WEB-INTEGRATED TAXONOMY AND SYSTEMATICS OF THE PARASITIC WASP FAMILY SIGNIPHORIDAE (HYMENOPTERA, CHALCIDOIDEA)

A Dissertation

by

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ABSTRACT

This work focuses on the taxonomy and systematics of parasitic wasps of the family Signiphoridae (Hymenoptera: Chalcidoidea), a relatively small family of chalcidoid wasps, with 79 described valid species in 4 genera: *Signiphora* Ashmead, *Clytina* Erdös, *Chartocerus* Motschulsky and *Thysanus* Walker. A phylogenetic analysis of the internal relationships in Signiphoridae, a discussion of its supra-specific classification based on DNA sequences of the 18S rDNA, 28S rDNA and COI genes, and taxonomic studies on the genera *Clytina*, *Thysanus* and *Chartocerus* are presented. In the phylogenetic analyses, all genera except *Clytina* were recovered as monophyletic. The classification into subfamilies was not supported. Out of the four currently recognized species groups in *Signiphora*, only the *Signiphora flavopalliata* species group was supported. The taxonomic work was conducted using advanced digital imaging, content management systems, having in sight the online delivery of taxonomic information. The evolution of changes in the taxonomic workflow and dissemination of results are reviewed and discussed in light of current bioinformatics. The species of *Thysanus* and *Clytina* are revised and redescribed, including documentation of type material. Four new species of *Thysanus* and one of *Clytina* are described. The taxonomy of *Chartocerus* is reviewed, including redescriptions of 25 out of 33 currently valid species, most based on type or topotypical material.

To my grandparents.

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CHAPTER I

INTRODUCTION

Chalcid wasps represent one of the most diverse groups of Hymenoptera, with about 22,000 described species and possibly up to 500,000 species (Noyes 2003). The present work focuses on the taxonomy and systematics of the parasitic wasps of the family Signiphoridae (Hymenoptera: Chalcidoidea), a relatively small family of chalcidoid wasps, with 79 described valid species (Noyes 2013) in 4 genera: *Signiphora, Clytina, Chartocerus* and *Thysanus*. These minute (less than 0.5 to 2mm) wasps are mostly primary or secondary parasitoids of sternorrhynchous Hemiptera (scale insects, mealybugs, psyllids); some species parasitize fly puparia and others have been reared from the eggs of mirid bugs and buprestid beetles (Woolley 1997; Woolley and Hanson 2006). Most species are Neotropical, although some seem to be cosmopolitan and might represent complexes of cryptic species. There is scarce information about the biology of signiphorids (Appendix A: Table 1); detailed life history studies are available for only four species: *Signiphora borinquensis* (Quezada et al. 1973), *Signiphora coquilletti* (Woolley and Vet 1981), *Chartocerus elongatus* (Clausen 1924) and *Chartocerus subaeneus* (Rosen et al. 1992).

Studies on material collected in the past 20 years have revealed a significant number of new species, notably from Costa Rica (Gaston et al. 1996, Noyes 2012) and Ecuador (Erwin 1982). The last comprehensive taxonomic review at the species-level was by Girault (1913). Rozanov (1965) published a review at the generic level, and Woolley (1988) redefined the genera based on phylogenetic relationships. Some regional accounts were published (DeSantis 1973 for Argentina, Myartseva 2005 for Mexico, Hayat 2009 for India), but most of the available recent literature present lists and keys only go to genus-level (Gibson 1993, Hanson 1995, Woolley 1997, Woolley and Hanson 2006, Gibson 2006). The current intrafamilial classification is based on hypotheses of morphological synapomorphy only (see Woolley 1988, Gibson et al. 1999). Therefore, phylogenetic studies including molecular data would contribute to the stability of the classification of this group.

Homoplasy of morphological characters made the production of a phylogeny for Chalcidoidea a formidably challenging task which has recently been addressed with the collective effort of over twenty researchers (Munro et al. 2011, Heraty et al. 2013) and development of specialized techniques of curation and visualization. Such difficulties have historically impacted the classification to the point that some authors have openly refrained from proposing taxonomic changes until a solid phylogeny had been achieved (Hanson and LaSalle 1995). Signiphoridae is not an exception. It has already been nested within Eulophidae, Encyrtidae and Aphelinidae (see Chapter III); taxonomic instability is very evident in the group as well. Woolley (1986) published a complete account of the tortuous path of the many nomenclatural issues involving this family.

The main difficulties for taxon identification in Signiphoridae, as with other chalcidoids, are the markedly reduced dimensions and accompanying numerous modifications of morphological features, many of which are characters that are only observable on slides. Many species are superficially similar, and their differentiation only became apparent after reviews in the 1980s, resulting in large amounts of misidentified material, which also impacts host records. This also has implications for economic entomology, since hyperparasitoids are considered a problem in IPM programs based on biological control, and Signiphoridae includes both primary parasitoids and hyperparasitoids. Thus, a phylogenetically meaningful classification is desirable because it would not only contribute to the taxonomic stability of the group, but also to the understanding of evolution of hyperparasitism, host shifts between very distinct groups (Hemiptera and Diptera) and biogeographic distribution.

SUMMARY OF CHAPTER CONTENTS

While incorporating both “traditional” and “new” approaches, as described originally among the objectives of the NSF-PEET (Partnerships for Enhancing the Expertise on Taxonomy) grant (Heraty and Woolley 2007), the present work has been produced in a context in which workflows in taxonomy have been under intensifying scrutiny by governmental entities and non-taxonomist scientists for about 10 years. One of the earliest meetings of this project was a workshop at UC-Riverside in May 2008, for the discussion of available tools to establish a workflow for the future taxonomic studies. We wanted especially to attend the new demands for the publication of results, which presently go beyond the publication of a journal article.

In an effort to understand these demands and what they actually meant in terms of workflow for a taxonomist, a brief discussion of context and the evolution of the changes in the workflow and dissemination of results is presented in Chapter II. It is not an attempt to list every application resulting from the efforts in developing Biodiversity Informatics, especially because large efforts have already performed this task (Tann and Flemons 2009, iDigBio 2011, TDWG), but an attempt to understand how the expansion of digital formats affect the individual researcher.

In the following chapters, we present a phylogenetic analysis of the internal relationships in Signiphoridae and a discussion of its supra-specific classification (Chapter III), and taxonomic studies on the genera *Clytina*, *Thysanus* and *Chartocerus* (Chapters IV and V), where the tools discussed in Chapter II were applied.

DISSERTATION OBJECTIVES

The following objectives were the aim of this work:

1. Revise the genera and species of *Thysanus* Walker, 1840, *Clytina* Erdös, 1957 and *Chartocerus* Motschulsky, 1859 (Signiphoridae), applying methods of content management, digital imaging, and online delivery of taxonomic information.
2. Explore the internal phylogenetic structure within Signiphoridae, integrating morphological and molecular data with phylogenetic methods.

CHAPTER II

BACKGROUND

OVERVIEW

Taxonomy was one of the first branches of biology to embrace digital technologies for management of raw data, beginning with museum initiatives in the 1970s. Almost 40 years later, the accelerated development of information technologies has led to unprecedented availability of content to users of taxonomic information, both academics and the general public. All taxonomic research involves management of a considerable assortment of types of primary data, such as specimen records, geographic information, molecular data, image archives and controlled vocabularies. However, most of the resources available to recognize, compile, manage and share this kind of information are focused on institutional data providers. The decisions that have to be taken by the individual researcher have only recently started to be the focus of discussions, in spite of the importance of taxonomic revisions in the validation and consequently reliability of data that reaches public databases. In this chapter, I discuss some issues we faced when producing the taxonomic work presented in chapters IV and V, focusing on the increasing identity of taxonomy with other disciplines of information science. This hopefully will be useful not only to provide background information on the epistemological context in which the taxonomic studies for this dissertation were conducted, but also to help future work in digital content-rich taxonomic revisions.

INTRODUCTION

Taxonomy and systematics (a.k.a. biodiversity studies) have changed substantially since the second half of the 20th century, and especially in the last 15 years. The increase in availability of digitization resources, the popularization of the Internet and advances in information technology can make taxonomic information promptly available to other academics and the general public through online databases and data mining. At the same time, there has been increasing political pressure for changes on environmental policies, which creates demand for information about diversity and species richness in formats beyond the ones usually provided by publication in scientific journals (Godfray and Knapp 2004, Smith et al. 2009, 2013).

The necessity of management, annotation and dissemination of primary data is part of a series of changes that began to affect taxonomy in the 20th century, starting with the paradigm shift when phylogenetic systematics became a significant guiding principle to taxonomic practice. The current changes relate to how Internet databases became a disruptive technology (*sensu* Christensen 1997, Hardisty et al. 2013) that impacted the workflow and tools used by taxonomists mainly by changing the means through which the results, or part of the results, are published (Smith 2009).

“TAXONOMIC IMPEDIMENT”

The pressure to “change” and “speed up” the discovery of species started to increase in the early 1990s, when international meetings such as the Convention for Biological Diversity (CBD) (United Nations 1993), political entities (e.g. Select Committee on

Science and Technology 2002) and scientific committees (e.g. NSB 1989, Systematics Agenda 2000) started to stress the central role of taxonomy in discovering and managing biodiversity on a global scale. The debates that led to these documents brought to focus a sense of urgency to "name and document all species in the world before they go extinct", which was already familiar to naturalists and environmentalists (Wilson 1988, Wheeler et al. 2012).

With estimates of extant species ranging from 3 million to as high as 100 million (Caley et al. 2014), and only 1.2 million species described (Mora et al. 2011) since the beginning of biological nomenclature with the Systema Naturae, it is not surprising that some would attribute these discouraging estimates to the methods of taxonomy itself, which allegedly have not changed much since the 1700s. Among the most common criticisms are that it is "too slow to modernize itself" or "too bound by tradition" (Hine 2008). These criticisms were intensified after the Earth Summit 2002 (Rio+10) conference in Johannesburg, after which proposals such as the Encyclopedia of Life (Wilson 2003) and DNA Barcoding (Hebert et al. 2003) came forward, resulting in intensifying scrutiny of workflows in taxonomy by governmental entities and non-taxonomist scientists. Taxonomic methods have been challenged by proponents of new ways to manage names (DeQueiroz & Gauthier 1994) or even to validate taxa (Godfray 2002; Tautz et al. 2003; Godfray et al. 2007; Mayo et al. 2008; Riedel et al. 2013) under the assumption that traditional methods are not efficient enough (but see discussions in Lipscomb et al. 2003; Mallet & Willmott 2003; Knapp et al. 2004; Carvalho et al. 2007).

The CBD and later discussions highlighted two main issues: first, the "taxonomic impediment", or the effect of scarcity of taxonomists in biology (Taylor 1983; New 1984; Wheeler 1990; Hoagland 1995); second, "data repatriation", refers to overcoming an overall inequality in the distribution of taxonomic resources, i.e. while expertise and archives tend to be located in richer nations, the core of undescribed biodiversity is concentrated in developing nations (GBIF 2008). The proposed solution was to make resources openly available (United Nations 1993, art. 17), including taxonomic information, type material, basic literature, etc., and support the work of scientists in the region of origin of the described organisms by cooperating in education and training of personnel. In this sense, "making resources openly available" would translate into massive digitization projects.

ISSUE 1: PUBLICATION VS. DISSEMINATION

Publication Format

After the CBD, many initiatives were started in the 1990s, such as large-scale inventories, funding programs for training new taxonomists, development of new methods to voucher specimens, and organizing and serving taxonomic and ecological information to the public (Rodman and Cody 2003; Canhos et al 2004; Los and Hof 2007). The immediate result was a proliferation of alternative database models applied to biodiversity studies, many of them redundant in structure and purpose (Mallet and Wilmott 2003; Johnson 2007). The Biodiversity Information Projects of The World database (TDWG 2014) currently lists 684 projects ranging from regional checklists to worldwide data aggregators.

There is also an increased expectation that taxonomy should have a strong component of web services and computational frameworks, as well as open access to primary data (Costello 2009). As described by Johnson (2007), there is considerable structure in place to facilitate data capture and sharing by collections, especially for material collected after the database structures are in place. However, for "retrospective data capture", that is, capture of information from specimens collected and sorted previously to a database structure, often this has to be done in a specimen-by-specimen basis, due to the variability of label formats and need for interpretation. For this and several other curatorial reasons, the ECN (Entomological Collections Network) has recommended that this retrospective data capture be done as part of taxonomic research (Thompson et al. 1990; Thompson 1994). Some institutions have also turned to crowdsourcing as an alternative approach to this problem (Smithsonian Transcription Center; Notes from Nature).

For the individual researcher, however, specimen data capture and related activities are seen as tasks preliminary to research, though important nonetheless. The first complicating factor is that there are few clear pathways in place for the researcher to easily share primary data, in spite of the obvious value added to data quality with the examination by experts (Soberón and Peterson 2004; Smith 2009). Second, besides being a time-consuming enterprise, this effort usually does not result in a peer-reviewed publication in a scientific journal (Costello 2009, McDade et al. 2011, Smith et al. 2013). Third, specimen data capture brings back to focus questions involving data management, intellectual property (Patterson et al. 2014), authorship credit (Graves 2000), verifiability, and stability (Bastow and Leonelli 2010; Vision 2010; Duke and Porter 2013).

Huang et al. (2012) published the results of a questionnaire submitted to scientists working in biodiversity and conservation, and the overall result evidences that authorship credit is still an important concern: while 84% of the respondents agreed that sharing primary data is a basic responsibility of researchers and 91% considered this "very important", 65% said they are unwilling to share data that was not published, i.e. in scientific journals. Thus, they conclude that there is an "underdeveloped culture of data sharing". Agosti and Johnson (2002, 2005) also point out that intellectual property laws also delay or block access to data relevant to biodiversity research. Costello et al. (2013) revised the authorship credit issues and pointed at proposed solutions to peer-review, publish and reference data sets independently from scientific papers. Fortunately, some data repositories, data aggregators and the ICZN have been proving to be notably good at acknowledging publication and attribution issues, by encouraging researchers' feedback and suggestions and by including data usage disclaimers whenever their system receives a query.

The acceptance of species names published in electronic journals by the International Commission on Zoological Nomenclature (ICZN 2012) validated the digital medium as a publishing format for taxonomy. There is indication that online activity and digital works, including publication of primary data, are starting to be seen positively in terms of scientific production (Informe ENSP 2012, Mewburn and Thompson 2013), and new solutions to make the publication of data citable (Chavan and Penev 2011), i.e. out of the realm of "grey literature". This is especially important for taxonomy because it rewards the efforts made by this academic community to increase its representation in media for the general public, moving away from the stereotypical image of "outdated" or "cheap" science (Hine 2006, 2008). This image continues to have a negative impact on research, funding, and public image, which can range from comic to disastrous. Thus, when selecting the tools to produce the taxonomic revisions, we looked for solutions for publishing our species descriptions that would make them Internet-friendly (hypertext-friendly, and ideally, XML-friendly), going beyond the journal text article format.

Taxonomy as Multi-Layered Discipline

Taxonomy can be understood as both a traditional, hypothesis-and-fact driven science and an information science. The work of a taxonomist, when analyzing specimens, is driven by decisions and hypotheses about what species do these specimens represent (Gaston and Mound 1993, Wheeler 2004). Names are produced after studies that include both evolutionary relationships and ecological context; results that are needed by other areas of biology. Upon identification of characters and phylogenetic analyses, the scientist tests if the proposed groups are defensible as a meaningful group (i.e. a real species) or not. This process is not always straightforward, and what sets of traits should be used to make inferences about where the limit between two species lies has been the object of an extensive scientific debate also known as the "species problem" (Coyne and Orr 2004; Wilkins 2009, 2011 provide lists and reviews of a number of the concepts involved). On the other hand, taxonomy is also the branch of biology responsible for and organizing the basic units, the names, to which all information on organisms, from molecular data to behavior and community ecology, are attached (Wagele et al. 2011).

While managing nomenclatorial issues, one of the central matters of taxonomy could be summarized as ensuring that for each species there is only one valid scientific name. At one end, this is made by anchoring names to specimens and identifying any synonymies; at the other, by preventing homonyms. This principle is at the very base of the reasoning of controlled vocabularies in information science. In zoological taxonomy, a formal set of rules similar to controlled vocabularies was already being proposed as early as the 1840s and originated the ICZN (Melville 1995; Strickland et al. 1843). Early forms of indexing in zoological taxonomy also date from the same period: Louis Agassiz published the first Nomenclator Zoologicus between 1842 and 1847, the Zoological Record was started in 1864, and the Index Animalium was published in 1902 (Bowley and Smith 1968, Michel et al. 2009, ICZN 2014).

A lack of understanding of the two scientific roles played by taxonomy can explain much of the post-CBD criticism posed by non-taxonomists (Carvalho et al. 2007), such as calls for automation of the process of description of new species and proposals to adopt one single taxonomy ("*the point is for the user community to be protected from the confusion of a plethora of different hypotheses*"- Godfray et al. 2007). In fact, the display of multiple taxonomic concepts, so that the scientific process of taxonomy is less "hidden" from the public, has been demonstrated to be possible– see Franz and Peet (2009) and Jones et al. (2011).

Perhaps part of the reason why some researchers fail to perceive the hypotheses testing aspect of taxonomic work is the structure of taxonomic papers themselves. The telegraphic language of descriptions, jargon, and conventions used in taxonomic catalogues are rather cryptic to researchers in other life sciences; unlike in other areas, the omission of the methods section apart from mentioning sources of materials is common, and the equivalent to a "discussion" section is usually included in a "comments" or "remarks" paragraph within the species descriptions. Nevertheless, it is often not obvious even to taxonomists themselves that this problem in communication exists (Joppa et al. 2011; Garnock-Jones 2013). The result is that much of the hypotheses-driven work in taxonomy presents itself as “common knowledge” or even non-existent to other authors, and therefore descriptions, keys and revisions are not included in reference citations. Thus, other authors often omit the information on how the very organisms used in their articles were identified, and taxonomic papers are not cited, thus creating a “citation gap” between taxonomy and the other areas of biology (Agnarsson and Kuntner 2007; Seifert et al. 2008, Wagele et al. 2011). This “citation gap” is one among a variety of problems faced by the taxonomists. As indicated by Rafael et al. (2009), for these researchers, the undervaluing of taxonomic works in terms of impact factor (IF) is an additional challenge in a list that also includes infrastructural problems and difficulties of access to material, as discussed previously. Because citation indexes are increasingly used as measurement units of academic productivity, much criticism and alternative measures of productivity have been published (Ebach et al. 2011; Valdecasas 2011).

Unfortunately, there seems to be little that an individual researcher can do to address these particular problems. One possible change, which can already be noticed in some recent publications (for example, Talamas et al. 2009, Winterton 2011, Liew et al. 2014), is to provide as much methodological details as possible in the taxonomic papers, including everything from search criteria in databases, tools, etc. to highlighting scientific arguments to follow or propose a taxon concept. This might help a non-taxonomist peer to understand that the research includes more than descriptive information that could be summarized by pictures. Another change that could help strengthen the perception of taxonomy as producer of data, besides organizing it, would be to submit data to journals that legitimize the publication of primary data as peer-reviewed articles (Costello 2009, Smith 2009, Chavan and Penev 2011), especially while the digital publication of data is not formally accepted as publication in terms of academic productivity. However, the change that could potentially produce the most impact would come from the user of taxonomic information, by citing the sources that allowed the identification of the material used for a study, including identification keys, species descriptions, or direct help from specialists, and it is interesting to note that some journal editors have begun to encourage authors to include such information in their articles.

ISSUE 2: HYPERTEXT IS NOT JUST TEXT

Shifts in Media Format

The information-storage role of taxonomy was strongly impacted by advances in library and information science, which induced changes in the format of taxonomic publication: there has been a shift from books and journals stored in libraries to online articles, digital books and databases (Curry and Humphries 2007, Miller et al. 2012). The availability of electronic tools has increased in an almost geometric progression, and a few years can mean a complete transformation in the way the information is served to the public (Bisby 2000) or to researchers themselves.

When a new type of medium or technology appears, it is often understood as a replacement to another, doing something with more efficiency; however, as it develops, it transcends its “original” use (McLuhan 1964; McLuhan and Fiore 1967; Eno 2013). As the usage of a medium evolves, its own “language” begins to diverge and acquire its own set characteristics. In other words, it develops its own set of tools that are able to store kinds of information that other media cannot. In the case of the present work, this is illustrated by the relationship between electronic text versus print journals, or “cybertaxonomic” publications and “traditional” revisionary monographs.

Two of the most important elements that distinguish electronic text from the print journal are hyperlinks and marked-up text. Hyperlinks (or “links”) are defined simply as a “reference to data” in an electronic document (Merriam-Webster 2014). Markup languages are used to annotate digital text with elements that are syntactically different from the text itself, such as typeset appearance instructions. Because of those two elements, an electronic document can store a lot of information but display very few words. This goes a level beyond “intertextuality” as it occurs in literary text (see Chandler 2014), because not only the information exchanged between texts or documents may be referenced, but it is also explicitly displayed, or even contained in the same document.

In the case of electronic publications, one could understand them as originally intended as a “replacement” to print text, i.e. text ownership is very clear and links only allow the user to move between documents (web 1.0). As the digital medium and markup languages evolved, the instructions passed by the user interface could then interact with scripts that store content in a database. That way, content produced by the user can be contributed and appear online in real time. Thus, the user/reader is no longer just a consumer of information, but also producing and sharing (web 2.0). In a next step, markup languages connect not only a page and a database that stores content, but also contains instructions to connect databases by submitting queries that are embedded in hyperlinks. Therefore, markup may not only carry information that would facilitate the user’s work (viewing formatted text or submitting content), but allow content to be identified and read by applications. This step allows content to be curated, and therefore semantic meaning (read by applications, not the user) is added to the code (web 3.0).

For example, a scientific name can be displayed with the tags <i>Genus species</i>, but that would only tell the web browser to display those words in italics. Extended markup (XML, XHTML and later) allows tags such as <scientificname>Genus species</scientificname>. This is not relevant for the user who is seeing the name displayed on the screen, but can be used by applications external to that site to find all scientific names in that document. Note that all three levels of organization (web 1.0, 2.0, 3.0) can occur at the same time, for example, semantic markup annotation (3.0) can be applied to a regular electronic text (1.0), while at the same time a user can be adding notes about that document (2.0) in a different section of the same page.

The central point to be noted here is that an electronic publication is very different from a print paper, even if their structures are visually similar, and this has consequences for the author. First, the amount of data contained in both documents is not really comparable. The electronic format can store far more of the information produced in taxonomic revisions, because it increases the visibility of the background work on primary data and allows the researcher to send this data to permanent repositories (such as GenBank, MorphBank) and still embed this information in the publication (Johnson 2007). Second, the data in electronic documents can be fragmented by the use of tags and re-used in other documents and research (Hardisty et al. 2013). This can bring up questions regarding authorship credit, as discussed previously, but also allows research products to be more efficiently discovered and integrated in other projects (Walls et al. 2014), helping address the issues of data repatriation and taxonomic impediment.

Unique Identifiers and Semantics

Two elements that increased in importance with electronic publications were the attribution of unique identifiers to objects (to specimens, lots, images, DNA sequences, among others) and data annotation. These issues are interrelated, since data annotation in this context would be made aiming at database interoperability, which, to be achieved for online documents, needs unique identifiers and markup standards.

Edwards et al. (2000) discussed the need for unique identifiers and standardization in biodiversity science so that databases could communicate, when describing the basic elements for the GBIF Data Portal. That necessity arises from a problem that has been acknowledged since museums started to “computerize” their collections: there is nothing mandating a standard structure or application when these databases are developed (Sarasan 1983, Johnson 2007, Vandervalk et al. 2009), consequently limiting the distribution of queries and data across databases. The term “Deep Web” was coined by Bergman (2001) to refer to this large amount of information that does not have a discoverable web address, i.e. is “hidden” in databases that are not read by any site other than its own portal, thus only available when requested and not found by search engines.

Vanderwalk et al. (2009) give a history of development of semantic elements, unique identifiers and databases and discuss further the concepts of URI (Unique Resource Identifier), the importance of their stability (see also Berners-Lee 1998, Lassila et al. 2011), models for sharing data across databases, and the search for algorithms that are able to retrieve data from the “deep web” sources. Page (2008) discussed the issue of identifiers applied to biodiversity databases, given that taxonomic names themselves cannot be used as such due to not being stable (they are subject to revisions) or unique (synonymies, homonymies). Thus, the premise of assigning unique identifiers and use of semantic tagging is to bring the biodiversity data that is in the “deep web” of taxonomists’ and institution databases to the “surface”. These identifiers can be produced for many different kinds of objects (images, genetic sequences, specimens) as long as there is a database or data provider that will “translate” these identifiers into information. Hardisty et al. (2013, sections 2 and 3) present a more recent review of the main issues regarding data curation and sharing, including implementation, the role of standardized vocabularies, ontologies, identifiers and reliability of primary data that gets to be shared. More specifications about kinds of identifiers and their use in biodiversity informatics can be found in GBIF (2009) and Berendsohn et al. (2011).

The main practical consequence for our taxonomic revisions was that, in the first place, identifiers (unique accession numbers with an institutional coden) needed to be attributed to specimens and locality data from the labels had to be manually captured. Issues with the identifiers arise because the material used in a taxonomic revision often is on loan from several different museums, and more often than not, they do not yet have identifiers assigned until they are curated for the purposes of the revisionary work. The ECN has indicated that specimen identifiers, which are usually barcode labels, are only indications of the data capture and not ownership (Thompson 1994). However, not all museums agree, often because their own database systems will not handle identifiers produced by other systems. Therefore, a single specimen may end up with multiple identifiers, which has informally been referred to as “identifier schizophrenia”. The consequences are not limited to curatorial issues such as aesthetics and space, since the specimen can generate duplicate entries coming from the different sources of the identifiers. This produces a cascade effect on aggregator portals such as GBIF (Page 2012). In order to avoid this problem, we tried to obtain identifiers from each of the loaning institutions. For older loans, this sometimes had to be done retroactively.

Much has been written about its importance of data annotation and metadata, but there are few guides about how to incorporate it into taxonomic publications. A guide to including information for phenotypic data was published by Seltmann et al. (2012). Both GBIF and the EOL have been favoring DarwinCore data standards and have published tools to help data submission (GBIF 2014, EOL 2014, and see discussion below). GoldenGATE is an editor with a graphic interface that allows the annotation of legacy taxonomic literature using TaxonX markup (Agosti and Egloff 2009, PLAZI n.d.). Three XML schemas have been proposed for use in taxonomic literature (TaXMLit, TaxonX, TaxPub); Sautter et al. (2007) and Penev et al. (2011) reviewed the context in which each is being used, in spite of their large overlap in features and function. Some of the work in incorporating semantic tags to scientific papers is being accomplished by the publishers themselves (for example, Pensoft uses TaxPub XML and incorporates URI, LSID and GUID links in their publications) (Penev et al. 2009, 2010). It is also possible to annotate the data a posteriori to some extent, as it is being done for legacy literature, using text mining tools like Taxongrab (Koning et al. 2005) and NetiNeti (Akella et al. 2012).

Stability

Another issue that results from the option for digital publication concerns data curation and archival. As mentioned above, as a consequence of the use of markup, a “cybertaxonomic paper” will contain information that is actually stored elsewhere, in other documents and databases. The positive side is that the necessity of duplicating information (such as authors in the 19th century duplicating descriptions that had been published elsewhere) is decreased. On the other hand, one needs to keep in mind that in an electronic paper, the full set of information is not fully contained in the text, and every time an entry or the structure of the databases is changed and a link is broken, information is lost.

The stability of the medium in which information is stored is not a trivial issue in taxonomy, given that descriptions and taxonomic acts are potentially valid forever (Polaszek et al. 2005, Kullander 2008, Pyle 2008). Access to raw scientific data declines with the age of an article (Vines et al. 2014), and this actually applies to any data on the Internet, an observation that can be verified today by running a search for web sites that existed in the late 1990s or early 2000s—at the very least, the URL will have changed (a phenomenon referred to as “link rot”), if the content can be found at all. Thus, the concerns that information may suddenly disappear are clearly not restricted to taxonomy (Brand 1998, Bollacker 2010, Rice 2013).

Probably the most widely indicated solution for data preservation is to create repositories with redundant copies in several different places. For example, the Internet Archive was created in 1996 aiming at addressing this issue. It has also been demonstrated that data archiving does help reduce research data loss (Vines et al.

2013). Goddard et al. (2011) reviewed the landscape regarding services, tools and standards for archival of primary biodiversity data and point out that a common goal between these data storage centers are that they rely on data replication and effective metadata management. They presented a plan to develop specialized storage for biodiversity data, by comparison with general scientific data repositories, and also pointed out the main difficulties to such an enterprise. Besides development of the infrastructure, these difficulties consist of poor archiving of the raw information, the scientists' own conceptions of what is worth long-term storage and their backup habits, besides their concern that the data could be used by other research groups without attribution or collaboration.

The most commonly used format for storage and exchange of biodiversity data (in this case, specimen collection and locality data) is XML in DarwinCore standard (DwC 2009, Goddard et al. 2011). However, at this moment in time, it is still not possible to predict which standard will "survive", as explained by Yoder (2009), and no "tool" database (meaning the one that is used for the capture of data by the researcher) should be relied upon as a definitive repository of data. Therefore, in addition to submitting our information to public databases to the extent that it was possible, we followed the recommendation from the Library of Congress (NDIPP 2013) and Borer et al. (2009) to have the data stored in a "sustainable" format, meaning a format that can be easily read and converted to other formats, such as plain text or CSV tables, and have it stored in more than one type of device (for example, hard drive and media disk) which should have its integrity checked periodically.

The complexity of the process in which taxonomic information is produced and delivered by electronic media is increased by the fact that "old" storage media do not necessarily “phase out”. While “phasing out” is evident for several electronic storage formats (e.g. tapes, diskettes, laser discs), physical storage – paper – is still the most fundamental source of information for areas that rely on historical research, although the existence of multiple digital copies residing in servers in different locations has often been seen as an acceptable alternative. This was reflected in the ICZN’s decisions about what constitutes a “published work”: the requirements about availability of “numerous identical and durable copies” was expanded to accept descriptions published in digital-only journals, provided that the work is registered in ZooBank (ICZN 2012).

While the ICZN (Ride et al. 1999) does not make it mandatory to link every name to the ZooBank for publications that are released in print, the format of taxonomic publications is changing to accommodate increasing integration with data repositories (Pyle & Michel 2008, 2009, Polaszek et al. 2005, 2008), as well as making the published descriptions as widely accessible as possible (e.g. Penev et al. 2009, 2010).

ISSUE 3: TOOLS AND DATA REPOSITORIES

In taxonomy, primary data may translate into a number of data types: names and their status, specimen archiving information, descriptive (morphological) information, literature, site locality information / GIS, molecular data, digital image vouchers, ecological associations/niche information, and often additional illustrations such as sounds and other natural history information. These used to be organized in print through the publication of catalogues, but the predominance of the digital format has made print-only catalogs somewhat obsolete, and it is now difficult to justify the production of this kind of publication without an online database interface.

Managing all the different aspects of taxonomic data is well within the scope of information science and has been referred to as the "original bioinformatics" (Mallett and Wilmott 2003). In the last decades, numerous systems for managing and organizing taxonomic data have been developed.

A first group of such tools are desktop systems based on software that stores and operates databases locally: Microsoft Access, used in Platypus (Australian Biological Resources Study 2005) and 3i (Dmitriev 2003), or FileMaker, used by Mantis (Naskrecki 2008) and Mandala (Kampmeier & Irwin 2009). The usual route for these systems to make the data available on the internet is to export an image of the database, which may or may not conform to database markup standards. Thus, what the user sees is a snapshot of the database. The updates are not immediately made available. Unfortunately, at present, several of these systems no longer have support for development or users.

In the last few years, the popularization of dynamic web pages ("Web 2.0") led to content management systems that went from simple blogging interfaces like Blogger to complex systems like Drupal. These changes were incorporated into a new type of web-based management systems, such as MX (Yoder et al. 2006), Scratchpads (Smith et al. 2009), and the EDIT WP5 platform for cybertaxonomy (Berendsohn 2010).

Besides programs for management of original data, public repositories of data have become available. Much of the information that comes with a formal taxonomic description can now be stored in specific databases, such as specimen images (Morphbank), DNA sequences (GenBank, Benson *et al.* 2012), collecting event and repository information (GBIF data portal), taxonomic literature (Plazi.org, Biodiversity Heritage Library), besides names and hierarchies themselves (e.g. ITIS, Catalogue of Life/species2000, uBio, and even Entrez and Wikipedia), and finally, aggregators of data available from other databases, like the Encyclopedia of Life. Generic repositories of data are also available (Data Dryad, FigShare).

Many of the systems cited above have redundant functions, since they were elaborated by different institutions and research groups for basically the same kinds of information. This has been criticized because it makes the exchange of data between databases more difficult (Johnson 2007), but this is not a new problem. Overseeing data management issues has been an unfortunate repeated pattern in systematics (see Sarasan 1983). In fact, the main criticisms of these data management systems have not changed in a long time, as one can observe in the first words in the abstract of the opening chapter of a volume on databases in systematics, referring to works in the late 1960s and 1970s, saying "taxonomists have paid scant regard to the effectiveness of the information-processing side of their subject until recent years" (Heywood 1984). Heywood proceeds to discuss the application of computers in data management, producing keys, and in cladistics analyses. In the same volume, Bisby (1984) already considered: "Why does the community need taxonomists (...)? 'to systematize data for the use of other disciplines'. Despite these passing references, in practice remarkably little attention is given to studying these 'serious responsibilities towards society' " Lenore Sarasan was more specific when she described the problems faced by the community:

> Retrieval considerations, which should have preceded the start of data entry, had been deferred until data entry was completed. In many cases, data had been entered into the computer in a form not easily retrieved. Though there were some significant achievements, most new projects continued to repeat the mistakes made earlier. The lack of communication between projects, the lack of available written materials on existing projects, and the difficulty and frustration of trying to gather information about projects all contributed to this problem. (Sarasan 1983:7)

The problem of interoperability and data exchange, as described in previous sessions, has largely been addressed with the adoption of XML standards. Thus, when considering the choice of a program for data management, the main issue becomes not what the user feels more comfortable with, but how does the program deal with data standards. Some of the tools and central repositories applicable to each kind of data have been mentioned previously, more comprehensive reviews have been published by Smith (2007), Tann and Flemons (2009), iDigBio (2011), Goddard et al. (2011) and TDWG (2014). Johnson (2007) provided a more detailed explanation of how current biodiversity database services import and use these mechanisms and how they are tentatively standardized. Costello and Wieczorek (2014) present an updated list of best practices for management of biodiversity data. A summary of such services is presented in Table 2 (Appendix B) and a graphic representation of the relation between data portals mentioned here is presented in Figure 1 (Appendix B).

CONCLUSIONS

The aspects I have tried to implement in my descriptions based on this review were aimed at producing an Internet-friendly result that could go beyond the production of a publication with photography plates. This was accomplished in part by the use of several features in MX:

a. A code snippet generated by MX allows a certain OTU content page to be embedded in Internet pages. This allows the content to be dynamically updated from within the database;
b. Relevant content-types in MX were mapped to EOL defined subjects (EOL 2014), so once the species pages are public, they can feed data into the Encyclopedia of Life;

c. The list of material examined is georeferenced (as far as possible), and can be exported both as a Google Earth file (KML format) and as a Darwin Core standardized table, and therefore compatible with GBIF requirements. However, only institutions can contribute data to GBIF (GBIF 2014). At the moment, the alternative GBIF recommends is to publish species occurrence data papers with Pensoft Publishers, and use their Integrated Publishing Toolkit (Chavan and Penev 2011);
d. Images of the taxa will be available via image collections in Morphbank (which will be made public at the moment of publication);
e. The same applies for DNA sequences, which were submitted to GenBank;
f. The EOL entry for each taxon is provided, since that portal aggregates information from the databases cited above.

Besides these modifications, new features that I have not been able to implement at this time, but intend to do so in the future include better integration with the Hymenoptera Anatomy Ontology (Yoder et al. 2010, Deans et al. 2012, Seltmann et al. 2012) and SDD standards (Hagedorn et al. 2005) or equivalent. With regards to data preservation, besides submitting data to public databases to the extent that it was possible, the specimen information used in this study is also stored as worksheets and plain text files (Appendix B: Figure 2). Regarding the specimen identifiers reported in the lists of material examined, when it was not possible to obtain barcode labels or museum accession numbers, we used barcodes produced by the Texas A&M University Insect Collection (TAMUIC). Using project-specific identifiers would be clearly an erroneous decision, for the reasons explained below and because it would be pointless to create a public database only for signiphorid specimens (the maintenance of database, server security and other stability matters show that is not a long term option). TAMUIC submits data to GBIF; however, they do not submit data from specimens that do not belong to their collection. Therefore, we anticipate that a separate submission will have to be organized in order to handle this particular set of data.

In conclusion, it is common sense that the Internet is generally good for the researcher (Friedlander and Bessette 2003): it is extremely powerful to bring visibility to research; it expands the possibilities of collaborations, funding, interaction with the public, and of course discovery of information. It is important to keep in mind, however, that the print medium and electronic publications are very different. As "cybertaxonomy" grows, the amount of information contained in each work will lead us to rethink not only workflows but also the ways we understand authorship, credit, and our concept of publication itself. There are characteristics of the Internet that need to be considered: 1) impermanence: web documents can be edited and/or disappear suddenly; 2) information (content) can as easily be separated from context as it is from format: this is a result especially from issues 2 and 3 discussed previously – once tagged, content can be re-used in other documents without necessarily explicitly referencing its origin. Expecting credit for every re-use is utopic; 3) hypertext is non-linear: there is nothing indicating that an article will be read as a whole, or even displayed as a whole document, for the same reasons as #2. These characteristics will likely force us to rethink what publishing means, whether it is a complete journal article or primary data.

CHAPTER III

MOLECULAR PHYLOGENY OF THE PARASITIC WASPS OF THE FAMILY SIGNIPHORIDAE (HYMENOPTERA: CHALCIDOIDEA), WITH NOTES ON CURRENT SUPRASPECIFIC CLASSIFICATION

OVERVIEW

This work presents the first phylogenetic analysis of Signiphoridae to include molecular data covering all recognized supra-specific groups for this family, based on nuclear ribosomal DNA (18S, 28S expansion regions D2 through D5) and mitochondrial DNA (COI). The ingroup consisted of 74 taxa covering four signiphorid genera and four species groups of *Signiphora*. The data sets were analyzed in maximum parsimony and maximum likelihood frameworks. The phylogenetic results are compared with previous hypotheses and classifications of the group, and the sensitivity of the support for the groups to multiple sequence alignment approaches is evaluated. The overall results support the hypotheses of monophyly of Signiphoridae, as well as all genera except for *Clytina*. *Chartocerus* is sister to the other three genera. Two of the four species groups of *Signiphora* are supported: *flavopalliata* group and *coleoptrata* group. These results are mostly congruent with the hypotheses previously proposed based on morphological data and molecular data of the Chalcidoidea Tree of Life initiative. Optimization of life history strategies over the obtained trees suggests hyperparasitism may be a primitive condition for the group, with secondary reversal to primary parasitism. However, this

hypothesis needs further scrutiny, due to the fragmented knowledge of the biological niches occupied by most of the known species.

INTRODUCTION

Signiphoridae is a cosmopolitan family of minute (less than 0.5 to 2mm) chalcidoid wasps, most of which are associated with sternorrhynchous Hemiptera (scale insects, mealybugs, whiteflies, psyllids) as parasitoids, hyperparasitoids or parasitoids of their predators. The wasps in this family are distinctive and easily recognized by conspicuous characters such as the antenna with 4 to 7 segments (scape, pedicel, 1 to 4 anelliform segments and a usually long, unsegmented clava), the absence of external notauli, the transverse scutellum, the propodeum bearing a well-defined medial triangular area, a sessile metasoma, and wings mostly bare except for a marginal fringe, strong setae along the venation, and occasionally setae in characteristic locations.

Numerically, this is one of the smallest families in Chalcidoidea, with only about 80 valid species in 4 genera. However, in the last couple of decades, a significant number of new species have been discovered thanks to collecting efforts in several parts of the world with the use of specialized collecting techniques and bulk collecting such as canopy fogging. The undescribed diversity of Signiphoridae in the Neotropics is staggering. Based on previous faunistic surveys in Central America (Gaston et al. 1996, Heraty and Gates 2003), considerable diversity was expected from Neotropical samples. In fact, samples from Ecuador (Erwin 1982) and Costa Rica (Noyes 2012) have yielded an impressive number of signiphorid morphospecies per sample. In some of these, there were over 500 individuals in more than 30 morphospecies, most undescribed. For comparison, a regular sample obtained with the same collecting methods usually contained less than ten individuals and only one or two morphospecies. Noyes (2012) suggested that the number of undescribed species contained in the Costa Rican samples could possibly match the number of known species worldwide. There is, therefore, a great need for descriptive taxonomy of this group of insects.

Signiphoridae is not only a good illustration of how little we know about the diversity of parasitic Hymenoptera, but also of how the lack of a phylogenetic framework has produced problems for the taxonomy of the group. There is a consensus among Chalcidoidea researchers that the highly plastic morphological diversity observed in this superfamily resulted in a great amount of homoplasy, which has hampered the production of natural classification schemes for decades (Hanson and LaSalle 1995, Gibson et al. 1999). In Signiphoridae, this resulted in a number of synonymies, reversal of synonymies, genus transfers, re-transfers, changes of status and even different family-level classifications. A solid phylogenetic framework, considering both morphological and molecular evidence, would help not only the taxonomy of this group, but also the study of the evolution of its host relationships, host-switching, and the transition between primary parasitism and hyperparasitism.

Diversity, Distribution and Biology

The greatest known diversity of Signiphoridae is found in the Neotropics, particularly in the equatorial forest regions of Central America and South America: 39 out of the 79 described species occur in this region, 33 of which belong to the genus *Signiphora* (Noyes 2013). Some species groups of *Signiphora* (*dipterophaga*, *bifasciata*, *coleoptrata*) seem to be exclusively found in the New World. Of the four genera, only *Chartocerus* has a majority of species described from the Old World. These patterns are reinforced by the known distribution of new, undescribed species (Woolley and Dal Molin, unpublished data). *Signiphora* is both the most speciose and most morphologically diverse genus, ranging from small wasps in the *S. flavopalliata* species group to relative "giants" of about 2mm in size in the *S. dipterophaga* species group.

Signiphorid wasps present several parasitoid biologies (Woolley 1997, Woolley and Hanson 2006, and unpublished data from collection specimens): *Chartocerus* are known as obligate hyperparasitoids on scales and mealybugs or primary parasitoids on chamaemyiid flies (Chapter V), *Clytina's* only host record is as a pupal parasitoid of gall-making chloropid flies and their inquilines, most *Thysanus* are primary parasitoids of armored scales (although there are records as egg parasitoids of plant bugs and beetles) (Chapter IV), and *Signiphora* are primary or secondary parasitoids (hyperparasitoids) of sternorrhynchous Hemiptera. They have also been recorded from other fly puparia, eggs of mirid bugs and buprestid beetles, and one derived lineage contains pupal parasitoids of flies. However, the host for most species is unknown, increasing the importance of phylogenetic hypotheses that allow inference of putative ecological niches.

Economically, *Chartocerus* has often been a source of concern because it could disrupt biological control of mealybugs (e.g. Goergen and Neuenschwander 1992, Agricola and Fischer 1994). Several other species (e.g. *S. aleyrodis, S. xanthographa* and others) are also recorded as hyperparasitoids of silverleaf whitefly and woolly whiteflies (Woolley and Hanson 2006), but their effect on the primary parasitoid populations has not yet been quantified.

Classification and Relationships within Signiphoridae

Although Signiphoridae is a relatively small family, a fair amount of taxonomic instability is evident in the literature since the beginning of the 20th Century. About half of the known species had already been described by 1917, most by Ashmead (1900) and Girault (1913, 1915, 1916). After the addition of *Thysanus* to the group (Mercet 1917) and genus transfers made by Silvestri (1918), much confusion has resulted from lack of conceptual consensus on genus-group and family-group names, especially but not limited to the delimitation of genus *Thysanus*. This eventually resulted in the suggestion of a new family name, Thysanidae (Peck 1951). The history of these nomenclatural changes was reviewed by Woolley (1986), who established Signiphoridae as the correct name for the family, based on lack of general acceptance of the name Thysanidae.
The conflicts in the classification of genus-group names in this family also make evident the impact of difficulties in achieving a classification due to the lack of comprehensive analysis of the available specimens, literature and pre-Hennigean approaches to the inference of evolutionary relationships.

Thysanus was originally described without being assigned to a family (Walker 1840). Howard (1895) placed it in Aphelininae, which he considered a subfamily of Eulophidae. *Signiphora* also was not assigned to a family when it was described (Ashmead 1880), but Howard (1894) established the subfamily Signiphorinae, which can be interpreted in that work as being in the same level as Aphelininae (presently Aphelinidae) in Chalcididae (presently Chalcidoidea). Ashmead (1900) transferred Signiphorinae to Encyrtidae.

Girault (1913) was the first to propose subgroups in Signiphoridae in the first extensive work published on this group, with the classification of *Signiphora* in six species groups, based on color: *nigra*, *unifasciata*, *rhizococci*, *flavopalliata*, *maculata* and *aleyrodis*. The genus *Neosigniphora* was published (Rust 1913) in the same year in which Girault's monograph was published and therefore was not mentioned in that text. *Signiphorella* and *Matritia* were proposed as subgenera of *Signiphora* by Mercet (1916). Mercet also transferred *Thysanus* to Signiphoridae, keeping it as a second genus in this family (Mercet 1917) (there still is no mention of the name *Neosigniphora* in either of his works). *Xana* was described under Aphelininae (Kurdjumov 1917), and was transferred to Signiphoridae as a synonym of *Matritia* only in 1950, in the same work in which *Signiphorina* was described (Nikol'skaya 1950).

Silvestri (1918) transferred several species from *Signiphora* to *Thysanus,* and treated *Matritia* as a junior synonym. It is not clear from this publication whether his intention was the complete synonymy, since he lists *Signiphora* as per Ashmead (1900) and not the original description, but he does state that "probably all of Ashmead's species" belonged in *Thysanus,* as well as all the species treated by Girault (1913) under the *nigra* species group. Peck (1951, 1963) synonymized *Thysanus, Signiphora* and *Neosigniphora*, resulting in the treatment of all the species of this family under the genus *Thysanus*. These synonymies seem to have been done independently, i.e. Peck may have overlooked Silvestri's publication, since many of the species already transferred to *Thysanus* by Silvestri were indicated as "n. comb." by Peck. Peck (1951) did not discuss the reasons for such synonymy, but Kerrich (1953) presented a comparative table among 11 representatives of the then available generic names, and while he correctly concluded that *Thysanus ater* and *Neosigniphora nigra* (currently

Thysanus niger) were more closely related, he also considered that the "characters occur in so many different combinations" in the remainder of the group that it was preferable to keep all the species under the genus *Thysanus*.

In the next comprehensive revision, Rozanov (1965) did recognize *Thysanus, Signiphora, Chartocerus, Kerrichiella* and *Clytina* as separate genera, but synonymized *Neosigniphora* under *Thysanus, Signiphorella* under *Signiphora,* and put *Xana* (=*Matritia*) and *Signiphorina* as subgenera of *Chartocerus*. Adding to the confusion concerning generic concepts, uncertainties about the date of publication resulted in both *Xana* and *Matritia* having been used as senior synonyms (the former by Rozanov, and the latter by Nikol'skaya). Subba Rao (1974) followed Rozanov's (1965) classification and described *Rozanoviella*. Finally, *Neocales*, described by Risbec (1957), was considered *incertae sedis* in Aphelinidae by Hayat (1983), and then transferred and synonymized under *Chartocerus* by Polaszek (1993).

Besides the twelve available generic names in this family, there are also two unnecessary replacement names for *Thysanus* proposed by Förster (1856) (*Triphasius* and *Plastocharis*). Woolley (1988) consolidated all these names into a classification with four genera recovered as monophyletic based on 28 morphological characters (*Signiphora, Chartocerus, Thysanus* and *Clytina*), and subdivided *Signiphora* in four species groups (*bifasciata, coleoptrata, dipterophaga* and *flavopalliata*). His decision to keep the classification of *Signiphora* in species groups rather than subgenera was based on the fact that the relationships between these lineages, which include *Rozanoviella* and *Kerrichiella*, were not clear enough to propose phylogenetically meaningful taxonomic groups. *Rozanoviella* and *Kerrichiella* were kept as the *S.*

dipterophaga and *S. coleoptrata* species groups, respectively. This classification was followed by Hayat in his revision of the Signiphoridae from India (Hayat 2009).

De Santis (1968) divided Signiphoridae in two subfamilies, Signiphorinae and Thysaninae, based on the number of antennal annelli in males and females and presence of a discal seta on the forewing or hind wing. He placed *Signiphora* and *Kerrichiella* (now a junior synonym of Signiphora) in Signiphorinae and *Thysanus, Clytina, Chartocerus* and *Neosigniphora* (now a junior synonym of Thysanus) in Thysaninae. This subdivision was followed by Gordh (1979) and mentioned again by Woolley (1997) and Gibson et al. (1999). However, the usefulness of such classification has been questioned since the 1980s, for according to Woolley (1983, 1988), based on phylogenetic analyses, the subfamily Thysaninae could only be maintained as valid if limited to only *Thysanus* and *Clytina*, having *Chartocerus* as *incertae sedis*. Signiphorinae would become monotypic, given the synonymies of *Rozanoviella* and *Kerrichiella* under *Signiphora*. Furthermore, the characters proposed by De Santis (1968) do behave as expected in his key if looking only at his “Thysaninae”, but not for *Signiphora* (see characters 5, 6, 20 and 24 in Woolley 1988, which refer to the annelli and to the discal setae: the states described by De Santis for “Thysaninae”—4 annelli and absence of discal seta in forewing—are highly homoplastic). Therefore, there are only four valid genera and subfamilies are not recognized in the currently accepted classification (Noyes 2013).

The first formally proposed phylogeny of the genera of Signiphoridae was published by Woolley (1988) (Appendix C: Figure 3), based on a matrix of 21 out of the 28 morphological characters discussed in that paper, and treating the multistate characters as ordered. Woolley (1983, 1986) places *Chartocerus* as the sister group to all other Signiphoridae, supported by the absence of an epiproct in male *Chartocerus,* which causes the subfamily Thysaninae to be paraphyletic, as discussed above. *Thysanus* and *Clytina* appear as sister-groups, sharing the round shape of the occipital margin of the head and the loss of seta M6. *Signiphora* appears as a lineage well supported in multiple analyses, including the species that were under *Rozanoviella* and *Kerrichiella*. The pectinate calcar on foretibia and the extension of a lamelliform process beyond the median, triangular part of the propodeum are pointed out as synapomorphies defining *Signiphora*. However, as discussed in Woolley (1988), this hypothesis is sensitive to the polarization of the male epiproct character, which is the sole synapomorphy for grouping *Thysanus*, *Clytina* and *Signiphora*.

There are no other published analyses specifically on Signiphoridae, but recent studies in Chalcidoidea did involve multiple signiphorid terminals. The analyses from Munro et al. (2011) (23 signiphorids, based on ribosomal DNA) reflected an internal structure in Signiphoridae which is very similar to the Woolley (1988) hypothesis, with *Chartocerus* sister to the other three genera, except for the fact that the two *Clytina* terminals were split, one nested in *Chartocerus* and one as sister to *Thysanus*. Heraty et al. (2013) constructed a phylogeny based on the molecular data from Munro et al. (2011) and added morphological data; however, it only presented four coded signiphorid terminals, which makes it difficult to compare to previous analyses, although the same *Clytina* species that appeared nested in *Chartocerus* did again appear as its sister group, and *Thysanus* + *Signiphora* on the other branch. None of these recent studies included extensive sampling within Signiphoridae, especially regarding the species groups of *Signiphora*. Therefore, there is still the need for studies of phylogenetic relationships within Signiphoridae to facilitate further comparative studies.

