width of the genital foramen (ca. 86% of genital foramen width in *A. alexanderi*; 59–66% of genital foramen width in *A. repandirostris*).

DESCRIPTION: Female. Total body length 6.7 mm; forewing length 5.6 mm. Apical margin of clypeus procurved; distal half of clypeus extending below lower tangent of compound eyes; angle of epistomal sulcus only slightly less than orthogonal. Supraclypeal area moderately protuberant. Frontal line carinate between antennal sockets, otherwise a strongly impressed line extending to median ocellus. Preoccipital ridge carinate, strongly so dorsally (almost slightly lamellate). Intertegular distance 1.7 mm. Basal vein distad ca by twice vein width; first submarginal cell slightly longer than combined lengths of second and third submarginal cells; second submarginal cell approximately equal to that of

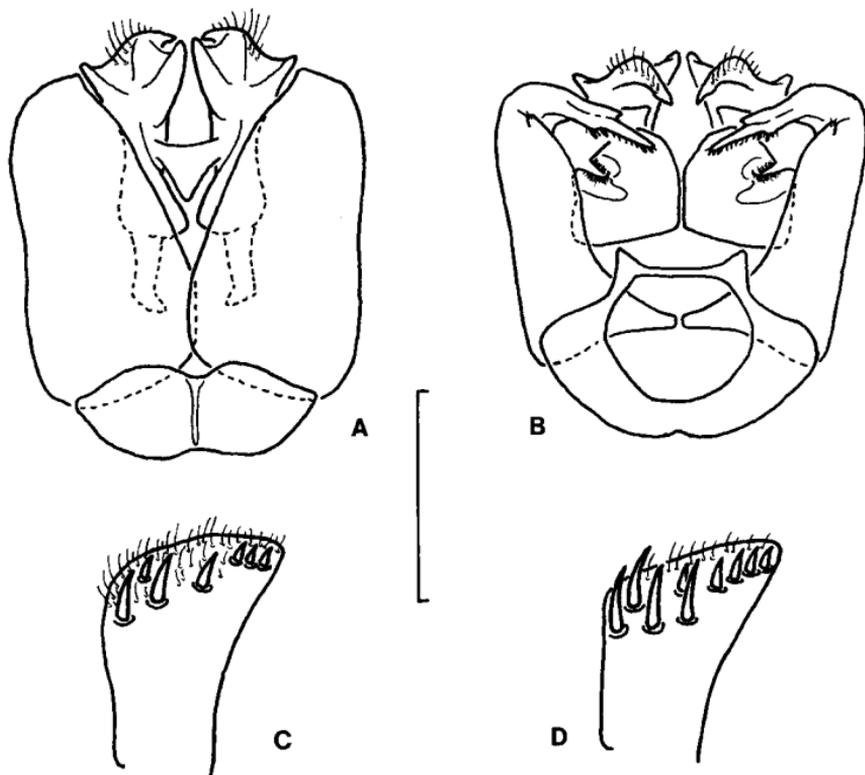


Fig. 5. Male terminalia: A–C of *Augochlora (Augochlora) alexanderi* Engel, new species; D of *A. (A.) repandirostris* (Vachal). A. Dorsal view of genital capsule. B. Ventral view of genital capsule. C. Ventral surface of ventral gonostylar process. D. Ventral surface of ventral gonostylar process for *A. (A.) repandirostris*. Scale bar = 0.5 mm (for A & B), 0.25 mm (for C & D).

integument between smooth; punctures becoming weak and gradually blending into imbricate surface along anterior margin; tegula weakly imbricate; scutellum with punctures slightly more faint and smaller than those of mesoscutum, separated by 0.5–1 times puncture width, integument between smooth; metanotum with shallow, coarse punctures separated by 1.5–2 times puncture width, integument strongly imbricate. Preepisternum with large, coarse punctures separated by a puncture width or less, integument between smooth, punctures gradually more spaced ventrally until reaching separation of 1.5 times puncture width; metepisternum with minute punctures separated by less than a puncture width except dorsal quarter with punctures distinctly larger than remainder of metepisternum. Basal area of propodeum with strong striae extending from basal margin to apex; lateral and posterior surfaces of propodeum imbricate, with coarse punctures separated by 2–3 times puncture width. Metasomal terga with minute punctures except apical margins impunctate, punctures of T1 sparse, punctures of remaining terga separated by 1.2 times puncture width; sterna faintly imbricate, with minute punctures separated by a puncture width or less on apical two-thirds.

Head and mesosoma brilliant metallic green with strong metallic blue highlights and scattered, faint golden or coppery highlights except for the following structures black: mouthparts, mandible, labrum, apical third of clypeus, scape, pedicel, and F1; F2–10 and legs dark brown except tarsi and protibia brown to light brown. Wing venation brown to dark brown; membrane hyaline. Metasoma black with strong metallic blue-green or green highlights.

Pubescence off-white except lightly golden on tibiae and tarsi.

Male. As described for the female except for typical sex differences of structure and pubescence, with the following modifications: Total body length 7.2 mm; forewing length 5.9 mm. Male genitalia depicted in Fig. 5.

Punctures of hypocpimeron nearly contiguous over entire surface; punctures of mesepisternum separated by a puncture width or less, punctures not becoming more widely separated ventrally.

Head and mesosoma brilliant metallic green with strong metallic blue highlights and scattered, faint golden or coppery highlights except the following structures: mouthparts and antenna black; mandible (except reddish-brown apex), labrum, and apical quarters of clypeus amber; legs dark brown except tarsi, protibia, and apices of meso- and metatibiae brown to amber.

