

# CLASSIFICATION OF THE BEE TRIBE AUGOCHLORINI (HYMENOPTERA: HALICTIDAE)

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# CLASSIFICATION OF THE BEE TRIBE AUGOCHLORINI (HYMENOPTERA: HALICTIDAE)

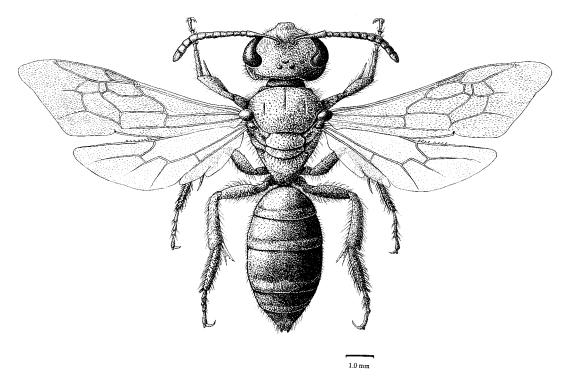
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FRONTISPIECE. Dorsal habitus of Neocorynurella seeleyi Engel and Klein (from Engel and Klein, 1997).

"Go to the bee, and learn how diligent she is, and what a noble work she produces, whose labors kings and private men use for their use, she is desired and honored by all, and though weak in strength she values wisdom and prevails."

-Proverbs, Chapter 6, Septuagint<sup>1</sup> version of the Bible

<sup>&</sup>lt;sup>1</sup> The Septuagint, sometimes known as *Interpretatio secundum septuaginta seniores* (Transl.: "Translation According to 70 Elders") or η εκκλησιαστικη εκδοσις (Transl.: "The Ecclesiastic Edition"), is the oldest Greek version, perhaps also the oldest extant version, of the Old Testament; believed to have been translated in Alexandria at the request of Ptolemy II Philadelphus (285–247 B.C.) by 70–72 Jewish scholars. The number 70 for the scholars would have been based on the tradition that 70 elders accompanied Moses when he received the commandments, while it is believed by some that the number was increased to 72, with six scholars representing each of the 12 Hebrew tribes. Later versions, such as those based on the Vulgate Latin translation, remove this portion of this text and retain only the reference to the "ant."

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## CONTENTS

#### ABSTRACT

The halictid bee tribe Augochlorini is revised at the level of genus and subgenus. Fortyone genera and subgenera are recognized with two being extinct. New subgenera of *Augochlora*, *Electraugochlora*, and of *Oligochlora*, *Soliapis*, are described for new fossils from Tertiary amber of the Dominican Republic. Complete taxonomic histories are given along with information on revisions at the species level, biological studies, and general distribution for each family- and genus-group taxon. The following subgenera are newly synonymized: *Aethechlora* new junior subjective synonym of *Oxystoglossella*, *Mycterochlora* new junior subjective synonym of *Augochlora*, *Vachalius* new junior sybjective synonym of *Neocorynurella*, and *Neocorynuroides* new junior subjective synonym of *Neocorynura*. The group *Glyptochlora* is resurrected from synonymy as a valid subgenus of *Augochloropsis*. The males of *Chlerogella* and *Micrommation* are described for the first time. A key to the genera and subgenera of the tribe is presented along with a key to the species of the rare *Augochloropsis* (*Glyptochlora*).

Suprageneric relationships in the tribe are explored cladistically. Characters of adult external morphology (72 characters) and ethology (12 characters) are coded for all recognized augochlorine genera as well as outgroups from the Halictini, Nomioidini, and Nomiinae. Results of the cladistic analysis are remarkably resolved but not very robust. The cladogram is summarized and infratribal groups defined. Most notably, the tribe is divided into two monophyletic subtribes: the **Corynurina** (new subtribe), containing the southern South American genera *Corynura, Halictillus, Rhectomia*, and *Rhinocorynura*; and the nominate subtribe, Augochlorina. Implications of the cladistic analysis on diversification in the Augochlorini and evolutionary patterns within the tribe are discussed.

New distribution records are given for three species which extend the known ranges of their respective genera. Augochlora essequibensis is a new junior subjective synonym of A. nigrocyanea while A. cladopyga, A. seminigra, Augochlorella bidentata, Halictus caucasicus, H. cerasis, H. chrysaspis, H. myrrhites, H. simotes, and Pereirapis rhizophila are all new junior subjective synonyms of P. semiaurata. Megalopta intermedia, Augochlora nitidior, Augochlorella eusticta, Augochlorodes clementis, and Augochloropsis scabriceps are all recognized as nomina nuda. Vachalius cosmetor, from Colombia and Venezuela, is transferred to Neocorynurella while Corynura biciliata, from Costa Rica, is recognized as a species of Halictini and is transferred to the genus Lasioglossum (Evylaeus) (new combinations). Four fossil and recent species new to science are described as Augochlora (Electraugochlora) leptoloba (fossil), Augochlora (Oxystoglossella) rightmyerae (extant), Oligochlora (Soliapis) rozeni (fossil), and Pseudaugochlora pulchra (extant).

## INTRODUCTION

Bees are one of the most ecologically important groups of arthropods and are by far the most significant group of insect pollinators. There are approximately 20,000 species worldwide, with the greatest diversity found in xeric regions. The living bees are segregated into six families; Colletidae<sup>2</sup>, Halictidae, Andrenidae, Melittidae, Megachilidae, and Apidae; and together form a monophyletic group within the aculeate superfamily Apoidea. Among the major lineages of bees, the family Halictidae is one of the more basal, apparently being sister to all other bees except the most primitive family, Colletidae. The family is relatively large, consisting of approximately 3500 described species. Three main lineages are recognized within the family; the plesiomorphic and certainly paraphyletic subfamily Rophitinae (= Dufoureinae of some authors), the Nomiinae, and the Halictinae. The halictines, by far, dwarf the other two subfamilies in size, and make up approximately 80% of the specific diversity for the family. The Halictinae is itself presently divided into three tribes: Nomioidini, Halictini, and Augochlorini. The present study focuses on the last-named tribe and provides a revised supraspecific classification.

The Augochlorini is remarkable among halictids for having its greatest diversity concentrated in the warm tropics of the New World, while lineages of the others are diversified either in xeric, temperate, or cool tropical habitats. The tribe consists of approximately 525 valid species and is most noted for the brilliant metallic coloration, which is frequently green (hence their name: Greek auge + chloros meaning "shining green"). Coloration throughout the tribe is quite variable, with a small number of species being dull metallic or black (similar to most species of Halictini), others brown to amber, while the majority are metallic red, gold, green, blue, violet, or any combination of these. Species are distributed from southern Canada to northern Argentina and Chile and east into the West Indies. Most taxa are of a moderate size, being around 6-10 mm in length, although some "giants" do occur in the nocturnal genus *Megalopta*, etc. (ca. 18 mm) and minute species are known in *Halictillus*, etc. (ca. 3 mm).

Many augochlorine species are gregarious, nesting in societies ranging from communal to primitively eusocial, semisocial societies apparently being the most common type and perhaps part of the augochlorine groundplan. Nest architecture within the tribe is varied. with nests ranging from simple tubular burrows with lateral cells to more elaborate chambers with supported clusters of brood cells constructed either in soil or rotting wood. This diversity has attracted the attention of comparative ethologists and several hypotheses have been presented to explain the patterns of change seen among augochlorine nests (e.g., Sakagami and Michener, 1962; Eickwort and Sakagami, 1979). Like most halictines, augochlorines are polylectic, visiting an array of flowers for resources; however, some modified foraging behaviors have arisen in the tribe. Most notably, the transition to nocturnal flower visitation in genera such as Megalopta is a peculiarity among bees. True nocturnal behavior, not simply crepuscular, has apparently arisen at least eight times among all bees; it is noteworthy that three of these derivations have been within the Augochlorini (see Discussion). Likewise, based on their anatomy, specific groups appear to have specialized on flowers with deep corollas (e.g., *Chlerogas*).

#### TAXONOMIC REVIEW

The first known augochlorine species was described by Fabricius (1793) as *Andrena metallica* (currently *Augochloropsis metallica*). Fabricius went on to name the second augochlorine in 1804, but over a quarter of a century would pass before another species would be recognized (*Halictus rubellus* Haliday, 1836). From 1836 to the present, every decade has seen activity on the species-level taxonomy of augochlorines, although after 1970 augochlorine taxonomy ground to a near halt with only two subgenera and two species named over the next quarter of a century (one of them, however, was merely a

 $<sup>^2\,{\</sup>rm I}$  consider the Australian family Stenotritidae to be a subfamily, at best, of Colletidae.

replacement name for a preoccupied species of *Caenaugochlora*). Not until 1995 did studies on the tribe resume.

At the generic level, most authors throughout the nineteenth century followed Latreille (1804) and placed augochlorines in the genus Halictus. It was Spinola (1851) who first proposed a currently recognized augochlorine genus, Corynura. During the remainder of that decade, four other genus-group names were proposed for augochlorine species (more than were proposed during the remainder of that century). In the early twentieth century the generic classification of the Augochlorini exploded with the number of genera more than doubling (to 20) by 1910, mostly owing to the efforts of Schrottky. Although a few groups were proposed over the intervening years, it was not until the 1940s and 1960s that work on the tribe resumed with any concentration. At this time Moure proposed 18 genera in connection with his studies designed to monograph the New World halictine fauna. In 1969, Eickwort (1969a) provided the first synthesis of augochlorine genera; relegating several names to synonymy. Eickwort recognized 24 genera and an additional seven subgenera. At the time of his study, the genera Chlerogella and Rhectomia were known only on the basis of females, and the genus Chlerogas only on the basis of males. In the same year, Moure (1969) described one additional genus, Micrommation, and later proposed two new subgenera in Augochlora and Megommation (Moure and Hurd, 1987), bringing the total composition of the Augochlorini to 25 genera and nine additional subgenera. Since then several genera have been added to the tribe by the present author and coauthors as well as an additional genus, Vachalius, by Moure (1999).

Kirby (1802) divided the Linnean genus *Apis* (Linnaeus, 1758), which was equivalent to all six bee families of today, into short-tongued and long-tongued bees [the Andrenetae and Apiariae of Latreille (1802)]; a higher classification which was perpetuated by Smith (1853, 1879). Under this classificatory structure the few augochlorines known at the time were placed in the Andrenetae along with the genus *Halictus* and, as indicated earlier, frequently *within* that genus. Ashmead (1899) proposed a supraspe-

cific classification of the Apoidea in which he placed the then recognized augochlorine genera (namely Augochlora, Corynura, Megalopta, and Temnosoma) into two different groups: Augochlora, Corynura, and Megalopta (under the lapsus Megaloptera) were placed in the Halictinae (then a subfamily of Andrenidae) along with genera such as Agapostemon, Nomioides, and Systropha, whereas the parasitic genus Temnosoma was grouped with other parasitic short-tongued bees (e.g., Sphecodes) in the subfamily Sphecodinae. Although Beebe (1925) later proposed the family-group name Augochloridae, the group as he conceived it was equivalent to the Halictinae of Ashmead (1899). The first suprageneric recognition of a group corresponding to the tribe of today was by Schrottky (1909b) who proposed the tribal name Oxystoglossini for those genera allied to the genus Oxystoglossa (a junior synonym of Augochlora); for the first time separating the augochlorines from Halictus and its allied genera. At approximately the same time, Vachal was involved in developing his classification of New World halictines (all under the genus *Halictus*!) in the form of a lengthy identification key. Vachal (1911) proposed the division Halicti hexagoni which approximately corresponded to Schrottky's Oxystoglossini. Moure (1943a), perhaps unaware of Beebe's use of the name Augochloridae as well as Schrottky's tribal name, defined the tribe Augochlorini as new and to accommodate the Halicti falcati subdivision of Vachal's Halicti hexagoni. At the same time Moure proposed the tribe Augochloropsini and the subfamily Megaloptinae for other subdivisions of Vachal's group; the three suprageneric groups together being equivalent to the Augochlorini of today. Eickwort (1969b) presented the first modern diagnosis of the tribe, distinguishing it from the Halictini on the basis of both adult morphology and nest architecture. Eickwort was apparently unaware of both Beebe's (1925) article and of the older tribal name Oxystoglossini, using Augochlorini as the valid name and attributing it to Moure. The usage of Augochlorini has become universal and Oxystoglossini has not been used since Schrottky's proposal of the name in 1909. An application to suppress Oxystoglossini has been made with the

I.C.Z.N. and is currently pending (Engel, 1999a).

As of 31 December 1999, 697 speciesgroup and 64 genus-group (table 1) names have been proposed in the Augochlorini, including nomina nova, nomina nuda, and names newly proposed herein.

#### THE PRESENT STUDY

The present study provides a revised classification of the Augochlorini above the level of species, an attempt to elucidate phylogenetic relationships among the supraspecific taxa, and to provide commentary on the evolution of the tribe. The classification developed here recognizes 30 genera and an additional 11 subgenera. Four genus-group taxa are newly placed into synonymy while a subgenus of Augochloropsis is resurrected from synonymy. Table 1 associates each genusgroup name with its current status. Megaloptilla, previously considered a subgenus of *Megommation*, is elevated to generic rank as it is not closely related to the later genus. The males of Chlerogella and Micrommation are described for the first time. By means of synonymies, a taxonomic history is given for each family- and genus-group taxon. In addition, for each genus information on the biology and distribution of the included taxa is summarized and references provided for any revisions or keys to species. A new key is provided for the identification of all valid genera and subgenera. A cladistic analysis of affinities among augochlorine genera is explored based on 84 characters of adult external morphology and ethology. All suprageneric groups are defined based on the cladogram and commentary provided on evolution within the tribe.

#### ACKNOWLEDGMENTS

This work is adapted from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Cornell University (Engel, 1998). I am indebted to my doctoral committee: James K. Liebherr, Richard G. Harrison, Thomas D. Seeley, and Charles D. Michener. Jerome G. Rozen, Jr., David A. Grimaldi, and Molly G. Rightmyer have, with great enthusiasm, provided me with constant encouragement and support while at the AMNH. The numerous curators (listed below) as well as a number of individuals too numerous to mention generously provided assistance and support; to each of them I am sincerely thankful. I am grateful for the influence of two men whose Earthly labors have since come to a close: my late advisor, George C. Eickwort, and Byron A. Alexander. During his life George was mentor to many and I am blessed that our paths crossed, even if only for a short time. George and Byron were noteworthy researchers, masterful teachers, inspiring mentors, and close friends. Lastly, I thank my parents, Rev. A. G. Engel and Donna G. Engel, for their constant support and encouragement.

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## MATERIALS AND METHODS

In the section below on Systematics, the taxonomic history of each group is presented followed by a brief diagnosis separating the taxon from close relatives or superficially similar genera. Genera are presented alphabetically under each subtribe; their order should not be taken as a reflection of relationship. Phylogenetic relationships are elaborated on in the Discussion. Following the diagnosis for each genus a short description

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Name	Current status	Name	Current status
Aethechlora Moure and Hurd	= Augochlora (Oxystoglossella)	Megaloptina Eickwort	Subgenus of Megommation
Andinaugochlora Eickwort	Valid genus	Megommation Moure	Valid genus
Ariphanarthra Moure	Valid genus	Micraugochlora Schrottky	= Temnosoma
Augochlora Smith	Valid genus	Micrommation Moure	Valid genus
Augochlorella Sandhouse	Valid genus	Mycterochlora Eickwort	= Augochlora (Augochlora)
Augochlorodes Moure	Valid genus	Neocorynura Schrottky	Valid genus
Augochloropsis Cockerell	Valid genus	Neocorynurella Engel	Valid genus
Cacosoma Smith	= Neocorynura	Neocorynuroides Eickwort	= Neocorynura
Caenaugochlora Michener	Valid genus	Noctoraptor Engel et al.	Subgenus of Megalopta
Callistochlora Michener	Subgenus of Corynura	Odontochlora Schrottky	= Augochlora (Augochlora)
Callochlora Moure	Corynura (Callistochlora)	Oligochlora Engel	Valid genus
Ceratalictus Moure	Valid genus	Oxystoglossa Smith	= Augochlora (Augochlora)
Chlerogas Vachal	Valid genus	Oxystoglossella Eickwort	Subgenus of Augochlora
Chlerogella Michener	Valid genus	Oxystoglossidia Moure	= Augochlorella
Chlerogelloides Engel et al.	Valid genus	Paraugochlora Schrottky	= Augochloropsis (Paraugochloropsis)
Cleptommation Engel et al.	Subgenus of Megommation	Paraugochloropsis Schrottky	Subgenus of Augochloropsis
Corynura Spinola	Valid genus	Paroxystoglossa Moure	Valid genus
Corynurella Eickwort	= Rhectomia	Pereirapis Moure	Valid genus
Corynogaster Sichel	= Corynura (Corynura)	Pseudaugochlora Michener	Valid genus
Corynuroides Sandhouse	= Rhinocorynura	Pseudaugochloropsis Schrottky	= Augochloropsis (Paraugochloropsis)
Corynuropsis Cockerell	= Rhinocorynura	Rhectomia Moure	Valid genus
Ctenaugochlora Eickwort	Subgenus of Caenaugochlora	Rhinocorynura Schrottky	Valid genus
Ctenocorynura Schrottky	= Rhinocorynura	Rhopalictus Sichel	= Corynura (Corynura)
Electraugochlora Engel	Subgenus of Augochlora	Rivalisia Strand	= Augochloropsis (Paraugochloropsis)
Glyptobasia Moure	= Augochloropsis (Paraugochloropsis)	Soliapis Engel	Subgenus of Oligochlora
Glyptobasis Moure	= Augochloropsis (Paraugochloropsis)	Stilbochlora Engel et al.	Subgenus of Megommation
Glyptochlora Moure	Subgenus of Augochloropsis	Tennosoma Smith	Valid genus
Halictillus Moure	Valid genus	Temnosomula Ogloblin	= Temnosoma
Ischnomelissa Engel	Valid genus	Tetrachlora Schrottky	= Augochloropsis (Paraugochloropsis)
Megalopta Smith	Valid genus	Thectochlora Moure	Valid genus
Megaloptella Schrottky	= Megalopta (Megalopta)	Tmetocoelia Moure	= Megalopta (Megalopta)
Megaloptidia Cockerell	Valid genus	Vachalius Moure	= Neocorynurella
Megaloptilla Moure and Hurd	Valid genus	Xenochlora Engel et al.	Valid genus
a Evolution longing colomi and nom	wise such		

TABLE 1 Summary of Genus-Group Names of Augochlorini<sup>a</sup>

<sup>a</sup> Excludes lapsus calami and nomina nuda.

providing important morphological traits is appended. Lastly, appended to each entry are brief summaries on (1) the current classification of each genus-group taxon, providing references to revisions, if they exist; (2) information and references to the biology of each group; and (3) distribution information. If, however, nothing is known concerning the biology for a given group, this section has been omitted. A list of species examined during the course of this study to construct the cladistic matrix is presented in appendix 3.

In the descriptions the following abbreviations are used: F, flagellomere; S, metasomal sternum; T, metasomal tergum. The length of the prementum and size of ocelli are characters used to separate genera. An elongate prementum is taken to mean that its length is greater than seven times its width, and conversely a prementum considered not elongate has the length less than seven times its width. Similarly, "ocelli greatly enlarged" is used for those taxa in which the distance from the upper margin of the compound eye to the lateral ocellus is less than the diameter of the median ocellus. Further details on morphological terminology are provided below (under General Morphology).

Specimens were prepared for scanning electron microscopy as follows: (1) pinned specimens were disarticulated and mounted directly onto carbon-covered stubs; (2) specimens originally stored in 70-90% ethanol were disarticulated and then transferred stepwise to 100% ethanol in which they were kept for at least 24 hours, before transfer to hexamethyldisalizane (HMDS) for one hour, and again to a fresh bath of HMDS. After the second wash of HMDS, the specimens were placed under a fume hood and allowed to remain there until all of the HMDS had evaporated (procedure further described by Brown, 1993; Rumph and Turner, 1998; and other authors). Each specimen was then mounted on an electron microscopy stub for study.

The following institutions and curators provided material that was examined during the course of this study. Abbreviations for institutions are taken from Arnett et al. (1993), except those collections not listed by them for which acronyms were newly created: **AMNH**, American Museum of Natural History, New York, New York, J. G. Rozen, Jr., and E. Quinter; ANSP, Philadelphia Academy of Natural Sciences, Philadelphia, Pennsylvania, D. Azuma; BMNH, The Natural History Museum, British Museum, London, United Kingdom, G. Else, S. Lewis; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, R. L. Davidson; CNC, Canadian National Insect Collection, Ottawa, Canada, G. Gibson and L. Dumouchel; CUIC, Cornell University Insect Collection, Ithaca, New York, J. K. Liebherr and E. R. Hoebeke; DZUP, Museu de Entomologia Padre Jesús Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil, J. S. Moure; EMUS, U.S.D.A. Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah, T. L. Griswold; FMNH, Field Museum of Natural History, Chicago, Illinois, P. P. Parrillo; FSCA, Florida State Collection of Arthropods, Gainesville, Florida, J. Wiley and M. C. Thomas; GARM, Gabriel A. R. Melo Private Collection, Ribeirão Preto, Brazil (formerly of SEMC); IIRB, Museo de Invertebrados, Instituto de Investigación de Recursos Biológicos "Alexander von Humboldt," Santa Fé de Bogotá, Colombia, F. Fernandez; INPA, Instituto Nacional de Pequisas da Amazônia, Manaus, Brazil, A. Y. Harada; IZAV, Universidad Central de Venezuela, Maracay, Venezuela, J. A. Clavijo and M. A. Ganiani; LACM, The Natural History Museum of Los Angeles County, Los Angeles, California, R. R. Snelling; MACT, Morone Amber Collection, Turin, Italy, E. Morone (D. A. Grimaldi, AMNH); MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, P. Perkins and S. Cover; MEMU, Mississippi State Insect Collection, Mississippi State, Mississippi, R. L. Brown; MIUP, Museo de Invertebrados "G. B. Fairchild," Universidad de Panamá, Panamá City, Panamá, D. Quintero; MNHC, Museo Nacional de Historia Natural, Havana, Cuba, J. A. Genaro; MNHN, Museum National d'Histoire Naturelle, Paris, France, J. Casevitz-Weulersse; MRSN, Spinola Collection, Museo Regionale Scienze Naturali, Turin, Italy, P. L. Scaramozzino; MSUC, Michigan State University, Department of Entomology Collection, East Lansing, Michigan, F. Stehr; PMAE, Provincial Museum of Alberta, Edmonton, Canada, A. Finnamore; **SEMC**, Snow Entomological Collection, Natural History Museum, University of Kansas, Lawrence, Kansas, C. D. Michener and R. W. Brooks; **STRI**, Smithsonian Tropical Research Institute, Balboa, Panamá, D. W. Roubik; **UADE**, University of Arkansas, Fayetteville, Arkansas, S. A. Cameron and J. B. Whitfield; **UCD**, Bohart Museum of Entomology, Davis, California, L. S. Kimsey and L. A. Baptiste; **UFVB**, Museu Entomologico de Universidade Fed-

#### GENERAL MORPHOLOGY

The general morphology of the augochlorine *Pseudaugochlora graminea* (Fabricius) was examined in detail by Eickwort (1969a: as a species of *Pseudaugochloropsis*), and such a study need not be repeated here. Instead, only those characters employed in this classification are briefly examined. The most common state of each character is presented along with a discussion of variations found in the tribe. Morphological terminology generally follows that of Michener (1944, 1965) and Eickwort (1969a).

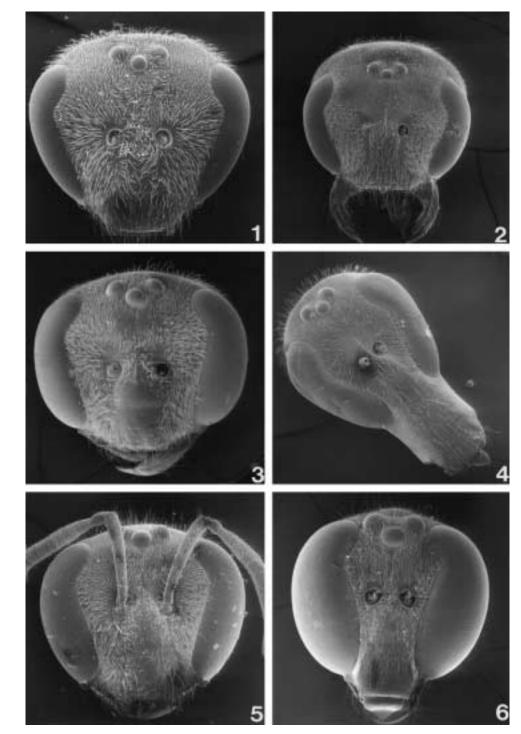
#### FEMALES

The mandible is often equipped with a subapical tooth that is little differentiated from the apex and is positioned slightly basad the apex on the upper margin of the mandible (fig. 16). This tooth can become strongly produced from the apex with a deep concavity differentiating it and sometimes the tooth reaches apicad as far as the mandibular apex. In these cases, the mandible is frequently has smaller supplementary tubercles or teeth on the inner surface, basal to the subapical tooth (fig. 16). In a few genera (e.g., *Temnosoma, Cleptommation*), the mandible lacks subapical or supplementary teeth (fig. 15).

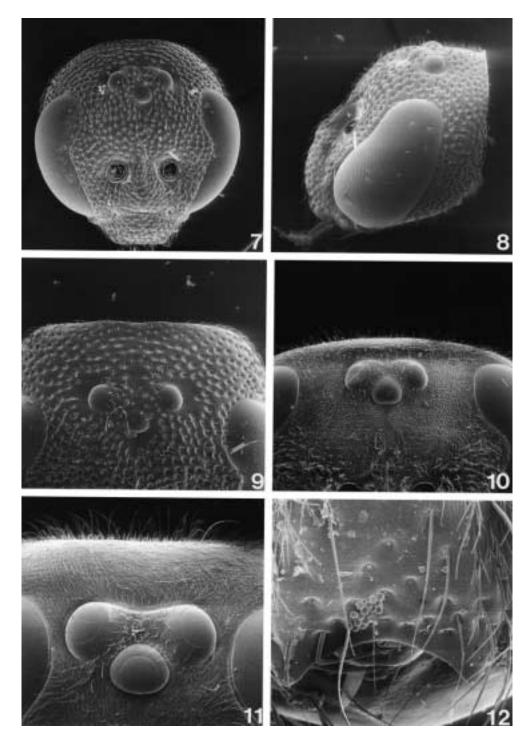
The labrum consists of a transverse basal area that may bear various blunt tubercles ranging in shape from orbicular to strongly bilobed. Extending apicad and set below this basal region is a triangular distal process, positioned such that the pointed apex of the triangle forms the most distal point of the labrum (fig. 17). The base of this process, where it joins with the basal area, is often slightly narrower than the width of the basal eral de Viçosa, Viçosa, Brazil; **UNCB**, Universidad Nacional de Colombia, Santa Fé de Bogotá, Colombia, G. Nates-Parra; **USNM**, United States National Museum, Smithsonian Institution, Washington, D.C., R. J. McGinley and M. Mello; **YUDB**, Department of Biology, York University, North York, Canada, L. Packer; **ZMHB**, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany, F. Koch and A. Kleine-Möllhoff.

area (fig. 17), but the base of the distal process can be expanded (e.g., Megalopta and Xenochlora) such that it is as broad as the basal area (broadly triangular) (fig. 18). In the genera Augochloropsis and Temnosoma the distal process is broad on both ends, becoming almost quadrate (fig. 20). The distal process bears on its dorsal surface a longitudinal carina or ridge (the distal keel; figs. 17-19). In two groups the distal keel becomes expanded at its base such that it forms a small plateau (fig. 19). The labral teeth along the lateral margins of the distal process can be completely absent (fig. 18) or developed into strong projections such that the lateral margins appear nearly pectinate (fig. 17). The apex of the clypeus in Megommation s.s. and Megaloptina is deeply concave (figs. 5, 12) rather than being approximately straight between two weakly developed lateral tubercles (figs. 1-4, 6). In the genus Rhinocorynura the clypeus frequently bears armature such as tubercles.

The prementum is typically much less than seven times as long as wide (fig. 14). However, in some genera (e.g., *Megaloptidia* and relatives) it is greatly narrowed and elongate, being seven or more times longer than wide (fig. 13). The base of the galea frequently extends to the stipital base or nearly so (fig. 22), but in a few genera (treated below as the subtribe Corynurina) it extends only half of this distance (fig. 21). In most augochlorines the maxillary palpi are much shorter than the prementum, or at most as long as the prementum. However, in *Ariphanarthra* they are greatly elongate and flattened so that the palpi reach to the metasoma in repose. The ga-

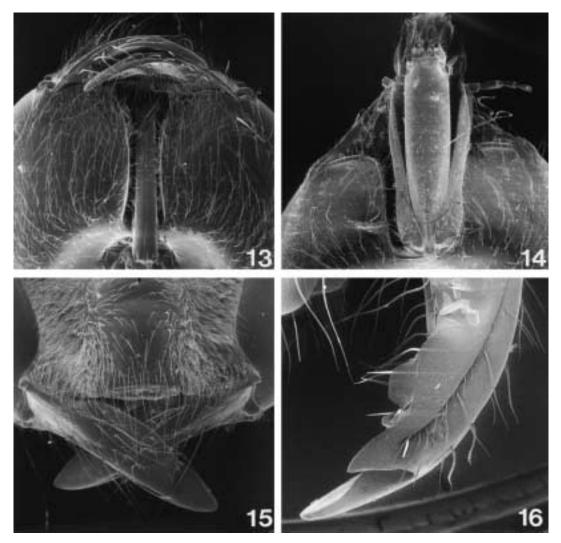


Figs. 1–6. Heads of Augochlorini, frontal aspect. **1.** *Thectochlora alaris* (Vachal), female. **2.** *Rhinocorynura briseis* (Smith), female. **3.** *Megommation* (*Cleptommation*) *minutum* (Friese), female. **4.** *Chlerogella* sp., female. **5.** *M.* (*Megaloptina*) *ogilviei* (Cockerell), female. **6.** *Megalopta* (*Megalopta*) *genalis* Meade-Waldo, male.



Figs. 7–12. Head modifications of female Augochlorini. 7. Temnosoma metallicum Smith, dorsal aspect. 8. T. metallicum, profile. 9. T. metallicum, vertex. 10. Pseudaugochlora graminea (Fabricius), vertex. 11. Megalopta (Megalopta) genalis Meade-Waldo, vertex. 12. Clypeal apex of Megommation (Megaloptina) ogilviei (Cockerell).