Relationships of Signiphoridae within Chalcidoidea

Signiphoridae is currently established as a well-defined, monophyletic group (Gibson et al. 1999). It has consistently been recovered as a strongly supported group in recent large-scale phylogenetic analyses: Munro et al. (2011), using 18S and 28S rDNA of 722 taxa, recovered the family with over 95% bootstrap support in maximum likelihood analyses of 5 out of his 7 alternative approaches to sequence alignment, the bootstrap support falling to 80% when regions of ambiguous alignment were removed. Combining this molecular data set with a matrix of 233 morphological characters (Heraty et al. 2013), the family had 99% bootstrap support in maximum parsimony analysis, and 100% support in model-based methods (bootstrap support in maximum likelihood and Bayesian posterior probabilities).

Several morphological synapomorphies have been proposed for this family, starting with seven cited by Woolley (1988): (1) forewing without microtrichiae; (2) flagellar structure unique (one to four anelli and unsegmented clava); (3) propodeum with triangular median region delineated by lateral sulci; (4) mesoscutum without notauli; (5) axillae not externally visible; (6) mesofemur with at least one long spine anteroventrally and (7) mesotibia obconic and with long dorsal spines (the anteroventral spine in the mesofemur and shape of mesotibia are homoplastically reversed in *Clytina*). The analysis by Heraty et al. (2013: table 2) expanded this set to 21 characters that are at least locally (relative to its lineage in Chalcidoidea – clades “A” and “C” in the same paper) synapomorphic for Signiphoridae, such as the increased length of the antennal radicle, the relationship between metapleuron and prepectus, the reduction or absence of the stigmal vein, and the clustering of uncal campaniform sensillae.

A putative relationship between Signiphoridae and Aphelinidae[1] had already been mentioned relatively early in the literature (Mercet 1917, Domenichini 1954), but beyond that, deeper phylogenetic relationships were not well known, which is reflected in the family-level classification. In the literature, two parallel histories can be identified in earlier classifications: one regarding *Signiphora* and another regarding *Thysanus*. While *Signiphora* was usually considered a group (subfamily or tribe) within Encyrtidae (or Encyrtinae) (Ashmead 1900, 1904, Schmiedeknecht 1909, Girault 1929), *Thysanus* had been frequently placed under Aphelinidae (Howard 1895, Ashmead 1900, Ashmead 1904, Schmiedeknecht 1909). There is also a pattern in several earlier classifications to group signiphorids and aphelinids either under Eulophidae or under Encyrtidae (Ashmead 1904, Schmiedeknecht 1909, Gordh 1979).

None of these interpretations precluded the possibility of Signiphoridae rendering Aphelinidae paraphyletic. In one of the earliest discussions on potential relationships (an "intuitive phylogeny"), Noyes (1990; dendrogram 1 in Heraty et al. 1997) included both Aphelinidae and Signiphoridae in his "eulophid lineage" along with Trichogrammatidae and Eulophidae (including Elasminae) based on reductional characters. In response, Gibson (1990) argued that Aphelinidae and Signiphoridae should actually be placed in the "pteromalid lineage" because they retain the putative primitive state of the fore tibial spur, which is bifurcated and not reduced, and do not present a reduction of the number of tarsomeres, consequently placing these two families closer to Encyrtidae.

Both molecular and morphological evidence have to some degree pointed at a cluster formed by Eulophidae, Trichogrammatidae, Signiphoridae, Aphelinidae and

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[1] Aphelinidae *sensu lato,* including Azotidae and Eriaporidae, cf. Heraty et al. (2013).

occasionally Encyrtidae. Compère and Annecke (1961) and Rosen and DeBach (1990) considered Aphelinidae to be more closely related to Signiphoridae and Encyrtidae; Viggiani and Battaglia (1984) proposed that Aphelinidae were morphologically allied with Eulophidae and Trichogrammatidae. Gibson (1989) also considered that the metafurcal pits openings in the middle of the metasternum indicate a relationship with Aphelinidae. The artificiality of concepts used by different authors to define subfamilies in Aphelinidae based on morphology (Hayat 1994), and the scattering of aphelinid subfamilies and genera across Chalcidoidea in molecular studies (Campbell et al. 2000; Munro 2009, 2011) may at least partially explain the classification problems.

Most evidence supports a relationship between Signiphoridae and the genus *Ablerus* (s.l.) (Azotidae) (Woolley 1988, Gibson et al. 1999, Heraty et al. 2013), suggested by the anterior projections of metasomal sternites 3-6, unsegmented clava and presence of an epiproct (Woolley 1988), as well as some features of larval morphology (tubercules over spiracles, Pedata and Viggiani 1991).

The sister group relationship between Signiphoridae and *Ablerus* was supported in the maximum likelihood phylogeny presented by Heraty et al. (2013), using rDNA combined with morphological data. That phylogeny placed Signiphoridae and *Ablerus* as sister groups, and *Ablerus* + Signiphoridae sister to a group containing Trichogrammatidae and Aphelinidae (excluding Eriaporinae). This hypothesis justified raising Azotinae and Eriaporinae to family level. Still in Heraty et al. (2013), the implied weight parsimony phylogeny placed Signiphoridae sister to *Ablerus* + Trichogrammatidae, again suggesting Noyes' "eulophid lineage". We used these studies to direct the choice of outgroups included in our analysis.

Age of the Group

There are no formal fossil records of Signiphoridae, but an undescribed specimen has been obtained from Baltic amber (approx. 44mya) that presents many similarities to current signiphorids, including wing venation and antennal structure. The thoracic and propodeal modifications do not seem to yet be present. Another specimen from Dominican amber (15-20mya, Iturralde-Vinent and MacPhee 1996) is closer to recent morphology.

Heraty and Darling (2009) listed several other records of chalcidoid families from Baltic amber. They argue that given the record of sister groups to other Chalcidoidea (Mymaridae and Mymarommatoidea) from late Jurassic or early Cretaceous deposits (Rasnitsyn et al. 2004, Engel and Grimaldi 2007), and the absence of Paleocene records, it appears that the major diversification of Chalcidoidea families happened during the Eocene (55-35mya). Recent records of chalcidoids (Mymaridae, Eulophidae and Trichogrammatidae) from Ethiopia (Schmidt et al. 2010) may push this diversification to late Cretaceous (93-95mya). One can expect Signiphoridae to be one of the families that established itself during the post-Cretaceous diversification of Chalcidoidea (Heraty et al. 2013).

Objectives of This Study

The main objectives of this work are to: 1) conduct a genus-level phylogenetic analysis of Signiphoridae, aiming at producing a phylogenetic framework to serve as a foundation for a stable classification; 2) test the monophyly of the groups taxonomically recognized in the current classification; and 3) contribute to the understanding of the evolution of the described and newly discovered biological diversity of this group, its distribution and life histories.

MATERIALS AND METHODS

Taxonomic Sampling

Our data set comprises a total of 98 terminals, including 74 Signiphoridae plus outgroups. The choice of outgroups was based on the analyses of Munro et al. (2011) and Heraty et al. (2013). We used all available data from these studies for *Ablerus* (Azotidae), plus representatives of Coccophaginae, Aphelininae, Eretmocerinae and Trichogrammatidae. Within Signiphoridae, we added terminals representing the four genera. The diversity of each taxonomic group is proportional to the taxonomic sampling: we included replicates of the two known species of *Clytina*, and both Old and New World representatives of *Thysanus* and *Chartocerus*. In the case of *Signiphora*, which is the most morphologically diverse group, we sampled species presenting the contrasting morphologies from the four species groups identified by Woolley (1988): *flavopalliata*, *dipterophaga*, *coleoptrata* and *bifasciata*. Voucher and sequence information are provided in Table 3 (Appendix C).

Collection and Treatment of Molecular Data

The sequences used in this study were obtained at the Heraty Lab (UC-Riverside) and Medina Lab (Texas A&M University). The data analyses were run locally in a quad-core Intel Q9550 PC running Bio-Linux 6 (NERC Environmental Bioinformatics Centre, UK), at the Brazos Computing Cluster (Texas A&M University) and at the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway (UC San Diego), except where noted. The detailed protocols for molecular laboratory work are provided in Appendix G.

DNA Extraction

Non-destructive DNA extraction was conducted using a modification of the Chelex® protocol (Walsh et al. 1991) developed at UC-Riverside or the Qiagen DNeasy Blood and Tissue kit (Qiagen cat. no. 69504), also with slight modifications of the manufacturer's protocol, which are detailed below. For the Chelex extractions, whole specimens were exposed to 80μL 5% Chelex-100 solution (BioRad cat. no. 143-2832) and 10μL proteinase-K (New England Biolabs cat. no. P812S, 20mg/mL) in a 55°C water bath for 45-60 minutes, then 100°C *water* bath for 8 minutes. The supernatant was separated from the resin beads and from the specimen and stored at -20°C, whereas the specimen was cleaned with distilled water and stored in 80% ethanol for posterior mounting. For the Qiagen protocol, the modifications involved using the whole specimen instead of macerating it, recovering it as voucher after the prot-K/buffer ATL incubation bath, followed by cleaning and storage in alcohol, and reducing by half (100μL) the amount of buffer AE in the final elution process. The vouchers were kept in 80% ethanol, and then card-mounted or slide-mounted. A high-resolution image library of vouchers was also constructed to ensure traceability of the results to species determinations, available through Morphbank (Table 3- Appendix C).

DNA Sequencing

Amplification of DNA followed standard PCR protocols at UCR (Babcock and Heraty 2000). We used the Qiagen *Taq-polymerase* kit with Q-solution added to the master mix for the amplification of rDNA, since it increased the probabilities of obtaining all loops (David Hawks, pers. comm.). Primers and reaction conditions are provided in Table 4 (Appendix C). PCR products were purified using Glassmilk™ and NaI (MP Biomedicals GeneClean kit, cat. no. 111001200) and sequencing was conducted by the UCR Genomics Core Facility. The sequences were assembled and edited using Geneious v. 5.6.2 (Biomatters 2012).

Molecular Markers and Partitioning

The analyzed data set consists of four partitions corresponding to 28S rDNA expansion regions D2 and D3-5, 18S rDNA, and the barcoding segment of cytochrome oxidase subunit I (COI), with the final alignment consisting of 4137 characters.

The choice of markers was made so that the set would include genes that would offer resolution for deeper and for more recent relationships, prioritizing taxon coverage rather than relative completeness of data sets, as recommended by Wiens et al. (2005). Previous results from the analyses for the Tree of Life project (Munro et al. 2011, Heraty et al. 2013) and other studies in Chalcidoidea (Campbell et al. 1993, Rasplus et al. 1998, Campbell et al. 2000, Gauthier et al. 2000, Babcock et al. 2001, Gumovsky 2002, Manzari et al. 2002, Chen et al. 2004, Heraty et al. 2004, Krogmann and Abraham 2004, Jousellin et al. 2006, Sha et al. 2006, Erasmus et al. 2007, Heraty et al. 2007, Owen et al. 2007; see also discussion in Desjardins and Gates 2001), as well as in other

Hymenoptera (Dowton and Austin 2001, Rokas et al. 2002, Lin and Danforth 2004, Danforth et al. 2006, Laurenne et al. 2006 and others), suggested that the combination of 18S and 28S data sets were adequate for resolving most family through tribal relationships in Chalcidoidea. The expansion region D2 of 28S rDNA is also considered to be fast-evolving, and therefore potentially having signal to resolve more recent divergences such as generic through species level (Heraty 2004). We added a faster-evolving gene, COI, to help with resolution of species-level relationships. The COI gene is a popular molecular marker used in studies of population genetics, species boundaries and phylogeography (Avise 2000, but see Moritz and Cicero 2004 for a discussion of the issues of diagnosis and proposed inference of species based on this gene).

Sequence Alignment

Each partition was aligned separately. The rDNA (18S and 28S) sequences were initially added to a subset of the available secondary structure alignment for Chalcidoidea (Gillespie et al. 2005, Munro et al. 2011) using MAFFT v. 7 (Katoh et al. 2002, Katoh and Toh 2008, Katoh and Frith 2012, Katoh and Standley 2013) (see below). The alignment was then visualized in Mesquite (Maddison and Maddison 2007), using the color module with the option to “highlight apparently slightly misaligned” characters. Finally, the alignments were manually annotated and compared with the secondary structure template from Munro et al. (2011) to further identify sequencing artifacts and manually adjust small alignment issues.

The alignment of the COI sequences was obtained using MACSE (Ranwez et al. 2011) and visually examined using color-coding by codon to search for possible frameshifts, stop codons or other abnormalities which could be indicative of pseudogenes, damaged templates, miscalled bases or other sequencing artifacts (see Schizas 2012). Three tools were used the most to visualize and edit the alignments: Mesquite v. 2.75 (Maddison and Maddison 2007), SeaView v. 4 (Gouy et al. 2010) and Notepad++ (Ho 2011). The quality of the alignments was evaluated using GBlocks v.0.91b (Castresana 2000). This alignment file is indicated as MAFFT+MSS (MAFFT + manual refinement on secondary structure) in illustrations and tables.

Alternative Alignments

The regions of ambiguous alignment (RAA's) in rDNA are a constant source of concern and often discarded from analyses due to the difficulty of producing homology hypotheses for nucleotide positions. Manual editing of alignments ("by-eye") is also often a source of concern due to their being allegedly difficult to reproduce and subjective. In order to address these issues, we ran preliminary analyses of unedited alignments obtained from different MAFFT algorithms: E-INS-i, L-INS-i, G-INS-i and Q-INS-i, with and without the use of a structural alignment "seed" (a subset of Munro et al. 2011). Each of the gene partitions was aligned separately and in the end combined with the COI alignment described above, resulting in 18 alternative alignments. These sets are named according to the MAFFT algorithm used to align the rDNA partitions, SS indicating where a secondary structure alignment seed was used. Each set was submitted to RAxML (Stamatakis et al. 2008) (GTR-CAT model, no constraints, 1000 bootstrapped trees). The resulting best ML tree of each of those alignments was compared to currently accepted hypotheses of relationship and results obtained by Heraty et al. (2013); clearly spurious relationships among higher-level groups were taken as an initial indication of a suboptimal alignment. The alignment files and respective trees are provided as supplemental material.

Phylogenetic Analyses

Parsimony analyses were run on TNT v.1.1 (Goloboff et al. 2008). Heuristic searches were conducted as recommended at the TNT wiki (2009), gaps being considered a 5th state (see Ogden and Rosenberg 2007), starting with driven new technology searches, with initial search level set to 100 (the most aggressive) and allowing it to be reevaluated every 3 hits, 50 initial addition sequences, and find the best score 10 times. The resulting trees were kept in RAM and re-analyzed with TBR. This procedure was repeated with different combinations of new technology searches (sectorial search, drift, ratchet and tree fusing) until the length and number of trees found stabilized. These trees were summarized in a strict consensus.

Maximum likelihood analyses were run using RAxML v.7.7.1 (Stamatakis et al. 2006, 2008) with 1000 rapid bootstrap replications, under the GTRCAT+I followed by slow maximum likelihood search (RAxML combines partitions when the same model is used for all of them). The CAT model of rate heterogeneity is an approximation to GTR (General Time-Reversible) and is recommended for data sets with more than 50 taxa, yielding superior results than GTR-Gamma (Stamatakis 2006 and RAxML manual). The program was set to halt search using the autoMRE criterion to evaluate result convergence. The best scoring maximum likelihood tree was saved keeping branch lengths and bootstrap support values.

RESULTS

Alternative Alignments

A summary of the basic statistics of each data set is provided in Table 5 (Appendix C). The main difference between the alignment algorithms in MAFFT that were used in this study is how they handle gap costs in the iterative refinement procedure, and ultimately handle unalignable residues. When the options were set to "auto" to let the program opt between the available progressive alignment methods (FFT) and iterative refinement (L-INS-i), the program consistently proceeded to iterative refinement. Based on the authors' descriptions, E-INS-I is preferred when long internal gaps are expected; L-INS-i assumes long terminal gaps; G-INS-i treats the fragments as global (as opposed to local) homologs; Q-INS-i uses an automated estimation of secondary structure available from the Vienna RNA package (Katoh et al. 2009). With this in mind, one would expect the best results from E-INS-i when RAA's a significant component of the sequence, such as in the 28S gene, especially expansion regions D4 and D5, and in fact the likelihood values obtained with this algorithm are lower, along with L-INS-i, when associated to a secondary structure alignment seed (Appendix C: Table 6).

When a secondary structure alignment seed was provided to the program, the number of parsimony-informative characters decreased; however, the likelihoods consistently improved. The best likelihood obtained was from the approach using the structural alignment as a guide for refining the MAFFT output, which was significantly higher than any of the alternatives. The clades obtained from different approaches were generally the same, with differences in support (Appendix C: Table 6). The most discrepant results were obtained with the Q-INS-i alignment, in which most groups that were consistently well-supported by other analyses were either not recovered or recovered with low support.

Phylogenetic Analyses

The parsimony consensus tree and the best maximum likelihood tree are presented in Figure 4 (Appendix C). The maximum parsimony searches resulted in 48 trees with 4662 steps (CI=0.436, RI=0.738). The likelihood of the final optimized tree was -23761.233. When invariable sites were not considered, this value decreased to -23946.615. The supra-specific groups in Signiphoridae recovered for each alignment approach and their respective supports were tabulated. A summary of the tree statistics and clade retention is provided in Table 6 (Appendix C). Figure 4A (Appendix C) is represents the RAxML analyses of the MAFFT+MSS data set. Figure 4B (Appendix C) is the strict consensus of the shortest trees of the maximum parsimony analysis.

DISCUSSION

The results obtained in both parsimony and maximum likelihood analyses generally support the groups recognized in the current classification.

Family-level groups. The family Signiphoridae is supported as a monophyletic group and recovered as such in all alignment cases, and this has been demonstrated several times in the literature (Woolley1983, 1988, 1997, Gibson et al. 1999, Munro et al. 2011, Heraty et al. 2013). The group has consistently strong (97%) ML bootstrap support when secondary structure of the rDNA genes is incorporated in the alignment.

The classification in subfamilies Signiphorinae and Thysaninae, as defined by DeSantis (1968), is not justified: Signiphorinae would include *Signiphora* alone and Thysaninae, the other three genera: *Chartocerus, Clytina* and *Thysanus*. Thysaninae was only monophyletic in two of the alternative alignments analized (global alignment refinement without use of secondary structure and the Q-INS-i algorithm with automatic estimation of secondary structure), and in both cases with low (< 50%) support. In this last case, Thysaninae excludes basal *Chartocerus* and Old World *Clytina*, and renders *Signiphora* itself paraphyletic. Therefore, since Thysaninae is not supported in the majority of analyses, it is hereby rejected.

Genus-level groups. The genera *Signiphora*, *Thysanus* and *Chartocerus* were recovered as monophyletic with significant support. *Signiphora* was not monophyletic or had lower support in the analysis of the Q-INS-i alignment likely due to Thysaninae being nested within that clade. *Thysanus* was not as strongly supported as *Signiphora* or *Chartocerus*, but was consistently recovered with more than 65% support. *Chartocerus* was recovered as monophyletic with 100% support in all but two alternative alignment analyses.

Clytina was the only genus not recovered as monophyletic—instead, the Old World specimens (*Clytina giraudi*) consistently grouped with *Chartocerus,* whereas the New World exemplars were mostly recovered in a clade with *Thysanus*. Both of these clades were obtained with very high (over 95%) support except in one alternative alignment case. The grouping of *Clytina giraudi* with *Chartocerus* had already been observed in the Tree of Life data set analyses (Munro et al. 2011, Heraty et al. 2013). Our analyses, with additional and distinct samples, have converged to the same result. However, we do not propose any taxonomic changes at this point. Accepting the relationship between *C. giraudi* and *Chartocerus* would require the assumption of parallel evolution of several morphological characters, such flattened body, the occipital margin of the head rounded rather than with acute, the pronotum larger in dorsal view than mesonotum and metanotum, the shape of lateral plates of the propodeum (broadly rounded in *Clytina* with a smaller area covered by the medial triangle, whereas in *Chartocerus* the propodeum is approximately crescent-shaped as in the other signiphorids), reduced proportions of forelegs, with slightly enlarged protibiae, and the shape of the midtibiae (approximately cylindrical in *Clytina* while it is obconic in other signiphorids). The strongest evidence is probably the presence of an epiproct in males of *C. giraudi*, which does not occur in *Chartocerus* and also is evidence to put *Chartocerus* as sister to all other Signiphoridae as discussed by Woolley (1988). Also, it is difficult to interpret the molecular evidence, but by comparison with the structural alignment in Munro et al. (2011), most positions that support *C. giraudi* + *Chartocerus* are in regions of ambiguous alignment (as RAA, RSC or REC – see Gillespie 2004) or flanking regions of ambiguous alignment.

Sub-generic groups. *Chartocerus* was recovered as monophyletic (albeit including *Clytina giraudi*) in all analyses but the one resulting from the Q-INS-i alignment. However, it was not possible to obtain samples to produce enough sequences to test satisfactorily the monophyly of the three subgenera as defined by Rozanov (1965). *Signiphora* is the other genus that could potentially be divided in subgenera. However, only one out of the four species groups of *Signiphora* (sensu Woolley 1988) has consistently been recovered as monophyletic in all analyses: the *Signiphora flavopalliata* group. In fact, in the parsimony analysis, *Signiphora* becomes a polytomy except for the *S. flavopalliata* group.

Tree topologies. The tree topologies do not vary substantially, especially when a secondary structural alignment is provided. The parsimony consensus tree reflects that the data set used in this study has signal to resolve supraspecific relationships in Signiphoridae, but not sufficient signal to resolve relationships at species level. This is evidenced by the collapsing of the nodes at the generic level. The collapsing at genus level is also observed in *Ablerus*, which supports this conclusion.

The relationships recovered in the latest phylogenies (Heraty et al. 2013) for family level groups suggested that Signiphoridae was part of a group that included *Ablerus* and other Aphelinidae. Most maximum-likelihood analyses put Signiphoridae and *Ablerus* (Azotidae) as sister groups; when this does not happen (due to *Eretmocerus*, in both cases), the support is substantially lower. In the parsimony analysis, there is a polytomy at the node leading to Signiphoridae, Azotidae, and other Aphelinidae. These results are similar to the behavior of analyses in Munro et al. (2011) and Heraty et al. (2013), where Signiphoridae was recovered as the sister group to Azotidae with the combined molecular + morphology sets, but not with molecular data alone.

CONCLUSION

This study presents phylogenetic hypotheses based on a data set containing nuclear ribosomal DNA and mitochondrial DNA, fixed alignments with and without manual refinement based on secondary structure, maximum parsimony and maximum likelihood analyses. The results obtained are largely congruent with the currently accepted classification of Signiphoridae in formal taxonomic ranks, with four genera and no subfamilies. The informal ranks (species groups), with the exception of the *Signiphora flavopalliata* species group, have not been confirmed. Further studies should include morphological data and faster-evolving molecular markers that provide resolution at sub-generic ranks. It is also desirable to obtain quality material of the genus *Chartocerus*, which has a different distribution than the remaining genera, being mostly known from outside the Neotropics. The use of third-generation sequencing approaches should be explored as it is likely to provide resolution at specific level.

CHAPTER IV

REVISION OF THE GENERA *Thysanus* WALKER, 1840 AND *Clytina* ERDÖS, 1957 (HYMENOPTERA: SIGNIPHORIDAE)[2]

INTRODUCTION

Thysanus Walker and *Clytina* Erdös are two of four genera in the family Signiphoridae, a group of minute (approximately 1mm body length) parasitic wasps. Both genera were originally described from Europe, but subsequently recorded in the New World. They are the two smallest genera in the family, *Thysanus* with 4 valid species and *Clytina* with only one described species. However, a study of Neotropical material has revealed new species, approximating these genera to the diversity pattern observed in *Signiphora*, which in spite of being found in several biogeographic regions, is better represented in the Neotropics.

Thysanus and *Clytina* are putatively sister groups constituting a branch of Signiphoridae sister to *Signiphora* (Woolley 1988, but see Chapter III for new results based on ribosomal DNA data). The two genera share morphological characteristics such as the rounded shape of the occipital margin of the head (as opposed to acute, *sensu* Woolley 1988, found in the other two genera), the loss of seta M6 (e.g. Appendix D: Figure 6C, 7C, 9C, 10C), and the enlarged pronotum (more so in *Clytina*), which often has an angular anterior margin rather than being crescent-shaped in dorsal view

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[2] None of the taxonomic acts proposed in the present document are intended as formally valid (*sensu* ICZN).

(e.g. Appendix D: Figure 6B, 7E, 9E, 10E). The presence of an epiproct in both sexes is shared between these genera and *Signiphora*.

The genus name *Thysanus* has been a source of considerable taxonomic confusion in the past. It was described by Walker (1840), but not included in the same family-level group as *Signiphora* Ashmead, 1880 until much later by Mercet (1917). The subsequent instability of the concept of this genus was reflected broadly in the literature in the first half of 20th Century. Woolley (1986) provided a detailed account of those changes, which are summarized in the taxonomic treatment below. The lack of a consensus in the genus concept culminated with the synonymy of all genera in the family Signiphoridae (then including *Signiphora, Neosigniphora, Xana* and *Matritia*) under *Thysanus* by Peck (1951), after which the family was treated by several authors as Thysanidae. The change in the family name was in accordance with the Rules of Zoological Nomenclature valid at the time (ICZN 1905:art. 4). However, the usage of Thysanidae for a family name was not unanimous, as Nikol'skaya (1952), Erdös (1957) and Peck (1963) all used Signiphoridae.

In the last 30 years, faunistic surveys especially in the Neotropics have revealed a number of new species of Signiphoridae, including *Thysanus* and *Clytina*. Other new species of *Thysanus* have also been reared during studies of pest insects. The present text is an update on the knowledge of the species that could be formally described so far.

METHODS

Material Preparation and Analysis

Specimens that were not obtained already slide-mounted were initially observed under stereomicroscope (Leica MZ16), mounted on pinned points or cards. Further study of point- or card-mounted specimens required releasing them from the mounting medium by submerging the point or card in distilled water or ethanol 95–100%, followed by clearing with KOH 10%, dehydration and preparation of slides with Canada balsam. The protocol followed for preparation of slides is similar to the described by Schmidt (2005), with slight differences in the positioning of the insect. When the preparation of slides was not possible, images of the specimen were captured using either a compound microscope, as described by Buffington and Gates (2008), but using 4 fiber-optic light sources and mylar paper rather than a LED ring, or using a Leica M205 series stereomicroscope. All images are digital micrographs processed with image-stacking software (Helicon Focus) followed by color correction (Adobe Photoshop CS4).

Data Management

Specimen information (identifier, repository, collecting and locality information) was first captured in a local spreadsheet file. When geographic coordinates were not provided in the locality (collecting event) label, they were estimated, when possible, using online tools: GeoHack (Wikimedia), Google Maps and Global Gazetteer (Falling Rain Genomics). The data were then batch loaded to MX (Yoder et al., 2006). The data stored in MX were used to generate distribution maps and lists of material examined, as well as producing content pages displaying the information obtained about a taxon, including illustrations scanned from the literature, photographs produced in the course of this study, literature citations and specimen information. These pages can be embedded in HTML for display in any web page. However, MX is not meant to be a final repository for data (Yoder 2009); therefore, primary data will be submitted to public databases indicated under "Repositories" below and as detailed in Chapter II of this dissertation.

Literature Sources

Selected literature references are provided for the taxa treated in this text. The surveyed citations were initially compiled from the Universal Chalcidoidea Database (Noyes 2003, 2013) and complemented with searches using the literature search engines Web of Knowledge (Thomson Reuters, covering Zoological Record, Biological Abstracts/BIOSIS, SciELO), OVID (covering CAB Abstracts and Agris), EBSCO Host (covering Agricola, Biological and Agricultural Index), and ProQuest (Entomology Abstracts, Theses and Dissertations) with closing date of July 2014. Primary sources were preferred. For the present purposes, we avoided citing catalogues and lists if they did not bring any new information. The non-Signiphoridae names cited follow the classification at the Catalogue of Life (Roskov et al. 2014) and ScaleNet (Ben-Dov et al. 2014).

Repositories

The following acronyms have been used to designate museum repositories: ANIC (Australian National Insect Collection- CSIRO, Canberra, Australia), BMNH (Natural History Museum, London, UK), CNC (Canadian National Collection of Insects, Ottawa, Canada), HDOA (Hawaii Department of Agriculture, Honolulu, USA), IEUC (Istituto di Entomologia Agraria dell'Università Cattolica, Piacenza, Italy), MLP (Museo de La Plata, La Plata, Argentina), MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain), MHNG (Muséum d'Histoire Naturelle, Geneva, Switzerland), SAMC (Iziko Museums of Cape Town, Cape Town, South Africa), SANC (South Africa National Collection, Pretoria, South Africa), SDEI (Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany); UCR (University of California, Riverside, CA, USA), USNM (National Museum of Natural History, Washington D.C., USA), WSU (Washington State University, Maurice T. James Entomological Collection, Pullman, WA, USA), ZIS (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia). When possible, we requested unique specimen identifiers to the owner institutions. Unique specimen identifiers are indicated as "ISSUER ###### (Repository)", where "issuer" indicates the institution that produced the barcode label, and "repository" indicates the owner institution. The n-dash (–) indicates an interval of identifiers.

In order to prevent conflicts arising from the public availability of the present electronic document, we have opted to designate lectotypes for series with cotypes only when this revision is published formally as a journal article.

Digital images were deposited in Morphbank[3], and each description includes the morphbank ID for the collection of images associated with it. DNA sequences were submitted to GenBank (Appendix C). For each extant species, we provide a link to the Encyclopedia of Life (EOL) page, which aggregates information from the two databases mentioned above, as well as several others, including open access literature through the Biodiversity Heritage Library. Digital copies of the scanned literature are being contributed to the Universal Chalcidoidea Database (Noyes, 2013)[4].

A dynamic content page was set up through the MX database (Yoder et al. 2006) consisting of a) taxonomic history, b) description fields, c) images, d) distribution, e) literature and f) material examined, all automatically fed from the database content. The images include available pictures from the authors as well as scanned illustrations from the literature. The distribution maps are generated from the georeferenced locality data from the specimens in the database using a Google Maps API; the locality information is displayed by clicking each "pin" in the map. The literature was associated to the content page through a new MX content module, "tags through taxon names", which results in categorized entries listed and annotated at the page similar to a catalogue. MX can export content in Darwin Core standards (DwC Task Group 2009) compatible with EOL and GBIF.

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[3] These entries will be made available to public at the time of journal publication.

[4] Due to copyright restrictions, only the PDF files of publications prior to 1923 or with explicitly authorized distribution are public.

Morphological Terms and Abbreviations

Terminology follows Woolley (1988), Heraty et al. (2013), Gibson et al. (1998) and Krogmann and Vilhelmsen (2006). In Signiphoridae, the propodeum is divided in two areas: a medial triangular plate separated from lateral areas, the metasoma is sessile, and the first metasomal tergite (Mt1) is modified, sometimes continuous with Mt2, and often bilobed. TII. Some authors preferred to number the tergites according to their position in the abdomen thus referring to the propodeum as TI and the bilobed tergite as TII. A third system of numbering the tergites takes into account that the bilobed tergite (Mt1) represents the petiole of other hymenoptera, and thus counting the next tergite (Mt2) as the first tergite of the gaster. We follow the first system, numbering metasomal tergites, which allows for a more direct comparison with the tagmata in other apocritan Hymenoptera. Length ratios, e.g. among anelli, are represented with the shortest measurement converted to 1. The setae at the outer margin of the wings are referred to as the "marginal fringe". The abbreviations M1–M6 refer to the setae projecting from the upper surface of the marginal vein of the forewing (also referred to as "marginal setae") and S, to a seta in the stigmal vein of the forewing (e.g. Appendix D: Figure 6C), in contrast with the expression as used by Gibson et al. (1998), which refers to the marginal fringe. *Thysanus* and *Clytina* have fewer marginal setae on the forewing than other signiphorid genera. Thus, the setae are numbered according to their relative positions, by comparison to those other genera: M1–M4 project from the anterior margin and M5–M6, from the posterior margin of the marginal vein (see Woolley 1988, figures 19–21, and Gibson 1998). M1 is usually smaller than the other setae and is opposite to or basal to M5; M3 and M4 are apical to M6. A sensillum can be observed in the posterior margin of the forewing vein next to M5 in some taxa; if this sensillum is postulated to be a landmark for a parastigma, then M1 and M5 would actually belong to the parastigma and therefore to the submarginal vein. However, the transition between the submarginal, marginal and S is not clearly defined, and to avoid adding new terminology, we use the numbering convention proposed in Woolley (1988). In *Thysanus,* the frontovertex and the rest of the face often have different cuticle sculpture and color. The frontovertex is often also less sclerotized and collapses in air-dried specimens. We use the terminology from Gibson et al. (1998) and refer to the sulcus separating these two regions as frontofacial sulcus, because most of it is homologous to the part of frontofacial sulcus indicated as upper ocular sulcus (uos) in Heraty et al. (2013). The fold immediately above the toruli in some *Thysanus* is a scrobal sulcus formed by narrowing and collapsing the scrobal depressions; in *Clytina, Signiphora* and *Chartocerus*, a scrobal area is defined. An image labeled with the structures as treated here has been added to Appendix H of this document. The notation <F> and <M> were used to indicate the Venus and Mars symbols when they were used to indicate sex of the specimen in the transcribed labels.

TAXONOMY

Genus *Clytina* Erdös, 1957

(Figures 5–7).

Original description. Erdös (1957:62). Type species: *Clytina giraudi* Erdös by monotypy and original designation.

Generic diagnosis. Body dorsoventrally compressed, head prognathous, dorsoventrally elongated and laterally compressed, mandibular glands tubuliform (not enlarged distally); pronotum larger than mesoscutum; the medial sclerite of the propodeum does not reach the posterior margin of that plate; midtibia subcylindrical, without dorsal spines; male genitalia digits with 1 apical denticle each and 2 medial denticles (Appendix D: Figure 6H).

Distribution. The known species present a highly disjunct distribution: temperate Eurasia, Neotropical rainforest and Indian tropical savanna.

Literature. Peck (1964): keyed, illustrated. Trjapitsyn (1978): keyed. Woolley (1988): phylogenetics, taxonomy, morphology. Munro et al. (2011): phylogenetics. Heraty et al. (2013): phylogenetics.

Remarks. We follow the genus concept as defined by Erdös (1957) in the original description, and Woolley (1988) based on phylogenetic analysis of morphological characters. We continue to treat *Clytina* as a single genus in spite of results from the molecular phylogenetics studies (Chapter III, Munro et al. 2011) in which the genus was not recovered as monophyletic in spite of the evident morphological support (Figures 5–

7). In these studies, *Clytina giraudi* was consistently recovered among *Chartocerus,* whereas *Clytina* n.sp.1 was recovered as sister group to *Thysanus*. However, accepting the non-monophyly of *Clytina* would require assuming parallel evolution of traits such as the flattened habitus with expansion and modification of the same sclerites (e.g. the pronotum, the lateral plate of the propodeum, a medial projection in the scutellum), the occipital margin of the head rounded rather than acute, the shape of lateral plates of the propodeum (broadly rounded in *Clytina* with a smaller area covered by the medial triangle, whereas in *Chartocerus* the propodeum is approximately crescent-shaped as in the other signiphorids), reduced proportions of forelegs, with slightly enlarged protibiae, and the shape of the midtibiae (approximately cylindrical in *Clytina* while it is obconic in other signiphorids). In addition, although the molecular result is consistent in these studies, most of the characters supporting it are in or flanking regions of ambiguous alignment in 28S rDNA.

A sample from India may represent a third species; however, it is known only from a single female specimen in suboptimal condition, and therefore we have not included a description: INDIA, Karnataka, E of Hassan, 923m, 12°58'36''N, 76°14'34''E, 26.xi.2003, J. Heraty, H03-140, sweeping scrub/sugarcane, UCRC_ENT 159630 (UCR).

Key. A key for the identification of the species of *Clytina* treated below is provided in Appendix I.

Clytina giraudi **Erdös, 1957**

Appendix D: Figure 5A–B, 6A–F. Morphbank collection ID: TBD.

Original description. Erdös (1957:63). Holotype <F>, HMNH.

Diagnosis. Besides the distinctive aspect of this genus, *Clytina giraudi* can be recognized by the dark coloration, the surface sculpture of the head in frontal aspect being very faint; short, inconspicuous setae throughout the body and antennae short for a signiphorid, being about 1/4 of length of the body measured from pronotum to epiproct.

Description. **Females.** *Length* (pronotum to apex of the epiproct): 0.8–1.3mm (n=15). *Habitus*: Body flattened, uniformly black to dark brown, except for tarsi and distal part of fore tibiaeforetibiae, which are pale yellow and antennae slightly lighter (dark brown). Sparse, delicate, short setae throughout the body, wings hyaline.

Head prognathous, flat, shape rounded-square in frontal view (Appendix D: Figure 6A); sculpture faintly strigulate noticeable only in genae and frons; small setae and sensillae concentrated around eyes and proximities of antennal insertion; frontofacial suture absent; scrobal area smooth and little differentiated. Mandibles bidentate, mandibular glands tubuliform. Eyes bare, about 1/3 of head height. Antennae (Appendix D: Figure 6F) with 4 anelli (1:4:3:5); clava 1.5X length of scape, 4.5x as long as wide; pedicel about ½ length of scape, about 2x as long as wide; scape 3.5x as long as wide; radicle about 2x as long as broad.

Mesosoma: pronotum and mesoscutum faintly imbricate; mesoscutum and metanotum with very faint sculpture; medial propodeal sclerite hexagonally imbricate (Appendix D: Figure 6B). Pronotum approximately 1.5x the length of mesoscutum, with about 15 setae randomly dispersed; mesoscutum with 4 setae, the two lateral ones advanced relative to the two medial ones. Scutellum bearing 4 setae along its posterior margin plus one on top of each axilla, 1 or 2 scutellar sensilla, asymmetrically positioned if paired. Protibia and profemur approximately the same size, and protibia slightly shorter than midtibia. Midtibia shape subcylindrical; midtibial spur simple, without setation, dorsal spines on midfemur absent (1 strong subapical seta). Medial propodeal sclerite acute, ending approximately 3/4 of the length before posterior margin of the propodeum. *Forewing* (Appendix D: Figure 6C) hyaline, at most with faint basal infuscation, oblanceolate, approximately 3.5x as long as wide; longest marginal setae approximately ½ wing width; 1 seta in submarginal vein; M6 absent; 1 seta in costal cell; sensillae on submarginal present (Appendix D: Figure 6C). *Hindwing* with parallel margins; discal seta present; 1 seta in marginal vein (Appendix D: Figure 6D).

Metasoma. Mt1 visible dorsally as two lobes; a medial third lobe weakly pronounced (medial lobe shorter, inconspicuous under propodeum), visible in slide preparation under the posterior margin of the propodeum (Appendix D: Figure 5B, 6B). Anterodorsal margin of Mt8 with slight medial emargination. Anterior projections of sternites long; ovipositor internally about half of the length of the metasoma, reaching Ms6, apex serrulate.

Males. Similar to females, except for antenna: 2 anelli, scape slightly wider, proportion (scape, pedicel, anellus, clava): 3:1.5:1:3.2.

Type material. Holotype female, paratype male, card-mounted (HMNH): HUNGARY, “Gardony, June 1955, ex *Haplegis flavitarsis* Mg. (Dipt. det. Soós) in *Phragmite communi* [sic]”. Other paratypes: 2 females, “Gardony, 1954”; 11 females, Gardony, dated 9–22.June.1955; 1 female, Vörs, 16.vi.1966; 1 female, “Budapest, 17.IV.1952, leg. Domokos”.

Other material examined. DENMARK: 2 females. TAMU-ENTO X0424818 (TAMU); UCRC_ENT 174771/D2226 (UCR). FRANCE: 1 female. USNM 763271 (USNM). HUNGARY: 5 females, 1 male. TAMU-ENTO X0424810, X0424811, X0852624, X0852625, X0852630 (ZIS); USNM ZIL_42 (USNM). KAZAKHSTAN: 2 females, 1 unknown (wing). TAMU-ENTO X0852626-628 (ZIS) (additional material in alcohol: 7 individuals). MOLDOVA: 2 females. TAMU-ENTO X0424819, X852631 (TAMU). ROMANIA: 1 female, BMNH(E) #1038820 (BMNH). UZBEKISTAN: 30 females, 2 males, 1 slide with 10 females. TAMU-ENTO X0852617–623, X0852629, X0855073–

090 (ZIS); TAMU-ENTO X0424812–817 (TAMU (additional material in alcohol: approx. 40 individuals).

Biology. All specimens studied bearing host records were obtained as pupal parasitoids of grass flies. Erdös (1957) reared the type series from pupae of *Cryptonevra flavitarsis* (Meigen, 1830) (=*Haplegis flavitarsis*) (Dip.: Chloropidae) and some of the paratypes from pupae of *Lipara lucens* Meigen, 1830 (Dip.: Chloropidae). *Cryptonevra* Lioy, 1864 is an inquiline in galls induced by *Lipara* Meigen, 1830 on common reed, *Phragmites australis* (Cav.) Trin. Ex Steud (cited as *Phragmites communis* Trin.) (Poaceae) (Grochowska 2008). Krogmann (2005) also reared this species from stem galls of *L. lucens* on *Phragmites australis*. Erdös (1957) reported two to five *Clytina* per host pupa. One of the paratypes (HMNH Hym Typ. 8936) is labeled "ex *Leptomyza gracili* Mg. in spice / *Phragmitis / vulgaris*"; however, this host information was not listed by Erdös (1957). Trjapitsyn (1978) lists other chloropid genera as additional hosts: *Elachiptera* Macquart, 1835*, Calamoncosis* Enderlein, 1911 and *Anacamptoneurum* Becker 1903 on cereals.

Distribution. Europe, Central Asia.

Literature. Erdös (1957): description, biology. Trjapitsin (1978): host records. Krogmann (2005): distribution record, biology, SEM, notes. Krogman and Vilhelmsen (2006): comparative morphology, SEM. Munro et al. (2011), Heraty et al. (2013): phylogenetics.

Remarks. Type series kept as card mounts at request of HMNH curator. Woolley (1988) mentions 3 anelli for the male. This seems to be in error, probably caused by a mislabeled specimen (TAMU-ENTO X0952627, ZIS) from Kazakhstan, which has its metasoma dissected. That specimen is labeled as male, but has a note in Cyrillic by Rozanov indicating it must be a female. That seems to be the source of the male antenna illustration by Rozanov (1965), which was also reproduced by Trjapitsyn (1978).

***Clytina* n.sp.1 Dal Molin and Woolley**

Appendix D: Figure 5C–D, 7A–F. Morphbank collection ID: TBD.

Diagnosis. The most conspicuous characters that distinguish this species are: head and clava darker than the rest of the body, long, robust, dark setae throughout the whole body, including head and eyes, wings infuscated, with an abrupt transition between submarginal and marginal vein. Compared to *Clytina giraudi,* the pilosity is longer and the coloration is distinct as described above, the scrobe and facial sutures are more conspicuous, antennal clava is longer, the pronotum is slightly more elongated in comparison to mesoscutum and Mt2 is shorter. This species has only been collected in the Neotropics, whereas *C. giraudi* is known only from the Old World.

Description. **Female.** *Length* (pronotum to apex of the epiproct): 0.96–1mm (n=6). *Habitus*: Body flattened, mostly brown. Head black or dark brown, except for yellowish mandibles; antenna light brown, with distal segments (distal portion of pedicel or anelli through clava) dark brown; mesosoma and metasoma brown; axillar areas and tegula sometimes slightly darker; coxae and femora dark brown; tibiae and tarsi light brown to yellow; wings infuscated from base to apex, often slightly darker under wing vein.

Head prognathous, quadrate in frontal view (Appendix D: Figure 7A); frons and gena longitudinally corinulate, transversally corinulate in vertex, with long (~0.15mm) setae; frontofacial suture present; scrobal area well defined and reaching above lower level of the eyes. Mandibles tridentate; mandibular glands well developed, tubuliform. Eyes pilose, about ½ head height. Antenna (Appendix D: Figure 7B) with 3 anelli

(4:2:1); clava about 1.2x length of scape, 3.5x as long as wide; pedicel about ½ length of scape, about 2.5x as long as wide; scape 4.5x as long as wide, proximally expanded; radicle about 2x as long as broad.

Mesosoma: pronotum, mesoscutum, scutellum and medial area of propodeum transvers striate to reticulate (Appendix D: Figure 7E). Pronotum 1.5x longer than mesoscutum, with more than 20 more or less uniformly dispersed strong setae; mesoscutum with 6 setae, being 4 of them medially aligned with (directly anterior to) scutellar sensillae, scutellum with 3 or 4 setae along its posterior margin plus 1 on each axilla; with one pair of scutellar sensilla. Protibia and profemur approximately the same size, and protibia ½ the length of midtibia. Midtibia shape subcylindrical to slightly obconic; midtibial spur simple, without setation; dorsal spines on midfemur absent (1 strong apical seta). Medial propodeal sclerite acute, not reaching posterior margin of propodeal segment. *Forewing* (Appendix D: Figure 7C) oblanceolate, approximately 3.5x as long as wide; longest marginal setae approximately as long as wing width; 2 setae in submarginal vein; setae M1 and M6 absent; 2 setae in costal cell; 3 ventral setae on marginal vein; sensillae on submarginal vein absent (Appendix D: Figure 7C). *Hindwing* with parallel margins; discal seta present; 2 setae in marginal vein; 1 seta in submarginal (Appendix D: Figure 7D).

Metasoma. Mt1 trilobed (Appendix D: Figure 5D, 7E) (medial lobe much shorter but visible in dorsal view); Mt8 transverse, Mt7 medially concave. Sternites setation: only one medial pair of setae; one extra pair closer to medial line in Ms7). Anterior projections of sternites long; ovipositor reaching up to Ms6; apex of the ovipositor very acute (Appendix D: Figure 7F).

Male. unknown.

Type material. Holotype female, UCRC_ENT 300241 (UCR): “COSTA RICA, Cartago, S.A.T.I.E., Turrialba, 10.xi.1980, coll. J.B. Woolley 80/104, screen-sweeping rainforest, reventazon gorge". Paratype: COSTA RICA, Heredia: 1 female, CNCHYMEN 122544 (CNC).

Material examined. Holotype (female): COSTA RICA, Cartago. UCRC_ENT 00300241. Other material: COLOMBIA: 1 female. CNCHYMEN 122499 (CNC). COSTA RICA:Guanacaste: 1 female. BMNH(E) #990995 (BMNH). COSTA RICA, Heredia: 1 female. CNCHYMEN 122544 (CNC). ECUADOR:Pichincha: 1 female. CNCHYMEN 122585 (CNC). ECUADOR:Sucumbios: 1 female. CNCHYMEN 122495 (CNC). GUATEMALA:Izabal: 3 females. CNCHYMEN 122496–122498 (CNC). TRINIDAD AND TOBAGO: 1 female. CNCHYMEN 122500 (CNC). VENEZUELA:Aragua: 2 females. TAMU-ENTO X0616350 (TAMU); CNCHYMEN 122501 (CNC).

Biology. The Guatemalan specimens were obtained by "sifting bark and bracket fungi" (J. Huber, pers. comm.). There is no additional information about hosts of this species.

Distribution. Neotropics (Central America through Equatorial South America).

Literature. Woolley (1988): note, phylogenetics (as *Clytina* n.sp.). Munro et al. (2011): phylogenetics (as *Clytina* sp. extract D1043).

Genus *Thysanus* Walker, 1840

(Figures 8–16)

Original description. Walker (1840:234). Type species: *Thysanus ater* by monotypy.

Synonyms:

> *Triphasius* Förster, 1856: 83. Unnecessary replacement name for *Thysanus* Walker, as Tetrastichoidae (=Eulophidae, Tetrastichinae).
>
> *Plastocharis* Förster, 1856:145. Unnecessary replacement name for *Triphasius* Förster.
>
> *Thusanus* Walker, 1872:114. Lapsus: misspelling.
>
> *Neosigniphora* Rust, 1913:164. Type species: *Neosigniphora nigra* Rust, 1913 by monotypy. Synonymy by Timberlake (1924:245).

Generic diagnosis. Woolley (1988) restricted *Thysanus* to species presenting the following combination of characters: male antenna with four anelli, each digitus of male genitalia with two denticles (one apical, one pre-apical) (Appendix D: Figure 9H), mandibles with 3 teeth, mandibular glands distally globular and lack of seta M6 on the forewing. The lack of M6 and a narrow, almost parallel-sided hindwing are shared with *Clytina,* from which *Thysanus* is clearly distinguished by the globular head, long legs and antennae, and midbasitarsus subequal in length to midtibia. The pronotum in *Thysanus*, in dorsal view, tends to be longer than in *Signiphora* and *Chartocerus*, but not as long as in *Clytina*. The head is globular, unlike in *Clytina*, *Signiphora* and *Chartocerus*.

Distribution. Known from North, Central and South America, Europe, Africa, Middle East and India.

Literature. Förster (1856): unnecessary replacement names; he mentions having examined a single specimen and having difficulties in observing the characters, therefore reporting the specimen as having 4 and not 5 tarsomeres (the reason why he placed it in his 'Tetrastichoidae') and counting only one ring in the male and 3 in the female. Both replacement names were proposed unnecessarily because of their plant homonyms *Thysanus* Lour. (Connaraceae) and *Triphasia* Lour. (Rutaceae). Förster (1878): redescription (as *Plastocharis*).: he rectified his observation on the number of tarsomeres and confirmed that *Triphasius* should be replaced by *Plastocharis* due to the plant homonym. Howard (1895): catalogue (as *Plastocharis*, under Aphelininae). Dalla Torre (1898): synonymy (*Thysanus* as valid name, *Triphasius* and *Plastocharis* junior synonyms), under Aphelinae (sic). Ashmead (1900): listed, under Aphelinidae. Ashmead (1904): listed, under Aphelininae (Eulophidae). Schmiedeknecht (1909): listed, as *Thusanus*, under Aphelinini (Eulophinae). Mercet (1912:122–124): notes on morphology and nomenclature (under Aphelininae). Mercet (1917): placement: *Thysanus* transferred to 'Signiforinos'. Nikol'skaya (1952:517): keyed, notes. Kerrich (1953:806–808): notes on classification, comparative morphology. Peck (1964): keyed, descriptive notes. Woolley (1986): notes on nomenclature. Woolley (1988): phylogenetics, taxonomy, morphology. Munro et al. (2011): phylogenetics. Heraty et al. (2013): phylogenetics.

Remarks. We use the genus concept as defined in Woolley (1988). The genus *Thysanus* presents a particularly convoluted taxonomic history, described in detail by Woolley (1986). Following the synonymy of all then known genera of Signiphoridae under *Thysanus* by Peck (1951), *Thysanus* sensu lato became equivalent to the whole family, as discussed by Kerrich (1953). *Thysanus* s.l. (=*Thysanus, Signiphora* and *Chartocerus*) is still used occasionally in applied entomology publications.

Key. A key for the identification of the species of *Thysanus* treated below is provided in Appendix I.

Thysanus ater **Haliday in Walker, 1840**

Appendix D: Figure 9A–F. Morphbank collection ID: TBD.
Original description: Haliday in Walker (1840:234). Syntypes, 1 <F>, 2 <M>, BMNH.

