



Bayesian and parsimony phylogeny of *Augochlora* bees (Hymenoptera: Apoidea) based on morphology: insights for their biogeography and natural history

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Abstract

Augochlora Smith, with 127 valid species, is the most widespread genus of Augochlorini bees, ranging from Argentina to southern Canada, including the Caribbean islands. The genus is divided into three subgenera, *Augochlora* s. str., *Oxystoglossella* Eickwort, and the fossil *Electraugochlora* Engel. The extant subgenera were traditionally diagnosed by their nesting substrate, social behavior and morphology. However, accumulating evidence suggests that these features are not reliable for their separation, especially with the discovery of an enigmatic species sharing characteristics from both subgenera. Our objective is to provide a phylogenetic hypothesis to evaluate the monophyly of the extant subgenera and to place a new species, *Augochlora* (*Augochlora*) *intermedia* sp. nov. For this purpose, we compiled 110 unordered characters for 40 species of *Augochlora* plus seven outgroup species and analyzed under parsimony and Bayesian inference. Topologies were very similar under both frameworks, allowing us to consistently characterize a few major lineages. Our results demonstrate that the extant subgenera correspond to monophyletic groups and the new species is sister group to remaining *Augochlora* s. str. species. Both subgenera are widespread in the Western Hemisphere, with species groups differing in range and distributional patterns. Our interpretation is that *Augochlora* arose in South America, subsequently colonizing Mesoamerica, the Caribbean and North America several times. Facultative social behavior can be found in both subgenera and in most lineages, indicating that the exclusive solitary behavior found in *Augochlora pura* is an exception. Based on morphological clues we interpret that the habit of nesting out of the soil arose once in *Augochlora* s. str.

Keywords

Augochlorini, Biogeography, Halictidae, Homoplasy, Neotropical, Partitioning

1. Introduction

Augochlorini Beebe is restricted to the western hemisphere, representing a major component of the Neotropical bee fauna (Eickwort 1969; Danforth and Eickwort 1997; Engel 2000; Pinheiro-Machado et al. 2002). These

bees are remarkable among other Halictinae by their diversity of specializations, embracing both behavioral and morphological aspects. The tribe is mostly composed of soil-nesting diurnal species, but nocturnal/crepuscular

behavior, cleptoparasitism and capacity of using decaying wood as nesting substrate are often found among its representatives (Eickwort 1969; Michener 1990, 2007; Engel 2000). Each of these characteristics evolved independently at least two times in different lineages within the tribe, somewhere during the Cenozoic (Gonçalves 2016). These bees also exhibit many levels of social organization, including solitary species with small nests and primitively eusocial species with large multifemale nests (Michener and Lange 1958; Ordway 1965; Stockhammer 1966; Danforth and Eickwort 1997; Gonzalez et al. 2014). Such behavioral diversity is often linked with morphological adaptations, for example the allometric growth of cephalic structures in some females of eusocial species, enlargement of eyes and ocelli in crepuscular or nocturnal species, and well-developed ridges on mandibles of females that build nests within wood (Sakagami and Moure 1965; Eickwort 1969; Gonçalves and Melo 2012; Lepeco and Gonçalves 2018). Even though many of these aspects have been investigated since the last century, the elucidation of their evolutionary pathways is still unclear, since species-level phylogenies are lacking for the speciose genera.

Augochlora Smith is the most widespread genus of Augochlorini, ranging from the province of Neuquén in central Argentina to southern provinces of Canada (Engel 2000; Packer et al. 2007; Lepeco and Gonçalves 2020a), being one of the few lineages of the tribe occurring in the Caribbean islands (Eickwort 1969; Engel 2000; Michener 2007). In the Neotropical region, these bees can be found in virtually all environments, with the exception of some xeric areas of Argentina and Chile (Dalmazzo and Roig-Alsina 2011). The diversity of *Augochlora* decreases in temperate regions with an apparent higher diversity in forested areas (Lepeco and Gonçalves 2020a). Presently, there are 127 valid species (Moure 2012; Ascher and Pickering 2021; Lepeco and Gonçalves 2020a, 2020b; this study), a number only outreached by *Augochloropsis* Cockerell within the tribe. *Augochlora* is a monophyletic group that belongs to the *Augochlora* genus group along with *Augochlorella* Sandhouse, *Ceratalictus* Moure and *Pereirapis* Moure (Engel 2000; Gonçalves 2016, 2019). The acute angle of epistomal sulcus and the truncate and appendiculate marginal cell apex are distinctive features of the genus (Eickwort 1969). According to Engel (2000) and Coelho (2004) *Augochlora* is related to *Ceratalictus* + *Pereirapis*, with *Augochlorella* as the sister group with the remaining genera, while Gonçalves (2016, 2019) considered *Augochlora* as sister group with *Augochlorella*.

Currently, the genus is found in three valid subgenera: *Augochlora* s. str., *Electraugochlora* Engel, and *Oxystoglossella* Eickwort (Engel 2000; Michener 2007; Moure 2012), but other four genus group names are available. Smith (1853) described *Augochlora* and included diverse augochlorine bees, mostly species currently placed in *Augochloropsis*. Later, Cockerell (1923) designated *Augochlora pura* (Say, 1837) as the type species of *Augochlora* and then Sandhouse (1937) properly delimited the genus as recognized by subsequent authors. Before 1937 the *Augochlora* species were placed on *Oxystoglossa*

Smith or *Odontochlora* Schrottky. *Oxystoglossa* was proposed by Smith in the description of *Augochlora decorata* (Smith, 1853) and this name was used by some authors (e.g., Schrottky 1909b) for *Augochlora* species without a spine in the first metasomal sternum. Posteriorly, Schrottky (1909a) proposed the subgenus *Odontochlora* for *Augochlora* species with a projection on the first metasomal sternum, designating *Augochlora mulleri* (Cockerell, 1900) as the type species. Both genus names were synonymized under *Augochlora* by Sandhouse (1937). Eickwort (1969) considered *Augochlora repandirostris* (Vachal, 1911) remarkably different from other *Augochlora*, due to the epistomal angle weakly produced and the clypeus apical margin prolonged, proposing *Mycterochlora* Eickwort as a subgenus to accommodate this and other similar species. Later, *Mycterochlora* was synonymized with *Augochlora* s. str. by Engel (2000). *Augochlora cordiaefloris* Cockerell, 1907 is the type species of a second valid subgenus, *Oxystoglossella*, described by Eickwort (1969) to accommodate species with preapical tooth of mandibles not produced. The subgenus *Aethochlora* was proposed by Moure and Hurd (1987) mostly based on the enlarged gena of *Augochlora matucanensis* Cockerell, 1914, but this name was synonymized under *Oxystoglossella* by Engel (2000). The third subgenus, *Electraugochlora* was described by Engel (2000) for one fossil species, *A. leptoloba* Engel, 2000, which lacks the distinctive acute angle of epistomal sulcus.

A broad sample of the behavioral diversity found in Augochlorini is present also in *Augochlora*, since species have particular nesting substrate preferences and sorts of social organization (Michener and Lange 1958; Stockhammer 1966; Dalmazzo and Roig-Alsina 2012, 2015, 2018a, 2018b). Previously, it was believed that eusocial behavior was restricted to the subgenus *Oxystoglossella*, especially due to long-term observations of nests of the solitary *A. (Augochlora) pura* (Michener and Lange 1958; Stockhammer 1966; Eickwort and Eickwort 1972, 1973; Engel 2000). Posteriorly, it was noted that other *Augochlora* s. str. species exhibit eusociality (Wcislo et al. 2003; Dalmazzo and Roig-Alsina 2012, 2015, 2018a, 2018b). In the primitively eusocial species, morphological variation among nestmates may be restricted to overall body size, as in *A. (A.) phoemonoe* (Schrottky, 1909), or with allometric growth of the head and its structures, as seen in *A. (Oxystoglossella) iphigenia* Holmberg, 1886 and *A. (A.) daphnis* Smith, 1853 (Dalmazzo and Roig-Alsina 2012, 2015; Lepeco and Gonçalves 2018). The phylogenetic placement of the genus within the *Augochlora* group of genera suggests a secondary loss of eusociality at least in *A. (A.) pura*, given that *Augochlorella* Sandhouse and *Pereirapis* Moure are eusocial as far as is known (Michener 1990; Wcislo and Danforth 1997). Nothing is known about the behavior of the species of *Ceratalictus* (Wcislo and Danforth 1997; Engel 2000).