Pupa. As described above for *A. isthmii*.

HOLOTYPE: Male; COLOMBIA: Caquetá, Paujil, 500 m, 3 July 2000, V. H. Gonzalez, ex. nest in twig. Deposited in Laboratorio de Investigaciones en Abejas, Universidad Nacional de Colombia, Santafé de Bogotá, Colombia.

PARATYPE: Female; COLOMBIA: Caquetá, Paujil, 500 m, 3 July 2000, V. H. Gonzalez, ex. nest in twig. Deposited in SEMC.

ADDITIONAL MATERIAL: A single male pupa; COLOMBIA: Caquetá, Paujil, 500 m, 3 July 2000, Victor H. Gonzalez, ex. nest in twig. Deposited in SEMC.

ETYMOLOGY: The specific epithet is a patronymic honoring Alexander Barr—a young entomologist who understands the importance of nature—in gratitude to him and his family for their inspirational insect collecting expedition to Panamá with the Make-a-Wish Foundation. Alexander was diagnosed with leukemia in 1997 and visited STRI in 2000. Three years off treatment, Alexander continues to enthusiastically collect insects, and is an active member of the entomological community in Seattle.

Discussion

The fact that the behavior of so few halictid species has been studied means that it is difficult to draw general conclusions about their behavioral evolution. From available data, the predominant architectural style for augochlorine bees is an earthen nest with a cluster of cells that are supported on pillars within an empty, underground cavity (Eickwort and Sakagami, 1979; Danforth and Eickwort, 1997; Engel, 2000). Some soil-dwelling augochlorines have cells dispersed along a main tunnel, which is thought to be a secondary reversion to a simpler nest architecture (*op. cit.*). Various workers have suggested that cell clusters may function to help drain water away from the developing brood (Sakagami and Michener, 1962; Eickwort and Sakagami, 1979; Packer and Knerer, 1986), and such a function might be especially important in soils of the wet tropics. Drainage would be relatively unimportant for tropical species nesting in dead wood, and nests of some other wood-nesting augochlorines (e.g., *Megalopta*) lack well-defined clusters. *Augochlora isthmii* and *A. alexanderi* nests are a mosaic: nest architecture is similar to that of *A. (Oxytroglossella)* in that cells are not clustered together in a chamber, while nest-site

preference resembles that of *Augochlora* s. str. in using wood as a nest substrate. In the tribe Augochlorini wood-nesting has evolved independently in *Augochlora*, *Neocorynura*, and *Megalopta* (Eickwort and Sakagami, 1979; Danforth and Eickwort, 1997; Engel, 2000). Some species of wood-nesting bees can be induced to nest in soil, at least in the laboratory (e.g., Barrows, 1973), but it is not known if such behavioral flexibility is expressed in nature. Our study supports Eickwort's (1979) hypothesis that certain structural features (e.g., expanded mandibles) are associated with wood-nesting behavior, indicating that these traits can be used with relative confidence to infer nest site preference for behaviorally unstudied species.

The behavioral and morphological characters of *A. isthmii*, and the newly discovered species, *A. alexanderi*, support the synonymy of *A. (Mycterochlora)* with *Augochlora* s. str. (Engel, 2000; Michener, 2000). If our limited behavioral observations are corroborated, then social behavior of *Augochlora* is more variable than previously thought. Our data suggest a few changes to the character state matrix in Appendix 2 of Engel (2000) for *Augochlora*: character 72 should be coded as a subset polymorphism (states 0 and 3) since both social and solitary behavior are apparently present, and character 76 should be changed to a subset polymorphism (states 0 and 1) since cell chambers are not present. Analysis of the data matrix with these alterations made no changes to the topology.

Evolutionary changes in the social behavior within the "*Augochlora* group" [*Augochlorella*, *Ceratalictus*, *Pereirapis*, *Augochlora (Oxystoglossella)*, and *Augochlora* s.str.] have been of considerable interest because of the possible loss of social behavior (see discussion in Wcislo and Danforth, 1997; also Danforth, 2002). A cladistic analysis of Eickwort's (1969) phenetic data supported Michener's (1990) hypothesis that solitary behavior in *Augochlora* s. str. was derived from eusocial ancestry (Danforth and Eickwort, 1997), which also was supported by an additional analysis (Engel, 2000). Danforth and Eickwort (1997) rightly concluded that behavioral information on unstudied lineages in the "*Augochlora* group" such as *Ceratalictus* and *A. (Mycterochlora)* would be particularly informative for differentiating between alternative cladistic reconstructions that they presented. They also noted that Michener's hypothesis of a reversal in social behavior would receive additional support if females of species then placed in *A. (Mycterochlora)* proved to be social, as suggested by our study. These earlier studies, however, assumed that the terminal taxa were monophyletic, and that behavioral data for known species also characterized basal members of each clade. The monophyly of some of these taxa is now doubtful (Engel, 2000; Michener, 2000; Coelho, 2001), and the typological characterization of the behavior of species and higher taxonomic units is a well-known problem in reconstructing historical changes for halictid bees and other taxa (Michener, 1974; Wcislo, 1997b; Crespi and Choe, 1997). Consequently, the reconstructions mentioned above are necessarily tentative hypotheses. Ideally, future studies would identify critical species based on their phylogenetic position and describe behavior from nests in multiple populations, to better understand evolutionary changes in social biology. Due to the vagaries of field research, however, opportunistic studies like the one presented here are more likely.

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