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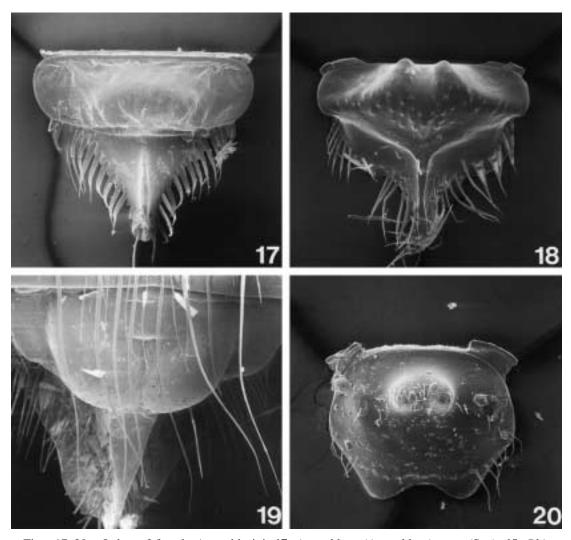


Figs. 13–16. Female mouthparts. **13.** Labiomaxillary complex and hypostomal fossa of *Megommation (Megaloptina) ogilviei* (Cockerell), ventral aspect. **14.** Labiomaxillary complex and hypostomal fossa of *Corynura (Corynura) chilensis* (Spinola), ventral aspect. **15.** Clypeus and mandibles of *M. (Cleptommation) minutum* (Friese). **16.** Mandible of *Megalopta (Megalopta) genalis* Meade-Waldo.

lea bears a broad, rounded lobe at its apex (fig. 24) and the inner surface typically lacks modifications (fig. 23); however, in a few genera (e.g., *Pseudaugochlora* and relatives) the galea is sharply pointed at its apex (fig. 23). In the corynurine genera the inner surface bears a strong galeal comb (figs. 24, 25).

A strong ridge separates the hypostomal fossa from the postgenal area. This ridge is usually developed into the hypostomal carina which runs from the posterior border of the head anteriorly (figs. 13, 14). At the anterior border of the head it gently turns outwards, running behind the articulation of the mandible (fig. 14), or in some augochlorines the point at which this carina turns outward it is developed into a strong point or angle instead of a broad curve. The hypostomal ridge is lamellate in *Megommation* s.s. and projects behind the posterior border of the head.

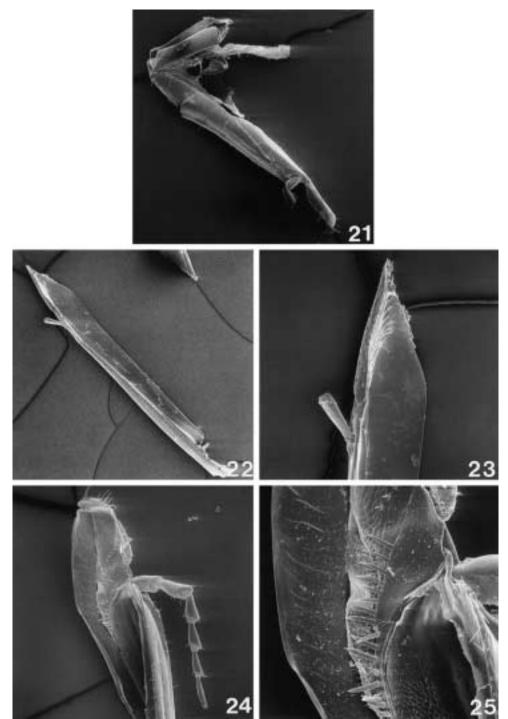
The area of integument between the lower border of the compound eye and the mandibular base is the malar space. In most groups this space is extremely short with the com-



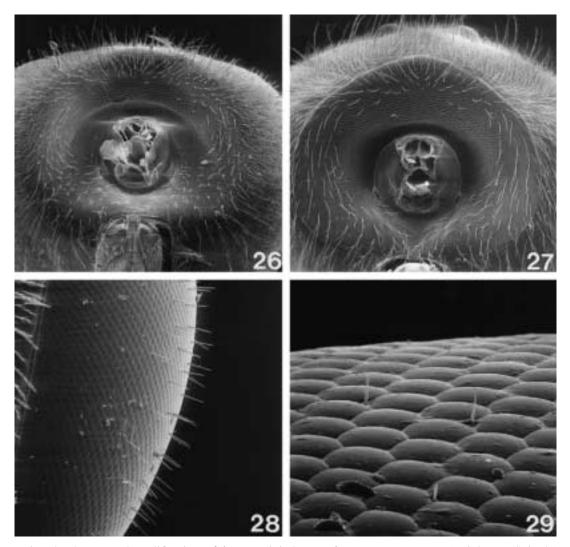
Figs. 17–20. Labra of female Augochlorini. **17.** Augochlora (Augochlora) pura (Say). **18.** Rhinocorynura briseis (Smith). **19.** Megalopta (Megalopta) genalis Meade-Waldo. **20.** Temnosoma metallicum Smith.

pound eye seemingly in contact with the mandibular base (i.e., the length of the malar space is much shorter than the basal mandibular width: figs. 1-3, 5, 6, 8). In certain augochlorine groups this space becomes greatly elongate with a separation between the mandibular base and the compound eye at least three quarters of the basal mandibular width, but frequently many times longer (fig. 4).

The epistomal sulcus is subdivided into a number of individual sulci. The angle created between the dorsal clypeo-genal sulcus and the lateral clypeo-genal sulcus which opens towards the compound eyes is variously constructed. In a few genera (e.g., *Augochlora*) this angle is strongly acute and projecting into the clypeal base as a small lobe. In *Chlerogelloides* this is the most well developed with the lobe being extremely narrow and nearly reaching to the apical margin of the clypeus. In scattered genera the angle is approximately orthogonal (i.e., almost right angular), whereas in still others (e.g., *Corynura*) it is broadly obtuse (in some cases almost not forming an angle, the two sulci being almost linear with one other).



Figs. 21–25. Labiomaxillary complex structures of Augochlorini. **21.** Maxilla in profile *Corynura* (*Corynura*) chilensis (Spinola). **22.** Maxilla of *Pseudaugochlora graminea* (Fabricius). **23.** Galeal apex of *P. graminea*. **24.** Galeal apex of *C. chilensis*. **25.** Galeal comb of *C. chilensis*.

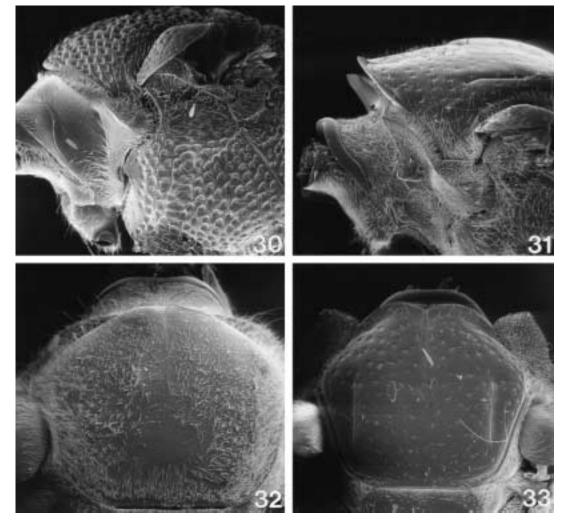


Figs. 26–29. Head modifications. **26.** Preoccipital area of *Corynura* (*Corynura*) *chilensis* (Spinola). **27.** Preoccipital area of *Pereirapis semiaurata* (Spinola), carina present. **28.** Compound eye of *C.* (*Callistochlora*) *chloris* (Spinola), elongate setae. **29.** Compound eye of *Augochlora* (*Augochlora*) *pura* (Say), minute setae.

The antennal flagellum of bees is composed of 10 units (flagellomeres) in females and 11 in males. In the genus *Chlerogas* the number of these segments is reduced by one in each sex.

The ocelli of most augochlorines are typical for bees (figs. 1–5, 7–10), being separated from the compound eyes by their own diameter or more. In a few taxa the ocelli are greatly enlarged, coming into close proximity with the compound eyes (figs. 6, 11). The compound eyes support setae which are about as long as the diameter of an ommatidium (fig. 29). In a few groups (e.g., *Callistochlora* or *Caenaugochlora* s.s.), these setae are greatly lengthened, many times as long as an ommatidial diameter, and are frequently visible on pinned specimens without the aid of a microscope (fig. 28).

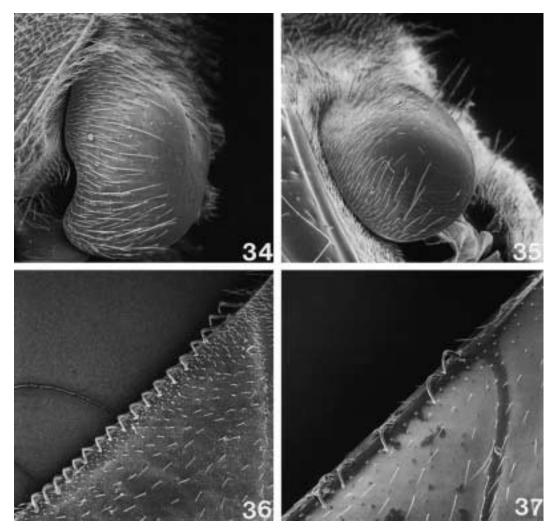
The vertex is gently rounded or slightly flattened behind the ocelli but in some genera it can be fairly long (figs. 2, 7–9). In the



Figs. 30–33. Mesosomae of female Augochlorini. **30.** *Temnosoma metallicum* Smith, profile. **31.** *Rhinocorynura briseis* (Smith), profile. **32.** Mesoscutum of *Megommation* (*Cleptommation*) *minutum* (Friese), dorsal aspect. **33.** Mesoscutum of *R. briseis*, dorsal aspect, pronotal dorsal lamellae evident on upper corners of mesosoma.

genera *Megalopta* s.l. and *Xenochlora* a deep interocellar furrow runs between and just behind the lateral ocelli (fig. 11). In *Pseudaugochlora*, a strong transverse ridge is present on the vertex behind the ocelli (fig. 10). The preoccipital area is gently rounded in most augochlorines (fig. 26); however, in a few groups it bears a strong carina or a weak lamella (fig. 27).

The sculpturing of the mesosoma is quite variable among augochlorines. A few genera have distinctive sculpturing patterns that help distinguish close relatives. In these cases the mesosoma is strongly and coarsely punctured (fig. 30). The pronotum extends latero-posteriorly to form the pronotal lobe and in so doing forms a dorsal surface that creates the lateral angle as it bends posteriorly to form the lobe. This angle can be strongly produced so that it projects anteriorly and forms a large dorsal surface. The ridge between this dorsal surface and the lateral surface of the pronotum is the pronotal dorsal ridge (fig. 31), while the ridge running from the point of the

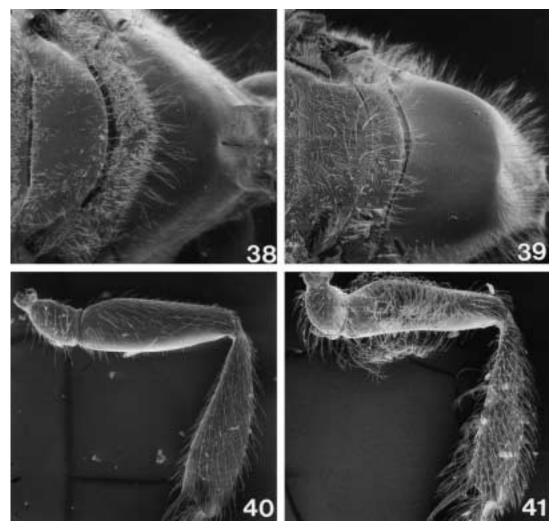


Figs. 34–37. Characteristics of female Augochlorini. **34.** Tegula of *Augochloropsis (Paraugochloropsis) sumptuosa* (Smith), depicting notch on inner posterior margin. **35.** Tegula of *Rhinocorynura briseis* (Smith). **36.** Distal hamuli of hind wing of *Megalopta (Megalopta) genalis* Meade-Waldo. **37.** Distal hamuli of *Chlerogella* sp.

angle ventrally along the lateral surface is the pronotal lateral ridge (fig. 31). These ridges can be rounded, carinate, or in more unusual cases, lamellate. The dorsal surface of the pronotum is greatly expanded and convex, forming an inflated surface in *Chlerogella* and *Chlerogelloides*. The anterior border of the mesoscutum is frequently gently convex and broadly rounded when viewed from above (fig. 32). In some genera (e.g., *Neocorynura, Rhinocorynura*), however, the medio-anterior margin is produced anteriorly

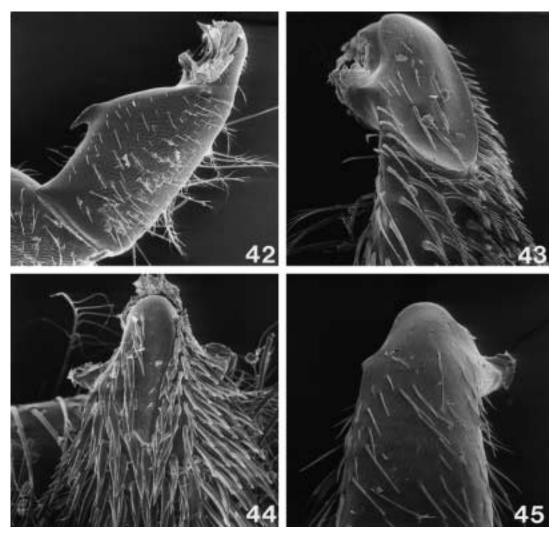
forming a slight bottleneck appearance (fig. 33) that can also be seen in profile (cf. figs. 30, 31). The tegula is ovoid and usually slightly narrower on the anterior end than is the broadly rounded posterior portion (fig. 35). In *Augochloropsis* s.l., however, the inner posterior border of the tegula is indented or deeply notched (fig. 34), so that the posterior part of the tegula is narrowed and bent inward.

The probasitarsus is frequently equipped on its outer edge with a distinctive row of



Figs. 38–41. Features of female Augochlorini. **38.** Scutellum, metanotum, and basal area of propodeum of *Megommation (Cleptommation) minutum* (Friese). **39.** Scutellum, metanotum, and basal area of propodeum of *Chlerogella* sp. **40.** Hind leg of *Temnosoma metallicum* Smith, scopa absent from femur and tibia. **41.** Hind leg of *Augochlora (Augochlora) pura* (Say), scopa on femur and tibia.

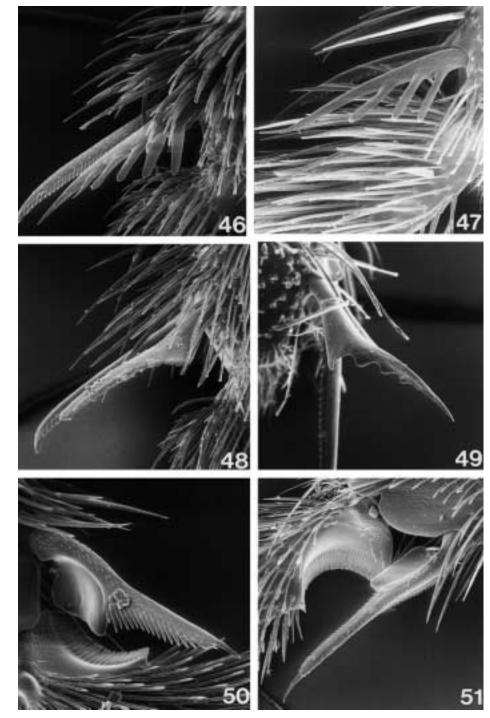
stiff setae known as the anterior basitarsal brush. In bees the protibial spur is modified into an antenna cleaner consisting of a backbone spine referred to as the malus and a flat, inner extension called the velum. The free portion of malus (not attaching to the velum) is variously modified and its margin can be serrated, minutely ciliate (fig. 51), or densely pectinate with the teeth progressively becoming shorter towards the apex (fig. 50). Although this structure is quite variable among and within the genera, it is mentioned here in order to draw future students to this feature as it appears to be a good character for species and species-groups. The mesotrochanter is gently rounded on its upper border in all augochlorines except in *Thectochlora* a strong hooked tubercle is present on this surface (fig. 42). The metafemur and metatibia bear the scopa, which is formed of dense, plumose setae used in the transport of pollen (fig. 41). Three groups lack the scopa and have scattered simple setae over these leg surfaces (fig. 40). On the outer



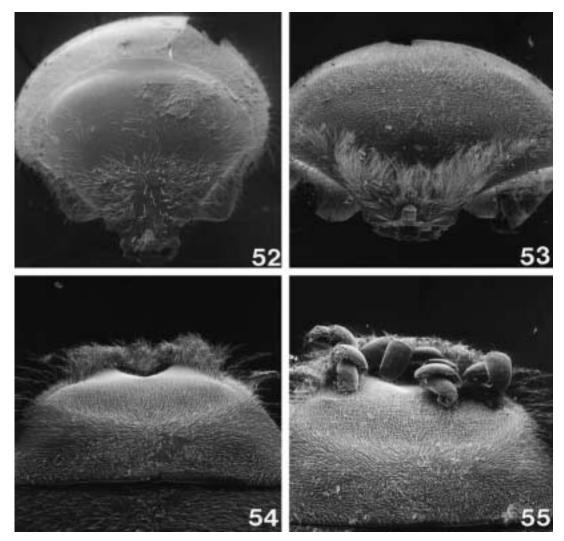
Figs. 42–45. Leg modifications of female Augochlorini. **42.** Inner surface of mesotrochanter of *Thectochlora alaris* (Vachal) showing hook on dorsal surface. **43.** Basitibial plate of *Augochlora (Augochlora) pura* (Say). **44.** Basitibial plate of *T. alaris.* **45.** Outer surface of metatibial base of *Megommation (Cleptommation) minutum* (Friese), showing absence of basitibial plate.

margin of the metatibial base is frequently found a small, raised area, termed the basitibial plate. The plate is glabrous, although a few groups have some short setae located on this plate. In most genera the plate is bordered on all sides except the base by a distinct rim or edge (fig. 43). In scattered genera, the plate slopes anteriorly and blends into the integument of the tibia without a distinct border along this margin (fig. 44), while in others the plate is completely absent (fig. 45). The inner margins of the metatibial spur range from serrated (figs. 48, 49) to pectinate, and bear a variable number of teeth usually between 3 and 10 (figs. 46, 47); in *Ischnomelissa* and *Ctenaugochlora*, there are more than 10 teeth densely packed together.

The marginal cell of the forewing is bordered anteriorly by vein R and posteriorly by Rs. The apex of this cell is typically acute, with Rs gently curving anteriorly before meeting R. In some genera, Rs turns more sharply anteriorly and bears a feeble distal



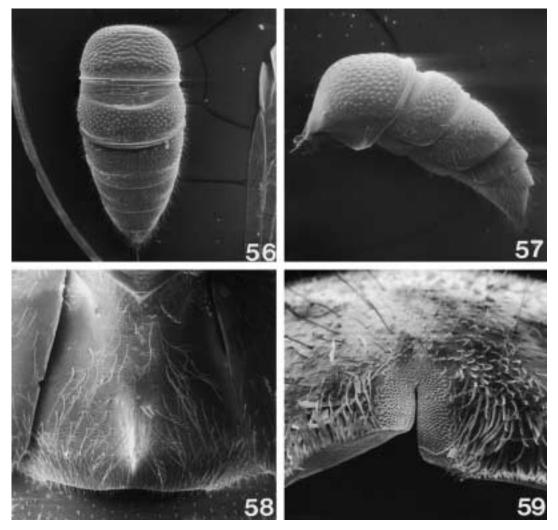
Figs. 46–51. Spurs and antenna cleaners of female Augochlorini. 46. Inner hind tibial spur of *Chlerogella* sp. 47. Inner hind tibial spur of *Thectochlora alaris* (Vachal). 48. Inner hind tibial spur of *Augochlora (Augochlora) pura* (Say). 49. Inner hind tibial spur of *Pereirapis semiaurata* (Spinola). 50. Antenna cleaner of *Chlerogella* sp. 51. Antenna cleaner of *Megommation (Cleptommation) minutum* (Friese).



Figs. 52–55. Tergal modifications of female Augochlorini. **52.** Anterior surface of T1 of *Pereirapis semiaurata* (Spinola). **53.** Anterior surface of T1 of *Thectochlora alaris* (Vachal) with acarinarium, mites removed. **54.** Dorsal aspect of T1 of *T. alaris* with acarinarium, mites removed. **55.** Same view as in figure 54 with mites present.

spur which extends towards the wing apex (feebly truncate and appendiculate). The distal hamuli along the anterior margin of the hind wing are typically arranged irregularly with a distinct spacing pattern produced by large separations between subgroups of the hamuli (fig. 37). In *Megalopta* and *Noctoraptor*, the hamuli are regularly spaced and numerous (fig. 36).

The basal area of the propodeum is the dorsal-facing surface of the first abdominal segment (fused into the thorax to form the mesosoma). The sculpturing of the basal area is quite variable; in some groups it is either uniformly striate or imbricate. The basal area is typically about as long as the scutellum (fig. 38), although in some groups it is strongly declivitous and only as long as the metanotum. In three augochlorine genera the basal area is elongate and as long as, or frequently longer than, the scutellum and metanotum combined (fig. 39). The posterior surface of the propodeum bears a narrow median depression termed the propodeal pit



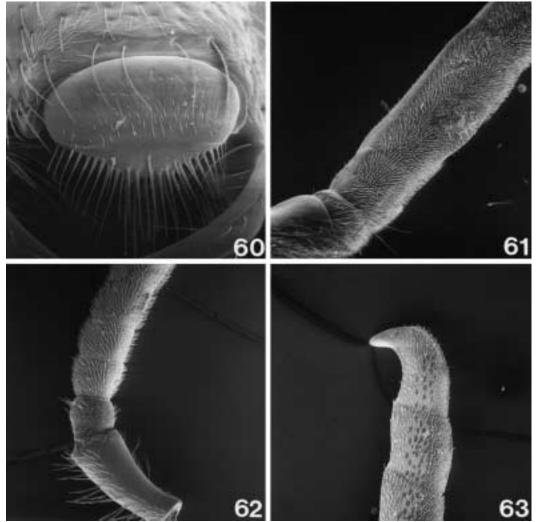
Figs. 56–59. Metasomal modifications of female Augochlorini. 56. Metasoma of *Temnosoma metallicum* Smith, dorsal aspect. 57. Metasoma of *T. metallicum*, profile. 58. S1 of *Augochlora (Augochlora) pura* (Say), median apical ridge. 59. Apex of T5 of *Megalopta (Megalopta) genalis* Meade-Waldo, medioapical cleft of pseudopygidial area.

(seen on the far right side of fig. 38), the typical state is a simple, narrow pit; however, in some corynurine genera this pit is set into a distinct V-shaped depression.

The anterior surface of the first metasomal tergum is typically flattened with scattered setae over smooth, imbricate, or lightly punctured integument (fig. 52). In two groups, this surface is strongly concave and bordered by dense setae forming an acarinarium (figs. 53– 55). In one genus the apical borders of T1-2 are strongly depressed and rimmed posteriorly (figs. 56, 57). The medio-apical margin of T5 bears a strong cleft (fig. 59) that is lost in the parasitic genus *Temnosoma*. Some species of the genus *Augochlora* bear a strong median spine or ridge on S1 (fig. 58). In all other instances this surface is gently rounded.

#### MALES

The basal area of the male labrum has a similar construction to that of the female, although it is less developed, typically being much shorter than that of the female. The

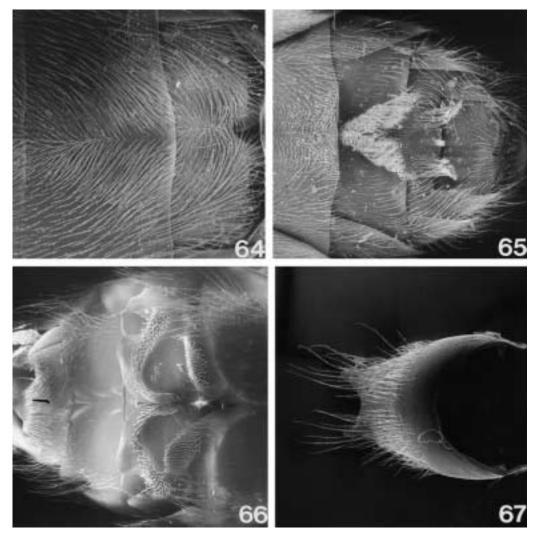


Figs. 60–63. Features of male Augochlorini. **60.** Labrum of *Caenaugochlora (Caenaugochlora)* costaricensis (Friese). **61.** From left to right: apex of scape, pedicel, F1, F2, and basal margin of F3 for *Corynura (Callistochlora) prothysteres* (Vachal). **62.** From bottom to top: scape, pedicel, F1, F2, F3, and basal margin of F4 for *Pereirapis semiaurata* (Spinola). **63.** Distal flagellomeres of *Pseudaugochlora graminea* (Fabricius), F11 hooked at apex.

basal area sometimes bears a small notch. The distal process is typically absent, although a small distal process is sometimes present as a broad triangular extension of the apical margin (fig. 60).

The male antennae are variously constructed. The length varies dramatically with some genera having short antennae whereby the flagellum extends only posterad to the posterior border of the mesoscutum. In moderately developed antennae the flagellum extends to the posterior border of the scutellum, while long antennae extend to the propodeum or beyond. The relative lengths of F1 and F2 are often diagnostic. In most instances these flagellomeres are of approximately equal length (fig. 62), although some genera have the second many times longer than the first (fig. 61), while others have the first many times longer than the second. The apical flagellomere (F11) in *Pseudaugochlora* is hooked at its apex (fig. 63).

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Figs. 64–67. Metasomal modifications of male Augochlorini. **64.** Relatively unmodified sterna (S5–S6) of *Neocorynura papallactensis* Engel. **65.** S3–S6 of *Pseudaugochlora graminea* (Fabricius). **66.** S3–S6 of *Megalopta* (*Megalopta*) genalis Meade-Waldo. **67.** T7 of *Temnosoma metallicum* Smith.

Typically, the legs of males are like those of females, excluding the usual sex differences (e.g., lack of pollen-collecting apparati in males). However, in one species of *Chlerogelloides* the mesofemur and mesotibia are greatly expanded and equipped with short, blunt processes on their inner surfaces. The inner hind tibial spur of males bears a finely serrated margin except in the genus *Chlerogas* where it is pectinate with long teeth.

Mesosomal pubescence varies dramatically among the genera, but distinctive patches of plumose setae surround the propodeal spiracles in *Megaloptina* and *Cleptommation*.

The male metasoma is typically elongated, the terga being as long as wide or longer, but in various genera, the metasoma is constructed like that of the female, with each tergum wider than long. In other groups the metasoma is petiolate, T1 being much longer than wide and greatly narrowed along its basal half.

The apical margin of T7 is typically unmodified, uninterrupted by processes or emarginations. In the genus Temnosoma, however, the apical margin of this tergum is deeply concave and bilobed (fig. 67). The proctiger includes the membranous remnants of the internalized T9. The apical margin of the proctiger is sometimes equipped with distinct anal filaments and/or an apical fringe of microtrichiae. The sterna are variously modified and some of these features are constant among species of a given genus. The apical margins of the sterna are typically entire, lacking processes or emarginations (fig. 64). In some genera, however, median processes are found on the apical margins of S3-S5, while in others the apical margins of S4-S6 genera bear depressions or clefts (fig. 66). Megalopta and Noctoraptor also possess deep lateral notches in the apical margin of S4 (fig. 66). The fourth sternum can also be adorned with a dense triangular setal patch medially (fig. 65). In Caenaugochlora s.s. this setal patch is positioned on a series of median tubercles. Other setal patterns exist and, while typically constant within a species, do not appear to be shared across groups of higher rank. The seventh and eighth sterna are fused and hidden within the body just ventral to the genital capsule. The apical margins of these sterna can be unmodified, or equipped with processes (e.g., figs. 68–71). Along the anterior margin of S8 is a median process referred to as the spiculum. This structure is present among all augochlorine genera and is frequently longer than it is wide (figs. 69-71), although in some groups it is quite broad (fig. 68).

The gonobase possesses two arms on its

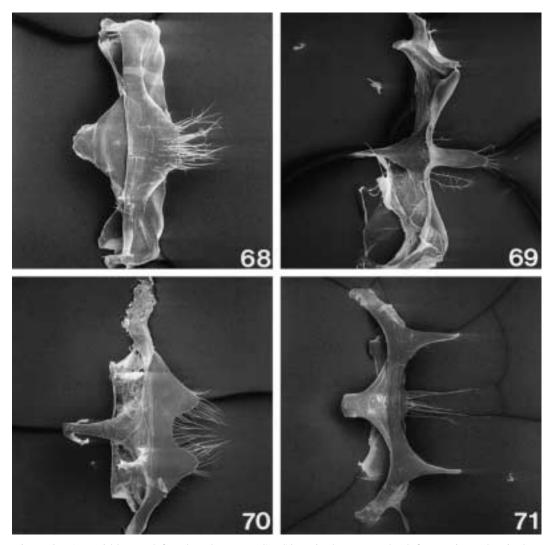
ventral surface that meet medially to produce the gonobasal bridge. This ventral bridge ranges from membranous to sclerotized. Dorsally, the gonobase is depressed along its medio-apical margin, producing two lobes. In many genera these lobes are strongly developed with a deep cleft or concavity separating the two; however, some augochlorines have merely a shallow depression, so that the lobes are scarcely developed. The ventral surface of the penis valve is equipped with a broad prong (fig. 72). In a few genera this is replaced by a stiff keel, while in others it is lost altogether. In the genus Temnosoma, the dorsal surface of the penis valve bears a large apically directed process (fig. 76). The base of the gonostylus is infrequently equipped with a small thumblike projection known as the basal process (figs. 74, 75). This process is normally covered by short setae (figs. 74, 75); however, in *Callistochlora* the setae are absent (fig. 77). A parapenial lobe often arises from just below the gonostylar processes on the inner surface of the gonostylus (fig. 73). This does not appear to be homologous with the retrorse lobe found among the Halictini. The retrorse lobe arises from the ventral surface of the gonocoxite and somewhat below where the parapenial lobe found among the augochlorines originates. The ventral gonostylar process is a well-developed lobe of various shapes. In Augochlorella and Ceratalictus it is deeply divided along its apex. The dorsal gonostylar process is also variously shaped, but in a few groups it is reduced to a distinctive setose ridge. The degree to which the dorsal process is sclerotized is also diagnostic for some genera.

## **SYSTEMATICS**

## TRIBE AUGOCHLORINI BEEBE

DIAGNOSIS: Augochlorines are most readily recognized from other Halictinae by their brilliant metallic coloration; however, this is not a universal character, being neither unique to nor fixed across Augochlorini. The medio-apical cleft of the female fifth metasomal tergum and the absence of a pygidial plate on the apical margin of the male seventh metasomal tergum separates Augochlorini from other Halictinae. Among New World halictines, the augochlorines are most similar to (and likely most closely related to) genera of the *Caenohalictus* and *Agapostemon* generic complexes; these groups also frequently exhibit metallic-green body coloration.