Both subgenera apparently diverge in nesting substrate usage – *Augochlora* s. str. construct nests from cavities within soft wood, while all *Oxystoglossella* so far studied exhibit the ancestral soil-nesting behavior. *A. (A.) esox* is the only known species to nest within the hummus accu-

mulated in the rosettes of bromeliads (Zillikens 2001), but this species was also collected nesting in wood. All known females of *Augochlora* s. str. have strongly bidentate mandibles with more conspicuous ridges on the outer surface, characteristics associated with excavation of soft wood (Eickwort 1969; Eickwort and Sakagami 1979). This trend is reinforced by the presence of even more developed mandibular ridges on larger females of some *Augochlora* s. str., that may represent foundresses in charge of nesting construction (Dalmazzo and Roig-Alsina 2012, 2015; Lepeco and Gonçalves 2018). On the other hand, the preapical tooth of *Oxystoglossella* females is small and largely separated from the apex of the mandible. Both subgenera also may differ in the pubescence of the pseudo-pygidial area, which is considered as related to the differing nesting substrate preferences (Engel 2000; Wcislo et al. 2003; Michener 2007). In addition, nesting architecture may differ within subgenera, as some species do not construct cell clusters, differing from the typical nest architecture of most Augochlorini (Eickwort and Sakagami 1979; Wcislo et al. 2003).

Although regional taxonomic revisions and species descriptions have been made in recent years (see Dalmazzo and Roig-Alsina 2011; Engel et al. 2012; Genaro 2016; Lepeco and Gonçalves 2020a, 2020b), the subgeneric classifications were not properly evaluated. In the present study we describe a new species bearing a mosaic of morphological characteristics found in both subgenera and explore the morphological variation within *Augochlora*, in order to propose a phylogenetic hypothesis for its main extant lineages. With this hypothesis in mind, we thereby discuss its implications for interpreting macro-evolutionary patterns of: biogeography, nesting substrate and architecture; and for social behavior and related morphological polymorphisms.

2. Methods

We selected 40 species of *Augochlora* as ingroup taxa, including all generic and subgeneric type species, with the exception of *Augochlora* (*A.*) *decorata*, whose type specimen is in poor conditions (images available in the British Natural History Museum website). We included seven species for the outgroups. *Augochlorella comis* (Vachal, 1911), *Augochlorella ephyra* (Schrottky, 1910), *Ceratalictus clonius* (Brèthes, 1909) and *Pereirapis semiaurata* (Spinola, 1853) as members of the *Augochlora* group of genera (Eickwort 1969; Engel 2000; Gonçalves 2016, 2019). We also included species of Augochlorini from other groups of genera, *Pseudaugochlora graminea* (Fabricius, 1804), *Neocorynura codion* (Vachal, 1904) and *Thectochlora brachycera* Gonçalves & Melo, 2006. Males and females were coded for all terminals, with the exception of males of *A.* (*A.*) *azteca* (Vachal, 1911) and *Augochlorella comis* (Vachal, 1911), the latter being coded for as many characters as possible using the literature. Also, male genitalia information is lacking for *A.*

(*O.*) *matucanensis* Cockerell, 1914 and *A.* (*O.*) *rightmyerae* Engel, 2000. All specimens examined for the present analyses are permanently housed in the Coleção Entomológica Pe. Jesus Santiago Moure at the Departamento de Zoologia, Universidade Federal do Paraná (DZUP), Curitiba, Paraná, Brazil.

Morphological terminology follows Michener (2007) except for mandibular structure following Michener and Fraser (1978) and genital capsule following Eickwort (1969). We use the abbreviations F1, F2 etc. to denote antennal flagellomeres; T1, T2 etc., to denote the metasomal terga; and S1, S2 etc., to denote metasomal sterna. We measure setae length in comparison to mid ocellus diameter (OD) and punctures interspaces in comparison to puncture diameter (PD). To study male genitalia characters, specimens were softened in a wet chamber for two or three days. Genitalia were removed with entomological pins and clarified in 10% KOH for 24 hours and then analyzed and preserved immersed in glycerol. Most of had type material of *Augochlora intermedia* sp. nov. is deposited in DZUP, with exception of one female paratype deposited in RPSP—Coleção Entomológica “Prof. J. M. F. Camargo”, Universidade de São Paulo, Ribeirão Preto, Brazil. The species description, including measurements and sculpturing terminology follows Lepeco and Gonçalves (2020a, 2020b).

Specimens were examined under Olympus SZ51 and SZ61 microscopes, using led ring illumination. Measurements were taken with the aid of a micrometric rule coupled to a Leica Stemi DV4. Specimens were photographed with a Nikon D7000 with a 105 mm Sigma Macro lens, controlling image capture with Helicon Remote. The illumination techniques used were those suggested by Kawada and Buffington (2016). Image stacking was made using the software Helicon Focus (version 6.18), based on Method C (Pyramid). Final image adjustments, including unsharp mask filtering and level control, and plate design were made with GIMP 2.8.16 (©The GIMP Team).

The morphological matrix was largely based on characters from previous studies (Engel 2000; Coelho 2004; Gonçalves 2016, 2019), with reinterpretations and additions where needed (Supplementary file 1: List of characters). The final matrix comprised 110 unordered characters and 47 terminals (Supplementary file 2: Morphological matrix). Inapplicable characters were coded with “-” and missing data with “?”. For most of the terminals, more than one specimen was observed during character construction and coding processes. Construction of characters was based on the method proposed by Sereno (2007). Autapomorphic characters were included, since they are used in estimation of branch lengths under parametric frameworks (Lewis 2001).

Parsimony analyses were taken using new search methods (Goloboff et al. 2008), under the following settings in TNT software: ratchet weighting probability 5%, 200 iterations, tree-drifting (50 cycles), and tree-fusing (five rounds, minimum length set to be hit 100 times). Analyses were conducted under equal weights and implied weighting, with different values for the concavity parameter (*k*) tested. Since there were no significant

alterations in tree topology under different k values, we used the standard $k = 3$ to calculate Goloboff's measure of homoplasy (f). Bootstrap and Jackknife values (1000 replications) and Bremer support were also calculated using TNT. Trees were viewed and edited using WinClada 1.00.08 (Nixon 2002).

The original character matrix was partitioned using the f values, following the methodology of Rosa et al. (2019). Final partitioning scheme comprised five partitions, with non-homoplastic and parsimony uninformative characters included in the same partition (Supplementary file 3: Partitioning scheme). We considered the minimum partition length = 6, to ensure that each partition would include at least 5% of the characters and, thus, avoiding excessive partitioning of the dataset. Branch lengths were linked among partitions, exponential prior on branch lengths with scale parameter = 10 and without assessment of site-specific rates within partitions. MCMC analyses were conducted in MrBayes 3.2.6 (Ronquist et al. 2012), using the Mk model accounting for ascertainment bias, since only variable characters were scored (*lset coding = variable*). The analysis ran for a total of 5,000,000 generations, sampling every 100th state and with four independent runs. Convergence was assessed with Tracer 1.6 (Rambaut et al. 2018) and majority-rule consensus trees (*Contype = Allcompat*) were computed with TreeAnnotator. A similar analysis was conducted without partitioning the data, accounting for among-character rate heterogeneity using a discretized Gamma distribution with four rate categories.

3. Results

3.1. Phylogenetic analyses

All analyses recovered *Augochlora* as monophyletic with strong support values (Fig. 1) and high posterior probabilities (PP > 95, Fig. 2, Supplementary file 4: Phylogenetic trees, Fig. 1). According to implied weighting and partitioned Bayesian analyses *Augochlora* is sister group to *Augochlorella*. However, unpartitioned Bayesian analysis found *Augochlorella* as the sister group to the remaining genera while *Augochlora* as related to *Ceratalictus* + *Pereirapis* (Supplementary file 4: Phylogenetic trees, Fig. 2) and parsimony under equal weights recovered a polytomy at this node (Supplementary file 4: Phylogenetic trees, Fig. 3). For simplification purposes, support values and posterior probabilities mentioned henceforward are based on results of the implied weighting parsimony and partitioned Bayesian analyses.

Both valid extant subgenera of *Augochlora* were recovered as monophyletic. The subgenus *Oxystoglossella* has 73 bootstrap and 80 jackknife support values (Fig. 1) and PP value equal to 0.95 (Fig. 2). Its synapomorphies are the pale yellowish hind basitarsus on males and the setae on the outer lobe of ventral gonostylus longer than inner lobe length (Fig. 1). The relationships among species are stable among analyses and two main clades

are found, herein the *A. iphigenia* and *A. morrae* species groups. Each species group has three synapomorphies, with the basal elevation of the labrum slightly produced in *A. iphigenia* group and orbicular in *A. morrae* group. The *A. iphigenia* group (PP = 0.96) is also defined by the broad mandible and not expanded preoccipital carina, and *A. morrae* group (PP = 0.97) by slightly pointed hypostomal carina and long S7 pre-apodemal projection.

