Systematics, Morphology and Biogeography

Phylogeny of the Augochlora clade with the description of four new species (Hymenoptera, Apoidea)

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A R T I C L E   I N F O

Article history:
Received 19 September 2018
Accepted 20 December 2018
Available online 3 January 2019
Associate Editor: Rodrigo Feitosa

Keywords:
Augochlorini
Bees
Neotropical
Systematics
Taxonomy

A B S T R A C T

The Augochlora clade includes four genera: Augochlora Smith, Augochlorella Sandhouse, Ceratalictus Moure, and Pereirapis Moure. This is one of the richest and most widespread groups of Augochlorini bees. There are about 150 species, which occur from Argentina to Canada. The species of Augochlora clade are considered solitary to facultatively social, except Ceratalictus for which nothing is known. Wood nesting behavior arose once in the clade, in Augochlora sensu strictu. The objective of this study is to describe four new species and to present a revised phylogenetic analysis of the Augochlora clade for the placement of these species. The morphological matrix comprised 77 characters and 42 terminals, and resulted in two most parsimonious trees. The monophyly of the Augochlora clade is corroborated. Ceratalictus and Pereirapis are considered as sister groups and Ceratalictus inflexus sp. nov. came as sister to other species of Ceratalictus. Augochlora and Augochlorella are monophyletic and sister groups. Both extant subgenera of Augochlora were corroborated as monophyletic. Augochlorella comis is considered as sister group to the rest of Augochlorella species. All Augochlorella new species described belong to the Augochlorella ephrya group. Augochlorella kellae sp. nov. is phylogenetically related to Augochlorella una. Augochlorella proctiva sp. nov. and Augochlorella mavricera sp. nov. constitute a clade with Augochlorella acarinata. Including the new species, Augochlorella has 19 species and Ceratalictus 11 species. A revised key for species of Augochlorella and Ceratalictus is also presented in the Supplementary Information.

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Introduction

Augochlorini is a monophyletic bee tribe and the main lineages divergence dating around 55–20 Ma (Hedtke et al., 2013; Gonçalves, 2016). The tribe comprises 663 described species primarily distributed in the Neotropical region (Moure, 2007). Species of Augochlorini have a remarkable range of behaviors and habits, including solitary, semisocial, primitively eusocial, crepuscular, nesting in the soil and wood, and cleptoparasitism (see Michener, 2007 for a review). These diverse and ecologically interesting habits make the augochlorine bees a good group for the evolution studies of such behaviors. In a recent molecular and morphological phylogeny, Gonçalves (2016) recognized seven suprageneric clades for the tribe and the Augochlora clade was recovered sister to the Megalopta group (Gonçalves, 2016; Meira and Gonçalves, 2018).

The Augochlora clade includes Augochlora Smith, Augochlorella Sandhouse, Ceratalictus Moure, and Pereirapis Moure (Eickwort, 1969). The taxonomic treatment of these genera vary among authors, Michener (2007) considered Ceratalictus and Pereirapis as subgenera of Augochlorella, but others treated them as separate genera (Eickwort, 1969; Danforth and Eickwort, 1997; Engel, 2000; Coelho, 2004; Moure, 2007; Coelho and Gonçalves, 2010; Eickwort and Eickwort, 1973). The late classification is supported by multiples phylogenies (Danforth and Eickwort, 1997; Engel, 2000; Coelho, 2014; Gonçalves, 2015, 2016) in which the genus Augochlorella does not form a monophyletic group with Ceratalictus and Pereirapis. Michener’s classification creates a paraphyletic group in relation to Augochlora.

Augochlora is the most speciose genus of the group, with 115 species, ranging from Argentina and Chile to Canada (Moure, 2007). Augochlora has three subgenera: Augochlora s.s. (87 species), Electraugochlora Engel (one fossil species), and Oxystoglossella Eickwort (27 species). No revisionary or phylogenetic studies have been conducted for the genus. Pereirapis is distributed from southern Brazil to Mexico, and it has eight species according to Moure (2007), although Engel (2000) considered the genus to be monotypic with all species synonym with P. semiurata (Spinola, 1853). Coelho (2004) revised Augochlorella, recognizing 16 species distributed from Argentina to Canada. The Augochlorella phylogeny supports the placement of Augochlorella as a sister group to the rest of the Augochlora clade (Coelho, 2004). Ceratalictus taxonomy

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https://doi.org/10.1016/j.rbe.2018.12.003
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was revised by Coelho and Gonçalves (2010) who recognized 10 species. Gonçalves (2015) provided a phylogeny of Ceratalictus species and also supported the placement of Augochlorella as sister to the remaining genera. Recently, however, Gonçalves (2016) recovered the following different topology using morphology and DNA ((Augochlora, Augochlorella), (Ceratalictus, Pereirapis)). The nesting biology and behavior for some species of all genera are known, except Ceratalictus. Studied species of Augochlora (Oxytoglossella), Augochlorella and Pereirapis are soil nesters and can be facultatively eusocial (Eickwort, 1969; Eickwort and Eickwort, 1972; Danforth and Eickwort, 1997 see Michener, 2007 for a review). Augochlora s.s. species nest in rotten–wood and are also solitary or facultatively eusocial (Stockhammer, 1966; Dalmazzo and Roig-Alsina, 2012, 2015; Wcislo et al., 2003) and are not exclusively solitary as previously postulated (Stockhammer, 1966; Danforth and Eickwort, 1997). Interestingly, intraspecific variation is also known for some species of the Augochlora clade, such as Augochlora iphigenia Holmberg, 1899, Augochlorella conis (Vachal, 1911) and Augochlorellara aurata (Smith, 1853) (see Danforth and Eickwort, 1997 for a review).

Since the taxonomic revisions of Coelho (2004) and Coelho and Gonçalves (2010) new species accumulate in Augochlorella and Ceratalictus. A new Ceratalictus was already known by the author but with uncertainty on generic placement, mainly due a peculiar genital capsule. The main goal of this study is to present a revised phylogenetic analysis for the Augochlora clade for the placement of four new species. Other objectives are to compile and revise the morphological characters of previous studies into a more complete dataset, and to describe one new Ceratalictus and three new Augochlorella species. A revised key for species of Augochlorella and Ceratalictus is also presented in the Supplementary Information.