DESCRIPTION: **Female.** Compound eyes frequently with emargination just above level of antennae (figs. 1–7). Distal wing venation strong; basal vein strongly arcuate. Apical margin of T5 cleft (except in *Temnosoma*)

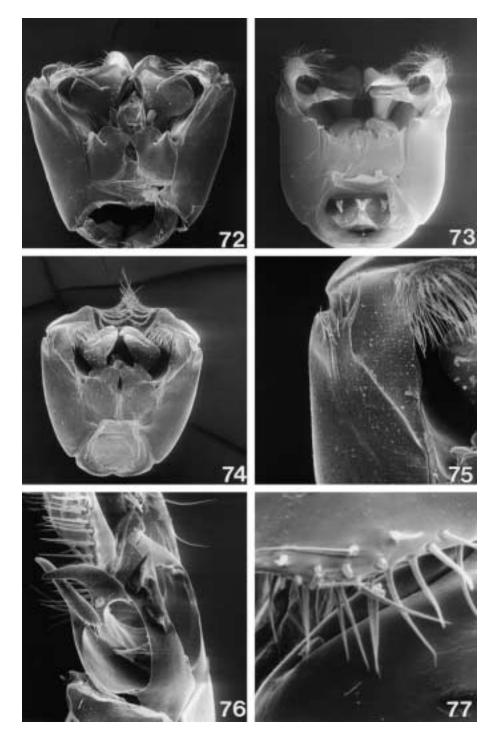


Figs. 68–71. Hidden and fused male sterna S7–S8; spicula are on the left margin and apical processes are shown on the right. **68**. Augochloropsis (Paraugochloropsis) sumptuosa (Smith). **69**. Temnosoma metallicum Smith. **70**. Megalopta (Megalopta) genalis Meade-Waldo. **71**. Pseudaugochlora graminea (Fabricius).

(fig. 59). **Male.** Apical margin of T7 without pygidial plate, margin not recurved. Apical margin of S6 cleft (except in *Halictillus* and some *Augochlora*). Spiculum present on anterior border of S8 (figs. 68–71). Retrorse lobe of gonocoxite absent.

COMMENTS: A potential larval character for the Augochlorini is the development of the mandibular cusp into an acute, elongate projection (McGinley, 1981). Larvae, however, are known for only a few, scattered genera (table 2) and until further work on augochlorine immatures is undertaken, the validity of this character in supporting the monophyly of the tribe remains uncertain.

Authorship of the tribe has universally been given to Moure (1943a). In actuality, Beebe (1925), in a semipopular treatment of the fauna of Guyana, mentions the name "Augochloridae" to include tropical species of the genera *Augochlora* and *Halictus*. Although Beebe (op. cit.) proposed the group



Figs. 72–77. Male genitalic structures. **72.** Genital capsule of *Thectochlora alaris* (Vachal), ventral aspect. **73.** Genital capsule of *Megalopta (Megalopta) genalis* Meade-Waldo, ventral aspect. **74.** Genital capsule of *Rhinocorynura briseis* (Smith), ventral aspect. **75.** Gonocoxite-gonostylus junction in *R. briseis* depicting basal gonostylar process on ventral surface, process with strong setae at apex. **76.** Penis valve of *Temnosoma metallicum* Smith, profile, with large dorsal processes. **77.** Basal gonostylar process of *Corynura (Callistochlora) prothysteres* (Vachal) lacking setae, partially hidden by setose ventral process.

Taxon	Larva	Pupa	Reference
AUGOCHLORINA <sup>a</sup>			
Augochlora cordiaefloris	Х	Х	Eickwort and Eickwort, 1972
Augochlora hallinani	Х	х	Eickwort and Eickwort, 1973b
Augochlora nominata	Х	х	Eickwort and Eickwort, 1972
Augochlora pura	Х	х	Michener, 1953, 1954a; McGinley, 1981
Augochlora sidaefoliae	Х	х	Eickwort and Eickwort, 1973b
Augochlorella edentata	Х	х	Eickwort and Eickwort, 1973a; McGinley, 1981
Neocorynura colombiana	Х	Х	Eickwort, 1979a
CORYNURINA <sup>b</sup>			
Corynura chloris	Х		Claude-Joseph, 1926
Corynura cristata	х		Claude-Joseph, 1926
Halictillus glabrescens	Х		Claude-Joseph, 1926

TABLE 2 Presently Described Immature Stages of Augochlorini

<sup>*a*</sup> Immatures stages of two species of *Megalopta* have been discovered and will be described in a forthcoming paper (Engel and Wcislo, in prep.).

<sup>b</sup> The descriptions of the corynurine immatures by Claude-Joseph (1926) are anecdotal and these taxa should be restudied.

cavalierly, he is to be considered as the correct author of the family-group name based on *Augochlora* (Engel, 1999b).

#### SUBTRIBE AUGOCHLORINA BEEBE

- Oxystoglossini Schrottky, 1909b: 482. Type genus: *Oxystoglossa* Smith, 1853. Suppression in favor of Augochlorini Beebe, 1925, pending with I.C.Z.N. (Engel, 1999a, b).
- Augochloridae Beebe, 1925: 102. Type genus: *Augochlora* Smith, 1853. Corrected authorship (not Moure, 1943a: see Engel, 1999b).
- Augochloropsini Moure, 1943a: 462. Type genus: Augochloropsis Cockerell, 1897b.
- Megaloptinae Moure, 1943a: 479. Type genus: *Megalopta* Smith, 1853.

DIAGNOSIS: This is the largest group of Augochlorini and is quite heterogeneous. The elongate medial process of the premental apex that extends anteriorly beyond the apices of the lateral processes is unique to the Augochlorina and readily separates them from the more primitive subtribe, Corynurina.

DESCRIPTION: As for the tribe with the following additions: **Female.** Angle formed by epistomal sulcus variable. Premental apex with median process elongate, extending beyond apices of lateral processes. Strong galeal comb absent (figs. 22, 23); galeal apex variable, frequently rounded; galeal base extends posteriorly to near stipital base (fig. 22). Marginal cell with apex variable. Integument frequently brilliant metallic. **Male.** Distal process of labrum frequently present. Apical margins of S4–S5 frequently modified.

#### Genus Andinaugochlora Eickwort

Andinaugochlora Eickwort, 1969a: 407. Type species: Andinaugochlora micheneri Eickwort, 1969a, monobasic and original designation.

DIAGNOSIS: Species of Andinaugochlora superficially resemble larger species of the more widely distributed genus Neocorynura and even more similarly the related genus Neocorynurella. From the former group, Andinaugochlora can be separated by the broadly rounded mesoscutal anterior border and the obsolescent anterior border to the metabasitibial plate, while from the latter genus it differs in these same characters and also by the nearly orthogonal epistomal sulcus and carinate preoccipital ridge.

DESCRIPTION: **Female.** Mandible with strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending nearly to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus nearly orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex neither

expanded nor ridged behind ocelli. Preoccipital ridge carinate. Pronotal lateral angle not produced and obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered posteriorly, margin obsolete anteriorly. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum granular; propodeal pit narrow. Male. Mandible simple. Labrum with weak distal process; basal area not notched. Antenna long, extending beyond propodeum; scape short; F2 longer than F1. Metasoma elongate. Apical margins of S4 and S5 straight, unmodified. Apical margin of S6 emarginate. Apical margins of S7 and S8 with medial projections; spiculum broad. Proctiger unmodified. Gonobasal bridge narrow, dorsal lobes strong. Basal process of gonostylus and parapenial lobe absent. Ventral surface of penis valve with prong.

REVISIONS: The genus has not been revised. There are presently two named species, *Andinaugochlora joannisi* (Vachal) and *A. micheneri* Eickwort, along with at least four undescribed species (personal obs.).

DISTRIBUTION: The genus is found in Colombia, Ecuador, and Peru. Based on the available collection information, species seem to be restricted to montane regions. An undescribed species has recently been identified from high altitude localities in Costa Rica (personal obs.). This species will be described at a later date by the author.

#### Genus Ariphanarthra Moure

Ariphanarthra Moure, 1951: 137. Type species: Ariphanarthra palpalis Moure, 1951, monobasic and original designation.

DIAGNOSIS: This monotypic genus resembles the nocturnal genus *Megaloptidia* in its head structure, both having the face slightly concave around the antennal sockets and the greatly narrowed and elongate prementum. *Ariphanarthra*, however, is not nocturnal, with dark integumental pigmentation and normal-sized ocelli. The genus is remarkable for the elongate maxillary palpi that in repose extend posteriorly to the metasoma, a feature unique among the Augochlorini.

DESCRIPTION: Female. Mandible with moderately strong subapical tooth. Labral distal process broadly triangular; basal elevation orbicular; teeth absent. Prementum greatly elongate; maxillary palpus elongate, extending posterad to metasoma. Galeal apex pointed, comb absent. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex short, barely as long as diameter of median ocellus. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate with well-developed borders. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum with weak basal striae. Male. Mandible simple. Labrum without distal process; basal area not notched. Antennae extending posterad to scutellum; F1 longer than F2. Inner hind tibial spur serrate. Metasoma oval. S4 unmodified. Apical margin of S5 weakly emarginate. Apical margin of S6 emarginate. Apical margins of S7 and S8 unmodified; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe of gonostylus present; basal process absent; dorsal process large and membranous. Ventral surface of penis valve with prong.

REVISIONS: At present Ariphanarthra contains only the type species. Moure (1951) presents a thorough description of the species.

BIOLOGY: Moure (1951) suggested that *Ar*iphanarthra may be crepuscular even though specimens have been captured only during the day and nothing about its morphology suggests this habit. Nothing is presently known of *Ariphanarthra* biology.

DISTRIBUTION: Ariphanarthra has an extensive range along the western half of South America. Individuals of A. palpalis Moure are recorded from northern Argentina, southern Brazil, Paraguay, Peru, as well as southern Colombia (Engel, 1996c).

#### Genus Augochlora Smith

DIAGNOSIS: This large, diverse group is second only to the genus *Augochloropsis* in number of recorded species. *Augochlora* is most similar to the genera *Augochlorella*, *Ceratalictus*, and *Pereirapis*. It can be distinguished from them all, however, by the acute epistomal sulcus that forms a lobe protruding into the basal margin of the clypeus.

DESCRIPTION: Female. Lateral margins of labral distal process with strong teeth. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent. Hypostomal ridge carinate; anterior angle pointed or produced into a short tubercle. Length of malar space less than basal mandibular width. Epistomal sulcus acute, protruding into clypeus. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not ridged behind ocelli. Preoccipital ridge carinate among living species (rounded in one extinct species: see below under subgenus Electraugochlora). Pronotal lateral angle produced, acute to obtuse; dorsal ridge carinate; lateral ridge angled, but distinctly not carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate with well-developed borders. Inner hind tibial spur serrate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum striate or rugose. S1 frequently bearing anterior median ridge or spine. Male. Mandible simple. Labrum without distal process; basal area not notched. Antennae of moderate length, extending posterad to scutellum; F2 length approximately equal to F1. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 unmodified. Apical margin of S6 usually emarginate (a few species are unmodified). Apical margins of S7 and S8 with median projection; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe absent; basal process present; dorsal process reduced to strong ridge with setae. Ventral surface of penis valve with prong.

**REVISIONS:** Refer to subgeneric treatments.

Michener (1954b) gave a key to the Panamanian species and Cockerell (1897b) provided a key to the Mexican species; however, this latter key is somewhat out of date and should be used with caution. Neither of these keys utilize the currently recognized subgeneric groupings and species identities should, therefore, be cross-referenced with Moure and Hurd (1987) for subgeneric associations and appropriate synonymies.

> Subgenus Augochlora Smith s.s. Figures 17, 41, 43, 48, 58

- *Augochlora* Smith, 1853: 73. Type species: *Halictus purus* Say, 1837, designated by Cockerell (1923).
- Oxystoglossa Smith, 1853: 83. Type species: Oxystoglossa decorata Smith, 1853, monobasic.
- Angochlora Schrottky, 1901: 212. Lapsus calami.
- Odontochlora Schrottky, 1909a: 141. Type species: Augochlora mulleri Cockerell, 1900 [= Augochlora muelleri Schrottky, 1909a, nomen emendatum (unjustified)], original designation.
- Oxystoglosss Moure, 1940: 57. Lapsus calami.
- *Odontochlor* Mitchell, 1960: 456. Lapsus calami. *Auglochlora* Dodson, 1967: 6. Lapsus calami.
- Augochlora (Mycterochlora) Eickwort, 1969a: 423. Type species: Halictus repandirostris Vachal, 1911, original designation. NEW SYN-ONYMY.

DIAGNOSIS: The nominate subgenus is most easily separated from the other subgenera by the strongly bidentate mandible and the transverse basal elevation on the labrum.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible strongly bidentate. Labral distal process usually narrowly triangular (a few species have broadly triangular processes); basal elevation transverse, protuberant. Angle of epistomal sulcus strongly protruding into clypeus. Pre-occipital ridge carinate. **Male.** Ridge bordering ventral gonostylar process with short setae, not surpassing gonostylar apex.

REVISIONS: There has been no revision of *Augochlora* s.s. Moure and Hurd (1987) listed 85 described species, although one, *Augochlora essequibensis* Cockerell, is newly synonymized with *A. nigrocyanea* Cockerell below (appendix 1). Three previously unplaced species have been recently transferred to this subgenus (Moure, 1999).

BIOLOGY: Species of Augochlora are soli-

tary and form nests in rotting wood (Eickwort and Eickwort, 1973b; Stockhammer, 1966). Immature stages have been described by Michener (1953, 1954a) and Eickwort and Eickwort (1973b) (table 2).

DISTRIBUTION: This subgenus has the greatest distribution of any augochlorine group. Species range from northern Argentina to southern Canada and into the West Indies.

## *Electraugochlora,* new subgenus Figures 79–81

TYPE SPECIES: Augochlora (Electraugochlora) leptoloba, new species (described in appendix 1).

DIAGNOSIS: This monotypic subgenus is unique among *Augochlora* species in the absence of a preoccipital carina, instead having an entirely rounded preocciptal area (a derived feature among the enitre *Augochlora*group of genera). The acute epistomal sulcus places it among *Augochlora*, but the lobe is very small, in this way differing from living species of the genus. The orbicular basal elevation on the labrum is similar to *Oxystoglossella*, but in this subgenus the elevation is strongly protuberant. Further details of this groups morphology are presented below as well as in appendix 1, where the type species is described.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible with moderate subapical tooth. Labral basal elevation orbicular, low and not protuberant (figs. 80, 81). Angle of epistomal sulcus only weakly protruding into clypeus (figs. 80, 81). Preoccipital ridge rounded. S1 without median ridge or spine. **Male.** Unknown.

ETYMOLOGY: The new generic name is a combination of *electrum* (L. amber) and the genus *Augochlora*, type genus of the tribe.

REVISIONS: There is only the one included species (described in appendix 1).

DISTRIBUTION: Presently known only from Miocene Dominican amber.

## Subgenus Oxystoglossella Eickwort

- *Augochlora (Oxystoglossella)* Eickwort, 1969a: 422. Type species: *Augochlora cordiaefloris* Cockerell, 1907, original designation.
- *Augochlora (Aethechlora)* Moure and Hurd, 1987: 275. Type species: *Augochlora matucanensis*

Cockerell, 1914, monobasic and original designation. NEW SYNONYMY.

DIAGNOSIS: *Oxystoglossella* differs from *Augochlora* s.s. by the less bidentate mandibular apex and orbicular basal elevation on the labrum. From *Electraugochlora* it differs in the presence of a preoccipital carina and a strong epistomal lobe.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible with moderate to strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular, protuberant. Angle of epistomal sulcus strongly protruding into clypeus. Preoccipital ridge carinate. **Male.** Ridge bordering ventral gonostylar process with long setae, greatly surpassing gonostylar apex.

REVISIONS: The species of *Oxystoglossella* have not been revised. Moure and Hurd (1987) listed 28 described species, although two of these have since been synonymized (Engel, 1996c) and a new species is described in appendix 1.

BIOLOGY: Oxystoglossella species are primitively eusocial and excavate nests in the soil (Eickwort and Eickwort, 1972). The mature larva and pupa have been described for A. cordiaefloris Cockerell and A. nominata Michener (Eickwort and Eickwort, 1972) (table 2).

DISTRIBUTION: *Oxystoglossella* has a wide distribution; species occur from Argentina to the southwestern United States and east into the West Indies.

## Genus Augochlorella Sandhouse

*Augochlorella* Sandhouse, 1937: 66. Type species: *Augochlora gratiosa* Smith, 1853, original designation.

Oxystoglossidia Moure, 1943a: 473. Type species: Oxystoglossidia uraniella Moure, 1943a [= Oxystoglossa ephyra Schrottky, 1911], original designation.

DIAGNOSIS: This genus can be separated from other members of the Augochloragroup (*Augochlora*, *Ceratalictus*, and *Pereirapis*) by the combination of an orthogonal epistomal sulcus, the acute marginal cell apex, and the absence of a large basal lobe on the inner metatibial spur.

DESCRIPTION: Female. Mandible with

weak subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular to transverse; teeth weak. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex neither expanded nor ridged behind ocelli. Preoccipital ridge carinate. Pronotal lateral angle not produced, orthogonal to obtuse; dorsal ridge carinate; lateral ridge angled, but distinctly not carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate with well-developed borders. Inner hind tibial spur serrate. Apex of marginal cell apex acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum striate, rugose, or granular. Male. Mandible simple. Labrum with distal process; basal area not notched. Antenna extending back to scutellum; F2 shorter than F1. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margins of S7 and S8 with median processes; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes variously produced. Parapenial lobe and basal process of gonostylus absent; ventral process divided; dorsal process variously constructed, a large partially membranous or sclerotized flange. Ventral surface of penis valve with prong.

REVISIONS: The species of Augochlorella occurring in the United States and Mexico have been revised by Ordway (1966b). A new revision of the genus, including the South American species, is currently under preparation (B. Coelho, in prep.). Moure and Hurd (1987) listed sixteen extant species; however, their Augochlorella cladopyga (Cockerell) is a junior synonym of Pereirapis semiaurata (Spinola) (see appendix 1).

BIOLOGY: Species of *Augochlorella* are primitively eusocial and nest in the soil (Eickwort and Eickwort, 1973a; Knerer, 1968; Knerer and Atwood, 1962, 1966; Ordway, 1961, 1964, 1966a; Sakagami and Moure, 1967). One species, *A. striata* (Provancher), has been the focus of a number of studies concerning nestmate relatedness (Mueller, 1991, 1996; Mueller et al., 1994) and social development (Ordway, 1965; Packer, 1990). The mature larva and pupa have been described for *A. edentata* Michener by Eickwort and Eickwort (1973a) (table 2).

DISTRIBUTION: Species of Augochlorella are distributed from northern Argentina to southern Canada. No species occur in the West Indies.

## Genus Augochlorodes Moure

Augochlorodes Moure, 1958a: 53. Type species: Augochlorodes turrifaciens Moure, 1958a, monobasic and original designation.

Augochlorocles Sakagami, 1979: 83. Lapsus calami.

DIAGNOSIS: Augochlorodes is similar to the genera of the Augochlora-group (Augochlora, Augochlorella, Ceratalictus, and Pereirapis) but differs by the pectinate inner metatibial spur and the rounded preoccipital ridge.

DESCRIPTION: Female. Mandible with moderately developed subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth weak. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate with well-developed borders. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum weakly striate basally; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area not notched. Antenna extending back to scutellum; F2 length approximately equal to F1. Inner hind tibial spur serrate. Metasoma elongate. Apical margin of S4 produced laterally, with long setae. Apical margin of S5 unmodified, with dense medial patch of setae. Apical margin of S6 weakly emarginate.

Apical margin of S7 with median process. Apical margin of S8 unmodified; spiculum broad. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes weak. Parapenial lobe and basal process of gonostylus absent; dorsal process large and weakly sclerotized. Ventral surface of penis valve with prong.

REVISIONS: At present there is only the one included species.

BIOLOGY: The biology of the type species was studied by Michener and Seabra (1959). This species nests in the soil and is apparently semisocial.

DISTRIBUTION: *Augochlorodes* is currently known only from southern Brazil.

#### Genus Augochloropsis Cockerell

DIAGNOSIS: This is the most speciose genus of the tribe. *Augochloropsis* s.l. can be quickly identified by the presence of a notch on the inner, posterior margin of the tegula as well as the pectinate inner metatibial spur and the lamellate pronotal dorsal ridge.

DESCRIPTION: Female. Mandible with moderate to strong subapical tooth. Labral distal process quadrate; basal elevation bilobed; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Pronotal lateral angle produced, orthogonal to obtuse; dorsal ridge lamellate; lateral ridge rounded to angled. Tegula with inner posterior border notched. Anterior basitarsal brush present. Basitibial plate bordered on all sides, extremely short. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Male. Mandible simple. Labrum without distal process; basal area not notched. Antennae extending back to scutellum; F2 approximately equal in length to F1. Inner hind tibial spur serrate. Metasoma oval. Apical margin of S4 produced laterally, with setae at apices of projections, also produced medially. Apical margin of S6 emarginate. Apical margin of S7 and S8 with median process, that of S8 usually bilobed; spiculum broad. Proctiger unmodified. Gonobasal bridge narrow, or completely membranous; dorsal lobes strong. Basal process of gonostylus and parapenial lobe absent; ventral process with long, thin process. Ventral surface of penis valve with keel. Volsella with inner apical angle produced into thin projection.

REVISIONS: There is no revision of any *Augochloropsis* subgenus, and many species are not placed to subgenus. Excluding the four species placed in the subgenus *Glyptochlora* (although one placed there only provisionally), there are 134 species listed by Moure and Hurd (1987) as belonging to *Augochloropsis* and *Paraugochloropsis*. Since the time of their catalog two species of *Paraugochloropsis* have been synonymized (Engel, 1996c) and a third has been newly transferred to the genus bringing the total specific diversity of the genus to 133.

BIOLOGY: The nesting biology of species in this genus have been studied by several authors (Gimenes et al., 1991; Michener and Lange, 1959; Michener and Seabra, 1959; Sakagami and Moure, 1967; Smith, 1901). All are soil nesters and are presumably communal. The peculiar quadrate pollen masses serve as an ethological synapomorphy for the genus.

DISTRIBUTION: The genus ranges from Argentina to southern Canada, although the three species occurring in the United States and Canada belong to the subgenus *Paraugochloropsis*. Species are known from the island of Trinidad, but do not occur in the West Indies.

#### Subgenus Augochloropsis Cockerell s.s.

- Augochlora (Augochloropsis) Cockerell, 1897b:
  4. Type species: Augochlora (Augochloropsis) subignita Cockerell, 1897a [= Augochlora ignita Smith, 1861], original designation.
- Angochlora (Angochloropsis) Schrottky, 1901: 213. Lapsus calami.
- Augochlora (Auhochloropsis) Moure, 1940: 45. Lapsus calami.
- Augochlora (Autochloropsis) Moure, 1940: pl. 2. Lapsus calami.
- Augoschloropsis Moure, 1943b: 197. Lapsus calami.
- Auochloropsis Roubik, 1989: 392. Lapsus calami.

DIAGNOSIS: Among the subgenera of Au-

*gochloropsis*, the nominate subgenus is most similar to *Paraugochloropsis* from which it can be separated by the presence of striae on the basal area of the propodeum.

DESCRIPTION: As for the genus with the following additions: **Female.** Vertex not greatly shortened, longer than diameter of median ocellus. Preoccipital ridge carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Basal area of propodeum striate. **Male.** Apical margin of S5 emarginate.

REVISIONS: See the account of the genus. BIOLOGY: See the account of the genus.

DISTRIBUTION: See the account of the genus.

# Subgenus *Glyptochlora* Moure, **revised** status

*Augochloropsis* (*Glyptochlora*) Moure, 1958b: 188. Type species: *Megalopta ornata* Smith, 1879, original designation.

DIAGNOSIS: The species of *Glyptochlora* are the most distinctive among all *Augochloropsis* species. The coarse punctation of the body resembles to some degree that of the cleptoparasitic genus *Temnosoma*. The extremely short vertex, sharply carinate preoccipital ridge, and the strongly narrowed and lamellate anterior border of the mesoscutum separate *Glyptochlora* from all other *Augochloropsis*.

DESCRIPTION: As for the genus with the following additions: **Female.** Head and mesosoma coarsely punctured. Vertex short, barely one ocellar diameter in length. Preoccipital ridge strongly carinate and coming to a sharp angle. Mesoscutal anterior border narrowed; mesoscutal lip lamellate. Basal area of propodeum strongly striate. **Male.** Unknown.

REVISIONS: At present *Glyptochlora* contains three species, *A. atropos* (Smith), *A. ornata* (Smith), and *A. refulgens* (Smith), which are identified by the key provided below. A fourth species, *A. cyclis* (Vachal), has been referred to this subgenus by Moure and Hurd (1987). This last species is included here only provisionally until further work can be done on the subgenus. *Glyptochlora* might eventually be recognized at the generic level, should the male exhibit additional striking differences from *Paraugochloropsis* and *Augochloropsis* s.s.

DISTRIBUTION: All three species are known only from northwestern Brazil (Amazonas, São Paulo de Olivença), while the uncertain species, *A. cyclis*, is from Peru. Unidentified material of *Glyptochlora* has recently been collected in French Guiana (R. W. Brooks, personal commun.).

#### KEY TO THE SPECIES OF AUGOCHLOROPSIS (GLYPTOCHLORA)

- Metasomal T1–T2 with conspicuous apical fringe of setae ..... atropos (Smith)
- Basal area of propodeum not encircled by a strong carina ..... *refulgens* (Smith)
  - Subgenus *Paraugochloropsis* Schrottky Figures 34, 68
- Augochloropsis (Paraugochloropsis) Schrottky, 1906: 312. Type species: Augochloropsis (Paraugochloropsis) lycorias Schrottky, 1906 [= Augochlora epipyrgitis Holmberg, 1903], monobasic.
- Augochloropsis (Pseudaugochloropsis) Schrottky, 1906: 313. Type species: Augochloropsis (Pseudaugochloropsis) sthena Schrottky, 1906, designation of Sandhouse (1943). The designation of Halictus nigromarginatus Spinola, 1841 [= Megilla graminea Fabricius, 1804], as the type by Schrottky (1909b) and supported by Moure (1944) is erroneous as it was not an originally included species (Sandhouse, 1943; Michener, 1954b, 1994).
- *Augochlora (Tetrachlora)* Schrottky, 1909b: 481. Type species: *Halictus multiplex* Vachal, 1903, monobasic.
- Paraugochlora Schrottky, 1910: 540. Type species: Augochlora spinolae Cockerell, 1900, original designation.
- Rivalisia Strand, 1921: 270. Type species: Rivalisia metallica Strand, 1921 [= Augochloropsis (Paraugochloropsis) aenigma Engel, 1996c], monobasic.
- Augochlora (Glyptobasis) Moure, 1940: 48. Type species: Augochlora (Glyptobasis) chloëra Moure, 1940, original designation. Nomen praeoccupatum [nec Glyptobasis M'Lachlan, 1871 (Neuroptera: Ascalaphidae) and others].

*Glyptobasia* Moure, 1941: 98. *Nomen novum pro Glyptobasis* Moure, 1940. Type species: autobasic with *Glyptobasis* Moure, 1940.

Tetrachlor Mitchell, 1960: 463. Lapsus calami.

DIAGNOSIS: See Diagnosis for Augochloropsis s.s.

DESCRIPTION: As for the genus with the following additions: **Female.** Vertex not greatly shortened, longer than diameter of median ocellus. Preoccipital ridge carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Basal area of propodeum rugulose or granular. **Male.** Apical margin of S5 unmodified.

REVISIONS: See the account of the genus.

BIOLOGY: See the account of the genus.

DISTRIBUTION: See the account of the genus.

#### Genus Caenaugochlora Michener

DIAGNOSIS: Species of *Caenaugochlora* are similar in general appearance to those of the genus *Pseudaugochlora*; the later genus has, however, a strong ridge on the vertex and a pointed galeal apex. From the related genus *Augochloropsis*, *Caenaugochlora* differs in the absence of a notch on the tegula, the nonlamellate pronotal dorsal ridge, and the orthogonal epistomal sulcus.

DESCRIPTION: Female. Mandible with subapical tooth variously defined. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge angled or carinate. Pronotal dorsal ridge carinate; lateral ridge rounded to carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area notched. Antennae extending back to scutellum; F2 about as long as F1. Inner hind tibial spur serrate. Metasoma oval. Triangular setal patch on S4. Apical margins of S5 and S6 emarginate. Apical margin of S7 with median projection. Spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes weak. Basal process of gonostylus and parapenial lobe absent; dorsal process partly membranous. Ventral surface of penis valve with prong.

### Subgenus *Caenaugochlora* Michener s.s. Figure 60

*Caenaugochlora* Michener, 1954b: 76. Type species: *Caenaugochlora macswaini* Michener, 1954b, original designation.

Coenaugochlora Michener, 1954b: 85. Lapsus calami.

DIAGNOSIS: *Caenaugochlora* s.s. is distinguished from *Ctenaugochlora* by the normal pectination of the inner metatibial spur, frequent presence of long compound eye hairs, strong anterior border of the basitibial plate, and propodeal striae not reaching to the apical margin.

DESCRIPTION: As for the genus with the following additions: **Female.** Compound eyes usually with long hairs. Pronotal lateral angle usually produced, angle slightly acute to obtuse. Basitibial plate with well-developed borders. Inner hind tibial spur pectinate. Basal area of propodeum with basal striae, not reaching apical margin. **Male.** Apical margin of S4 concave, with dense setal patches raised on tubercles toward apex. Apical margin of S8 with median projection, sometimes bilobed at apex. Volsella indented on inner margin.

REVISIONS: There has been no revision of *Caenaugochlora* species. At the present time, there are 15 described species in the subgenus, but many more await study.

BIOLOGY: The soil-nesting biology of *Cae-naugochlora costaricensis* (Friese) was studied by Michener and Kerfoot (1967: as a species of *Pseudaugochloropsis*), this species is possibly semisocial.

DISTRIBUTION: *Caenaugochlora* ranges from Colombia to Mexico. No species are known to occur in the West Indies.

#### Subgenus Ctenaugochlora Eickwort

Caenaugochlora (Ctenaugochlora) Eickwort, 1969a: 435. Type species: Neocorynura perpec-

*tinata* Michener, 1954b, monobasic and original designation.

DIAGNOSIS: Refer to Diagnosis for *Caenaugochlora* s.s.

DESCRIPTION: As for the genus with the following additions: **Female.** Compound eyes with minute hairs. Pronotal lateral angle not produced, obtuse. Basitibial plate bordered posteriorly, margin obsolete anteriorly. Inner hind tibial spur densely pectinate, with more than 10 long teeth. Basal area of propodeum with strong striae radiating from basal margin to apex. **Male.** Apical margin of S4 concave, dense triangular setal patch, patch not raised on tubercles. Apical margin of S8 unmodified. Inner margin of volsella rounded.