Augochlora s. str. have 72 bootstrap and 82 jackknife support values (Fig. 1) and PP value equal to 0.73 (Fig. 2). Its synapomorphies are the thin apical black band on clypeus and the metapostnotum about 1.5x longer than metanotum, and the black basal area of the labrum (only at fast optimization). There are five major clades within *Augochlora* s. str. recognized here as species groups. Despite the low support values in the parsimony analysis, relationships among the species groups are relatively well supported in the Bayesian analysis (PP > 0.7). All species groups defined herein were stable among analyses and have posterior probabilities higher than 0.95, with the exception of the *A. pura* species group. *Augochlora* (*A.*) *intermedia* sp. nov. has an isolated placement and is sister group to the remaining groups according to three out of four analyses (Fig. 1–2). The remaining *Augochlora* s. str. are grouped by three non-homoplastic synapomorphies: preapical tooth of mandible sharp and produced near apex of mandible, pseudo-pygidial area without appressed scale-like setae, and T1 with a relatively large impunctate area near apical dark band. On the other hand, the unpartitioned Bayesian analysis recovered the *A. hestia* species group as the sister group with the remaining *Augochlora* s. str. (Supplementary file 4: Phylogenetic trees, Fig. 2). This group has a strong support (PP = 1) and several synapomorphies, including the orbicular elevation and yellowish basal area of labrum, features shared with some *Oxystoglossella*. Also, females in this group have a flattened mesofemur, with a characteristic depression near the brush posteriorly.

The remaining *Augochlora* s. str. species are grouped by the presence of a long dark area between the premarigal setae apex and the T3 apex, the acute shape of apical spine on outer surface of hind tibia, and by the S2 apex acute medially on males (Fig. 1). The presence of a median longitudinal impression on the scutellum is a synapomorphy of the *A. daphnis* species group (PP = 0.98), being valuable to diagnose the group. Another synapomorphy for this group is the angulation between the anterior and posterior surfaces of the hind coxae, sometimes forming a slight longitudinal carina, a condition also found in *A. (A.) intermedia* sp. nov. The *A. repandirostris* species group has strong support (PP = 1) and several synapomorphies, some of them useful to readily distinguish its species, such as the projected anterior portion of the clypeus, the less projected epistomal angle, and the depressed face around the antennal sockets. The *A. repandirostris* and *A. pura* species groups are defined as a clade by the absence of tiny setae among long setae on the outer surface of hind tibia and the inflexed apex of T1, both features observed in males. The *A. pura* group (PP = 0.62) is singly supported by homoplasies and rela-

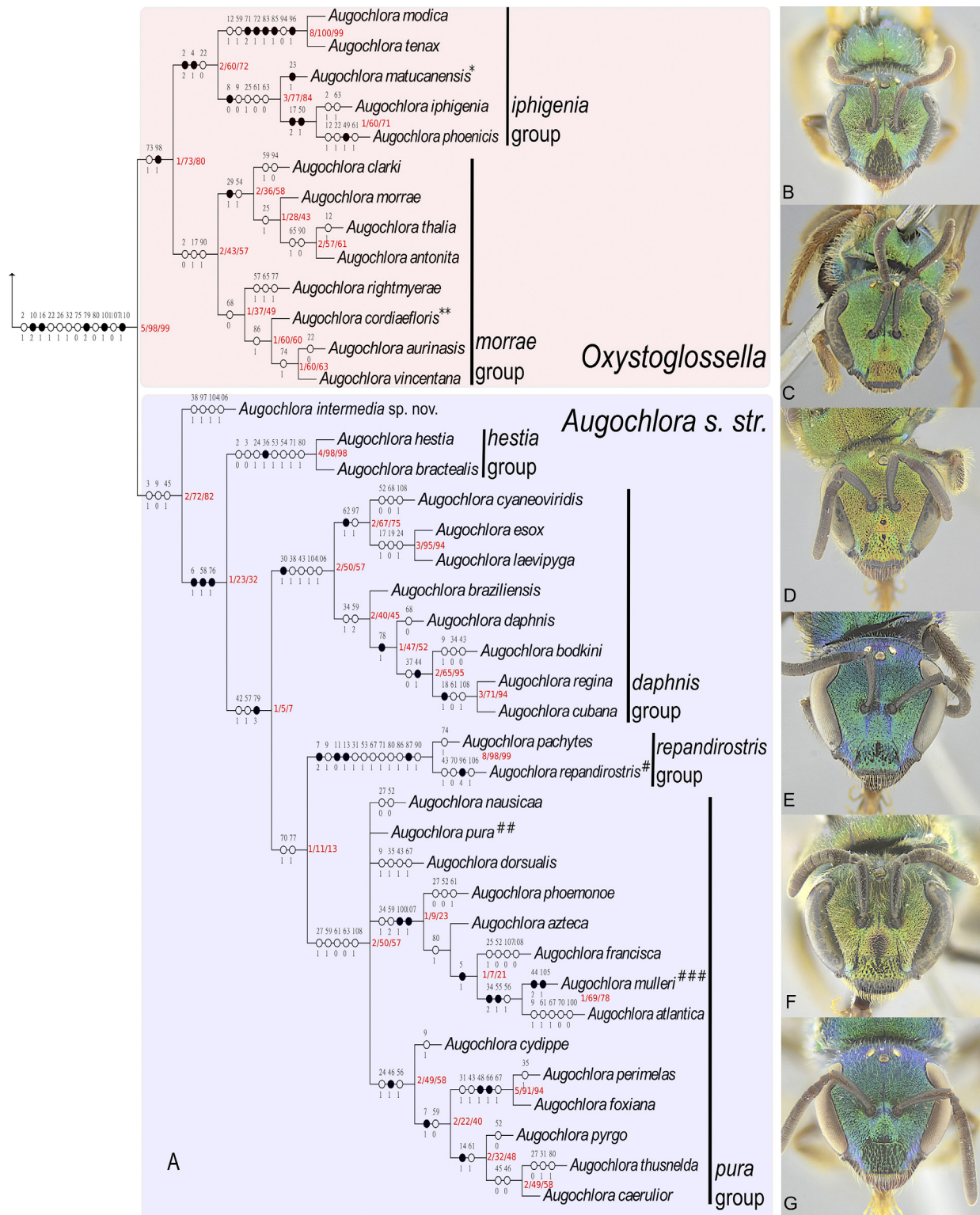


Figure 1. Phylogeny and subgeneric classification of *Augochlora* Smith. A) Parsimony analysis under implied weighting ($k=3$, fast optimization). Black and white circles indicate unique and homoplastic changes, respectively. B) *Augochlora iphigenia* Holmberg, 1886; C) *Augochlora morrae* Strand, 1910; D) *Augochlora hestia* Lepeco & Gonçalves, 2020; E) *Augochlora daphnis* Smith, 1853; F) *Augochlora repandirostris* (Vachal, 1911); G) *Augochlora pura* (Say, 1837). * type of *Aethechlora* Moure & Hurd, ** type of *Oxystoglossella* Eickwort, # type of *Mycterochlora* Eickwort, ## type of *Augochlora* Smith, ### type of *Odontochlora* Schrottky. Bremer, Bootstrap and Jackknife support values are indicated in red.

tionships among some clades are not clearly identifiable through morphology. While the consensus trees of parsimony analyses resulted in a polytomy at the base (Fig. 1 and Supplementary file 4: Phylogenetic trees, Fig. 3), the

Bayesian analysis with partitioned data indicated *A. (A.) nausicaa* as the sister group with remaining species and *A. (A.) pura* and *A. (A.) dorsualis* as related to a clade with *A. (A.) cydippe*.