Diagnosis. *Thysanus ater* is distinguishable from the other species in the genus by the pronotum with angular anterior margin, medially projected in dorsal view, the body predominantly brown, with the frontovertex less sclerotized, bright yellow to salmon pink, this pattern sometimes extending towards the vertex along and beyond the eyes, and white tarsi. Some females of *T. nigrellus* and *Thysanus* n.sp.6 are similarly colored, but the light areas in the head of these species does not extend over the whole frontovertex as in *ater* (Appendix D: Figure 9A). Also, *T. ater* has the scrobal depressions narrowed, usually only apparent as a sulcus, lacks M1, has 1 discal seta in the hindwing and the lobes of Mt1 are longitudinally elongated and well defined.

Description. **Female.** *Length* (pronotum to apex of the epiproct): 0.54 –0.82mm (n=15). *Habitus*: Body roughly cylindric, elongate, brown, except for frons through vertex, which is yellowish to salmon pink, and the mandibles, which are white; antenna slightly lighter brown, their apex slightly darker; legs the same color as body, except the articulation between foreleg femur and tibia and all tarsi, which are yellowish-white. Forewing (Appendix D: Figure 9C) infuscated from base to below stigma vein, with a hyaline spot below submarginal vein.

Head (Appendix D: Figure 9A) globular; gena and face longitudinally corinulate, antennal scrobe and vertex transversally striate, interantennal area slightly raised and matching face and gena in color and sculpture. Interantennal area reaches 1/3 to ½ of height of eyes. Frontovertex conspicuously defined by the differences in color, sculpture and limited by a frontofacial sulcus and a scrobal sulcus. Eyes glabrous, about ½ head height. Antenna with 4 anelli (Appendix D: Figure 9B) (2:1:1:1); clava about 2.75x length of scape, 8.5x as long as wide; pedicel about ¾ length of scape, about 3x as long as wide; scape 4x as long as wide; radicle about 3 times as long as broad; toruli on lower margin of the face. Mandibles tridentate; mandibular glands well developed, distally globular.

Mesosoma (Appendix D: Figure 9E) with pronotum, mesoscutum and scutellum imbricate; medial area of propodeum striate to approximately hexagonally reticulate. Pronotum about half of the length of mesoscutum in dorsal view; mesoscutum with 4 setae, the 2 lateral anterior to medial 2, scutellum with 2 or 3 setae aligned with posterior margin plus 1 on top of each axilla, 2 scutellar sensilla. Profemur slightly (1/4 length) longer than protibia. Midtibia obconic, 2x length of protibia, midbasitarsus 1.5x length of protibia, midtibial spur with 4 to 6 teeth; midfemur with 2 basal and 2 apical spines, hindtibia 3x length of protibia. Apex of median propodeal triangle touching posterior margin of propodeal segment. *Forewing* (Appendix D: Figure 9C) oblanceolate, approximately 3x as long as wide; longest marginal setae approximately as long as wing width; 1 seta in submarginal vein; setae M1 and M6 absent; 2 setae in costal cell; sensillae on submarginal present towards apical half. *Hindwing* with parallel margins; discal seta present; 2 setae in marginal vein.

Metasoma. Mt1 bilobed (Appendix D: Figure 9E), extending 1.5x the length of propodeum posteriorly to the propodeum, the lobes relatively close together, the distance between them subequal to length of their exposed area beyond propodeum; Mt8 tranverse, Mt7 slightly curved. Anterior projections of sternites long; ovipositor internally reaching Ms5; few delicate, fine setae along outer plates of the ovipositor.

Male similar to female, but with antenna more elongate (Appendix D: Figure 9G): clava 13.7x as long as wide, with longitudinal sensillae distributed close to each other, 4 anelli subequal in size, pedicel 3.5x as long as wide, scape 6x as long as wide, radicle 3x as long as wide. Digiti of genitalia (Appendix D: Figure 9H) with apical denticles, preapical denticles and a seta in the basal half of each digitus.

Type material. Syntypes, 1 female, 2 males (BMNH) card-mounted. Observed one male: “Syntype || Thysanus ater | Haliday <M> | Syntype. | M. de V. Graham” and the female: “Syntype || Thysanus ater | Haliday <F> | Syntype. | M. de V. Graham”. No locality label. Based on journal article, presumably from Britain.

Other material examined. ENGLAND: 4 females, 1 male, BMNH(E) #990656–658 (BMNH), 1 female (SDEI), USNM_ENT 763255 (USNM). CANADA, Ontario: 1 female, CNC 122400 (CNC). CROATIA: 3 females, 6 males (MNHG). FRANCE: 11 females, 13 males (MHNG). ITALY: 2 females (IEUC). UNITED STATES: California: 22 females, 10 males, UCRC_ENT 299673–684, 299689–697 (UCR), TAMU-ENTO X0460209–220. Connecticut: 1 female, UCRC_ENT 299691 (UCR); Idaho: 2 males, 2 females, CNCHYMEN 122397–399, 122401 (CNC); Maryland: 1 female, UCRC_ENT 299698 (UCR). Montana: 1 male, 15 females (WSU).

Biology. The European specimens that have host records were reared from *Diaspidiotus perniciosus* (Comstock, 1881) (San Jose scale) and *Leucaspis signoreti* Signoret, 1870 (Southern Europe pine scale). Nikol’skaya (1952) listed also *Diaspidiotus ostreaeformis* (Curtis, 1843) as host. The exemplar from Connecticut was also reared from San Jose scale. The specimens from California and Idaho were reared from highly discrepant hosts (see remarks below): central California specimens associated with plant bugs (Hemiptera: Miridae) on *Larrea tridentata* (Richard Rice, letter to JBW) and the specimens from Idaho, from *Coleotechnites milleri* (Busck, 1914) (Lepidoptera: Gelechiidae).

Distribution. Cosmopolitan. Hayat (1970, 2009) reported this species from India.

Literature. Förster (1878): redescription (as *Plastocharis ater*). Nikol'skaya (1952): keyed, host record. Thompson (1954): host records. Hayat (1970): keyed, descriptive notes. Gordh (1979): catalog, host records, distribution records. Hayat and Verma (1980): catalog, host record. Hayat & Subba Rao (1986): keyed, descriptive notes. Woolley (1988): notes, phylogenetics. Kreiter et al. (1997): host record, distribution record. Hayat (2009): regional revision (India), descriptive notes.

Remarks. This species has previously appeared in catalogs attributed to "Walker, 1840". The original description as it appears in Walker's text is between quotation marks and attributed to Haliday (ICZN art. 50). The year 1839 corresponds to the actual publication date of the fascicle (Evenhuis 2003), whereas 1840 is the volume (cover) date. The cosmopolitan distribution and discrepant host records indicate that *T. ater* as treated here is probably a complex of at least 3 cryptic species: one associated with Diaspididae, one associated with Gelechiidae, and one associated with mirid eggs. Further studies using molecular markers and detailed documentation of habitus and color would be necessary for an appropriate assessment. The lighter part of the frontovertex tends to collapse in specimens card- or point-mounted.

Thysanus melancholicus **(Girault, 1913)**

Appendix D: Figure 8A–B, 10A–F. Morphbank collection ID: TBD.

Original description. Girault (1913:218), as *Signiphora melancholica*. Holotype <F>, USNM.

Diagnosis. *T. melancholicus* can be recognized by the 8–14 thick setae in a single row parallel to the posterior margin of scutellum, the 1–2 rows of thick setae along the outer plate of the ovipositor, the elongated shape of the epiproct, and the coloration: black, with a white transversal band along the posterior margin of the pronotum, which is wider in front of the tegulae, The wing vein is hyaline between M1 and M3 in the forewing and marginal vein of hindwing.

Description. **Female.** *Length* (pronotum to apex of the epiproct): 1.0–1.26mm (n=5). *Habitus*: Body predominantly black, except for a white band extending transversally along the posterior margin of the pronotum; distal part of hind femur, proximal part of hind tibia and all tarsomeres white. Wings hyaline, with faint patch at the base of forewing, extending to middle of submarginal vein.

Head (Appendix D: Figure 10A) globose; frons and genae longitudinally corinulate. Frontovertex pale, finely transversally striate; interantennal area raised, with coloration and sculpture matching remainder of the head, reaching about ½ height of eyes. Mandibles tridentate; mandibular glands well developed, globose. Eyes glabrous, about ½ head height. Antennae (Appendix D: Figure 10B) with 4 anelli (1:1.5:2:3); clava about 8x as long as wide, 2.5x length of scape; pedicel subequal in length to scape, about 3.5x as long as wide; scape 4.5x as long as wide; toruli on lower margin of the face.

Mesosoma (Appendix D: Figure 10E) with pronotum and mesoscutum transversally striate, scutellum finely reticulate, metanotum transversally striate (wide striations), and medial area of propodeum reticulate. Very fine longitudinal striations are visible in slides using DIC or phase contrast, among the reticulae in the medial propodeal area. Pronotum 1/3 length of mesoscutum in dorsal view; mesoscutum with 4 to 6 small setae, scutellum with 6 to 14 thick setae in a row parallel to the posterior margin of the tergite plus 1 on top of each axilla; 2 scutellar sensilla. Profemur longer (about ¼ length) than protibia. Midtibia obconic, 2x the length of protibia; midbasitarsus length subequal to midtibia (midtibia 1/5 longer); midtibial spur usually with 9 teeth; midfemur with 2 distal spines on posterior margin, one large and one smaller. Median propodeal triangle reaching posterior margin of propodeal segment with a very small medial projection; posterior margin of propodeal segment transverse. *Forewing* (Appendix D: Figure 10C) obovate, approximately 2.5x as long as wide; longest marginal setae approximately ½ of wing width; 2 setae in submarginal vein; 1 seta in costal cell, 4 very small setae in basal area; 3 ventral setae on marginal vein; sensillae on submarginal present. *Hindwing* (Appendix D: Figure 10D) with parallel margins; 2 discal setae; 2 setae in marginal vein. In both fore and hindwing, the medial vein is pale.

Metasoma. Mt1 bilobed, practically transverse, with the lobes widely round and well separated, extending posteriorly less than ½ of the length of the propodeum at midline; Mt8 transverse. Sternites setation strong and conspicuous; 1 or 2 lines of robust setae along outer plates of ovipositor. Anterior projections of sternites long. Ovipositor internally about the same length of the metasoma. Epiproct subtriangular, about half as wide as long.

Male. Similar to female, differing in antennal proportions: clava 10x as long as wide, 3.5x longer than scape; 4 anelli (2.5:1.5:1.5:1); pedicel ½ length of scape; scape 3.6x longer than wide; radicle 3x as long as wide, 0.4x the length of scape. Digiti of genitalia with apical denticles, subapical denticles, and a subapical seta in the apical 1/3 of the digitus.

Type material. USNM Type No. 14200. Holotype female, slide-mounted in balsam "1°3f | Gn. 2sp. 7 | Samán | Jul. 16–10. T.". The same label has notes in pencil: "C. H. Signiphora sp. H. minor". The specimen lacks head and legs.

Other material examined. BRAZIL, Santa Catarina: 2 females, BMNH(E) #990350, #990351 (BMNH); TRINIDAD & TOBAGO: 1 male, CNCHYMEN 122403, 1 female, CNCHYMEN 122402 (CNC); URUGUAY: 2 females, USNM_ENT 763259 – 60 (USNM); USA, Texas: 1 female, USNM_ENT 763261 (USNM).

Biology. The type specimen was reared from *Pinnaspis dysoxyli* Maskell (as *Hemichionaspis minor*).

Distribution. Uruguay through Southern United States.

Type locality. Peru, Samán.

Literature. Woolley (1988): taxonomy.

Remarks. The "silvery white" band described by Girault (1913) as being across the mesoscutum is actually in the posterior margin of the pronotum.

***Thysanus nigrellus* (Girault, 1913)**

Appendix D: Figure 8C, D, 11A–F. Morphbank collection ID: TBD.

Original description. Girault (1913:223), as *Signiphora nigrella*. Holotype <M>, USNM.

Diagnosis. This species has been described from males, which are completely brown and do not present any single conspicuous characters that distinguishes this species on its own. They can be separated from other *Thysanus* by using a combination of the shape of Mt1 (Appendix D: Figure 11E), broadly bilobed with a transverse area between lobes, the short, oval mesoscutum and the number of setae in scutellum. If coloration is not evident, the females will look similar to *T. ater*, from which they can be further distinguished by the 2 setae in submarginal vein, presence of M1 and setae along the outer plate of the ovipositor. These setae, although clearly apparent in slides, are not as robust as in *T. melancholicus*.

Description. **Male.** *Length* (pronotum to apex of the epiproct): 0.96–1mm (n=6). *Habitus*: Body all brown (Appendix D: Figure 11A), with tarsi light brown to yellow; forewing infuscation from base to below seta M4 and reaching the posterior margin of the wing, darker under marginal vein, lighter and interrupted by two hyaline patches under submarginal vein (Appendix D: Figure 11C). Girault (1913) described the type specimen as black, with lighter (brownish) thorax. In the non-type material, a paler H-shaped area can sometimes be observed in the head, extending along the two compound eyes and between lateral ocelli. The vertex is brown; the frons is lighter. Specimens in alcohol tend to have a blueish luster.

Head globose; frons and genae longitudinally striate. Mandibles tridentate; mandibular glands well developed, globular distally. Scrobal area defined by sulci. Eyes bare, slightly larger than ½ height of head capsule. Antennae with 4 anelli (2:1:1:1; hard to observe on type); clava about 1.2X larger than the scape, 3.5x as long as wide; pedicel about ½ length of scape, about 2.5x as long as wide; scape 4.5x as long as wide, proximally expanded; radicle about 2 times as long as broad; toruli on lower margin of the face.

Mesosoma with pronotum, and mesoscutum transversally striate; scutellum, metanotum and medial area of propodeum reticulate. Pronotum short, about 5x as wide as long in dorsal view, ½ length of mesoscutum; mesoscutum with 4 setae, the 2 setae medially aligned with scutellar sensillae and the 2 lateral setae anterior to medial ones; scutellum with 4 setae in line along posterior margin plus 1 on top of each axilla, 1 or 2 scutellar sensilla; protibia and profemur approximately the same size, and protibia ½ the lenth of midtibia. Midtibia obconic, 5.5x as long as wide; midbasitarsus ½ length of midtibia, midtibial spur with 4 teeth, 0.6x length of basitarsus, midfemur with 1 spine. Apex of median propodeal triangle reaching posterior margin of propodeal segment, with a rounded apex. *Forewing* oblanceolate, approximately 2.7x as long as wide; longest marginal setae approximately 0.8x wing width; 2 setae in submarginal vein; seta M1 present and opposite to M5; 2 setae in costal cell; 3 ventral setae on marginal vein; 3–5 small setae in basal area; sensillae on submarginal absent. *Hindwing* with parallel margins; discal seta present; 2 setae in marginal vein (2 on basal third); 1 seta on submarginal vein.

Metasoma. Mt1 bilobed, with transverse area separating each of them which is overlapped by the posterior margin of the propodeum, which is also transverse.

Female. As in male, but clava shorter, 2.25x length of scape, distal anellus 3x larger than the most basal one (3:1.6:1.6:1).

Type material. Holotype male, USNM Type No. 14204, slide-mounted in balsam: “Signiphora | nigrella Girault | 471^{01}. Iss. 16| Jan. ’94. Par: | Asp. tenebricosus | Waco, Tex. | USNM | Type <M>". The specimen is in fair condition; it is not possible to observe part of the antennae, apex of metasoma and genitalia, which are obscured.

Other material examined. MEXICO: Michoacán, 5 males, 3 females, UCRC-ENTO 299700 – 707 (UCR); USA: Alabama, 2 males and 1 female, USNM_ENT 763262 – 264 (USNM).

Biology. The type specimen and the specimens from Alabama were reared from *Melanaspis tenebricosa* (Comstock, 1881) (Hemiptera: Diaspididae).

Distribution. The distribution of the samples is somewhat disjunct, but all from warm areas of the New World; North of South America, Southern North America.

Literature. Woolley (1988): taxonomy, first placement in *Thysanus* s.s., phylogenetics.

Remarks. The anterior margin of the mesoscutum of the specimens from Mexico is angular and therefore the mesoscutum is larger than in the other specimens. All other characteristics in coloration and setation are equivalent.

***Thysanus rusti* Timberlake, 1924**

Appendix D: Figure 8E, F, 12A–F. Morphbank collection ID: TBD.

Original description. Rust (1913:164), as *Neosigniphora nigra*, preoccupied by *Thysanus niger* (Ashmead, 1900) (see Timberlake 1924). Holotype (1 of 3 individuals) <F>, USNM.

Thysanus rusti nom nov. Timberlake, 1924, nec Ashmead 1900.

Diagnosis. Thysanus rusti can be distinguished from the other species by the transverse, almost trapezoid shape of Mt1; the legs are predominantly clear, the scutellum+metanotum are lighter than the rest of the body. The forewing infuscation is also distinct, occurring in two patches at the base of the wing and below the marginal vein.

Description. **Female.** *Length* (pronotum to apex of the epiproct): 0.82–1 mm (n=6). *Habitus*: Body predominantly brown or tan, the antennal clava slightly darker; vertex and dorsal part of frons yellowish, lateral-posterior angles of pronotum, mesoscutum, and scutellum+metanotum lighter than other sclerites; legs yellowish to white, tan at the apex of midfemur and basal half of all tibiae; forewing (Appendix D: Figure 12C) infuscated in basal portion only, a patch in posterior half below the submarginal vein and a separate, darker diffuse patch under the marginal vein.

Head globose; genae without any conspicuous sculpturing, although the setae and sensillae have a clear pattern, aligned with the scrobal suture. Mandibles tridentate; mandibular glands well developed, globular distally. Scrobal area depressed; interantennal area with the same color of the rest of the head extending to half of the height of the eyes; frons and vertex light, little sclerotized, transversally striated. Eyes glabrous, a little less than ½ head height. Antennae with 4 anelli (1:1.5:1.5:2.5); clava about 1.5X longer than the scape; pedicel about ½ length of scape.

Mesosoma with pronotum transversally striate; mesoscutum, scutellum and medial area of propodeum reticulate; the scutellum and propodeum with very fine longitudinal costulae perpendicular the reticular sculpture. Pronotum 1/3 length of mesoscutum; mesoscutum with 2 setae, scutellum with 2 setae aligned with posterior margin plus 1 on top of each axilla; 2 scutellar sensilla. Protibia ½ the length of midtibia. Midfemur with 1 large and 1 small spine; mesotibia with 2 basal spines, 1 large apical, 3 strong setae in a transverse line in apical half; midbasitarsus 2/3 length of midtibia, midtibial spur 0.6x the length of basitarsus; hindtibia 1.5x length of midtibia. Apex of median propodeal triangle round rather than acute, not reaching posterior margin of propodeal segment. *Forewing* oblanceolate, approximately 3x as long as wide; longest marginal setae approximately as long as wing width; discal seta absent, 2 setae in submarginal vein; no setae in costal cell; 4 small setae in basal area. *Hindwing* with parallel margins; discal seta absent; 1 seta in submarginal vein and 1 in marginal vein.

Metasoma. Mt1 not lobed, but with a transverse posterior margin. However, there are striae projecting from latero-posterior portions of the tergite where it fuses with Mt2. Anterior projections of sternites long; outer plates of the ovipositor long, internally reaching propodeum; epiproct ovate.

Male unknown.

Type material. 3 females, USNM Type No. 19065. In the original description, Rust indicated that 1 out of the 3 specimens on slide would be a holotype. However, there is no indication of which specimen it would be. “1^{o}3d. type. | Neosigniphora | nigra Rust | Ex *Hemichionaspis* | *minor*. | Chaquira, Perú | Aug. 10 ’10- T”.

Other material examined. BRAZIL, Santa Catarina: 15 females (BMNH). HAITI: 2 females, USNM_ENT 763267 – 268 (USNM). PERU: 2 females, USNM_ENT 763265–266 (USNM). TRINIDAD & TOBAGO: 1 female, CNCHYMEN 122404 (CNC). USA, Florida: 3 females, TAMU-ENTO X0616339, X0616342, X0616343 (FSCA).

Biology. The type specimens and the non-type specimens from Peru were reared from *Pinnaspis dysoxyli* (Maskell, 1885) (listed as *Hemichionaspis minor*). One specimen from Haiti was reared from *Coccus viridis* (Green, 1889) and the other, from *Vinsonia stellifera* (Westwood, 1871). Two specimens from Florida were reared from *Pseudaulacaspis pentagona* (Tozzetti, 1886). Thompson (1954) lists also *Pinnaspis strachani* (Coolley, 1899) as a host (listed as *Pinnaspis temporaria*), after Fulmek

(1943). Coccidae are unusual hosts for *Thysanus*, which is more commonly reared from Diaspididae. The fact that this species has been reared from both families of hosts may suggest this species is a hyperparasite.

Distribution. New World (Subtropical South America, Neotropics through Florida).

Literature. Fulmek (1943): host record. Woolley (1988): morphology, phylogenetics.

Thysanus **n.sp.2**[5] **Dal Molin & Woolley**

Appendix D: Figure 13A–F. Morphbank collection ID: TBD.

Diagnosis. Most similar to *T. nigrellus*; it can be distinguished by the shape of mesoscutum, which has an angular anterior margin in n.sp.2, the axillae do not conspicuously project anteriorly from the scutellum, the scutellar sensilla are much closer to each other than to the lateral margins of the mesosoma; wing infuscation is faint and at the base of the wing; the third valvulae of the ovipositor are elongated and somewhat darker than the remainder of the ovipositor; males with enlarged scape and clava.

Description. **Male.** *Length* (pronotum to apex of the epiproct): 0.6–0.8mm (n=3). *Habitus*: Body predominantly brown or tan; dorsal part of frons lighter, less sclerotized, yellowish to salmon pink; legs brown, dorsal surface slightly darker, mid and hind tarsi pale brown to white; wings mostly hyaline, infuscated at basal portion posterior to the submarginal vein.

Head globose; genae longitudinally striate. Mandibles tridentate; mandibular glands well developed, globular distally. Scrobal area depressed; interantennal area with

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[5] The working temporary numbers of the new species have been retained. Thus, the new species numbers are not necessarily consecutive.

the same color as the frons; frontovertex with the same color as the body, sometimes with lighter areas close to the eyes and transfacial suture or frons light, little sclerotized, transversally striate. Eyes glabrous, a little more than ½ head height. Antennae with 4 anelli (1:1:1:1); clava about 8x longer than wide and 4x longer than the scape; pedicel about ½ length of scape.

Mesosoma with pronotum and mesoscutum transversally striate; scutellum, metanotum and medial area of propodeum reticulate; the reticle in the scutellum smaller than in metanotum and propodeum. Pronotum 1/3 length of mesoscutum; mesoscutum with 4–5 setae, scutellum with 3–4 setae aligned with posterior margin plus 1 on top of each axilla; 2 scutellar sensilla. Protibia ½ the length of midtibia. Midfemur with 2 long spines and 3 strong, short spines posteroapically; mesotibia with 1 basal spine and 1 large apical spine; midbasitarsus 3/4 length of midtibia, midtibial spur 0.6x the length of basitarsus, with 4 teeth; hindtibia 1.5x length of midtibia. Apex of median propodeal triangle round rather than acute, not reaching posterior margin of propodeal segment. *Forewing* oblanceolate, approximately 3x as long as wide; longest marginal setae slightly shorter than wing width; discal seta absent, 1 seta on submarginal vein; 1 seta in costal cell; 2 small setae in basal area of wing disc. *Hindwing* with parallel margins; discal seta present; 1 seta on submarginal vein and 1 on marginal vein.

Metasoma. Mt1 bilobed; epiproct ovate; apical and subapical denticles present in digiti of genitalia.

Female Similar to males, but slightly larger (0.7–0.9mm). Anterior projections of sternites long; outer plates of the ovipositor long, internally reaching propodeum, 3rd valvulae conspicuously darker than other pieces of ovipositor, elongated.

Type. Holotype male, BMNH(E) #990344: "Brazil: Sta. Cat. | Nova Teutonia | 26.i.1944 | F. Plaumann | B.M. 1957–341". Paratypes: BRAZIL, Santa Catarina: 3 males, 3 females BMNH(E) #990345–349 (BMNH, TAMU, USNM).

Biology. Unknown.

Distribution. Southern Brazil.

***Thysanus* n.sp.3 Dal Molin & Woolley**

Appendix D: Figure 14A– F. Morphbank collection ID: TBD.

Diagnosis. This species can be distinguished from other *Thysanus* by the imbricate/reticulate sculpture of the face, lack of a less sclerotized area between interantennal area and transfacial sulcus, large eyes (about 2/3 height of head), female antennal segments not elongated (clava and scape each about 5x as long as wide), distal anellus of the male larger than the other anelli, forewing elongated (1.25x as long as wide), ovipositor elongated, with 3rd valvulae conspicuous and projecting beyond apex of metasoma. The mesosoma+Mt1 resembles *T. nigrellus* and *Thysanus* n.sp.2. These species can be separated based on the number and distribution of setae and relative distance of the scutellar sensilla (much closer to each other in n.sp.3).

Description. **Female.** *Length* (pronotum to apex of the epiproct): 0.5–0.8 mm (n=8). *Habitus*: Body predominantly brown or tan, the antennal scape and pedicel slightly lighter; light patches near upper margins of eyes and on upper face, next to transfacial sulcus; legs with same color as body, lighter in distal part of tibiae and tarsi; wings infuscated from basal portion to below apex of stigma vein vein (S) and faintly infuscated distally through apex.

Head globose; genae striate, face imbricate to reticulate. Mandibles tridentate; mandibular glands well developed, distally globular. Antennal scrobes depressed with an interantennal area elevated; the antennal scrobes not confluent dorsally, each reaching the transfacial sulcus. Eyes glabrous, about 2/3 head height. Antennae with 4 anelli (1:1:1:3); clava little less than ¾ of its length longer than the scape; pedicel about ¾ length of scape.

Mesosoma with pronotum, mesoscutum and metanotum transversally striate; scutellum faintly, finely reticulate; medial area of propodeum reticulate. Pronotum ½ length of mesoscutum; mesoscutum with 6–7 setae, scutellum with 4–6 fine setae aligned with posterior margin plus 1 on top of each axilla; 2 scutellar sensilla. Length of protibia little more than ½ the length of midtibia; profemur subequal to midtibia in length. Midfemur with 1 spine; mesotibia without conspicuous spines and only a strong basal seta; midbasitarsus ½ length of midtibia, midtibial spur 0.6x the length of basitarsus; hindtibia 2x length of midtibia. Apex of median propodeal triangle acute, reaching posterior margin of propodeal segment. *Forewing* oblanceolate, approximately 3.5x as long as wide; longest marginal setae approximately as long as wing width; discal seta absent, 2 setae on submarginal vein; 1 seta on costal cell; 6 small setae in basal area. *Hindwing* with parallel margins; discal seta present; 1 seta on submarginal vein and 1 on marginal vein.

Metasoma. Mt1 bilobed, with transverse margin between lobes (Appendix D: Figure 14E). Anterior projections of sternites long; outer plates of the ovipositor internally reaching Mt4 (Appendix D: Figure 14F); epiproct elongate.

Males as females, including antennal proportions. Digiti of genitalia with subapical and apical denticles; unlike in other species, the digiti project laterally beyond the base of the apical denticles.

Type. Holotype female, CNCHYMEN 122504: “Canada:ON, | Sault Ste. Marie | 46°30.259’N | 84°18.283”W, |17.vii.2007 | D. B. Lyons, ex. | *Agrilus anxius* | egg #0112.” Paratypes: CNCHYMEN 122405–412 (CNC): see material examined.

Material examined. CANADA, New Brunswick: 9 males, 5 females, CNCHYMEN 122409122405–412 (CNC), UCRC_ENT 299713, 299716–18 (UCR); Ontario: 1 female, CNCHYMEN 122504 (CNC). USA, Maine: 1 female, 1 male, USNM_ENT 763269 (USNM); Pennsylvania: 1 male, 3 females, UCRC_ENT 299708–711 (UCR); Tennessee: 1 male, UCRC_ENT 299712 (UCR).

Biology. All specimens except for UCRC_ENT 299712 were reared from eggs of *Agrilus anxius* Gory, 1841 (Coleoptera, Buprestidae). Katovich et al. (2000) mention a parasitism of 50 percent of borer eggs in New Brunswick sites, and 7 percent of eggs in Pennsylvania sites, but no list of parasitoids was provided.

Distribution. North America, along the Eastern coast (distribution range of several birch species native to Northeast US and Southeast Canada.).

***Thysanus* n.sp.5 Dal Molin & Woolley**

Appendix D: Figure 15A–F. Morphbank collection ID: TBD.

Diagnosis. *Thysanus* n.sp.5 can be easily distinguished from the other species by the distinctive color pattern, especially in the head, the 4-toothed mandibles, the short antenna, the wide curve of the 1st valvula in comparison to the position of the valvifers, and the conspicuous, darker pieces of the apical part of the metasoma (Mt8+9 and epiproct).

Description. **Females.** *Length* (pronotum to apex of the epiproct): 0.8–2mm (n=10). *Habitus*: Body predominantly brown or tan; head: the antennal clava, anelli, pedicel and clypeus dark brown, vertex and upper face white, interrupted by a curved v-shaped brown band anterior to the medial ocellus. Mesosoma and metasoma uniformly light brown; Mt6-7 slightly darker, syntergum, cerci, epiproct and 3rd valvulae of the ovipositor dark brown. Legs tan, the protibia slightly darker posteriorly; tarsi the same color as legs. Wings mostly infuscated, only two hyaline patches, one at the base and one at the very apex covering half of the wing disc posterior to the vein or less.

Head globose, the clypeus slightly above the genae, exposing the mandibles; sculpture ranging from colliculate at the genae to striate/imbricate closer to the antennae. Mandibles quadridentate; 2 mandibular glands well developed, globular distally. Scrobal area depressed; interantennal area not differentiated by color but slightly raised, going up to half of the height of the eyes; sculpture continuous to that of the face. Eyes glabrous, large, little more than ½ head height. Antennae with 4 anelli, all of the same size; scape about ¾ length of the clava; pedicel about 1/3 length of scape.

Mesosoma with pronotum and mesoscutum transversally striate, mesoscutum reticulate to striate, metanotum striate, propodeal triangle smooth to faintly reticulate. Pronotum 1/2 length of mesoscutum in dorsal view; mesoscutum with 6–8 setae, scutellum with 4 setae aligned with posterior margin plus 1 on top of each axilla; 2 scutellar sensilla. Protibia 1/3 length of profemur and midtibia. Midfemur with 2 large apical spines; midbasitarsus 0.6x length of midtibia, midtibial spur 0.6x the length of basitarsus; hindtibia 1.3x the length of midtibia. Apex of median propodeal triangle acute, reaching posterior margin of propodeal segment. *Forewing* oblanceolate, 2.5–3x as long as wide; longest marginal setae 0.6x of wing width; discal seta absent, 2 setae on submarginal vein; setae M1 and M6 absent; 2 setae; 5 small setae in basal area. *Hindwing* with parallel margins; discal seta present; 1 seta in submarginal vein and 1 in marginal vein.

Metasoma. Mt1 bilobed, with curved connection between the two lobes. Anterior projections of sternites short and fine; outer plates of the ovipositor reaching Mt5; epiproct ovate, the anterior margin projecting medially to articulate with an indentation in the syntergum.

Male unknown.

Type. Holotype female (HDOA): "Trinidad, | Curepe | Coll. R. | Burkhart | IX-22-1981 | ex. Angraecum | Scale" (TAMU-ENTO X0855960)

Material Examined. HONDURAS: 1 female, BMNH(E) #990935 (BMNH). TRINIDAD & TOBAGO: 6 females, CNCHYMEN 122413 (CNC), TAMU-ENTO X0855959–963 (HDOA). USA: Florida: 7 females, TAMU-ENTO X0616333–338, TAMU-ENTO X0626307–308 (FSCA); Hawaii: 1 female, BPBM_TCN 0344 (BPBM). VENEZUELA: 1 female, TAMU-ENTO X0616310 (FSCA).

Biology. The specimens from Trinidad, Florida and Hawaii were reared from *Conchaspis angraeci* Cockerell, 1893.

Distribution. Northern Neotropics through Florida, Hawaii.

Thysanus **n.sp.6 Dal Molin & Woolley**

Appendix D: Figure 16A–F. Morphbank collection ID: TBD.

Diagnosis. Thysanus n.sp.6 is most similar to *Thysanus* ater. It can be distinguished from that species by the white flanks of the pronotum, which are similar to *T. melancholicus*, the presence of a depressed antennal scrobe rather than a scrobal sulcus, the vertex is reticulate rather than striate, two submarginal setae, and the setae along the outer plates of the ovipositor, which are short and stout.

Description. **Female.** *Length* (pronotum to apex of the epiproct): 2–2.3 mm (n=2). *Habitus*: Body predominantly brown or tan, the apical 1/3 of the antennal clava slightly darker; vertex and dorsal part of frons lighter, lateral-posterior angles of pronotum, articulations of legs (distal femur, basal part of tibia, distal tibia) and tarsi white; distal tarsomeres tan. Wings infuscated from base through stigmal vein, with two hyaline patches towards the base.

Head globose; vertex reticulate, frons transversally striate, face colliculate to striate and reticulate. Genae slightly darker than remainder of head. Frons pale and less sclerotized above interantennal ridge and along eye margins. Mandibles tridentate; 2 mandibular glands well developed, globular distally. Antennal scrobes narrow, depressed, converging into the pale area of the frons. Interantennal area raised, with the same color and sculpture of the rest of the head, extending to half of the height of the eyes. Eyes glabrous, a little less than ½ head height. Antennae with 4 anelli (anelli length ratio approximately 1:1.5:2:3); clava about 2.5X longer than the scape; pedicel about 0.6x length of scape.

Mesosoma with pronotum transversally striate; mesoscutum striate to widely articulate, scutellum and medial area of propodeum reticulate. Pronotum 2/3 length of mesoscutum; mesoscutum with 4 setae, scutellum with 4 setae aligned with posterior margin plus 1 on top of each axilla; 2 scutellar sensilla. Protibia not too much shorter (0.8x) than midtibia. Midfemur with 1 large and 1 small apical spine and 7 strong setae; mesotibia with 1 large basal and 2 apical spines; midbasitarsus 2/3 length of midtibia, midtibial spur 0.6x the length of basitarsus; hindtibia 1.8x length of midtibia. Apex of median propodeal triangle acute, reaching posterior margin of propodeal segment. *Forewing* oblanceolate, approximately 3x as long as wide; longest marginal setae about 0.8x of wing width; discal seta absent, 2 setae in submarginal vein; setae M1 and M6 absent; 2 setae in costal cell; 4 small setae in basal area. *Hindwing* with parallel margins; 2 discal setae present; 1 seta above marginal vein in hindwing costa.

Metasoma. Mt1 bilobed, with medial portion broadly rounded. Anterior projections of sternites long; outer plates of the ovipositor reaching Mt4; epiproct subtriangular.

Male unknown.

Type material. Holotype female: "Brazil,| S. Paulo,| Teodoro Sampaio| Coll:| F. M. Oliveira| xi.1973" CNCHYMEN 122415 (CNC). 1 Paratype female : same data, CNCHYMEN 122414.

Material examined. BRAZIL: Sao Paulo: 2 females, CNCHYMEN 122414 – 15 (CNC) (=type material).

Biology. unknown.

Distribution. Neotropical.

CHAPTER V

REVIEW OF THE SPECIES OF THE GENUS *Chartocerus* MOTSCHULSKY, 1859 (HYMENOPTERA: SIGNIPHORIDAE)[6]

INTRODUCTION

Chartocerus is the second largest genus in the family Signiphoridae, with 33 valid species (Noyes 2013). Most of these species are associated with mealybugs (Hemiptera: Pseudococcidae) and other sternorrhynchous Hemiptera. Two species have had their life cycles studied in detail: *Chartocerus elongatus* (Clausen 1924) and *Chartocerus subaeneus* (Rosen et al. 1992). In both cases, they were found to be hyperparasitoids on encyrtids (Hymenoptera: Chalcidoidea) that parasitized mealybugs. Hyperparasitoids are generally considered organisms that can be harmful in biological control programs, though the significance and type of this impact vary (Bennett 1981, Sullivan 1987, Sullivan and Völkl 1999) and scenarios have been proposed in which hyperparasitism might even be positive (Luck et al. 1981). Rozanov (1965) mentioned that *C. subaeneus* reduced the effectiveness of *Pseudaphycus malinus* Gahan in the control of the Comstock mealybug in Central Asia, and Timberlake and Clausen (1924) considered that *C. elongatus* had a negative impact on the control of *Pseudococcus maritimus* (Ehrhorn). *Chartocerus* has a cosmopolitan distribution and, unlike other signiphorid genera, the majority of species are known not from the Neotropics, but Old World and Australia. The overall instability of genus-level classification of Signiphoridae during

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[6] None of the taxonomic acts proposed in the present document are intended as formally valid (*sensu* ICZN).

most of the 20th century has produced a somewhat atypical situation, in which a species such as *C. elongatus* ended up classified in four different genera (*Neosigniphora, Signiphorina, Thysanus* and *Chartocerus*) in less than 80 years. Also, as in many chalcidoid wasp groups, the largely conservative external morphology and the lack of comprehensive comparative studies creates great difficulties for the identification of these wasps. The present work is an attempt to contribute to the production of more geographically comprehensive and generally accessible knowledge resources for these species. We provide descriptive notes and images for 25 of the 33 valid species in this genus, most based on type material, including notes and pictures of A. A. Girault's material deposited in the collection of the Queensland Museum and South Australian Museum, prepared by JBW during his visit in the early 1980s. We were not able to review species from India and China. The species from India have been recently revised by Hayat (2009). Basic literature information for these and other species have been provided for reference.

MATERIALS AND METHODS

Literature searches, preparation of specimens and terminology followed the same approach described in Chapter IV. Host records were initially surveyed from the Universal Chalcidoidea Database (Noyes 2013), plus further searches on ProQuest Search (ProQuest LLC) to include theses and dissertations, and Google Books (Google Inc.), which tends to be more efficient in searching 'gray' literature. The following acronyms have been used to designate museum repositories: ANIC (Australian National Insect Collection- CSIRO, Canberra, Australia), BMNH (Natural History Museum, London, UK), CNC (Canadian National Collection of Insects, Ottawa, Canada), CNEP (Collection of Natural Enemies of Pests, Hubei University, China), DEAP (Department of Agriculture, Perth, Australia), FAC (Fujian Agricultural College, China), FSCA (Florida State Collection of Arthropods, Gainesville, FL, USA), IARI/NPCI (Indian Agriculture Research Institute, National Pusa Collections, New Delhi, India), IEUC (Istituto di Entomologia Agraria dell'Università Cattolica, Piacenza, Italy), INHS (Illinois Natural History Survey, Champaign, IL, USA), MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina), MLP (Museo de La Plata, La Plata, Argentina), MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain), MNHN (Muséum National d'Histoire Naturelle, Paris, France), MHNG (Muséum d'Histoire Naturelle, Geneva, Switzerland), QM (Queensland Museum, South Brisbane, Australia), SAM (South Australian Museum, Adelaide, Australia), SAMC (Iziko Museums of Cape Town, South Africa), TAMU (Texas A&M University Insect Collection, College Station, TX, USA), UCR (University of California, Riverside, CA, USA), USNM (National Museum of Natural History, Washington D.C., USA), ZAMU (Zoological Museum, Aligarh Muslim University, Uttar Pradesh, India), ZIS (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia), ZSI (Zoological Survey of India, Calcutta, India). Unique specimen identifiers are indicated in the following format: “IDENTIFIER ###### (repository)”, where IDENTIFIER indicates the institution that captured the data, #### corresponds to the accession number, and (repository) indicates the owner institution where the material is deposited. When transcribing label information, a pipe (|) indicates a line break and a double pipe (||) indicates another label; the abbreviations <F> and <M> correspond respectively to the Venus and Mars symbols used to indicate sex of the specimens.

RESULTS

Classification and Phylogeny

As described in chapters III and IV, the overall classification of Signiphoridae has been relatively unstable, especially between the 1950s and 1980s. *Chartocerus* was described from Sri Lanka by Motschulsky (1859), but was not transferred to Signiphoridae for over a century (Rozanov 1965), appearing as *incertae sedis* in catalogues prior to Rozanov's work (Dalla Torre 1898, Ramakrishna Ayyar 1925, Mani 1938). Three other available names are found in the literature as subgenera or, more currently, synonyms of *Chartocerus* (Woolley 1988): *Matritia* Mercet, *Xana* Kurdjumov, *Signiphorina* Nikol'skaya and *Neocales* Risbec. *Matritia* was originally described by Mercet (1916) as a subgenus of *Signiphora*. *Xana* was described under Aphelininae (Kurdjumov 1917), and was transferred to Signiphoridae as a synonym of *Matritia* only in 1950, in the same work in which *Signiphorina* was described (Nikol'skaya 1950). At that point, two historical nomenclatural questions concerning *Chartocerus* and its synonyms appeared: the diverse combinations in which they have been recognized either as valid, as synonyms or as subgenera of one another, and the priority of *Matritia* vs. *Xana*. Woolley (1986) reviewed nomenclatural changes in Signiphoridae.

Probably the most stable classification scheme that kept most involved generic names as valid was proposed by Rozanov (1965), who transferred *Chartocerus* to Signiphoridae and divided it in three subgenera: *Chartocerus, Xana* (with *Matritia* as junior synonym) and *Signiphorina*, thus establishing a generic concept that has changed little in comparison to those used by other authors that subsequently treated all subgenera as synonyms. Woolley (1988) proposed a generic concept based on phylogenetics. *Neocales* was the last name added to the list of synonyms of *Chartocerus*. This happened in the 1990s after the types for the genus were discovered by Rozanov (1965, 1969) at the MNHN, Paris.

In this study, we follow the generic concept from Woolley (1988), which has also been followed by Hayat (2009). Two of the proposed synapomorphies for *Chartocerus* are good diagnostic characters, namely the presence of seta M2b (i.e. two large setae opposite to the space between M5 and M6) and the absence of an epiproct in the male. The seta M1, when present, is shorter than the other robust setae on the marginal vein and it is positioned opposite to M5; M3, M4 and S are distal to M6. *Chartocerus* is the only genus in Signiphoridae in which males do not have an epiproct, that is, the metasomal tergites Mt8 and Mt9 are fused in a syntergum, as in most other Chalcidoidea. In the other signiphorid genera and in the female *Chartocerus*, there is a sclerite after Mt8, which is referred to as epiproct (Domenchini 1953, Woolley 1988: figures 12–14), because it does not bear the cerci (the cerci would be in Mt9 in Symphyta and Ichneumonoidea and therefore in the syntergum in most Chalcidoidea). The presence of an epiproct in females is one of the characters shared with the putative sister group to Signiphoridae, Azotidae (formerly Azotinae, a subfamily of Aphelinidae, see Heraty et al. 2013). Woolley (1988) discussed further the problem of homologizing these sclerites, especially by comparative analysis of *Ablerus* and *Aphelinus*.

Chartocerus shares with *Signiphora* the robust body, the head crescent-shaped in dorsal view (i.e. occipital margins acute), the appendages not significantly elongated, middle basitarsus shorter than tibia, hind wing normally expanded, and the pronotum wider than long, as discussed in chapter III. These morphological similarities are likely why in some works (e.g. Peck et al. 1964) *Matritia, Xana* and *Signiphorina* have been treated as subgenera of *Signiphora*.

A summary of the taxonomic questions concerning *Chartocerus* is presented in Table 7 (Appendix E) with the characters that were proposed by different authors to distinguish each of the subgroups that are currently part of the genus. The table demonstrates that most of the characters used to differentiate between these groups were based on measurements, such as the ratio between the length of the marginal fringe of the wings and the wing width, or the length ratio between certain sclerites.

One of the main problems with such characters in this particular case is that most of the specimens are in slide preparations, and thus the measurements are affected by the optical deformation caused by the angle in which the specimen is positioned. Also, the measurement-based diagnoses would likely be defensible when one is looking at extremes of morphological modification; however, their usefulness is greatly reduced when most individuals present measures and ratios that are close enough to the diagnostic "cut line" that expected measurement errors, or degrees of uncertainty, could lead to misidentification. Table 8 (Appendix E) lists the currently valid species (as in Noyes 2013) along with their putative classification under such subgroups and known biological information, as a first attempt to try to identify patterns in this genus. However, the problem of assessing the validity of subgenera in *Chartocerus, i.e.* the biological informativeness of such classification, clearly needs to be approached from a phylogenetic perspective with the addition of new sources of character data, including molecular information.

Hosts and Distribution

Most species of *Chartocerus* for which hosts are known are associated with mealybugs (Hemiptera: Pseudococcidae). However, species are also found parasitizing other sternorrhynchous Hemiptera, Diptera, and atypical records, such as spider egg sacs (Girault 1929). The genus is cosmopolitan, and most of the known species were described from Australia or from the Old World. One could speculate that this pattern could be reflecting sampling effort and not actual distribution. However, in at least two comprehensive surveys conducted in the tropics (Noyes 1989, 2012), *Chartocerus* continued to be as underrepresented as usually found in regular collecting events. The surveyed records for distribution and parasitism relationships have been summarized in Table 8.

TAXONOMIC NOTES

Genus *Chartocerus* Motschulsky, 1859

Original description. Motschulsky (1859:171).

Type species. *Chartocerus musciformis*, by monotypy. Repository: Moscow State University (Rozanov 1965, 1969).

Synonyms:

Matritia Mercet, 1916:525, as *Signiphora (Matritia)*. Type species: *Signiphora conjugalis* Mercet, 1916, by original designation. Junior synonym of *Xana* (Nikol'skaya 1950) (see remarks). Junior synonym of *Chartocerus* (Trjapitzin 1978).

Xana Kurdjumov, 1917:80. Type species *Xana kurdjumovi* Nikol'skaya, 1950, *nom. nov.pro Xana nigra* Kurdjumov, 1917 (nec Ashmead, 1900), by monotypy. Junior synonym of *Matritia* (Ferrière 1953) (see remarks). Junior synonym of *Chartocerus* (Trjapitzin 1978).

Signiphorina Nikol'skaya, 1950: 321. Type species: *Signiphorina mala* Nikol'skaya, 1950, by original designation. Junior synonym of *Chartocerus* (Trjapitzin 1978).

Neocales Risbec, 1957:271. Type species: *Neocales philippiae* Risbec, 1957, by monotypy. Junior synonym of *Chartocerus* (Polaszek 1993).

Generic diagnosis. The most fundamental characters used for diagnosis of this genus are the presence of seta M2b (i.e. two large setae opposite to the space between M5 and M6) (fig. 2B) and the absence of an epiproct in the male. Other characteristics that may be helpful in combination with these features include a female antenna with 4 anelli, maxillary palps 2-segmented, mesotibial spur with more than 6 teeth, usually three or four long spines in the mid femur, and the marginal fringe of the wings proportionally shorter than in most other signiphorids.

Most *Chartocerus* present the same pattern in coloration, with small variations: the body black, the appendages the same color as the body or brownish, the mid and hind tarsi white, and the fore wing with a dark infuscation at the base and light infuscation towards the apex, with a hyaline band medially. The pattern of setae on the wing veins also changes very little: M1 is usually absent, M2b is present as mentioned above, 2 setae on the submarginal vein, 1 on the costal cell. The hind wing has a small discal cell and 1 seta on the marginal vein. Thus, most of the variation is observed in the antennae, relation between propodeum and Mt1, shape of Mt1, surface sculpture of scutellum, metanotum and medial sclerite of the propodeum. The color usually varies in the extension of the light areas of the appendages and the extension of infuscation of the fore wing. Domenichini (1955) described variation in proportions and direction of denticles in male genitalia.

Distribution. Cosmopolitan.

Literature. Rozanov (1965): revision, key, classification in subgenera, new combinations. Woolley (1988): phylogenetics, descriptive notes, systematics, new combinations. Hayat (2009): revision of species from India.

Remarks. The problem of priority between *Matritia* and *Xana* stems from the lack of information on the actual date of publication for these two descriptions. Both are dated from 1916, but only the work by Mercet (1916) displays explicitly the date, December 1916; Kurdjumov's displays the year 1916. Rozanov (1965) stated that *Xana* was described earlier than *Matritia*. Subba Rao (1974) argued for the priority of *Matritia*, mentioning the actual date of publication of *Xana* is 1917. Woolley (1986) considered that based on the ICZN and the printed dates, both publications should be considered as published on December 31st, 1916. We follow Noyes'catalogue (2013), which indicates 1917 as the date of publication.

Type species: *Chartocerus musciformis* Motschulsky

Original description. Motschulsky (1859:171).

Type material. From Nura Ellia Mountains, Sri Lanka (Ceylon), ex *Pseudococcus* on coffee. Holotype <F>, microscope preparation #679, ZMMU.

Remarks. It was not possible to examine this type. However, Rozanov (1965, 1969) redescribed it in detail after the type material was located at ZMMU. He not only redescribed the genus but also transferred it to Signiphoridae for the first time.

***Chartocerus australiensis* (Ashmead, 1900)**

Appendix E: Figure 17; Morphbank ID 576508 (type material)

EOL taxon ID: 847913

Original description. Ashmead (1900:410), as *Signiphora australiensis*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.5–0.8mm (n=3). *Habitus and coloration*: Body predominantly dark, originally described as black with metallic tones, scutellum "with a bluish tinge" and mesonotum "with a bronzy tinge". It is perceptible in the type slide that the scutellum is slightly darker than most of the mesoscutum, metanotum and medial area of propodeum. Head brown, as in pronotum and most of metasoma, antennal clava and anelli lighter than pedicel and scape. Legs tan, lateroposterior part of protibiae and mesotibiae lighter, tarsi white. Fore wings infuscated, darker patch extending from base to apex of stigmal vein, lighter infuscation on apex, and two hyaline patches: one at basal-posterior area, and one posterior to stigma vein, slightly curved towards base of wing.

Head sculpture punctuate and longitudinally striate, more conspicuous punctuations along outer margin of antennal scrobes and inner margins of eyes, 1.3x as wide as high. Antennal scrobes well defined, extending through 3/4 of height of head. Other sulci absent. Eyes large, glabrous, about 2/3 of head height. Antenna with 4 anelli 1:1:1:1.2), clava 5x as long as wide, scape about ¾ length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through metanotum striate or striate to reticulate, fainter in scutellum and metanotum; pronotum barely visible dorsally, mesoscutum about 3.5x longer than scutellum, with about 13–15 small setae, most closer to medial-posterior area, scutellum with 7 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; internally marked axillae project anteriorly from scutellum to about ½ of mesoscutum; metanotum about 2/3 length of scutellum; medial triangle of propodeum finely reticulate. Protibia about 2/3 of length of mesotibia. Mesofemur with 3 large apical spines; mesobasitarsus little more than 1/3 length of mesotibia, mesotibial spur about 2/3 of length of basitarsus; hindtibia as long as mesotibia. Apex of medial sclerite of propodeum curved, reaching posterior margin of propodeal segment. Propodeal segment reaches, but does not overlap the area between the lobes of Mt1. Fore wings about 2.5x as long as wide; longest setae of marginal fringe about ¼ of wing width; discal seta absent, 1 seta in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 2 setae on base of marginal vein.

Metasoma. Mt1 bilobed, with slightly curved connection between the two lobes. Imbricate sculpture evident on tergites. Plates of ovipositor almost reach base of gaster.

Male unknown.

Type material. Syntypes (examined): 3 females (USNM Type No. 4771), mounted in balsam. “Signiphora | australiensis Ash. | <F> Type no. | 4771. USNM | Australia. | Koebele. 12.”, The original description does not provide further information. Girault (1913) redescribed the type material, having remounted the specimens in slides. The slide locality label is in Girault’s handwriting. One of the three females is damaged, located in resin outside of the coverslip.

Distribution. Australia.

Biology. In the original description, Ashmead mentions an unidentified “rhynchotan” (i.e. Hemiptera) as host. Girault (1913) reported on other slide (USNM: not located) “Acanthococcid on *Eucalyptus*” from Koebele material collected in New South Wales.
Literature. Girault (1913): notes on type material, descriptive notes, host record, distribution record. Girault (1915): descriptive note, distribution record. Woolley (1988): transfer to *Chartocerus*.