REVISIONS: There has been no revision of *Ctenaugochlora*, although Engel (1995a) provided a key to the four described species.

DISTRIBUTION: *Ctenaugochlora* is currently known from Costa Rica and Panama al-though undescribed species occur in Trinidad and Mexico (personal obs.).

### Genus Ceratalictus Moure

*Ceratalictus* Moure, 1943a: 463. Type species: *Oxystoglossa theia* Schrottky, 1911 [= Augo*chlora clonia* Brèthes, 1909], original designation.

Ceratilictus Roubik, 1989: 392. Lapsus calami.

DIAGNOSIS: This genus is most similar to *Augochlorella* and it may be prudent in the future to consider *Ceratalictus* a junior synonym of the former. *Ceratalictus* can be separated from *Augochlorella* by the obtuse epistomal sulcus and the obsolescent anterior border of the basitibial plate.

DESCRIPTION: **Female.** Mandible with moderately developed subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth weak. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge carinate. Pronotal lateral angle produced, acute; dorsal ridge carinate; lateral ridge angled. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered posteriorly, margin obsolete anteriorly. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum striate; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area not notched. Antennae extending back to scutellum; F1 about as long as F2. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 unmodified. Apical margin of S8 with median process; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe present; basal process of gonostylus present; ventral process divided. Ventral surface of penis valve with prong.

REVISIONS: The genus has not been revised. At present there are six recognized species (Moure and Hurd, 1987; Moure, 1999). Moure (1999) recently synonymized the type species, *Ceratalictus theius* (Schrottky), with *C. clonius* (Brèthes).

DISTRIBUTION: The genus occurs in southern Brazil, Bolivia, Paraguay, and southeastern Peru.

#### Genus Chlerogas Vachal

*Chlerogas* Vachal, 1904: 127. Type species: *Halictus chlerogas* Vachal, 1904, monobasic and absolute tautonymy.

DIAGNOSIS: The elongate heads produced by a greatly lengthened malar space serves to separate *Chlerogas* from other Augochlorini except the genera *Chlerogella* and *Ischnomelissa*. The genera, however, are not related and although *Chlerogas* resembles the latter two in the structure of the head, this genus is unique for the pectinate inner hind tibial spur of the male, the reduced flagellomere count, the shorter propodeal basal area, and the larger body sizes.

DESCRIPTION: **Female.** Mandible with moderately defined subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to

base of stipes. Hypostomal ridge carinate; anterior angle rounded. Malar space much longer than basal mandibular width. Epistomal sulcus very slightly acute, only a little less than 90°. Flagellum with only 9 flagellomeres. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge angled. Pronotal lateral angle not produced, obtuse; dorsal ridge angled; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate border on all sides. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum about as long as scutellum, granular or striate; propodeal pit narrow. Male. Mandible simple. Labrum with short distal process; basal area not notched. Antennae long, extending back to propodeum; flagellum with only 10 flagellomeres. Inner hind tibial spur pectinate. Metasoma elongate. Apical margins of S4-S5 concave. Apical margin of S6 emarginate. Apical margin of S7 with median projection. Apical margin of S8 with median projection; spiculum broad. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes moderately developed. Parapenial lobe and basal process of gonostylus absent; dorsal process a large lightly melanized mass. Volsella indented on inner margin at base of digitus; digitus sometimes elongated apically. Ventral surface of penis valve unmodified.

REVISIONS: The genus has recently been revised by Brooks and Engel (1999) who recognize nine species.

BIOLOGY: Nothing is known of *Chlerogas* biology, although Brooks and Engel (1999) speculated that the elongate heads are an adaptation for tubular flowers.

DISTRIBUTION: Species of *Chlerogas* are found throughout northern South America, although the range of any single species is seemingly restricted. Species are known from the mountains of Bolivia, Colombia, Ecuador, Peru, and Venezuela.

### Genus *Chlerogella* Michener Figures 4, 37, 39, 46, 50

*Chlerogella* Michener, 1954b: 75. Type species: *Chlerogella elongaticeps* Michener, 1954b, monobasic and original designation. DIAGNOSIS: The genus *Chlerogella* is most similar and closely related to the genera *Chlerogelloides* and *Ischnomelissa*, sharing with these genera the elongate propodeum. From the former *Chlerogella* differs in the elongate malar space, the pectinate inner metatibial spur, strong basitibial plate, and in the structure of the epistomal sulcus; while from the later genus *Chlerogella* differs in the normal pectinations of the inner metatibial spur, the acute epistomal sulcus, and the inflated dorsal surface of the pronotum.

DESCRIPTION: Female. Mandible with moderately developed subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular to bilobed; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space as long as or frequently longer than basal mandibular width. Epistomal sulcus acute. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal dorsal surface frequently inflated, rendering lateral ridge and angle obsolete; dorsal ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip absent. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum longer than scutellum, smooth to granular; propodeal pit narrow. Male. Mandible simple. Labrum without distal process; basal area not notched. Antennae long, extending back to posterior border of propodeum; F2 longer than F1. Inner hind tibial spur serrate. Metasoma elongate. Apical margin of S4 emarginate. Apical margin of S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 with median projections. Apical margin of S8 with median projection; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes weak. Parapenial lobe and basal process of gonostylus absent. Ventral surface of penis valve with prong.

REVISIONS: A revision of *Chlerogella* is being completed by Brooks and Engel (in prep.) and currently recognizes 17 species (15 new to science), although one, *Chlero*-

*gella bouyssoni* (Vachal), is uncertainly placed in the absence of the holotype (Engel, personal obs.).

BIOLOGY: The biology of *Chlerogella* remains undiscovered. The elongate heads may indicate an association with flowers possessing deep corollas similar to that hypothesized for species of *Chlerogas* (Brooks and Engel, 1999).

DISTRIBUTION: Species of *Chlerogella* are distributed throughout southern Central America and northern South America. Their range includes mountainous regions of the following countries: Bolivia, Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela.

### Genus *Chlerogelloides* Engel, Brooks, and Yanega

*Chlerogelloides* Engel, Brooks, and Yanega, 1997: 3. Type species: *Chlerogelloides femo-ralis* Engel, Brooks, and Yanega, 1997, monobasic and original designation.

DIAGNOSIS: This genus is remarkably similar to *Chlerogella*; both having the peculiar inflation of the pronotal dorsal surface. *Chlerogelloides*, however, has a deeply acute epistomal sulcus protruding into the basal margin of the clypeus such that the epistomal lobe nearly reaches to the clypeal apex. In addition, *Chlerogelloides* has a serrate inner metatibial spur and a short malar space.

DESCRIPTION: Female. Mandible with strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular and weak; lateral teeth absent. Prementum greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge feebly carinate on anterior half, carina disappearing on posterior half; anterior angle rounded. Malar space less than basal mandibular width. Epistomal sulcus acute, projecting deeply into clypeus as a thin line nearly reaching clypeal apex. Ocelli not greatly enlarged; ocellar furrow absent. Vertex short, approximately one ocellar diameter in length. Preoccipital ridge rounded. Pronotal dorsal surface inflated, lateral angle feebly present and obtuse; lateral ridge absent; dorsal ridge rounded. Mesoscutal anterior border weakly narrowed; mesoscutal lip absent. Tegula oval. Anterior

basitarsal brush absent. Basitibial plate represented by slightly elevated glabrous region. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum longer than scutellum and metanotum combined, smooth; propodeal pit narrow. Male. Mandible simple, with strong double curve towards apex. Labral basal elevation absent; distal process absent. Antenna short, extending posteriorly to mesoscutum; F1 longer than F2. Inner hind tibial spur serrate. Metasoma elongate. S3-S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 with bilobed projection. Apical margin of S8 with median projection; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes weak. Gonostylus without basal process; parapenial lobe present. Venter of penis valve with prong.

REVISIONS: The genus presently contains two species that have been revised by Engel and Brooks (1999b).

BIOLOGY: Nothing is known of *Chlerogelloides* biology, although the peculiarly modified midlegs of the type species, *C. femoralis*, are likely involved in mating.

DISTRIBUTION: Individuals of the type species have been collected in Colombia, Ecuador, and Peru, whereas the second species occurs in French Guiana (Engel and Brooks, 1999b).

#### Genus Ischnomelissa Engel

*Ischnomelissa* Engel, 1997b: 42. Type species: *Ischnomelissa zonata* Engel, 1997b, monobasic and original designation.

DIAGNOSIS: This group is similar to the more diverse genus *Chlerogella*, both genera having an elongate propodeum and a frequently elongate malar space that makes the head much longer than wide. *Ischnomelissa* differs by a densely pectinate inner metatibial spur, an orthogonal epistomal sulcus, and a pronotum that is not dorsally inflated.

DESCRIPTION: **Female.** Mandible with moderately developed subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate; an-

terior angle rounded. Length of malar space usually less than basal mandibular width, except in some species in which the length is equal to the basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge angled, but distinctly not carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate border posteriorly, margin obsolete anteriorly. Inner hind tibial spur densely pectinate, with more than 10 teeth. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum as long as or longer than scutellum and metanotum combined, nonstriate, smooth; propodeal pit narrow. Male. Mandible simple. Labrum without distal process; basal area not notched. Antenna long, extending beyond posterior border of propodeum; F1 much shorter than F2. Inner hind tibial spur serrate. Metasoma elongate. S3-S5 unmodified. Apical margin of S6 cleft. Apical margin of S7 with short median process. Apical margin of S8 with median process; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes weak. Basal process of gonostylus and parapenial lobes absent; gonostylus not divided into ventral and dorsal gonostylar processes. Ventral surface of penis valve with prong.

REVISIONS: The genus has recently been revised by Brooks and Engel (1998) who recognize six species.

DISTRIBUTION: Species are known from Colombia and Ecuador.

## Genus Megalopta Smith

DIAGNOSIS: This is a large genus of nocturnal bees exhibiting the typical characters of large ocelli and pale integumental pigmentation. *Megalopta* is related to the genus *Xenochlora*, but this group has normal-sized ocelli, lacks the densely packed, single series of distal hamuli, and has stiff, black setae on the hindlegs. Among the other nocturnal genera, *Megaloptidia* and *Megommation*, *Megalopta* lacks the strongly narrowed and elongate prementum and the pointed galeal apex. The pectinate inner metatibial spur and densely packed hamuli can also separate *Megalopta* from other nocturnal augochlorines.

DESCRIPTION: Female. Labral distal process broadly triangular; keel expanded basally; basal elevation bilobed; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate to weakly lamellate; anterior angle rounded. Malar space less than basal mandibular width. Epistomal sulcus acute, gently projecting into clypeus. Ocelli greatly enlarged; ocellar furrow present. Vertex expanded behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced; dorsal ridge rounded; lateral ridge carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli closely and evenly spaced. Basal area of propodeum smooth or striate, strongly declivitous; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area not notched. Antennae extending back to scutellum, metanotum, or propodeal triangle; F2 much longer than F1. Inner hind tibial spur serrate. Apical margin of S4 emarginate medially, with lateral notches, setal patches bordering emargination. Apical margin of S5 emarginate, medial surface with tubercle fitting into emargination of S4. Apical margin of S6 emarginate. Apical margin of S7 with median process bilobed. Apical margin of S8 unmodified; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes weak. Parapenial lobe present; basal process of gonostylus absent. Ventral surface of penis valve with prong.

### Subgenus *Megalopta* Smith s.s. Figures 6, 11, 16, 19, 36, 59, 66, 70, 73

Megalopta Smith, 1853: 83. Type species: Megalopta idalia Smith, 1853 [= Halictus amoenus Spinola, 1853], designation of I.C.Z.N. (1966), petition by Michener and Moure (1964). Designation of Megalopta bituberculata Smith, 1853, as the type species by Cockerell (1900) and Meade-Waldo (1916) is invalid.
Megaloptera Ashmead, 1899: 92. Lapsus calami. Megalopta (Megaloptella) Schrottky, 1906: 312.

Type species: *Halictus ochrias* Vachal, 1904, monobasic and original designation.

*Tmetocoelia* Moure, 1943a: 481. Type species: *Megalopta sulciventris* Friese, 1926, original designation.

DIAGNOSIS: The nominate subgenus differs from the cleptoparasitic species of *Noctoraptor* by the presence of scopal hairs, a basitibial plate, and the normally developed mandibles. The apical margin of the male clypeus is white and F2 is about as long as F3 in *Megalopta* s.s., while the clypeus is black and F2 is much shorter than F3 in *Noctoraptor*.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible multidentate, with supplementary teeth. Scopa present. Basitibial plate bordered posteriorly, margin obsolete anteriorly. **Male.** Apical margin of clypeus white. Scape anteriorly white; F2 approximately equal in length to F3. Metasoma oval to elongate. Apical margin of S5 narrowly emarginate.

REVISIONS: Friese (1926) revised the species of *Megalopta*, although he included species of *Megaloptidia* and *Megommation*. There has been no modern treatment of the genus. Moure and Hurd (1987) listed 28 species, although their *Megalopta ianthina* and *M. nigrofemorata* are species of *Xenochlora* and were transferred to that genus by Engel et al. (1997). *Megalopta intermedia*, listed by Sakagami (1979) is a nomen nudum (see append. 1).

BIOLOGY: Species of *Megalopta* are nocturnal. Individuals can be readily captured at lights just after dusk until just before dawn (personal obs.). Brief accounts of the nesting biology of two *Megalopta* species have been given by Sakagami (1964) and Janzen (1968), while accounts of their seasonal abundance and nocturnal activity are given by Wolda and Roubik (1986) and Roulston (1997) respectively. Immatures for two Panamanian species are currently being studied (Engel and Wcislo, in prep.), as are finer details of the nesting and social biology of these species (W. T. Wcislo, personal commun.).

DISTRIBUTION: *Megalopta* s.s. ranges from southern Brazil to Mexico.

### Subgenus *Noctoraptor* Engel, Brooks, and Yanega

Megalopta (Noctoraptor) Engel, Brooks, and Yanega, 1997: 12. Type species: Megalopta (Noctoraptor) byroni Engel, Brooks, and Yanega, 1997, original designation.

DIAGNOSIS: See Diagnosis for *Megalopta* s.s. (above).

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible long, scythe-shaped, without supplementary teeth. Scopa absent. Basitibial plate absent. **Male.** Apical margin of clypeus black. Scape anteriorly black; F2 approximately two-thirds length of F3. Metasoma elongate. Apical margin of S5 broadly emarginate.

REVISIONS: At present there are two species included in *Noctoraptor*; the type species and *M*. (*Noctoraptor*) *noctifurax* Engel et al.

BIOLOGY: *Noctoraptor* species are cleptoparasitic, based on their anatomy, presumably on other species of *Megalopta*.

DISTRIBUTION: The two known species occur in Panama (*M. byroni*) and Ecuador (*M. noctifurax*).

#### Genus Megaloptidia Cockerell

Megalopta (Megaloptidia) Cockerell, 1900: 373. Type species: Megalopta (Megaloptidia) contradicta Cockerell, 1900, monobasic and original designation.

DIAGNOSIS: This is a genus of moderately large, robust, nocturnal bees generally resembling the larger nocturnal genus *Megalopta*; they were at one time included as a subgenus. The genus can be readily separated from *Megalopta* by the narrowed, elongate prementum, the serrate inner metatibial spur, the enlarged compound eyes, and the irregularly spaced distal hamuli. Like most nocturnal bees, species are generally pale in coloration and have greatly enlarged ocelli.

DESCRIPTION: **Female.** Mandible with strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum greatly elongate. Galeal apex acute; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than

basal mandibular width. Epistomal sulcus orthogonal. Compound eyes greatly enlarged, reaching above vertex in profile. Ocelli greatly enlarged; ocellar furrow absent. Vertex short, barely one ocellar diameter in length. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge rounded; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur serrate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum granular, nonstriate; propodeal pit narrow. Male. Mandible simple. Labrum without distal process; basal elevation absent. Antenna extending to posterior border of mesoscutum; F2 shorter than F1. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 concave. Apical margin of S6 emarginate. Apical margin of S7 with bilobed median process. Apical margin of S8 with short median projection; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes strong. Basal process of gonostylus absent; parapenial lobe present. Ventral surface of penis valve with prong.

REVISIONS: *Megaloptidia* was revised by Engel and Brooks (1998) who recognized three species; *Megaloptidia contradicta* (Cockerell), *M. nocturna* (Friese), and *M. saulensis* Engel and Brooks.

BIOLOGY: Species of *Megaloptidia* are nocturnal and can be captured at lights. Nothing is known of their nesting or social biology. A female of *M. nocturna* has been captured at flowers of the monocotyledon *Dichorisandra ulei* (Commelinaceae) (Engel and Brooks, 1998).

DISTRIBUTION: The genus occurs in northern South America. Individuals are known from Brazil, Colombia, Ecuador, French Guiana, Peru, and Venezuela.

#### Genus Megaloptilla Moure and Hurd

- Megommation (Megaloptilla) Moure and Hurd, 1987: 241. Type species: Halictus callopis Vachal, 1911, monobasic and original designation.
- *Emgaloptilla* Moure and Hurd, 1987: vi. Lapsus calami.

DIAGNOSIS: The genus *Megaloptilla* is most similar to as well as most closely related to *Paroxystoglossa*. *Megaloptilla* can be separated from *Paroxystoglossa*, however, by a rounded preoccipital ridge, a transverse labral basal elevation, an acute marginal cell apex, and a very weakly narrowed anterior border of the mesoscutum.

DESCRIPTION: Female. Mandible bidentate, with weak supplementary teeth. Labral distal process narrowly triangular; basal elevation transverse; teeth weak. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridge behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate, weakly lamellate in some places; lateral ridge rounded. Mesoscutal anterior border slightly narrowed; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum subequal to scutellum, rugulose; propodeal pit narrow. Male. Mandible simple. Labrum without distal process; no elevation. Antenna extending back to scutellum; F2 longer than F1. Inner hind tibial spur serrate. Metasoma oval. Apical margin of S4 unmodified. Apical margin of S5 weakly emarginate. Apical margin of S6 emarginate. Apical margin of S7 with median projection. Apical margin of S8 with bilobed median projection; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes weak. Parapenial lobe and basal process of gonostylus absent. Ventral surface of penis valve unmodified.

REVISIONS: Engel and Brooks (1999a) have recently revised *Megaloptilla* and recognized two species: *Megaloptilla callopis* (Vachal) and *M. byronella* Engel and Brooks.

DISTRIBUTION: *Megaloptilla callopis* is recorded from Colombia, Ecuador, and Peru while the second species is presently known only from Panama.

## Genus Megommation Moure

DIAGNOSIS: This is a heterogenous group of taxa with strongly narrowed mouthparts (e.g., *Megaloptidia*, *Ariphanarthra*). *Megommation* in the broad sense can be most easily separated from these other genera by normalsized compound eyes (greatly enlarged in *Megaloptidia*) and normal maxillary palpi (greatly lengthened in *Ariphanarthra*). See also the diagnoses for *Megaloptidia*, *Ariphanarthra*, and *Micrommation*.

DESCRIPTION: Female. Labral distal process broadly triangular. Prementum greatly elongate. Galeal apex acute; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate to weakly lamellate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush absent. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Male. Mandible simple. Inner hind tibial spur serrate. Gonobasal bridge narrow; dorsal lobes strong. Apical margin of S6 emarginate. Proctiger with anal filaments. Basal process of gonostylus absent; parapenial lobe present; dorsal process of gonostylus partially membranous. Ventral surface of penis valve with prong.

> Subgenus *Cleptommation* Engel, Brooks, and Yanega Figures 3, 12, 13, 15, 32, 38, 45, 51

Megommation (Cleptommation) Engel, Brooks, and Yanega, 1997: 19. Type species: Megalopta minuta Friese, 1926, monobasic and original designation.

DIAGNOSIS: This cleptoparasitic subgenus can be quickly identified by the simple, bladelike mandibles (fig. 15), the absence of a basitibial plate, and the absence of a scopa. It is most similar to *Megaloptina*, both sharing the dense, plumose setae surrounding the propodeal spiracle in males. *Megaloptina*, however, is not parasitic and has a well-developed scopa, a basitibial plate, and normal mandibles. The serrate inner metatibial spur also distinguishes *Cleptommation* from *Me-galoptina*.

DESCRIPTION: As for the genus with the following additions: Female. Mandible simple, bladelike (fig. 15). Labral basal elevation absent; teeth absent. Clypeal apex relatively straight. Hypostomal ridge carinate. Ocelli not greatly enlarged. Pronotal dorsal ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Scopa absent. Basitibial plate absent. Inner hind tibial spur serrate. Male. Labrum without distal process; basal area not notched. Antenna extending back to scutellum or metanotum; F1 longer than F2. Dense patch of plumose setae at propodeal spiracle. Metasoma slightly elongate. Apical margins of S2 and S3 with slight median projection. Apical margins of S4 and S5 unmodified. Apical margins of S7 and S8 with median process.

REVISIONS: There is only one included species, although there may be a second species (R. W. Brooks, personal commun.; D. Yanega, personal commun.).

BIOLOGY: Based on the adult anatomy, *Cleptommation* is cleptoparasitic, perhaps on other species of *Megommation* (most likely *Megaloptina* or *Stilbochlora*).

DISTRIBUTION: *Cleptommation* occurs in Bolivia, Brazil, Costa Rica, Ecuador, Panama, and Peru.

# Subgenus *Megaloptina* Eickwort Figures 5, 12–13

Megommation (Megaloptina) Eickwort, 1969a: 441. Type species: Augochlora (Pseudaugochloropsis) ogilviei Cockerell, 1930, original designation.

DIAGNOSIS: This subgenus is most similar to *Cleptommation*, particularly in the male sex where both share the presence of dense, plumose setae surrounding the propodeal spiracle. *Cleptommation*, however, lacks a scopa, has a bladelike mandible, lacks a basitibial plate, and differs in the structure of the male metasomal sterna. *Megaloptina* differs from *Stilbochlora* in the presence of a propodeal tuft of setae in males and the short basitibial plate with weakly developed borders.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible with

moderate subapical tooth. Labral basal elevation orbicular; teeth weak. Clypeal apex concave (fig. 12). Hypostomal ridge carinate. Ocelli not greatly enlarged. Pronotal dorsal ridge rounded. Scopa present. Basitibial plate extremely short, borders faint. Inner hind tibial spur pectinate. Male. Labrum without distal process. Antenna extending back to scutellum; F1 longer than F2. Dense patch of plumose setae at propodeal spiracle. Metasoma oval. Apical margin of S2 unmodified. Apical margin of S3 with median projection. Apical margin of S4 unmodified. Apical margin of S5 emarginate. Apical margin of S7 with median projection. Apical margin of S8 unmodified.

REVISIONS: There are presently only two described species, *Megommation festivagum* (Dalla Torre) and *M. ogilviei* (Cockerell), and at least one undescribed species (personal obs.).

DISTRIBUTION: *Megaloptina* is known from Ecuador, Guyana, and Brazil.

Subgenus Megommation Moure s.s.

- Megommation Moure, 1943a: 479. Type species: Halictus insignis Smith, 1853, monobasic and original designation.
- Megammation Sakagami and Michener, 1962: 88. Lapsus calami.

DIAGNOSIS: This monobasic subgenus is nocturnal in habit and exhibits the typical features of nocturnal bees: pale integumental pigmentation and greatly enlarged ocelli. The nocturnal characters can readily distinguish *Megommation* proper from the other subgenera. This group can be easily confused with the related nocturnal genus *Megaloptidia*, but *Megaloptidia* has the compound eyes greatly enlarged and the marginal cell apex feebly truncate and appendiculate.

DESCRIPTION: As for the genus with the following additions: **Female.** Mandible with moderate subapical tooth. Labral basal elevation orbicular; teeth weak. Clypeal apex concave. Hypostomal ridge weakly lamellate on posterior half. Ocelli greatly enlarged. Pronotal dorsal ridge rounded. Scopa present. Basitibial plate extremely short, borders faint. Inner hind tibial spur serrate. **Male.** Labrum without distal process. Antenna extending back to scutellum; F1 longer than F2.

Metasoma oval. Apical margin of S2 unmodified. Apical margin of S3 with median projection. Apical margin of S4 with median projection. Apical margin of S5 emarginate. Apical margin of S7 with bilobed median projection. Apical margin of S8 unmodified.

REVISIONS: *Megommation* proper contains only the type species.

BIOLOGY: The nesting biology of *M. insigne* (Smith) was studied by Jörgensen (1912), Michener and Lange (1958b), and Sakagami and Moure (1967).

DISTRIBUTION: *Megommation insigne* occurs in northern Argentina, southern Brazil, and Paraguay.

Subgenus *Stilbochlora* Engel, Brooks, and Yanega

Megommation (Stilbochlora) Engel, Brooks, and Yanega, 1997: 15. Type species: Megommation (Stilbochlora) eickworti Engel, Brooks, and Yanega, 1997, monobasic and original designation.

DIAGNOSIS: Refer to Diagnosis for subgenus *Megaloptina* (above).

DESCRIPTION: As for the genus with the following additions: Female. Mandible with strong subapical tooth. Labral basal elevation orbicular; teeth weak. Clypeal apex relatively straight. Hypostomal ridge carinate. Ocelli not greatly enlarged. Pronotal dorsal ridge carinate. Scopa present. Basitibial plate not shortened, bordered posteriorly. Inner hind tibial spur pectinate. Male. Labrum with distal process, without basal elevation. Antenna extending back to scutellum; F2 longer than F1. Metasoma oval. Apical margins of S2 and S3 unmodified. Apical margin of S4 with median projection. Apical margin of S5 unmodified. Apical margin of S7 unmodified. Apical margin of S8 with median projection.

REVISIONS: There is only the one included species.

DISTRIBUTION: *Megommation eickworti* is found in Brazil, Bolivia, Colombia, Ecuador, and Peru.

#### Genus Micrommation Moure

Micrommation Moure, 1969: 247. Type species: Micrommation larocai Moure, 1969, monobasic and original designation.

DIAGNOSIS: This genus appears to be sim-

ilar to the nocturnal genus *Megaloptidia*; however, *Micrommation* does not have enlarged ocelli nor a feebly truncate marginal cell apex. Likewise, *Micrommation* is not nocturnal and has brilliant metallic-green integument, whereas *Megaloptidia* has the typically pale integument pigmentation of nocturnal bees.

DESCRIPTION: Female. Mandible with strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum greatly elongate. Galeal comb absent. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate strongly rimmed on all borders. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum as long as scutellum, smooth; propodeal pit narrow. Male. Mandible simple. Labral distal process absent. Antenna extending to posterior border of mesoscutum; F1 longer than F2. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 concave. Apical margin of S6 emarginate. Apical margin of S7 with bilobed median process. Apical margin of S8 with short median projection; spiculum narrow. Proctiger with anal filaments. Gonobasal bridge narrow; dorsal lobes strong. Basal process of gonostylus absent; parapenial lobe present. Ventral surface of penis valve with prong.

REVISIONS: Only the type species is currently recognized in *Micrommation*. Douglas Yanega is preparing a new description of Moure's type as well as of the only known male (Yanega, in prep.).

DISTRIBUTION: *Micrommation* is only known from the type locality in Paraná, Brazil (at 900 m).

COMMENTS: I have not seen specimens of *Micrommation*, which is known only on the basis of the female holotype, a single female paratype, and one nontype male. My generic diagnosis is taken from Moure's original description and figures as well as information provided to me by D. Yanega (personal com-

mun.) who has examined the as of yet undescribed male of *Micrommation*. For further details on *Micrommation* morphology refer to Yanega (in prep.).

# Genus *Neocorynura* Schrottky Figure 64

- Cacosoma Smith, 1879: 39. Type species: Cacosoma discolor Smith, 1879, designation of Sandhouse (1943). Nomen praeoccupatum (nec Cacosoma Felder In Felder and Rogenhofer, 1874 [Lepidoptera: Zygaenidae]).
- Neocorynura Schrottky, 1910: 540. Nomen novum pro Cacosoma Smith, 1879. Type species: autobasic with Cacosoma Smith, 1879.
- *Neocorynura (Neocorynuroides)* Eickwort, 1969a: 404. Type species: *Halictus rhytis* Vachal, 1904, monobasic and original designation. NEW SYNONYMY.

DIAGNOSIS: The speciose genus *Neocorynura* contains a heterogenous assemblage of primitive Augochlorina. The combination of an obtuse epistomal sulcus, frequently narrowed mesoscutal anterior margin, carinate preoccipital ridge, pectinate inner metatibial spur, and strongly bordered basitibial plate distinguishes the genus from similar genera such as *Andinaugochlora* and *Neocorynurella*.

DESCRIPTION: Female. Mandible with moderate to strong subapical tooth. Labral distal process narrowly triangular; basal elevation transverse; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded to carinate. Pronotal lateral angle variable; dorsal ridge carinate; lateral ridge carinate to lamellate. Mesoscutal anterior border frequently narrowed; mesoscutal lip rounded to angled. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum granular, striate, or rugose; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area not notched. Antenna extending back to propodeum or beyond; F2 longer than F1. Inner hind tibial spur serrate. Metasoma frequently petiolate. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 unmodified. Apical margin of S8 with median projection; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe and basal process of gonostylus absent. Ventral surface of penis valve with or without prong, never with keel.

REVISIONS: There has been no revision of *Neocorynura*. There are presently 67 valid species.

BIOLOGY: The biology of *Neocorynura* is varied with species nesting in the soil (Michener, 1977; Michener and Lange, 1958b; Michener et al., 1966; Sakagami and Moure, 1967) or rotten wood (Lüderwaldt, 1911; Schremmer, 1979). *Neocorynura colombiana* Eickwort and *N. erinnys* (Schrottky) may be semisocial (Lüderwaldt, 1911; Schremmer, 1979). Immatures have been described for *N. colombiana* by Eickwort (1979a).

DISTRIBUTION: The genus ranges from Argentina to Mexico. Although *Neocorynura* is unknown from the West Indies today, one fossil species, *N. electra* Engel, has been found as a Miocene amber inclusion from the Dominican Republic (Engel, 1995c).

#### Genus Neocorynurella Engel

- *Neocorynurella* Engel *in* Engel and Klein, 1997: 156. Type species: *Neocorynurella seeleyi* Engel and Klein, 1997, original designation.
- Vachalius Moure, 1999: 74. Type species: Halictus cosmetor Vachal, 1911, monobasic and original designation. NEW SYNONYMY.

DIAGNOSIS: The genus is most similar to *Andinaugochlora*. Refer to the diagnosis of *Andinaugochlora* for features separating the two genera.