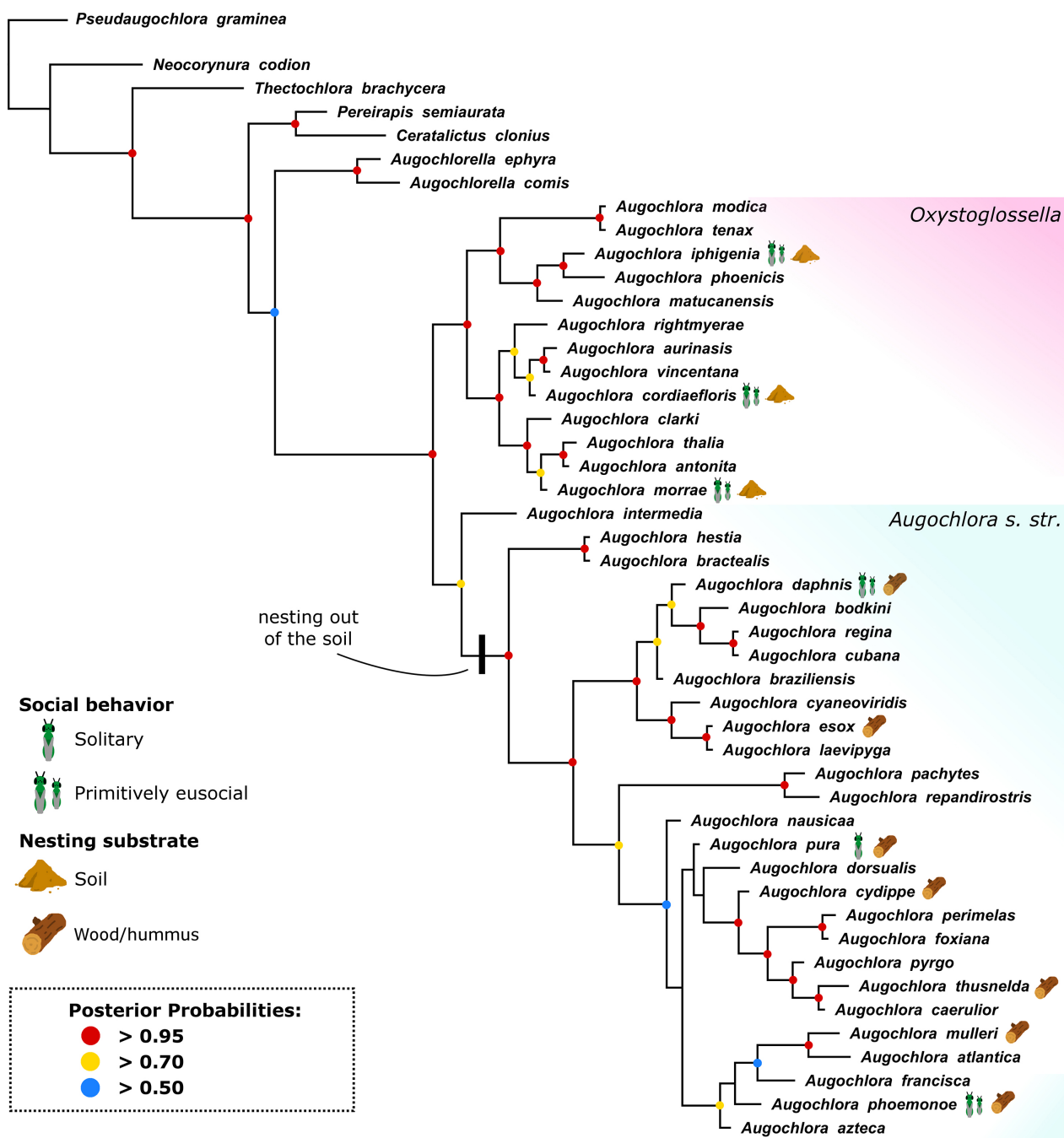


Figure 2. *Augochlora* Smith majority-rule consensus tree derived from Bayesian analysis of partitioned data. Social behavior and nesting substrate annotated where known. Origin of the behavior of nesting out of the soil was inferred based on morphological clues and on the scattered knowledge about the biology of *Augochlora* species.

3.2. Taxonomy

3.2.1. *Augochlora (Augochlora) intermedia* sp. nov.

<http://zoobank.org/NomenclaturalActs/A26D6FDD-D726-4A-41-B553-FE5F086B205D>

Figure 3A–E

Type material. Holotype female (DZUP), “DZUP\568723” “LIMA San Bartolomé\ 26.VII.75\ Coll: R. García” “RG: 537”. Paratypes

(DZUP), male “DZUP\568724” “LIMA San Bartolomé\ 17.VII.75\ Coll: R. García” “RG: 537”; female “DZUP\568725” “Lima (Peru)\ 1.6.1939\ leg. Weyrauch” “WKW\3773”; one female and two males pinned together “DZUP\568726” “LIMA, Perú\ I-1949\ P. Aguilar” “FC-64A”; female “DZUP\568727” “LIMA, Perú\ I-1949\ P. Aguilar L.” “FC-64A”; female “DZUP\568728” “No. 606-35\ Hda. Nanipol\ Jequetepeque\ 21-XII-1934” “J. Lamas coll.”; (RPSP) one female “RPSP\ 15.2461” “Peru, Cajamarca, San\ Miguel, Florida, 06 51S\ 79 07 28W 20.vi.2008\ on *Nasa olmosiana*”.

Diagnosis. Females of the new species can be readily distinguished from most other *Augochlora* by the distinctly contiguous coarse punctuation, especially on tergal mar-

ginal area, in combination with the mandible with a small preapical tooth produced far from mandibular apex. In addition, females can be separated from other *Augochlora* s. str. species by the T5 pseudo-pygidial area covered by scale-like appressed setae (similarly with *Oxystoglossella* species). From *Oxystoglossella* species it can be separated by the darkened basal area of labrum and hind coxa angulate on ventral transition between anterior and posterior surfaces. Males are diagnosed by the combination of: F1 as long as F2; hind basitarsus black; metapostnotum shorter than scutellum; T1 with reduced impunctate area medially adjacent to apical dark band (similarly with *Oxystoglossella* species); T2 with premarginal setae almost reaching apex on sublateral surfaces (similarly with *Oxystoglossella* species); and outer lobe of gonostylus ventral process with setae shorter than inner lobe.

Description. Holotype Female. Measurements (in mm). Distance between eye notches: 1.8; head length: 2.2; clypeus width: 0.6; clypeus length: 0.5; clypeoantennal distance: 0.4; clypeus ocellar distance: 1.3; intertegular distance: 1.6; T1 width: 2.1; T2 width: 2.3; body length: 8. — **Head.** Labrum basal surface black; basal elevation transverse. Mandible mostly black, apex brown; medial portion minimum width about 0.7x basal width; pre-apical tooth small and rounded, relatively distant from apical tooth apex; distal part of adductor ridge not swollen, but conspicuous in frontal view. Clypeus mostly green with golden reflection, apical black band as long as OD; mostly densely punctate ($I < PD$), punctures large, medially with an impunctate longitudinal path, imbricate among punctures. Supraclypeal area green with golden reflection; mostly contiguously punctate, sparser towards clypeus, imbricate among punctures. Lower paraocular area green with golden reflection; contiguously punctate; long setae (3 OD) intermixed with tiny setae. Antennae: mostly black, flagellum ventrally brownish. Frons green with golden reflection; contiguously punctate; not protuberant above antennal sockets. Preoccipital carina not enlarged near post-gena. Gena with golden reflection. Post-gena darkened; microreticulate, some scattered weak punctures; setae length < 3 OD. Hypostomal carina not projected anteriorly. — **Mesosoma.** Pronotum dorsolateral angle obtuse, not strongly projected. Fore leg: entirely dark brown, longer setae length = 3 OD. Mesoscutum green; mostly contiguously punctate, anterior portion crowded punctate to imbricate; with long dark setae (2 OD) intermixed with tiny setae. Scutellum green; without strong medial furrow; contiguously punctate; with long dark setae (3 OD) intermixed with tiny setae. Mesepisternum green with golden reflection; mostly contiguously punctate, anterior portion crowded punctate; with long setae (3 OD) intermixed with tiny setae. Mid leg: entirely dark brown, longer setae length = 3 OD; trochanter ventral margin straight; femur posterior surface flat; mesofemoral brush yellowish. Tegula dark brown. Metanotum longer setae length = 2 OD. Metepisternum green; contiguously punctate, becoming crowded to rugose above metapleural pit. Hind leg: mostly dark brown, except for green anterior surface of coxa; transition between

anterior and posterior surfaces of coxa ventrally making a strong angulation; without black setae on tibia and basitarsus. Metapostnotum green; as long as 0.7x scutellum length; with almost straight radiating carinae, slightly imbricate in between. Propodeum green with golden reflection; with long setae (3 OD) intermixed with tiny setae; posterior surface mostly imbricate with some scattered distinct punctures, lateral surfaces crowded to contiguously punctate near metepisternum. — **Metasoma.** T1 anterior surface densely punctate ($I = 0.5$ PD), loosely imbricate among punctures; with long setae (2 OD) intermixed with tiny decumbent setae. T1 dorsal surface contiguously punctate, mostly with small and deep punctures, larger punctures on lateral surfaces; mostly green, apical black band shorter than OD; apex not inflexed. T2 green; densely punctate ($I = 0.5$ PD), mostly with small and deep punctures, smooth in between, larger punctures on lateral surfaces; marginal zone with punctate portion 4x longer than apical brown band on sublateral surfaces. T3 green; densely punctate ($I = 0.5$ PD), loosely imbricate in between; apex of tiny setae surpassing apex of T3 sublaterally. T4 green; weakly punctate, imbricate in between. T5 light brown; pseudo-pygidial area medially without scale-like decumbent setae, colliculate. Pygidial plate dark brown, apex rounded. S1 brown; very slightly prominent medially, without distinct projection; long setae (< 5 OD) medially, margin with tiny decumbent setae. S2 brown; sparsely punctate, microreticulate in between; long setae (< 4 OD) on posterior half. S3–5 as S2. S6 dark brown.