Material and methods

Phylogenetic analysis

As ingroup I selected seven species of Augochlora representing the extant subgenera, one species of Pereirapis, and all known species of Augochlorella and Ceratalictus. The new species of Augochlorella and Ceratalictus were also included as terminals. The included Augochlora species are distributed from Argentina, Brazil and Paraguay. There are several genus level names available for Augochlora but they are not tested here. All species were directly examined except some of Augochlorella aurata group. For those species, the character coding was the same present by Coelho (2004) with few modifications based on the original drawings and descriptions. As outgroup I selected four species of Augochlorini including two species of the Megalopta clade (the sister group of Augochlora clade (Gonçalves, 2016; Meira and Gonçalves, 2018). Pseudaugochlora graminea (Fabricius, 1804) was used to root the cladogram based on the topologies of Gonçalves (2016) and Meira and Gonçalves (2018). For the character statements, I firstly revised the original datasets of Coelho (2004), and Gonçalves (2015, 2016). The later incorporated previous characters from Eickwort (1969) and Engel (2000). The character coding from the original studies were completely rescoped based on direct observation and new interpretations. The second step was the inclusion of new characters statements based on external morphology and male genitalia. The writing of all characters statements followed the recommendations of Sereno (2007). Inapplicable character states for contingent characters are indicated by “-”, missing character states by “?” The final matrix comprised 77 characters and 42 terminals, both matrix and character list are provided in the Supplementary Information. Parsimony analyses were carried out in Tree Analysis using New Technology Search (TNT, Goloboff et al., 2008), using equal weights, and the following settings (ratchet weighting probability 5%, 200 iterations), tree-drifting (50 cycles), and tree-fusing (five rounds, minimum length set to be hit 1000 times). All characters were treated as non-additive. Bootstrap (1000 replications) and Bremer support were also calculated with TNT. Trees were viewed and edited with WinClada ver. 1.00.08 (©KC Nixon) and GIMP 2.8.16 (©The GIMP Team).

Taxonomy

The descriptions were organized following the body organization, tagmata, segments, and sclerites, with special attention given to the following: structure (general organization), sculpturing (impressions and elevations on sclerite surface), color and pubescence. Structure terminology follows Eickwort (1969) and Michener (2007) except the basal area of propodeum referred here as the metapostnotum. I use the abbreviations T1, T2, etc., to denote the metasomal terga; S1, S2, etc., to denote metasomal sterna; and F1, F2, etc., to denote the flaggomeranes. For examined material the quotation marks surround exact transcriptions of individual labels, while the backslash (\) indicates different lines on the same label. The material cited here is deposited in the following institutions: BMNH – British Museum of Natural History, London, UK; DZUP – Coleção Entomológica Pe. Jesus Santiago More, Curitiba, Brazil; MZSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; SEMC – Snow Entomological Museum Collection, Lawrence, USA; UFMG – Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; UFV – Universidade Federal de Viçosa, Viçosa, Brazil; USNM – Smithsonian National Museum of Natural History, Washington, USA.

I measured the following: eye notch width (as a measure of head width); head length (distance from base of clypeus to vertex apex); glossa length; clypeus maximum width and length; supraclypeal length (distance from clypeus base to lower tangent of alveoli); distance between upper tangent alveolus and tangent of lower median ocellus; intertropical distance; first tert-gum maximum width; second tert-gum maximum width; total length (approximate by measuring head and mesosoma plus metasoma). All measurements are in millimeters. Relative size comparisons used the mid ocellus diameter (=OD) or eye maximum width in lateral view (=EW). The punctures interspaces (i) are described in relation to puncture diameter (pd). Sculpture terminology follows Harris (1979) including conflated for crowded punctures. For some sculpturing I use two terms to describe mixed or transitional patterns, as areolate–rugose. For punctuation, sparsely punctate is used for punctures separated by more than one puncture diameter, coarsely punctate for punctures comparatively coarser than ordinary covering punctures. For microsculpture, visible only in magnifications above 50x, I use the prefix micro-, the term polished is applied for the absence of microsculpture.

Most specimen examination was made with Olympus SZ51 and SZ61 using white led ring illumination. Measurements were made with a Leica Stermi DV4 and an eyepiece micrometer. Photographs were taken with a Nikon D700 and 107 mm Sigma Macro lens using Helicon Remote for controlling image capture. Illumination followed the system of Kawada and Buffington (2016), Image stacking was made with Helicon Focus (version 6.0.18) – render method based on Method C (Pyramid), Final image adjustments (unsharp mask filtering, level control, background color setting) were with GIMP 2.8.16 (©The GIMP Team).
Results

Phylogenetic analysis

The phylogenetic analysis resulted in two most parsimonious trees with 158 steps, the consensus tree is presented in Fig. 1. The Augochlora clade is monophyletic and supported by five synapomorphies (Fig. 1). Ceratalictus and Pereirapis are sister groups with four synapomorphies in fast optimization (one in unambiguous optimization). Ceratalictus is supported by seven synapomorphies (six in unambiguous optimization) and Ceratalictus inflexus sp. nov. is sister group to the remaining Ceratalictus species. Augochlora and Augochlorella are sister groups sharing four synapomorphies, from these only one supports the group unambiguously. Augochlora is monophyletic and the clade shows high support values compared to other genera, its extant subgenera are also corroborated as monophyletic. Augochlorella comis is considered as sister group to the remaining Augochlorella species. The three new species of Augochlorella belong to the "ephyra group" from Coelho (2004). Augochlorella kelliae sp. nov. is related to Augochlorella una. Augochlorella prociva sp. nov. and Augochlorella m'avricera sp. nov. constitute a clade with Augochlorella acarinata. Based on these results, the generic classification from Moure (2007) was corroborated and the new species are described under Augochlorella and Ceratalictus at the generic level.