DESCRIPTION: Female. Mandible with weak subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus

obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex slightly expanded behind ocelli. Preoccipital ridge rounded or weakly carinate. Pronotal lateral angle not produced, obtuse; dorsal ridge rounded; lateral ridge angled. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate with well-developed borders. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum as long as metanotum, striate; propodeal pit narrow. Male. Mandible simple. Labrum with short distal process; basal elevation not notched. Antennae extending back to propodeum; F2 longer than F1. Inner hind tibial spur serrate. Metasoma elongate. Apical margins of S4 and S5 weakly depressed. Apical margin of S6 deeply emarginate. Apical margin of S7 with broad median projection. Apical margin of S8 with narrow median projection; spiculum broad. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe and basal process of gonostylus absent; ventral process twisted apically. Ventral surface of penis valve unmodified.

REVISIONS: The genus currently contains three species; *Neocorynurella cosmetor* (Vachal) (see appendix 1), *N. seeleyi*, and *N. virida* Engel and Klein (*nomen emendatum*, from *N. viridis*).

DISTRIBUTION: The genus occurs in mountainous areas of Colombia and Venezuela.

COMMENTS: Thanks to Frank Koch (ZMHB) I have had the opportunity to examine the lectotype of *Halictus cosmetor* designated by Moure (1999) and to confirm the synonymy of *Vachalius* with *Neocory-nurella*. Moure did not have a male, nor is one present in the original series; however, several females that are clearly conspecific with the types are in the AMNH and SEMC (see appendix 1).

#### Genus Oligochlora Engel

DIAGNOSIS: This fossil genus is not without affinities to *Neocorynura* but differs by the broadly rounded mesoscutum, the rounded preoccipital ridge, the unproduced pronotal lateral angle, and in some species (*Oligo*- *chlora* s.s.) by the obsolescent anterior border to the basitibial plate and the presence of a weak acarinarium on T1.

DESCRIPTION: Female. Mandible with strong subapical tooth. Labral distal process narrowly triangular; lateral teeth strong. Prementum not greatly elongate. Galeal apex rounded. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded nor ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, acute to obtuse; dorsal ridge carinate; lateral ridge rounded or carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Inner hind tibial spur pectinate. Apex of marginal cell feebly truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum smooth to weakly striate and granular, not elongate; propodeal pit narrow. Male. Unknown.

DISTRIBUTION: The genus is presently known only from the Miocene amber deposits of the Dominican Republic (Iturralde-Vinent and MacPhee, 1996). The Eocene dates which have been estimated for some of these mines based on NMR studies (Lambert et al., 1985) have not been substantiated.

### Subgenus Oligochlora Engel s.s.

*Oligochlora* Engel, 1996b: 336. Type species: *Oligochlora eickworti* Engel, 1996b, original designation.

DIAGNOSIS: This subgenus differs from *Soliapis* by the presence of an acarinarium and the obsolescent anteior border of the basitibial plate. The only other augochlorine with an acarinarium is the South American genus *Thectochlora*. *Oligochlora* is distinguished from *Thectochlora* by an unproduced pronotal lateral angle, absence of a lamella on the pronotal dorsal ridge, a broadly rounded mesoscutum, absence of a dorsal hook on the mesotrochanter, and abence of dense tomentum on the basal area of the propodeum.

DESCRIPTION: As for the genus with the following additions: **Female.** Basitibial plate bordered posteriorly, margin obsolete ante-

riorly. Anterior surface T1 weakly modified into an acarinarium. **Male.** Unknown.

REVISIONS: At present this group contains three species. The subgenus was newly diagnosed by Engel (1997a) based on the discovery of a third species.

PALEOBIOLOGY: Two of the three species of *Oligochlora* are associated with astigmatid mites (Engel, 1996b; Fain et al., 1999). Mitebee associations are common, although poorly understood (Eickwort, 1979b, 1994; Fain et al., 1999). *Oligochlora*, like the genus *Thectochlora* (see below), possesses an acarinarium on the first metasomal tergum suggesting a mutualistic association between these ancient bees and mites.

### *Soliapis,* new subgenus Figure 82

TYPE SPECIES: Oligochlora (Soliapis) rozeni, new species (appendix 1).

DIAGNOSIS: See Diagnosis for *Oligochlora* s.s. (above).

DESCRIPTION: As for the genus with the following additions: **Female.** Basitibial plate strongly bordered on all sides. Anterior surface of T1 unmodified, not developed into an acarinarium. **Male.** Unknown.

ETYMOLOGY: The subgeneric name is a combination of the Latin words *sola* (meaning "alone") and *apis* (meaning "bee") and is a reference to the lack of an acarinarium and thereby the mutualism with mites in these species.

REVISIONS: Two species are included in this subgenus. The first is described in appendix 1 as the type species of the group while a second is treated by Engel and Rightmyer (in press).

### Genus Paroxystoglossa Moure

- *Paroxystoglossa* Moure, 1940: 59. Type species: *Oxystoglossa jocasta* Schrottky, 1911, original designation.
- Paraoxystoglossa Roubik, 1989: 392. Lapsus calami.

DIAGNOSIS: Refer to the Diagnosis for *Me-galoptilla* (above).

DESCRIPTION: Female. Mandible with moderate subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth weak. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge angled, distinctly not carinate. Pronotal lateral angle variable; dorsal ridge carinate; lateral ridge rounded to angled. Mesoscutal anterior border narrowed; mesoscutal lip angled. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur serrate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum weakly striate to rugulose; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area notched. Antenna long, extending back to propodeum; F2 longer than F1. Inner hind tibial spur serrate. Metasoma oval to slightly elongate. Apical margins of S4-S6 emarginate. Apical margins of S7 and S8 with median projection. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Parapenial lobe and basal process of gonostylus absent. Ventral surface of penis valve with prong.

REVISIONS: The genus was revised by Moure (1960), who recognized nine species.

BIOLOGY: The nesting biology of *Paroxystoglossa* has been studied by Michener and Lange (1958a, 1958b) and Michener and Seabra (1959).

DISTRIBUTION: Species of the genus range in Argentina, southern Brazil, and Paraguay.

### Genus *Pereirapis* Moure Figures 27, 49, 52, 62

- Pereirapis Moure, 1943a: 461. Type species: Pereirapis rhizophila Moure, 1943a [= Halictus semiauratus Spinola, 1853], monobasic and original designation.
- Pereirapsis Alves dos Santos, 1997: 6. Lapsus calami.

DIAGNOSIS: *Pereirapis* generally resembles species of the more common genera *Augochlorella* and *Augochlora*. It can be separated from the latter genus by the absence of a deeply acute epistomal sulcus that projects into the base of the clypeus and by the acute marginal cell apex. *Pereirapis* differs from *Augochlorella* in the presence of a large basal lobe on the inner metatibial spur. *Pereirapis* are small, brilliant metallic bees that are frequently green, with some populations slightly bluish and others more cupreous.

DESCRIPTION: Female. Mandible with moderate to strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth strong. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridge behind ocelli. Preoccipital ridge carinate. Pronotal lateral angle not produced, orthogonal to obtuse; dorsal ridge carinate; lateral ridge angled. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush absent. Basitibial plate bordered on all sides. Inner hind tibial spur serrate, basally with an expanded tooth (fig. 49). Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum striate; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area not notched. Antenna extending back to scutellum; F2 approximately equal in length to F1. Inner hind tibial spur serrate. Metasoma oval. Apical margin of S4 concave. Apical margin of S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 unmodified. Apical margin of S8 with median process; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Basal process of gonostylus present; parapenial lobe absent. Ventral surface of penis valve unmodified.

REVISIONS: There is only the one included species (see appendix 1).

BIOLOGY: The nesting biology, phenology, and primitively eusocial behavior of *Pereirapis* was investigated by Oliveira Campos (1980). McGinley (1989) cited the description of immature stages for *Pereirapis edentata* (Michener), but this is a species of *Augochlorella*.

DISTRIBUTION: Pereirapis ranges from

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Mexico eastward into the West Indies and south to southern Brazil.

### Genus *Pseudaugochlora* Michener Figures 10, 22–23, 63, 65, 71

 Caenaugochlora (Pseudaugochlora) Michener, 1954b: 77. Type species: Halictus nigromarginatus Spinola, 1841 [= Megilla graminea Fabricius, 1804], original designation.

DIAGNOSIS: *Pseudaugochlora* is superficially most similar to *Caenaugochlora*. The genus can be separated from *Caenaugochlora* by the presence of a strong ridge on the vertex, pointed galeal apex, and hooked apex of F11 in males.

DESCRIPTION: Female. Mandible with strong subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth weak. Prementum not greatly elongate. Galeal apex acute; galeal comb absent; galeal base extending to stipital base. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus orthogonal. Ocelli not greatly enlarged; ocellar furrow absent. Vertex with ridge behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum rugose; propodeal pit narrow. Male. Mandible simple. Labrum with distal process; basal area notched. Antenna extending back to scutellum or metanotum; F2 approximately equal in length to F1; F11 hooked at apex. Inner hind tibial spur serrate. Metasoma oval. Apical margins of S4 and S5 emarginate; S4 with medio-apical setal patch; S5 with lateroapical setal patches. Apical margin of S6 emarginate. Apical margin of S7 produced laterally. Apical margin of S8 with median process; spiculum broad. Proctiger with anal filaments. Gonobasal bridge narrow or membranous; dorsal lobes strong. Parapenial lobe present; basal process of gonostylus absent. Ventral surface of penis valve unmodified.

REVISIONS: The genus has never been revised. Moure and Hurd (1987) list seven named species while an eighth species is proposed in appendix 1.

BIOLOGY: The nesting biology of *P. graminea* and *P. sordicutis* (Vachal) has been investigated by Michener and Kerfoot [1967: as species of *Pseudaugochloropsis*, the latter under the name *P. nigerrima* (Friese)].

DISTRIBUTION: *Pseudaugochlora* extends from the southwestern United States to Argentina and east into the West Indies.

COMMENTS: This group has generally been known under the name Pseudaugochloropsis by recent authors (e.g., Eickwort, 1967; Michener, 1974; Eickwort and Sakagami, 1979; Moure and Hurd, 1987; Roubik, 1989; Michener et al., 1994; Radchenko and Pesenko, 1994b; Griswold et al., 1995; Danforth and Eickwort, 1997). However, the type species of *Pseudaugochloropsis* is a species of Augochloropsis (Paraugochloropsis), and thus the valid name for the genus is Pseudaugochlora (see also discussions in Michener, 1954b, 1994). As if this confusion were not enough, the type species of this genus has been consistently cited as Halictus nigromarginatus Spinola, 1851 (Eickwort, 1969a; Michener, 1994, 1997), which is obviously a homonym of the actual type species of Pseudaugochlora (namely, H. nigromarginatus Spinola, 1841). Spinola's 1851 nigromarginatus is in actuality a species of Caenohalictus (= Caenohalictus oblitus Moure and Hurd, 1987).

#### Genus Temnosoma Smith

Figures 7-9, 20, 30, 40, 56-57, 67, 69, 76

- Temnosoma Smith, 1853: 38. Type species: Temnosoma metallicum Smith, 1853, monobasic.
- Tamnosoma Taschenberg, 1883: 93. Lapsus calami.
- *Micraugochlora* Schrottky, 1909a: 138. Type species: *Micraugochlora sphaerocephala* Schrottky, 1909a, monobasic.
- Temnosoma (Temnosomula) Ogloblin, 1953: 2. Type species: Temnosoma (Temnosomula) platensis Ogloblin, 1953 [= Micraugochlora sphaerocephala Schrottky, 1909a], monobasic and original designation. Proposed as new again in Ogloblin, 1954.
- *Themnosoma* Sakagami, 1979: 83. Lapsus calami. *Microaugochlora* Schlindwein, 1998: 52. Lapsus calami.

DIAGNOSIS: This is one of the most distinctive genera of Augochlorini. The coarse sculpturing of the body gives these cleptoparasitic bees the general appearance of chrysidid wasps. Among augochlorine genera, *Temnosoma*'s appearance comes closest to species of *Glyptochlora*. *Temnosoma* can be separated from *Glyptochlora* by an oval tegula, absence of a scopa, the depressed apical margins of the first two metasomal terga, absence of a medio-apical cleft in the fifth metasomal tergum of females, and the presence of a broad division in the seventh metasomal tergum of males, among other characters.

DESCRIPTION: Female. Body coarsely punctured. Mandible simple. Labral distal process quadrate; basal elevation weakly bilobed; keel absent; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex expanded behind ocelli. Preoccipital ridge sharply angled and weakly carinate. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip weak and rounded. Tegula oval; coarsely punctured. Anterior basitarsal brush absent. Mesofemoral brush absent. Scopa absent. Penicillus absent. Basitibial plate absent. Inner hind tibial spur serrate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum strongly striated. Apical margins of T1 and T2 strongly depressed and rimmed; apical margin of T5 without cleft. Male. Mandible simple. Labrum with quadrate distal process. Antenna extending back to mesoscutum; F2 longer than F1. Inner hind tibial spur serrate. Metasoma oval. Apical margin of T7 with broad division. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 medially unsclerotized. Apical margin of S8 with median projection; spiculum narrow. Proctiger unmodified. Gonobasal bridge broad; dorsal lobes weak. Gonostylus with parapenial lobe present; basal process absent; ventral process greatly expanded with long setae; dorsal process reduced, small ridge with setae. Ventral surface of penis valve unmodified, with large dorsal process.

REVISIONS: Friese (1925) revised the species of *Temnosoma* known at the time recognizing six species. Moure and Hurd (1987) list seven species. There has been no modern treatment of the genus.

BIOLOGY: The biology of *Temnosoma* remains unstudied, but the species are presumably parasitic, perhaps on species of the genus *Augochloropsis* or *Augochlora* (Michener, 1978a).

DISTRIBUTION: *Temnosoma* occupies a wide distribution with species found from as far south as northern Argentina, throughout South and Central America, north to Arizona (Timberlake, 1958), as well as occurring in Cuba and Jamaica (Eickwort, 1988). One potential host, *Augochloropsis*, does not occur in the West Indies, but the other, *Augochlora*, does.

Genus *Thectochlora* Moure Figures 1, 42, 47, 53–55, 72

*Thectochlora* Moure, 1940: 51. Type species: *Halictus alaris* Vachal, 1904, monobasic and original designation.

DIAGNOSIS: *Thectochlora* resembles to some degree the genera of the *Augochlora*group (e.g., *Augochlorella*, *Pereirapis*), but differs most notably in the presence of a well-developed acarinarium on the first metasomal tergum, presence of a strong dorsal hook on the mesotrochanter, a lamellate dorsal pronotal ridge, and the presence of dense tomentum on the basal area of the propodeum. The genus also differs in the combination of an obtuse epistomal sulcus and a pectinate inner metatibial spur.

DESCRIPTION: **Female.** Mandible with weak subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; teeth strong. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent; galeal base extending to base of stipes. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle produced, obtuse; dorsal ridge lamellate; lateral ridge rounded. Mesoscutal anterior border narrowed; mesoscutal lip lamellate. Tegula oval. Anterior basitarsal brush absent. Mesotrochanter with strong dorsal hook. Basitibial plate rimmed on posterior edge, anterior border obsolete. Inner hind tibial spur pectinate. Apex of marginal cell truncate. Distal hamuli with irregular spacing pattern. Basal area of propodeum striate, extremely short, covered in dense tomentum. Anterior surface T1 modified into an acarinarium (a depressed shiny area bordered basally and partly on lateral margins by long plumose hairs). Male. Mandible simple. Labrum with weak distal process; basal area not notched. Antennae extending just beyond posterior margin of propodeum; F2 much longer than F1. Inner hind tibial spur serrate. Metasoma oval. S4 with lateral processes on apical margin possessing strong setae at apices; central patch of dense setae on disc. Apical margin of S5 emarginate. Apical margin of S6 emarginate. S7 unmodified. Apical margin of S8 with medial process; spiculum narrow. Proctiger unmodified. Gonobasal bridge narrow; dorsal lobes strong. Gonostylus with parapenial lobe present; basal process absent. Penis valve with prong on ventral surface.

REVISIONS: There is currently only one species recognized in the genus.

BIOLOGY: Nothing is known of *Thecto-chlora* biology, aside from its association with a specific genus of acarid mites — *Thectochloracarus* (Fain et al., 1999). The modified anterior surface of T1 for the transport of mites suggests that this is perhaps a mutualistic relationship.

DISTRIBUTION: *Thectochlora* occurs in northern Argentina, southern Brazil, Paraguay, and Guyana.

# Genus Xenochlora Engel, Brooks, and Yanega

Xenochlora Engel, Brooks, and Yanega, 1997: 7.Type species: Xenochlora ochrosterna Engel, Brooks, and Yanega, 1997, original designation.

DIAGNOSIS: This group is most similar to the nocturnal genus *Megalopta* and most species were at one time included therein. *Xen*- *ochlora*, however, is not nocturnal and lacks the greatly enlarged ocelli of *Megalopta*, has irregularly spaced distal hamuli along the anterior margin of the hind wing, and has stiff, black setae on the hindlegs.

DESCRIPTION: Female. Mandible bidentate, with supplementary teeth. Labral distal process broadly triangular; basal elevation bilobed; keel expanded basally; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb absent. Hypostomal ridge lamellate; anterior angle rounded. Malar space less than basal mandibular width. Epistomal sulcus acute, gently protruding into clypeus. Ocelli not greatly enlarged; ocellar furrow present. Vertex expanded behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced; dorsal ridge angled to weakly carinate; lateral ridge carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Metatibia and metabasitarsus covered with stiff, black setae. Basitibial plate rimmed posteriorly, anterior border obsolescent. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum about as long as metanotum and strongly declivitous. Male. Unknown.

REVISIONS: There are currently four included species, *Xenochlora chalkeos* Engel et al., *X. ianthina* (Smith), *X. nigrofemorata* (Smith), and *X. ochrosterna* Engel et al., all identified by the key provided in Engel et al. (1997).

BIOLOGY: A nest of *X. ianthina* was reported by Bates in a rotten twig (as a species of *Megalopta*; Smith, 1861). Unfortunately, no further details were given.

DISTRIBUTION: *Xenochlora* species are distributed in Amazonian Brazil, Ecuador, and Peru.

### CORYNURINA, NEW SUBTRIBE

TYPE GENUS: *Corynura* Spinola, 1851, present designation.

DIAGNOSIS: This is the most primitive group of Augochlorini and is restricted to southern South America. The species are generally small, although females of at least one species, *R. inflaticeps*, can be moderately large. Most species are dull metallic (except *Callistochlora*) or nonmetallic in coloration. The presence of a strong galeal comb, the short galea that extends posteriorly only half-way to the stipital base, and the short median process on the premental apex all serve to separate this group from the larger and more diverse Augochlorina.

DESCRIPTION: **Female.** Epistomal sulcus forming an obtuse or nearly linear angle. Premental apex with median process as long as or shorter than lateral processes. Strong galeal comb present (figs. 24, 25); galeal apex rounded (fig. 24); galeal base extending only halfway to stipital base (fig. 21). Marginal cell apex acute. Integument frequently dull metallic. **Male.** Distal process of labrum frequently absent (except in *Rhinocorynura*). Apical margins of S4–S5 unmodified.

#### Genus Corynura Spinola

DIAGNOSIS: Species of *Corynura* s.l. can be distinguished from other Corynurina by the combination of a broad hypostomal fossa, a nonproduced pronotal lateral angle, and a triangular recess surrouding the propodeal pit.

DESCRIPTION: Female. Mandible with moderate to strong subapical tooth. Labral distal process broadly triangular; basal elevation transverse; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb present; galeal base extending about half of distance to stipital base. Hypostomal fossa as long as wide or wider; hypostomal ridge carinate; anterior angle rounded. Malar space length less than mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush present. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Propodeal pit set into notch. Male. Mandible simple. Labrum without distal process; basal are not notched. Antennae long, extending back to propodeal triangle; F2 much longer than F1, usually longer than or as long as scape. Inner hind tibial spur serrate. Metasoma petiolate. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 unmodified. Apical margin of S8 with median projection; spiculum broad. Proctiger unmodified. Gonobasal bridge broad; dorsal lobes weak. Basal process of gonostylus present; parapenial lobe absent; dorsal gonostylus reduced, present as a ridge bearing setae. Ventral surface of penis valve with keel.

### Subgenus *Callistochlora* Michener Figures 28, 61, 77

Callochlora Moure, 1964: 269. Type species: Halictus chloris Spinola, 1851, original designation. Nomen praeoccupatum (nec Callochlora Packard, 1864 [Lepidoptera: Bombycidae]).

Callistochlora Michener, 1997: 12. Nomen novum pro Callochlora Moure, 1964. Type species: autobasic with Callochlora Moure, 1964.

DIAGNOSIS: Refer to Diagnosis for *Cory*nura s.s. (below).

DESCRIPTION: As for the genus with the following additions: **Female.** Compound eyes with long eye hairs. Basitibial plate rimmed posteriorly, anterior border obsolete. Inner hind tibial spur pectinate. Basal area of propodeum striate. **Male.** Basal process of gonostylus without setae.

REVISIONS: Moure and Hurd (1987) list four species included in *Callistochlora* (as *Callochlora*); however, two of these have since been moved to other genera (Engel, 1996c). These taxonomic changes have left the subgenus with only the two originally included species, *C. chloris* (Spinola) and *C. prothysteres* (Vachal), both of which can be identified by Moure's key (1964).

BIOLOGY: The nesting biology and mature larva of *C. chloris* were studied by Claude-Joseph (1926, as a species of *Halictus*).

DISTRIBUTION: *Callistochlora* occurs in Chile and Argentina, with one record of *C. prothysteres* from Peru.

Subgenus *Corynura* Spinola s.s. Figures 14, 21, 24–26

*Corynura* Spinola, 1851: 296. Type species: *Corynura gayi* Spinola, 1851 [= *Halictus rubellus* Haliday, 1836], designation of Alfken (1926).

Corynogaster Sichel, 1867: 146. Type species: Corynura gayi Spinola, 1851 [= Halictus ru*bellus* Haliday, 1836], designation of Daly et al. (1987). Designation of *Halictus (Corynura)* gayi Spinola, 1851 [meaningless combination] by Dalla Torre (1896) and Sandhouse (1943) is invalid. This name was interpreted as a possible lapsus calami for *Corynura* Spinola, 1851, by Eickwort (1969a).

*Rhopalictus* Sichel, 1867: 146. Type species: *Corynura flavofasciata* Spinola, 1851 [= *Halictus chilensis* Spinola, 1851], designation of Alfken (1926).

DIAGNOSIS: The dull metallic coloration, strongly bordered basitibial plate, and granular propodeum separates species of *Corynura* s.s. from *Callistochlora*. The monophyly of this subgenus, however, could not be confirmed. Those species with a pectinate inner metatibial spur may be more closely related to *Callistochlora* than to other *Corynura* proper. Until this can be confirmed I have not attempted to alter the classification of *Corynura* in the broad sense.

DESCRIPTION: As for the genus with the following additions: **Female.** Basitibial plate bordered on all sides. Inner hind tibial spur serrate or pectinate. Basal area of propodeum granular. **Male.** Basal process of gonostylus with setae.

REVISIONS: Alfken (1926) described and provided a key to the species known to him, and later updated this work (Alfken, 1931). Moure and Hurd (1987) list 18 species.

BIOLOGY: The nesting biology and mature larva of *C. cristata* (Smith) were studied by Claude-Joseph (1926, as a species of *Halic-tus*).

DISTRIBUTION: Species occur in Argentina and Chile.

#### Genus Halictillus Moure

Halictillus Moure, 1947: 7. Type species: Chloralictus loureiroi Moure, 1941, monobasic and original designation.

DIAGNOSIS: Species of *Halictillus* are the most Halictini-like among all augochlorines and strongly resemble the genus *Dialictus* (in fact, more often than not, they are misidentified as species of *Dialictus*). The strong distal wing venation, medioapical cleft in the female T5, the absence of a pygidial plate in males, and the presence of a spiculum on S8 in males all attest to the placement of this

group in Augochlorini. Species are minute, dark, and dull metallic blue-green.

DESCRIPTION: Female. Mandible with moderate subapical tooth. Labral distal process narrowly triangular; basal elevation orbicular; lateral margins of distal process serrated. Prementum not greatly elongate. Galeal apex rounded; galeal comb present; galeal base extending about half of distance to stipital base. Hypostomal ridge carinate; anterior angle rounded. Malar space less than mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex not expanded or ridged behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle not produced, obtuse; dorsal ridge carinate; lateral ridge rounded. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Basitibial plate bordered posteriorly, margin obsolescent anteriorly. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum granular; propodeal pit set into notch. Male. Mandible simple. Labrum without distal process; basal area not notched. Antennae long, extending beyond propodeum; F2 much longer than F1, usually longer than or as long as scape. Inner hind tibial spur serrate. Metasoma elongate. Apical margins of S4 and S5 unmodified. Apical margin of S6 not emarginate. Apical margin of S7 with median process. Apical margin of S8 with median process; spiculum broad. Proctiger unmodified. Gonobasal bridge broad; dorsal lobes weak. Basal process of gonostylus and parapenial lobe absent; dorsal process reduced to a ridge bearing setae. Ventral surface of penis valve unmodified; dorsal bridge near apices.

REVISIONS: There has been no attempt to revise the species of *Halictillus*. At present only two species, *H. glabrescens* (Cockerell) and *H. loureiroi* (Moure), are included in the genus.

BIOLOGY: The biology of *H. glabrescens* was investigated by Claude-Joseph (1926, under the name *Halictus glabriventris* Friese).

DISTRIBUTION: *Halictillus* occurs in northern Argentina, southern Brazil, and Chile.

#### Genus Rhectomia Moure

- *Rhectomia* Moure, 1947: 9. Type species: *Rhectomia pumilla* Moure, 1947, monobasic and original designation.
- *Corynurella* Eickwort, 1969a: 398. Type species: *Corynurella mourei* Eickwort, 1969a, monobasic and original designation.

DIAGNOSIS: *Rhectomia* is most closely related to *Rhinocorynura*. The genus differs from *Rhinocorynura* by a broadly rounded mesoscutal anterior margin, a rounded mesoscutal lip, and the absence of clypeal armature and the anterior basitarsal brush.

DESCRIPTION: Female. Mandible with weak subapical tooth. Labral distal process narrowly triangular; basal elevation bilobed or orbicular; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb present; galeal base extending only halfway to stipital base. Hypostomal ridge carinate; anterior angle rounded. Length of malar space less than basal mandibular width. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex expanded behind ocelli. Preoccipital ridge rounded. Pronotal lateral angle produced, orthogonal to obtuse; dorsal ridge carinate, usually with medial interruption separating dorsal ridge into anterior and posterior halves on different planes; lateral ridge angled or carinate. Mesoscutal anterior border rounded; mesoscutal lip rounded. Tegula oval. Anterior basitarsal brush absent. Basitibial plate bordered on all sides. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum smooth or very finely striate; propodeal pit narrow. Male. Mandible simple. Labrum without distal process; basal area not notched. Antenna extending back to scutellum; F2 roughly equal to F1. Inner hind tibial spur serrate. Metasoma elongate. S4 unmodified. Apical margins of S5 and S6 emarginate. Apical margin of S7 unmodified. Apical margin of S8 unmodified; spiculum narrow. Proctiger with microtrichial fringe. Gonobasal bridge broad; dorsal lobes strong. Basal process of gonostylus present; parapenial lobe absent. Ventral surface of penis valve unmodified.

REVISIONS: The genus was recently treated by Engel (1995b) who recognized four species and presented a key for their identification.

BIOLOGY: Nothing is known of *Rhectomia* biology, although the head size polymorphism present in at least one species (*R. harrisoni* Engel) suggests the possibility of social behavior.

DISTRIBUTION: Species of *Rhectomia* occur in northern Argentina, southern Brazil, Bolivia, Paraguay, and southern Peru.

> Genus *Rhinocorynura* Schrottky Figures 2, 18, 31, 33, 35, 74–75

- Corynura (Corynuropsis) Cockerell, 1901: 220. Type species: Corynura (Corynuropsis) darwini Cockerell, 1901 [= Augochlora briseis Smith, 1879], original designation. Nomen praeoccupatum (nec Corynuropsis Scott, 1894 [Crustacea: Entomostraca]).
- *Rhinocorynura* Schrottky, 1909a: 147. Type species: *Halictus (Corynura vel Corynuropsis) inflaticeps* Ducke, 1907, monobasic and original designation.
- Ctenocorynura Schrottky, 1914: 628. Type species: Ctenocorynura vernoniae Schrottky, 1914 [= Halictus (Corynura vel Corynuropsis) inflaticeps Ducke, 1907], monobasic and original designation.
- *Corynuroides* Sandhouse, 1943: 540. *Nomen novum pro Corynuropsis* Cockerell, 1901. Type species: autobasic with *Corynuropsis* Cockerell, 1901.
- Rhynocorynura Sakagami and Moure, 1965: 303. Nomen emendatum (unjustified).

DIAGNOSIS: Refer to Diagnosis for *Rhec-tomia*.

DESCRIPTION: Female. Mandible with strong subapical tooth. Labral distal process broadly triangular; basal elevation bilobed; teeth absent. Prementum not greatly elongate. Galeal apex rounded; galeal comb present; galeal base extending only halfway to stipital base. Hypostomal ridge carinate or weakly lamellate; anterior angle rounded. Length of malar space less than basal mandibular width. Clypeus frequently with armature of some design. Epistomal sulcus obtuse. Ocelli not greatly enlarged; ocellar furrow absent. Vertex expanded behind ocelli. Preoccipital ridge rounded (except one species is carinate). Pronotal lateral angle produced, orthogonal to obtuse; dorsal ridge lamellate; lateral ridge angled. Mesoscutal anterior border narrowed; mesoscutal lip lamellate. Tegula oval. Anterior basitarsal brush present. Basitibial plate bordered on all sides. Inner hind tibial spur pectinate. Apex of marginal cell acute. Distal hamuli with irregular spacing pattern. Basal area of propodeum smooth. Male. Mandible simple. Labrum with distal process; basal area not notched. Antenna extending back to scutellum; F2 approximately equal in length to F1. Inner hind tibial spur serrate. Metasoma elongate. Apical margins of S4 and S5 unmodified. Apical margin of S6 emarginate. Apical margin of S7 with median projection. Apical margin of S8 unmodified; spiculum narrow. Proctiger with microtrichial fringe. Gonobasal bridge broad; dorsal lobes weak. Basal process of gonostylus present; parapenial lobe present or absent. Ventral surface of penis

valve with keel.

REVISIONS: There has been no revision of the genus, which currently includes five described species.

BIOLOGY: The nesting biology of one species, *R. inflaticeps* (Ducke), was investigated by Eickwort and Sakagami (1979).

DISTRIBUTION: Species of *Rhinocorynura* occur in northern Argentina, southern Brazil, Bolivia, southern Ecuador, Paraguay, and Peru.

# KEY TO GENERA AND SUBGENERA OF AUGOCHLORINI

The groups *Electraugochlora*, *Glyptochlora*, *Oligochlora*, *Soliapis*, and *Xenochlora* are excluded from the male portion of this identification key as males are unknown for these taxa. The key presented in Engel (1998) mistakenly treated the marginal cell apex of *Oligochlora* as acute while in all species the apex is, in truth, feebly truncate.