Description. Paratype male. Measurements (in mm). Distance between eye notches: 1.6; head length: 2.1; clypeus width: 0.6; clypeus length: 0.5; clypeoantennal distance: 0.4; clypeoocellar distance: 1.2; intertegular distance: 1.3; T1 width: 1.4; T2 width: 1.5; scape length: 0.6; body length: 9. — **Head.** Labrum basal surface light yellowish. Mandible dark brown. Clypeus mostly green with golden reflection, apex yellowish, apical border exposed, yellowish; densely punctate, $I = 0.5$ PD, punctures large and shallow, loosely imbricate in between. Supraclypeal area green with golden reflection; mostly contiguously punctate, sparser towards clypeus, loosely imbricate among punctures. Paraocular area green with golden reflection; densely punctate, $I < 0.5$ PD, smooth in between; long setae (2 OD) and short setae intermixed. Antennae: mostly black, flagellum ventrally yellowish; F1 as long as F2; F3 as long as wide; remaining flagellomeres progressively longer. Frons mostly green, with golden and blue iridescences intermixed; mostly contiguously punctate, crowded punctate near mid ocellus. Gena green with golden reflection. Post-gena darkened, with golden reflections; loosely imbricate, some scattered weak punctures; sparse long setae (< 4 OD). — **Mesosoma.** Pronotum dorsolateral angle obtuse, not strongly projected. Fore leg: mostly brown, except for green coxae anteriorly and femur outer surface; trochanter and femur not strongly swollen. Mesoscutum green; densely punctate ($I = 0.5$ PD), mostly loosely imbricate in between, anteriorly microrreticulate among punctures; with long

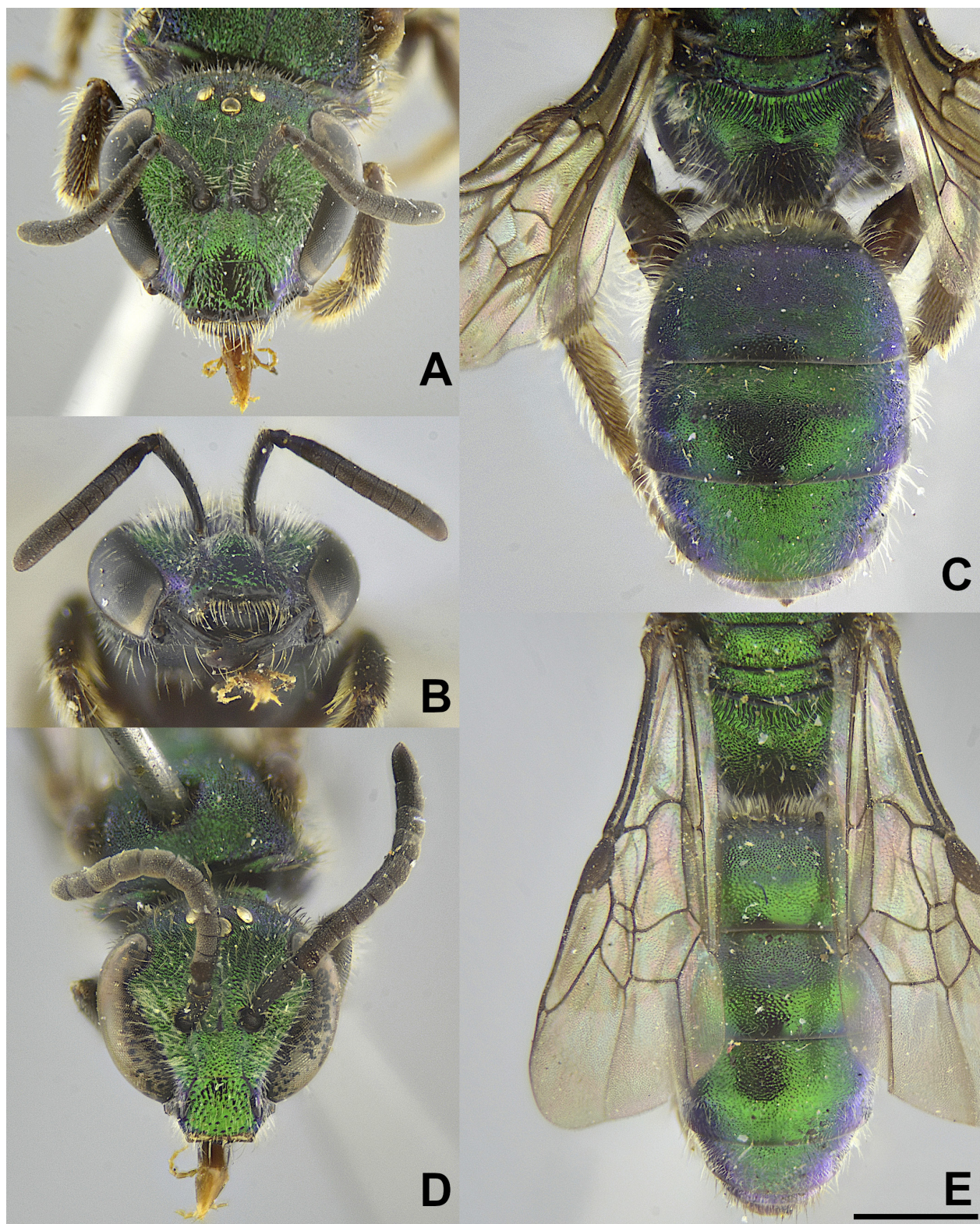


Figure 3. *Augochlora intermedia* sp. nov. Female (holotype): A) frontal view of head, B) anterior view of head, C) dorsal view of mesosoma and metasoma; male (paratype): D) frontal view of head; E) dorsal view of mesosoma and metasoma. Scale bar: 1.0 mm, all at same scale.

dark setae (2 OD) intermixed with tiny setae. Scutellum green with golden reflection; medial furrow inconspicuous; densely punctate ($I < 0.5$ PD), punctures coarse; with long dark setae (2 OD) intermixed with tiny setae. Mesepisternum green with golden reflection; mostly densely punctate ($I < 0.5$ PD), anterior portion crowded punctate;

with long setae (3 OD) intermixed with tiny setae. Mid leg: coxa mostly dark brown, except for green femur posterior surface; longer setae length = 2 OD; femur not strongly swollen. Tegula dark brown. Metanotum longer setae length = 2 OD. Metepisternum green with golden reflection; contiguously punctate, becoming crowded to

rugose above metapleural pit. Hind leg: coxa mostly dark brown, except for coxae posterior surface green and trochanter and femur with faint bluish iridescences; femur outer surface with tiny setae among longer setae; basitarsus about 6x longer than maximum width, parallel sided. Metapostnotum green; about as long as metapostnotum; gently depressed transversally; mostly with sinuous radiating carinae, posteriorly rugose. Propodeum densely punctate ($I < 0.5 PD$), loosely imbricate in between; with long setae (2 OD) intermixed with tiny setae. — **Metasoma.** T1 anterior surface sparsely punctate, punctures deep, loosely imbricate in between; only with long setae (2 OD). T1 dorsal surface mostly contiguously punctate, becoming densely punctate ($I = 0.5 PD$) towards apex, coarser punctures on lateral surfaces; mostly green with golden reflection, apical black band = 0.5 OD; apex not inflexed. T2 mostly green with golden reflection; mostly contiguously punctate, becoming sparser towards apex; marginal zone with punctate portion 3x longer than apical brown band on sublateral surfaces; T3 mostly green with golden reflection, apex darkened; punctate ($I = PD$), smooth in between. T4 mostly green with golden reflection, apex darkened; punctate ($I = PD$), smooth in between. T5 mostly green with golden reflection, apex darkened; sparsely punctate, punctures weak, smooth in between. T6 brown, with faint green reflection; weakly punctate. T7 light brown. S1 brown; with a slight longitudinal sulcus medially. long setae ($< 2 OD$) medially, margin with tiny decumbent setae. S2 mostly brown, apical portion yellowish; sparsely punctate, microreticulate in between; with short setae ($= OD$), more abundant near apex. S3–4 as S2. S5 apical portion not depressed; covered with tiny setae throughout medial glabrous path. S6 brown; with tiny setae, more abundant near apex. S7 lateral apodemes longer than half S8 width. S8 anterior projection more than four times longer than apical width; posterior margin acuminate. **Genitalia:** gonobase 2.0 times wider than long; gonobase ventral arms slightly curved on apex. Gonocoxite about 2.0 times longer than wide. Gonostylus, dorsal surface glabrous. Ventral process of gonostylus: inner lobe slender; with long and short setae intermixed; outer lobe with short setae with length = 0.7 inner lobe size. Gonapophysis ventral prong well produced and broad; dorsal bridge margin weakly projected; ventral bridge absent; apodeme narrow and strongly hooked.

Etymology. Nominative feminine of *intermedius*, meaning in the middle, a reference to intermixed features of *Augochlora* subgenera found in this species.

Distribution. Specimens were collected in Lima and La Libertad departments (Peru), western of Andean Mountains.