Chartocerus axillaris **De Santis, 1973**

Appendix E: Figure 18; Morphbank ID TBD (type material)

EOL taxon ID: 847847

Original description. DeSantis (1973:152), as *Chartocerus (Xana) axillaris*

Description. **Female.** *Length* (pronotum to apex of epiproct): 0.97–1.2mm. *Habitus and coloration*: Body uniformly reddish brown in slide preparation; there are no notes about coloration of the fresh material in the original description. Legs tan, fore tarsi and hind tarsi tan, midtarsi light yellow to white except for the two distal tarsomeres, which are tan, head and antennae brown, pedicel, basal anelli, mandibles and interantennal area slightly lighter than other parts. Fore wing infuscation extending posteriorly between M5 and M4, then a lighter apical infuscation, with a roughly straight hyaline band separating the two infuscated areas. Basal part of the wing, posterior to the submarginal vein, hyaline.

Head round in frontal view (crescent-shaped in dorsal view), not more than 1.2x as wide as tall, sculpture punctuate, punctuations somewhat uniformly distributed in frontovertex and face, faint striae perceptible along outer margins of antennal scrobe. Antennal scrobes well defined, length ¾ height of head. Other sulci absent. Eyes large, glabrous, about ½ of head height. Antenna with 4 anelli (6:4:3:1), clava 8.5x as long as wide, scape little more than 1/3 length of clava; pedicel little more than 1/3 length of clava. Scape basally expanded, 3x as long as width at its widest point, pedicel 2.5x as long as wide and slightly wider than basal annellus. Scape and pedicel with small punctuations with small, delicate setae.

Mesosoma with pronotum and mesoscutum faintly striate, scutellum and metanotum practically smooth, some faint reticulation in lateral portions. The fact that the specimen is rather dark and the sculpture so faint may explain why De Santis (1973) described the mesoscutum as lacking sculpture. Dorsally visible part of pronotum about 1/10 of length of mesoscutum at medial line. Mesoscutum about 2.5x longer than scutellum, with 14 small setae, somewhat symmetrically distributed in relation to midline, scutellum with 11 setae: 7 aligned parallel with posterior margin, plus a pair between that line and placoid sensillae, plus one larger seta on top of each axilla; axillae project anteriorly from scutellum to about ½ of mesoscutum; metanotum about ½ of length of scutellum; medial triangle of propodeum reticulate. Protibia about 2/3 of length of mesotibia. Mesofemur with 3 large apical spines; mesobasitarsus 1/2 length of mesotibia, mesotibial spur about ¾ of length of basitarsus, with 5 teeth; metatibia as long as mesotibia. The two basal tarsomeres of the midleg about the same length, and the third about ¾ of their length. Apex of medial sclerite of propodeum acute, reaching posterior margin of propodeal segment. Propodeal segment does not reach the area between the lobes of Mt1. Fore wings about 3x as long as wide; marginal fringe short, about 0.2 of wing width; discal seta absent, 2 setae in submarginal vein; 1 seta in costal cell, seta M1 absent; 3 unaligned small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 1 seta on submarginal and 1seta at the base of the marginal vein.

Metasoma. Mt1 bilobed, with a small third lobe connecting the two typical lobes. The plates of the ovipositor reach the anterior 1/3 of the gaster.

Male unknown.

Type material. Holotype female (examined), mounted in Canada Balsam (MLP 3927/1): "Det. Chartocerus | (Xana) | axillaris | De Santis | Holotipo | Museo de La Plata || Chacras de Coria | (Prov. De Mendoza) | s/ cochinilla del | quillo-quillo | Col: Exp. Museo | 25/II/1957", in pencil: "n.sp? | Chartocerus | (Xana)".

Distribution. South America (Argentina, Paraguay).

Biology. The specimen label cites as host a cochineal (?) insect ("cochinilla del quillo-quillo"); however, in the original description, De Santis (1973) recorded this species as reared along with *Apoanagyrus lopezi* De Santis, 1964 from an unidentified mealybug (*Pseudococcus* sp.) collected on *Solanum eleagnifolium*. In his subsequent catalogue (De Santis 1979), this species is recorded from *Hypogeococcus* and *Pseudococcus*.

Literature. DeSantis (1973): description, host record (*Pseudococcus*). DeSantis (1979): host record (*Hypogeococcus*). Woolley (1988), placement in *Chartocerus*. Loiácono et al. (2003): list of type material at MLP.

***Chartocerus conjugalis* (Mercet, 1916)**

Appendix E: Figure 19; Morphbank ID TBD (type material)

EOL taxon ID: 847844

Original description. Mercet (1916:525), as *Signiphora (Matritia) conjugalis*.

Description. **Female.** *Length* (pronotum to apex of epiproct): 1mm. *Habitus and coloration*: Body predominantly dark, originally described as very dark blue, ventrally reddish, legs mostly with same color as body, two basal tarsomeres of fore legs, three basal tarsomeres of midlegs and basal tarsomere of hind leg light yellow to white, the others ranging from tan to black. The dark brown coloration of the specimen in the slide corresponds to the bluish/black areas of the original description; apex of tibiae and articulation between mesotibia and mesofemur are lighter than remainder of legs. The head is described as dark as the body (very dark in the slide mount), scape and pedicel also dark, anelli and clava lighter, tan. In the mounted specimen, the clava does not seem much lighter than the pedicel, unlike the anelli. Fore wing infuscation extends from just before M5 to M4, and then there is another, lighter infuscated band midway between the apex of the wing vein and the apex of the wing itself.

Head The head of the slide-mounted specimen is very damaged. Mercet provided a relatively detailed description, mentioning that the occelli were positioned almost equidistantly from each other and the shape approximately round in frontal view. It is possible to observe punctuation in the face and frontovertex, but it is not possible to describe a pattern due to the fragmentation of the head capsule. Sculpture not visible. Eyes large, about 2/3 head height in frontal view.Antenna with clava little more than 6x as long as wide, 4 anelli (4:2:3:1), pedicel about 2.5x as long as wide and less than 1/3 length of clava. scape seems to have been lost.

Mesosoma. The pronotum has been separated from the remainder of the mesosoma and metasoma in the slide. The mesoscutum is also fragmented and the body has been deformed by the preparation. Mesoscutum with transverse striations and at least 16 setae concentrated in the posterior half. Scutellum and metanotum with very faint surface sculpture. Even though Mercet (1916) described the axillae as invisible, as in other cleared specimens of Signiphoridae, they are visible as internal ridges in the slide preparation. Scutellum with 6 setae aligned in parallel with posterior margin and one longer seta on top of each axilla. Apex of medial sclerite of propodeum round. Protibia about 1/2 of length of mesotibia. Mesofemur with 3 large apical spines; mesobasitarsus little more than 1/3 length of mesotibia, mesotibial spur about 2/3 of length of basitarsus; hindtibia as long as mesotibia. Apex of medial sclerite of propodeum curved, reaching posterior margin of propodeal segment. The fore wings of the specimen are folded in the holotype slide preparation; 3x as long as wide; longest setae of marginal fringe about1/10 of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 4 small setae in basal area. Hind wings about 3.5x as long as wide, longest setae of marginal fringe less than1/4 maximum width of wing; discal seta present. It was not possible to observe details and setae in the hind wing vein.

Metasoma. Mt1 not bilobed, following the shape of propodeal sclerite. Metasomal tergites with evident imbricate/reticulate. Plates of the ovipositor almost reach the base of the gaster.

Male unknown.

Type material. Holotype female (examined), mounted in balsam (MNCN): "S.| (Matritia) | conjugalis M. || MNCN | Cat. Tipos No. 12058 || sobre Aesculus | hippocastanum | Madrid 25-7-16 || MNCN_Ent No. Cat. 71291."

Distribution. Palearctic (Europe).

Biology. Associated with *Pinus halepensis*, *Chionaspis pinifoliae* (Mercet 1916), *Phenacaspis pinifoliae* (Thompson 1954), *Planococcus citri* (Herting 1972), *Marietta picta* (Hayat 1986).

Literature. Mercet (1916): Compared with *C. thusanoides* and *C. argentinus*. Nikol'skaya (1952:522): keyed, as *Xana*. Woolley (1988): transfer to *Chartocerus*.

Chartocerus dactylopii **(Ashmead, 1900)**

Appendix E: Figure 20; Morphbank ID 576512 (type material)

EOL taxon ID: 847842

Original description. Ashmead (1900:410), as *Signiphora dactylopii*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.76mm (n=4). *Habitus and coloration*: Body predominantly dark, originally described as blueish black, mesonotum "with an aeneous tinge anteriorly". Girault (1913) described the coloration of the card-mounted specimens as metallic green in the vertex and mesoscutum. In the slide mounts, the mesoscutum and the metanotum seem lighter than the rest of the body. Legs the same color as body, except for tarsi: fore tarsi tan, midtarsi and hind tarsi white, but with two distal segments tan. Head same color as body. Fore wings infuscation extends posteriorly as a band between M5 and M4, slightly constricted medially. Areas closest to the wing vein, anterior to this constriction, appear darker in some specimens and the posterior part of this infuscation very faint to imperceptible.

Head sculpture punctuate in vertex to longitudinally striate in face and genae, round in frontal view. Antennal scrobes well defined, extending to level of upper margin of eyes. Other sulci absent. Eyes large, glabrous, less than 1/2 of head height. Antenna with 4 anelli, (5:3:3:1), clava 6–6.5x as long as wide, 1.5x length of scape. Pedicel ½ length of scape.

Mesosoma with pronotum and mesoscutum transversally striate, scutellum, metanotum and medial area of propodeum reticulate. Pronotum about 1/5 of mesoscutum when measured at the midline, with lateral portions more visible due to shape of mesoscutum; mesoscutum 2–2.5x longer than wide, with 6–14 very small setae. Scutellum about 0.4x length of mesoscutum measured along midline, with 6-8 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla. Protibia about 2/3 of length of mesotibia. Mesofemur with 3 large spines; mesobasitarsus almost 1/2 length of mesotibia, mesotibial spur about about same length of basitarsus, with 7 teeth; hindtibia 1.5x length of mesotibia. Apex of medial sclerite of propodeum acute, practically touching the posterior margin of propodeal segment, which projects posteriorly in parallel to the margins of the medial area. Fore wings 2.7–3x as long as wide; longest setae of marginal fringe about 1/3 of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 3 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe little less than ½ maximum width of wing; discal seta present; 1 seta on submarginal vein.

Metasoma. Mt1 transverse. Imbricate sculpture evident. Plates of the ovipositor almost reach the base of the gaster.

Male. Body slightly smaller than females.

Type material. Syntypes (examined): 1 male, 3 females (USNM Type No. 4772), mounted in Canada Balsam: “4713° | Par.: on Dactylo-|pius ephedrae | Coq. | Remounted from [illegible] | A.A.G.” No further locality information: recorded from District of Columbia in original publication, “bred at Department of Agriculture”. The male has the head attached; the females don’t. There is a head towards the margin of the coverslip. Gordh (1979) states that the correct type locality is Los Angeles, CA, and reared from *Dactylopius ephedra* Coq.

Other material examined. USA: California: 3 males, 5 females, UCRC-ENTO 299799-802, 299813–816 (UCR), INHS_18 (INHS), 2 males reared from *Leucopis*, USNM 763211 (USNM); New Mexico: 3 females in 1 slide, USNM 763213 (USNM); Texas: 3 females, 2 males in one slide, USNM 763210 (USNM), Arizona: 2 females, 1 male, USNM 763212 (USNM).

Distribution. USA: California, Hawaii (Thompson 1954), New Mexico, Texas, Arizona.

Biology. Hyperparasitoid through encyrtid hosts on Hemiptera, Pseudococcidae: *Anisococcus ephedrae* (Ashmead 1900, as *Dactylopius*), *Phenacoccus solenopsis* (Ashmead 1902, as *P. cevalliae*), *Phenacoccus gossypii* (Gordh 1979). Parasitoid of Diptera, Chamaemyiidae: *Leucopis* sp. (Gordh 1979), a genus of flies that prey on sternorrhynchous Hemiptera.

Literature. Ashmead (1900): original description, host record, keyed. Ashmead (1902): distribution record (NM), host record (*Phenacoccus cevalliae*). Schmiedeknecht (1909): imprecise distribution record: “Columbia” (=D.C.). Girault (1913): descriptive notes, notes on type material, host record (*Anisococcus ephedrae*). Thompson (1954): host record (Encyrtid hosts), distribution record (Hawaii). Peck (1951, 1963): new combination, citation (as *Thysanus*). Gordh (1979): transfer to *Chartocerus*. Woolley (1988): as *Chartocerus*.

***Chartocerus elongatus* (Girault, 1916)**

Appendix E: Figure 21, Morphbank ID: 573445 (type material)

EOL taxon ID: 848108

Original description. Girault (1916:41), as *Neosigniphora elongata*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.72mm

Habitus and coloration: Body more or less uniformly dark, Mt2–4 slightly darker than rest of body. Head and antennae uniformly brown. Legs same color as body, but distal portion of profemur, basal portion of protibiae and hindtibiae, and distal 1/3 of metatibiae lighter fore tarsi tan, midtarsi and hind tarsi white except for distal tarsomeres. Fore wings infuscated, darker patch extending from base to apex of stigmal vein, lighter infuscation on apex, and two hyaline patches: one at basal-posterior area, and one posterior to stigma vein, slightly curved towards the base of the wing.

Head 1.3x as wide as high, sculpture punctuate with striae along the antennal scrobe, punctuations more or less distributed along outer margin of antennal scrobes and inner margin of eye. Antennal scrobes well defined, extending through 2/3 of height of head. Other sulci absent. Eyes large, glabrous, about 2/3 of head height. Antenna with 4 anelli (1:2:2:4), clava 6x as long as wide, 1.5x length of scape; pedicel about ¼ length of scape.

Mesosoma with pronotum and mesoscutum striate; scutellum, metanotum and medial sclerite of propodeum reticulate. Striae and the reticulation more widely spaced in comparison to other species. Anterior margin of pronotum transverse in dorsal view. Mesoscutum about 3x longer than scutellum, with about 15 setae, a row of 7 along the anterior margin and another 8 distributed in symmetric pairs relative to the medial line.

Scutellum with 9–10 setae aligned in parallel with the posterior margin plus one larger seta on top of each axilla; internally marked axillae project anteriorly from scutellum to about ½ of mesoscutum; metanotum about 2/3 of length of scutellum; medial triangle of propodeum finely reticulate. Protibia about 3/4 of length of mesotibia. Mesofemur with 2 large postero-apical spines; mesobasitarsus about 1/2 length of mesotibia, mesotibial spur about 3/4 of length of basitarsus; hindtibia about 1.3x length of mesotibia. Apex of medial propodeal sclerite acute, lateral areas of propodeal plate protruding posteriorly along with medial sclerite, almost reaching the medial posterior margin of Mt1. Fore wings 3.5–4x as long as wide; longest setae of marginal fringe about 0.7–0.8x wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 4 small setae in basal area. Hind wings 6x as long as wide, with parallel margins, longest setae of marginal fringe slightly shorter than maximum width of wing; discal seta present; 1 setae on marginal vein.

Metasoma. Mt1 bilobed, similar to *C. axillaris*, with a transverse part connecting the two lobes. Plates of the ovipositor almost reach about ½ of the gaster.

Males similar to females, clava longer (7–8x as long as wide).

Type material. Holotype <F> USNM 19210 (examined): "Webster No. 11824 | Elkpoint, S.D. | March 28, 1914. | Reared from coccid on *Muhlenbergia* | C.N. Ainslie Collector". Type label reads "*Neosigniphora elongata* Gir. <F> type | 19210." (the last number is fading).

Distribution. New World (USA, Caribbean), Africa (Ivory Coast, Senegal), India.

Biology. External, obligate hyperparasidoid reared from mealybugs and other Coccoidea: *Pseudococcus maritimus* (Ehrhorn)*, Coccus hesperidum* Linnaeus, *Ferrisiana virgate* Cockerell, *Planococcus citri* Risso, *Pseudococcus comstocki* (Kuwana), through parasitoids *Zarhopalus corvinus* (Girault)*, Acerophagus notativentris* (Girault)*, Anagyrus pseudococci* (Girault)*, Anagyrus yuccae* (Coquillet), *Clausenia purpurea* Ishii, *Leptomastix dactylopii* Howard, *Pseudaphycus mundus* Gahan, *Pseudleptomastix squammulata* Girault, and occasionally tertiary on *Aprostocetus minutus* (Howard) and *Prochiloneurus modestus* (Timberlake) (Clausen, 1924, Timberlake and Clausen 1924, Thompson 1955, Peck 1963, Herting 1972, 1977, DeSantis 1979, Gordh 1979). *Xanthogramma aegyptium* (Diptera: Syrphidae) (Herting 1978) is an outlier host record.

Literature. Girault (1916): compared with *C. australicus*. Timberlake and Clausen (1924): distribution record, host record, descriptive notes (identified by Gahan), description (male), compared with *C. niger*. Clausen (1924): biology, life cycle. Kerrich (1953): note (as *Thysanus*). Domenichini (1954, 1955): morphology, descriptive notes, morphometry, compared with *C. subaeneus* and *C. novitzkyi*, illustrations (as *Thysanus*). Nikol'skaya (1952:523): keyed, as *Signiphorina*. Novitzky (1954): comparative notes. Thompson (1955): host records, distribution. Peck (1963): host records, distribution. Rozanov (1965): transfer to *Chartocerus*. Gordh (1979): host records, distribution. DeSantis (1979): host records, distribution. Meyerdirk et al. (1981): biological control. Woolley (1988): systematics.

Remarks. A record from Italy is considered misidentification (Novitzky 1954).

***Chartocerus fimbriae* Hayat, 1970.**

Appendix E: Figure 22; Morphbank ID TBD (paratype)

EOL taxon ID: 848106

Original description. Hayat (1970:396), as *Chartocerus (Signiphorina)*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.8mm. The diagnostic characters, sculpturing and and the measurements for the examined material of this species are coincident with those of *C. elongatus*.

Type material. Holotype female, India (not examined): Tamil Nadu, Tenkasi, 6.iii.1967, M. Hayat, ex. *Nipaecoccus vastator* (Maskell), on *Acacia arabica*. At Aligarh Muslim University, Zoology Museum. Hayat and Verma (1980) mention the type is actually at the National Collection, Zool. Survey of India, Calcutta. Paratypes listed to ZSI, ZMAMU and Hayat personal collection.

Material examined. INDIA: Tamil Nadu: 3 paratypes: 2 females, 1 male BMNH(E) #990936–938, PAKISTAN: 1 female, CIE ai8333/3183/9 (BMNH); BARBADOS: 2 females, det. A. Polaszek (BMNH).

Biology. Associated to *Nipaecoccus vastator* (Maskell), on *Acacia arabica* (Hayat 1970), *Ceroplastes cajani* (Hayat 1976).

Literature. Hayat (1970): description (*C. fimbriae*), illustrations, compared with *C. subaeneus*. Hayat (1976): host record, illustration, compared with *C. subaeneus* and *C.*

novitzkyi. Hayat and Verma (1980): note on type material. Hayat (2009): revision for India.

Remarks. By comparison of the paratype with the holotype of *C. elongatus,* it is likely that these species are synonyms.

Chartocerus kerrichi **(Agarwal, 1963)**

Appendix E: Figure 23; Morphbank ID TBD

EOL taxon ID: 848100

Original description. Agarwal (1963:389), as *Matritia kerrichi.*

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.7–0.8mm (n=5). *Habitus and coloration*: Body predominantly dark. Agarwal describes the coloration of the dry material as follows: head "black with bluish reflections", mesosoma "brown with violaceous reflections" and metasoma "brown with bluish reflections"; legs brown, except for midtarsi and two basal tarsomeres of hind leg. Fore wing infuscation is described as extending posteriorly from the marginal vein. In the specimens observed, the infuscation extends from the base of the wing to the end of the marginal vein. Hind wings hyaline. None of the examined slides retained enough pigmentation for comparison of the body coloration.

Head sculpture punctuate and longitudinally striate, punctuations more or less follow along the outer margin of antennal scrobes and inner margins of eyes, 1.5x as wide as high. Antennal scrobes well defined, extending through 3/4 head height. Other sulci absent. Eyes large, glabrous, about 1/2 of head height. Antenna with 4 anelli

(4:2:2:1), clava 4.5x as long as wide, the extremities finer than midlength, giving it a feather-like shape in side view (the author describes it as flattened), scape about 2/3 length of clava; pedicel little less than 1/3 length of clava.

Mesosoma with pronotum through mesoscutum striate, metanotum reticulate, medial sclerite of propodeum reticulate to longitudinally imbricate. pronotum medially about 1/3 of length of mesoscutum, mesoscutum about 3.5–4x longer than scutellum, with 5 very small setae, scutellum with 7 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about the same length as scutellum. Mesotibia 1.5x length of protibia, mesofemur with 3 large apical spines; mesobasitarsus ½ length of mesotibia, mesotibial spur about 2/3 of length of basitarsus; hindtibia 1.5x length of mesotibia but ½ as thick. Apex of medial sclerite of propodeum rounded, almost touching posterior margin of propodeal segment. Propodeum transverse, medial part projecting posteriorly along with medial triangle. Fore wings about 3x as long as wide; longest setae of marginal fringe about 1/3 of wing width; discal seta absent, 2 setae on submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 1 seta on marginal vein.

Metasoma. Mt1 bilobed, with transverse connection between the two lobes. Imbricate sculpture evident on tergites. The plates of the ovipositor reach up to Mt3.

Males. As females, but pedicel smaller (1/8 of clava) and 3 anelli, the 2 distal about the same size, basal one ½ of length of others. Clava with larger concentration of sensillae.

Type material. Described from Aligarh, India (not examined). “Reared holotypes and paratypes on 19.8.1959 and the following dates. Endoparasite of *Eriococcus greeni* Newst. *Saccharum spontanium* L.” (Agarwal 1963). Hayat (1980): repository of types was not given in original description but probably at ZAMU (see Hayat 1970, 1976, 1980).

Material examined. INDIA: 4 males, 8 females, CIE A18572-2, 3 and 5; CIE A19035/11/4/1, 2; CIE A19035/11/1/1, 19035/11/1/2, 19035/11/2/2; 31.MC 1, 2, 3 (BMNH).

Distribution. India.

Biology. Hosts include Coccidae and Pseudococcidae Hayat (1970, 1976). The species was originally obtained from *Eriococcus greeni*; the material examined was reared from *Sacchariococcus sacchari* and *Nipaecoccus vastator*.

Literature. Rozanov (1965): in *Chartocerus*. Hayat (1970): illustrations. Hayat (1976): illustrations, notes: male genitalia. Woolley (1988): placement in *Chartocerus*.Hayat (2009): revision of species from India.

Chartocerus kurdjumovi **(Nikol'skaya,1950)**

Appendix E: Figure 24; Morphbank ID TBD

EOL taxon ID: 848097

Original description. Kurdjumov (1917), as *Xana nigra*.

> *Xana kurdjumovi* Nikol’skaya, 1950*,* nom. nov. for *Xana nigra* (junior secondary homonym of *Chartocerus niger* (Ashmead, 1900)).
>
> *Chartocerus kurdjumovi* (Nikol’skaya, 1950)

Description. **Females.** *Length* (pronotum to apex of the epiproct): 1.1mm.

Habitus and coloration: Body predominantly dark, the scutellum and Mt2–5 slightly darker; head somewhat uniform; legs slightly lighter than body, tarsi light brown to white except apical tarsomeres, which are tan. Fore wings infuscated, darker patch extending posteriorly between M5 and M6, medially narrowed; lighter infuscation at apex, and two hyaline patches: one at the basal area through M5, and one below M3/M6 crossing the wing at the midpoint.

Head sculpture punctuate and longitudinally striate, punctuations more conspicuous along the outer margin of the antennal scrobes and inner margins of the eyes, 1.3x as wide as high. Antennal scrobes well defined, extending through 3/4 of the height of the head. Other sulci absent. Eyes large, glabrous, about 2/3 of the head height. Antenna with 4 anelli, more or less the same size (the distal one slightly longer), clava 5x as long as wide, scape about ¾ length of the clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through medial sclerite of the propodeum striate or striate to reticulate, though originally described as “smooth, shining, reticulate under high magnification”. Pronotum barely visible dorsally, mesoscutum about 4x longer than scutellum, with more than 20 small setae randomly distributed; scutellum with 7 setae aligned in parallel with the posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of the length of the scutellum. Protibia about 2/3 of the length of mesotibia. Mesofemur with 3 or 4 large apical spines; mesobasitarsus little less than 1/2 length of mesotibia, mesotibial spur about the same length of basitarsus. Apex of medial sclerite of propodeum acute, almost touching the posterior margin of propodeal segment. Fore wings about 2.5x as long as wide; longest setae of marginal fringe about 1/7 of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 8 small setae in basal area. Hind wings about 3.5–4x as long as wide, longest setae of marginal fringe about 0.4x the maximum width of the wing; discal seta present; 2 setae on venation.

Metasoma. Mt1 trapezoid as the propodeum, the posterior margin transverse. bilobed. Imbricate sculpture evident. The plates of the ovipositor almost reach the base of the gaster.

Male as female, but with much wider clava (3–3.5x as long as wide), the anelli all the same size, pedicel and scape also proportionally shorter. Scape with medial part slightly bulging in both sexes.

Type material. Described from Poltova, Ukraine (not examined). Syntypes, “1 <M> reared 1911 at Poltaw. Agr. Exp. Sta from *Eriococcus greeni* Newst., 2 <F><F> and 1 <M> reared august-september 1913 by N.A. Grossheim in Crimea from puparia of *Leucopis* sp.?” (Kurdjumov 1917). Repository unknown.

Material examined. “GEORGIA (Telavi) on *Ps. citri* | 1938 | A”. (ZIS)

Distribution. Europe, India.

Biology. The type series was reared from *Eriococcus greeni* Newst. and from puparia of flies tentatively identified as *Leucopis* sp.

Literature. Nikol'skaya (1950): *new name* for *Xana nigra*, which became preoccupied by *Signiphora nigra* Ashmead, 1900 when both were placed in *Xana*. Nikol'skaya (1952:521): keyed, diagnosis, as *Xana*. Notes: Hayat (1980). Woolley (1988): under *Chartocerus*. *Hayat (2009): revision of species from India.*

Chartocerus niger **(Ashmead, 1900)**

Appendix E: Figure 25; Morphbank ID 576525 (type material)

EOL taxon ID: 848095

Original description. Ashmead (1900:410), as *Signiphora nigra*. Syn. *Signiphora argentina* Brèthes (1913:97) Syntypes <F> (MACN). Junior synonym of *Chartocerus niger* (as *Signiphora nigra*) (DeSantis 1957).

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.5–0.6mm (n=5). *Habitus and coloration*: Body predominantly dark, with midtarsi and hind tarsi white, apical tarsomere from midleg and of hind leg tan. Dry material originally described as "polished black, impunctate, with a decided aeneous tinge" (Ashmead 1900). Head brown as rest of the body, clava slightly lighter. Fore wings infuscated from base to M3, and light apical infuscation, interrupted by two hyaline patches: one in posterior half of the base of the wing and one medial band, as in several other species. Hind wing hyaline.

Head sculpture punctuate and longitudinally striate, punctuations roughly parallel to scrobes and inner margins of eyes, producing a uniform pattern. Eyes large, about 2/3 head neight. Antennal scrobes converge at about height of frons. Other sulci absent. Antenna with 4 anelli (4:3:2:1), clava 5.5x as long as wide, scape about the same length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through metanotum striate or striate to reticulate; pronotum barely visible medio-dorsally, mesoscutum about 3.5x length of scutellum, with 7–10 small setae in posterior half, organized in symmetric pairs, scutellum with 6–8 thick setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of length of scutellum; medial triangle of propodeum transversally striate to reticulate. Protibia about 2/3 of length of mesotibia. Mesofemur with 4 large apical spines; mesobasitarsus 1/2 length of mesotibia, mesotibial spur about same length of basitarsus; hindtibia 1.5 length of mesotibia, but mesotibia 2.5x thicker than metatibia. Apex of medial sclerite of propodeum round, almost reaching posterior margin of propodeal segment. Propodeal segment reaches, but does not overlap the area between the lobes of Mt1. Fore wings about 2.5–2.8x as long as wide; longest setae of marginal fringe little more than 1/3 of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe little more than ½ of maximum width of wing; discal seta present; 1 seta at on marginal vein.

Metasoma. Mt1 bilobed, with transverse connection between the two lobes. Retoiculate sculpture on tergites. Plates of the ovipositor almost reach the base of the gaster.

Male similar to females.

Type material: Syntypes, 3 males, 2 females (examined), mounted in Canada balsam (USNM type no. 4767): "'Signiphora | nigra Ashm. | <F>. Type no | 4767. U.S.N.M.' Washington, | D.C. | 3 <M>'s | 2 <F>'s | Remounted. || (red label) Signiphora | nigra | Ashm | Type No. 4767 U.S.N.M.". The type of *Signiphora argentina* Brèthes was found at MACN, but it is in poor conditions (Roig-Alsina, pers. comm.) and therefore could not be obtained on loan.

Distribution. Neotropics to Nearctic, Europe.

Biology. *C. niger* has been reared in association to encyrtids (*Aphycus lounsburyi, Clausenia purpurea, Leptomastidea abnormis*) on armored scales (*Quadraspidiotus perniciosus*), mealybugs (*Planococcus citri*, *Pseudococcus adonidum*, *P. comstocki*.) and scales (*Coccus hesperidum*). The synonym *C. argentinus* has been associated with *Dactylopius* sp. and *Paranusia bifasciata* (Brèthes 1913).

Literature. Girault (1913): notes on type material, descriptive notes, host record, distribution record. Girault (1915): descriptive note, distribution record. Smith and Compere (1928): review of hosts. Peck (1951): distribution records, host records.

Kerrich (1953): comparative morphology, taxonomy, as *Thysanus*. Thompson (1954): distribution.

Chartocerus novitzkyi **(Domenichini,1955)**

Appendix E: Figure 26; Morphbank ID TBD (type material)

EOL taxon ID: 848094

Original description. Domenichini (1955:18), as *Thysanus novitzkyi*

Description. **Male.** *Length* (pronotum to apex of the epiproct): 0.45–0.5mm (n=2). *Habitus and coloration*: The dry specimen was originally described as “black, with blueish and greenish tinge and antennae tan”. Body brown, the metanotum, propodeum and Mt1 light brown, the fore legs the same color as the body with tarsi tan, midlegs, hind legs and tarsi tan. Head and antennae the same color as body. Fore wings lightly infuscated from base to stigmal vein.

Head almost round in frontal view, sculpture longitudinally striate, with sparse short setae. Antennal scrobes well defined, extending to the height of upper margin of eyes, converging after the basal 1/3. Other sulci absent. Eyes large, glabrous, about 1/2 of head height. Antenna with 3 anelli, more or less same size (distal one slightly longer), clava 5x as long as wide, scape about ¾ length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through scutellum transversally striate, metanotum more widely so, propodeal triangle with large reticulation; pronotum barely visible dorsally, mesoscutum about 2x longer than scutellum, with 6 small setae concentrated in posterior half, scutellum with 6 setae aligned in parallel with posterior margin plus

one larger seta on top of each axilla. Metanotum about 2/3 of length of scutellum. Protibia about 2/3 of length of mesotibia. Mesofemur with 2 shorter apical spines and 2 large posterior spines; mesobasitarsus little less than 1/3 length of mesotibia, mesotibial spur same length of basitarsus; hindtibia slightly longer than mesotibia. Apex of medial sclerite of propodeum acute, reaching posterior margin of propodeal segment.
Metasoma. Mt1 trilobed, two lateral larger lobes connected by a short one. Genitalia with medial denticles projecting straight, one seta laterally to each of the medial denticles.

Female. Not observed. Domenichini (1955) described females and provided illustrations.

Type material. The type material is not in Novitzky's collection in Wien (Dominique Zimmermann, pers. comm.), as stated in the original description. There was also no response from the University in Piacenza.

Material examined. Two slides sent by Domenichini himself, one of them labeled "Turchia sp. n." and the other "Thysanus novitzkyi sp.n.". Based on these labels, it is possible that this last specimen might be type material.

Distribution. Palearctic.

Biology. Unknown.

Literature. Domenichini (1955): comparative morphology. Rozanov (1965): transferred to *Chartocerus*. Woolley (1988): listed in *Chartocerus*.

Chartocerus philippiae **(Risbec, 1957)**

Appendix E: Figure 27; Morphbank ID TBD (type material)

EOL taxon ID: 848092

Original description. Risbec (1957:271), as *Neocales philippiae*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 0.6–0.7mm (n=3). *Habitus and coloration*. Body predominantly dark, described originally as “black, with legs tan, tarsi transparent” (Risbec 1957). Propodeum and metasoma appear darker than the rest of the body in slide preparation. Head brown, as in pronotum and most of metasoma, antennal clava and anelli lighter than pedicel and scape. Legs tan, the lateroposterior part of protibiae and mesotibiae lighter, tarsi white. Fore wings infuscated, darker patch extending from base to apex of stigmal vein, lighter infuscation on apex, and two hyaline patches: one at the basal-posterior area, and one posterior to the stigmal vein, slightly curved towards the base of the wing.

Head sculpture punctuate and longitudinally striate, more conspicuous punctuations along outer margin of antennal scrobes and inner margins of eyes. Antennal scrobes well defined. Other sulci absent. Eyes large, glabrous. Antenna with 4 anelli, (1:2:2:3), clava 5x as long as wide, scape about ¾ length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through propodeum finely striate; pronotum visible dorso-laterally, mesoscutum about 4x length of scutellum, with about 20 small setae, concentrated in the posterior half, scutellum with 12 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of length of scutellum. Protibia about 3/4 of length of mesotibia. Profemur as long as mesotibia. Mesofemur with 3 large posteroapical spines; mesobasitarsus little more than 1/3 length of mesotibia, mesotibial spur about the same length as basitarsus; hindtibia as long as mesotibia. Apex of medial sclerite of propodeum acute, almost reaching posterior margin of propodeal segment. Fore wings about 3x as long as wide; longest setae of marginal fringe little less than 1/2 of wing width; discal seta absent, 1 seta in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 1 seta on base of marginal vein.

Metasoma. Mt1 is difficult to observe in both the lectotype and the paralectotype. It appears to be broadly bilobed with a transverse connection between the lobes, but the medial area is obscured. Plates of the ovipositor almost reach the base of the gaster.

Male similar to female, genitalia similar to *C. fimbriae* and *C. subaeneus*. The paralectotype male has no head.

Type material. Lectotype female (examined), remounted in Canada balsam (MNHN): “1014 (3) Aphelinidae ex coch[enille]. s[ur] Philippia”. Paralectotypes: 2 females, 1 male. Polaszek (1993) redescribed the species based on the type slide. That slide contained 4 individuals. Polaszek remounted each in an individual slide and designated the lectotype.

Distribution. Africa (Madagascar).

Biology. Unknown.

Literature. Polaszek (1993): redescription, notes on types, compared with *C. subaeneus, C. novitzkyi, C. hyalipennis*.

Chartocerus rosanovi **Sugonjaev, 1968**

Appendix E: Figure 28; Morphbank ID TBD (type material)

EOL taxon ID: 847841

Original description. Sugonjaev (1968:602).

Description. **Females.** *Length* (pronotum to apex of epiproct): 1.4mm.
Habitus and coloration: Body predominantly dark, originally described as black with "a bronzy luster" (Sugonjaev 1968). The type specimen (slide-mounted) is uniformly dark brown, including head and antennae, the anelli and clava slightly lighter. Legs the same color as body, lateroposterior part of protibiae and mesotibiae lighter, tarsi white, except for apical tarsomere, which is dark brown. Fore wing infuscation only under M2 to M4, and then at the apex of the wing. Apex of hind wing lightly infuscated.

Head sculpture punctuate and longitudinally striate close to antennal scrobes, round in frontal view. Antennal scrobes well defined, extending through 2/3 of height of head. Other sulci absent. Eyes large, glabrous, about 1/2 of head height. Antenna elongated, with 4 anelli (1:2:2:3, distal segments less than 1.5x as wide as long), clava about 10x as long as wide, scape about 2/3 length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through scutellum striate; scutellum and medial sclerite of propodeum finely reticulated. Pronotum barely visible dorsally, mesoscutum about 2.5x length of scutellum, with about 20 small setae concentrated in posterior half, scutellum with 8 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of length of scutellum; medial triangle of propodeum finely reticulate. Protibia about 2/3 of length of mesotibia. Mesofemur with 4 large posteroapical spines; mesobasitarsus 1/2 length of mesotibia, mesotibial spur about as long as basitarsus; hindtibia as long as mesotibia. Apex of medial sclerite of propodeum acute, reaching posterior margin of propodeal segment. Propodeal segment projecting posteriorly. Fore wings about 2.5x as long as wide; longest setae of marginal fringe about ¼ of wing width; discal seta absent, 1 seta in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 2 setae on base of marginal vein.

Metasoma. Mt1 not bilobed, parallel to propodeum, the midline longer than the flanks. Fine reticulation sculpture evident on tergites.

Male unknown.

Type material. Holotype female (examined): 1 slide with 3 coverslips, one with the body, one with the wings and one with the legs (ZIS): labels read clockwise: "(written directly on slide) <F> Kartocerus (sic) || (red label) Hartocerus (sic) | rosanovi | Sugonjaev || (red label) Holotypus || (written directly on slide, in cyrillic) 5km W

Bakanasa | at Ili River, clay desert | from galls of Caillardia | (along with Psyllae[phagus] caillardiae), on saxaul), 18–20.vii.63 || (written directly on slide) 1694.

Distribution. Palearctic (Kazakhstan).

Biology. The holotype was originally reared from galls of *Caillardia robusta* and associated with *Psyllaephagus caillardiae; paratypes* were reared from nymphs of psyllids on *Anabasis* sp.

Literature. Sugonaev (1968): compared with *Chartocerus kurdjumovi*.

Chartocerus simillimus **(Mercet, 1917)**

Appendix E: Figure 29; Morphbank ID TBD (type material)

EOL taxon ID: 847838

Original description. Mercet (1917:170), as *Signiphora simillima*.

Description. **Females.** *Length* (pronotum to apex of epiproct): 1.0–1.1mm. *Habitus and coloration*: Body predominantly dark, head dark, antenna slightly lighter, anelli and club light brown. Basal and distal extremes of all 3 tibiae white, the remainder as dark as body. Fore wing infuscation darker in area extending from base to under stigmal vein; then another infuscated area at the distal portion of the wing.

Head sculpture punctuate. Antennal scrobes well defined, reaching median line of eyes. Other sulci absent. Eyes large, glabrous, about 3/4 of head height. Antenna with

4 anelli (1:2:2:3), clava 5x as long as wide, scape about ¾ length of clava; pedicel about 1/3 length of clava.

Mesosoma with pronotum through metanotum striate or striate to reticulate, not visible in metanotum and propodeum. Pronotum visible dorsally, about 1/3 of mesoscutum; mesoscutum about 3x longer than scutellum, scutellum with 10 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla;; metanotum about 1/2 of length of scutellum. Protibia about 2/3 of length of mesotibia. Mesofemur with 3 large apical spines; mesobasitarsus little more than 1/3 length of mesotibia, mesotibial spur about 2/3 of length of basitarsus; hindtibia as long as mesotibia. Apex of medial sclerite of propodeum round, almost reaching posterior margin of propodeal segment. Propodeal segment reaches, but does not overlap the area between the lobes of Mt1. Fore wings about 3.5x as long as wide; longest setae of marginal fringe about ¼ of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 2 setae on base of marginal vein.

Metasoma. Mt1 transverse. Imbricate sculpture evident. Plates of the ovipositor almost reach the midline of the gaster.

Male unknown.

Type material. Syntypes female (examined), mounted in balsam (MNCN): "Signiphora simillima | Mercet | tipo | Madrid -16-2-67 || MNCN Cat. Tipos No. 12089 || MNCN_Ent No. Cat. 71292)." Mercet (1917) did not explicitly indicate the repository for the type of this species.

Distribution. Palearctic (Spain).

Biology. Unknown. The type material was collected on pine trees, as reported by the author (Mercet 1917).

Literature. Woolley (1988): transferred to *Chartocerus*.

***Chartocerus subaeneus* (Förster, 1878)**

Appendix E: Figure 30; Morphbank ID TBD (type material)

EOL taxon ID: 1500589

Original description. Förster (1878:69), as *Plastocharis subaenea*.

Syn. *Signiphorina mala* Nikol'skaya, 1950:320. Junior synonym of *Chartocerus subaeneus* (Novitzky 1954). (type repository unknown)

Description. **Males.** *Length* (pronotum to apex of epiproct): 1–1.2mm (n=6). *Habitus and coloration*: Body predominantly dark, originally described as black with metallic "bronze/green tones". Head brown, as in pronotum and most of metasoma. Mesoscutum and Mt2–4 slightly darker than the rest of the body. Legs the same color as scutellum and metanotum; distal part of mesotibia, hindtibia and respective tarsi lighter. Fore wing infuscation extending from the distal point of submarginal (parastigma) to M3 or M4.

Head sculpture uniformly punctuate, striate along margins of antennal scrobe, genae and clypeus, striation absent in vertex), with scattered small punctuations along outer margin of antennal scrobes and inner margins of eyes, approximately round in frontal view. Antennal scrobes well defined, extending to level of dorsal 1/3 of compound eyes. Eyes large, glabrous, about ½ of head height. Antenna with 4 anelli (1:2:2:3), clava 6x as long as wide, scape about ¾ length of clava; pedicel about 1/9 length of clava.

Mesosoma with pronotum through metanotum transversally striate, axillae longitudinally striate, propodeum striate to poligonally reticulate. Mesoscutum about 3x longer than scutellum, with about 3–5 small setae, scutellum with 4 setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of length of scutellum. Protibia about ¾ of length of mesotibia; mesotibia ¾ of length of metatibia. Mesofemur with 3 large spines; mesobasitarsus approximately ½ length of mesotibia, mesotibial spur slightly shorter than length of basitarsus (less than 1/3 length difference), with 7 teeth. Apex of propodeum triangular area acute, reaching posterior margin of propodeal segment. Propodeal sclerite transverse, does not overlap the area between the lobes of Mt1. Fore wings 2.75–3x as long as wide; longest setae of marginal fringe little less than ½ of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 5 small setae in basal area. Hind wings 4x as long as wide, longest setae of marginal fringe about ½ maximum width of wing; discal seta present; 1 seta on submarginal and 1 in marginal vein.

Metasoma. Mt1 bilobed, with transverse connection between the two lobes.

Type material. Lectotype male (Berlin): “17/610 || (pink label) Frst || (in pencil) Plastocharis | subaenea Forst. || Zool. Mus. Berlin || (red label) Plastocharis | subaenea Förster | lectotype <M> | design. J.B.Woolley ’89 || (white label) GBIF-ChalCISD | ID: ChalD0126”. The lectotype is mounted in resin between two fragments of coverslips embedded in a perforated card.

Other material examined. GERMANY: 4 females (MHNG). ISRAEL: 6 males, 9 females (TAMU, UCR). ITALY: 3 males, 9 females (IEUC).

Distribution. Palearctic, Nearctic, Afrotropics.

Biology. Rosen et al. (1992) described the life cycle and immature stages of *C. subaeneus* as a parasitoid of Pseudococcidae.

Literature. Domenichini (1955): comparative morphology. Novitzky (1954): synonymy of *S. mala*. Nyiazov (1969): distribution, parasitism, quantification of parasitism. Rosen et al. (1992): redescription, natural history, electron microscopy, designation of lectotype. Woolley (1988): systematics, placement in *Chartocerus*.

Chartocerus walkeri **Hayat, 1970**

Appendix E: Figure 31; Morphbank ID TBD (type material)

EOL taxon ID: 847836

Original description. Hayat (1970:393).

Description. **Females.** *Length* (pronotum to apex of epiproct): 1–1.2mm (n=6). *Habitus and coloration*: Body predominantly dark, legs the same color as the body from coxa to apex of tibia, tarsi white, except for distal tarsomere of midleg and hind leg, which is tan. Fore wings and hind wings hyaline.

Head sculpture striate to reticulate, transverse in frontovertex. Antennal scrobes well defined, merging at about the midline of eyes, extending through 3/4 of head height. Other sulci absent. Eyes large, glabrous, about 2/3 of head height. Antenna with 4 anelli (1:3:4:4), clava 5.5x as long as wide, scape about 1/2 length of clava; pedicel elongate, about 1/3 length of clava.

Mesosoma with pronotum through metanotum striate or striate to reticulate, fainter in scutellum; pronotum barely visible dorsally, mesoscutum about 3.5x longer than scutellum, with some sparse very small setae, scutellum with 6–8 very fine setae aligned in parallel with posterior margin plus one larger seta on top of each axilla; metanotum about 2/3 of length of scutellum; medial triangle of propodeum striate to finely reticulate. Protibia about 1/2 of length of mesotibia. Mesofemur with 3 large posteroapical spines; mesobasitarsus little more than 1/3 length of mesotibia, mesotibial spur about 2/3 of length of basitarsus; hindtibia slightly longer than mesotibia. Apex of medial sclerite of propodeum acute, not reaching posterior margin of propodeal segment. Fore wings about 3x as long as wide; longest setae of marginal fringe about 1/5 of wing width; discal seta absent, 2 setae in submarginal vein; seta M1 absent; 3 small setae in basal area. Hind wings 3x as long as its maximum width, longest setae of marginal fringe about 1/3 maximum width of wing; discal seta present; 1 seta in distal half of marginal vein.

Metasoma. Mt1 bilobed, medial-posterior portion of propodeum overlapping it (NB. Not a process, as in *Signiphora*). Plates of the ovipositor almost reach the base of the gaster.

Male unknown.

Type material. Holotype <F> at ZSI, Calcutta (Hayat 1980) not at Aligarh (not examined). Described from India: Uttar Pradesh, Aligarh, on *Rastrococcus iceryoides*

(Green.) on *Capparis* sp. Coll. Hayat 25.xii.1968. The publication mentions paratypes at ZIASL (Leningrad), ZMAMU (Aligarh), ZSI (Calcutta). 2 paratypes examined: “Chartocerus | walkeri Hayat | ex Rastrococcus iceryoides | on Zizyphus | 105.MC.1 || INDIA: HP | Joginder Nagar | 27.vi.1967 | AP prep x.87” (BMNH(E) #990939–940) *Other material examined.* INDIA: Bangalore: 4 males, 1 female (CIE-BMNH); Tamil Nadu: 1 male (CIE-BMNH); Uttar Pradesh: 1 male, 1 female (BMNH). MALAYSIA: 2 males, 3 females (CIBC-BMNH).

Distribution. Oriental (India, Southeast Asia).

Biology. Type material reared from *Rastrococcus iceryoides* (Green.). Hayat (1980) rectified host information, mentioning having reared it from *Diaphorina cardiae* (Psyllidae).

Literature. Hayat and Verma (1980): listed, notes on morphology. Hayat (2009): revision of species from India.

Chartocerus DESCRIBED BY A. A. GIRAULT AT THE QUEENSLAND MUSEUM

The following descriptive notes are based on data sheets and photographs taken by JBW during his visit to the Queensland Museum.

Chartocerus australicus (Girault, 1913)

Appendix E: Figure 32A; Morphbank ID TBD (type material)

EOL taxon ID: 847848

Original description. Girault (1913:226), as *Signiphora australica.*

Remarks. Holotype male under cracked resin and coverslip, along with a specimen of *Aphelinoidea howardi* Gir. Transcription of labels from Dahms (1983): “From window of a workmen's quarters. Sugar farm, Nelson [= Gordonvale], N.Q. XII.21.1911 [GH]", "Signiphora australica Girault, i Type, Hy/773 [GH] 4412, 4412" and on the reverse of the slide, "Queensland Museum. TYPE, Hy/773 S". Dahms (1983) also mentions one paratype and one specimen at the USNM, topotypical.

Description. **Male.** *Length* (pronotum to apex of epiproct): 0.6mm. *Habitus and coloration*: Body brown; metasoma and propodeum darker than head and thorax; antennae, genae and clypeus slightly lighter than surrounding areas. *Head.* Several structures cannot be observed. Head approximately rounded in frontal view, antennal scrobes evident, clava 7x as long as wide, 3 anelli (2:2:1), pedicel 2.5x as long as wide, scape 4x as long as wide, clava 2.5x length of scape. *Mesosoma*. Wings not visible. Pronotum about 8x as wide as long. The other sclerites seem crushed; margins are indiscernible. Median propodeal sclerite seems to be coarsely reticulated like the remainder of the abdomen. *Metasoma*. Mt1 visibly bilobed.

Chartocerus australiensis orbiculatus **(Girault, 1915)**

Appendix E: Figure 33; Morphbank ID TBD (type material)

Original description. Girault (1915:68), as *Signiphora australiensis orbiculata*

Remarks. Girault (1915) defined this subspecies based on differences of the wing infuscation; the anterior part of the infuscation which extends from the base to S is darker than the posterior. The distal portion of the wing is faintly infuscated as in *C. australiensis australiensis*.

Holotype <M>, Hy2965 at QM. The label, in Girault's handwriting, indicates: "Type | Hy/2965 | A.A. Girault || Signiphora | australica Gir. || (red label) 4409 | Signiphora | australiensis | orbiculata | Gir. 2 Described from Gordonvale (Cairns), North Queensland. This locality information is not provided in the type label. Dahms (1983:92) describes the slide which contains the holotype as "slide #3" in his discussion of *C. australicus* material*:* "2 coverslip fragments; the one closest to "TYPE" label contains *Signiphora australiensis orbiculata* Girault; the other fragment contains a *Signiphora australica*, head, wings and some legs separated".

Description. **Male.** *Length* (pronotum to apex of epiproct): 2.2mm. *Habitus and coloration*: Body brown; legs slightly lighter, tarsi of midleg and hind leg white, and apical tarsomere of hind leg tan. The head has been crushed. Mandibles bidentate, scape wide (approximately 3x as long as wide (?), pedicel 2x as long as wide, anelli not visible, clava fairly short and wide (4x as long as wide). Mesoscutum about 2x as long as scutellum, with 12 setae; 8 setae in posterior margin of scutellum plus 1 on top of each axilla. Mesotibiae ½ length of metatibiae, mesobasitarsus about ½ length of mesotibia, mesotibial spur slightly shorter than basitarsus, with 5 teeth. Mesofemur with 3 spines. Fore wings 3x as long as wide, marginal setae about 1/3 of maximum wing width, 1 seta in submarginal vein. Hind wing 4x as long as wide, marginal fringe about ½ width of wing, 1 seta in marginal vein. Mt1 bilobed, with a transverse extension between two lobes.

Chartocerus beethoveni **(Girault 1915)**

Appendix E: Figure 34; Morphbank ID TBD (type material)

EOL taxon ID: 847846/

Original description. Girault (1915:71), as *Signiphora beethoveni*

Remarks. Holotype <F>, Hy2969, QMB: Chindera, New South Wales, 9.v.1914, A.P. Dodd, “sweeping forest on sand-ridges near coast”. Partially dissected.