Taxonomy

Augochlorella kelliae sp. nov.  
(Figs. 2 and 3)

Diagnosis. Females of this species are similar to Augochlorella una and can be separated from the remaining Augochlorella by the olive green head and mesosoma (not olive in other species), elongate head (wider than longer in other species), and microreticulate posterior and lateral surfaces of the propodeum (not microreticulate in other species) (Fig. 2). From A. una, the new species can be separated by the metapostnotum with strong posterior marginal angles, being almost trapezoidal (Fig. 2C), preoccipital ridge carinate, mesoscutum punctures sparser on the median surface (intervals equal to one puncture diameter on A. una, and about two puncture diameter on A. kelliae sp. nov.) and the scutellar punctures are not strong and contiguous. The male can be separated from other species by
the combination of clypeus with a transverse yellow band, hind leg with short setae, preoccipital ridge carinate, and metapostnotal carinae almost reaching the posterior margin (Fig. 3).

**Description.** *Holotype female. Measurements (mm).* Eye notch width: 1.3; head length: 2.0; glossa length: 1.2; clypeus width: 0.7; clypeus length: 0.5; supraclypeal length: 0.4; clypeus ocular distance: 0.8; interocular distance: 1.4; T1 width: 1.8; T2 width: 2.0; body length: 7.5. *Head.* Labrum basal elevation orbicular, black. Mandible black with subapical amber spot; subapical tooth not strongly produced; long setae (2–3 OD) on outer and ventral margins. Epistomal angle orthogonal. Clypeus sparsely punctate, microreticulate on basal portion; erect setae with 1–1.5 OD; apical surface darkened, most surface olive green. Supraclypeal area sparsely punctulate, microreticulate near clypeus; fine erect setae; olive green. Paraocular area punctate, strongly microreticulate; olive green, some weak copper reflections near eye notch; branched setae with 1–1.5 OD. Antennae: scape dark brown with very weak metallic highlights; flagellomeres amber ventrally, especially on F9–10; F1–2 and base of F3 setose, with inconspicuous sensilla, remaining flagellomeres with conspicuous sensilla. Frons not depressed; confluent punctate, strongly microreticulate; weak blue iridescence; short and fine setae. Preoccipital ridge carina not reaching the gena. Vertex coarsely punctate becoming rugose near ridge; long plumose (short branches) setae. Gena puncticulate, microlineate on postgena; green with very weak copper reflections; white plumose setae (1.5–2 OD). Hypostomal ridge carinate. *Mesosoma.* Pronotum dorso ridged weakly carinate; lateral angle not projected, rounded; lateral ridge rounded; dorsal surface lineate and puncticulate; green; with few tomentum on dorsal surface. Propleuron brown with green highlights. Prosternum green. Fore leg: coxa dark green, trochanter and femur brown, tibia light brown on outer surface, base of tibia and pretarsus yellow; long white setae on coxa to femur, yellow erect setae on tibia and tarsus. Mesoscutum anterior border weakly acuminate; median sulcus well impressed; parapsidal lines weakly impressed; punctate laterally, more sparse on median surface, microlineations more conspicuous on anterior surface; olive green; short (=0D) and sparse white setae. Scutellum median sulcus very weakly impressed; puncticulate, some scattered punctures, polished; bright olive green; longer setae (2.5–3 OD) on posterior margin. Mesepisternum rugulose on preepisternum, irregularly punctate on hypoepimeral area, sulci weakly foveate, densely punctate near scrobe, becoming more evenly punctate ventrally; olive green, weak copper reflections; covered with plumose setae (=1.5 OD). Mid leg brown; yellow setae on femur to tarsus. Tegula concentric lineate; dark amber, weak green reflections anteriorly. Fore wing: marginal cell apex rounded; membrane hyaline; black microtrichia. Metanotum median sulcus very weakly impressed; puncticulate to rugulose; green with bluish iridescence; long plumose setae (2–3 OD). Metepisternum lineate above superior metapleural pit, rugulose–punctate below; green with copper and bluish reflections. Hind leg: basitibial plate apex rounded; tibial spur serrate; brown; long plumose setae on ventral coxa to femur; ventral tibial setae short and branched. Hind wing hyaline. Metapostnotum weakly inclined; weakly depressed; apex rounded; less twice as long as metanotum; rugulose on most surface, except a stripe on posterior margin, microreticulate; olive green. Propodeum posterior surface puncticulate, few scattered punctures, microreticulate; olive green; short plumose and some erect (1–2 OD) setae; propodeum lateral surface puncticulate, few scattered punctures, microreticulate; olive green; with thicker and longer (3–4 OD) setae. *Metasoma.* T1 anterior and dorsal surfaces not angled between; sparsely puncticulate, microlineate; olive green on anterior and lateral surfaces, dark brown on median surface. T2 puncticulate; olive green on anterior and lateral surfaces, dark brown on median surface; short. T3–T4 puncticulate; olive green with some dark brown on median surface, brown on marginal area; short. T5 punctate; dark brown; covered with black long erect setae. Pygidial plate short, truncate. S1 without tubercle; lineate; amber with green highlights on median surface; very long setae (>3 OD) on median surface. S2–S4 lineate; brown to light brown; subapical setae very long (about 5 OD) and with recurved apices. S5 lineate; brown; long setae (about 4 OD), plumose. S6 lineate; brown; yellowish setae on apical margin.