Comments. The holotype and a couple of paratypes have bluish reflections while remaining specimens are mostly green with few reddish reflections, besides this color variation the specimens have very similar body ornamentation and imperceptible differences in size.

3.2.2. *Augochlora (Augochlora) bractealis* (Vachal, 1904), new combination

Halictus bractealis Vachal, 1904. Holotype male (MNHP) from Peru, ‘Villanota’ [probably lapsus for Vilcanota, in Cuzco, Peru]. Examined through photographs.

Halictus pyrrhias Vachal, 1911. Lectotype female (MNHP) from Peru, Marcapata. Examined through photographs. New synonym.

Comments. Moure and Hurd (1987) designated the lectotype for *Halictus pyrrhias* and considered both names under *Oxystoglossella*, a decision followed by Moure (2007). We examined the photographs of the types from both names (Muséum d’Histoire Naturelle, Paris, France) and the specimens belong to the *A. hestia* species group in *Augochlora* s. str. We also consider that the male and female are the same species proposing the synonymy for these names. As discussed herein, this species superficially resembles *Oxystoglossella* and shares labral modifications with that subgenus, what justified Moure and Hurd’s (1987) generic assignment.

3.2.3. *Electraugochlora* Engel, new status

Electraugochlora Engel, 2000. Type species: *Augochlora (Electraugochlora) leptoloba* Engel, 2000 by original designation. Not examined.

Comments. We made some efforts to include this species in our analysis based on the original description, but the results were very unstable, probably due to the large amount of missing data. According to the original description and a revised phylogeny of Augochlorini (Gonçalves et al. *in press*), *A. leptoloba* could be a sister group with all other *Augochlora*. However, the uncertainty on several morphological attributes of this species and the lack of the acute angle of epistomal sulcus, a distinctive feature of *Augochlora*, are indicative for us to consider *Electraugochlora* as a separate genus.

4. Discussion

4.1. Phylogeny and taxonomy of *Augochlora*

Herein we analyzed a morphological matrix for *Augochlora* under two different approaches – parsimony criterion and Bayesian inference. The genus and both extant subgenera were recovered as monophyletic, with relatively high support values on all analyses. Within the genus, both approaches provided very similar topologies, allowing us to consistently identify major lineages. Partitioning using characters’ level of homoplasy resulted in trees more alike those generated by implied weighting parsimony, which is expected since both approaches do not treat characters as equally influential for topology estimation.

tion. This kind of approach yielded trees with outgroup relationships identical to those recovered by molecular and total-evidence analyses (Gonçalves 2016; Gonçalves et al. *in press*). The use of parsimony is widespread for morphological datasets, probably as a reflex of tradition and simplicity. On the other hand, the use of model-based approaches for phylogeny estimation of discrete morphological data is increasing and revealing many advantages over other methods (see Wright and Hillis 2014; O'Reilly et al. 2016). We understand that the concomitant use of parsimony and Bayesian approaches helps to better explore available information.

One of our main goals was to evaluate the valid subgeneric classification (*sensu* Engel 2000, Michener 2007; Moure 2007). As both extant subgenera were recovered as monophyletic, their use should be maintained for stability. To achieve this, a species placed in *Oxystoglossella* in the current classification (Moure and Hurd 1987; Moure 2007), *A. bractealis* should be transferred to *Augochlora* s. str. This species superficially resembles *Oxystoglossella*, and also have some labral modifications shared with that subgenus, but it belongs to the *A. hestia* species group in *Augochlora* s. str. (synapomorphies supporting a close relationship between *A. (A.) bractealis* and *A. (A.) hestia* are shown in Fig. 1). Our results support the use of *Aethechlora* as a separate subgenus for *A. iphigenia* species group, but this can unnecessarily inflate the taxonomy of the group and besides the original description by Moure and Hurd (1987) no other author considered the validity of this subgenus. We also favor maintaining *Augochlora* s. str. as a subgenus with no further modifications, since the use of *Mycterochlora* as a separate subgenus for the *A. repandirostris* species group would unnecessarily require raising three new subgenera. The unique *A. (A.) intermedia* sp. nov. is remarkable in having mandibles and pseudo-pygidial area modifications characteristic of *Oxystoglossella* while its genital capsule is typical from *Augochlora* s. str. Despite the monophyly of the subgenera, we found that characters frequently used to separate them (Eickwort 1969; Engel 2000) are variable along the phylogeny. The single exception is the length of the setae on the outer lobe of gonostylus – the long setae are a synapomorphy of *Oxystoglossella*, while *Augochlora* s. str. have short setae, as in the outgroup.

The large and produced preapical tooth was considered as a characteristic feature of *Augochlora* s. str. females (Eickwort 1969; Engel 2000), and besides *A. (A.) intermedia* sp. nov., the remaining species of the subgenus have this modification. Although mandibular teeth can bear some degree of wear depending on the specimens, it is clear that some species have a broadly rounded preapical tooth, less detached from the upper margin of the rutellum. The mandibles also have distinct modifications in other clades. In the *A. iphigenia* species group they are elongated with a broad apical tooth, a condition taken to the extreme in some macrocephalic forms, as in *A. (O.) matucanensis* and *A. (O.) phoenicis*. In some species of the *A. pura* group, there is a strong constriction before the distal part of aductor ridge in frontal view, as was noted in *A. (A.) atlantica*, *A. (A.) francisca* and *A.*

(A.) mulleri, also occurring in *A. (A.) genalis* Lepeco & Gonçalves (Lepeco and Gonçalves 2020a: Fig. 1). The shape of the elevation on the basal area of the labrum was also considered diagnostic of the subgenera, with the transverse elevation being typical for *Augochlora* s. str. and an orbicular shape for *Oxystoglossella* (Engel 2000). However, the shape is quite variable among species. The orbicular form is found only in the *A. morrae* group from *Oxystoglossella* and also on the *A. hestia* group. *A. (A.) iphigenia* also has a transverse elevation as interpreted by Gonçalves (2019), and its allied species have a slight elevation, without a well-defined shape, as discussed for *A. (O.) modica* and *A. (O.) tenax* by Lepeco and Gonçalves (2020b).

We noted that the pseudo-pygidial area on the fifth tergum is a key element in the systematics of *Augochlora*, but it has been described in different ways by previous authors. Eickwort (1969) considered that species in *Augochlora* s. str. bear scale-like setae in the pseudo-pygidial area of T5, while *Oxystoglossella* lack these setae. This character was not mentioned by Engel (2000), but posteriorly Dalmazzo and Roig-Alsina (2011) considered that species of *Oxystoglossella* bear setae-like spicules, while *Augochlora* s. str. bear globose spicules (see Figures 11 and 12 of the latter work). Lepeco and Gonçalves (2020a) suggested that the structures found in *Augochlora* s. str. are simply the colliculate integument exposed due to the absence of scale-like setae found in *Oxystoglossella*. All species of *Oxystoglossella* and the outgroup bear appressed setae on the pseudo-pygidial area, somewhat resembling scales, while most *Augochlora* s. str. lack these setae and have a more sclerotized irregular surface on each side of the medial cleft of T5. This irregular surface is formed by many tiny protuberances, clearly shown by Dalmazzo and Roig-Alsina (2011: Fig. 12), that are not similar with setae or scales. We maintain the interpretation of Lepeco and Gonçalves (2020a), adding the indication that the setae found in the medial area of T5 in *Oxystoglossella* are appressed, to avoid confusion with the terms coined by Eickwort (1969) and Dalmazzo and Roig-Alsina (2011). The presently described *A. (A.) intermedia* sp. nov. is the single *Augochlora* s. str. to bear appressed scale-like setae on the pseudo-pygidial area, although the coverage is sparser than observed in *Oxystoglossella*, maybe representing an intermediate state.

4.2. Implications for biogeography

Augochlora is a widespread genus in the Western Hemisphere, but much of its diversity and distribution patterns are largely unknown. In the case of the revised fauna from Southern South America (Lepeco and Gonçalves 2020a), it is clear that species exhibit different ranges and habitat tolerances, with some of them occurring in areas strictly covered by rainforests and others also reaching regions of open vegetation. An important observation derived here is that the main lineages, the species groups, have a widespread distribution on western hemisphere. Our taxon sampling is inadequate for a formal biogeographic re-

construction, as we did not sample regions equally within species groups, leaving many distributional gaps in our data. In addition, the diversity of some regions, such as Mesoamerica and Amazonia, is not fully known, leaving an obstacle for any phylogenetic and biogeographic exploration. Therefore, in light of our knowledge on the subject, we bring some insights also considering species not represented in our phylogeny.