*Description.***Female.** *Length* (pronotum to apex of epiproct): 1.15mm. *Habitus and coloration*: Head and body appear uniformly light brown; head (frontovertex) slightly darker; fore legs and tarsi of all legs lighter brown to almost transparent. Frontovertex finely transversally striate, punctuations typical of most *Chartocerus* are not visible. Antennal scrobes well defined. The morphology of the antenna very distinctive, similar to that described for males of *C. kerrichi*: clava wide, ellipsoid, 3x longer than maximum width; 4 anelli (4:2:2:1), pedicel 2x as long as wide, scape 4x as long as wide and about ¾ of length of clava. Pronotum, mesoscutum, scutellum and metanotum transversally striate to finely, faintly reticulate; axillae reticulate, medial area of propodeum reticulate at lateral margins to striate medially, with cells 2-3x wider than long. Mesoscutum about 3.5x length of scutellum. Fore wing 3x as long as wide, marginal fringe slightly longer than ½ of maximum width of wing, 2 setae in submarginal vein, M1 lacking, 5 small setae in basal area of wing, 1 wing in costal cell. Mesotibiae 2x as long as protibiae; hindtibiae only slightly longer than protibiae, mesofemur with 3 spines, mesobasitarsus about ½ length of mid-tibiae and mesotibial spur about same length of basitarsus, with 5 teeth. Mt1 bilobed.

Chartocerus corvinus **(Girault, 1913)**

Appendix E: Figure 35; Morphbank ID TBD (type material)

EOL taxon ID: 847843

Original description. Girault (1913:225), as *Signiphora corvina*.

Remarks. Holotype <F> mounted with *Gonatocerus huxleyi* and specimens of *Signiphora australiensis, Abbella subflava, Ufens* and *Aphelinoidea,* "from a window in a granary and barn on a wheat farm at Roma, Queensland, October 6, 1911". Hy./772, QMB. The accession number Hy/772 is not indicated in the slide; number 4407 is indicated in a red label. According to Dahms (1983), the female is in fact the holotype: "QM: Slide - 1 cracked, complete coverslip (partly missing over 1 specimen) containing the Holotype = (head separated) of Signiphora corvina and other specimens as per labels. "Gonatocerus huxleyi Girault, 2 Type 1040. From windows of a granary, Roma, Q., 6 Oct., 1911 AAG [GH] 3691, 3691”. An arrow was added by JBW to indicate the holotype. The head of the specimen is off.

Description. **Female.** *Length* about 1.2mm. Body dark, femora and tibiae slightly lighter, protibiae especially light distally. Tarsi of all legs lighter than the rest of the legs. The basal infuscation of the wing extends to a diagonal crease positioned in direction of the stigmal vein. Head round in frontal view, genae reticulate, punctuations lateral to antennal scrobes; interantennal area seems lighter than clypeus and genae. Eyes relatively small, about 1/3 height of head. Antennal scape about 5x as long as wide, pedicel and ring segments cannot be observed, club about 2.6x as long as wide. Mesoscutum transversally striate, scutellum, metanotum and basal part of medial propodeal sclerite striate to reticulate towards margins. Mesoscutum at least 2x length of scutellum. It is not possible to count the setae on the mesosomal tergum. Fore wing very broad, at the broadest part about ½ length of wing. The wing vein reaches about half of the distance to the apex. Marginal fringe very short, not more than 1/8 of wing width, 2 setae on submarginal vein, M1 missing (M6 is broken in this type but the socket is visible). Hind wing also wide towards the apex, about 3.5x as long as wide, marginal fringe 1/5 of wing width, with discal seta. Mesobasitarsus less than ½ length of mesotibia; mesotibial spur slightly shorter than basitarsus and with 4 teeth. Mesofemur with 2 visible spines.

Chartocerus delicatus **(Girault, 1933)**

Appendix E: Figure 36; Morphbank ID TBD (type material)

EOL taxon ID: 848109/

Original description. Girault (1933:2), as *Matricia* (sic) *delicata*

Remarks. From the original description: “Taringa, No. 26, 1928”. The original description does not offer further information about specimens. Holotype <F> in balsam slide, head off. Dahms (1983:216) provides a longer explanation from Girault’s unpublished manuscript: “One female found upon the adhesive bracts of Passaflora [= Passiflora] foetida in my home garden was the type".” According to Dahm’s description, the slide cracked and was mended with paper, and it contains the female holotype together with several other insects. The label data reads: "Matritia delicata Girault, Type = [GH] || On adhesive bracts of Passaflora [sic], Taringa, Nov. 26, 1928 [GH] Ent. Div.Dep. Ag. & Stk., Qld".

Description. **Female.** *Length* 0.74mm. Body light brown; legs and tarsi yellowish or light brown, syntergum and ovipositor sheath seem slightly darker than the rest of the body. Wing infuscation seems to cover the entire wing; instead of a medial hyaline area, the infuscation only gets lighter close to the end of stigmal vein, and then also noticeably infuscated at the apex of the wing. Head roughly rounded in frontal view; punctate sculpturing. Pronotum, mesoscutum, scutellum and metanotum transversely striate; axillae reticulate, medial area of propodeum reticulate. Mesoscutum with about 14 small setae arranged somewhat symmetrically in posterior half of mesoscutum. Scutellum with 9-10 fine setae in posterior margin of scutellum and one on top of each axilla.

Protibia about 2/3 of length of mesotibia, mesotibia about 2/3 of length of metatibia; mesobasitarsus less than half of length of middle tibia, mesotibial spur with 5 teeth. Fore wing with 2 setae on submarginal vein, lacking M1, as described above for other Australian species of *Chartocerus*. Hind wing 6.5x as long as wide, marginal fringe little less than ½ width of wing. Mt1 bilobed, although faint. Girault (1933) mentions it differs from *C. australicus* by shorter marginal fringe in wings, and hindfemur infuscated only apically, which might have been an oversight, since several other species of *Chartocerus* present such coloration.

Chartocerus funeralis **(Girault, 1913)**

Appendix E: Figure 37; Morphbank ID TBD (type material)

EOL taxon ID: 848103

Original description. Girault (1913:224), as *Signiphora funeralis*.

Remarks. The photographed type material corresponds to Hy./771 holotype <F>, QM. In the original description, Girault mentions it was "captured from a window in an empty dwelling, December 28, 1911, at Heberton, North Queensland, Australia", mounted with "some trichogrammatids and an *Anagyrus*" (Girault 1913). "Girault number" 4410. The slide is described from QM (Dahms 1984) as consisting of 3 coverslip fragments: one with the intact holotype of *S. funeralis*, along with the other chalcidoids, one containing 1 male *S. funeralis* with head, 1 antenna and 1 leg separated (label: "Signiphora funeralis Gir. | Indooroopilly | window | VII.5.1933)" and one containing a specimen of *M. hebes*.

Description. **Female**. *Length* 0.74mm. The holotype has faded to yellowish tone, but it was originally described as dark as the other species of *Chartocerus*. Head with punctuations scattered on face and genae. Scape about 4.5x as long as wide, pedicel 2x as long as wide, ring segments in ratio (6:4:2:1), resembling *C. kerrichi,* clava 5x s long as wide. Mesoscutum little more than 3.5x length of scutellum, with scattered small setae; scutellum with 6 faint setae along posterior margin. Fore wing almost 3x as long as wide, marginal fringe roughly ½ width of the wing. Mesobasitarsus less than ½ length of mesotibia, mesotibial spur about 1/3 of the basitarsus. Mt1 bilobed, the two lobes connecting smoothly by a concave curve; propodeal sclerite projecting posteriorly gradually.

***Chartocerus hebes*(Girault,1929)**

Appendix E: Figure 38; Morphbank ID TBD (type material)

EOL taxon ID: 848102

Original description. Girault (1929), as *Matritia hebes*.

Remarks. Syntypes, females. In the original description, Girault mentions "three females from spider eggs in a leaf-nest, Tasmania" (Girault 1929). Dahms (1984) describes material at two institutions: 1 slide at SAM containing 3 females (Label: "TYPE | Matritia hebes Girault | type <F> S. Aus. Mus. Ent. Div. Dep. Ag. & Stk., Qld."), plus 1 card and 1 slide at QM. The card contains 2 females and a glue spot where a third specimen was attached, labeled "Tasmania || From eggs of spider in leaf nest || 4416 || Matritia hebes Girault | Cotype <F>'s", and the slide with one female ("Hy.235 | Matritia hebes Girault | also wing <F> cotype (inner) | Ent. Div. Dep. Ag. & Stk., Qld.

4416"). The data from the QM material matches the original description. Dahms (1984) deduced from these labels that Girault had more than the three specimens at hand when he described the species, and therefore all 6 females should be considered syntypes.

Description. **Female.** Body dark, legs also dark, but posterior part of fore leg and apical part of metatibiae lighter, tarsi yellowish. Wing infuscation is different from other species of *Chartocerus* because the apical part is darker than the basal part, with an extension of the darkened areas below the stigmal vein. Setae in fore and hind wing as in other *Chartocerus* (2 setae on fore wing submarginal vein, 1 costal seta, 6 setae on marginal veinm etc.). Basitarsus of midleg about 1/3 of length of midleg. Scutellum about 1/3 of length of scutum. The propodeum and Mt1 were not cleared enough in this preparation to be visualized; the same applies to setation of mesoscutum and scutellum.

Chartocerus reticulatus **(Girault,1913)**

Appendix E: Figure 39; Morphbank ID TBD (type material)

EOL taxon ID: 13795738

Original description. Girault (1913:166), as *Signiphora*.

Remarks. Unpublished notes from Girault put this species as *Matritia* (Dahms 1986). The original description indicates "Ayr, Queensland, sweeping forest. Holotype <F>, QM Hy/1281". Dahms (1986:474) describes 3 slides located at QM, one with the holotype and two with multiple individuals actually labeled as *(Signiphora) Matritia reticulata* (Girault). The holotype is in a slide under 1 complete coverslip, and a fragment of a coverslip that contains the type of *Australaphycus albioviductus* Gir.:

"Queensland Museum. TYPE | Hy/1281 | 2 || Australaphycus albioviductus Gir., Type <F> [GH] || Signiphora reticulata Girault, <F> type. Sweeping, forest, Ayr, Q., 6 Apr.,1912 [GH] 4408"."

Description. **Female.** *Length* 0.96mm. Body dark brown, legs lighter, golden-brown, tarsi of midleg and hind legs yellow. Head with somewhat equally spaced punctuations, and striae close to antennal scape. Scape 3-3.5x as long as wide, medially wider than in extremities, pedicel 2x as long as wide, 4 anelli (1:3:3:5), clava 6-7x longer than wide. Mesoscutum about 2x as wide as long, scutellum 1/3 of length of mesoscutum. Mesotibia about 2x length of protibia; hindtibia 1.25x length of mesotibia. Mesobasitarsus a little more than 1/3 of length of mesotibia; mesotibial spur ½ length of basitarsus and with 3 teeth visible. Mesofemur with 2 spines. Fore wing 3x as long as wide, setae not larger than 1/8 of width of wing. Setae in fore and hind wing as in other *Chartocerus* (2 setae on fore wing submarginal vein, 1 seta in costal cell of fore wing, 6 setae on marginal vein etc.). The wing infuscation is not discernible.

Chartocerus ruskini (Girault, 1921)

Appendix E: Figure 32B, 40; Morphbank ID TBD (type material)

EOL taxon ID: 847839

Original description. Girault (1921:188)

Remarks. *Type material*. Holotype <F> (QM Acc. No. 4406) on a slide in bad conditions, labeled: "Lathromeroidea nigrella <MF>, Anaphoidea linnaei 2<F>'s, *Signiphora ruskini* Gir. Type. <F> 4406 | (red label) 4406). Dahms (1986) describes the slide containing 5 coverslip fragments, with numerous specimens, one of which is the holotype. The slide does not have date information, but in the original description, Girault indicates "Nelson, forest, March 6, 1919". The propodeal sclerite was dissected in this specimen.

Description. **Female.** Length ~0.6mm. Body mostly brown, metanotum and medial area of propodeum much lighter ; scutellum, mesoscutum and pronotum slightly lighter than metasoma. Fore wing infuscation darker from base to M4. Remainder of wing lightly infuscated. Face striate, frontovertex with punctuations more evident. Scutellum a little less than ½ length of mesoscutum. Fore wing 2.7x as long as wide, marginal fringe as long as slightly less than ½ maximum wing width. The fore wing venation seems to be similar to other *Chartocerus,* but it is obscured. Mt1 bilobed.

Chartocerus thusanoides **(Girault, 1915)**

Appendix E: Figure 41; Morphbank ID TBD (type material)

EOL taxon ID: 847837

Original description. Girault (1915:71), as *Signiphora thusanoides*.

Remarks. Holotype <F>. Dahms (1986) published notes on the conditions of the type material: 2 coverslip fragments, one with the holotype, the other with an unidentified signiphorid (label: "TYPE || 4415 || (fading) Signiphora thusanoides Gir. <F> type || Holotype *Signiphora thusanoides,* Gir. Det. J. B. Woolley '79". The head is broken in fragments, and the mesosoma is broken in 2.

Description. ***Female.*** Length about 1.4mm, Body mostly brown, legs lighter, with apical tarsomeres of metatibiae tan; posterior face of mesotibiae yellowish white. The specimen head capsule has been completely crushed. Scape 4x as long as wide, pedicel little less than 2x as long as wide, 4 anelli (2:3:4:7). Clava about 4x as long as wide. Pronotum about 5x as wide as long, mesoscutum 2.5x longer than scutellum. Fore wing wide, 2.3x as long as wide. Hind wing about 3x as long as wide, marginal fringe about ¼ of width of my mesotibia. Mt1 slightly bilobed, the two lobes very close to each other, giving Mt1 with the same trapezoid appearance as propodeum. Ovipositor short, the outer plates not reaching ½ length of the metasoma.

SPECIES NOT COVERED IN THIS STUDY

Chartocerus bengalensis Hayat, 2004

EOL taxon ID: 847845

Original description. Hayat (2004 :1383-1385).

Type material. Holotype female, slide-mounted (IARI/NPCI). Acc. description: "Kalyani, West Bengal, India, ex *Aspidiotus* sp. on *Mangivera indica*, coll. B. K. Das".

Distribution. India.

Remarks. Species with yellow tones. This species was tentatively described in *Chartocerus,* however, it presents features that may indicate otherwise. Hayat indicates this species differs from other species because the female antenna has 3 and not 4 anelli, the fore wing has a discal seta, and the male has a distinct epiproct.

Literature. Hayat (2009): revision of species from India.

Chartocerus fujianensis **Tang, 1985**

EOL taxon ID: 1500764

Original description. Tang (1985:59), as *Chartocerus (Signiphorina) fujianensis*.

Type material. Holotype male (FAC accession no. 28), acc. description: “Hongtang, Fuzhou, Fujian, 1983-NOV-13”; Paratype male, same as holotype; 8 Paratype females, 7 males: “Hongtang, Fuzhou, Fujian, 1983-Oct-3 ~ Nov-10”. They were all cultured from a citrus parasite *Nipaecoccus vastator*.

Distribution. China.

Remarks. Since the description was only provided in Chinese, a translation of the text by Tang (1985) is included for reference at this project’s public taxon page for this species (http://tinyurl.com/cfujianensis).

Chartocerus gratius **(Girault, 1932)**

EOL taxon ID: 847836

Original description. Girault (1932), as *Matritia gratia*.

Type material. Syntypes, DEAP. Acc. description: “Western Australia, on *Dactylopius*, L. J. Newman)”. A single slide contains 10 damaged syntypes of both sexes (Dahms 1984).

Distribution. Australia.

Remarks. Described by comparison with *C. hebes*. Woolley (1988): new combination, as *Chartocerus*.

Literature. Dahms (1984:660): notes on type material.

***Chartocerus himalayanus* Hayat, 2009**

Original description. Hayat (2009 :23).

Type material. Holotype female (ZAMU reg. no. 13/6/70/5).

Distribution. India.

Remarks. Described in comparative diagnosis with *C. fimbriae*.

***Chartocerus hyalipennis* Hayat, 1970**

Original description: Hayat (1970:391), as Chartocerus (Xana) hyalipennis.

Type material. Holotype female (ZSI?), according to original description: "India, Tamil Nadu, Shenkottah, 6.ii.1967, M. Hayat, ex. Nipaecoccus vastator (Maskell) on Tephrosia purpurea".

Distribution. India, Ghana (Cudjoe et al. 1993), Nigeria (Goergen 1992), West Africa (Goergen and Neuenschwander 1994).

Remarks. There is conflicting information about the type repository; the original publication indicates ZAMU, but subsequently (Hayat and Verma 1980 and later publications and catalogues) as having been deposited at the ZSI.

Literature. Hayat and Subba Rao (1986): taxonomic position.*Woolley (1988): systematics, Chartocerus*. Hayat (2009): revision of species from India.

***Chartocerus intermedius* Hayat,1976**

Original description. Hayat (1976:162-3), as Chartocerus (Signiphorina) intermedius.

Type material. Holotype female (ZSI Acc. No. 373MA-1), acc. description: from "India, Uttar Pradesh: Bareilly, ex mealybug. Coll. Hayat 28.x.1969". Paratypes 1 female and 1 male labeled 373MA-2 and 373MA-3.

Distribution. India.

Literature. Hayat (1976): descriptive notes. Hayat (2009): revision of species from India.

***Chartocerus ranae* (Subba Rao, 1957)**

EOL taxon ID: 848090

Original description. Subba Rao (1957:388-90), as *Thysanus ranae*.

Type material. Holotype female (IARI/NPCI). Acc. description, from "New Delhi, N. India". Indicated as hyperparasitoid through encyrtid on *Sacchariococcus sacchari* (sugar cane mealybug).

Distribution. India.

Remarks. Transferred to *Chartocerus* by Rozanov (1965). According to Hayat (2009), the types of this species may be lost, since this material was not found at NPCI. Hayat (2009) also points out that this species might be a junior synonym of *C. subaeneus,* or a senior synonym of *C. fimbriae* or *C. intermedius*.

Literature. Hayat (2009): revision of species from India.

Chartocerus yunnanensis **Tan & Zhao, 1995**

Original description. Tan and Zhao (1995:204-206), as *Chartocerus (Signiphorina) yunnanensis*.

Type material. Holotype female, 2 males and 1 female paratypes (CNEP). Acc. description: “Datun, Mengzi County, Yunnan Province, 1998-7. Reared from *Planococus citri* Risso”.

Distribution. China.

Remarks. Since the description was only provided in Chinese, a translation of the text by Tan and Zhao (1995) is included for reference at this project’s public taxon page for this species (http://tinyurl.com/cyunnanensis).

OTHER TAXA PLACED IN *Chartocerus*

Gordh (1979:912) listed under *Chartocerus* four species that are now placed in *Signiphora*, as discussed by Woolley (1988): *Signiphora fasciata* Girault, 1913, *Signiphora mexicana* Ashmead, 1900, *Signiphora pulchra* Girault, 1913 and *Signiphora unifasciata* Ashmead, 1900. No reason was given for their placement in *Chartocerus*. Miller and Gimpel (2014) and Stauffer and Rose (1997) listed *S. fasciata* under this genus based on Gordh (1979).

CONCLUSION

The present work aimed at facilitating further comparisons in order to produce a comprehensive revision of the genus *Chartocerus*. A survey of the type material and comparison of host records already reveals some possible synonymies, as already hinted by Polaszek (1993). On the other hand, it is necessary to study in more depth the material of species involved in food webs of economically important insects and most commonly identified: *Chartocerus subaeneus, Chartocerus elongatus, Chartocerus dactylopii* and *Chartocerus niger*.

CHAPTER VI

CONCLUSION

Seven years ago, Matt Yoder wrote, in the conclusion of his dissertation:

> When new technologies are envisioned or described there is typically a significant lag between their inception and their usefulness in any widespread capacity. Only when databases and molecular phylogenies are not but an afterthought to the taxonomist/systematist will we be at the stage where the true efficiencies needed to treat the taxonomic impediment are met. (Yoder 2007)

In 2014, taxonomic publications using molecular data are ubiquitous, and if the use of databases is not, those too are starting to become widespread. However, at least part of taxonomic information has reached a scale of dissemination that was hard to imagine a few years ago. It used to be anticipated by any systematist that there would be difficulties posed by lack of access to publications and data, scarcity of tools, lack of integration between databases, redundancy and difficulties to discover sources of information. These are finally being very quickly remediated through initiatives that digitize literature, sites that connect researchers, encouraging them to share their publications, publishers that embrace more flexible intellectual property policies, and agreements on data schemas between biodiversity databases. All these factors have significantly transformed the landscape of the field of taxonomy. (Unfortunately, we are still not at the stage where the same can be said about access to specimens and funds for sampling.)

The challenge, therefore, changes: it is no longer about finding data, but sorting through all this information in order to produce meaningful taxonomic work. It is becoming clear that besides the practice of taxonomy, it is required that researchers in taxonomy acquire at least basic knowledge of programming and web development not only because one needs to manage increasing amounts of information, but also to make sense of the quickly transforming field of taxonomy (or "cybertaxonomy") and to make educated choices about the best practices for dissemination of scientific information. It is imperative to understand that hypertext works differently than the print medium, and the already high amount information contained in very few words in taxonomic text will increase exponentially, especially with the advent of semantic tagging.

Data management is only one of the facets of "new taxonomy", which also includes ever more powerful photomicroscopy, DNA sequencing and phylogenetics. Overseeing data management issues has been an unfortunate repeated pattern in this area (see Sarasan 1983), but there is no reason why it can't be broken. Hopefully in a few years these electronic workflows will be accessible enough to every researcher that streamlining the process of data capture and sharing will be a well-established third element in taxonomic studies, along with alpha-taxonomy and phylogenetics, rather than a challenge. Still, there is no substitute for careful direct observation and analysis of the organisms, and every effort put into helping the researcher to focus more on descriptive work and comparative biology should perhaps be more valued, or at least as valued as the efforts put into methods of displaying results.

With respect to the systematics of Signiphoridae, it became clear from the material available that the biodiversity represented by this group had been greatly underestimated both in number of species and on morphological variation. In the future, the phylogenetic framework presented in Chapter III will clearly benefit from the addition of new taxa and new data, especially from the emerging high-throughput approaches to DNA sequencing. Other issues that should be addressed with the availability of molecular data would be the cryptic species close to *Thysanus ater* and the subgenera of *Chartocerus*. I have no question that new technologies that allow for external and internal morphology, such as improvements in optics, the "desktop electron microscope" and micro-computerized tomography scanning, will reveal many unexplored structural complexities.

A large part of the work in this dissertation involved "behind the scenes" activities such as capture of basic data, digitizing information, data cleanup and transformation of storage formats, troubleshooting and optimizing protocols for each of these activities, and trying to apply them to "traditional" taxonomy. This is likely no surprise to any researcher in this area. It is also no surprise that doing so is a highly iterative process. In comparison to classic taxonomists, who could focus all their attention in alpha taxonomy, this clearly impacted the research in terms of numeric output at first instance. I am, however, left with a workflow which can be efficiently applied to future studies, and which I hope will be able to quickly absorb and interact with new technologies.

I conclude the work in this dissertation with an optimistic perspective, in view of the mostly positive interaction between taxonomy and the general public fostered by the new methods to disseminate science and the impressive accomplishments in biodiversity informatics that have been reached in the past 3-5 years. If the "classic" taxonomist has been said to be bound to extinction, information technologies could be considered a pre-adaptation that will allow for the survival of this "species", even if it is yet another diversion from pure alpha-taxonomy.

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APPENDIX A

MAIN TABLES AND FIGURES FOR CHAPTER I

Table 1. Genera and species groups of Signiphoridae, distribution, number of species and biology. Updated from Woolley and Hanson (2006) based on Noyes (2013). Numbers in parentheses indicate number of species with records in the Neotropics relative to total known species.

Genus / species group	**Distribution, number species**	**Hosts**
Chartocerus	Cosmopolitan (3/33)	Hyperparasitoids of Pseudococcidae, Coccidae, Psylloidea, Aphidoidea. Primary parasite on Chamaemyiidae
Clytina	Palearctic, Neotropical (1/2)	Chloropidae (puparia), n.sp. collected from litter and fungi
Signiphora	(33/41)	
flavopalliata species group	Cosmopolitan (21/24)	Primary parasites or hyperparasitoids on Diaspididae, hyperparasitoids on Aleyrodidae. Heteropteran eggs.
bifasciata species group	Mainly Neotropical (5/6)	Primary parasite on Psylloidea, Coccidae, Pseudococcidae
dipterophaga species group	Mainly Neotropical (5/6)	Diptera puparia, especially Tachinidae. Also Drosophilidae, predators of Pseudococcidae
coleoptrata species group	Neotropical (2/2)	Hyperparasitoids on Pseudococcidae
Thysanus	Cosmopolitan (3/4)	Diaspididae. Miridae and Buprestidae eggs.

APPENDIX B

MAIN TABLES AND FIGURES FOR CHAPTER II

Table 2. Summary of biodiversity informatics services.

Service	**Purpose**	**Relevance/contribution for researcher working on a revision**
ITIS, Species2000, uBIO, ECAT	Taxonomic name aggregators (produce "authority files" of species names")	Store classification hierarchies that are used by several other data portals.
GBIF	Keeps authority files and specimen information from different institutions.	Allows specimen data produced by different institutions to be accessed from a single portal, independent of their local management software.
UDDI (Universal Description, Discovery and Integration)	Registry of data providers	To provide data to GBIF, an institution must get into this registry. Data can be either mapped from institution database using XML schemas or exported in a table with the standardized fields. Not available for individual researchers.
TDWG	Working group that aims at producig standards for data sharing in XML so databases can be communicate.	If submitting data to several portals, including GBIF and EOL, it saves time if your database can export using their XML schemas. They also have a database of databases and services and documentation wikis.
DarwinCore	XML schema for specimen data	Allow data in electronic publication to be discovered and reused by other applications and web sites.
ABCD	XML schema for collection data	Same as DarwinCore, but more detailed (taxon-specific details)
TCS (taxonomic concept transfer schema)	XML schema for taxonomic concepts	Allows XML to understand when the same name is used in different meanings by different authors. Few implementations.
SDD (structure of descriptive data)	XML schema for characters	Used for characters in a matrix. Probably will have to interact closely with OWL. Lucid 3 can export it.

Table 2. Continued.

Service	**Purpose**	**Relevance/contribution for researcher working on a revision**
NeXML	XML schema for phylogenetic matrices	Allows semantic annotation of terminals and character data.
taXMLit, TaxonX, TaxPub	XML schemas for descriptions	Used to mark sections of a description, such as synonymy, diagnosis, description, material examined
DiGIR (distributed generic information retrieval protocol), BioCASE, TAPIR	Protocols for submission of queries between databases	DiGIR is the protocol used by GBIF and it is based in DarwinCore.
GUID (Globally Unique Identifier)	A reference number applied to an object in a database which can be resolved, and therefore reused by other databases	GUIDs are used for database interoperability. An example are DOIs. The standard recommended by the ECN for specimens is an alphabetic string (institution producing and storing the data) and a sequential number, usually a barcode.
LSID (life science identifier)	Entry identifier; a standard for GUIDs used in life sciences databases	LSIDs were recommended by the TDWG to identify entries in databases and thus facilitate interoperability.
ZooBank	Universal registry of animal names and works by the ICZN	Official database of the ICZN with lists of names, publications, etc.

Figure 1. Map of network connectivity between the main biodiversity data portals. Connections as reported by the Google database of related sites and calculated using the Touchgraph SEO application, July 2014. (See Appendix F for source link data.)

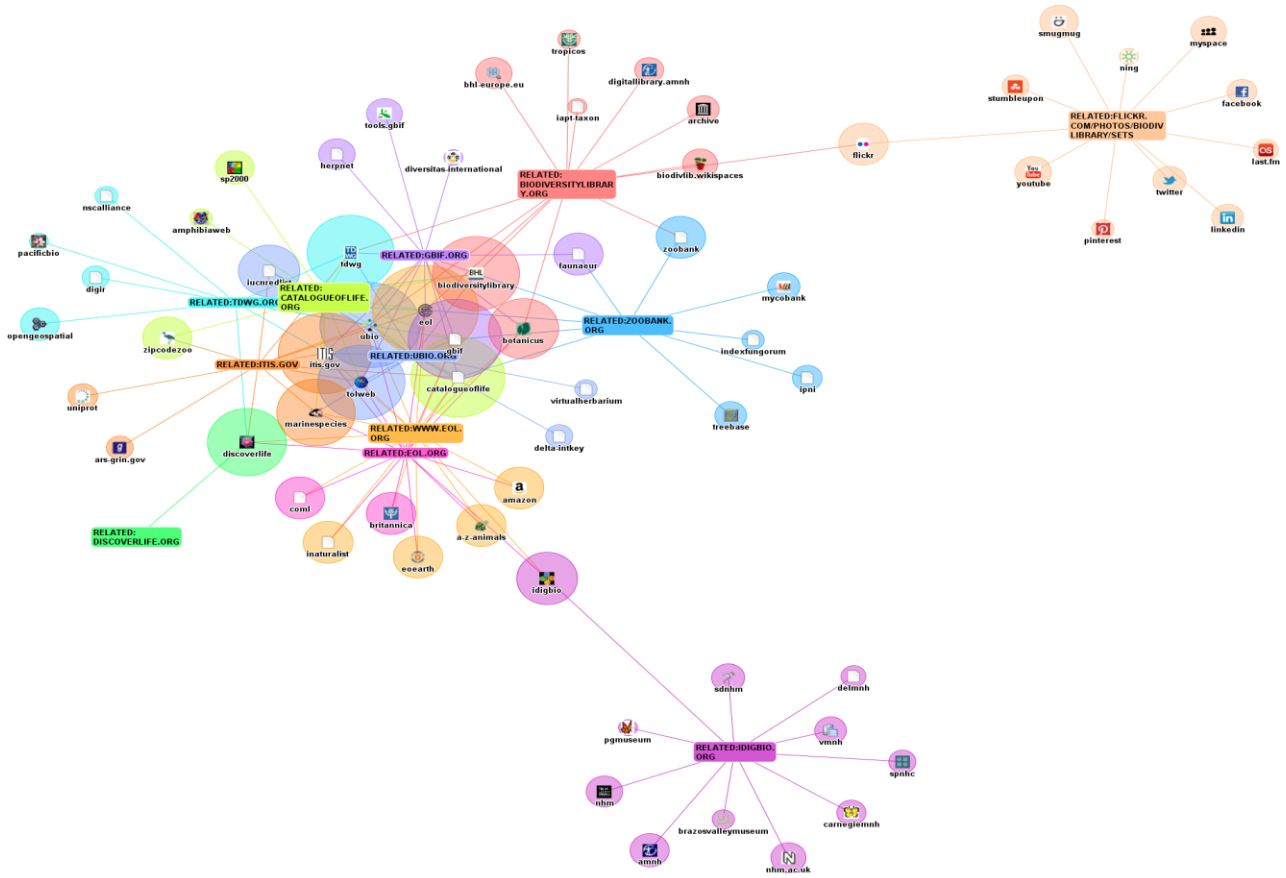
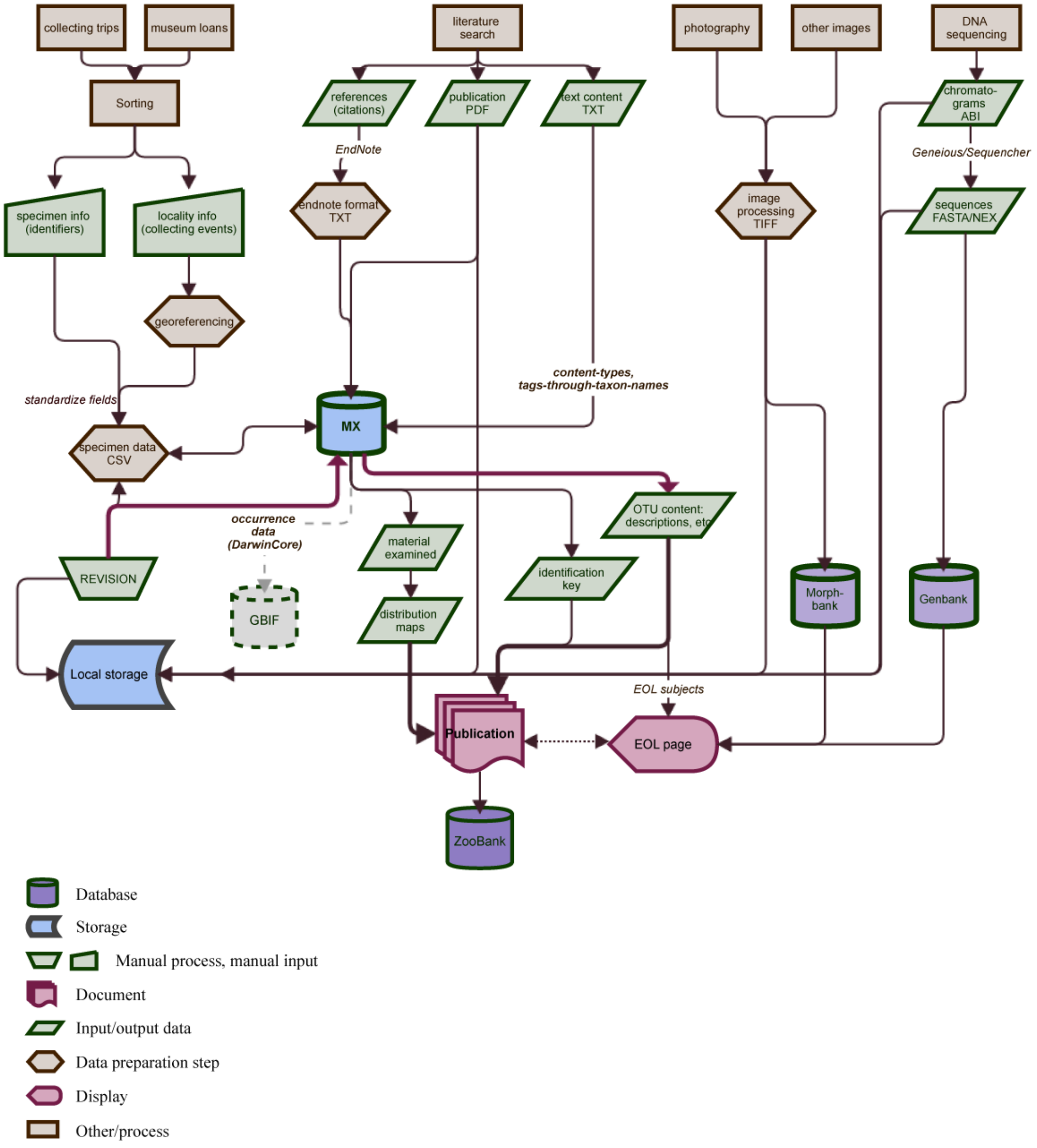


Figure 2. Resulting workflow of data for the present study. Gray and dotted lines represent communication that was not possible to implement at this moment or that cannot be done directly between researcher and data portal.



APPENDIX C

MAIN TABLES AND FIGURES FOR CHAPTER III

(see next page)

Table 3. List of taxa and gene regions sampled for Signiphoridae and outgroups. See text for details.

Taxon	Matrix name (DNA extract id)*	Specimen ID	Voucher Repository	Morphbank Entry	Genbank Accession Numbers				Source/Locality
					28S-D2	28S D3-D5	18S	COI	
Outgroups									
Azotidae									
Ablerus clisiocampae	AblD0401	UCRCENT 48962	UCR	–	AY599322	–	JN623105	–	USA: MD: Anne Arundel Co.
Ablerus sp.8	AblD0403	UCRCENT 48964	UCR	–	AY599330	AY599330, JN623917	JN623115	–	Bermuda: Southampton Parish
Ablerus sp.1	AblD0404	UCRCENT 48965	UCR	–	AY599323	AY599323, JN623912	JN623108	–	USA: CA: Riverside Co.
Ablerus sp.7	AblD0507	UCRCENT 48966	UCR	–	AY599329	AY599329, JN623916	JN623114	–	Ecuador: Orellana Province
Ablerus sp.9	AblD0816	UCRCENT 49017	UCR	–	AY599331	AY599331, JN623918	JN623116	–	Australia: NT: Simpsons Gap
Ablerus sp.10	AblD0827	UCRCENT 49026	UCR	–	AY599332	AY599332, JN623911	JN623106	–	South Africa: Western Cape Province
Ablerus sp.2	AblD0833	UCRCENT 49029	UCR	–	AY599324	AY599324, JN623913	JN623109	–	Ecuador: Orellana Province
Ablerus sp.3	AblD0834	UCRCENT 49030	UCR	–	AY599325	AY599325, JN623914	JN623110	–	Ecuador: Orellana Province
Ablerus sp.4	AblD0838	UCRCENT 49031	UCR	–	AY599326	–	JN623111	–	Honduras: Olancho
Ablerus sp.5	AblD0841	UCRCENT 49093	UCR	–	AY599327	AY599327 (partial)	JN623112	–	Ecuador: Orellana Province

Taxon	**Matrix name (DNA extract id)***	**Specimen ID**	**Voucher Repository**	**Morphbank Entry**	**Genbank Accession Numbers**				**Source/Locality**
					28S-D2	**28S D3-D5**	**18S**	**COI**	
Ablerus sp.6	AblD1022	UCRCENT 49032	UCR	–	AY599328	AY599328, JN623915	JN623113	–	Australia: NT: Georges Creek
Ablerus sp.11	AblD1061	UCRCENT 49065	UCR	–	AY599333	–	JN623107	–	Australia: WA: Margaret River
Aphelinidae									
Aphelininae									
Aphelinus glycinis	AphD3596	TBA	TAMU	TBD	TBD	TBD	TBD	–	China: Liaoning
Aphelinus coreae	AphD3597	TBA	TAMU	TBD	TBD	TBD	TBD	TBD	South Korea: Miliyang
Aphytis melinus	AphyAD89	TBA	TAMU	TBD	TBD	TBD	TBD		Green Methods/Beneficial Insectary (culture)
Coccophaginae									
Coccobius sp.	CbiD3256	(UCR)	UCR	–	TBD	TBD	TBD	TBD	J. Mottern
Coccobius sp.	CbiD3276	(UCR)	UCR	–	TBD	TBD	TBD	TBD	J. Mottern
Coccobius sp.	CbiD3314	(UCR)	UCR	–	TBD	TBD	TBD	TBD	J. Mottern
Coccophagus sp.	CphD2822	UCRCENT 252127	UCR	TBD	TBD	TBD	TBD	TBD	J. Mottern
Coccophagus (Euxanthellus) phillippiae	CphD2913	UCRCENT 239401	UCR	TBD	TBD	TBD	TBD	TBD	St. Helena, Cuckhold's Pt.
Encarsia formosa	EncaAD91	TBA	TAMU	–	TBD	TBD	TBD	TBD	Green Methods/Beneficial Insectary (culture)
Eretmocerinae									
Eretmocerus eremicus	EretAD90	TBA	TAMU	–	TBD	–	TBD	–	Syngenta "Eretline e" lot 0821-01 (culture)
Trichogrammatidae									
Trichogramma platneri	TplD1050	UCRCENT 49059	UCR	703233	AY599407	AY599407, JN624250	JN623531	–	USA: CA: Riverside Co. (culture)
Trichogramma pretiosum	TprD1048	UCRCENT 49057	UCR	703229	AY599408	AY599408 (D3)	AY940359	–	USA: CA: Riverside Co. (culture)
Ingroup									
Chartocerus									

Taxon	Matrix name (DNA extract id)*	Specimen ID	Voucher Repository	Morphbank Entry	Genbank Accession Numbers				Source/Locality
					28S-D2	28S D3-D5	18S	COI	
Chartocerus dactylopii	ChaD0512	UCRCENT 48969, UCRCENT 48970	UCR	703011	AY599336	AY599336, JN624212	JN623488	–	USA:CA:Riverside Co.
Chartocerus elongatus	ChaD0525	TAMU-ENTO X0855927, X0855928	TAMU	TBD	AY599334	AY599334, JN624214	JN623490	–	USA:TX:Uvalde Co.
Chartocerus dactylopii	ChaD0543	UCRCENT 48975	UCR	703023	AY599335	AY599335, JN624215	JN623491	–	USA:CA:Riverside Co.
Chartocerus sp.	ChaD0556	not found	UCR	N/A	AY599337	AY599337, JN624213	JN623489	–	USA:CA:Riverside Co.
Chartocerus cf. *elongatus*	ChaD0820	UCRCENT 49020, UCRCENT 49021	UCR	703131	AY599338	AY599338 (D3)	JN623492	–	South Korea: South Jeolla Province
Chartocerus cf. *elongatus*	ChaD1023	UCRCENT 49033	UCR	703189	AY599339	AY599339, JN624216	JN623493	–	China: Beijing
Chartocerus sp. ms6	ChaD1024	UCRCENT 49034	UCR	703193	AY599340	AY599340, JN624217	JN623494	–	China: Beijing
Chartocerus elongatus (group I)	ChaD3511	TAMU-ENTO X0855929	TAMU	TBD	TBD	TBD	TBD	–	USA:TX:Brewster Co.
Chartocerus sp. nr.elongatus	ChaD3525	TBA	TAMU	TBD	TBD	TBD	TBD	TBD	China: Beijing
Chartocerus cf. *elongatus*	ChaD3530	TBA	TAMU	TBD	TBD	TBD	TBD	TBD	USA:CA:Riverside Co.
Chartocerus sp.	ChaD3549	TBA	TAMU	TBD	TBD	TBD	–	TBD	USA:MO:Wayne Co.
Chartocerus dactylopii	ChaD3550	TBA	TAMU	TBD	TBD	TBD	–	TBD	USA:AZ:Pima Co.
Chartocerus subaeneus	ChaD3551	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Romania: IaSi
Chartocerus dactylopii	ChaD3563	TBA	TAMU	TBD	TBD	TBD	–	TBD	USA:FL:Highlands Co.

Taxon	Matrix name (DNA extract id)*	Specimen ID	Voucher Reposi-tory	Morph-bank Entry	Genbank Accession Numbers				Source/Locality
					28S-D2	28S D3-D5	18S	COI	
Clytina									
Clytina n.sp.1	ClyD1043	photo voucher	photo voucher	703700	AY599351	AY599351, JN624219	JN623496	–	Costa Rica: Alajuela
Clytina giraudi	ClyD2226	UCRCENT 174771	UCR	703624	JN623495	JN623495, JN623835	JN624218	–	Denmark: Kalvebod Faelled
Clytina giraudi	ClyD3509	BMNH(E) #1038820	BMNH**	TBD	–	TBD	TBD	TBD	Romania: IaSi
Clytina n.sp.1	ClyD3510	BMNH(E) #1038821	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Clytina n.sp.1	ClyD3548	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Costa Rica: Guanacaste
Signiphora									
S. bifasciata group									
Signiphora n.sp.6	SbiD3513	BMNH(E) #1038823	BMNH**	TBD	TBD	TBD	TBD	–	Costa Rica: Heredia
Signiphora n.sp.6	SbiD3514	BMNH(E) #1038824	BMNH**	TBD	–	TBD	–	–	Costa Rica: Heredia
Signiphora n.sp.6	SbiD3531	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Alajuela
Signiphora n.sp.	SbiD3532	TBA	BMNH**	TBD	TBD	TBD	–	–	Costa Rica: Alajuela
Signiphora n.sp.6	SbiD3543	TBA	BMNH**	TBD	TBD	–	–	–	Argentina: Misiones
Signiphora n.sp.35	SbiD3544	TBA	BMNH**	TBD	TBD	–	–	–	Costa Rica: Heredia
Signiphora sp, bif. gr.	SbiD3552	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Costa Rica: Guanacaste
S. coleoptrata group									
Signiphora giraulti	ScoAD92	TBA	BMNH**	TBD	TBD	TBD	TBD	–	Costa Rica: Alajuela
Signiphora n.sp.25	ScoD3517	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora cf *giraulti*	ScoD3518	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora giraulti	ScoD3546	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora sp. col. gr.	ScoD3560	TBA	TAMU	TBD	TBD	TBD	–	TBD	US:FL:Martin Co.

Taxon	Matrix name (DNA extract id)*	Specimen ID	Voucher Repository	Morphbank Entry	Genbank Accession Numbers				Source/Locality
					28S-D2	28S D3-D5	18S	COI	
Signiphora n.sp.25	SdiD3521	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
S. dipterophaga group									
Signiphora sp. ms5	SdiD2905	TBA	BMNH**	TBD	TBD	–	–	–	Costa Rica: Puntarenas
Signiphora n.sp.22	SdiD2906	TBA	BMNH**	TBD	TBD	–	–		Costa Rica: Puntarenas
Signiphora sp. gr3ms3	SdiD2907	TBA	BMNH**	TBD	TBD	–	–	TBD	Costa Rica: Puntarenas
Signiphora n.sp.22	SdiD3515	BMNH(E) #1038825	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora sp. ms5	SdiD3516	BMNH(E) #1038826	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora sp. nr. maxima	SdiD3533	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora nr. *zosterica*	SdiD3535	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Signiphora n.sp.22	SdiD3536	TBA	BMNH**	TBD	TBD	TBD	–	–	Costa Rica: Puntarenas
Signiphora cf. gr3ms12	SdiD3545	TBA	BMNH**	TBD	TBD	TBD	–	–	Costa Rica: Heredia
Signiphora n.sp.22	SbiD3554	TBA	BMNH**	TBD	TBD	TBD	–	–	Costa Rica: Heredia
Signiphora sp. dipt.gr	SdiD3555	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Costa Rica: Heredia
Signiphora sp. dipt.gr.	SdiD3556	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Costa Rica: Puntarenas
Signiphora sp. gr2ms5	SdiD3558	TBA	BMNH**	TBD	TBD	TBD	–	TBD	Costa Rica: Puntarenas
S. flavopalliata group									
Signiphora flavopalliata	SflD3519	TBA	BMNH**	TBD	TBD	TBD	TBD	–	Costa Rica: Heredia
Signiphora n.sp. 5	SflD3520	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Mexico: Veracruz
Signiphora n.sp.13	SflD3522	TBA	BMNH**	TBD	TBD	–	–	–	Costa Rica: Guanacaste
Signiphora coquilletti	SflD3523	TBA	UCR	TBD	TBD	TBD	TBD	TBD	USA:CA:Los Angeles Co.
Signiphora n.sp.13	SflD3524	TBA	BMNH**	TBD	TBD	TBD	TBD	TBD	Mexico: Veracruz
Signiphora aleyrodis	SflD3537	TBA	TAMU	TBD	TBD	–	–	–	Bermuda: Southampton Parish
Signiphora sp. nr. *borinquensis*	SflD3539	TBA	BMNH**	TBD	TBD	–	–	TBD	Costa Rica: Heredia
Signiphora n.sp. flavo. gr.	SflD3557	TBA	BMNH**	TBD	TBD	–	–	–	Costa Rica: Heredia
Signiphora n.sp. 2	SflD3561	TBA	TAMU	TBD	–	TBD	–	–	USA:FL:Collier Co.

Taxon	Matrix name (DNA extract id)*	Specimen ID	Voucher Reposi-tory	Morph-bank Entry	Genbank Accession Numbers				Source/Locality
					28S-D2	28S D3-D5	18S	COI	
Signiphora sp. ms4	SigD0515	TAMU-ENTO X0855094	UCR	TBD	AY599347	AY599347, JN624207	JN623482	–	Dominican Republic: Province Pedernales
Signiphora aleyrodis	SigD0516	TAMU-ENTO X0855102	UCR	TBD	AY599341	AY599341	–	–	Mexico: Veracruz
Signiphora sp. ms4	SigD0523	TAMU-ENTO X0855093	UCR	TBD	AY599348	AY599348	–	–	Dominican Republic: Province Pedernales
Signiphora n.sp.15	SigD0526	TAMU-ENTO X0855103	UCR	TBD	AY599342	AY599342	JN623480	–	USA: TX: Hidalgo Co.
Signiphora aleyrodis	SigD0536	UCRCENT 48971, UCRCENT 48972	UCR	703015	AY599343	AY599343 (D3)	JN623481	–	Bermuda: Southampton Parish
Signiphora sp.	SigD0538	not found	UCR	TBD	AY599344	AY599344, JN624208	JN623483	–	Bermuda: Southampton Parish
Signiphora coquilletti	SigD0817	UCRCENT 49018, UCRCENT 49019	UCR	703127	AY599345	AY599345, JN624209	JN623484	–	USA: CA: Los Angeles Co.
Signiphora sp. ms7	SigD0829	UCRCENT 49027	UCR	703143	AY599346	AY599346, JN624210	JN623485	–	Bermuda: Southampton Parish
Signiphora sp. ms8	SigD0832	UCRCENT 49028	UCR	703147	AY599349	AY599349 (D3)	JN623486	–	USA: NC: Carteret Co.
Signiphora n.sp.36	SigD1027	UCRCENT 49036	UCR	703197	AY599350	AY599350, JN624211	JN623487	–	USA: GA: Liberty Co.: St. Catherines Island
Thysanus									

Taxon	**Matrix name (DNA extract id)***	**Specimen ID**	**Voucher Repository**	**Morphbank Entry**	**Genbank Accession Numbers**				**Source/Locality**
					28S-D2	**28S D3-D5**	**18S**	**COI**	
Thysanus sp.	TspD0519	not found	TAMU	TBD	AY599352	AY599352 (D3)	–	–	Mexico: Veracruz
Thysanus sp.	TspD0535	not found	TAMU	–	AY599353	AY599353 (D3)	JN623497	–	USA: PA: Montgomery Co.
Thysanus sp. nr. *ater*	TspD0540	UCRCENT 48973	UCR	703019	AY599354	AY599354, JN624220	JN623498	–	USA: CA: Riverside Co.
Thysanus sp. nr. *ater*	TspD1038	UCRCENT 49049, UCRCENT 49050	UCR	703217	AY599355	AY599355, JN624221	JN623499	–	USA: NM: Hidalgo Co.
Thysanus ater	TspD3507	BMNH(E) #1038785	BMNH**	TBD	TBD	TBD	TBD	TBD	Romania:IaSi
Thysanus n.sp.8	TspD3508	BMNH(E) #1038822	BMNH**	TBD	TBD	TBD	TBD	TBD	Costa Rica: Puntarenas
Thysanus sp. nr. *ater*	TspD3527	TBA	TAMU	TBD	–	–	–	–	Costa Rica:Alajuela
Thysanus sp. nr. *ater*	TspD3528	TBA	TAMU	TBD	TBD	TBD	–	TBD	USA:CA:Riverside Co.
Thysanus sp. nr. *ater*	TspD3547	TBA	TAMU	TBD	TBD	TBD	–	–	USA:CA:Riverside Co.
Thysanus sp. nr. *ater*	TspD3562	TBA	TAMU	TBD	TBD	TBD	–	–	USA:FL:St. Lucie Co.

* The matrix name consists of three letters indicating the genus and species group followed by a four-digit "D" number corresponding to extract entry in Heraty Lab or the author's DNA extraction logs.

** Final repository not defined- individuals are part of very long series.

Table 4. Oligonucleotide primer sequences used in the present study.

Sequence	**Primer name**	**Primer sequence**	**Source**
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
	mtD-7.2F	ATTAGGAGCHCCHGAYATAGCATT	Brunner et al. (2002)
	C1-N-2329	TAAACTTCAGGGTGACCAAAAAATCA	Simon et al. (1994)
18S(a)	18Sa-1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. (1996), Schulmeister (2003)
	18Sa-591R (18S4R)	GAATTACCGCGGCTGCTGG	Giribet et al. (1996), Schulmeister (2003)
18S(b)	18Sb-441F (18S-H17F)	AAATTACCCCACTCCCGGCA	Munro et al. (2011)
	18Sb-1299R (18S-H35R)	TGGTGAGGTTTCCCGTGTT	Munro et al. (2011)
	18SFi (18Si-673F)	ATCGCTCGCGATGTTTAACT	Munro et al. (2011)
	18SRi (18Si-905R)	AGAACCGAGGTCCTATTCCA	Munro et al. (2011)
18S(c)	18Sc-1204F	ATGGTTGCAAAGCTGAAAC	Schulmeister et al. (2003)
	18Sc-1991R	GATCCTTCCGCAGGTTCACCTAC	Schulmeister et al. (2003)
28S-D2	D2F (D2-3551 F)	CGGGTTGCTTGAGAGTGCAGC	Modified from Campbell et al. (2000)
	D2FiA (D2i-3686 F)	GAAACCGTTCAGGGGTAAACC	Modified from Campbell et al. (2000)
	D2Ra (D2-4039 R)	CTCCTTGGTCCGTGTTTC	Modified from Campbell et al. (2000)
28S-D3-D5	D3Fa (D3-4046 F)	TTGAAACACGGACCAAGGAG	Modified from Nunn et al. (1996)
	D5Ra (D5-4625 R)	CGCCAGTTCTGCTTACCA	Modified from Schulmeister (2003)

Table 5. Basic statistics of alternative alignment data sets.