**Paratype male.** *Measurements (mm).* Eye notch width: 1.2; head length: 1.8; clypeus width: 0.6; clypeus length: 0.5; supraclypeal length: 0.3; clypeus ocular distance: 0.7; interocular distance: 1.3; T1 width: 1.2; T2 width: 1.3; body length: 9. *Head.* Labrum and mandible yellow. Clypeus, epistomal angle straight; sparsely punctate, weakly microreticulate; white setae on middle, longer setae on apex; yellow stripe on apical margin, green. Supraclypeal area sparsely punctate, weakly microreticulate; green. Paraocular area sparsely punctate, weakly microreticulate; green, coppery along eye margins; long (>2 OD) branched setae, yellow. Antennae F2 0.7x F1 length, F3 = F1.
longer; scape and pedicel light brown, flagellomeres yellowed ventrally; F11 not flattened; without sensillia placodea patches. Frons not depressed above antennal sockets; coarsely punctate; bright green, few coppery reflections near paraocular; fewer erect setae. Pre-occipital ridge carinate, some portions lamellate. Vertex punctate becoming rugose near ridge; very long plumose (short branches) setae. Gena puncticulate becoming linear on postgena; green, some coppery reflections; white plumose setae (1.5–2 OD). Hypostomal ridge carinate. Mesosoma. Pronotum dorsal ridge carinate; lateral angle almost orthogonal; lateral ridge rounded; dorsal surface rugose; bright olive green, weakly metallic laterally; with some plumose setae on dorsal surface. Fore leg: coxa to femur bright metallic green, tibia and tarsus light brown; short yellow erect setae. Mesoscutum anterior border slightly projected over pronotum, weakly lobed; median sulcus well impressed; parapsidal lines well impressed; punctate, sparsely on anterior lobe; bright olive green; posterior margin weakly covered with plumose setae. Scutellum median sulcus impressed; punctate, polished; bright olive green; anterior surface densely covered with erect setae. Metepisternum lineate above superior metapleural pit, rugulose–punctate below; bright olive green. Hind leg: coxa brown with metallic reflections, remaining leg light brown; short yellow erect setae. Tegula concentric lineate; brown, green reflections anteriorly. Forewing weakly infuscate on apex. Metanotum median sulcus weakly impressed; puncticulate, polished; bright olive green; anterior surface densely covered with erect setae. Metepisternum lineate above superior metapleural pit, rugulose–punctate below; bright olive green. Hind leg: coxa brown with metallic reflections, remaining leg light brown; short yellow erect setae, shorter than diameter of segments. Metapostnotum weakly inclined and depressed; twice as long as metanotum; apex rounded; carinate, posteriorly only weakly microreticulate; green. Propodeum: posterior surface posterior pit shallow, punctate, microreticulate, olive green, with fine setae; lateral surface punctate, olive green, with thicker setae. Metasoma. T1 very sparsely puncticate; light brown with metallic reflections, yellow marginal areas. T2–5 very sparse puncticate; light brown with metallic reflections, yellow marginal areas; vestiture white, with weak row of long white setae on basis. T6 green; long setae. T7 black; short black setae. S1 margin straight; sparsely punctate, microlineate; light brown; with very short setae. S2–S5 straight; brown; covered with short white setae on median surface, posterior surface with long setae (>4 OD). S4 margin concave; with median, triangular patch of setae; lateral setae longer. S6 weakly concave; brown; black setae on apicol margin. S7 posterior margin sinuose. S8 posterior margin not produced; 0.3 times S8 width. Genitalia (Fig. 3C). Gonapophysis broad, longer than gonostylus and without dorsal crest; with large ventral prong and lateral teeth. Gonobase short (0.6 times gonocoxite length); dorsal lobes weakly produced; ventral bridge narrow. Gonostylus basal process reduced; parapenial lobe reduced; ventral process with outer and inner lobes, inner lobe divided and asymmetric, setose; dorsal lobe transversal. Volsella longer than wider; oblique, corners acuminate; without hook.

Comments. Coelho (2004) listed a A. unio paratype female as “1?m#; Minas Gerais, Serra do Rola-Moça, Zona Metalúrgica, 15.9.x.1997 (E. A. B. Almeida) (BMNH)”, the author listed all specimens of A. unio with male symbols but the species is only known from females. As the question mark could represent a dubious identification I speculate that this paratype can be a specimen of A. kelliae sp. nov. In this case A. unio is known only from Central Brazil and A. kelliae sp. nov. is known only for Minas Gerais.


Etymology. In honor of Dr. Kelli S. Ramos, friend, melittologist, and collector of the type.

Augochlorella mavricera sp. nov.

(Figs. 4–6C,D)

Diagnosis. The female of this species is very similar to A. acarina. The body of A. mavricera sp. nov. is mostly dark green with some violet reflections on clypeus and supraclypeal area and black dorsal surfaces of terga (Fig. 4) while A. acarina is bright green with some copper reflections. Also, A. mavricera sp. nov. punctation is sparser than on A. acarina (>2pd on lower paraocular and >pd on mesoscutum). The male can be easily separated from A. acarina by the dark body, including legs (Figs. 5 and 6D), compared with yellowish color of A. acarina (Fig. 6A,B). The S4 is slightly bilobed (Fig. 6C) in the new species, while A. acarina males have S4 strongly bilobed (Fig. 6A).