Oxystoglossella is less speciose in comparison to *Augochlora* s. str., allowing us to identify some distribution patterns based on the studied species. The *A. iphigenia* species group is restricted to South America. Within this group, *A. (O.) modica* and *A. (O.) tenax* are recovered as sister species in our results, being typical from the Caatinga in Northeastern Brazil, a region characterized by dry conditions and high temperatures (Lepeco and Gonçalves 2020b). *Augochlora (O.) mendax* Lepeco and Gonçalves, 2020 is very similar to *A. (O.) modica*, and is found throughout the Cerrado formation, in central Brazil. A fourth species is known to us only from the Serra do Cipó locality, in Minas Gerais, Brazil, characterized by dry conditions. It seems clear that these four species presumably form a monophyletic group well-adapted to Brazilian open vegetational formations, being the single group bearing this characteristic within the genus. On the other hand, the clade composed of *A. (O.) iphigenia*, *A. (O.) phoenicis* and *A. (O.) matucanensis* is more heterogeneous. *A. (O.) iphigenia* is abundant from central Brazil to the Argentine Pampas, while *A. (O.) phoenicis* is found only within Western Amazonia, and *A. (O.) matucanensis* is the single species in the subgenus found in the Pacific side of the Andean mountain range in Peru. The *A. morrae* species group is mostly composed of commonly collected species, distributed throughout the almost entire range of the subgenus, with *A. (O.) vincentana* occurring at Caribbean islands (Moure 2012). Another species, not studied here, was described for Haiti: *A. (O.) haitiensis* (Vachal, 1911). Finally, a few species of *Oxystoglossella* occur in Central America, and at least three species occur in Mexico, with *A. (O.) aurifera* Cockerell, 1897 also recorded for the USA (Ascher and Pickering 2021).

Within *Augochlora* s. str., the *A. daphnis* and *A. pura* species groups are the more widespread, with the later also being the more speciose and morphologically diverse. Representatives of both groups are found in the USA, with *A. (A.) pura* reaching Canada and *A. (A.) nigrocyanea* Cockerell, 1897, a species undoubtedly belonging to the *A. daphnis* group, reaching southern USA (Sandhouse 1937; Moure 2012). Our results indicate that the occupation of the Nearctic region occurred within few derived taxa, disfavoring a scenario where *Augochlora* originated in North America. Interestingly, both species groups are found in the southernmost locality where *Augochlora* were ever collected – the Neuquén Province in Argentina – since *A. (A.) australis* Lepeco and Gonçalves, 2020 and *A. (A.) hirsuta* Lepeco and Gonçalves, 2020 are probably related to *A. pura* and *A. daphnis* species groups respectively. All *Augochlora* s. str. known to us from the Caribbean islands seem to be related to the *A. daphnis* species group, and, according to our results, the occupation of

Caribbean islands occurred at least three times within derived taxa of the genus. An early diversification of *Augochlora* in the Caribbean islands cannot be discarded if we consider that *E. leptoloba* is the sister group with all other *Augochlora* (Gonçalves et al. *in press*). From *A. daphnis* group came the only species recorded on Fernando de Noronha archipelago (545 km from Brazilian coast), *Augochlora laevipyga* is related to *Augochlora esox*.

The *A. repandirostris* species group is more abundant and diverse in the Amazon rainforest, but can also be found in the Panamanian Forest (e.g., *A. (A.) isthmii* Schwarz, 1934), and in the Atlantic Forest, (*A. (A.) helena* Lepeco and Gonçalves, 2020 and an undescribed species from Espírito Santo). The *A. hestia* species group has a similar distribution with two species from Amazonian Forest and one species widespread in the Atlantic Forest known to date. Species from both groups seems to be restricted to rainforests, with no representative being ever recorded in the open formations of South America. They also were not collected in the Caribbean.

The western coast of Peru appears to be an important region for the biogeography of the genus, with two species occurring there – *A. (A.) intermedia* sp. nov. and *A. (O.) matucanensis*. Both species are morphologically unique, and the former is the single representative of a lineage sister to all other *Augochlora* s. str. Nevertheless, the diversity of *Augochlora* in Peru, western to the Andean mountain range, seems to be low. The original label of *A. (O.) matucanensis* indicates that these bees were collected at Andean foothills, where vegetational conditions may diverge from that explored by most of *Augochlora* species. Another case to be addressed is *A. (A.) notialis* (Vachal, 1904), known only from the male holotype, labeled from Chile. Unfortunately, we did not examine the holotype and, according to Moure and Hurd (1987), it was probably mislabeled.

In summary we understand that the first evolutionary and biogeographic events of extant *Augochlora* lineages took place in South America. This seems to be evident by the diversity of *Oxystoglossella*, as a few groups with distinctive morphologies are restricted to South America. In the case of *Augochlora* s. str., two of its early branching lineages are endemic to South America (i.e., *A. intermedia* sp. nov. and *A. hestia* species group). Nevertheless, a refined elucidation of the biogeographic history of *Augochlora* can only be achieved with better understanding of its taxonomy and phylogeny.

4.3. The social behavior of *Augochlora*

Despite direct observation, the social behavior can be also positively inferred from intraspecific polymorphisms. *Augochlora (O.) iphigenia*, *A. (O.) matucanensis* and *A. (O.) phoenicis* are remarkable for the existence of females with distinct head enlargement, along with expansion of the apical portion of the mandible and projection of the hypostomal carina. These characteristics were also documented in *A. (O.) empusa* Engel, Hinojosa-Díaz and Bennett, 2012, which is probably a junior synonym of

A. phoenicis. Morphological polymorphisms of this sort are often linked to social interactions within the nest, as the large foundress females of primitively eusocial bees physically subjugate their subordinate daughters (Pabalan et al. 2000; Packer et al. 2003). Allometric growth of head structures in females is also present in species of the *A. daphnis* group (including the facultatively eusocial *A. daphnis*) and in *A. (A.) genalis* Lepeco and Gonçalves, 2020, a putative member of the *A. pura* species group (Lepeco and Gonçalves 2018; Lepeco and Gonçalves 2020a). It is unclear whether such modifications are invariably related to eusociality, even so, conspicuous cephalic polymorphism seems to have evolved at least three times independently in the genus.

Michener (1990) pointed out that solitary behavior in *Augochlora* s. str. represented a reversal from eusociality, since *Oxystoglossella* and the related genera are primitively eusocial (Eickwort 1969; see also Danforth and Eickwort 1997). *A. (A.) pura* is a well-known solitary species, and no signals of eusociality were found in *A. (A.) hallinani* Michener, 1954; *A. (A.) sidaefoliae* Cockerell, 1913; and *A. (A.) smaragdina* Friese, 1916 (Stockhammer 1966; Eickwort and Eickwort 1973). It is difficult to conclude whether these species are indeed solitary, due to the low number of nests observed. Given the presence of eusociality in *A. (A.) isthmii*, a member of the *repandirostris* species group, and in *A. (A.) daphnis* and *A. (A.) phoemonoe* (Dalmazzo and Roig-Alsina 2012, 2015, 2018a, 2018b), our results point to the presence of primitively eusocial species in at least three of the five *Augochlora* s. str. species groups, indicating that the exclusive solitary behavior of *A. (A.) pura* can be a reversion case.

Eusociality has been lost many times in eusocial Halictinae lineages (Danforth 2002; Gibbs 2012). Unlike in fixed-caste eusocial taxa (e.g., Apini, Meliponini), reversal to solitary behavior does not represent a large evolutionary obstacle for the Halictinae. Since all totipotent-caste eusocial bees pass through a solitary phase during the year (i.e., nest construction and provisioning before the first brood emerging) shift to solitary behavior would be acquired by simply changing from a multivoltine to univoltine cycle, where only reproductive brood is raised (Gibbs 2012; see also Almeida and Porto 2014). In fact, eusociality is facultative in many Halictinae species, being determined at the transcriptional level and influenced by climatic conditions, with females behaving as solitary in colder regions (Sakagami and Munakata 1972; Eickwort et al. 1996; Kapheim et al. 2020). Another important factor is resource limitation, species that nest in wood often have to cope with substrates with different sizes, shapes and diggability, which probably limit colony expansion (Dalmazzo and Roig-Alsina 2015).

Among *Augochlora*, facultative behavior can be suggested for *A. (A.) daphnis*, since individual nests were found both with a single female or with many females dividing activities (Dalmazzo and Roig-Alsina 2012). This is also the case of *A. (A.) isthmii* (Wcislo et al. 2003) and probably for the remaining *Augochlora* s. str.. Other kinds of social organization, such as communal nesting,

may be common within the genus, as it is the case for Halictinae (Michener 2007). We suggest that eusociality is a plastic characteristic in the genus, perhaps with multiple gains and losses along its evolution. Additionally, the eusocial behavior in *Augochlora* is probably facultative as a rule. Nevertheless, the evolutionary history of eusocial behavior will be only completely understood with nest observations and detailed records.