#### FEMALES

- Prementum not greatly narrowed or elongate, length less than seven times width (fig. 14)
- 2. Maxillary palpus not elongate, extending posteriorly to base of prementum at most . . 3
- Maxillary palpi greatly elongate, extending

posteriorly to posterior border of mesosoma or beyond ..... Ariphanarthra

- Basitibial plate with anterior border obsolete or all borders faint; inner hind tibial spur variable (*Megommation* s.l. in part) ... 7
- Basitibial plate with all borders well developed; inner hind tibial spur serrate (fig. 48) ..... Micrommation
- Scopa present (fig. 41); mandible normal, short with weak subapical tooth; inner hind tibial spur pectinate (figs. 46, 47) ..... 8
- Scopa absent (fig. 40); mandible long and slender; inner hind tibial spur serrate (fig. 48) .... Megommation (Cleptommation)

- 10. Malar space elongate, as long as or longer than basal mandibular width (fig. 4) . . 11

- 11. Flagellum with the normal complement of 10 flagellomeres; pronotal dorsal surface frequently inflated; basal area of propodeum as long as or longer than scutellum and metanotum combined (fig. 39), nonstriate ...
- Flagellum with only nine flagellomeres; pronotal dorsal surface not inflated; basal area of propodeum subequal to scutellum, shorter than scutellum and metanotum combined (fig. 38), frequently striate .... Chlerogas
- 12. Inner hind tibial spur densely pectinate, with more than 10 long teeth; epistomal sulcus forming orthogonal angle; pronotal dorsal surface not inflated (*Ischnomelissa* in part) ..... *Ischnomelissa*
- Inner hind tibial spur pectinate, fewer than 10 long teeth; epistomal sulcus forming acute angle; pronotal dorsal surface frequently inflated ...... Chlerogella
- 13. Inner hind tibial spur pectinate (figs. 46, 47)
- Inner posterior angle of tegula rounded, not notched (fig. 35); pronotal dorsal ridge variable; labral distal process variable, but never expanded at apex (figs. 17–19) .... 17

- 16. Basal area of propodeum striate or pitted ...
- ..... Augochloropsis (Paraugochloropsis) 17. Labral keel of distal process with basal ex-
- Labral keel of distal process without basal expansion (figs. 17, 18); mandible without

- 18. Ocelli enlarged, nearly touching compound eye (fig. 6); distal hamuli of hind wing closely packed and numerous (fig. 36); hairs of mesotibia, metatibia, and metabasitarsus variably colored, frequently amber, never stiff and black (*Megalopta* s.l.) ..... 19
- Ocelli normal, not enlarged, more than one ocellar diameter from compound eye (figs. 1–5); distal hamuli of hind wing normal, with distinct spacing pattern (fig. 37); hairs of mesotibia, metatibia, and metabasitarsus stiff and black ...... Xenochlora

- 20. Pronotal dorsal ridge lamellate (fig. 33) .... 21

- Anterior surface of T1 unmodified (fig. 52); mesotrochanter lacking a dorsal hook; vertex lengthened posteriorly; marginal cell apex acute; basitibial plate with strong borders (fig. 43); basal area of propodeum variable, but never covered with tomentum .
   *Rhinocorynura*

- Basitibial plate with well-developed borders (fig. 43); epistomal sulcus forming orthogonal or obtuse angle; mesoscutal anterior border frequently narrowed (fig. 33) . . 25
- 24. Inner hind tibial spur pectinate, teeth well spaced, with fewer than 10 long teeth (figs. 46, 47); pronotal dorsal ridge not produced

anteriorly; basal area of propodeum granular with fine basal striations .....

- Andinaugochlora
   Inner hind tibial spur densely pectinate, with more than 10 long teeth; pronotal dorsal ridge produced anteriorly; basal area of propodeum with strong striae reaching to apex ..... Caenaugochlora (Ctenaugochlora)
- 25. Angle of epistomal sulcus forming obtuse angle; mesoscutal anterior border sometimes narrowed (fig. 33); hairs of compound eyes minute, shorter than, or scarcely longer than diameter of a single ommatidium (fig. 29) ..... Neocorynura

- Vertex with transverse ridge posterior to ocelli (fig. 10); epistomal sulcus orthogonal; galeal apex pointed (fig. 23) .....
   *Pseudaugochlora*
- Pronotal dorsal ridge rounded; labral teeth absent; basitibial plate with well-defined bor-

ders; basal area of propodeum striate .... ..... Neocorynurella 31. Basitibial plate with all borders strongly defined (fig. 43); anterior surface of T1 unmodified (fig. 52) ..... ..... Oligochlora (Soliapis) - Basitibial plate with anterior border obsolete (fig. 44); anterior surface of T1 with weakly developed acarinarium (cf. fig. 53) .... ..... Oligochlora (Oligochlora) 32. Basitibial plate with well-developed borders (fig. 43) ..... 33 Basitibial plate with obsolete anterior border (fig. 44) ..... 35 33. Pronotal dorsal ridge not produced; anterior basitarsal brush present ..... 34 Pronotal dorsal ridge produced, frequently with median interruption setting anterior and posterior halves on separate planes, frequently with a small flange; anterior basitarsal brush absent ..... Rhectomia 34. Basal area of propodeum with striae along basal margin; labral distal process narrowly triangular (fig. 17); galeal comb absent (figs. 22, 23); propodeal pit not enclosed within a V-shaped notch ..... Augochlorodes - Basal area of propodeum lacking any striae, entirely granular or smooth; labral distal process broadly triangular (fig. 18); galeal comb present (figs. 24, 25); propodeal pit enclosed within a V-shaped notch ..... ..... Corynura (Corynura) part 35. Basal area of propodeum granular; hairs of compound eye short (fig. 29); labral distal process narrowly triangular (fig. 17); dull and dark metallic blue-green or black ... ..... Halictillus - Basal area of propodeum striate; hairs of compound eye long (fig. 28); labral distal process broadly triangular (fig. 18); brilliant metallic green ..... ..... Corynura (Callistochlora) 36. Epistomal sulcus forming obtuse angle ... 37

- Preoccipital ridge carinate (fig. 27); basitibial plate with obsolete anterior border (fig. 44); basal area of propodeum striate; galeal comb absent (figs. 22, 23) . . Ceratalictus
- 39. Preocciptial ridge rounded (fig. 26) .... 40
- Preoccipital ridge carinate (fig. 27) .... 41 40. Epistomal sulcus forming acute angle, very slightly protruding into clypeus (figs. 80, 81); mesoscutal anterior border rounded; apex of marginal cell feebly truncate and appendiculate (Dominican amber fossil: Augochlora s.l. in part, figs. 79-81) .... ..... Augochlora (Electraugochlora)
- Epistomal suclus forming orthogonal angle; mesoscutal anterior border slightly narrowed; marginal cell apex acute ..... ..... Megaloptilla
- 41. Epistomal sulcus forming acute angle, forming lobe which protrudes into basal margin of clypeus; marginal cell apex truncate and appendiculate (Augochlora s.l. in part) .. 42
- Epistomal sulcus forming orthogonal angle; marginal cell apex acute ..... 43
- 42. Mandible with large, strongly developed subapical tooth; basal labral elevation orbicular; S1 frequently with a median ridge or tubercle (fig. 58) ..... ..... Augochlora (Augochlora)
- Mandible normal, subapical tooth weak; basal labral elevation transverse; S1 rarely with median ridge or tubercle ..... ..... Augochlora (Oxystoglossella)
- 43. Inner hind tibial spur with an enlarged, broad, basal tooth (fig. 49) ..... Pereirapis
- Inner hind tibial spur normally serrated, without expanded basal tooth (fig. 48) ..... ..... Augochlorella

#### MALES

1.	Prementum greatly narrowed and elongate, length seven or more times longer than wide (fig. 13) 2
	Prementum not narrowed or elongate, length less than seven times longer than wide (fig. 14)
2.	Maxillary palpus not greatly elongate 3
_	Maxillary palpus greatly elongate, extending posterad beyond apex of mesosoma <i>Ariphanarthra</i>
3.	Pronotal dorsal surface not inflated; epistomal sulcus variable, but never forming a deep projection extending into clypeus; mandible unmodified
	Pronotal dorsal surface inflated; epistomal sul- cus forming a thin, deep projection extend- ing into clypeus, almost reaching clypeal

	apex; mandible thin and twisted towards
	apex Chlerogelloides
4.	Ocelli greatly enlarged (fig. 6) 5
	Ocelli not enlarged (figs. 1–5) 6
5.	Marginal cell apex feebly truncate; S4 emar-
	ginate Megaloptidia
	Marginal cell apex acute; S4 not emarginate
~	
6.	Propodeal spiracle surrounded by a dense patch of plumose setae
	Propodeal spiracle not surrounded by a dense
	patch of plumose setae
7.	Apical margins of S2–S3 unmodified; head
<i>.</i>	and mesosoma brilliant metallic blue-green
	Megommation (Megaloptina)
	Apical margins of S2-S3 with short medial
	projections; head and mesosoma mostly am-
	ber or brown
	Megommation (Cleptommation)
8.	F1 longer than F2; labral distal process absent
	Micrommation
	F2 longer than F1; labral distal process present
0	Megommation (Stilbochlora)
9.	Malar space elongate, as long as, or usually
	much longer than basal mandibular width (fig. 4)
	Malar space not elongate, shorter than basal
	mandibular width (figs. 1–3, 5, 8) 12
10.	Flagellum with only 10 flagellomeres; inner
	hind tibial spur pectinate (figs. 46, 47); pron-
	otal dorsal surface not inflated; basal area of
	propodeum approximately as long as scutel-
	lum (fig. 38) Chlerogas
	Flagellum with the normal complement of 11
	flagellomeres; inner hind tibial spur serrate
	(fig. 48); pronotal dorsal surface usually in-
	flated; basal area of propodeum elongated,
	as long as scutellum and metanotum com- bined (fig. 39) 11
11	Dorsal gonostylar process reduced without se-
11.	tae or with extremely short setae
	Ischnomelissa part
	Dorsal gonostylar process reduced with long
	setae, frequently surpassing ventral gonos-
	tylar process Chlerogella
12.	Pronotal dorsal ridge lamellate 13
	Pronotal dorsal ridge variable, but never la-
	mellate 16
13.	Inner posterior angle of tegula with notch (fig.
	34); preoccipital ridge carinate or sharply
	angled; S4 with medioapical lobe, laterally
	with apical processes (Augochloropsis s.l.)
	Inner posterior angle of tegula rounded, with-

out notch (fig. 35); preoccipital ridge rounded; S4 without medioapical lobe, laterally with or without apical processes ..... 15

14. S5 with medioapical emargination
Augochloropsis (Augochloropsis)
— S5 without apical emargination
Augochloropsis (Paraugochloropsis)
15. S5 with apical margin emarginate; vertex nor- mal, not swollen posteriorly; antennae
reaching beyond propodeum; F2 much lon-
ger than F1 (fig. 61) Thectochlora
— S5 without apical emargination; vertex swol-
len posteriorly; antennae reaching at most
to propodeum; F2 and F1 equal in length
(fig. 62) Rhinocorynura
16. S4 with apical margin strongly concave or
emarginate 17 — S4 with apical margin unmodified or weakly
depressed
17. Ocelli greatly enlarged (fig. 6); S4 with later-
oapical notches on apical margin (fig. 66);
epistomal sulcus forming slightly acute an-
gle; distal hamuli of hind wing dense and
numerous (fig. 36) ( <i>Megalopta</i> s.l.) 18 — Ocelli not enlarged; S4 without lateroapical
— Ocelli not enlarged; S4 without lateroapical
notches; epistomal sulcus variable; distal
hamuli exhibiting distinct spacing pattern,
not densely packed together in a series (fig. 37) 19
18. F2 about equal in length to F3; clypeus with
apical margin and scape anteriorly white;
antennal socket diameter much greater than
ocular-antennal socket distance; S5 narrow-
ly emarginate Megalopta (Megalopta)
— F2 about two-thirds length of F3; clypeus and
scape completely black; antennal socket di- ameter less than ocular-antennal distance;
S5 broadly depressed
19. Marginal cell apex acute
— Marginal cell apex feebly truncate 22
20. S5 with apical margin unmodified 21
— S5 with apical margin strongly depressed
Paroxystoglossa part
21. S5 with dense medial patch of setae; S6 with
weak medio-apical notch, apical margin not produced <i>Augochlorodes</i>
— S5 without medial patch of setae; S6 with
strong medio-apical notch, slightly pro-
duced along apical margin Pereirapis
22. F2 approximately equal to F1 (fig. 62)
- F2 much longer than F1 (fig. 61) $\ldots$
Paroxystoglossa part
23. Vertex unmodified; terminal flagellomere un-
modified ( <i>Caenaugochlora</i> s.l.) 24 — Vertex behind ocelli produced into a trans-
verse ridge (fig. 10); terminal flagellomere
(F11) produced into a hook (fig. 63)
Pseudaugochlora
24. S4 with medioapical tubercles covered in

	dense setae; compound eyes frequently
	with long hairs (fig. 28) <i>Caenaugochlora</i> ( <i>Caenaugochlora</i> ) S4 without medioapical tubercles, however,
	with a triangular medioapical setal patch; hairs of compound eyes short (fig. 29)
25.	S5 with apical margin strongly depressed or
25.	emarginate
26	S5 with apical margin unmodified 29 F2 much longer than F1 (fig. 61); marginal
20.	cell apex acute or truncated; pronotal lat- eral angle not produced
	Length of F2 roughly equal to F1 (fig. 62);
	marginal cell apex acute; pronotal lateral angle produced <i>Rhectomia</i>
27.	Antennae extending to posterior border of pro- podeum; mesoscutal anterior border rounded
	(fig. 32); metasoma elongate
	Antennae extending to scutellum; mesoscutal anterior border slightly narrowed; metaso-
	ma oval Megaloptilla
28.	Epistomal sulcus forming orthogonal angle; venter of penis valve with prong
	Andinaugochlora
—	Epistomal sulcus forming obtuse angle; ven- ter of penis valve without prong
29.	Marginal cell apex feebly truncate 30
30.	Marginal cell apex acute
	ing a lobe extending into clypeus; metaso-
	ma oval ( <i>Augochlora</i> s.l.)
31.	Outer ridge bordering gonostylus with short
51.	setae Augochlora (Augochlora)
_	Outer ridge bordering gonostylus with long setae, surpassing ventral gonostylus length
37	Augochlora (Oxystoglossella) Body variously sculptured, but not coarsely
52.	punctate; T1 and T2 not depressed on basal halves; T7 not bilobed along apical margin
_	Body coarsely punctate (fig. 30); T1 and T2 depressed on basal half (figs. 56, 57); T7 with apical margin bilobed (fig. 67)
22	Temnosoma
55.	Epistomal sulcus forming orthogonal angle
	Epistomal sulcus forming obtuse angle 35
34.	Preoccipital ridge rounded (fig. 26); F2 much longer than F1; basal area of propodeum
	elongated, as long as or longer than scutel- lum and metanotum combined (fig. 39)

lum and metanotum combined (fig. 39) ... ..... Ischnomelissa part

- Preoccipital ridge carinate (fig. 27); F1 longer than F2; basal area of propodeum subequal to scutellum (fig. 38) . . . . Augochlorella
- 35. Preoccipital ridge rounded (fig. 26) .... 36
- Preoccipital ridge carinate (fig. 27) .... 38
   36. Metasoma petiolate; apical margin of S6
- 37. Body brown, black, or dully metallic in coloration; hairs of compound eye short (fig. 29); basal process of gonostylus with setae ...... Corynura (Corynura)
- F2 much longer than F1 (fig. 61); mesoscutal anterior border narrowed (fig. 33); antennae frequently just surpassing posterior border of propodeum ..... Neocorynura part
- F2 roughly equal in length to F1 (fig. 62); mesoscutal anterior border rounded (fig. 32); antennae reaching back to mesoscutal posterior border or to scutellum ...... *Ceratalictus*

# **CLADISTICS**

### DESCRIPTION OF CHARACTERS

Eickwort's (1969a) comparative morphological study of the Augochlorini served as the primary resource for characters used below. His work was largely supplemented and modified by the my above study of the genera. A number of characters used by Eickwort (op. cit.) in his groundplans had to be excluded as the states could not be confidently differentiated. Examination of taxa for each group revealed overlapping variation for many of the features included in his study. For example, Eickwort (op. cit.), as well as a recent cladistic reinterpretation of his raw data (Danforth and Eickwort, 1997), utilized characters that were treated as "unmodified" versus "modified". Although these statements are not incorrect, the homology assessments and codings can be further refined. For example, the apical margin of the fourth male metasomal sternum is one in which "unmodified" refers to a straight, uninterrupted apical margin, whereas "modified" includes those taxa possessing a deep median cleft, a gently depressed or concave margin, a strong median process, or deep lateral notches. Thus, the state "modified" contains little or no true grouping information. Of the 80 characters employed in the earlier studies (Eickwort, 1969a; Danforth and Eickwort, 1997), 27 are used here and an additional 11 are reinterpreted based on direct study of numerous augochlorine species (appendix 3). At the same time my own studies revealed a number of new characters which are employed here for the first time (e.g., mesotrochanteral hook, arrangement of the hamuli, the interocellar furrow). In total, 46 new characters are used; 34 from adult morphology and 12 from behavior.

Homology was determined using the principle of connections as it has been classically defined (Geoffroy Saint-Hilaire, 1818; Owen, 1866; Remane, 1952). Identification of ethological homology follows the same principles as used for morphology (Baerands, 1958; Wenzel, 1992; Greene, 1994), namely topographic and phenetic similarity coupled with functional information.

The following 84 characters were coded for all 39 genera and subgenera of Augochlorini as well as 10 genera of Halictini, 1 genus of Nomioidini, and two genera of Nomiinae (summarized in the data matrix presented in appendix 2). As many species as possible were examined from each genus in order to survey variation in each group; in several cases all known species for a given genus were examined (appendix 3 presents a list of taxa examined for construction of the data matrix). In the character matrix (appendix 2), interrogative marks represent unknown information while dollar signs represent subset polymorphisms (elaborated on below). The matrix was constructed in the DADA (Nixon, 1995). Characters 0 through 33 are for the female sex, although some may equally apply to males, while 34 through 60 are derived from the male. Characters 61 through 71 are autapomorphic, used to support the monophyly of various genera, and not listed in sequence by gender. The last 12 characters (characters 72 through 83) are based on ethological traits. State number does not imply plesiomorphic versus apomorphic polarity. The nomiine genera *Dieunomia* and *Lipotriches* were used as outgroups to polarize the characters. For the definition of particular morphological structures refer to the above section on General Morphology.

### FEMALE-DERIVED CHARACTERS

**0.** Apical margin of clypeus: (0) straight; (1) concave (fig. 12).

**1.** Distal process of labrum: (0) base broadly joined to basal area, triangular (fig. 18); (1) base narrowly joined to basal area, triangular (fig. 19); (2) quadrate (fig. 20).

**2.** Keel of labral distal process: (0) thin ridge (figs. 17, 18); (1) expanded at base (fig. 19).

**3.** Lateral teeth of labrum: (0) absent (fig. 18, 19); (1) small, forming a serrated margin; (2) strong, forming a weakly pectinate margin (fig. 17).

**4.** Length of malar space: (0) short, less than basal width of mandible (figs. 1-3); (1) elongate, as long as, or longer than, basal width of mandible (fig. 4).

**5.** Angle formed between dorsal and lateral clypeogenal sulci and opening toward compound eye: (0) obtuse or linear; (1) approximately orthogonal; (2) acute, forming lobe projecting into clypeal base.

**6.** Apex of galea: (0) lobed (fig. 24); (1) distinctly acute (fig. 23).

**7.** Galeal comb: (0) absent; (1) present (figs. 24, 25).

**8.** Base of galea: (0) extending posterad to middle of stipes (fig. 21); (1) extending posterad or near to base of stipes (fig. 22).

**9.** Medioapical process of prementum: (0) short, extending apicad to lateral processes; (1) elongated, extending apicad beyond lateral processes.

**10.** Prementum: (0) unmodified, less than  $7 \times$  longer than wide (fig. 14); (1) greatly narrowed and elongate,  $7 \times$  or more longer than wide (fig. 13).

**11.** Anterior angle of hypostomal ridge: (0) rounded; (1) angled, coming to a distinct point.

12. Compound eye hairs: (0) minute, as

long as an ommatidium diameter (fig. 29); (1) long, much longer than several ommatidium diameters (fig. 28).

**13.** Ocelli: (0) normal (fig. 1–5); (1) greatly enlarged (fig. 6).

**14.** Interocellar furrow: (0) absent; (1) present (fig. 11).

**15.** Preoccipital area: (0) not carinate (fig. 26); (1) carinate (fig. 27) or lamellate.

**16.** Pronotal dorsal surface between lateral angles: (0) short, mostly covered by mesoscutum; (1) convex, inflated, and greatly expanded anteriorly, not obscured by mesoscutum.

**17.** Mesoscutal anterior border: (0) broadly rounded (fig. 32); (1) strongly narrowed and projecting forward (fig. 33).

**18.** Tegula: (0) oval (fig. 35); (1) inner posterior margin notched (fig. 34).

**19.** Propodeal triangle length: (0) no longer than metanotum; (1) subequal to scutellum (fig. 38); (2) as long as or longer than scutellum and metanotum combined (fig. 39).

**20.** Propodeal posterior pit: (0) set into triangular recess; (1) not set into a triangular recess.

**21.** Probasitarsal brush: (0) absent; (1) present.

**22.** Basitibial plate: (0) absent (fig. 45); (1) present, anterior border obsolete (fig. 44); (2) present, rimmed on all borders (fig. 43).

**23.** Metatibial spine: (0) absent; (1) present.

**24.** Inner metatibial spur: (0) serrate (fig. 48); (1) pectinate, fewer than 10 teeth well spaced (figs. 46–47); (2) pectinate, more than 10 teeth, densely packed.

**25.** Scopa: (0) absent (fig. 40); (1) present (fig. 41).

**26.** Basal area of propodeum: (0) normal, strongly angled from posterior surface; (1) declivitous.

**27.** Apex of marginal cell: (0) acute; (1) truncate, frequently feebly appendiculate.

**28.** Distal wing venation: (0) strong; (1) weakened.

**29.** Distal hamuli: (0) irregularly spaced (fig. 37); (1) uniformly spaced and numerous (fig. 36).

**30.** Acarinarium of anterior surface of T1: (0) absent (fig. 52); (1) present (figs. 53–55).

**31.** Median cleft in apical margin of T5: (0) absent; (1) present (fig. 59).

**32.** Gradulus of T6: (0) absent; (1) present.

**33.** Gradulus of S4: (0) absent; (1) present.

MALE-DERIVED CHARACTERS

**34.** Distal process of labrum: (0) absent; (1) present (fig. 60).

**35.** Relative lengths of F1 versus length of F2: (0) F1 equal to F2 (fig. 62); (1) F1 shorter than F2 (fig. 61); (2) F1 longer than F2.

**36.** Dense, plumose setae surrounding propodeal spiracle: (0) absent; (1) present.

**37.** Pygidial plate on T7: (0) absent; (1) present.

**38.** Anal filaments on apical margin of proctiger: (0) absent; (1) present.

**39.** Microtrichiae on apical margin of proctiger: (0) absent; (1) present.

**40.** Medio-apical process on S3: (0) absent; (1) present.

**41.** Gradulus of S4: (0) continuous; (1) medially interrupted.

**42.** Gradulus of S4: (0) separated from antecosta; (1) meeting antecosta medially.

**43.** Medio-apical margin of S4: (0) continuous, straight; (1) gently concave; (2) cleft; (3) posterior process.

**44.** Lateral notches on apical margin of S4: (0) absent; (1) present (fig. 66).

**45.** Triangular setal patch medially on S4: (0) absent; (1) present (fig. 65).

**46.** Medio-apical margin of S5: (0) continuous, straight (fig. 64); (1) gently concave; (2) cleft.

**47.** Gradulus of S6: (0) continuous; (1) medially interrupted.

**48.** Medio-apical margin of S6: (0) continuous, straight; (1) cleft (fig. 64).

**49.** Apical margin of S7: (0) continuous, straight; (1) with median process (figs. 68, 69); (2) with bilobed process (fig. 70); (3) with lateral processes (fig. 71).

**50.** Apical margin of S8: (0) continuous, straight; (1) with median process.

**51.** Spiculum of S8: (0) absent; (1) present, broad (fig. 68); (2) present, narrow (fig. 69).

**52.** Point of fusion between S7 and S8: (0)

at apodeme apex; (1) before apodeme apex. **53.** Gonobase: (0) broad; (1) narrow.

54. Gonobasal dorsal lobes: (0) narrow,

situated between apodemes of penis valves in dorsal view; (1) broad, situated at or lateral to apodemes of penis valves in dorsal view.

**55.** Inner apical corner of volsella: (0) variously produced; (1) modified into a thin hook.

**56.** Ventral surface of penis valve: (0) unmodified; (1) with broad prong; (2) with keel.

**57.** Parapenial lobes: (0) absent (fig. 74); (1) present (fig. 73).

**58.** Basal process of gonostylus: (0) absent; (1) present, without setae (fig. 77); (2) present, with setae (figs. 74, 75).

**59.** Ventral process of gonostylus: (0) single projection; (1) divided projection.

**60.** Dorsal process of gonostylus: (0) absent; (1) setose ridge; (2) present, partially membranous; (3) present, sclerotized.

AUTAPOMORPHIES

**61.** The female maxillary palpus: (0) unmodified, extending posterad to premental base at most; (1) greatly elongate, extending posterad to metasoma. [*Ariphanarthra*-1]

**62.** Hypostomal ridge posteriorly extended into a lamellate flange [female: *Megommation* proper—state 1]: (0) absent; (1) present.

**63.** Medio-dorsal hook of mesotrochanter [female: *Thectochlora*—state 1]: (0) absent; (1) present (fig. 42).

**64.** Depressed and rimmed apical margin of T1-2 [female: *Temnosoma*—state 1]: (0) absent; (1) present (figs. 56, 57).

**65.** Number of units comprising antennal flagellum (Nr. female/ Nr. male) [both sexes: *Chlerogas*—state 1]: (0) 10/11; (1) 9/10.

**66.** Dorsally extended transverse ridge behind ocelli on vertex [both sexes: *Pseudaugochlora*—state 1]: (0) absent; (1) present (fig. 10).

**67.** F11 [male: *Pseudaugochlora*—state 1]: (0) unmodified, gently conical at apex; (1) hooked at apex (fig. 63).

**68.** Mesofemoral and mesotibial expansion [male: *Chlerogelloides*—state 1]: (0) absent; (1) present.

**69.** Inner hind tibial spur [male: *Chlero-gas*—state 1]: (0) serrate; (1) pectinate.

70. Broad medio-apical cleft on T7 [male:

*Temnosoma*—state 1]: (0) absent; (1) present (fig. 67).

**71.** Long, anteriorly directed, dorsal process on penis valve [male: *Temnosoma*—state 1]: (0) absent; (1) present (fig. 76).

### ETHOLOGICAL CHARACTERS

Behavioral information, mostly from nest architecture, was derived from a number of sources. Appendix 4 provides information as to where pertinent ethological data were obtained for each genus.

**72.** Social structure: (0) solitary; (1) cleptoparasitic; (2) communal; (3) semisocial; (4) eusocial. The classification of social categories as defined by Michener (1969a, 1974) is followed here.

**73.** Augochlorines are oligolectic, so specific foraging preferences are not meaningful for phylogenetic analysis. However, augochlorine genera do vary in some aspects of their foraging behavior, most notably in the time of activity: diurnal (0); nocturnal (1).

**74.** Attachment of brood cell to burrow: (0) via long lateral; (1) sessile.

**75.** Brood cell distribution: (0) scattered; (1) clustered; (2) serial.

**76.** Chamber containing cell cluster: (0) absent; (1) present, along main burrow; (2) present, offset from main burrow.

**77.** Brood cell orientation: (0) horizontal or slanting; (1) vertical.

**78.** Nest plan: (0) branching before cells; (1) unbranched or branching only below first set of cells.

**79.** Cell location: (0) along a single burrow; (1) along multiple burrows.

**80.** Short lateral tunnels bordering cells: (0) absent; (1) present.

**81.** Nesting substrate: (0) soil; (1) wood.

**82.** Turret: (0) absent; (1) present.

**83.** Position of the pollen mass provisions within the brood cell: pollen mass placed at cell apex (0); pollen mass occupying a lateral position within the cell (1).

#### SUBSET POLYMORPHISMS

Taxa which are polymorphic were coded with an interrogative mark in the data matrix

(appendix 2). Subset polymorphisms (Nixon, 1993) were coded for those taxa exhibiting only two states of a multistate character. Subset polymorphisms are indicated with the dollar sign (\$) in the matrix and implemented with the Shift-\$ command in DADA (Nixon, 1995). The subgenus Augochlora was coded as having subset polymorphism for the shape of the labral distal process (character 1: states 0 and 1). Similarly, all nonparasitic taxa for which the social biology is unknown were coded as subset polymorphisms for social behavior (character 72), thereby excluding the parasitic state (the presence of a well-developed scopa, normal mandibles, and a basitibial plate indicates that these taxa are not parasitic). This coding allowed these taxa to have any of the possible social states (solitary through eusocial; states 0, 2-4), but not to have the cleptoparasitic state (state 1).

### DATA ANALYSIS

All characters were run with equal weights and considered nonadditive. Analyses were carried out using NONA (Goloboff, 1993) and were run in two parts. The first analysis consisted of 20 replications of random-taxonaddition with each replicate holding 500 trees in memory. This analysis was performed to identify a set of trees upon which more exhaustive branch-swapping could be undertaken. The memory was then reallocated to hold as many topologies as possible and the initial set of trees was submitted to the program and analyzed using the max\* command. Autapomorphic traits (characters 61 through 71) were excluded from the calculation of the consistency index (CI), retention index (RI), and tree length. The two nomiine genera (Dieunomia and Lipotriches) were used to root the tree, thereby allowing for the various halictine genera to potentially render the Augochlorini as nonmonophyletic. Trees were visualized and printed using CLADOS (Nixon, 1993). 5488 trees exhibited length 283, CI 0.31, and RI 0.61 (strict consensus in fig. 78).