Description. Holotype female. Measurements (mm). Eye notch width: 1.3; head length: 1.6; glossa length: 0.6; clypeus width: 0.7; clypeus length: 0.4; supraclypeal length: 0.3; clypeus ocellar distance: 0.9; interocular distance: 1.1; T1 width: 1.7; T2 width: 1.8; body length: 7.0. Head. Labrum basal elevation orbicular, black. Mandible black with subapical amber spot; subapical tooth
not strongly produced; long setae (2–3 OD) on outer and ventral margins. Epistomal angle orthogonal. Clypeus sparsely punctate, weakly microreticulate on basal portion; erect setae with 1–1.5 OD; apical surface darkened, subapical area violet, remaining surface bright green. Supracylpeal area sparsely punctulate, polished; fine erect setae; green with violet reflections. Paraocular area punctate, strongly microreticulate; olive green, some weak violet reflections near eye notch; branched setae with 1–1.5 OD. Antennae: scape dark brown with very weak metallic highlights, flagellomeres weakly amber ventrally; F1–3 setose, with inconspicuous sensilla, remaining flagellomeres with conspicuous sensilla. Frons not depressed; confected punctate, strongly microreticulate; olive green; short and fine setae. Preoccipital ridge not carinate. Vertex coarsely punctate becoming rugose near ridge; long plumose (short branches) setae. Gena puncticulate, microlineate on postgena; dark green to black; white plumose setae (1.5–2 OD). Hypostomal ridge carinate. *Mesosoma*. Pronotum dorsal ridge weakly carinate; lateral angle not projected, rounded; lateral ridge rounded; dorsal surface lineate and puncticulate; dark green; with few tomentum on dorsal surface. Propleuron brown with green highlights. Prosternum green. Fore leg: coxa dark green, trochanter and femur brown, tibia brown on outer surface, base of tibia and pretarsus light brown; long yellowish setae on coxa to femur, yellow erect setae on tibia and tarsus. Mesoscutum anterior border weakly acuminate; median sulcus well impressed; parapsidal lines weakly impressed; punctate laterally, more sparse on median surface (=pd), microlineations more conspicuous on anterior surface; green with violet reflections; short (=OD) and sparse white setae. Scutellum median sulcus very weakly impressed; punctate to confected punctate, microreticulate; bright olive green; longer setae (=2.5–3 OD) on posterior margin. Mesepisternum confected punctate, microreticulate; olive green, weak violet reflections; covered with plumose setae (=1.5 OD). Mid leg brown; yellow setae on femur to tarsus. Tegula concentric lineate; dark amber, weak green reflections anteriorly. Fore wing: marginal cell apex rounded; membrane hyaline; black microtrichia. Metanotum median sulcus very weakly impressed; rugulose, microreticulate; green with bluish iridescence; long plumose setae (2–3 OD). Metepisternum lineate above superior metaepimarginal pit, confected punctate below; green with violet reflections. Hind leg: basitibial plate apex rounded; tibial spur serrate; brown; long plumose setae on ventral coxa to femur, ventral tibial setae not too long and with short branches. Hind wing hyaline. Metapostnotum weakly inclined; weakly depressed; apex rounded to trapezoidal; less twice as long as metanotum; rugulose on median surface, carinate laterally, microreticulate; dark olive green with some violet reflections; Propodeum posterior surface puncticulate, few scattered punctures, microreticulate to granular; dark olive green; short plumose and some erect (1–2 OD) setae. Propodeum lateral surface puncticulate, microreticulate; olive green; with thicker and longer (3–4 OD) setae. *Metasoma*. T1 anterior and dorsal surfaces not angled between; sparsely puncticulate, microlineate; olive green reflections on lateral surfaces, black on median surface, few copper reflections elsewhere; short. T2 puncticulate; olive green reflections on lateral surfaces, black on median surface, few copper reflections elsewhere; short. T3–T4 puncticulate; olive green reflections on lateral and marginal surfaces, black on median surface, few copper reflections elsewhere; short. T5 punctate; dark brown; covered with black long erect setae. Pygidial plate short, truncate. S1 without tubercle; lineate; amber with green highlights on median surface; very long setae (=3 OD) on median surface. S2–4 lineate; brown to light brown; subapical setae very long (about 5 OD) and with recurved apices. S5 lineate; brown; long setae (about 4 OD). Plumose. S6 lineate; brown; yellowish setae on apical margin.

**Paratype male.** **Measurements (mm).** Eye notch width: 1.2; head length: 1.6; clypeus width: 0.6; clypeus length: 0.4; supraclypeal length: 0.3; clypeus ocellar distance: 0.9; intertentacular distance: 1.2; T1 width: 1.4; T2 width: 1.6; body length: 7.0. *Head*. Labrum and mandible amber; Clypeus: epistomal angle straight; punctate, very weakly microreticulate; white setae on middle, longer setae on apex; yellow marking on latero–apical margin, green. Supracylpeal area sparsely punctate, very weakly microreticulate; green. Paraocular area sparsely punctate, weakly microreticulate; olive green; long (>2 OD) branched setae, yellow. Antennae F2 0.8x F1 length, F3 = F1, remaining flagellomeres relatively longer; scape and pedicel light brown, flagellomeres mostly yellowed; F11 flattened dorso–ventrally; without sensilla placodea patches. Frons not depressed above antennal sockets; coarsely punctate; olive green; few erect setae. Preoccipital ridge not carinate. Vertex punctate becoming rugose near ridge; very long plumose (short branches) setae. Gena puncticulate, almost polished on postgena; olive green, some coppery reflections on postgena; white plumose setae (1.5–2 OD). Hypostomal area, ridge carinate. *Mesosoma*. Pronotum dorsal ridge carinate; lateral angle almost orthogonal; lateral ridge rounded; dorsal surface rugose; bright olive green, weakly metallic laterally; with some plumose setae on dorsal surface. Fore leg: coxa to femur with some metallic reflections, tibia and tarsus dark brown; short yellow erect setae. Mesoscutum anterior border slightly projected over pronotum, weakly lobed; median sulcus well impressed; parapsidal lines well impressed; punctate, sparsely on anterior lobe; bright olive green; posterior margin weakly covered with plumose setae. Scutellum median sulcus weakly impressed; punctate, polished; bright olive green;
anterior surface covered with plumose setae. Mesepisternum punctate, polished; bright olive green; short plumose setae. Mid leg: coxa brown with metallic reflections, remaining leg light brown; short yellow erect setae. Tegula concentric lineate; brown, green reflections anteriorly. Forewing weakly infuscate on apex. Metanotum median sulcus weakly impressed; puncticulate, polished; bright olive green; anterior surface densely covered with erect setae. Metepisternum lineate above superior metapleural pit, punctate below; bright olive green; Hind leg: coxa brown with metallic reflections, remaining leg light brown; apex of ventral surface of femur with apical very long thick setae (7 OD), apex of ventral surface of tibia with long setae (4 OD); ventral surface of basitarsus with tuft of erect setae (3 OD) on a convexity. Metapostnotum weakly inclined; weakly depressed; twice as long as metanotum; apex rounded; rugose, some carina laterally; green. Propodeum posterior surface posterior pit shallow, punctate, microreticulate, olive green, with fine setae; lateral surface punctate, olive green, with thicker setae. *Metasoma.* T1 very sparsely puncticate; brown with lateral metallic reflections; short; T2 very sparse puncticulate; light brown with metallic reflections, yellow marginal areas; vestiture white, with weak row of long white setae on basis. T3–T5 as T2, some bluish iridescence. T6 green; long setae. T7 black; short black setae. S1 margin straight; sparsely punctate, microlineate; light brown; with very short setae. S2–S3 and S5 straight; brown; covered with few short white setae on median surface, posterior surface with some long setae (>4 OD). S4 weakly bilobed (Fig. 6C); with apical row of thick setae; lateral setae very short. S6 weakly concave; brown; black setae on apical margin. S7 posterior margin sinuose. S8 posterior margin not produced. 0.3 times S8 width. *Genitalia* (Fig. 5C). Gonapophysis broad; longer than gonostylus; without dorsal crest; with large ventral prong; with lateral teeth. Gonobase short (0.6 gonocoxite length); dorsal lobes weakly produced; ventral bridge narrow. Gonostylus basal process reduced; parapenial lobe reduced; ventral process with outer and inner lobes, inner lobe divided and asymmetric, setose; dorsal lobe transversal. Volsella longer than wider; oblique, corners acuminate; without hook.