4.4. Nesting biology insights

Modified mandibles and absence of appressed scale-like setae on pseudo-pygidial area are found in primarily wood-nesting augochlorines. The studied nesting species of *Megalopta* Smith and allied genera (*Megaloptosyne* Engel and *Xenochlora* Engel, Brooks and Yanega) nest in decaying wood, and their females have strong mandibles with supplementary teeth on the inner surface (Michener and Fraser 1978; Santos et al. 2010) and colliculate pseudo-pygidial area, without appressed setae (see Engel 2000: Fig. 59). The same T5 modification and developed preapical tooth can be found in some species of *Neocorynura* Schrottky which nest in wood (Eickwort 1969; Brosi et al. 2006), but in this case a phylogeny to trace the origin of these traits is lacking. All species of *Augochlora* s. str. studied so far nest out of the soil (Table 1), and, using the mentioned morphological clues, we suggest that this behavior evolved in the common ancestor of the *A. hestia*, *A. daphnis*, *A. repandirostris* and *A. pura* species groups. Although the new species, *A. intermedia* sp. nov., is more related to *Augochlora* s. str. species, it has mandibles typical of soil-nesting species and sparse scale-like setae on the pseudo-pygidial area. Alternatively, the new species may be a facultative wood-nester, as is the case of *A. (A.) esox*, recorded nesting on bromeliad humus (Zillikens et al. 2001) but also found nesting in wood (G. A. R. Melo, personal communication). Nevertheless, *Augochlora* s. str. may not be strictly dependent on a single type of nesting substrate, a conclusion supported also by laboratory rearing of *A. (A.) pura* in soil (Barrows 1973).

In regard to nest architecture, bees exhibit a certain level of plasticity, adapting the organization of structures according to substrate conditions (Eickwort and Sakagami 1979). Nests with clusters of cells supported by earthen pillars within a hollow cavity are the commonest among Augochlorini, probably representing a plesiomorphy for the *Augochlora* group of genera (Danforth and Eickwort 1997; Engel 2000; Wcislo et al. 2003; Coelho 2004). These clusters facilitate the isolation of cells from the surrounding soil by means of a drainage cavity, protecting the provisions and brood from excessive moisture (Sakagami and Michener 1962; Eickwort and Sakagami 1979; Wcislo et al. 2003). Clusters surrounded by cavities are present in nests of *A. (A.) daphnis* within soft wood, but were not found in trunks with harder wood (Dalmazzo and Roig-Alsina 2012). In the other few *Augochlora* nests studied, clusters are either present or not, showing no consistent phylogenetic pattern. On the other hand, all

Table 1. Nesting substrate and social behavior of *Augochlora* Smith species.

Species	Nesting substrate	Social behavior	References
<i>A. (A.) alexanderi</i> Engel, 2003	wood	—	Wcislo et al. (2003)
<i>A. (A.) cydippe</i> (Schrottky, 1910)	wood	—	Lepeco and Gonçalves (2020a)
<i>A. (A.) daphnis</i> Smith, 1853	wood	Primitively eusocial	Dalmazzo and Roig-Alsina (2012,2018b); Lepeco and Gonçalves (2018)
<i>A. (A.) esox</i> (Vachal, 1911)	wood/hummus	—	Zillikens et al. (2001); unpublished data
<i>A. (A.) hallinani</i> Michener, 1954	wood	Solitary?*	Eickwort and Eickwort (1973)
<i>A. (A.) isthmii</i> Schwarz, 1934	wood	Primitively eusocial	Wcislo et al. (2003)
<i>A. (A.) mulleri</i> Cockerell, 1900	wood	-	Sakagami and Moure (1967)
<i>A. (A.) phoemonoe</i> (Schrottky, 1909)	wood	Primitively eusocial	Dalmazzo and Roig-Alsina (2018a)
<i>A. (A.) pura</i> (Say, 1837)	wood**	Solitary	Stockhammer (1966)
<i>A. (A.) sidaefoliae</i> Cockerell, 1913	wood	Solitary?	Eickwort and Eickwort (1973)
<i>A. (A.) smaragdina</i> Friese, 1916	wood	Solitary?	Eickwort and Eickwort (1973)
<i>A. (A.) thusnelda</i> (Schrottky, 1909)	wood	—	Lepeco and Gonçalves (2020a)
<i>A. (O.) cordiaefloris</i> Cockerell, 1907	soil	Primitively eusocial	Eickwort and Eickwort (1972)
<i>A. (O.) iphigenia</i> Holmberg, 1886	soil	Primitively eusocial	Michener and Lange (1958); Sakagami and Moure (1965)
<i>A. (O.) morrae</i> Strand, 1910	soil	Primitively eusocial?	Michener and Lange (1958)
<i>A. (O.) nominata</i> Michener, 1954	soil	Primitively eusocial	Eickwort and Eickwort (1972)

* Some species were studied based on a few nests and/or localities and conclusions are based on behavioral clues rather than on observation of the entire life cycles, making it difficult to determine if sociality is actually absent or occasionally not observed.

** *Augochlora pura* was induced to nest in soil under laboratory conditions by Barrows (1973).

Oxytroglossella studied so far do not construct cells in clusters (Eickwort and Sakagami 1979), suggesting that their absence is not necessarily linked to wood-nesting. Nevertheless, it is not known whether the absence of clusters and/or hollow cavities surrounding cells in nests of *Augochlora* s. str. is related to the better drainage proportioned by wood, as suggested by Wcislo et al. (2003), or due to heterogeneity of wood material in relation to soil, where conditions allow females to express their full construction capabilities (Dalmazzo and Roig-Alsina 2012). In the latter case, environmental conditions have a major role in defining architecture in relation to phylogenetic relationships.

Decaying wood has the disadvantage of being less abundant in comparison to suitable soil, but, on the other hand, it is more difficult to become soaked during periods of rainfall and retains humidity in dry periods (Stockhammer 1966). Regarding social behavior, nesting above ground did not limit *Augochlora* s. str. to the solitary lifestyle (Dalmazzo and Roig-Alsina 2012, 2015, 2018a, 2018b). Examining other augochlorine wood nesters, *Megalopta* and allied genera can be primitively eusocial (Kapheim et al. 2020), but for *Neocorynura* this behavior was not yet published (Brosi et al. 2006) and there are no morphological clues such as female polymorphisms. Michener (1990) suggested that the scarcity of suitable plant material, in contrast to soil, triggered the reversion to solitary behavior, as natural enemies in forest environments were less successful and, therefore, disadvantages of eusociality outweighed the advantages. This argument, if valid, is restricted to temperate species *A. (A.) pura* so far.

As is common for bees, *Augochlora* are parasitized by conopid flies and mutillids (Michener and Lange 1958).

The single putative cleptoparasite bees to attack nests of the genus are *Temnosoma* Smith: females of an unidentified species were already seen flying around and found within nests of *A. (A.) esox* (Silveira et al. 2002). Eickwort (1969) suggested that *Temnosoma* were cleptoparasites of eusocial species, given their distinctively coarse integuments. The association of *Temnosoma* with *Augochlora* is supported by the distribution of both genera – these are the only augochlorine genera occurring simultaneously at USA, Chile and the antilles, besides most of the Neotropical region (Eickwort 1969; Michener 2007; Moure 2012). If *Temnosoma* did not parasitize other groups, this association may represent an adaptation to host-seeking in an unusual substrate, i.e., decaying wood. A similar trend is found on the cleptoparasitic species of the wood nester *Megalopta* (Michener 2007). Considering this hypothesis, the utilization of decaying wood for nesting may have facilitated the origination of cleptoparasitic lineages within the tribe, with less competitors, since other soil nesting genera (e.g., *Augochlorella*) are usually attacked by the widespread genus *Sphecodes* Latreille (Ordway 1965).

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Supplementary material 1

List of characters

Authors: Lepeco A, Gonçalves RB (2022)

Data type: .docx

Explanation note: Besides the original characters, many were compiled – and modified, when necessary – from Eickwort (1969), Danforth & Eickwort (1997), Engel (2000), Coelho (2004), Gonçalves (2015), Gonçalves (2016), and Gonçalves (2019).

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Link: <https://doi.org/10.3897/asp.80.e71943.suppl1>

Supplementary material 2

Character matrix and examined material

Authors: Lepeco A, Gonçalves RB (2022)

Data type: .xlsx

Explanation note: This spreadsheet includes the matrix of characters used in all analyses and the specimens examined during morphological investigation.

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Link: <https://doi.org/10.3897/asp.80.e71943.suppl2>

Supplementary material 3

Partitioning schemes

Authors: Lepeco A, Gonçalves RB (2022)

Data type: .docx

Explanation note: Scheme of partitions used in Bayesian analysis, based on homoplasy values calculated in the software TNT.

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Supplementary material 4

Phylogenetic trees

Authors: Lepeco A, Gonçalves RB (2022)

Data type: .docx

Explanation note: Supplementary phylogenetic trees showing posterior probabilities and mapped synapomorphies.

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