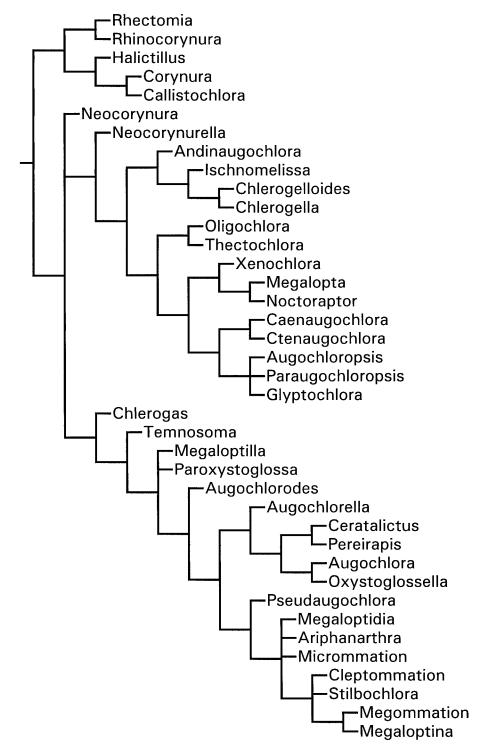


Fig. 78. Phylogeny of tribe Augochlorini (length 283, CI 0.31, RI 0.61, strict consensus).

# DISCUSSION

### PHYLOGENETIC RELATIONSHIPS

The phylogenetic analysis of augochlorine genera presented here is certainly not robust owing to the large number of trees, the low CI, and low RI; however, a strict consensus of these topologies retains a remarkable amount of resolution (fig. 78). On account of the high level of homoplasy in the analysis, I have conservatively avoided naming most of the nodes in the cladogram. However, certain clades are well supported and are discussed at length below. In the following discussion character and state numbers are provided in parentheses.

### TRIBE AUGOCHLORINI

The Augochlorini is supported as monophyletic among the Halictinae with the tribe Halictini apparently paraphyletic with respect to the augochlorines. This conclusion is not far removed from the one reached by Pesenko (1983), although he considered the Halictini to be monophyletic and his putative synapomorphies of the Augochlorini are not all identical with those resulting from my studies (Engel, 1996a, 1998, herein). The monophyly of the Augochlorini is supported by the medio-apical cleft of the fifth tergum of females (31-1), absence of a pygidial plate in males (37-0), the medio-apical cleft of the sixth sternum in males (48-1), presence of a spiculum (51-1,2), and sessile attachment of brood cells to the main burrow in nests (74-1). Additional possible synapomorphies, which are subsequently modified several times within the tribe, are an unmodified venter of the penis valve (56-0), the clustering of brood cells in the nest (75-1), and the presence of an excavated brood cell chamber (76-1). Although recent studies focusing on the phylogeny of short-tongued bee families (Alexander and Michener, 1995) failed to support augochlorine monophyly, these analyses suffered from sparse taxon sampling at lower ranks and therefore limited character choice. In the study of Alexander and Michener (op. cit.) the augochlorines were represented only by the genera Augochlora, Corynura, and Pseudaugochlora, while of the aforementioned synapomorphies for the tribe, only the medio-apical cleft of the female fifth tergum and the pygidial plate of males were included. An approximate outline of augochlorine classification is presented in table 3.

Because of the small sample of halictine genera examined, it was not possible to determine the sister-group of the Augochlorini, but members of the caenohalictine genera (Caenohalictus, Habralictus, etc.) seem to be the most likely candidates and should perhaps be treated as a tribe separate from the Halictini. In fact, a family-group name for these genera was already proposed by Michener (1954b) and could be reinstated to accommodate them as the tribe Caenohalictini. A tribal classification of this subfamily recognizing five monophyletic tribes seems more appropriate than the one in present use. The paraphyletic Halictini should be broken into three entities: the Gastrohalictini (= Lasioglossum group), the Halictini (= Halictus and Sphecodes groups), and the Caenohalictini (= Agapostemon and Caenohalictus groups) (table 4).

### SUBTRIBE CORYNURINA

The subtribes Augochlorina (discussed below) and Corynurina are both recognized as monophyletic. The corynurine genera form the basalmost clade of the tribe (fig. 78), united by the presence of a strong glaeal comb (7-1) and the absence of a distal process on the male labrum (34-0). All of these genera are distributed in northern Chile and Argentina, Paraguay, Bolivia, and the southernmost regions of Brazil and Peru. Moure and Hurd (1987) assigned the Ecuadorian species Halictus joannisi Vachal to Corynura thereby extending the range of this genus much further northward; however, this species actually belongs to the high-altitude genus Andinaugochlora and is a member of the Augochlorina (Engel, 1996c). The genera comprising the Corynurina had been considered paraphyletic with respect to the remainder of the tribe (Eickwort, 1969a; Danforth and Eickwort, 1997) and this is somewhat supported by the absence of a cleft in the male S6 of Halictillus, a character that could

Tribe AUGOCHLORINI Beebe	
Subtribe Corynurina, new subtribe (type: Corynura)	
Corynura Group	
Genus Corynura Spinola	
Subgenus Corynura Spinola	
Subgenus Callistochlora Michener	
Genus Halictillus Moure	
Rhinocorynura Group	
Genus Rhectomia Moure	
Genus Rhinocorynura Schrottky	
Subtribe Augochlorina Beebe	
Genus Neocorynura Schrottky	
Megaloptomorpha Clade	Augochloromorpha Clade
Genus Neocorynurella Engel	Genus Chlerogas Vachal
Genus Andinaugochlora Eickwort	Genus Temnosoma Smith
Ischnomelissiti, new infratribe (type: Ischnomelissa)	Paroxystoglossa Group
Genus Ischnomelissa Engel	Genus Paroxystoglossa Moure
Genus Chlerogelloides Engel et al.	Genus Megaloptilla Moure and Hurd
Genus Chlerogella Michener	Augochlorodes Group
Thectochloriti, new infratribe (type: Thectochlora)	Genus Augochlorodes Moure
Genus †Oligochlora Engel	Augochloriti Beebe
Subgenus †Oligochlora <sup>a</sup> Engel	Augochlora Group
Subgenus †Soliapis, <sup>a</sup> new subgenus	Genus Augochlora Smith
Genus Thectochlora Moure	Subgenus Augochlora Smith
Megaloptiti Moure	Subgenus † <i>Electraugochlora</i> , <sup>a</sup> new subgenus
Augochloropsis Group	Subgenus Oxystoglossella Eickwort
Genus Augochloropsis Cockerell	Genus Augochlorella Sandhouse
Subgenus Augochloropsis Cockerell	Genus Ceratalictus Moure
Subgenus Paraugochloropsis Schrottky	Genus Pereirapis Moure
Subgenus Glyptochlora Moure	Megaloptidiiti, new infratribe (type: Megaloptidia)
Genus Caenaugochlora Michener	Pseudaugochlora Group
Subgenus Caenaugochlora Michener	Genus Pseudaugochlora Michener
Subgenus Ctenaugochlora Eickwort	Megaloptidia Group
Megalopta Group	Genus Megaloptidia Cockerell
Genus Megalopta Smith	Genus Ariphanarthra Moure
Subgenus Megalopta Smith	Genus Micrommation Moure
Subgenus Noctoraptor Engel et al.	Genus Megommation Moure
Genus Xenochlora Engel et al.	Subgenus Megommation Moure
č	Subgenus Cleptommation Engel et al.
	Subgenus Megaloptina Eickwort
	Subgenus Stilbochlora Engel et al.

TABLE 3 Hierarchical Supraspecific Classification of Tribe Augochlorini Proposed Herein

<sup>a</sup> Fossil taxon from Tertiary amber of the West Indies.

potentially group the remaining corynurine genera with the Augochlorina. The paraphyly of the subtribe, however, was primarily based on the a priori assumption that the galeal comb was a primitive trait and its loss constituted a synapomorphy for the higher Augochlorini (here equivalent to the subtribe Augochlorina). Although this character is certainly primitively present among many higher-level bee groups (e.g., see distribution presented by Alexander and Michener, 1995) the a priori assumption that it is primitively present in the Augochlorini is not supported by outgroup comparisons. A galeal comb is not present among the Halictini and Nomioidini and must therefore be considered independently derived in the common ancestor of these genera and not as a trait carried over from a more distant ancestor with the Nomiinae or Rophitinae. The interpretation of the

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TABLE 4 Suggested Classification of Halictinae

Subfamily Halictinae Thomson
Tribe Nomioidini Börner
Tribe Halictini Thomson
Subtribe Halictina Thomson
Subtribe Sphecodina Schenck
Tribe Gastrohalictini Schrottky
Tribe Caenohalictini Michener
Subtribe Caenohalictina Michener
Subtribe Agapostemonina, new <sup>a</sup>
Tribe Augochlorini Beebe
Subtribe Corynurina, new
Subtribe Augochlorina Beebe

<sup>a</sup> Type: Agapostemon Guérin-Méneville. This group differs from Caenohalictina (*Caenohalictus* and *Habralictus*) in the fusion of the first and second metatarsomeres in males.

galeal comb as plesiomorphic for Augochlorini is also incongruent with the plesiomorphic presence of a strongly distad galea relative to the stipes and the numerous characters uniting *Halictillus* with *Corynura* (see discussion below) if the Corynurina is considered paraphyletic. The analysis presented here supports Corynurina monophyly and the absence of a cleft in the sixth sternum of *Halictillus* males is interpreteted as a secondary reversal.

Within the Corynurina two main clades are recognized (fig. 78: table 3); the Corynura group and the Rhinocorynura group. The genera of the Corynura group share the presence of a triangular recess surrounding the propodeal pit (20-0), an obsolescent anterior border to the basitibial plate (22-1), the presence of a metatibial spine (23-1), a broad spiculum (51-1), and the reduction of the dorsal gonostylar process to a setose ridge (60-1). In Corynura s.s. the basitibial plate structure is reversed to regain the anterior border. The Rhinocorynura group is united by the combination of the male F1 length being equivalent to that of F2 (35-0), the presence of microtrichiae on the proctiger (39-1), a medially interrupted gradulus on the sixth sternum of males (47-1), and the presence of a setose gonostylar basal process (58-2).

#### SUBTRIBE AUGOCHLORINA

The subtribe Augochlorina is supported by the elongation of the galea which extends posterad to meet the base of the stipes (8-1) as well as by the elongate median apical process of the prementum (9-1). Unlike the Corynurina, the Augochlorina is widely distributed covering the range of the corynurine genera and extending northward to southern Canada as well as east into the West Indies. The subtribe can be further divided into two primary clades; the Megaloptomorpha and the Augochloromorpha (discussed below). The enigmatic genus Neocorynura is left unassigned in the Augochlorina. A revision of the numerous species in Neocorynura is desperately needed in order to confirm its monophyly and to, it is hoped, confidently place the genus among the Augochlorina.

### MEGALOPTOMORPHA

The megaloptomorph augochlorines are weakly united by the presence of a feebly truncate marginal cell apex (27-1). This character, however, is homoplastic throughout the tribe and is reversed in some species of the Ischnomelissiti and Megaloptiti clades (see below); it also appears independently in scattered species of the Augochloromorpha. Thus, no single character change serves to identify a megaloptomorph bee, instead the apomorphic presence of a truncate marginal cell apex and the absence of augochloromoph synapomorphies are together required to recognize this clade. Although megaloptomoph monophyly is weakly supported, they can be confidently excluded from the Augochloromorpha and specific clades within the group can be confidently diagnosed (see below).

### ISCHNOMELISSITI

The Ischnomelissiti is a distinctive clade of genera that frequently have elongate heads, perhaps an adaptation for visiting flowers with deep corollas. The Ischnomelissiti are united by the elongate propodeum (19-2), the absence of distal process on the male labrum (34-0), and the reversal to an acute marginal cell apex (27-0). The genera *Chlerogella* and *Chlerogelloides* are further united by the presence of an acute epistomal sulcus (5-2), particularly so in *Chlerogelloides* (refer to description of this genus), and an inflated pronotal dorsal surface (16-1). The elongate head of *Chlerogas* is independently derived, as this is a genus of the Augochloromorpha (below).

### Thectochloriti + Megaloptiti

The two clades discussed below are united by the presence of a concave apical margin on the fourth sternum (43-1) and the presence of a deep medioapical cleft on the fifth sternum of males (46-2). The structure of the fourth sternum is further elaborated on in the genus *Megalopta* (refer to description of genus above).

### THECTOCHLORITI

The modification of the anterior-facing surface of the first metasomal tergum into an acarinarium is unique to the genera of Thectochloriti (30-1), although the charcter is reversed in two apomorphic species of Oligochlora (see discussion of the genus above). The acarinarium is described above under General Morphology and is designed for the transport of phoretic instars of mites (see also Fain et al., 1999). The modification of the bee's morphology for the transport of the mites as well as the frequently species-specific association between the bees and mites suggests that this relationship is a mutualistic one (at least within Augochlorini). No other Augochlorini have acarinaria.

#### MEGALOPTITI

This clade is united by the fusion of the gradulus with the antecosta on the fourth sternum of males (42-1), although this is reversed in *Ctenaugochlora* (this reversal being one of several synapomorphies for the subgenus).

Among the Megaloptiti, the *Augochloropsis* group is united by the apomorphic presence of a carinate preoccipital ridge (15-1), presence of a gradulus on the fourth metasomal sternum in females (33-1), and F1 and F2 being of equal lengths in males (35-0). Both of the included genera, *Augochloropsis* and *Caenaugochlora*, are diverse. The monophyly of *Caenaugochlora* s.l. is supported by the apomorphic presence of an orthogonal epistomal sulcus (5-1), a triangular setal patch medially on the fourth metasomal ster-

num in males (45-1), and the partially membranous dorsal gonostylar process (60-2). *Augochloropsis* s.l. monophyly is established by the quadrate distal labral process (1-2), the tegular notch (18-1), the absence of a male labral process (34-0), the presence of a medioapical process on the fourth metasomal sternum of males (43-3), the broad spiculum (51-1), the inner apical hook of the volsella (55-1), the presence of a strong keel on the venter of the penis valves (56-2), the vertical orientation of brood cells in the nest (77-1), and the presence of short lateral tunnels bordering the cell clusters (80-1).

The *Megalopta* group is a disinctive group of fairly robust bees and includes not only the largest members of the tribe (i.e., some species of Megalopta s.s.) but also the most diverse clade of nocturnal species within the tribe, inclusive of the only nocturnal parasitic bees of any family (Noctoraptor). The clade is supported by the broad distal labral process (1-0), the basal expansion of the distal labral keel (2-1), the formation of an acute angle by the epistomal sulcus that protrudes into the basal margin of the clypeus (5-2), the presence of the interocellar furrow (14-1), the shortened and declivitous basal area of the propodeum (19-0 and 26-1), and the utilization of a wood subtrate for nest construction (81-1).

### Augochloromorpha

The unique character of broadly separated gonobasal lobes (54-1) unites this large clade of genera. The genus *Chlerogas* is here considered the basalmost genus of the Augochloromorpha based on the pectinate inner metatibial spur. The serrate inner metatibial spur unites the remaining genera, although it is subsequently reversed in *Pseudaugochlora*, *Stilbochlora*, *Megaloptina*, and *Augochlorodes*. The next clade excludes *Temnosoma* by the apomorphic presence of serrated margins on the labral distal process (3-1). This character is independently modified in the genera *Augochlora* and *Pereirapis* and in some species of the *Megaloptidia* group.

Although the monophyly of the *Paroxy-stoglossa* group was not supported by the analysis presented here, the genera are difficult to separate morphologically and there is

enough cohesion to the taxa that I have opted to establish a group in the belief that it will eventually be recognized as monophyletic. The group can be recognized by the presence of medioapical cleft on the fifth metasomal sternum of males (46-2). If the monophyly of the *Paroxystoglossa* group is confidently established, then groups that I have herein retained at the generic level should be considered subgenera of a single genus.

The genus Augochlorodes is placed in its own monotypic genus group. The genus is remarkably similar to species of the Augochlora group (differentiated above in the diagnosis of the genus). It is difficult to consider the following characters as synapomorphies given that there is only one included species. However, Moure (in Schlindwein, 1998) has named a second species of the genus that may potentially share some of these features, thereby providing a good test for the predictive power of the cladogram. However, I have not seen seen material of this putative Augochlorodes, nor has Moure presented a description of the species (see systematic section on Augochlorodes above as well as appendix 1). Putatitive synapomorphies for the Augochlorodes group include the combination of a pectinate inner metatibial spur (24-1), the meeting of the gradulus and antecosta on the fourth metasomal sternum of males (42-1), the absence of apical processes on the eight metasomal sternum of males (50-0), and the broad spiculum (51-1).

The Augochlora-group of genera (Augochlora, Augochlorella, Ceratalictus, and Pereirapis) are perhaps the most well-known group of augochlorine genera. The presence of a carinate preoccipital ridge (15-1) and the presence of eusociality (72-4). One species of Augochlora s.l. (the fossil species, A. leptoloba, described in appendix 1) has secondarily lost the preoccipital carina, while the secondary loss of eusocial behavior is a synapomorphy of species in Augochlora s.s.

#### MEGALOPTIDIITI

The Megaloptidiiti includes thoe augochlorines with a sharply pointed galeal apex (6-1), the fusion of metasomal sterna seven and eight prior to their lateral apices in males (52-1), and the presence of a parapenial lobe

(57-1). The clade contains two distinctive groups. The first of these, the Pseudaugochlora group, possesses a pectinate inner metatibial spur (24-1), a feebly truncate marginal cell apex (27-1), the presence of lateral processes on the apical margin on the seventh metasomal sternum of males (49-3), an unmodified venter on the penis valves (56-0), and strong ridge on the vertex (66-1). The Megaloptidia group contains those augochlorine genera sharing the absence of labral teeth (3-0), the greatly narrowed prementum (10-1), and the presence of a labral distal process in males (34-1). Although relationships within the clade are not well resolved, Megaloptidia is likely the most primitive genus of the group owing to the sclerotized dorsal gonostylar process; the remaining genera share the apomorphic presence of a partially desclerotized dorsal process. Further work on the internal phylogeny of the Megaloptidiiti will need to explore this character more fully.

#### ANOMALIES

Some anomalous features of the topology (fig. 78) should be briefly noted. The positions of the genera Andinaugochlora, Temnosoma, and Ceratalictus are enigmatic and should be investigated further. The genera Andinaugochlora and Neocorynurella are remarkably similar and it is surprising that a sister-group relationship, or at least closer affinity, is not supported by these analyses. The placement of *Temnosoma* is also intuitively displeasing. It has been long believed that Temnosoma and Augochloropsis were sister taxa based on a unique labral morphology (1-2) and the coarse sculpturing of Temnosoma (figs. 7-9, 30, 56, 57), Glyptochlora, and a few primitive species of Paraugochloropsis. Of these characters only the labral morphology is discrete and could be successfully coded for cladistic analysis. The degree of sculpturing is quite variable, blending gradually from species of Temnosoma and Glyptochlora into the least sculptured species of Paraugochloropsis. Therefore, this feature, while suggestive, provides little conclusive information toward the grouping of these taxa. The quadrate labrum is incongruent with the pattern exhibited by other characters in the analysis and must therefore be interpreted, for the time being, as convergent between Augochloropsis and Temnosoma. Lastly, Ceratalictus also possesses a unique character that seemingly allies it with Augochlorella. Both of these genera have exceedingly similar genitalia with a divided ventral gonostylar process (59-1). As it is, Ceratalictus allies itself with Pereirapis in the phylogeny, a particularly distressing position. A more intuitive scenario would have Augochlorella and Ceratalictus as sisters and Augochlora and Pereirapis as sisters. It will be important to determine whether these relationships are stable to the addition of new character information. If a sister-group relationship is ever supported for Ceratalictus and Augochlorella, then it would probably be best to treat them as synonyms or as subgenera of a single genus.

## ETHOLOGICAL EVOLUTION

Details of behavioral evolution among the augochlorines will be presented in a forthcoming paper specifically focusing on this topic (Engel, in prep.). A preliminary outline of ethological evolution in Augochlorini is, however, presented here.

The nocturnal genera Megalopta, Megommation s.s., and Megaloptidia do not form a natural group, thereby suggesting independent derivations of this life-history strategy and convergence on a presumably adaptive morphology. Each of these groups possess greatly enlarged ocelli, large body size, and pale integumental pigmentation, all possibly specializations for activity at night. Interestingly, other nocturnal Hymenoptera, such as the nocturnal vespids Apoica and Provespa and the nocturnal ichneumonids of the subfamily Ophioninae, also exhibit strikingly enlarged ocelli as well as generally pale body pigmentation (coloration is not universal, however, as some species of all of these groups, including Megalopta and Megaloptidia, can be fairly dark). The general loss of body pigmentation may be the result of relaxed pressure from ultraviolet radiation. A cursory examination of the UV-reflectance abilities of diurnal and nocturnal augochlorines as well as other brilliant metallic-green bees (e.g., Euglossini) reveals a consistently lower percentage reflectance in the nocturnal representative for wavelengths below 450 nm (Engel, 1998, in prep.). Insect ocelli are potentially involved in the detection of subtle changes in light levels, especially at low intensities (Chapman, 1982). The enlargement of the ocelli in each of these groups is presumably an adaptation for navigating under the extreme conditions of night where subtle changes in light levels might aid in their orientation abilities. Many crepuscular and nocturnal bees have proportionally larger ocelli than diurnal species (Kerfoot, 1967).

The nest architecture of the augochlorines is varied and has been the subject of phylogenetic interpretation (e.g., Eickwort and Sakagami, 1979). When nest architecture traits are interpreted in light of the cladogram (fig. 78), the assumption that the primitive nest architecture for the Augochlorini must have been something closely resembling the general nest design seen in the tribe Halictini (Eickwort and Sakagami, op. cit.) is not supported. A more congruent pattern of characters entails a more complicated nest design with the following characteristics to be basal among the augochlorines: (1) nests constructed in the soil, (2) a single turretless burrow, (3) burrow opening into a cell chamber, (4) cells oriented horizontally. Those nests resembling the simple Halictini-type (e.g., lacking the cell chamber) are therefore reductions. The pathways of change suggested by the phylogeny are not as progressive as those of the previous studies (Sakagami and Michener, 1962; Eickwort and Sakagami, 1979). Instead of a series of changes, the topology suggests a major change between the Halictini and Augochlorini with subsequent independent derivations or reductions in the tribe each occurring without evidence of proceeding through one of the "simpler" plans (Engel, 1998, in prep.).

The genera *Temnosoma*, *Megommation* (*Cleptommation*), and *Megalopta* (*Noctoraptor*) are not closely related, indicating three derivations of cleptoparasitism in the tribe. Each exhibits the typical suite of morphological characters associated with parasitic behavior: absence of scopal hairs on the metatibia, absence of a basitibial plate, and the simple, bladelike or scythelike mandible. Information on the specific modes of parasitism and biology of these species is desperately needed. Until the hosts of these taxa and their specific biologies are discovered, little more can be determined regarding their evolution.

#### FOSSIL HISTORY

The augochlorines are the most speciose group in the Miocene fauna of Hispaniola as it is presently understood. There are six described augochlorine species representing three genera; Augochlora, Neocorvnura, and Oligochlora. The remainder of the Dominican amber bee fauna consists of the groups Protandrenini (Rozen, 1996), Chilicolini (Michener and Poinar, 1996; Engel, 1999e), Euglossini (Engel, 1999c; Poinar, 1998), Halictini (Michener and Poinar, 1996), Megachilinae (Engel, 1999d), and Meliponini (Wille and Chandler, 1964; Camargo et al., 2000). Although the Miocene species are the oldest augochlorine fossils presently known, the tribe is undoubtedly much older. None of the Miocene groups (Neocorynura, Augochlora s.l., Oligochlora s.l.) are basal in augochlorine phylogeny as it is presently understood (fig. 78). The tribe as a whole may be as old as the early Paleocene or, more likely, the Late Cretaceous, having diversi-

fied after the separation of the African and South American continents. Engel (1998) hypothesized that the primitive condition for augochlorine nests was a single, turretless burrow in the soil opening into a horizontally oriented cell chamber. Interestingly, trace fossils of the Late Cretaceous from Argentina assigned to the ichnogenus Uruguay (Roselli, 1938; Genise and Bown, 1996) strongly resemble nests made by extant augochlorine species and generally fit the primitive reconstruction hypothesized by Engel (1998). The tribe presumably originated in southern South America and extended northward, reaching at least the area of the West Indies by the early Miocene as shown by the presence of three genera in Dominican amber. The species from the West Indies, including the fossils, all share affinities with species occurring in northern South America (Eickwort, 1988; Engel, 1995c), supporting the notion that the West Indian augochlorine fauna is derived from South America and not North or Central America, thereby following the South American-Caribbean track of Rosen (1975). Finer level studies on the internal phylogenetic relationships of various genera (particularly Augochlora and Augochloropsis) will greatly facilitate an understanding of augochlorine biogeography.

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# **APPENDIX 1**

### Descriptions and Records of Bees Pertinent to this Study

The following species are treated in this work since they provide significant range extensions for their respective genera, are important taxonomic changes, are rare additions to the augochlorine fauna, or provide valuable information for a morphological understanding of a particular genus.

Augochlora (Augochlora) nigrocyanea Cockerell

Augochlora nigrocyanea Cockerell, 1897a: 144.

Halictus zophodes Vachal, 1911: 16.

Augochlora smaragdina variety atrata Friese, 1916: 312.

Augochlora smaragdina variety atra Friese, 1916: 313. Lapsus calami.

Augochlora (Odontochlora) essequibensis Cockerell, 1923: 445. NEW SYNONYMY.

Augochlora cyanaspis Cockerell, 1931: 552.

COMMENTS: The possible synonymy of *A. essequibensis* with *A. nigrocyanea* was first suggested to me by my late mentor George C. Eickwort (personal commun.) and I have since been able to confirm his suspicions through examination of the types. This synonymy is published here for the first time but should probably be attributed to Eickwort as he was the first person to correctly recognize the conspecific nature of the taxa.

Augochlora (Augochlora) nitidior Moure, nomen nudum

Augochlora (Augochlora) nitidior Moure in Schlindwein, 1998: 51.

# Augochlora (Electraugochlora) leptoloba, new species

### Figures 79-81

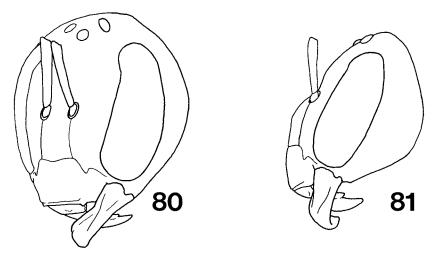
DIAGNOSIS: As for the subgenus (refer to page 32).

DESCRIPTION: **Female.** Total body length 8.5 mm; forewing length 4.6 mm. Head length 2.1 mm. Lower third of clypeus below lower tangent of compound eyes. Basal vein distad cu-a by 3 times vein width; 1r-m confluent with 1m-cu; 2r-m distad 2m-cu by 3 times vein width; first sub-marginal cell about as long as combined lengths of second and third submarginal cells; second submarginal cell parallel-sided; distal hamuli arranged 3-1-1-2.

Clypeus and supraclypeal area with widely scattered faint, coarse punctures, integument between faintly imbricate. Face and vertex minutely



Fig. 79. Photomicrograph of holotype female of *Augochlora* (*Electraugochlora*) *leptoloba*, new subgenus and new species, in Dominican amber (photograph by author).



Figs. 80–81. Augochlora (Electraugochlora) leptoloba, new subgenenus and new species, female. 80. Head, oblique anterior aspect. 81. Head in profile.

punctured, punctures separated by width or less, integument otherwise faintly imbricate. Gena as on face except punctures become separated by two times puncture width on lower third. Postgena faintly imbricate and impunctate. Pronotum faintly imbricate. Mesoscutum and scutellum imbricate with very widely scattered, faint punctures. Metanotum weakly rugulose. Preepisternum coarsely punctured, punctures contiguous on upper third, separated by width or less on lower twothirds. Mesepisternum coarsely punctured, punctures separated by puncture width or less, integument otherwise granular; hypoepimeron weakly rugulose with minute punctures along anterior third separated by less than a puncture width. Metepisternum weakly rugulose. Propodeal lateral surface faintly imbricate with widely scattered coarse punctures; posterior surface faintly imbricate; basal area imbricate with faint basal striae. Terga and sterna imbricate.

Mandible and labrum brown. Head dull metallic green with a few faint metallic copper highlights except clypeal apex brown. Mesosoma as on head; legs brown; wings hyaline, venation brown. Terga dark brown with a few faint metallic green highlights; sterna brown.

Pubescence golden and generally sparse except as indicated: on mesoscutum, scutellum, and metanotum fuscous; on outer surfaces of meso- and metatibiae, basitarsi, tarsomeres 2–4 long, simple, fuscous, and stiff; on terga fuscous.

Male. Unknown.

HOLOTYPE: Female, Miocene amber of the Dominican Republic (MACT), accession number M-2521.

ETYMOLOGY: The specific epithet is a combination of the Greek words *leptos* (meaning "small") and *lobos* (meaning "lobe") and refers to the weakly developed epistomal lobe that protrudes into the basal margin of the clypeus.

# Augochlora (Oxystoglossella) rightmyerae, new species

DIAGNOSIS: This species can be distinguished from other *Oxystoglossella* by the sculpturing of the clypeus, face, mesoscutum, and pleura and the coloration of the face and mesoscutum (all described below).

DESCRIPTION: Female. Total body length 8.8 mm; forewing length 5.8 mm. Head as long as wide (length, width 2.4 mm). Lower two-thirds of clypeus below lower tangent of compound eyes. Intertegular distance 1.8 mm. Basal vein distad cu-a by three times vein width; 1r-m confluent with 1m-cu; 2r-m distad 2m-cu by seven times vein width, 2r-m gently curved; first submarginal

cell longer than combined lengths of second and third submarginal cells; second submarginal cell slightly narrowed anteriorly; anterior border of third submarginal cell three-quarters that of posterior border; distal hamuli arranged 2-1-2.

Clypeus with small, weak punctures separated by 2-4 times puncture width, integument otherwise smooth. Supraclypeal area with minute punctures separated by 1-2 times puncture width, integument between smooth. Face at and below level of antennae with punctures separated by less than a puncture width, integument smooth; above level of antennae punctures become much smaller and contiguous except at emargination of compound eye where separated by less than width and forming impunctate spot bordering the crux of the eye. Punctures of vertex minute and separated by width, integument smooth. Gena as on vertex except punctures separated by 2-3 times puncture width. Postgena imbricate and impunctate. Pronotum faintly imbricate. Mesoscutum with minute punctures over smooth integument; medially punctures separated by width or slightly more on anterior half and separated by 2-5 times width on posterior half; lateral thirds with punctures separated by width. Scutellum with minute punctures separated by 1-2 times width, integument between smooth. Metanotum rugulose. Preepisternum strongly rugose. Punctures of mesepisternum separated by puncture width on smooth integument. Metepisternum with punctures separated by less than puncture width, integument smooth. Propodeal lateral and posterior surfaces imbricate; basal area of propodeum with strong striae radiating from basal margin, integument between striae smooth and shining. Anterior surface of T1 with punctures very widely spaced, integument between smooth; remainder of T1 with minute punctures separated 1-4 times puncture width, integument faintly imbricate; sculpturing of T2-T5 as on posterior half of T1; apical margins of terga imbricate and impunctate; sterna imbricate.