**Type material.** Holotype female (DZUP): “Parque Saint–Hilaire\ Brazil: RS, Viamão, 02/03/2017, Coletado em \ Euphorbia sel loi (11–14h)\ Saibreira\ Fogo Recente”. Paratype: one male (DZUP) “Parque Saint–Hilaire\ Brazil: RS, Viamão, 21/12/2015, Coletado em\ Richarda grandiflora (08–11h)\ NOVA\ Fogo Intermediário”.

**Etymology.** From Greek terms that mean black, mavros, and horn, ceros, in reference to the black F11, feminine.

*Augochlorella procliva* sp. nov.

(Fig. 7)

**Diagnosis.** Females of *A. procliva* sp. nov. can be separated from the similar *A. ephrya* and *A. iopoecila* by the combination of the weakly carinate preepicondripal ridge, green head and mesosoma (Fig. 7), rugulose and declivitous metapostnotum, and the granular posterior and lateral surfaces of propodeum. The carinæ of metapostnotum reach the edge posteriorly differently from *A. urania*, other similar species which presents carinate preepicondripal ridge. Males are not known.

**Description.** **Holotype female.** Measurements (mm). Eye notch width: 1.4; head length: 1.9; glosa length: 0.8; Clypeus width: 0.7; Clypeus length: 0.7; supraclypeal length: 0.3; Clypeus occular distance: 0.8; Intertepal distance: 1.4; T1 width: 2.0; T2 width: 2.2; body length: 7.6. *Head.* Labrum basal elevation weakly orbicular, amber. Mandible black with subapical and apical amber spot; subapical tooth not strongly produced; long setae (2–3 OD) on outer and ventral margins. Epistomal angle orthogonal. Clypeus sparsely punctate, polished; erect setae with 1–1.5 OD; apical surface darkened, most surface bright green. Supraoculæal area sparsely punctulate, polished; fine erect setae; bright green. Paraclypeal area punctate, sometimes conflcated, polished; green; branched setae with 1–1.5 OD. Antenna: scape brown with weak metallic highlights, flagellomeres amber ventrally, especially on F9–10; F1–3 setose, with inconspicuous sensilla, remaining flagellomeres with conspicuous sensilla. Frons not depressed: conflcated punctate; bright green. Short and fine setae. Preepicondripal ridge weakly carinate, carina not reaching the gena. Vertex coarsely punctate becoming rugose near ridge; long plumose (short branches) setae. Genal puncticulate, microlineate on postgena; green with very weak bluish reflections; white plumose setae (1.5–2 OD). Hypostomal ridge carinate. *Mesosoma.* Pronotum dorsal ridge weakly carinate; lateral angle not projected, rounded; lateral ridge rounded; dorsal surface lineate and puncticulate; green; with few tomentum on dorsal surface. Propleura brown with green highlights. Prosternum green. Fore leg coxa dark green, trochanter and femur brown, tibia light brown on outer surface, base of tibia and pre-tarsus yellow; long white setae on coxa to femur, yellow erect setae on tibia and tarsus. Mesoscutum anterior border weakly acuminate; median sulcus well impressed; parapsidal lines weakly impressed; punctate laterally, more sparse on median surface, microlineate; green, few copper reflections; short (=OD) and sparse white setae. Scutellum median sulcus very weakly impressed; punctate, becoming rugulose posteriorly; bright olive green; longer setae (=2.5–3 OD) on posterior margin. Mesepisternum rugulose, sulci weakly foveate; olive green, weak copper reflections; covered with plumose setae (=1.5 OD). Mid leg brown, tarsius light brown; yellow setae on femur to tarsus. Tegula concentric lineate; dark amber, weak green reflections anteriorly. Fore wing, marginal cell apex rounded; membrane hyaline; black microtrichia. Metanotum median sulcus very weakly impressed; puncticulate to rugulose; green with bluish iridescence; long plumose setae (2–3 OD). Metepisternum lineate above superior metapleural pit, rugulose–punctate below; green with copper and bluish reflections. Hind leg, basitibial plate apex rounded; tibial spur serrate; brown; long plumose setae on ventral coxa to femur, ventral tibial setae not too long and with short branches. Hind wing hyaline. Metapostnotum inclined; weakly depressed; apex rounded to trapezoidal; less twice as long as metanotum; entirely rugulose, some lateral carina extending to propodeum; green. Propodeum
posterior surface punctate rugulose, microreticulate; green; short plumose and some erect (1–2 OD) setae. Propodeum lateral surface punctate rugulose, microreticulate; green; with thicker and longer (3–4 OD) setae. Metasoma. T1 anterior and dorsal surfaces not angled between; sparsely puncticulate, microlineate; copper green on anterior and lateral surfaces, dark brown on median surface; short. T2 puncticulate; copper green on anterior and lateral surfaces, dark brown on median surface; short. T3–T4 puncticulate; copper green with some dark brown on median surface, brown on marginal area; short. T5 puncticulate; dark brown; covered with amber long erect setae. Pygidial plate short, truncate. S1 without tube cle; lineate; amber with green highlights on median surface; very long setae (=3 OD) on median surface. S2–S4 lineate; brown to light brown; subapical setae very long (about 5 OD) and with recurved apices. S5 lineate; brown; long setae (about 4 OD), plumose. S6 lineate; brown; yellowish setae on apical margin.