Data set name	Total characters[†]	18S	28S-D2	28S D3-5	Invariable	# parsimony informative characters
MAFFT+MSS	4137	1988	773	710	3127	741
Mafft –add	4628	2473	784	705	3409	741
E-INS-i	4928	2921	692	649	3392	933
E-INS-i + structure	4440	2383	742	649	3316	732
G-INS-i	4031	2025	692	648	2771	955
G-INS-i + structure	4027	1974	743	644	2831	767
L-INS-i	4928	2921	692	649	3393	933
L-INS-i + structure	4448	2391	742	649	3323	732
Q-INS-i	4065	2031	710	658	2817	913
Q-INS-i + structure	4039	1962	756	655	2969	755

[†] base composition of complete data set: 24.3%A, 22.8%C, 27.7%G, 25.2%T.

Table 6. Negative log-likelihoods and ML bootstrap support for clades recovered using different alignment approaches. See methods section for details.

Data set	**MAFFT +MSS**	**E-INS-i**	**E-INS-I + SS**	**G-INS-i**	**G-INS-I + SS**	**L-INS-i**	**L-INS-i + SS**	**Q-INS-i**	**Mafft --add**	**Parsimony**
-LnL (best tree)	23946.6155	28604.1462	25385.4322	27015.8259	26004.9346	28603.6111	25376.8606	26178.7627	26257.5862	n/a
Signiphoridae + *Ablerus*	35 (*Eretmocerus*)	73	10 (*Eretmocerus*)	33	-	60	30	48	35 (*Eretmocerus*)	100[**]
Signiphoridae	97	26	97	67	97	48	97	77	97	63
Signiphorinae	97	26	100	-	100	100	100	-	97	93
Thysaninae	-	-	-	21	-	-	-	48	-	-
Chartocerus + OW[†] *Clytina*	100	100	100	-	100	100	100	(52)[§]	100	100
NW[†] *Clytina*	84	-	95	89	69	-	90	95	84	77
Thysanus	74	68	96	25[††] (+Sig.)	76	66	96	68	74	(86)
Thysanus + NW[†] *Clytina*	98	92	100	37 (+Sig.)	100	96	100	100	98	86
Signiphora + *Clytina* + *Thysanus*	81	100	75	-	66	100	76	40 (+ Chart.)	81	-
Signiphora	97	100	100	-	100	100	100	40 (Thysaninae)	97	57

Data set	**MAFFT +MSS**	**E-INS-i**	**E-INS-I + SS**	**G-INS-i**	**G-INS-I + SS**	**L-INS-i**	**L-INS-i + SS**	**Q-INS-i**	**Mafft --add**	**Parsimony**
Signiphora bifasciata group	-	-	-	-	-	-	-	-	-	-
Signiphora coleoptrata group	-	-	-	-	-	-	-	-	-	-
Signiphora dipterophaga group	-	-	-	-	-	-	-	-	-	-
Signiphora flavopalliata group	98*	100*	98*	-	99*	100	99‡	-	98*	61*

†OW= Old World; NW= New World; *excludes *Signiphora* (*flavopalliata* group) sequences D0515, D0523, D3557, D3561. ‡excludes *Signiphora* sequences D0515, D0523 and D3561. §2 species of *Chartocerus*, 3551 and 0512 ††1027, 3522, 3524, 0526 in T+Cl **polytomy with remaining aphelinids

Figure 3. Previous phylogenetic hypotheses for intrafamilial relationships in Signiphoridae. Strict consensus of three most parsimonious solutions from Woolley (1988) based on 21 morphological characters.

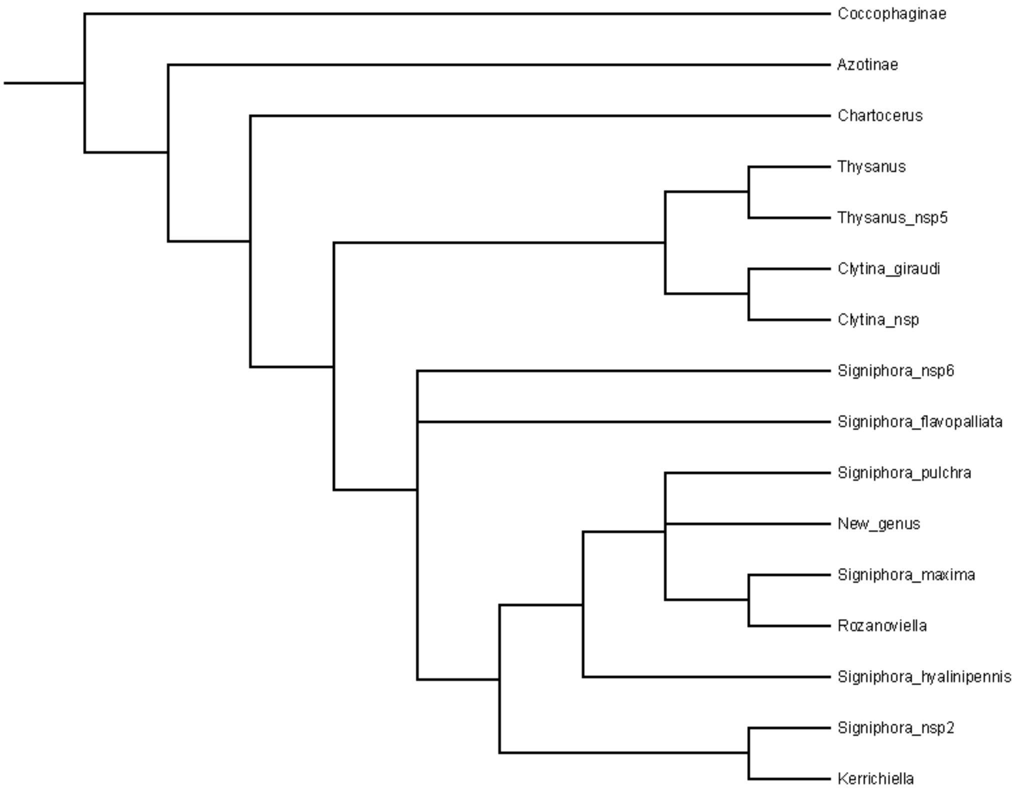
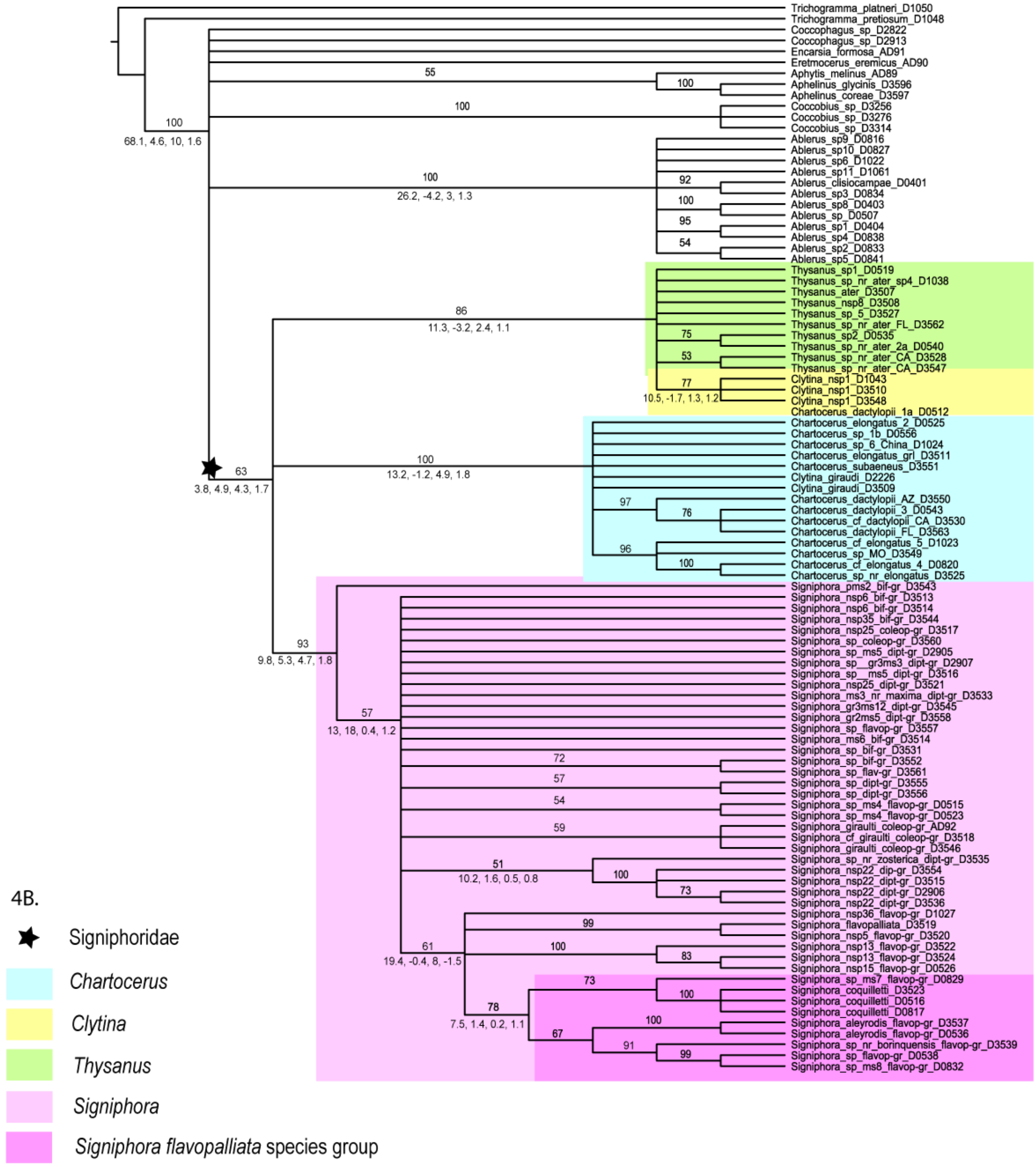


Figure 4. Results of phylogenetic analyses of the MAFFT+MSS data set. A, Maximum likelihood using RAxML. Values on branches correspond to bootstrap support. B, Parsimony analysis using TNT. Values above branches correspond to bootstrap support; values below branches correspond to partitioned Bremer support as implemented in Peña et al. (2006).

Figure 4. (cont.)



APPENDIX D

MAIN TABLES AND FIGURES FOR CHAPTER IV

Figure 5. *Clytina* habitus. A, *Clytina giraudi,* lateral; B, *Clytina giraudi*, dorsal; C, *Clytina* n. sp., lateral; D. *Clytina* n. sp., dorsal.

Figure 6. *Clytina giraudi*. A, head; B, mesosoma and Mt1; C; forewing vein, D, hindwing vein, E. metasoma showing ovipositor, F. antenna (Female TAMU-ENTO X0424818), G, male antenna; H, male genitalia (TAMU-ENTO X0852625).

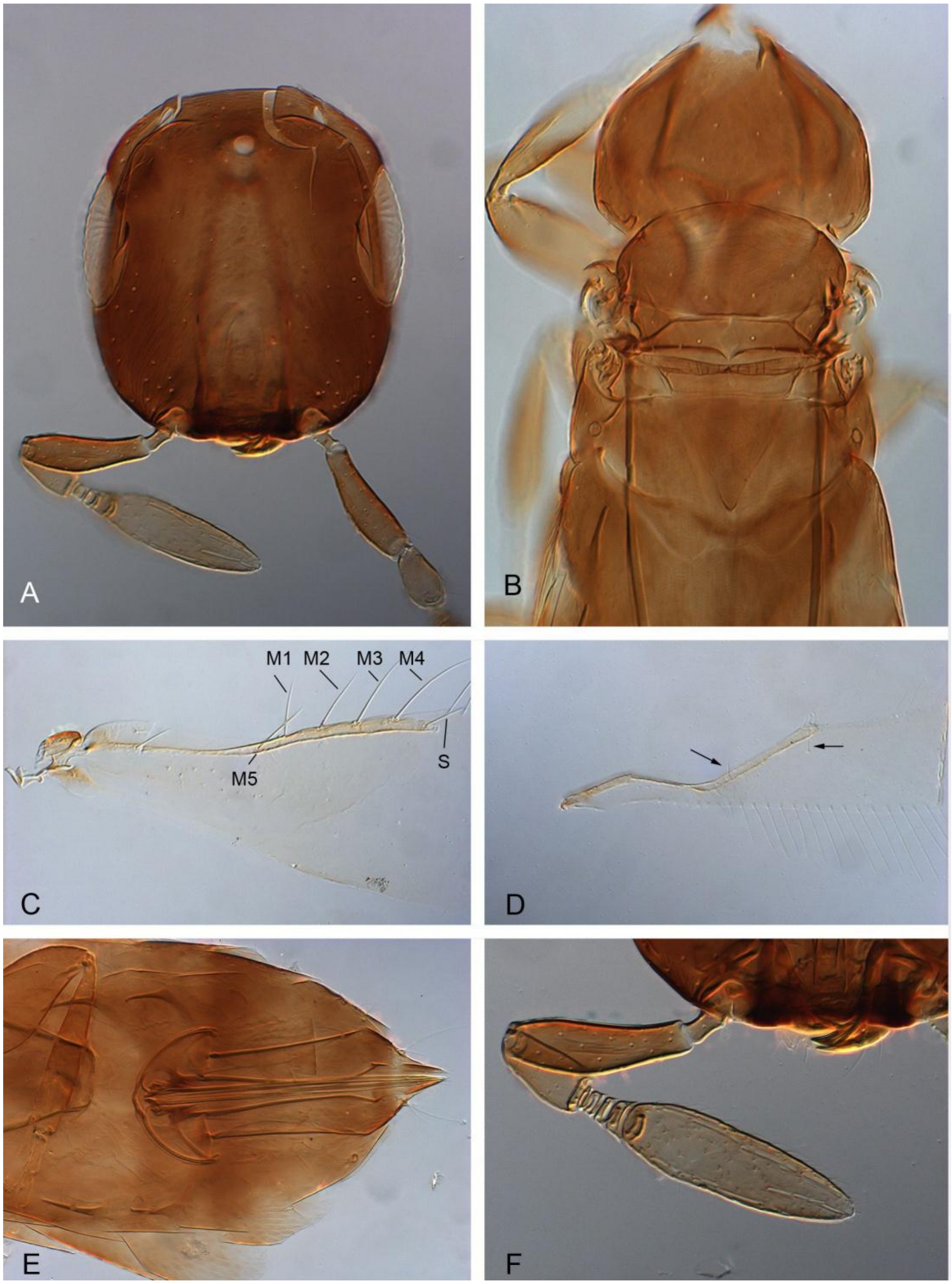


Figure 6 (cont.)

Figure 7. *Clytina* n.sp. 1. A, head; B,antenna; C; forewing vein; D, hindwing vein; E, mesosoma and Mt1; F, metasoma showing ovipositor (TAMU-ENTO X0424818).

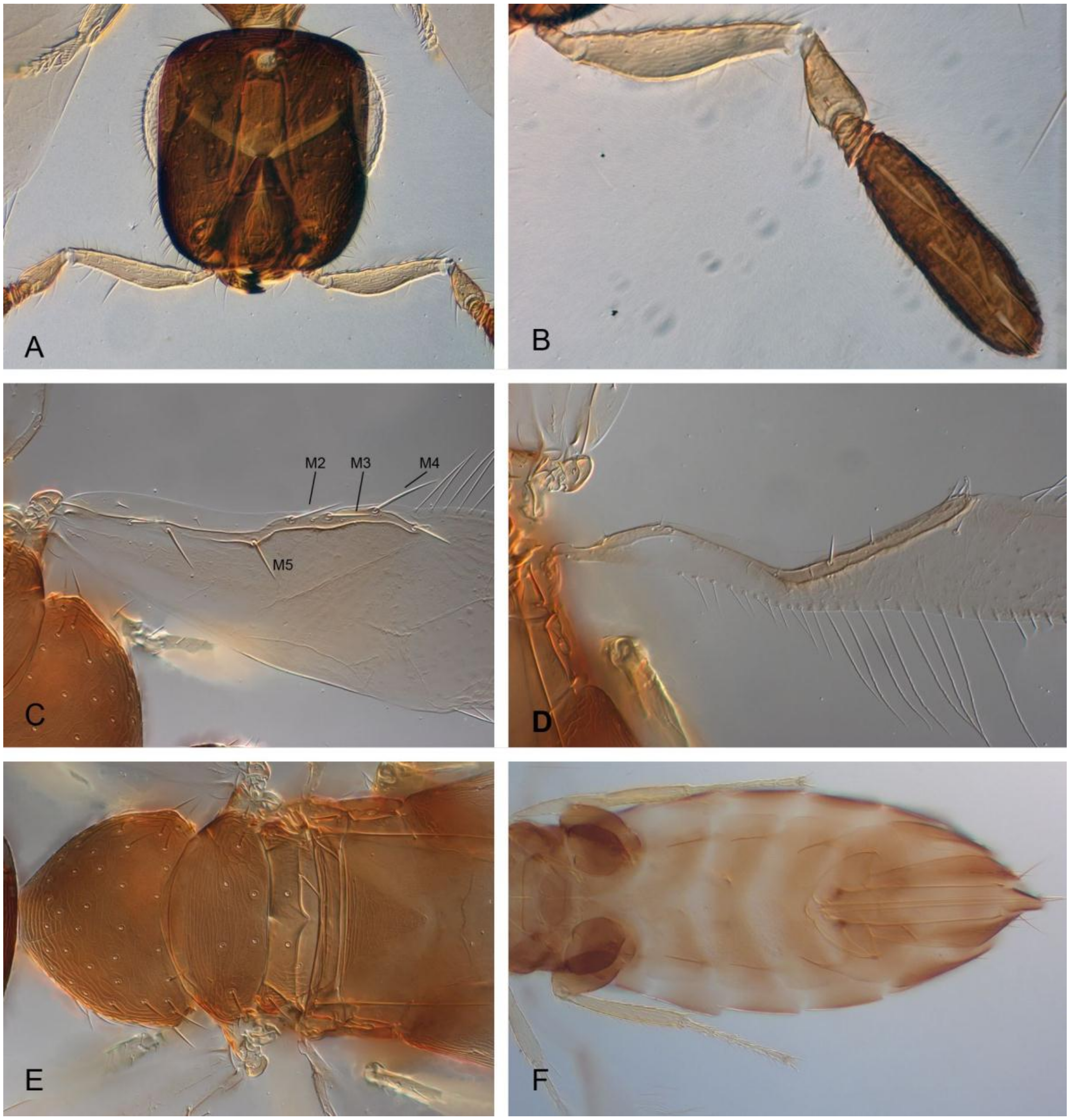


Figure 8. Slide-mounted type specimens deposited at USNM. A, *Thysanus melancholicus,* slide; B, *Thysanus melancholicus,* habitus; C; *Thysanus nigrellus*, slide; D, *Thysanus nigrellus*, habitus; E, *Thysanus rusti*, slide; D, *Thysanus rusti*, habitus.

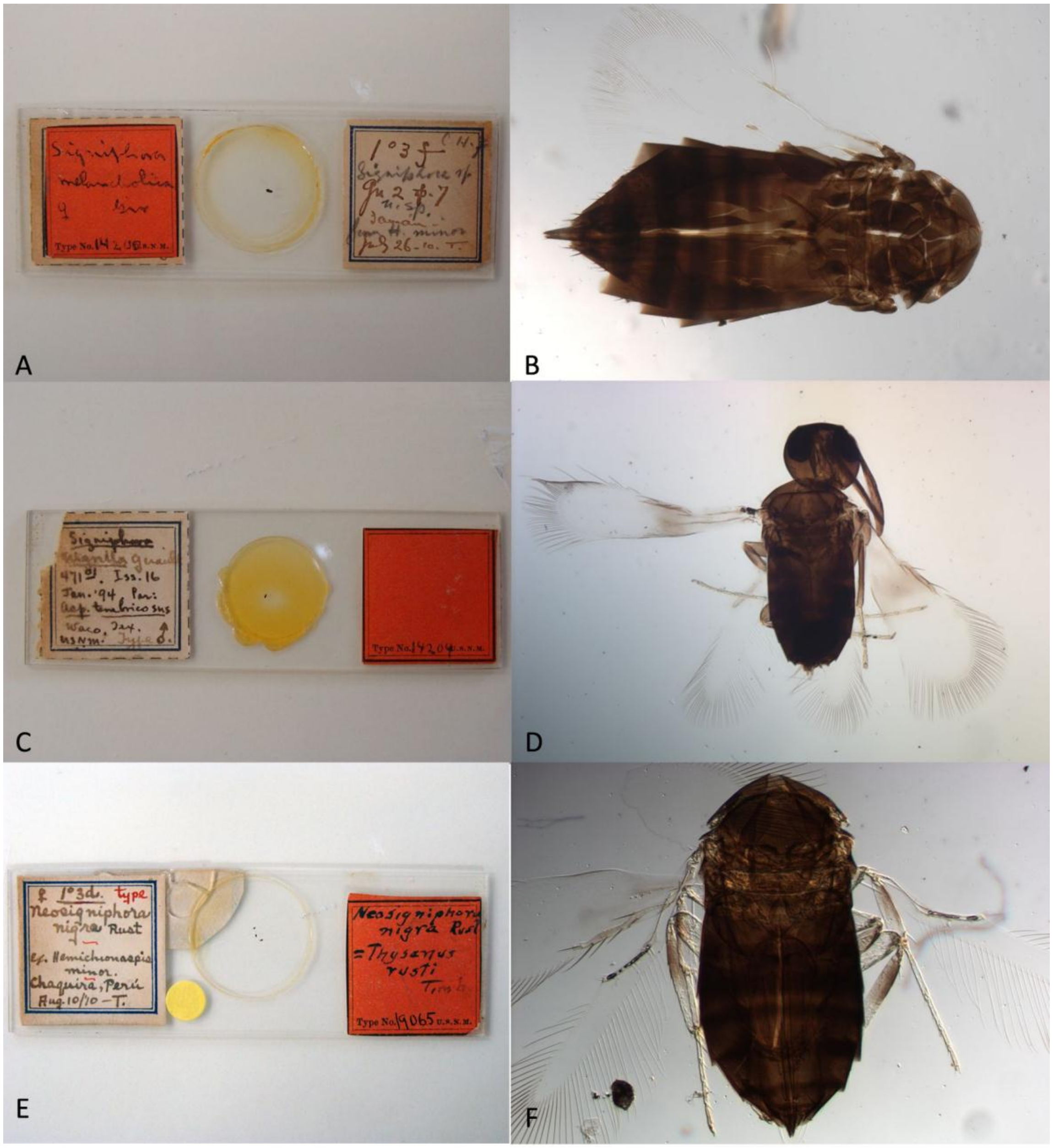


Figure 9. *Thysanus ater*. A, head; B, antenna; C; forewing vein; D, hindwing vein; E, mesosoma; F, metasoma showing ovipositor; G, male antenna; H, male genitalia (arrows indicate preapical and apical denticles) (female: BMNH(E) #1038786, male: BMNH(E) #990658).

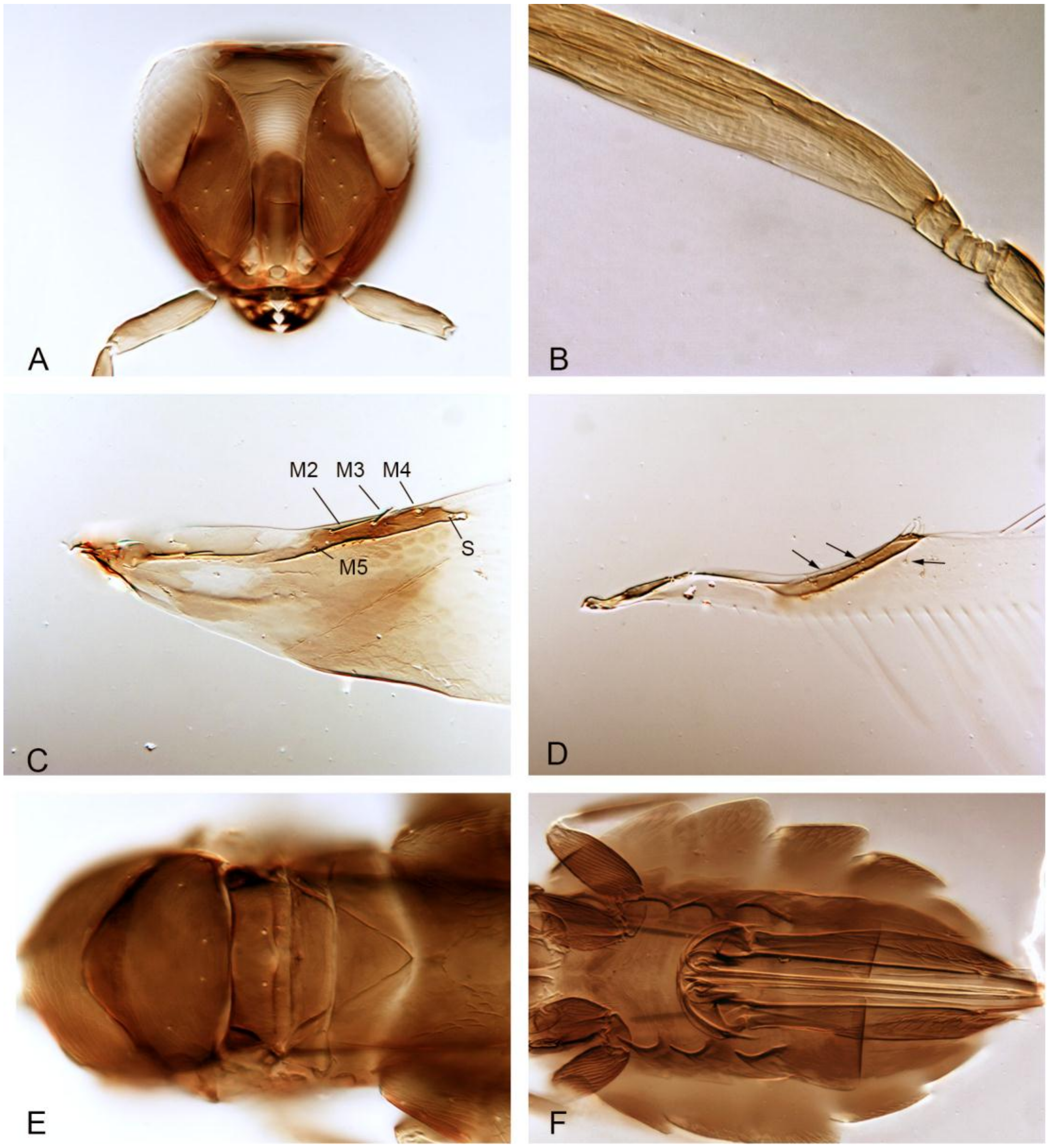


Figure 9 (cont.)

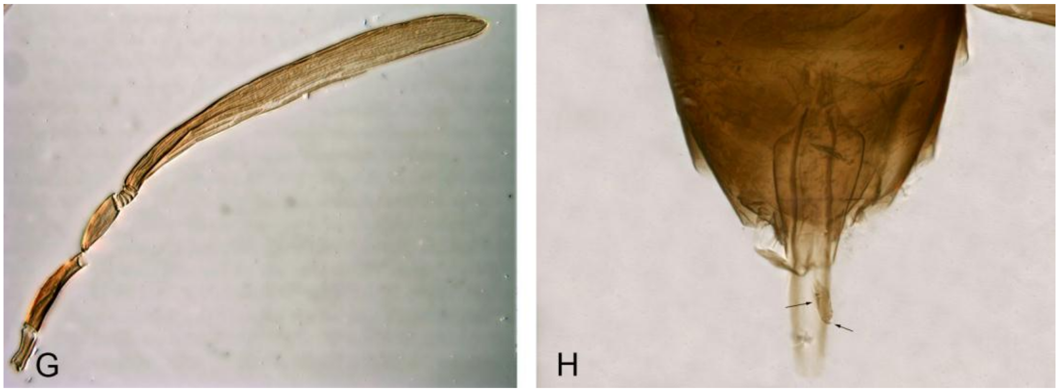


Figure 10. *Thysanus melancholicus*. A, head; B, antenna; C; forewing vein; D, hindwing vein; E, mesosoma; F, metasoma showing ovipositor; G, male antenna; H, male genitalia (female: USNM_ENT 763260; male: CNCHYMEN 122403).

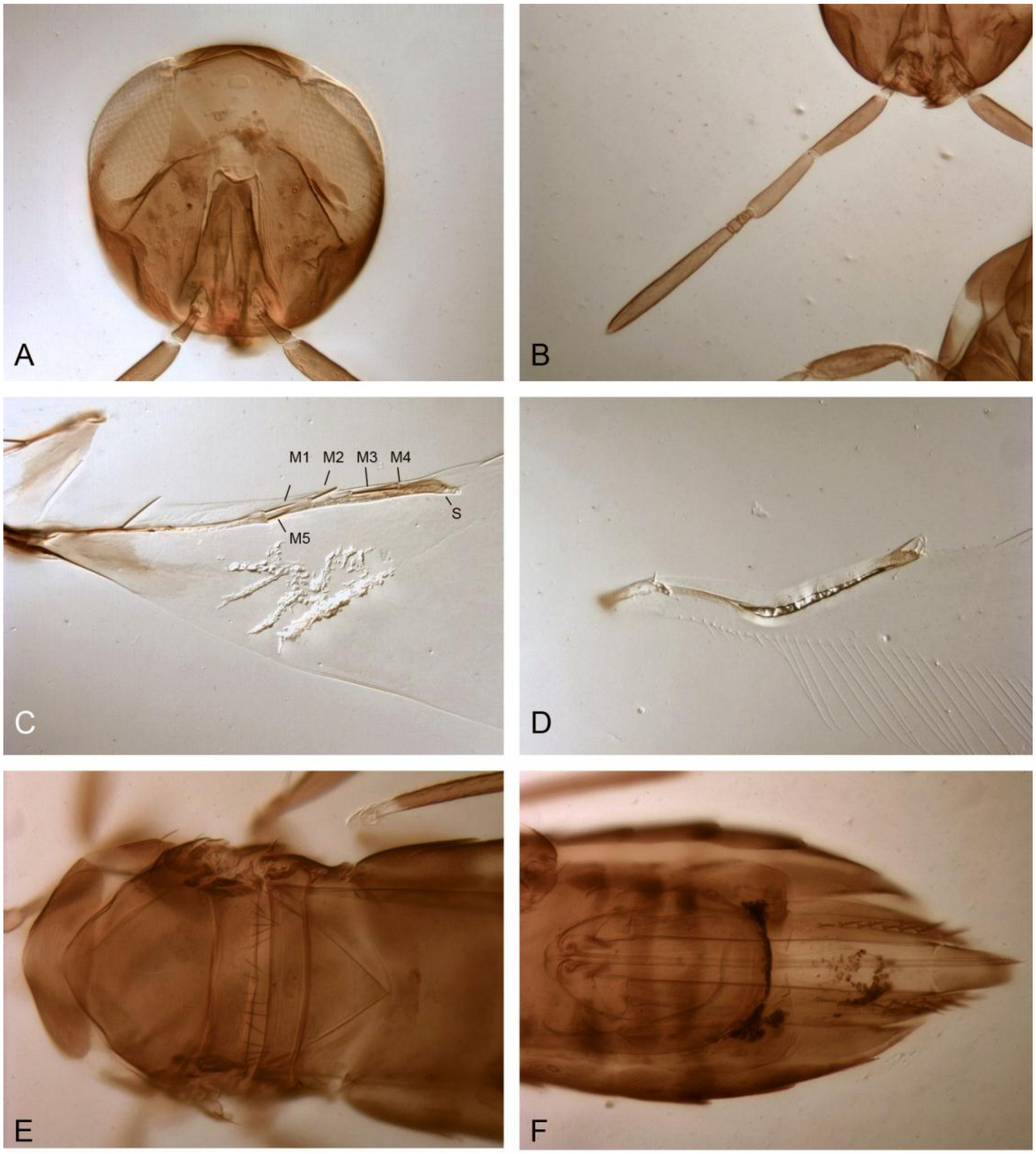


Figure 11. *Thysanus nigrellus*. A, head; B, antenna; C; forewing vein; D, hindwing; E, mesosoma; F, male genitalia (USNM Type No. 14204).

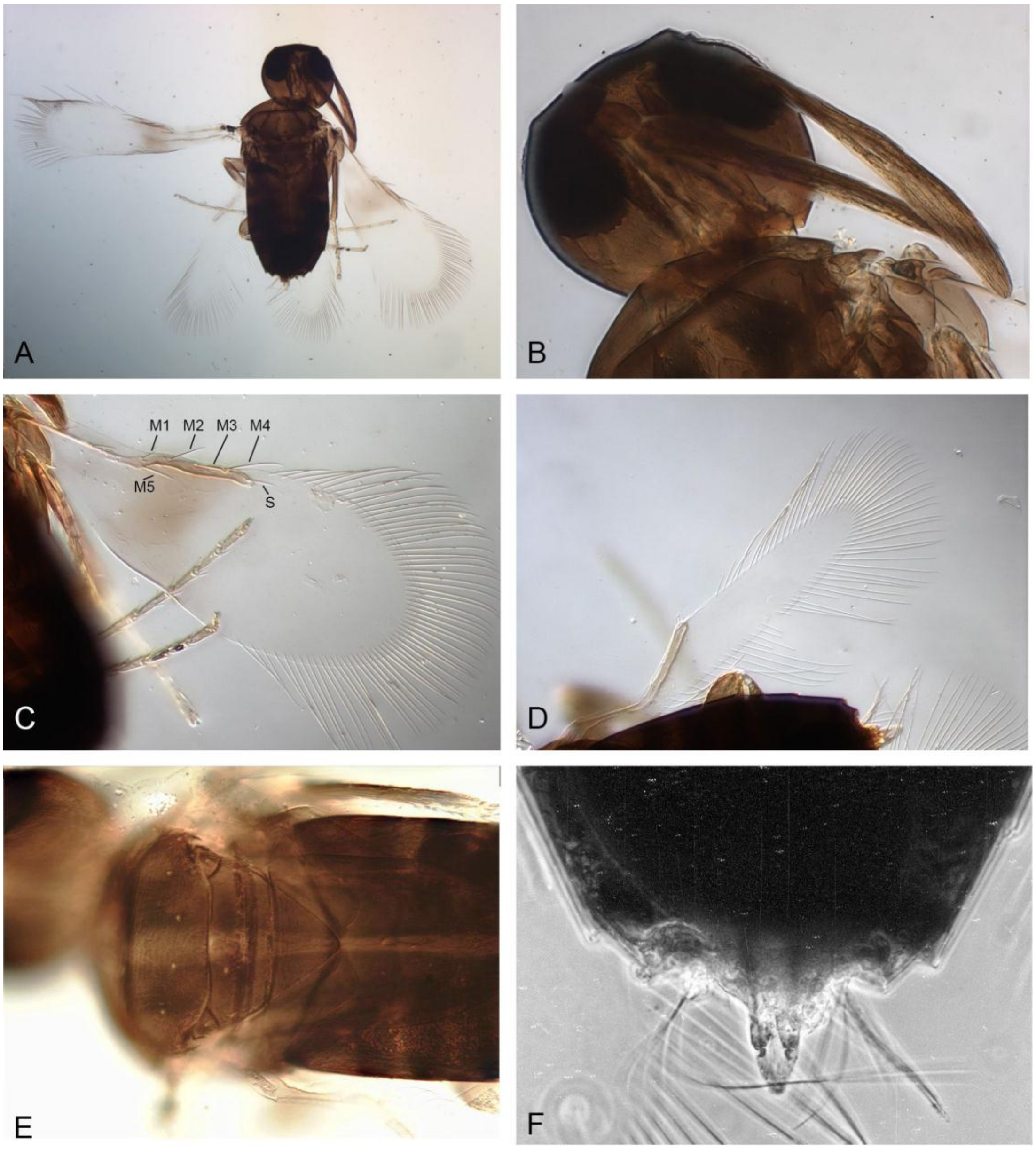


Figure 12. *Thysanus rusti*. A, head; B, antenna; C; forewing vein; D, hindwing; E, mesosoma, excluding pronotum and mesoscutum; F, metasoma showing ovipositor. (TAMU-ENTO X0616339).

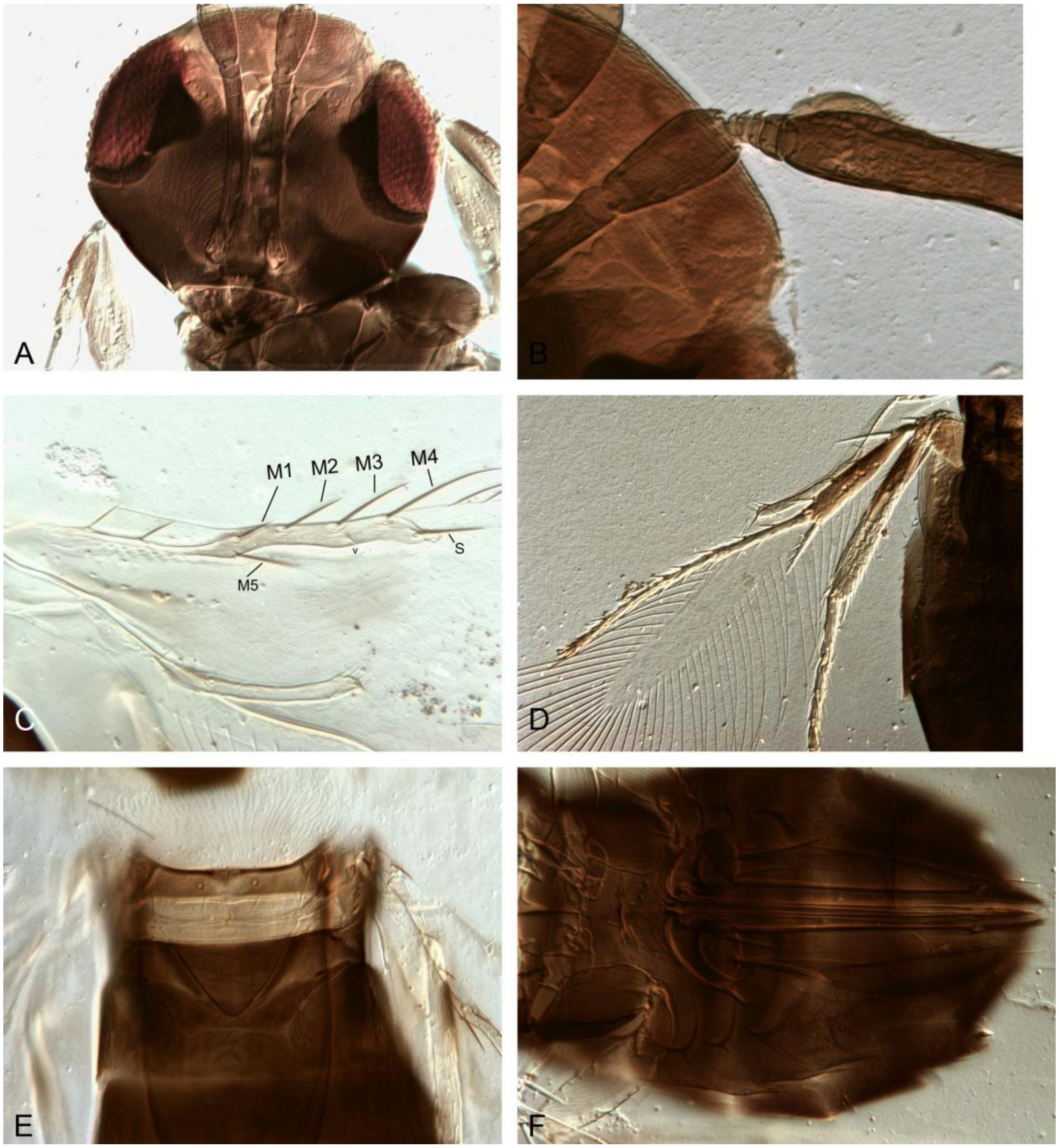


Figure 13. *Thysanus* n. sp. 2. A, head (BMNH(E) #990347); B, antenna (BMNH(E) 990344); C; forewing vein (BMNH(E) #990347); D, hindwing (BMNH(E) 990344); E, mesosoma (BMNH(E) 990349; F, male genitalia (BMNH(E) 990345).

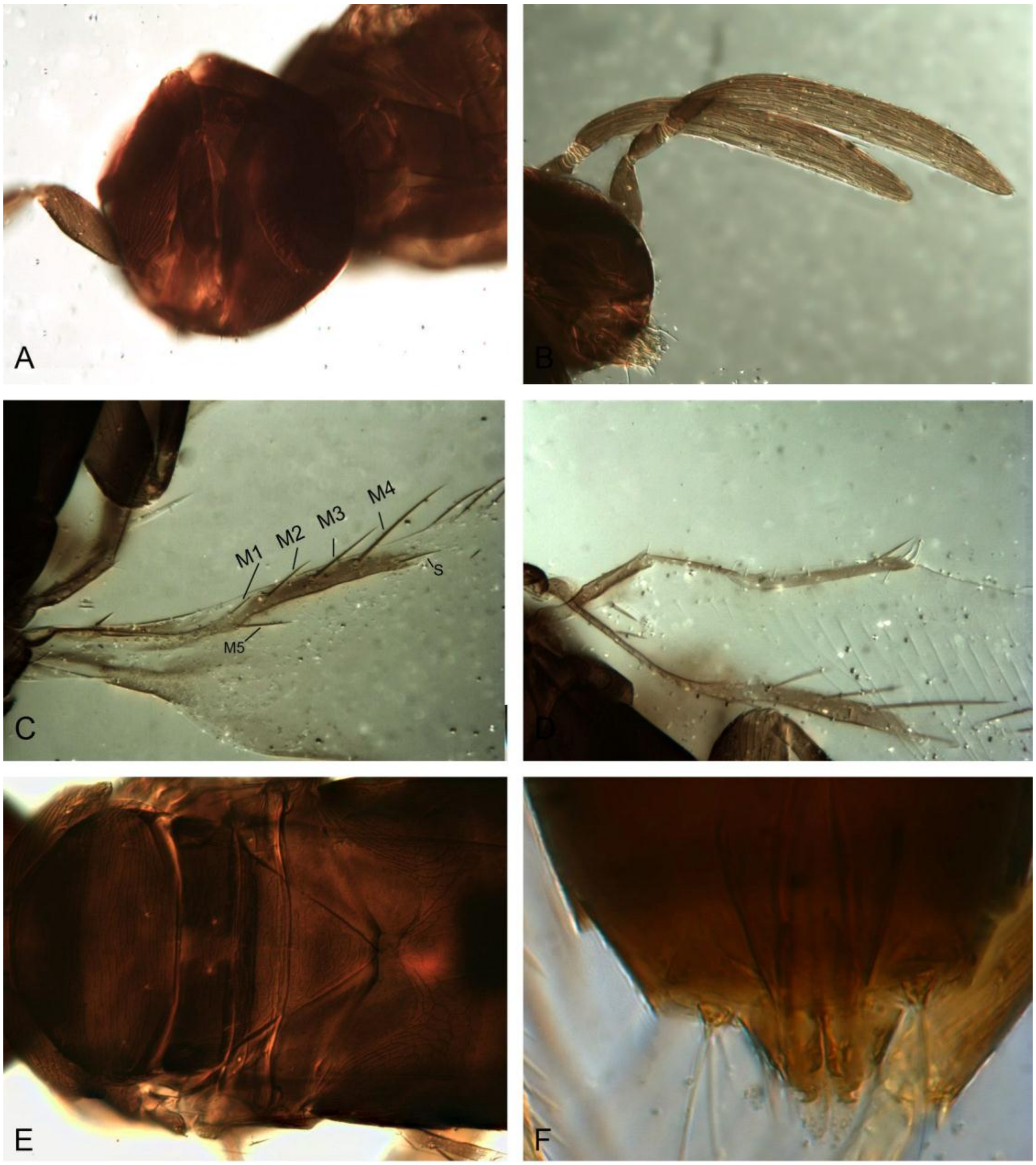


Figure 14. *Thysanus* n. sp. 3. A, head; B, antenna; C; forewing vein; D, hindwing; E, mesosoma, excluding pronotum and mesoscutum; F, metasoma showing ovipositor. (A-D, CNCHYMEN 122504; E-F, CNCHYMEN 122408).

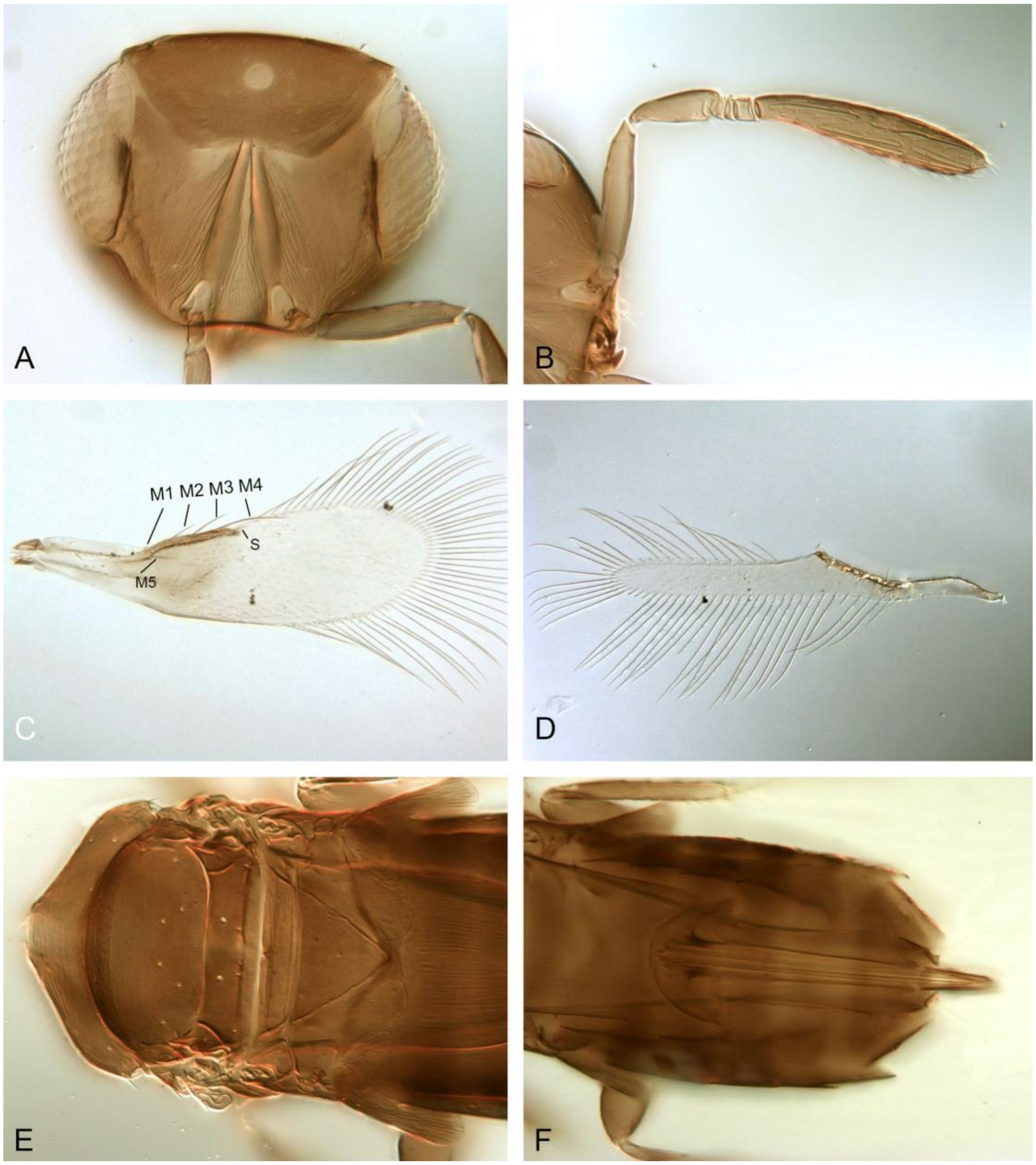


Figure 15. *Thysanus* n. sp. 5. A, head; B, antenna; C; forewing vein; D, hindwing; E, mesosoma, excluding pronotum and mesoscutum; F, metasoma showing ovipositor. (Hawaii DA RB-12-81 (1) and (2)).