Mandible dark brown except middle third which is amber and apex which is reddish brown. Labrum dark brown. Clypeus and supraclypeal area dark brown with strong metallic red or purple highlights except along upper border of supraclypeal area which is brilliant metallic green. Antenna brown. Remainder of head brilliant metallic green with scattered gold or weakly coppery highlights. Mesosoma brilliant metallic green except mesoscutum and scutellum which are dark brown, nearly black; mesoscutum with a few faint metallic red or purple highlights on borders; scutellum with stronger metallic red or purple highlights, particularly strong on axilla, and some metallic green highlights along anterior border. Tegula dark brown. Wing membrane hyaline; veins brown. Legs brown. Metasoma dark brown except metallic green highlights faint on central discs of T2–T5, stronger laterally on terga; sterna without highlights.

Pubescence golden or white except on scutellum and T5–T6, which is slightly fuscous. Anterior surface of T1 with mat of appressed, short plumose hairs.

Male. Unknown.

HOLOTYPE: Female; Bolivia, La Paz, Alto Río Beni, south of Rio Inicua, 1100 m, 15–18 January 1976, Luis E. Peña (AMNH).

ETYMOLOGY: The specific epithet honors Ms. Molly G. Rightmyer, talented artist and entomologist, who has offered every assistance in my efforts to curate the AMNH bee collection.

Augochlorella eusticta Moure, nomen nudum

Augochlorella eusticta Moure in Schlindwein, 1998: 51.

Augochlorodes clementis Moure, nomen nudum

Augochlorodes clementis Moure in Schlindwein, 1998: 51.

# Augochloropsis scabriceps Moure, nomen nudum

Augochloropsis scabriceps Moure in Schlindwein, 1995: 52.

### Caenaugochlora (Caenaugochlora) elisabethae Engel

Caenaugochlora (Caenaugochlora) elisabethae Engel, 1997c: 91.

NEW RECORDS: One male; Costa Rica, Puntarenas Coto Brus, Las Alturas Biological Station, near lecheria of Finca Las Alturas, near Cotón, 1540 m, 13 June 1992, J.V. McHugh, lot #CR92-183 (CUIC). One female, four males; Costa Rica, Puntarenas, Las Alturas Field Station, 20 km N. San Vito de Hava, 1400 m, 20–24 May 1991, De Vries, malaise trap (AMNH). One female; Costa Rica, Puntarenas, Las Alturas Field Station, 20 km N. San Vito de Hava, 1540 m, 10–31 July 1992, C. Snyder, malaise trap (AMNH).

### Caenaugochlora (Ctenaugochlora) donnae Engel

Caenaugochlora (Ctenaugochlora) donnae Engel, 1995a: 283.

NEW RECORD: One male; Costa Rica, Heredia Province, ca. 12 km SW Horquetas (Rara Avis), 550 m, 18-23 January 1989, D. A. Grimaldi (AMNH).

COMMENTS: This species was, until now, known solely on the basis of the holotype female in the collection of the LACM. A single male has recently been identified among unsorted Hymenoptera at the AMNH and is reported upon here. This is the second species of the subgenus for which males and females are both known.

# Lasioglossum (Evylaeus) biciliatum (Friese), new combination

Corynura biciliata Friese, 1916: 319.

COMMENTS: This Costa Rican species was placed by Friese (1916) in the augochlorine genus *Corynura*, which, as presently understood, does not occur outside of southern South America. Examination of the type (ZMHB) reveals that this species is, in fact, a member of the tribe Halictini (or Gastrohalictini: see Table 4), genus *Lasioglossum*. Padre Moure had also examined the type, a year before me, as evidenced by the date on his determination label, and arrived at the same conclusion.

### Megalopta (Megalopta) intermedia Sakagami, **nomen nudum**

Megalopta intermedia Sakagami, 1979: 86.

COMMENTS: This name appeared in a popular article on the diversity and biology of halictine bees. Unfortunately no species has ever been proposed with this epithet.

# Neocorynurella cosmetor (Vachal), new combination

Halictus cosmetor Vachal, 1911: 51.

*Augochlora cosmetor* (Vachal); Moure and Hurd, 1987: 276.

Vachalius cosmetor (Vachal); Moure, 1999: 76.

NEW RECORD: One female, Venezuela, Merida, La Montana, cable car station, 2442 m, 23–25 February 1968, P. and B. Wygodzinsky and M. Cormons (AMNH).

# Oligochlora (Soliapis) rozeni, new species Figure 82

DIAGNOSIS: As for the subgenus (refer to p. 47). DESCRIPTION: **Female.** Total body length 8.2 mm; forewing length 5 mm. Head apparently about as long as wide (length, width 2 mm). Compound eyes strongly convergent below. Pronotal lateral angle orthogonal. Basal vein distad cu-a by



Fig. 82. Photomicrograph of holotype female of *Oligochlora (Soliapis) rozeni*, new subgenus and new species, in Dominican amber (photograph by author).

two times vein width; Sc+R pigmented as other wing veins; 1r-m confluent with 1m-cu; 2r-m distad 2m-cu by four times vein width, 2r-m relatively straight; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell parallel-sided; anterior border of third submarginal cell approximately equal to that of second submarginal cell; distal hamuli arranged 3-1-2. Inner hind tibial spur with 4 teeth excluding apex.

Clypeus and supraclypeal area weakly granular, impunctate. Face below level of antennae weakly granular with faint, crowded punctures appearing by margin of compound eye, clypeus, and near antennal socket; upper half of face apparently weakly granular with faint, nearly contiguous punctures. Gena and postgena apparently faintly imbricate. Pronotum faintly imbricate. Mesoscutum (and apparently the same on scutellum) weakly punctured, punctures separated by puncture width or less, integument between imbricate. Metanotum imbricate. Preepisternum rugose. Mesepisternum granular with faint, coarse punctures separated by a puncture width or less. Metepisternum imbricate. Propodeal lateral surface granular; basal area granular, without basal striae. Terga faintly imbricate.

Mandible and labrum dark brown. Head brilliant metallic green-gold with scattered coppery highlights. Antenna brown except with yellow markings on inner surface of scape. Mesosoma as on head except tegula brown; wings hyaline, venation dark brown; legs brown. Terga dark brown with metallic green highlights and apical margins brown without highlights; sterna brown.

Pubescence golden except on mesoscutum and scutellum fuscous and on meso- and metatibiae and tarsi which is fuscous, highly branched, and long.

### Male. Unknown.

HOLOTYPE: Female; Miocene amber of the Dominican Republic (MACT), accession number M-2523.

ETYMOLOGY: The specific epithet is a patronymic honoring Dr. Jerome G. Rozen, Jr., of the AMNH. Jerry helped me enormously during the undertaking of my graduate research and since then in my postdoctoral studies at the AMNH. I am sincerely grateful for his support and friendship.

### Pereirapis semiaurata (Spinola)

- Halictus semi-auratus Spinola, 1853: 86.
- Augochlora Titania Smith, 1853: 75.
- Augochlora semiaurata (Spinola): Smith, 1853: 79.
- Halictus caucasicus Radoszkowsky, 1868: 77. NEW SYNONYMY.
- Augochlora titanea Dalla Torre, 1896: 96. Nomen emendatum (unjustified).
- Augochlora seminigra Cockerell, 1897a: 144. NEW SYNONYMY.
- Corynura titania (Smith): Cockerell, 1900: 375.
- Halictus hypixis Vachal, 1904: 127, 142.
- Halictus chrysaspis Vachal, 1911: 18. NEW SYNON-YMY.
- Halictus myrrhites Vachal, 1911: 18. NEW SYNONY-MY.
- Halictus simotes Vachal, 1911: 22, 55. NEW SYNON-YMY.
- Halictus cerasis Vachal, 1911: 55. NEW SYNONYMY.
- Augochlora cladopyga Cockerell, 1914: 324. NEW SYNONYMY.
- Pereirapis rhizophila Moure, 1943a: 461. NEW SYN-ONYMY.
- Augochlorella bidentata Michener, 1954b: 57. NEW SYNONYMY.
- Augochlorella cerasis (Vachal): Moure in Ordway, 1966b: 511.
- Augochlorella chrysaspis (Vachal): Moure in Ordway, 1966b: 511.
- Augochlorella semiauratus (Spinola): Moure in Ordway, 1966b: 512.
- Pereirapis rhysophila Ordway, 1966b: 512. Lapsus calami.
- Augochlorella simotes (Vachal): Moure in Ordway, 1966b: 512.
- Augochlorella cladopyga (Cockerell): Moure in Ordway, 1966b: 512.
- Pereirapis caucasica (Radoszkowsky): Ebmer, 1977: 575.
- Pereirapis cerasis (Vachal): Moure and Hurd, 1987: 247.
- *Pereirapis chrysaspis* (Vachal): Moure and Hurd, 1987: 247.
- Pereirapis simotes (Vachal): Moure and Hurd, 1987: 248.
- Augochlora myrrhites (Vachal): Moure and Hurd, 1987: 277.
- Pereirapsis [sic] risofila Alves dos Santos, 1997: 6. Lapsus calami.
- Pereirapis myrrhites (Vachal): Moure, 1999: 83.

COMMENTS: Two synonymies are proposed above even though I have not had the opportunity to examine the type material firsthand. The first is *H. caucasicus* the holotype for which is located in the Institute of Systematic Zoology, Polish Academy of Sciences, Krákow. According to the curator the holotype is in poor condition and not suitable for shipment (W. Celary, personal commun., 1996). Father Ebmer (1977), however, had examined the type and considered it identical to *A. seminigra* and *A. bidentata*. I have seen the types of both *A. seminigra* and *A. bidentata* and am confident of Ebmer's comparisons. I therefore have considered *H. caucasicus* as identical to these latter two taxa and thereby as a synonym of *H. semiauratus*.

I have also not had the opportunity to see Padre Moure's types of *P. rhizophila* (located in DZUP), although I have seen specimens of this species identified by Moure. In 1944 and 1950 Moure considered his species as a synonym of *A. seminigra*. I am similarly confident with Moure's determination which accords with the specimens identified by him that I have examined. I therefore consider *P. rhizophila* as a synonym of *H. semiauratus*.

### Pseudaugochlora pulchra, new species

DIAGNOSIS: This enigmatic species can be easily recognized from currently known *Pseudaugochlora* species by the strongly protuberant clypeus, the ventrally bent mandible with its mediodorsal flange, the long prementum which extends posterad to the procoxae, the serrate malus, the outer hind tibial spur bent strongly at its apex, and the strong rugae of the propodeal basal area.

DESCRIPTION: Female. Total body length 11.34 mm; forewing length 7.7 mm. Head slightly wider than long (length 2.7 mm, width 2.8 mm). Mandible strongly bent ventrally near its midpoint with dorsal flange or lamellae leading to strong, rounded, subapical tooth. Labral basal area strongly delimited from distal process by carina. Clypeus strongly protruding from face in profile. Hypostomal ridge weakly lamellate. Prementum very long (although not narrowed; approximately 5.5 times longer than wide), extending posteriorly to procoxae. Glossa nearly as long as prementum. Maxillary palpi relatively short. Compound eyes only weakly converging below; strongly emarginate above level of antennae. Intertegular distance 1.96 mm. Strong anterior basitarsal brush; malus of antenna cleaner serrate; mesotibial spine very short and strongly bent inward at apex; outer hind tibial spur strongly bent inward towards apex; inner hind tibial spur with four long teeth (excluding apex). Basal vein distad cu-a by 4.5 times vein width; 1m-cu distad 1r-m by vein width; 2r-m distad 2m-cu by five times vein width; pterostigma narrow, barely wider than distance from C to Sc+R (including widths of these veins); first submarginal cell slightly longer than second and third combined; second cell not narrowed anteriorly; anterior border of third cell longer than that of second; distal hamuli arranged 3-1-1-2.

Clypeus with weak, coarse punctures separated by less than a puncture width, integument between imbricate; supraclypeal area as on clypeus although faintly imbricate and shining. Face below antennae with coarse punctures separated by less than a puncture width, punctures stronger than those of clypeus, integument between imbricate. Face above level of antennae with punctures smaller and contiguous; punctures becoming very weak by ridged vertex. Gena smooth with minute punctures separated by 3-4 times puncture width. Postgena imbricate and impunctate. Pronotum smooth with minute punctures separated by puncture width or less; laterally punctures disappearing. Mesoscutum with punctures separated medially by puncture width, integument between smooth; at borders punctures separated by less than width and much smaller, contiguous around parapsidal lines. Scutellum smooth with scattered large punctures. Metanotum weakly roughened. Preepisternum rugulose on upper border, otherwise strongly and contiguously punctured. Mesepisternum smooth with punctures separated by less than puncture width except on lower half punctures widely spaced. Metepisternum with weak transverse striae on upper third, remainder with scattered punctures and smooth integument between. Propodeal lateral surface punctured, punctures separated by less than puncture width, although on border with metepisternum and dorsal surface faintly imbricate, a few weak transverse striae near metacoxal base; posterior surface smooth with widely spaced punctures; basal area with strong rugae, integument between smooth. Anterior surface of T1 smooth with widely spaced minute punctures, medially with larger punctures separated by width or less, posterior border with microscopic punctures widely spaced; T2 with minute punctures separated by width, posterior border as for that of T1; T3-T5 imbricate; sterna imbricate with weak widely scattered punctures.

Mandible dark brown with reddish apex. Head brilliant metallic green with a few coppery highlights except apex of clypeus and antennae dark brown. Mesosoma brilliant metallic green with scattered copper highlights, highlights strongest on mesoscutum and pleura; tegula brown except metallic green on inner border. Wing membrane hyaline; veins dark brown. Legs brown with metallic green highlights on all surfaces except tarsi. Metasoma brilliant metallic green except apical margins of T1–T3 brown; sterna brown with strong metallic green highlights on apical halves.

Mandible with row of long, simple hairs on ventral margin. Face with scattered fuscous hairs, such hairs with a few short branches. Hairs of gena suberect and golden with a few short branches, progressively becoming longer ventrally towards border of gena and postgena. Postgena with long, branched, white hairs. Pronotum with minute, simple, appressed hairs on posterior border, dorsally on anterior border and medially; laterally such hairs nearly obscure the surface, thinning by pronotal lobe. Mesoscutum with scattered fuscous hairs similar to those of face. Scutellum and metanotum with pubescence similar to that of mesoscutum although much longer. Pleura with a few fuscous hairs as on mesoscutum, mostly with scattered golden hairs each with a few short branches. Scopal hairs white; remaining pubescence of legs gold except fuscous on outer surfaces of mesotibia, metatibia, outer surface of protarsus, and entirety of meso- and metatarsus. Propodeal lateral surface with hairs like those of pleura except intermixed wih short, simple, suberect white hairs; posterior surface with short hairs like that of lateral surface plus long white hairs with short branches. Terga with scattered suberect white hairs; anterior surface of T1 with long, mostly simple, gold to white hairs; T2-T6 with gradually more numerous fuscous hairs intermixed on lateral and posterior borders, such predominant by T5. Sterna with scattered, long, mostly simple, gold or fuscous hairs; fuscous hairs most predominant on S5-S6.

Male. Unknown.

HOLOTYPE: Female; Peru, Huánuco, Cueva de las Pavas, Tingo Maria, 12 July 1974, C. Porter and L. Stange (CUIC).

ETYMOLOGY: The specific epithet is derived from the Latin word *pulcher* meaning "beautiful."

COMMENTS: This species is quite unique among *Pseudaugochlora* and as more material is acquired it might be worthy of its own subgenus (particularly if related species are discovered). For now, however, I hesitate to recognize subgenera in *Pseudaugochlora* and leave such a determination to future students of the Augochlorini.

### Rhectomia mourei (Eickwort)

*Corynurella mourei* Eickwort, 1969a: 514. *Rhectomia mourei* (Eickwort): Engel, 1995b: 308.

NEW RECORD: One female; Bolivia, La Paz, Alto Río Beni, south of Río Inicua, 1100m, 15– 18 January 1976, L.E. Peña (AMNH).

COMMENTS: This is the first record of this genus from Bolivia.

**APPENDIX 2** 

# Character State Matrix for Genera of Augochlorini

Genera of Augochlorini are listed first. Outgroup genera are listed at the end and include the subfamily Nomiinae (Dieunomia and Lipotriches), tribe Nomioidini (Nomioides), and tribe Halictini (all remaining outgroup genera). Character descriptions are provided in the text. Daggers (†) indicate fossil taxa.

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AUGOCHLORINI	
Andinaugochlora	01000100110000001000111101101101000110110000
Ariphanarthra	00000110111000000000011120010000011002001000000
Augochlora	$0 \ddagger 02 02 02 00 11 01 00 01 00 01 11 12 00 10 10 00 11 10 00 01 00 00 00 00 00 $
Oxystoglossella	010202001101000100011120010100011100001000000
Augochlorella	01010100100100000100011120010000011012001000000
Augochlorodes	01010000110000000000111201100000110100010001000100001101000000
Augochloropsis	0200000011000001001111201101000111000000
Glyptochlora	020000001200000010111120110100011177777777
Paraugochloropsis	0200000011000001001111201101000111000000
Caenaugochlora	010001001100?00?000111201101000111100000001101201112010010
Ctenaugochlora	01000100110000010001111021010001111000000
Ceratalictus	01010000110000010000111100100000111110000
Chlerogas	0100110011000000000000111201100000011011
Chlerogella	010012001100000000000000000110000001000000
Chlerogelloides	01000200111000001002101001000011002000000
Corynura	0000000000000000000
Callistochlora	0000000000000000000
Halictillus	010100010000000000000010111100000110010000
Ischnomelissa	0100?1001100000000000000001100100000000
Megalopta	0010020011000110000011101110110110110110
Noctoraptor	0010020011000110000011001010101010110110
Megaloptidia	0100011011100100000111200101000011002001001
Megaloptilla	0101010011000000000001112001000001100100
Megommation	100101101110010000011010010000010002001011100011120210101100201000000
Cleptommation	10111000000001100000000000000010101010
Megaloptina	101110000000110101011000001000210101110000111010000110000111000000
Stilbochlora	0000000\$05555555
Micrommation	010001101710000000000111200100000177020077777777

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	APPENDIX 2
	Continued
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AUGOCHLORINI (continued)	ted)
Neocorynura	010000001100000?0?01112011000001101100000000
Neocorynurella	01000000110000000000011120110100011011000000
†Oligochlora	0202000212000000000111101101101177777777
Paroxystoglossa	0101000011000000001011120010100011011000000
Pereirapis	01020100110000010001102001000001111000000
Pseudaugochlora	01010110110000000000011120110100011010001000020110131110000100300000110000301110100001
Rhectomia	0000000000001102011000001100000010000000
Rhinocorynura	1000000000001011120110000011010000101000001111201002720
Temnosoma	020000001100000100011000000000000001100000
Thectochlora	010200001100000001001001011011011001000000
Xenochlora	00100200110000100000111011100000110????????
INIGIOIMON	
Nomioides	0100020010000000000011020110100001011011
HALICTINI	
Agapostemon	01000100030000000000000000011000
Caenohalictus	0000100000111201100000001101000100000011000000
Habralictus	00000000000111201100000010; $1010000000000000000000000000000000000$
Habralictellus	112000000001112011001000122101000000000
Halictus	000000000011120110000001??1010000000000
Homalictus	$0 \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\$
Lasioglossum	0000000000011120110010?01??10100000?00?00?0011000001000300000000
Mexalictus	10030000000000000
Ruizanthedella	10000000000000000000
Zonalictus	0
NOMIINAE	
Dieunomia	
Lipotriches	0

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### APPENDIX 3

### Species of Augochlorini Examined for Phylogenetic Studies

Halictid bee species examined in the course of these studies. Daggers (†) indicate fossil species. Not all characters were coded from each species (e.g., males are unknown for some species and others are represented solely by the holotype, thereby excluding them from some of the dissections necessary to examine certain traits). Many additional species have been studied (particularly in the genera *Augochloropsis*, *Caenohalictus*, *Dialictus*, *Megalopta*, and *Neocorynura*), but these were not focused on in great detail or used in constructing the data matrix presented in appendix 2. Specimens are deposited in the institutions listed under Materials and Methods.

### SUBFAMILY HALICTINAE

AUGOCHLORINI: Andinaugochlora: A. joannisi (Vachal), A. micheneri Eickwort, Andinaugochlora spp. 1-3; Ariphanarthra: A. palpalis Moure; Augochlora (Augochlora): A. buscki Cockerell, A. decorata (Smith), A. esox (Vachal), A. essequibensis Cockerell, A. foxiana Cockerell, A. hallinani Michener, A. ignifera Crawford, A. mulleri Cockerell, A. nigrocyanea Cockerell, A. pachytes (Vachal), A. praeclara Cresson, A. pura (Say), A. regina Smith, A. repandirostris (Vachal), A. smaragdina Friese, Augochlora (Augochlora) spp. 1–4; Augochlora (Oxystoglossella): A. antonita Michener, A. aurifera Cockerell, A. cordiaefloris Cockerell, A. matucanensis Cockerell, A. nominata Michener, A. rightmyerae Engel (see appendix 1), A. thalia Smith, Augochlora (Oxystoglossella) spp. 1–3; Augochlorella: A. aurata (Smith), A. bracteata Ordway, A. comis (Vachal), A. edentata Michener, A. gratiosa (Smith), A. neglectula (Cockerell), A. persimilis (Viereck), A. pomoniella (Cockerell), A. striata (Provancher), A. urania (Smith), Augochlorella spp. 1-2; Augochlorodes: A. turrifaciens Moure; Augochloropsis (Augochloropsis): A. auriventris (Friese), A. brachycephala Moure, A. callichroa (Cockerell), A. flammea (Smith), A. ignita (Smith), A. multiplex (Vachal), A. notophos (Vachal), A. wallacei (Cockerell); Augochloropsis (Glyptochlora): A. atropos (Smith), A. ornata (Smith), A. refulgens (Smith); Augochloropsis (Paraugochloropsis): A. anonyma (Cockerell), A. auriferina Michener, A. aurifluens (Vachal), A. chloera (Moure), A. crassiceps Moure, A. cupreola (Cockerell), A. electra (Smith), A. hebescens (Smith), A. iris (Schrottky), A. metallica (Fabricius), A. smithiana (Cockerell) [= A. aphrodite (Schrottky)], A. sthena Schrottky, A. sumptuosa (Smith), A. vesta (Smith) [= A. nigriscopis (Vachal)], Augochloropsis (Paraugochloropsis) sp. 1-6; Caenaugochlora (Caenaugochlora): C. costaricensis (Friese), C. cupriventris (Vachal), C. elisabethae Engel, C. flagrans (Vachal), C. gemmella (Cockerell), C. inermis (Vachal), C. jeffreyi Engel, Caenaugochlora (Caenaugochlora) spp. 1-2; Caenaugochlora (Ctenaugochlora): C. algeri Engel, C. beethoveni Engel, C. donnae Engel, C. perpectinata (Michener); Ceratalictus: C. ischnotes (Vachal), C. stigon (Vachal), C. clonius (Brèthes) [= C. theius (Schrottky): see Moure, 1999]; Chlerogas: C. araguaensis Brooks and Engel, C. boliviensis Brooks and Engel, C. chlerogas (Vachal), C. colombiensis Brooks and Engel, C. cyaneus Brooks and Engel, C. hirsutipennis Cockerell, C. nephos Brooks and Engel, C. tiara Brooks and Engel, C. townesi Brooks and Engel; Chlerogella: C. elongaticeps Michener, C. nasus (Enderlein), Chlerogella spp. 1-15; Chlerogelloides: C. femoralis Engel et al., C. simplex Engel and Brooks; Corynura (Callistochlora): C. chloris (Spinola), C. prothysteres (Vachal); Corynura (Corynura): C. apicata (Spinola), C. chilensis (Spinola), C. corinogaster (Spinola), C. cristata (Smith), C. herbsti (Alfken), C. rubella (Haliday); Halictillus: Halictillus spp. 1-3; Ischnomelissa: I. cyanea Brooks and Engel, I. ecuadoriana Brooks and Engel, I. lescheni Brooks and Engel, I. octogesima Brooks and Engel, I. rhina Brooks and Engel, I. zonata Engel; Megalopta (Megalopta): M. amoena (Spinola), M. centralis Friese, M. ecuadoria Friese, M. fornix (Vachal), M. genalis Meade-Waldo, M. ochrias (Vachal), M. purpurata (Smith), M. sodalis (Vachal), Megalopta spp. 1-4; Megalopta (Noctoraptor): M. byroni Engel et al., M. noctifurax Engel et al.; Megaloptidia: M. contradicta (Cockerell), M. nocturna (Friese), M. saulensis Engel and Brooks; Megaloptilla: M. callopis (Vachal), M. byronella Engel and Brooks; **Megommation** (Cleptommation): M. minutum (Friese); Megommation (Megaloptina): M. ogilviei (Cockerell), M. festivagum (Dalla Torre), Megommation (Megaloptina) sp.; Megommation (Megommation): M. insigne (Smith); Megommation (Stilbochlora): M. eickworti Engel et al., Megommation (Stilbochlora) sp.; Neocorynura: N. cercops (Vachal), N. colombiana Eickwort, N. discolor (Smith), †N. electra Engel, N. fumipennis (Friese), N. oiospermi (Schrottky), N. panamensis Engel, N. papallactensis Engel, N. rhytis (Vachal), N. rufa Michener, N. sulfurea Engel, Neocorynura spp. 1-7; Neocorynurella: N. cosmetor (Vachal) (see appendix 1), N. seelevi Engel and Klein, N. virida Engel and Klein (nomen emendatum); †Oligochlora: †O. eickworti Engel, †O.

grimaldii Engel, †O. micheneri Engel, †O. rozeni Engel (appendix 1), *†Oligochlora* sp. (Engel and Rightmyer, in press); Paroxystoglossa: P. andromache (Schrottky), P. barbata Moure, P. brachycera Moure, P. crossotos (Vachal), P. jocasta (Schrottky), P. mimetica Moure, P. seabrai Moure, P. spiloptera Moure, P. transversa Moure; **Pereirapis:** P. semiaurata (Spinola) (see appendix 1); Pseudaugochlora: P. crawfordi (Vachal), P. graminea (Fabricius), P. pandora (Smith), P. praepotens (Vachal), P. sordicutis (Vachal) [= P. nigerrima (Friese)], P. pulchra Engel (see appendix 1); Rhectomia: R. harrisoni Engel, R. liebherri Engel, R. mourei (Eickwort), R. pumilla Moure, Rhectomia spp. 1-2; Rhinocorynura: R. briseis (Smith), R. crotonis (Ducke), R. inflaticeps (Ducke); Temnosoma: T. metallicum Smith, T. smaragdinum Smith; Thectochlora: T. alaris (Vachal); Xenochlora: X. chalkeos Engel et al., X. ianthina (Smith), X. nigrofemorata (Smith), X. ochrosterna Engel et al.

**NOMIOIDINI:** *Nomioides: N. variegatus* (Olivier).

HALICTINI: Agapostemon: A. poeyi (Lucas),

A. sericeus (Forster), A. texanus Cresson, A. viequesensis Cockerell; Caenohalictus: C. eberhardorum Michener, Caenohalictus spp. 1-5; Dialictus: D. breedi (Michener), D. busckiellus (Cockerell), D. mestrei (Baker), D. parvus (Cresson), D. proangularis (Ellis), Dialictus spp. 1-6; Habralictus: H. bimaculatus Michener, H. canalictulatus Moure, Habralictus spp. 1-2; Habralictellus: H. auratus (Ashmead), Habralictellus spp. 1-3; Halictus: H. farinosus Smith, H. ligatus Say; Homalictus: H. dampieri Cockerell, Homalictus sp.; Lasioglossum: L. coriaceum (Smith), crocoturum (Vachal), L. leucozonium L. (Schrank), L. trizonatum (Cresson); Mexalictus: M. arizonensis Eickwort, M. mexicanus Eickwort, M. micheneri Eickwort, Mexalictus spp. 1-3; Ruizanthedella: R. mutabilis (Spinola), R. nigrocaerulea (Spinola); Zonalictus: Z. rufobasalis (Alfken), Z. viridifilosus (Cockerell).

### SUBFAMILY NOMIINAE

Dieunomia: D. heteropoda (Smith), D. triangulifera (Vachal); Lipotriches: Lipotriches sp.

### **APPENDIX 4**

# Sources of Nest Architectural Characters

Information on the nesting biology of halictine genera was extracted from the sources indicated below. These data were used in constructing the matrix presented in appendix 2.

Agapostemon: Abrams and Eickwort (1980), Eickwort (1981), Eickwort and Eickwort (1969), Roberts (1969); Augochlora: Engel (personal obs.), Eickwort and Eickwort (1973b), Sakagami and Moure (1967), Stockhammer (1966); Augochlorella: Engel (personal obs.), Eickwort and Eickwort (1973a), Knerer and Atwood (1962), Ordway (1961, 1966a), Sakagami and Moure (1967); Augochlorodes: Michener and Seabra (1959); Augochloropsis: Michener and Lange (1959), Michener and Seabra (1959); Caenaugochlora: Michener and Kerfoot (1967: as Pseudaugochloropsis); Caenohalictus: Michener and Lange (1958b: as Caenaugochlora), Michener et al. (1979), Sakagami and Moure (1967); Callistochlora: Claude-Joseph (1926: as Halictus); Corynura: Claude-Jospeh (1926: as Halictus); Dialictus: Engel (personal obs.), Michener and Seabra (1959), Michener et al. (1979), Sakagami and Moure (1967); Dieunomia: Cross and Bohart (1960: as Nomia), Parker et al. (1986: as Nomia),

Rau (1929: as Epinomia), Wcislo (1993), Wcislo and Engel (1996); Habralictus: Michener and Lange (1958b), Michener et al. (1979); Halictillus: Claude-Joseph (1926: as Halictus); Halictus: Eickwort (1985); Lasioglossum: Knerer and Atwood (1962); Lipotriches (= Rhopalomelissa sensu Pauly, 1990): Hirashima (1961), Michener (1969b), Wcislo and Engel (1996); Megalopta: Janzen (1968), Sakagami (1964), Sakagami and Moure (1967); *Megommation*: Jörgensen (1912: as Megalopta), Michener and Lange (1958b), Sakagami and Moure (1967); Neocorynura: Michener et al. (1966), Sakagami and Moure (1967), Schremmer (1979); Nomioides: Pesenko (1983); Oxystoglossella: Eickwort and Eickwort (1972), Sakagami and Moure (1967); Paraugochloropsis: Eickwort and Sakagami (1979), Michener and Lange (1959); Paroxystoglossa: Michener and Lange (1958a, b), Michener and Seabra (1959); Pereirapis: Eickwort and Sakagami (1979), Oliveira Campos (1980); Pseudaugochlora: Michener and Lange (1958b), Sakagami and Moure (1967: as Pseudaugochloropsis); Rhinocorynura: Eickwort and Sakagami (1979); Ruizanthedella: Claude-Joseph (1926: as Halictus); Xenochlora: Engel et al. (1997), Smith (1861: as Megalopta).