**Type material.** Holotype female (DZUP): “MANAUS – AM; Brasil 1 61\ C. ELIAS leg.”. Paratype: one female (DZUP), with same data as holotype.

**Etymology.** From Latin term proclivus, meaning inclined.

*Ceratalictus inflexus* sp. nov.  
(Figs. 8 and 9)

**Diagnosis.** *Ceratalictus inflexus* sp. nov. is distinguished from other *Ceratalictus* by the combination of lateral angle of pronotum obtuse; surface of mesoscutal disk weakly microreticulate; carinae of metapostnotum not reaching edge posteriorly; metapostnotum similar with metanotum in length and shape, and by the metasoma with blue reflections (Figs. 8 and 9). The female has the basal elevation occupying all the longitudinal portion of labrum, the male has the antennae with sensilla placodea patches.

**Description.** **Holotype female.** Measurements (mm). Eye notch width: 1.5; head length: 1.7; glossa length: 0.4; cypleus width: 0.8; cypleus length: 0.4; supraclypeal length: 0.3; cypleus ocellar distance: 1.1; intertemporal distance: 1.5; T1 width: 2.0; T2 width: 2.2; body length: 8.0. *Head*. Labrum basal elevation orbicular, black. Mandible black with subapical amber spot; subapical tooth not strongly produced; long setae (2–3 OD) on outer and ventral margins. Epistomal angle obtuse. Clypeus coarsely punctate, microreticulate; erect setae with 1–1.5 OD; apical surface darkened, blue green. Supraclypeal area sparsely punctate, microreticulate; fine erect setae; blue green. Paracentral area coarsely punctate becoming confluent, strongly microreticulate; blue green; branched setae with 1–1.5 OD. Antennae, scape dark brown with very weak metallic highlights, flagellomeres amber ventrally, especially on F9–10; F1–2 and base of F3 setose, with inconspicuous sensilla, remaining flagellomeres with conspicuous sensilla. Frons not depressed; confluent punctate, strongly microreticulate; dark blue green; short and fine setae. Preoccipital ridge carinate, carina not reaching the gena. Vertex coarsely punctate becoming rugose near ridge; long plumose (short branches) setae. Gena puncticulate, microlineate on postgena; blue green, dark green on postgena; white plumose setae (1.5–2 OD). Hypostomal ridge carinate. *Mesosoma*. Pronotum dorsal ridge weakly carinate; lateral angle not projected, rounded; lateral ridge rounded; dorsal surface lineate and puncticulate; blue green; with few tomentum on dorsal surface. Propleura brown with green highlights. Prosternum green. Fore leg coxa dark green, remaining leg dark brown; long white setae on coxa to femur, yellow erect setae on tibia and tarsus. Mesoscutum anterior border weakly acuminate; median sulcus well impressed; parapsidal lines weakly impressed; punctate laterally, more sparse on median surface, punctures with different diameters intermixed, microlineations only on anterior surface and near median sulcus; blue green; short (≈OD) and sparse white setae. Scutellum median sulcus very weakly impressed; irregularly punctate, rugulose posteriorly; blue green; longer setae (2–2.5 OD) on posterior margin. Mesepisternum rugulose on preepisternum, sulci foveate, densely to confluent punctate, microreticulate; blue green, blue ventrally; covered with plumose setae (1.5 OD). Mid leg light brown; yellow setae on femur to tarsus. Tegula concentric lineate; dark amber, weak green reflections anteriorly. Fore wing. Marginal cell apex rounded; membrane hyaline; black microtrichia. Metanotum median sulcus very weakly impressed; puncticulate to rugulose; blue green; long plumose setae (2–3 OD). Metepisternum lineate above superior metapleural pit, rugulose–punctate below; green with copper and bluish reflections. Hind leg, basitibial plate apex rounded; tibial spur serrate; brown; long plumose setae on ventral coxa to femur, ventral tibial setae not too long and with short branches. Hind wing hyaline. Metapostnotum weakly inclined; weakly depressed; apex rounded; less twice as long as metanotum; carinate to irregularly carinate, carinae not reaching posterior margin, microreticulate; blue green. Propodeum posterior surface puncticulate, few scattered setose punctures, microreticulate; blue green; short plumose.
and some erect (1–2 OD) setae. Propodeum lateral surface puncticate, few scattered punctures, microreticulate; blue green; with thicker and longer (3–4 OD) setae. Metasoma. T1 anterior and dorsal surfaces not angled between; sparsely punctate, microlineate; blue green with some amber to brown portions on median surface; short. T2 puncticulate, weakly microreticulate; blue green, black on marginal area; short. T3–T4 puncticate, weakly microreticulate; blue green, black on marginal area; short. T5 punctate; dark brown; covered with black long erect setae. Pygidial plate short, truncate. S1 without tubercle; lineate; amber with green highlights on median surface; very long branched setae (=3 OD) on median surface. S2–S4 lineate; brown to light brown; subapical branched setae very long (about 4 OD). S5 lineate; brown; long setae (about 4 OD), plumose. S6 lineate; brown; yellowish setae on apical margin. 