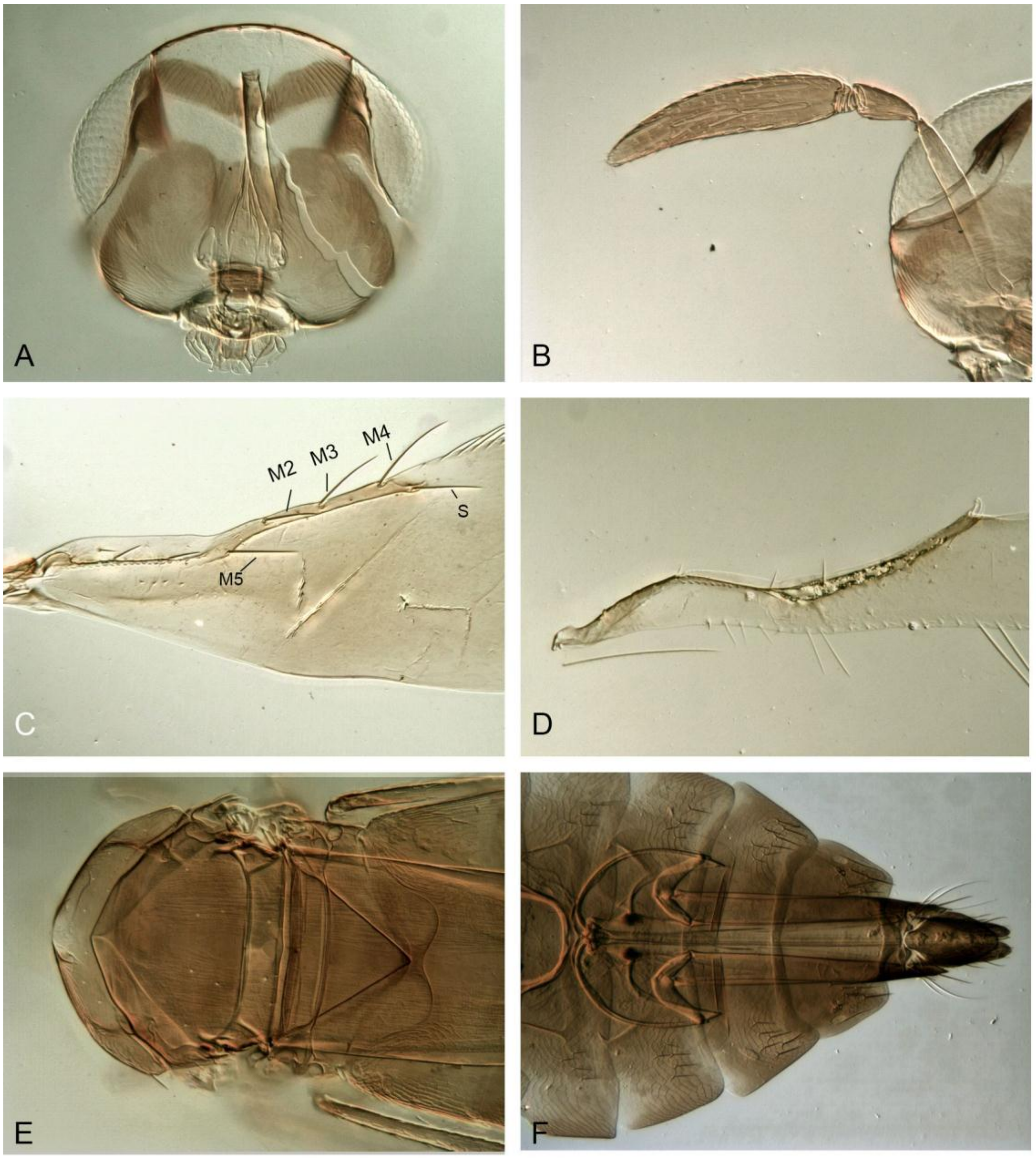
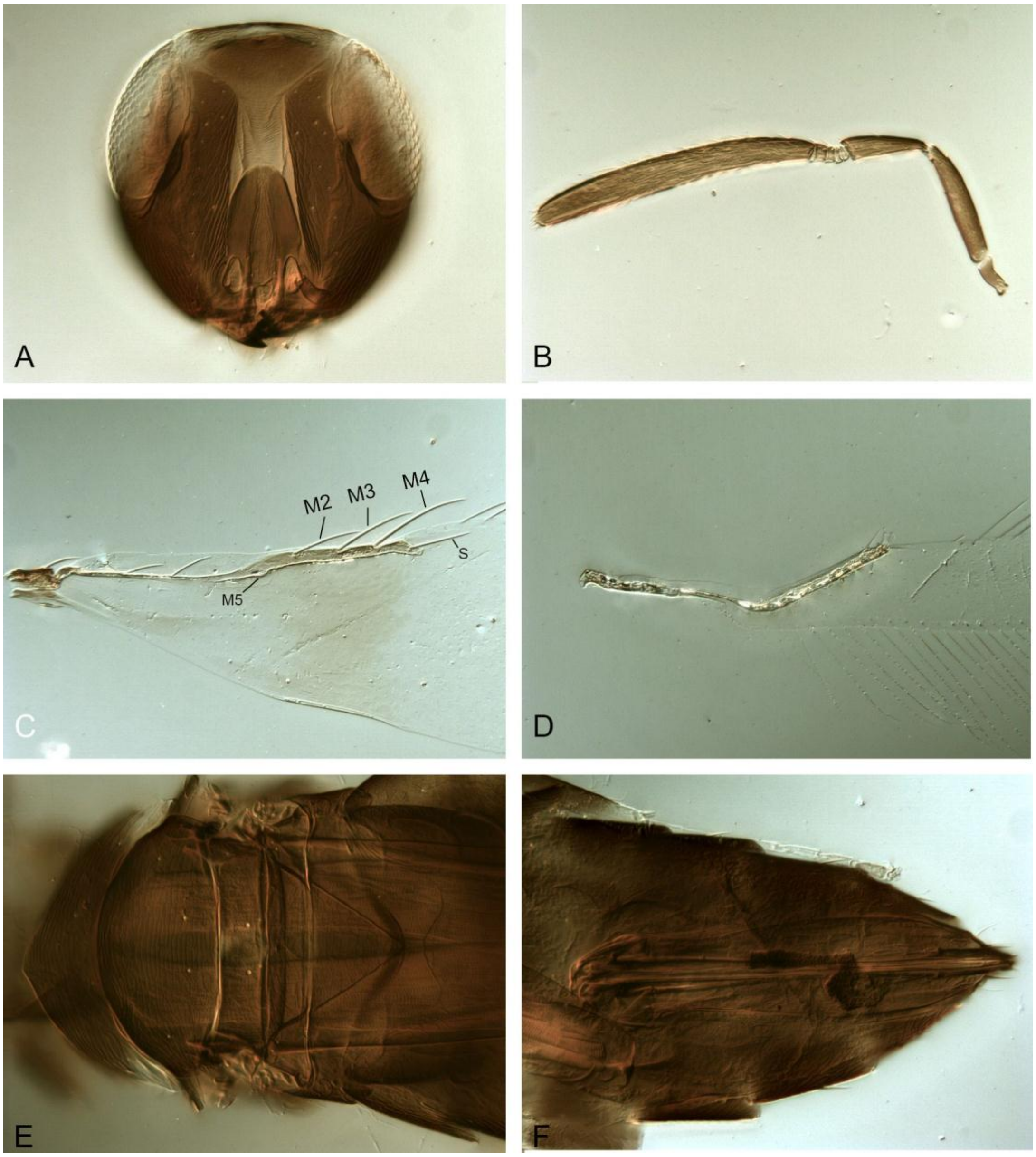


Figure 16. *Thysanus* n. sp. 6. A, head; B, antenna; C; forewing vein; D, hindwing; E, mesosoma, excluding pronotum and mesoscutum; F, metasoma showing ovipositor. (CNCHYMEN 122415).



APPENDIX E

MAIN TABLES AND FIGURES FOR CHAPTER V

Table 7. Summary of characters that were proposed to distinguish the subgenera of *Chartocerus*.

Subgenus	**Reference**	**Characters**
Chartocerus	Rozanov 1965 DeSantis 1968	- marginal fringe of fore wing shorter than ½ of width of wing - hind wing less than 4x as long as wide; - marginal fringe of hind wing not more than 1/3 width of the wing - pronotum almost 7x as wide as long, - spur of middle tibia with 14 teeth - papilliform processes distally in the male genitalia
Signiphorina	Nikol'skaya 1950	- fore wing fringe longer than 1/3 of wing width - 'body relatively longer and narrower' - antenna of male with 3 anelli - male scape and pedicel slender and long, as in female
Signiphorina	Rozanov 1965 DeSantis 1968	- marginal fringe of fore wing at least half as long as width of wing - hind wing more than 4x as long as wide - marginal fringe of hind wing longer than ½ of width of the wing.
Xana	Nikol'skaya 1956	- fore wing fringe short - 'body relatively shorter and wider' - antenna of male with 4 anelli - male scape and pedicel shorter, less expanded than in female
Xana	Rozanov 1965 DeSantis 1968	- marginal fringe of fore wing shorter than ½ of width of wing - hind wing less than 4x as long as wide; - marginal fringe of hind wing not more than 1/3 width of the wing - spur of middle tibia with 7-9 teeth - second to 4th annellus more than 2x as long as wide

Table 8. Summary of known distribution and host records of *Chartocerus* species

	Subgroup	**Reference**	**Nearctic**	**Neotropical**	**Palearctic**	**Africa**	**India**	**Oriental**	**Australia**	**Primary (Phytophagous) Host**	**Coccidae**	**Eriococcidae**	**Dactylopiidae**	**Pseudococcida**	**Diaspididae**	**Aphididae**	**Psylloidea**	**Diptera**	**Secondary (parasitoid host)**
australicus	*?Chartocerus*								x	–									
australiensis									x	–									
australiensis orbicularis	*?Signiphorina*								x	–									
axillaris	*Xana*			x						*Hypogeococcus* *Pseudococcus*				x					
beethoveni	*Matritia/Xana*	Rozanov 1965							x	–									
bengalensis	-									*Aspidiotus* sp.					x				
conjugalis	*Matritia/Xana*	Peck et al. 1964 Rozanov 1965			x					*Phenacaspis pinifoliae* *Planococcus citri*				x	x				Marietta
corvinus	*Matritia/Xana*	Rozanov 1965							x	–									
dactylopii	*Matritia/Xana*	Rozanov 1965	x							several				x				(1)	Anagyrus; Holcencyrtus
delicatus	*Signiphorina*								x	–									
elongatus	*Signiphorina*	Nikol'skaya 1952 Rozanov 1965	x	x	x	x				*Coccus hesperidium Ferrisiana virgata, Pseudococcus, Planococcus*	x			x				(2)	Encyrtidae, Pteromalidae, Eulophidae
fimbriae	*Signiphorina*	Hayat and Verma 1980					x			*Ceroplastes cajani; Nipaecoccus viridis; Pseudococcus vastator; Saccharicoccus sacchari;*	x			x					
fujianensis	*Signiphorina*	original description						x		–									

	Subgroup	Reference	Nearctic	Neotropical	Palearctic	Africa	India	Oriental	Australia	Primary (Phytophagous) Host	Coccidae	Eriococcidae	Dactylopiidae	Pseudococcida	Diaspididae	Aphididae	Psylloidea	Diptera	Secondary (parasitoid host)
funeralis	*Signiphorina*								x	–									
gratius	-	-							x	*Dactylopius conspictus*			x						
hebes	*Matritia/Xana*	Rozanov 1965							x	arachnid egg sac									
himalayanus	-	-					x			–									
hyalipennis	*Matritia/Xana*	original description				x	x			several				x					
intermedius	*Signiphorina*	Hayat and Verma 1980					x			Pseudococcidae				x					
kerrichi	*Matritia/Xana*	Rozanov 1965					x			several	x	x		x					Primary (?)
kurdjumovi	*Matritia/Xana*	original description			x		x	x		several		x				x		(1)	
musciformis	*Chartocerus*	type species			?		x	?		*Pseudococcus coffeae*				x					
*niger*Ashm.	*Signiphorina*	Rozanov 1965	x	x	x					several				x	x				Encyrtidae
novitzkyi	*Signiphorina*	Rozanov 1965			x					–									
philippiae	*Signiphorina*					x				–									
ranae	*Matritia/Xana*	Agarwal 1963 Rozanov 1965					x			*Saccharicoccus sacchari*				x					
	Signiphorina	Hayat and Verma 1980																	
reticulatus	*Matritia/Xana*	Rozanov 1965							x	–							?		
rosanovi	*Matritia/Xana*	Sugonaev 1968			x					–									
ruskini									x	–									
simillimus	*Matritia/Xana*				x					–									
subaeneus	*Signiphorina*	Nikol'skaya 1952			x	x				several				x	x				
(mala)	*Signiphorina*				x					–									

	Subgroup	Reference	Nearctic	Neotropical	Palearctic	Africa	India	Oriental	Australia	Primary (Phytophagous) Host	Coccidae	Eriococcidae	Dactylopiidae	Pseudococcidae	Diaspididae	Aphididae	Psylloidea	Diptera	Secondary (parasitoid host)
thusanoides	*Matritia/Xana*	Rozanov 1965							x	–									
walkeri	*Matritia/Xana*	original description					x	x		*Diaphorina cardiae; Phenacoccus iceryoides*				x			x		*Diaphorencyrtus aligarhensis*
	Chartocerus	Hayat and Verma 1980																	
yunnanensis	*Signiphorina*	Original description						x		*Planococcus citri*				x					

(1) *Leucopis* (Chamaemyiidae)

(2) *Xanthogramma* (Syrphidae)

Figure 17. *Chartocerus australiensis* (Ashmead), syntype. A, head; B, antenna; C, fore wing; D, fore wing vein; E, mesosoma; F, metasoma.

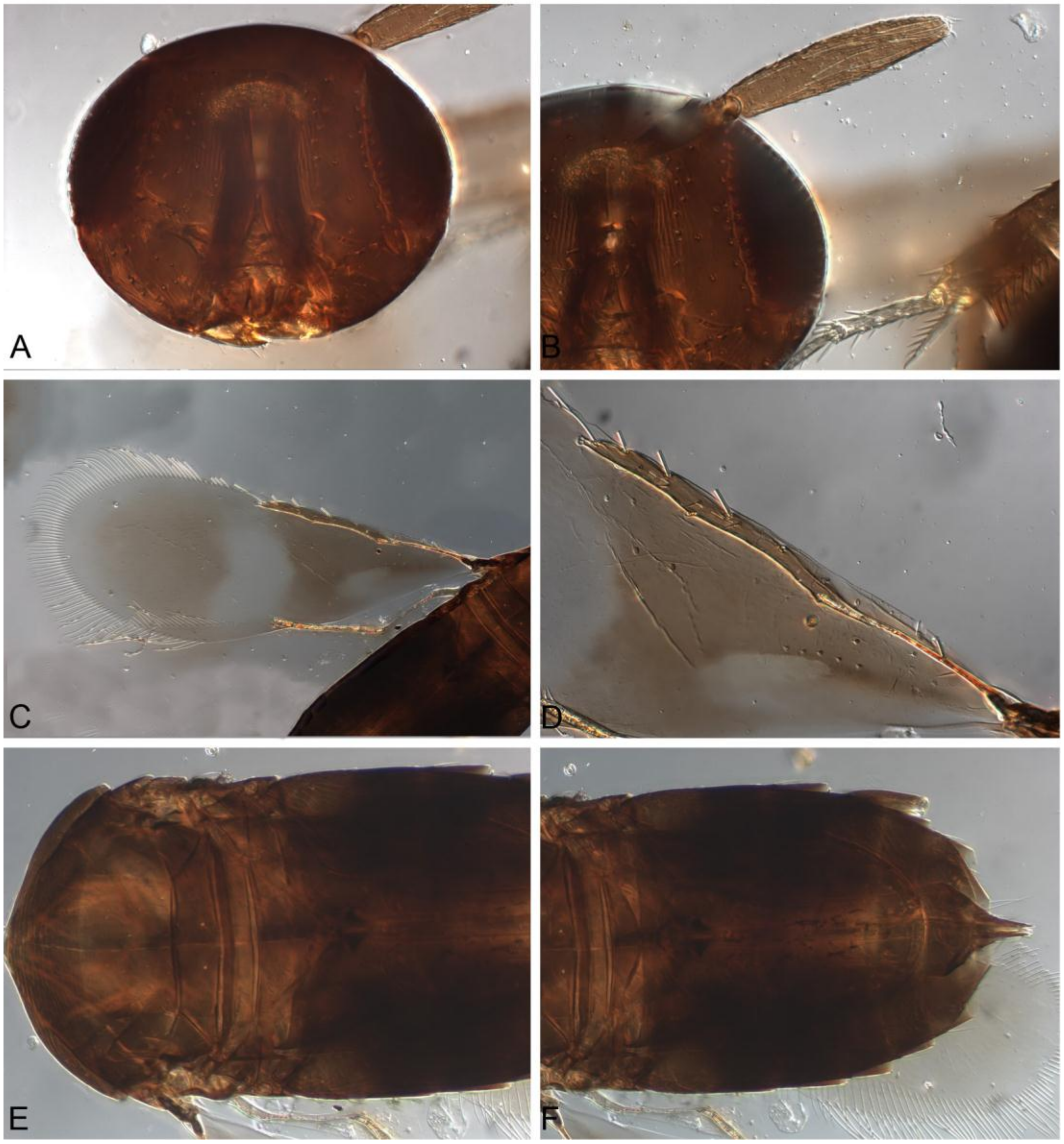


Figure 18. *Chartocerus axillaris* De Santis, holotype. A, head; B, antenna (detail: pedicel and anelli); C, fore wing; D, fore wing vein; E, mesosoma; F, metasoma.

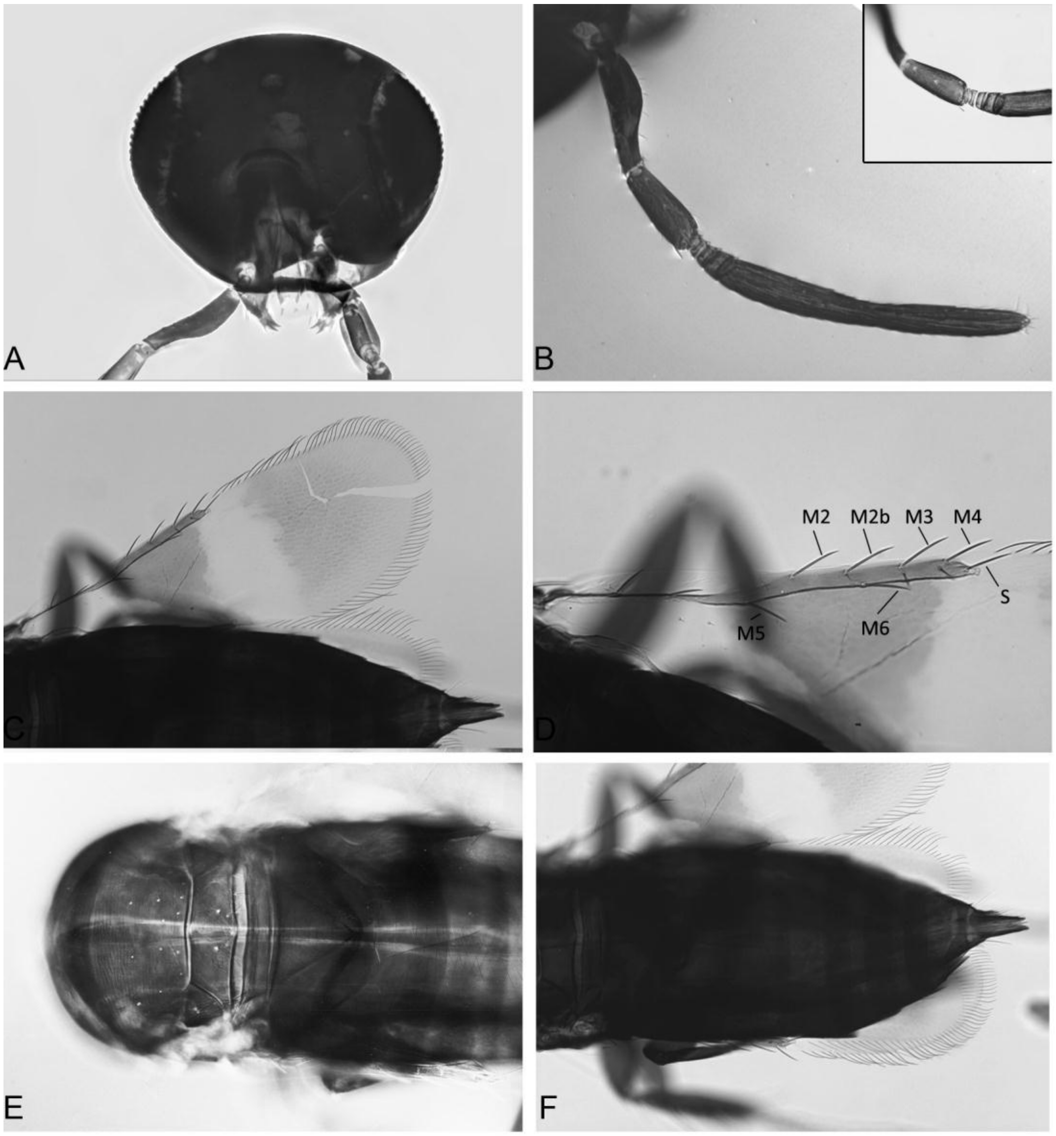


Figure 19. *Chartocerus conjugalis* (Mercet), holotype. A, habitus; B, antenna (missing scape); C, mesosoma; D, fore wing.

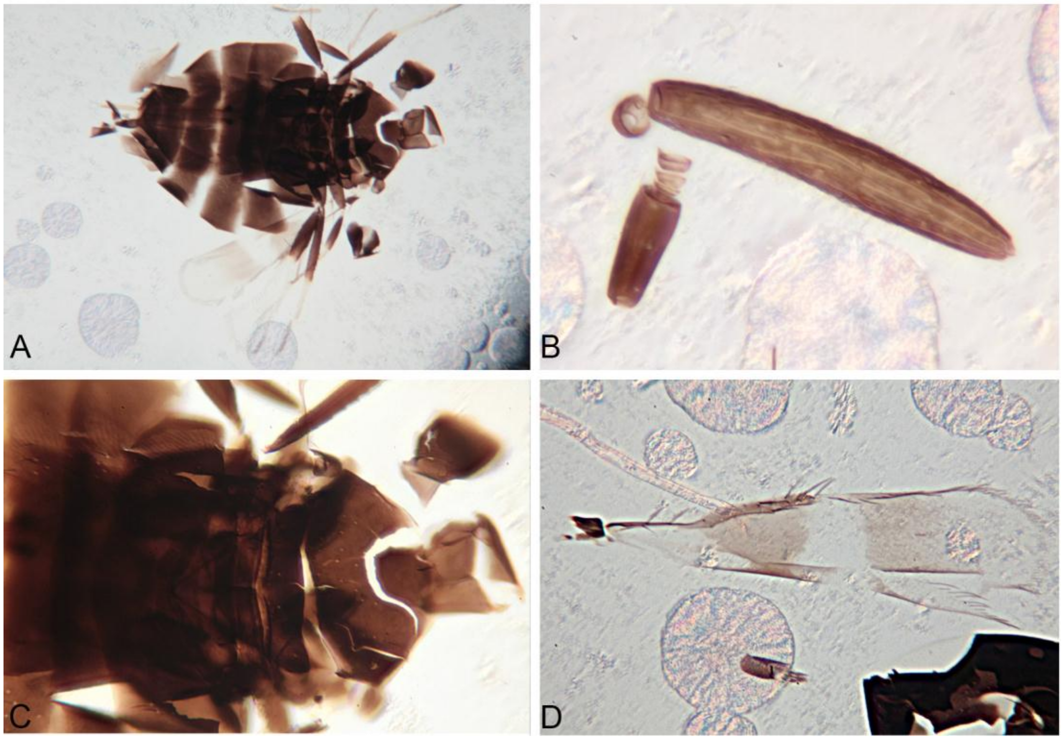


Figure 20. *Chartocerus dactylopii* (Ashmead), syntypes. A, C, E from one of the females; B, D, F from the only male. A, habitus (female); B, habitus (male); C, fore wing; D, antenna; E, mesosoma; F, male genitalia.

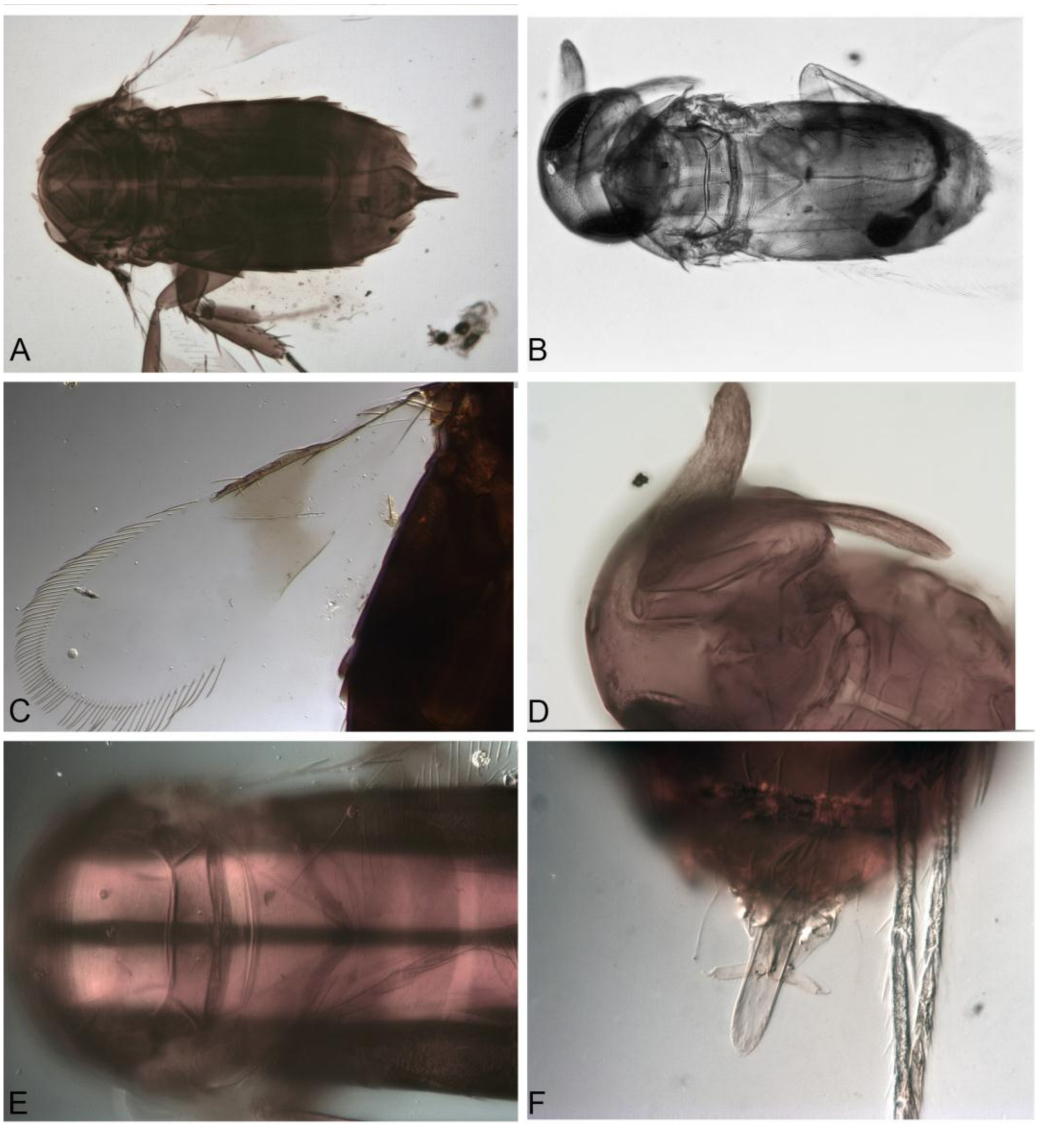


Figure 21. *Chartocerus elongatus* (Girault, 1916), holotype. A, head; B, antenna; C, fore wing; D, hind wing; E, mesosoma; F, metasoma.

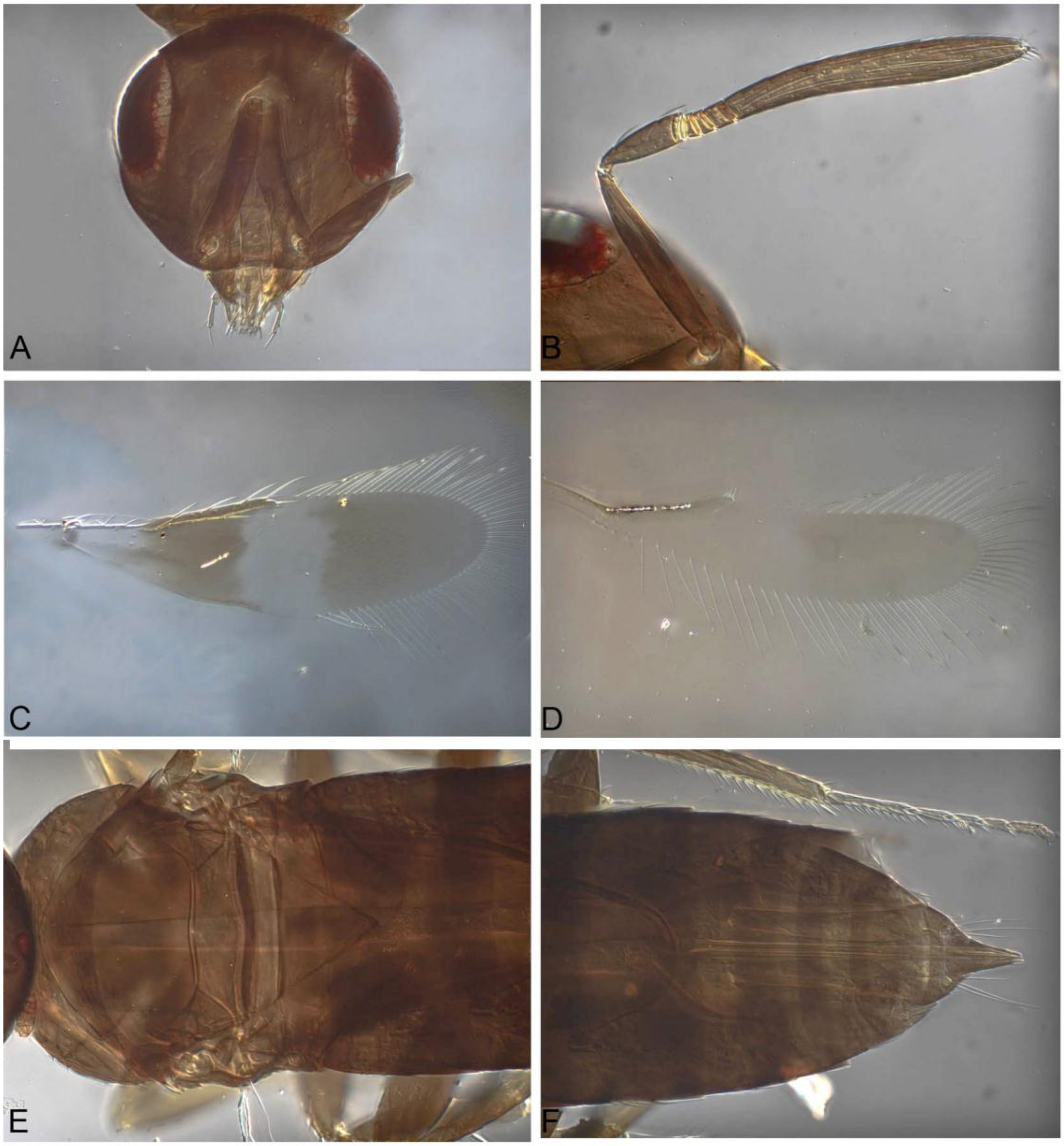


Figure 22. *Chartocerus fimbriae* Hayat, paratype. A, head; B, antenna; C, fore wing; D, hind wing; E, mesosoma; F, metasoma.

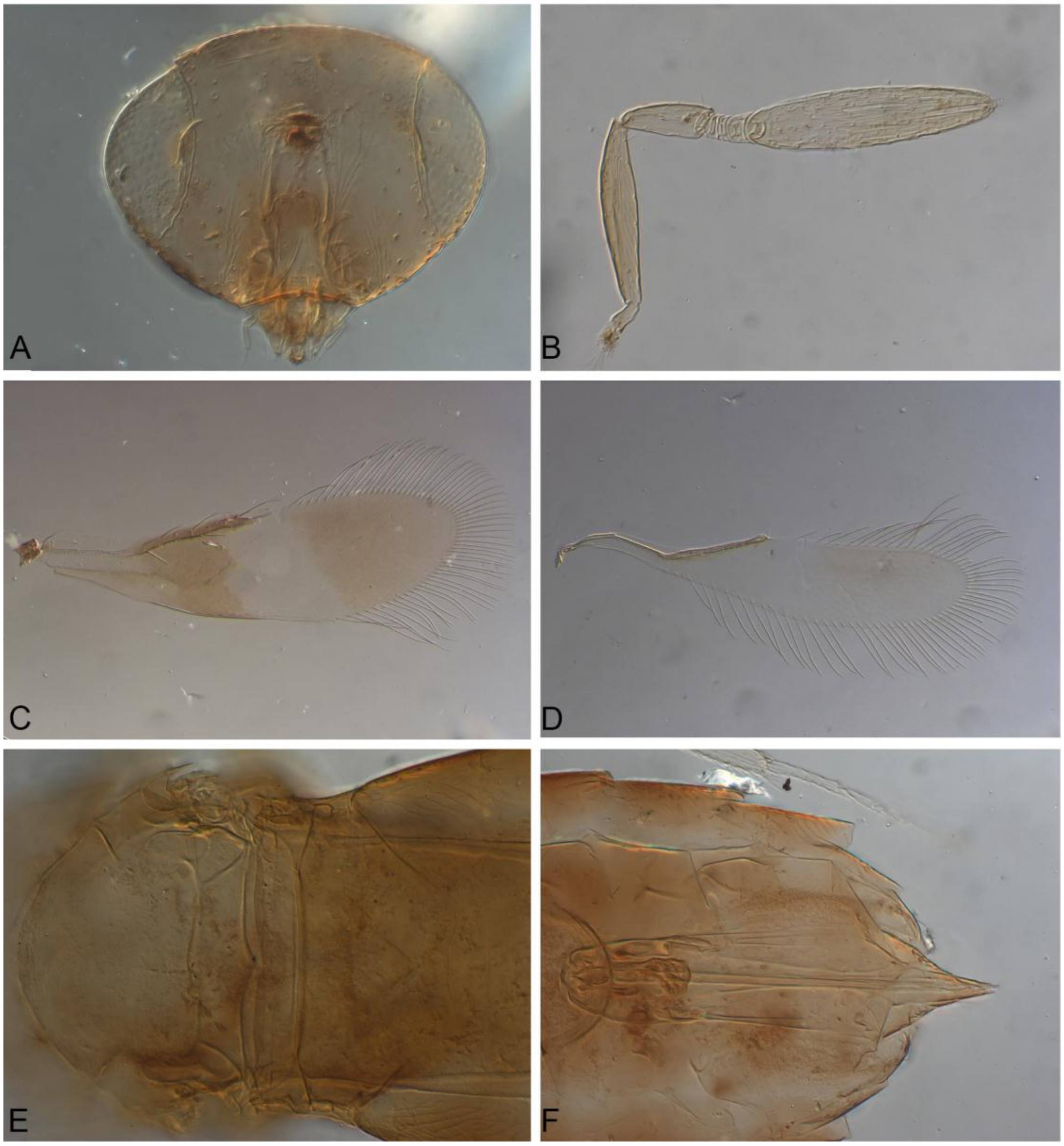


Figure 23. *Chartocerus kerrichi* (Agarwal). A, head; B, antenna; C, fore wing; D, hind wing; E, mesosoma; F, metasoma.

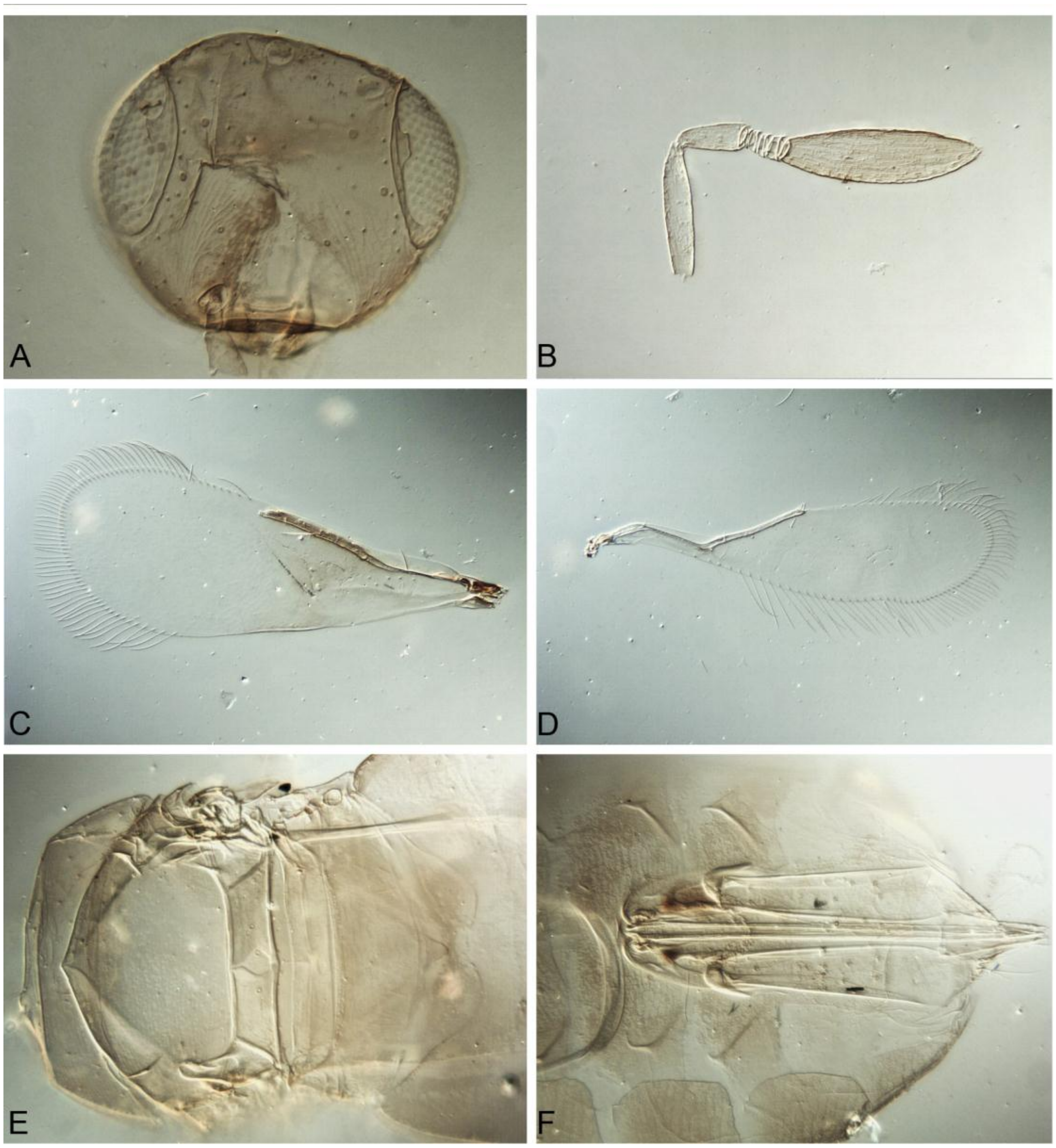


Figure 24. *Chartocerus kurdjumovi* (Nikol'skaya). A, head; B, antenna; C, fore wing; D, hind wing; E, mesosoma; F, metasoma.

Figure 25. *Chartocerus niger* (Ashmead), syntypes. A, female head; B, female antenna; C, female mesosoma; D, male genitalia.

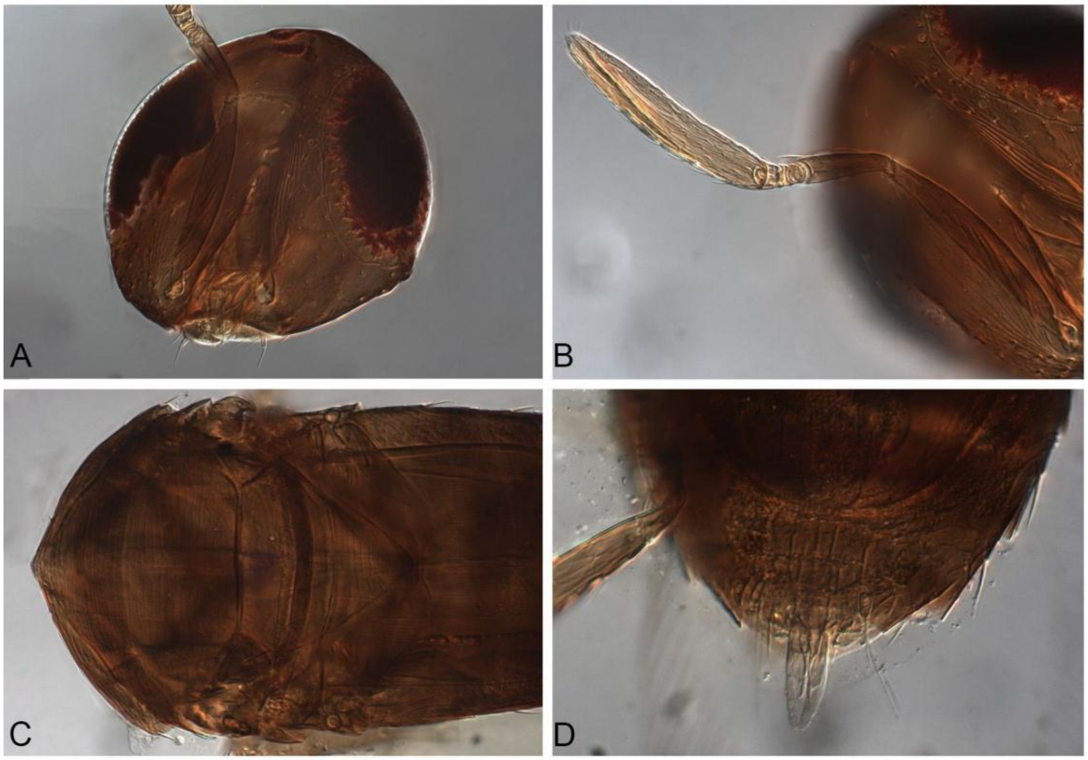


Figure 26. *Chartocerus novitzkyi* (Domenichini), putative syntype. A, head; B, antenna; C, fore wing; D, habitus and coloration; E, mesosoma; F, male genitalia.

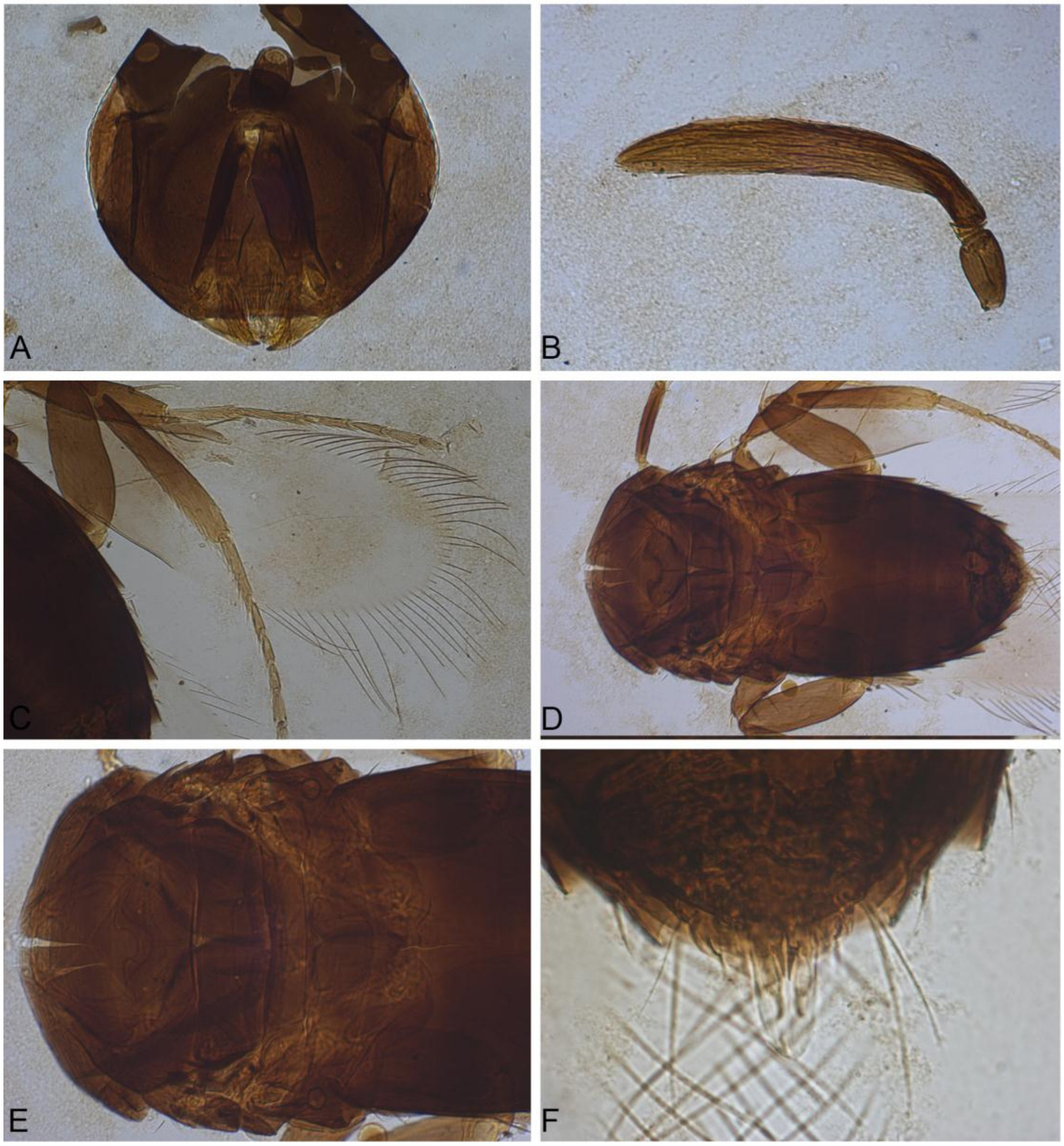


Figure 27. *Chartocerus philippiae* (Risbec), lectotype. A, habitus; B, antenna; C, fore wing; D, hind wing.

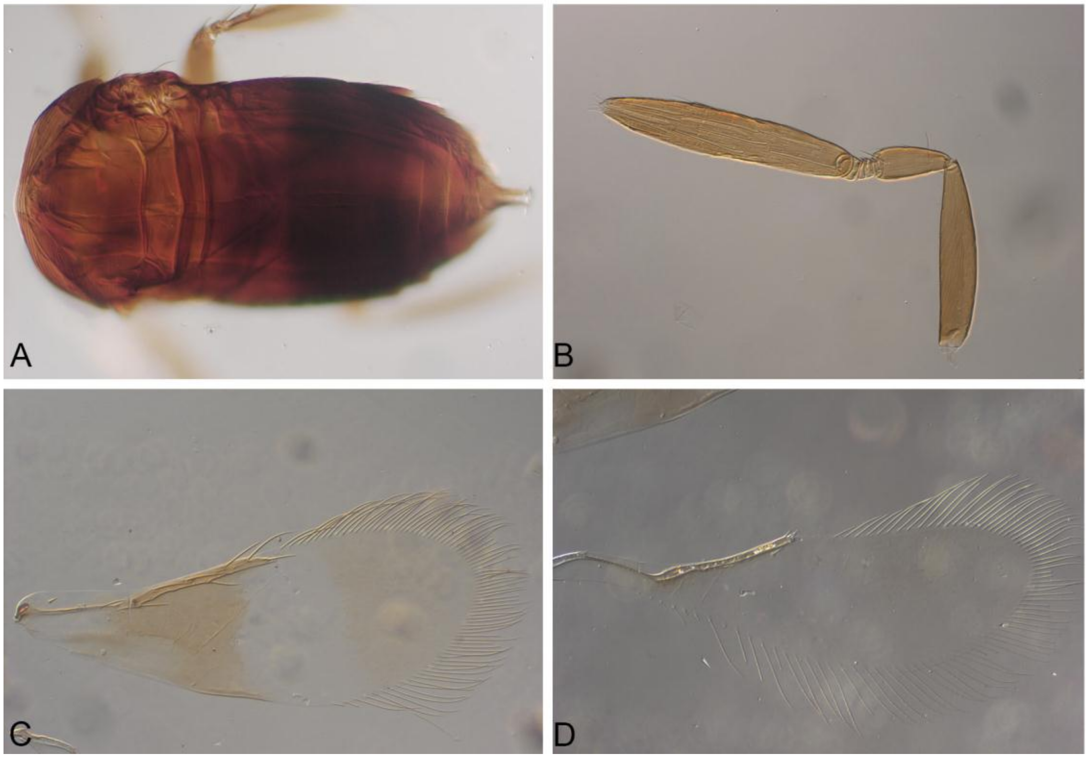


Figure 28. *Chartocerus rosanovi* Sugonaev, holotype. A, head; B, antenna; C, fore wing; D, hind wing, fragment (detail: basal fragment from opposite wing); E, mesosoma; F, metasoma.

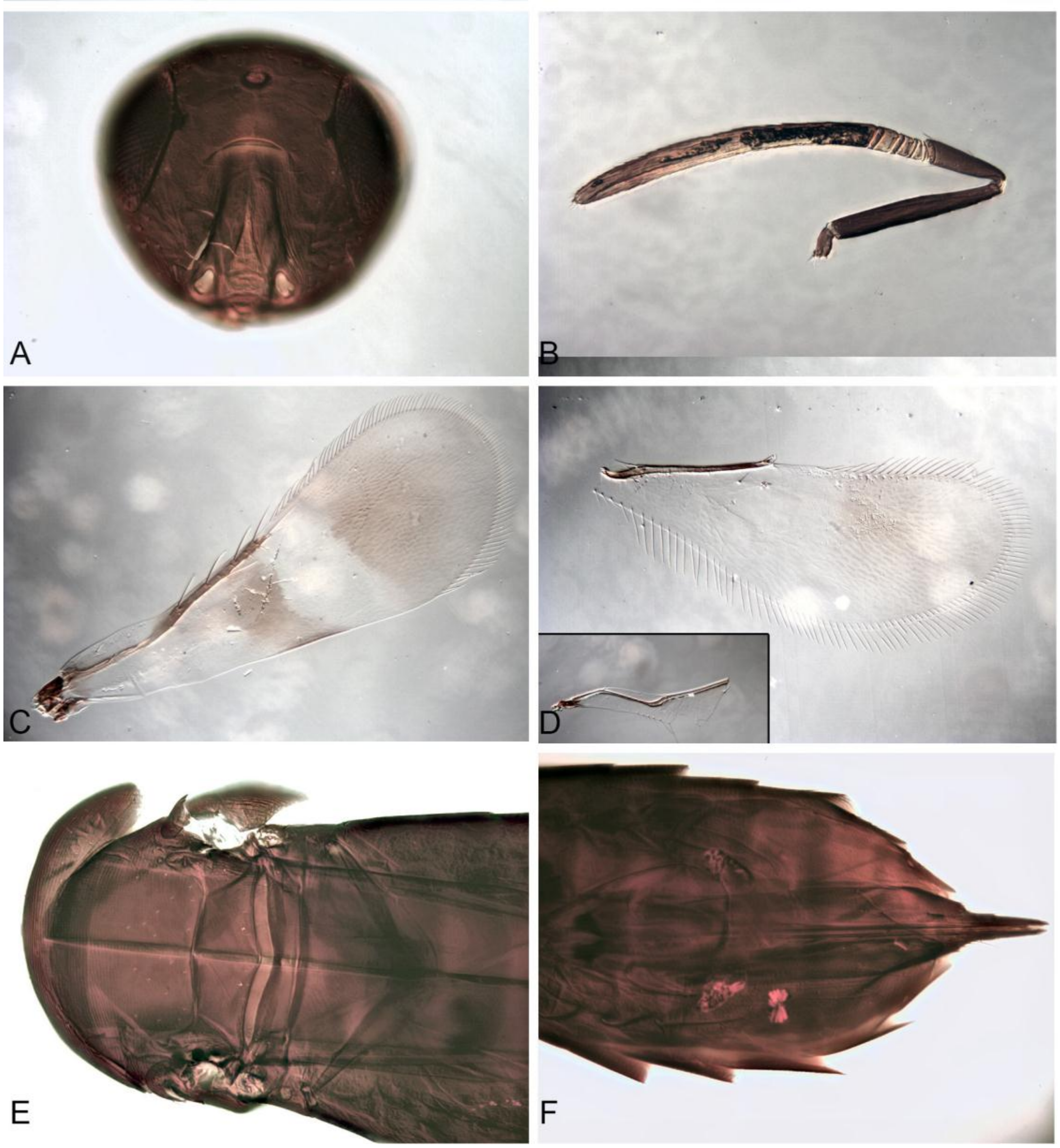


Figure 29. *Chartocerus simillimus* (Mercet), syntype. A, head; B, antenna; C, fore wing; D, mesosoma; E, metasoma; F, habitus.