**Paratype male.** Measurements (mm). Eye notch width: 1.3; head length: 1.8;clypeus width: 0.6; clypeus length: 0.5; supracypeal length: 0.3; clypeus ocellar distance: 1.1; intertegular distance: 1.6; T1 width: 1.9; T2 width: 2.0; body length: 8.0. Head. Labrum and mandible brown. Clypeus, epistomial angle obtuse; punctate, weakly microreticulate; white setae on middle, longer setae on apex; yellow stripe on apical margin, green. Supracypeal area sparsely puncticate, microreticulate; green. Paracoxal area sparsely puncticate, microreticulate; green; long (>2 OD) branched setae, yellow. Antennae F2 = F1, remaining flagellomeres relatively longer; scape and pedicel light brown, flagellomeres yellowed ventrally; F11 not flattened; F3–11 with sensilla placodea patches. Prons not depressed above antennal sockets; coarsely punctate; green with bluish iridescence; few erect setae. Preopercular ridge carinate, some portions lamellate. Vertex punctate becoming rugose near ridge; very long plumose (short branches) setae. Gena puncticulate weakly lineate on postgena; green, copper reflections on postgena; white plumose setae (1.5–2 OD). Hypostomal area, ridge carinate. Mesosoma. Pronotum dorsal ridge carinate; lateral angle almost orthogonal; lateral ridge rounded; dorsal surface rugose; green; with some plumose setae on dorsal surface. Fore leg coxa to femur with green reflections, tibia and tarsus brown; short yellow erect setae. Mesoscutum anterior border slightly projected over pronotum, weakly lobed; median sulcus well impressed; parapsidal lines well impressed; punctate, sparsely median surface, microreticulations only on lateral surface; green; posterior margin weakly covered with plumose setae. Scutellum median sulcus weakly impressed; punctate, rugulose on posterior margin, polished; green, blue iridescence posteriorly, weak copper reflections on middle surface; anterior surface covered with plumose setae. Mesepisternum punctate, densely microreticulate; green with some copper reflections; short plumose setae. Mid leg coxa brown with metallic reflections, remaining leg brown; short yellow erect setae. Tegula concentric lineate; brown, green reflections anteriorly. Forewing weakly infuscate on apex. Metanotum median sulcus weakly impressed; puncticulate, polished; bright blue green; anterior surface densely covered with erect setae. Metapostnotum lineate above superior metapleural pit, rugulose–punctate below; blue green. Hind leg coxa with metallic reflections, remaining leg brown; short yellow erect setae, shorter than diameter of sclerites. Metapostnotum weakly inclined; weakly depressed; 1.5 x as long as metanotum; apex rounded; carinate to irregularly carinate, carinae not reaching posterior margin, microreticulate; blue green. Propodeum posterior surface posterior pit shallow, densely punctate, microreticulate, blue green, with fine setae; lateral surface punctate, blue green, with thicker setae. Metasoma. T1 anterior surface not punctate, dorsal surface punctate, polished; blue green, dark marginal area short. T2–5 punctate, microreticulate; dark blue green, marginal area black; vestiture white, with weak row of long white setae on basis. T6 green; long setae. T7 black; short black setae. S1 margin straight; sparsely punctate, microlineate; light brown; with very short setae. S2–3 straight; brown; covered with short white setae on median surface, posterior surface with long setae (>4 OD). S4 apical margin straight; without median patch of setae; lateral setae short. S5 as S2. S6 weakly concave; brown; black setae on apical margin. S7 with median process. S8 apical margin bilobed. Genitalia. Gonopophysis broader; longer than gonostyli; without dorsal crest; with large ventral prong; with lateral teeth. Gonobase short (0.6 times gonocoxite length); dorsal lobes weakly produced; ventral bridge narrow. Gonostylus basal process absent; parapenial lobe present, short; ventral process with outer and inner lobes, inner lobe transversal setose on apex; dorsal lobe transversal. Volsella longer than wider; oblique, corners mostly rounded; without hook. 

**Variation.** Most examined material is blue green but some specimens from Paraná and Espírito Santo are green. The blue reflections vary among specimens, including some violet reflections. The mesoscutum punctuation is sparsor in some specimens. 


**Etymology.** From the Latin term *inflexus* means bend, curve, in reference to the form of the inner lobe of ventral process of gonostyli. 

**Discussion.** This study corroborates the monophyly of the Augochlorina clade recovered by previous studies (Eickwort, 1969; Danforth and Eickwort, 1997; Engel, 2000; Coelho, 2004; Gonçalves, 2015, 2016). The topology of *Goncalves* (2016) is corroborated in contrast to previous hypothesis (Eickwort, 1969; Danforth and Eickwort, 1997; Engel, 2000; Coelho, 2004; Gonçalves, 2015) (fig. 1). In spite of the peculiar genital capsule, *Ceratalictus inflexus* sp. nov. is sister lineage to the rest of the species of the genus. *Ceratalictus* is supported by seven synapomorphies. The phylogenetic relationships among the remaining *Ceratalictus* species were the same as found by Gonçalves (2015). *Ceratalictus*’ distribution shows biogeographical duplications in southeastern South America (Gonçalves, 2015) and the basal position of the new species reinforces the hypothesis of the origin of the genus in this region. 

The topology found for *Augochlorella* is different from that of Coelho (2004) due the placement of *A. comis*. This species is considered here sister to the rest of the genus, in contrast to the previous study where it was considered as related to the “aurata group”. The
male F2 shorter than F1 and the concave S4 are synapomorphies for Augochlorella excluding A. comis. The convex face and the almost obtuse epistomal angle of A. comis are also plesiomorphic features from other Augochlorella species and support this new phylogenetic hypothesis. Coelho (2004) postulate a vicariance between A. ephra and A. aurata (including A. comis) groups. In the present study, the hypothesis point to a different interpretation with the origin of Augochlorella in Central America and only later occupying North and South America. More effort is necessary to understand the biogeographical evolution of Augochlorella. This study described four new species of the Augochlora clade and provided a revised phylogeny for the placement of these species. This was the first attempt to include all species of Augochlorella and Ceratalictus in a phylogenetic analysis. There is still a lot of systematic work to be done with the clade: Pererapis has never been studied in detail; Augochlora taxonomy and systematics is still very poorly investigated due to large number of undescribed species; and the relationships of Augochlorella species remains with unresolved nodes.

**Funding**

This study was partially supported by Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico, number 443069/2014-0.

**Conflicts of interest**

The authors declare no conflicts of interest.

**Acknowledgements**

Thanks to Carlos Roberto Brandão and Gabriel Melo for assistance during the execution of this study. I am grateful to five anonymous reviewers for suggestions on the manuscript.

**Appendix A. Supplementary data**


**References**