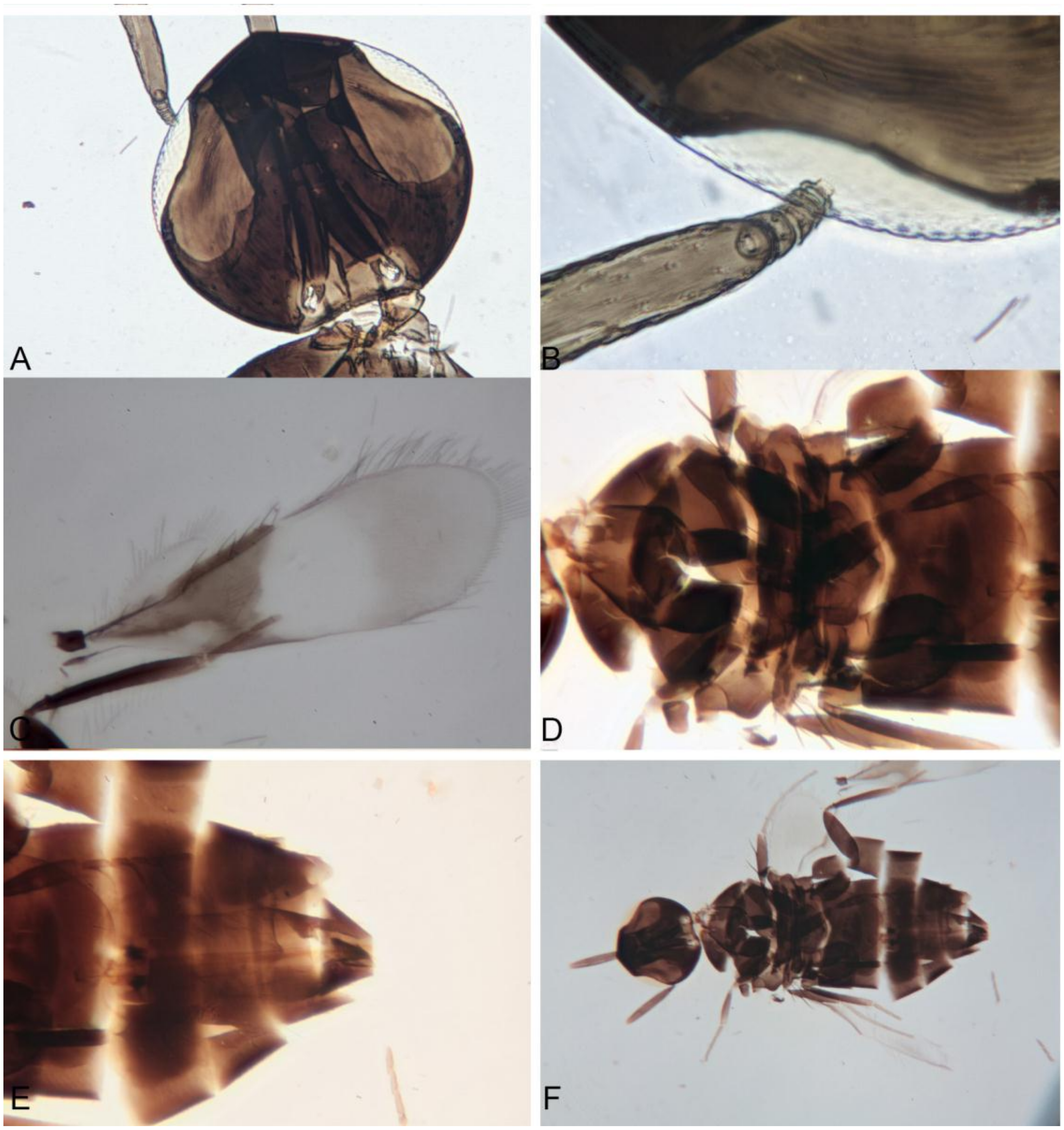


Figure 30. *Chartocerus subaeneus* (Förster), lectotype. A, head; B, antenna; C, fore wing; D, hind wing vein; E, mesosoma; F, metasoma and male genitalia.

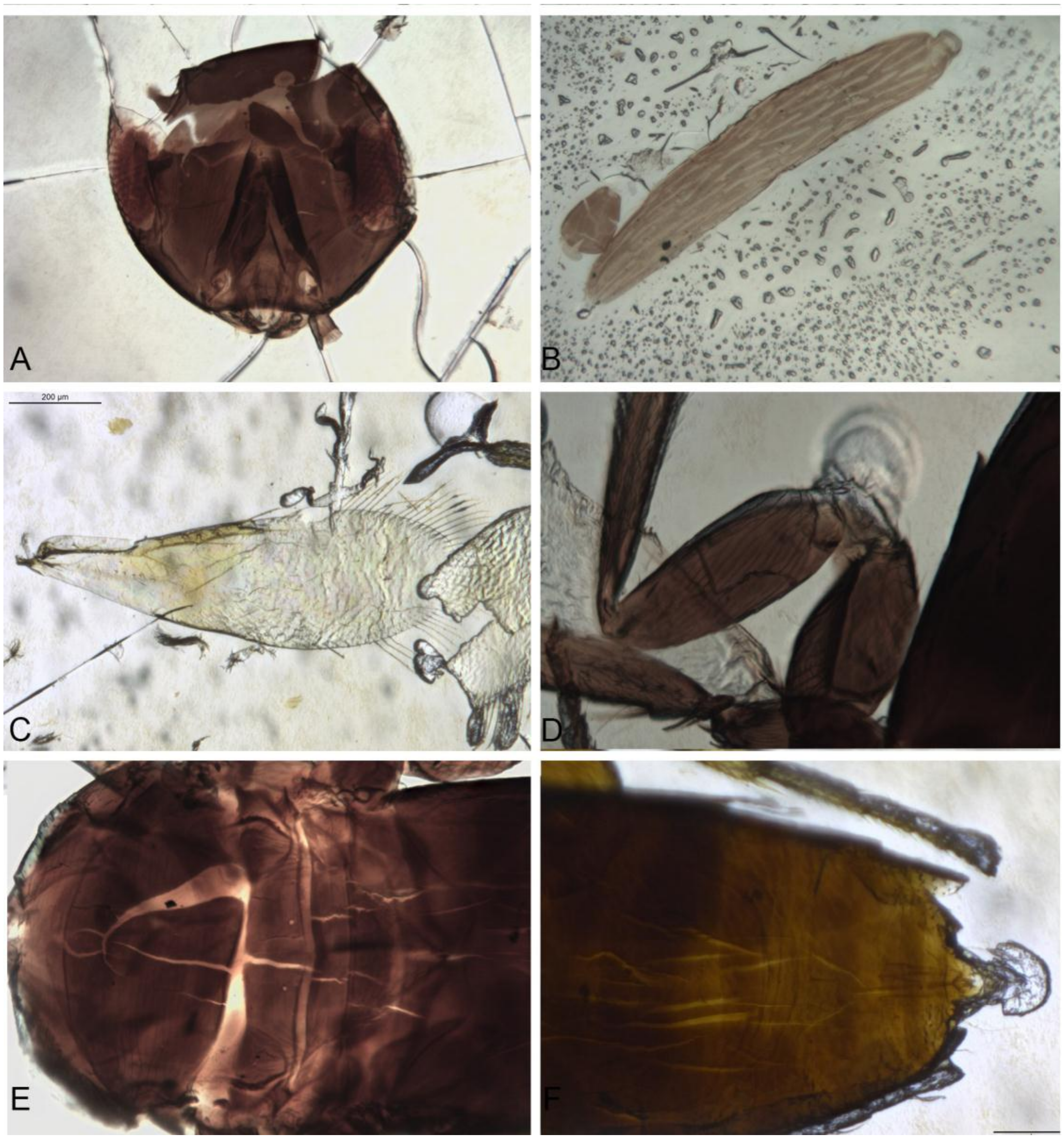


Figure 31. *Chartocerus walkeri* Hayat, paratype. A, head; B, antenna; C, fore wing; D, hind wing; E, mesosoma; F, metasoma.

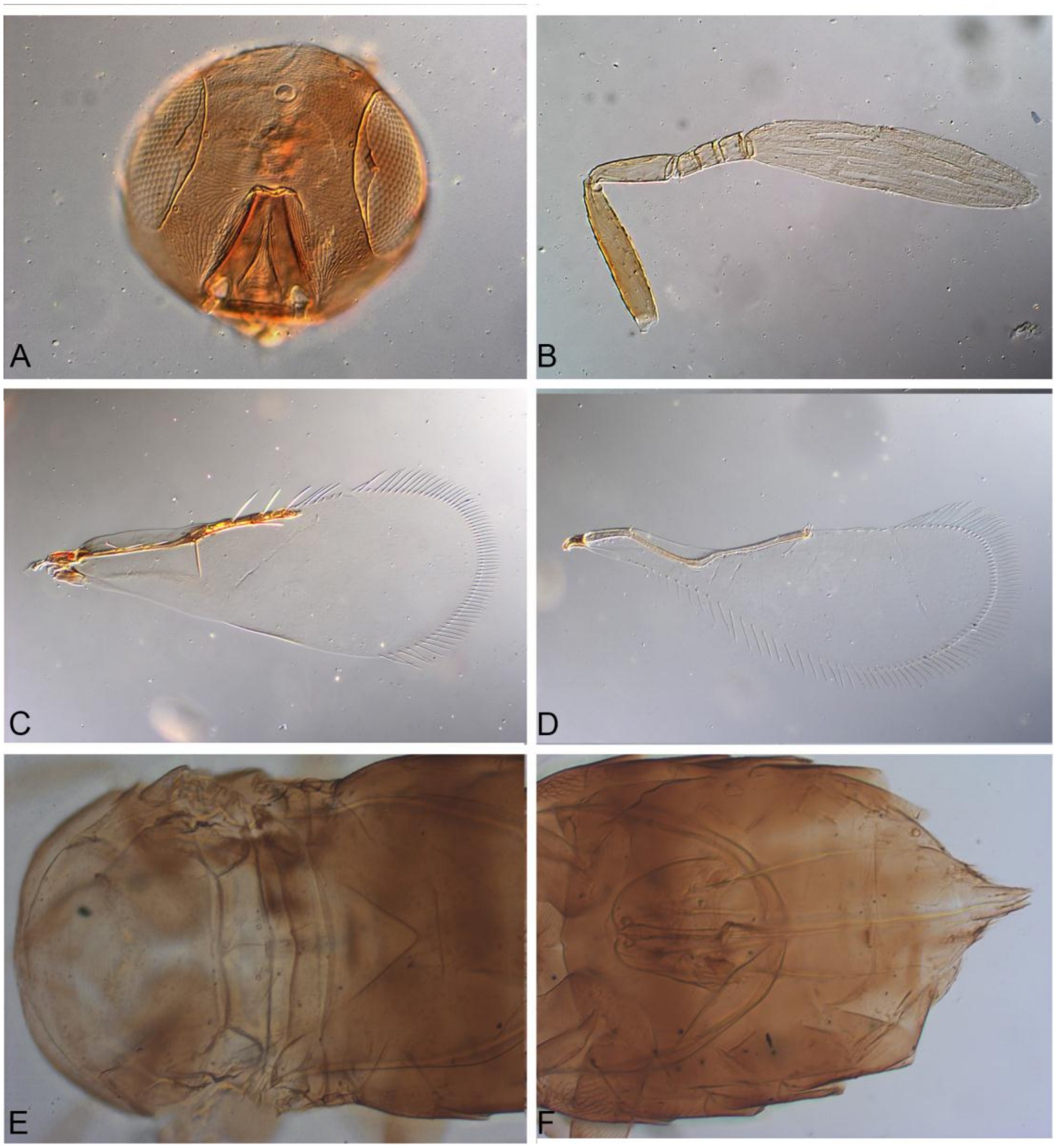


Figure 32. Slides with damaged Girault types. A, *Chartocerus australicus* (Girault), holotype slide. B, *Chartocerus ruskini* (Girault), holotype slide. The arrow indicates the dissected propodeum.

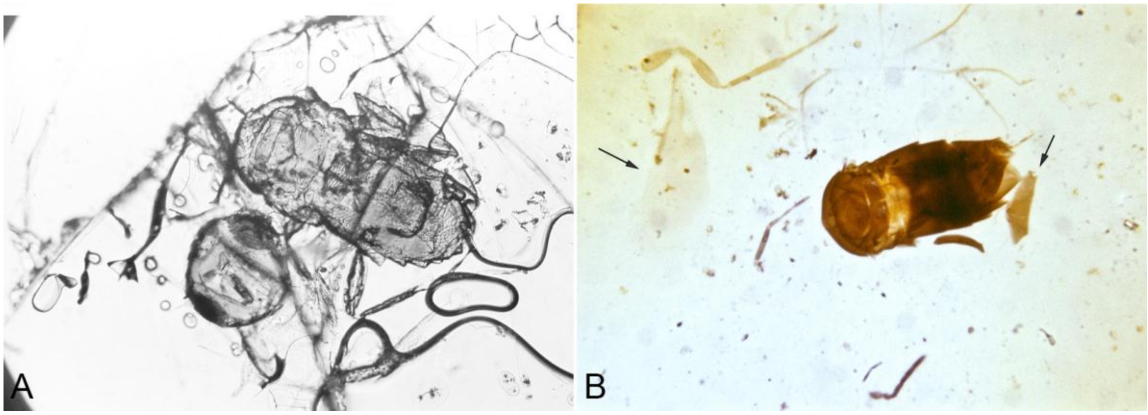


Figure 33. *Chartocerus australiensis orbicularis* (Girault), holotype. A, habitus and coloration; B, head; C, wings; D, detail of mesosoma showing propodeum and Mt1; E, metasoma; F, male genitalia.

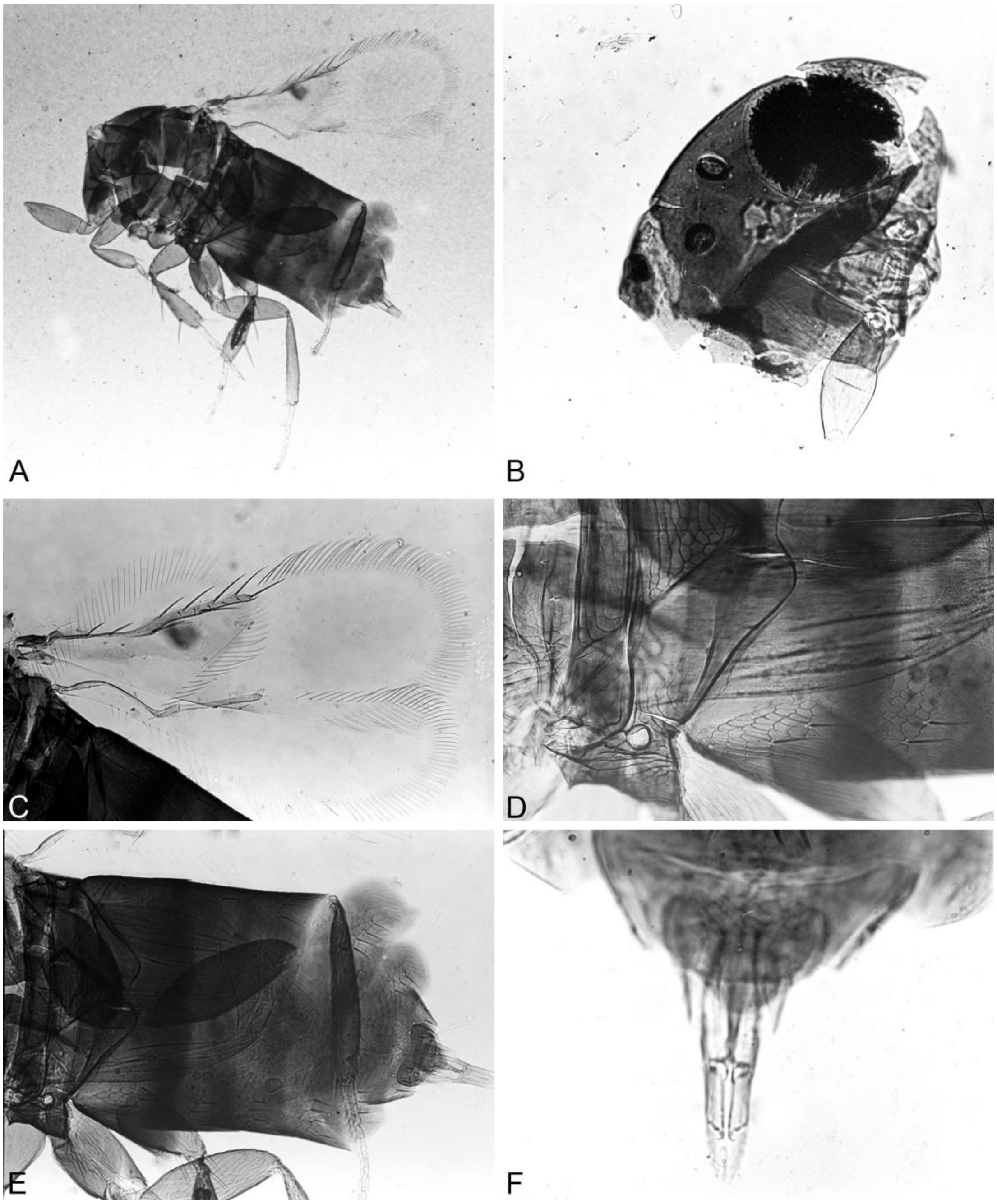


Figure 34. *Chartocerus beethoveni* (Girault), holoype. A, habitus and coloration; B, head; C, antenna; D, wings, E, mesosoma; F, detail of mesosoma showing propodeum and Mt1.

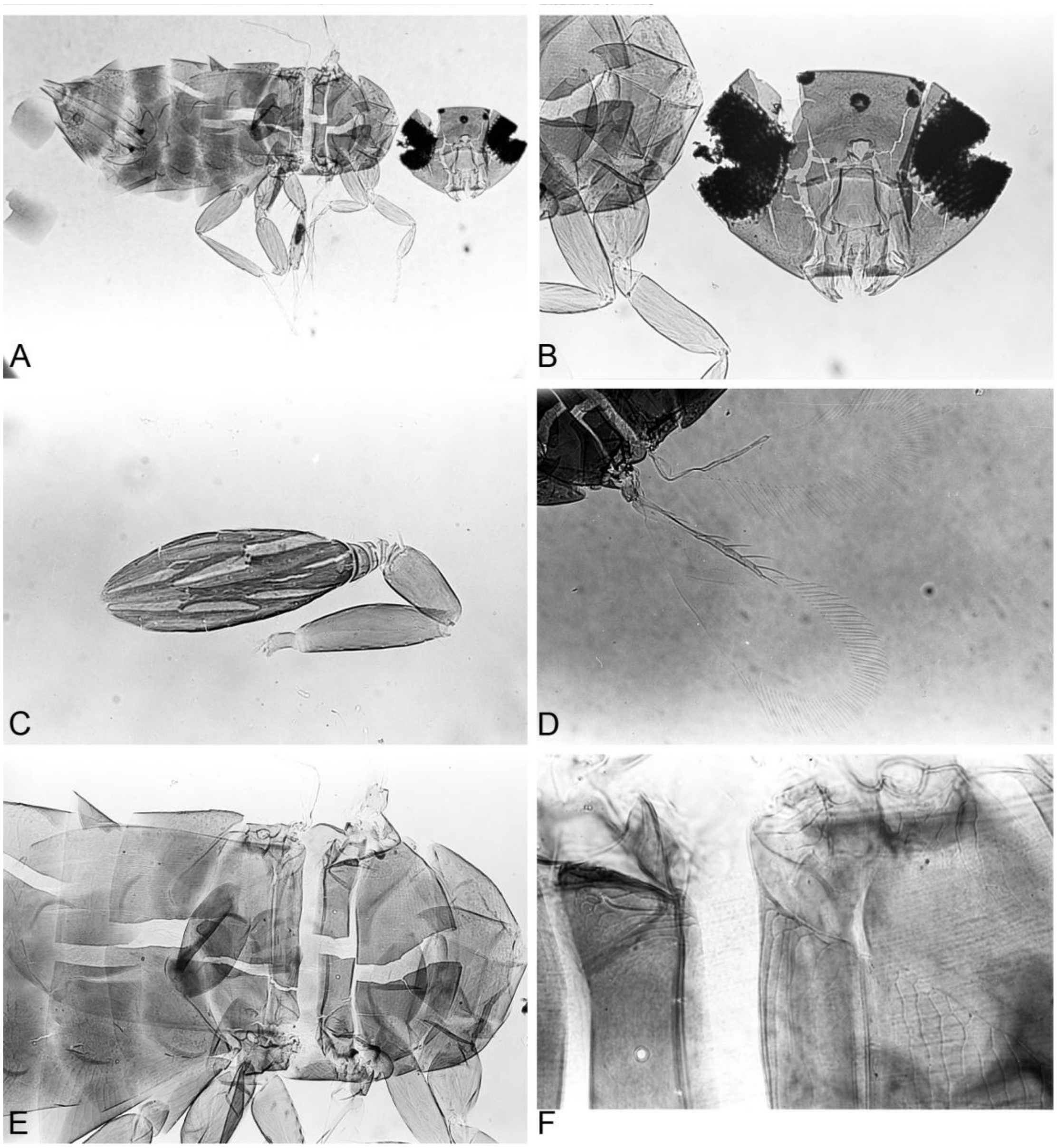


Figure 35. *Chartocerus corvinus* (Girault), holotype. A, habitus and coloration; B, head; C, mesosoma; D, fore wing.

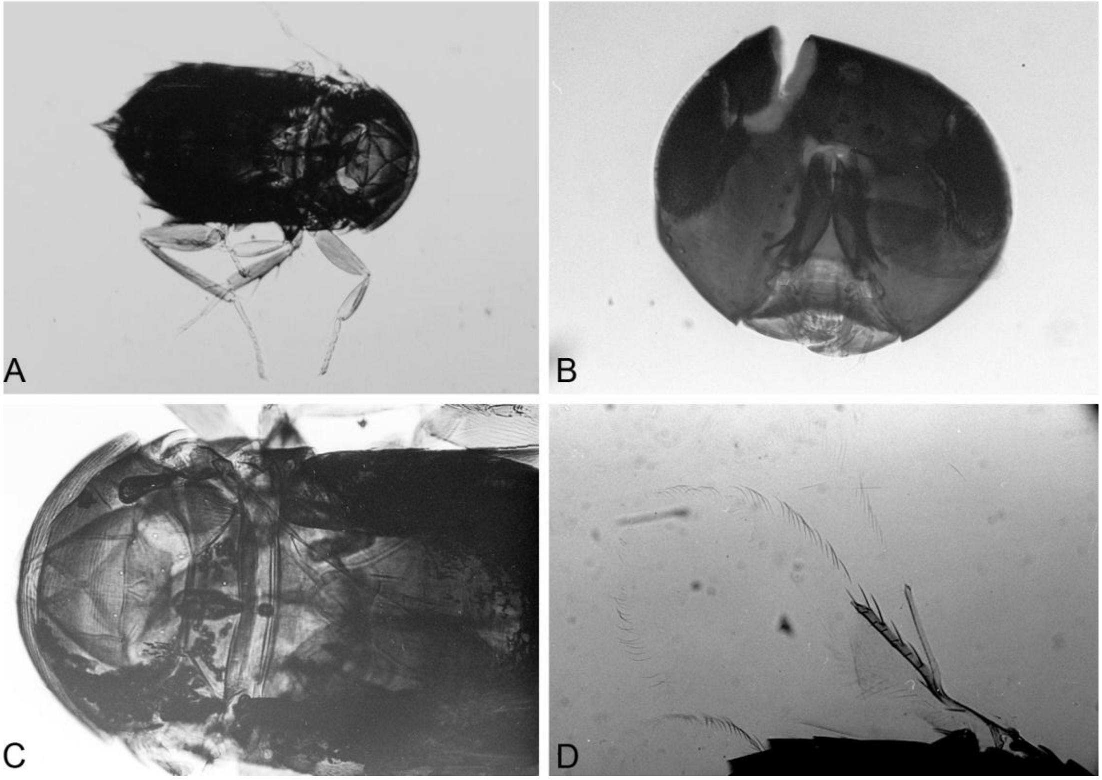


Figure 36. *Chartocerus delicatus* (Girault), holotype. A, habitus and coloration; B, head, C; antenna; D, wings; E, mesosoma; F, metasoma.

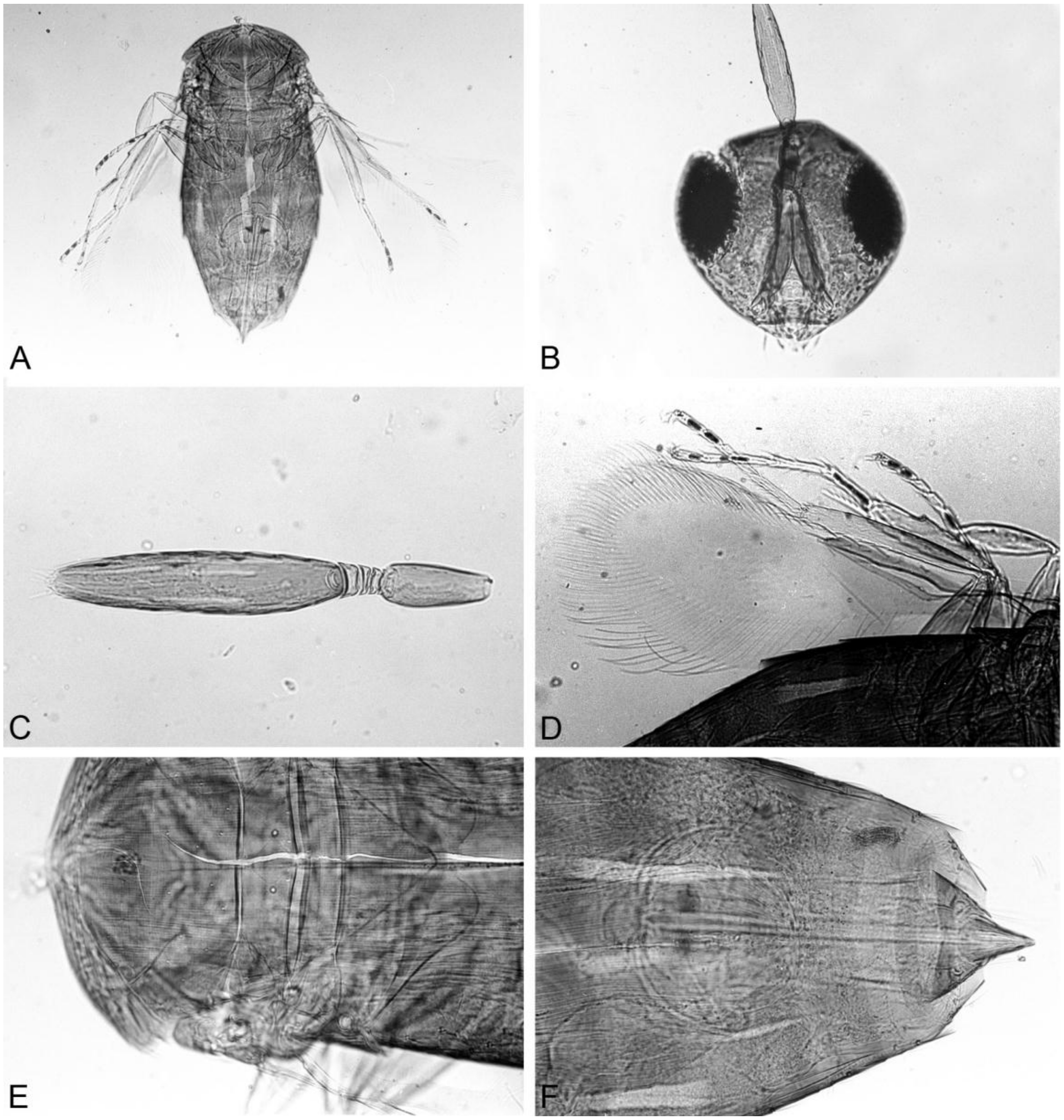


Figure 37. *Chartocerus funeralis* (Girault), holotype. A, habitus and coloration; B, head; C, mesosoma; D, wings.

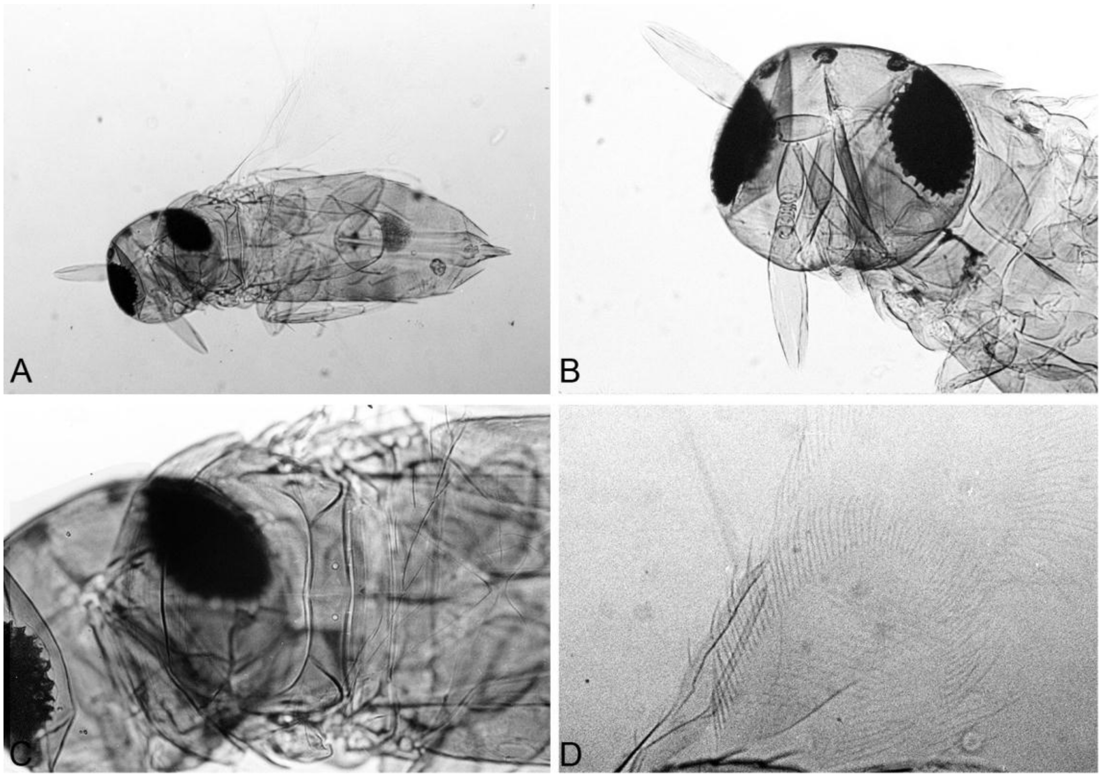


Figure 38. *Chartocerus hebes* (Girault), syntype. A, habitus; B, head; C, mesosoma; D, antenna (clava, anelli, pedicel).

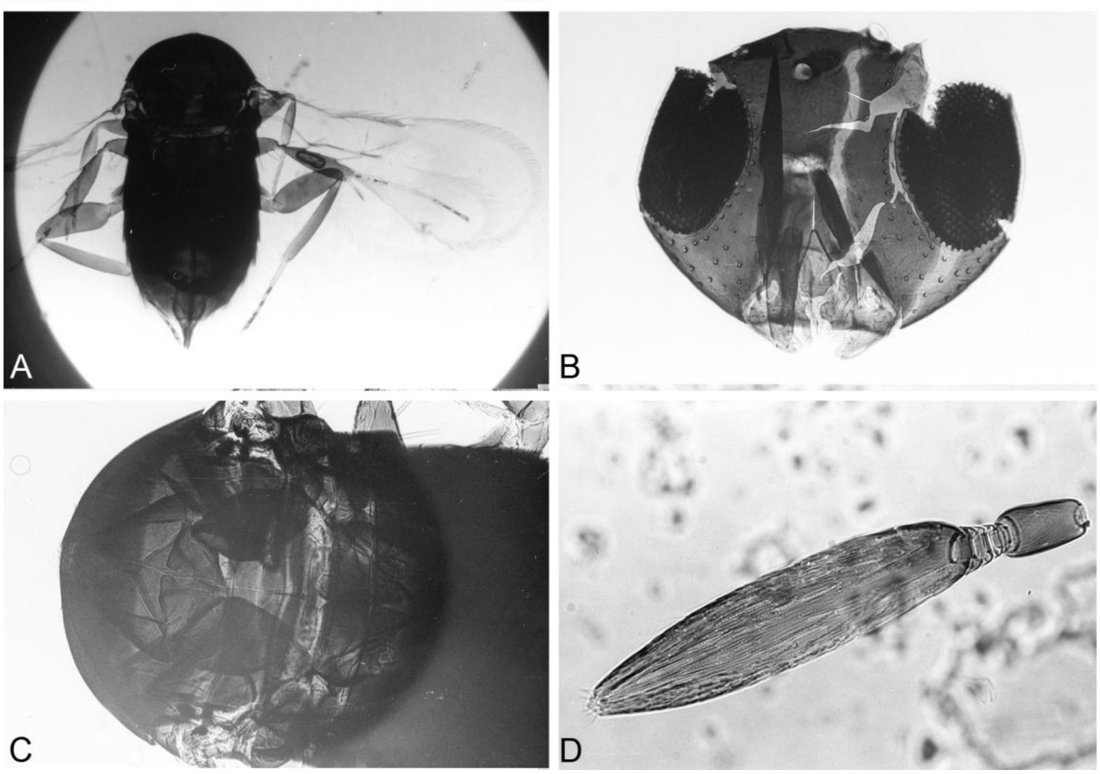


Figure 39. *Chartocerus reticulatus* (Girault), holotype. A, head; B, antenna, C, wings; D, legs; E, mesosoma (scutellum, metanotum, propodeum); F, metasoma.

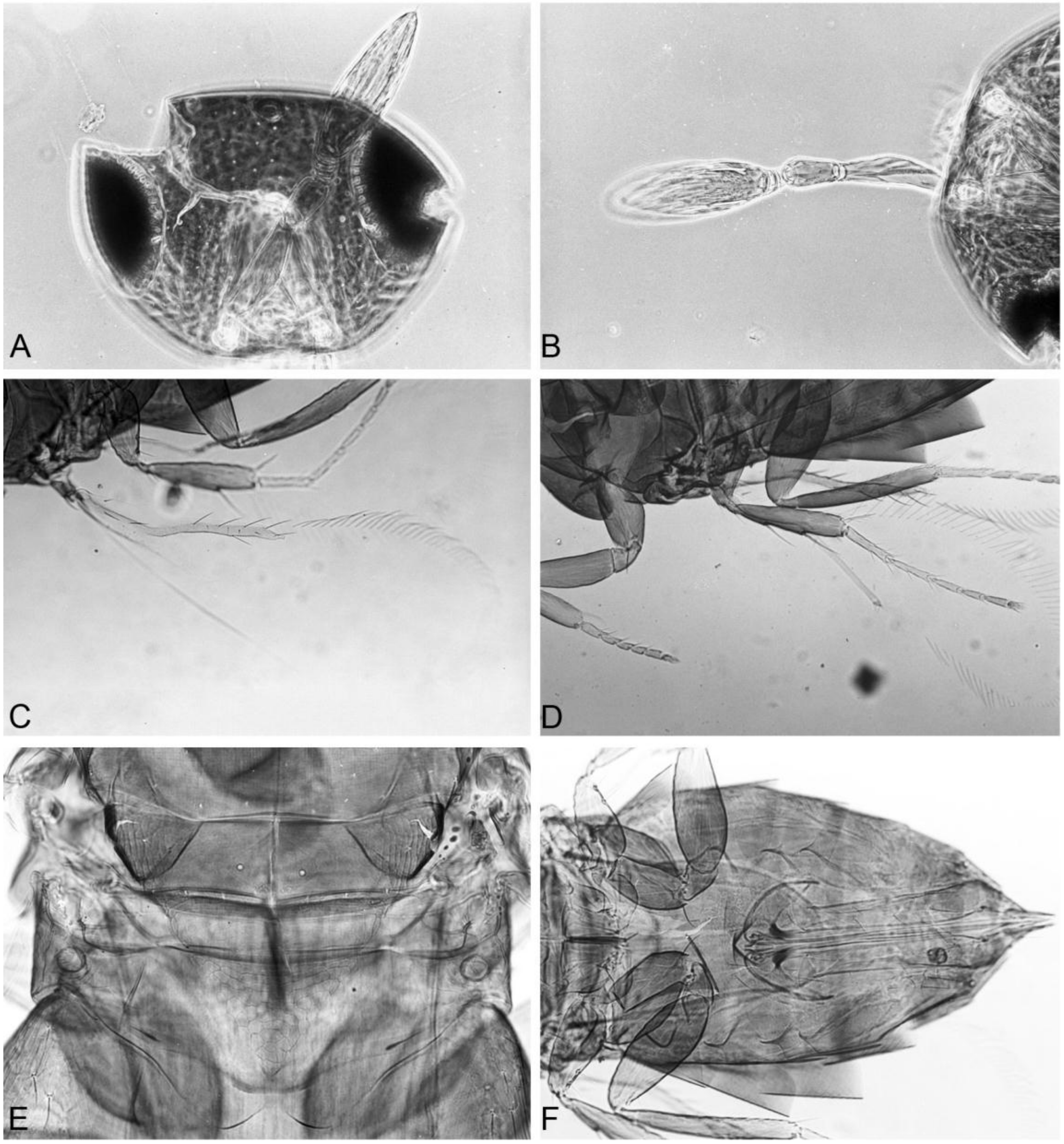


Figure 40. *Chartocerus ruskini* (Girault), holotype. A, head; B, fore wing; C, habitus; D, dissected propodeum.

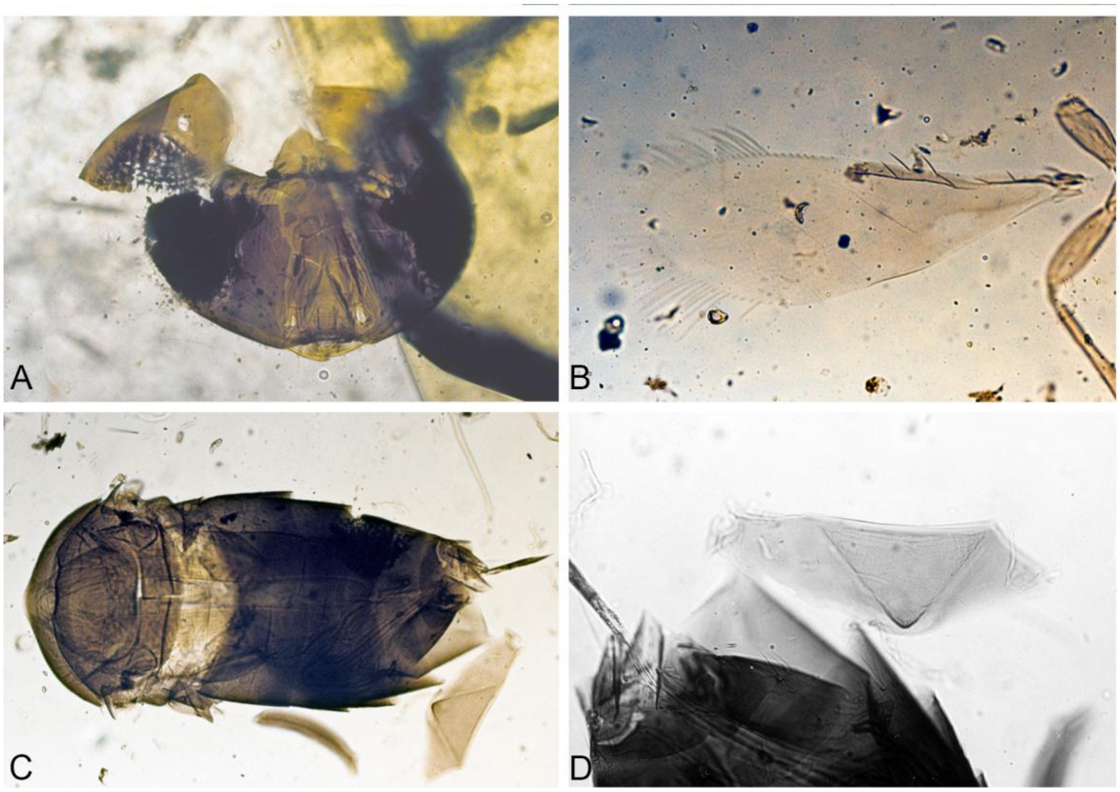
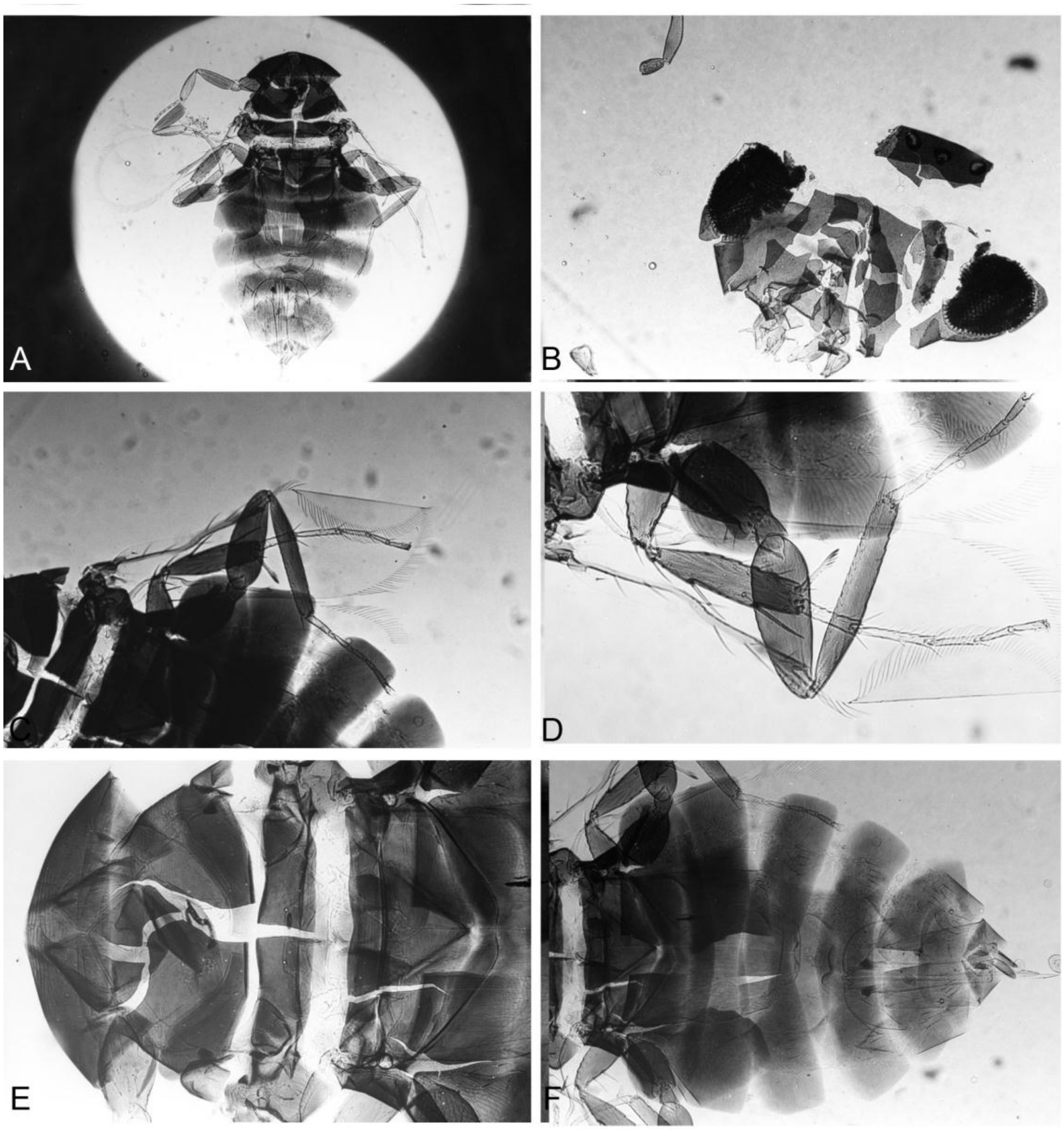


Figure 41. *Chartocerus thusanoides* (Girault), holotype. A, habitus; B, head, C; fore wing vein; D, midleg and hind leg; E, mesosoma; F, metasoma.



APPENDIX F

SOURCE LINKS AND ASSOCIATIONS

Search Term	Rank	Host	Url	Title
related:biodiversitylibrary.org	0	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:biodiversitylibrary.org	1	botanicus.org	http://www.botanicus.org	Botanicus.org - a freely accessible, Web-based encyclopedia of
related:biodiversitylibrary.org	2	bhl-europe.eu	http://www.bhl-europe.eu	BHL-Europe Portal
related:biodiversitylibrary.org	3	biodivlib.wikispaces.com	http://biodivlib.wikispaces.com	Biodiversity Heritage Library - About
related:biodiversitylibrary.org	4	en.wikipedia.org	http://en.wikipedia.org/wiki/biodiversity_heritage_library	Biodiversity Heritage Library - Wikipedia, the free encyclopedia
related:biodiversitylibrary.org	5	archive.org	https://archive.org/details/biodiversity	Biodiversity Heritage Library : Free Books : Free Texts : Download
related:biodiversitylibrary.org	6	digitallibrary.amnh.org	http://digitallibrary.amnh.org	AMNH DSpace Digital Repository - American Museum of Natural
related:biodiversitylibrary.org	7	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:biodiversitylibrary.org	8	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:biodiversitylibrary.org	9	tropicos.org	http://www.tropicos.org	Tropicos - Home
related:biodiversitylibrary.org	10	iapt-taxon.org	http://www.iapt-taxon.org	IAPT
related:biodiversitylibrary.org	11	zoobank.org	http://zoobank.org	ZooBank
related:biodiversitylibrary.org	12	ubio.org	http://www.ubio.org	uBio Home
related:biodiversitylibrary.org	13	theguardian.com	http://www.theguardian.com/environment/biodiversity	Biodiversity | Environment | The Guardian
related:biodiversitylibrary.org	14	flickr.com	https://www.flickr.com/photos/biodivlibrary/sets	BioDivLibrary's albums on Flickr
related:catalogueoflife.org	0	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:catalogueoflife.org	1	sp2000.org	http://www.sp2000.org	Species 2000 - Welcome to Species 2000 website
related:catalogueoflife.org	2	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:catalogueoflife.org	3	en.wikipedia.org	http://en.wikipedia.org/wiki/catalogue_of_life	Catalogue of Life - Wikipedia
related:catalogueoflife.org	4	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:catalogueoflife.org	5	marinespecies.org	http://www.marinespecies.org	World Register of Marine Species: WoRMS
related:catalogueoflife.org	6	iucnredlist.org	http://www.iucnredlist.org	The IUCN Red List of Threatened Species
related:catalogueoflife.org	7	ubio.org	http://www.ubio.org	uBio Home
related:catalogueoflife.org	8	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:catalogueoflife.org	9	amphibiaweb.org	http://amphibiaweb.org	AmphibiaWeb
related:catalogueoflife.org	10	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:catalogueoflife.org	11	lifedesks.org	http://www.lifedesks.org	LifeDesks
related:catalogueoflife.org	12	zipcodezoo.com	http://zipcodezoo.com	Welcome to ZipcodeZoo
related:catalogueoflife.org	13	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:catalogueoflife.org	14	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:discoverlife.org	1	discoverlife.org	http://www.discoverlife.org	Discover Life
related:discoverlife.org	2	discoverlife.org	http://www.discoverlife.org/mp/20q	IDnature guides - Discover Life
related:discoverlife.org	3	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dcaterpillars	Caterpillars -- identification guide -- Discover Life
related:discoverlife.org	4	discoverlife.org	http://www.discoverlife.org/mp/20q%3fsearch%3dapoidea	Apoidea - Bees, Apoid Wasps -- Discover Life
related:discoverlife.org	5	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dbutterflies	Butterflies -- identification guide -- Discover Life
related:discoverlife.org	6	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dapoidea_species	Apoidea species -- identification guide -- Discover Life
related:discoverlife.org	7	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dbumblebees	Bumblebees -- identification guide -- Discover Life
related:discoverlife.org	8	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dinsect_orders	Insect orders -- identification guide -- Discover Life
related:discoverlife.org	9	discoverlife.org	http://www.discoverlife.org/cricket/dc	Discover Life--DC/Baltimore Cricket Crawl
related:discoverlife.org	10	discoverlife.org	http://www.discoverlife.org/moth	Overview, Mothing -- Discover Life
related:discoverlife.org	11	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dwildflowers	Wildflowers -- identification guide -- Discover Life
related:discoverlife.org	12	discoverlife.org	http://www.discoverlife.org/mp/20m%3fact%3dmake_map	Global Mapper -- Discover Life
related:discoverlife.org	13	discoverlife.org	http://www.discoverlife.org/nh/tx/insecta	Insecta - Insects, Entognatha, Hexapods, Hexapoda -- Discover Life

Search Term	Rank	Host	Url	Title
related:discoverlife.org	14	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dtrees	Trees -- identification guide -- Discover Life
related:discoverlife.org	15	discoverlife.org	http://www.discoverlife.org/nh/id/20q/20q_help.html	Help -- Discover Life
related:discoverlife.org	16	discoverlife.org	http://www.discoverlife.org/mp/20q%3fguide%3dturtles	Turtles -- identification guide -- Discover Life
related:eol.org	0	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:eol.org	1	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:eol.org	2	a-z-animals.com	http://a-z-animals.com	A-Z Animals - Animal Facts, Information, Pictures, Videos
related:eol.org	3	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:eol.org	4	eoearth.org	http://www.eoearth.org	Encyclopedia of Earth
related:eol.org	5	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:eol.org	6	ubio.org	http://www.ubio.org	uBio Home
related:eol.org	7	inaturalist.org	http://www.inaturalist.org	iNaturalist.org · A Community for Naturalists
related:eol.org	8	amazon.com	http://www.amazon.com/national-geographic-animal-encyclopedia-animals/dp/1426310226	National Geographic Animal Encyclopedia: 2, 500 Animals with
related:eol.org	9	discoverlife.org	http://www.discoverlife.org	Discover Life
related:eol.org	10	botanicus.org	http://www.botanicus.org	Botanicus.org - a freely accessible, Web-based encyclopedia of
related:eol.org	11	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:eol.org	12	idigbio.org	https://www.idigbio.org	iDigBio Home | iDigBio
related:eol.org	13	en.wikipedia.org	http://en.wikipedia.org/wiki/encyclopedia_of_life	Encyclopedia of Life - Wikipedia
related:eol.org	14	marinespecies.org	http://www.marinespecies.org	World Register of Marine Species: WoRMS
related:eol.org	15	britannica.com	http://www.britannica.com	Encyclopedia Britannica
related:eol.org	16	coml.org	http://www.coml.org	A Decade of Discovery
related:flickr.com/photos/biodivlibrary/sets	0	flickr.com	https://www.flickr.com/photos/biodivlibrary/sets	BioDivLibrary's albums on Flickr
related:flickr.com/photos/biodivlibrary/sets	1	smugmug.com	http://www.smugmug.com	SmugMug: Photo Sharing. Stunning Photo Websites.
related:flickr.com/photos/biodivlibrary/sets	2	youtube.com	http://www.youtube.com	YouTube
related:flickr.com/photos/biodivlibrary/sets	3	myspace.com	https://myspace.com	Featured Content on Myspace
related:flickr.com/photos/biodivlibrary/sets	4	twitter.com	https://twitter.com	Twitter
related:flickr.com/photos/biodivlibrary/sets	5	linkedin.com	https://www.linkedin.com	LinkedIn: World's Largest Professional Network
related:flickr.com/photos/biodivlibrary/sets	6	facebook.com	https://www.facebook.com	Welcome to Facebook - Log In, Sign Up or Learn More
related:flickr.com/photos/biodivlibrary/sets	7	stumbleupon.com	https://www.stumbleupon.com	StumbleUpon.com: Explore more. Web pages, photos, and videos
related:flickr.com/photos/biodivlibrary/sets	8	last.fm	http://www.last.fm	Last.fm - Listen to free music and watch videos with the largest
related:flickr.com/photos/biodivlibrary/sets	9	pinterest.com	https://www.pinterest.com	Pinterest
related:flickr.com/photos/biodivlibrary/sets	10	ning.com	http://www.ning.com	Ning.com: Build and cultivate your own community
related:flickr.com/photos/biodivlibrary/sets	11	photobucket.com	http://photobucket.com	Photo and image hosting, free photo galleries, photo editing
related:flickr.com/photos/biodivlibrary/sets	12	tagged.com	http://www.tagged.com	Tagged
related:flickr.com/photos/biodivlibrary/sets	13	mog.com	http://mog.com	MOG
related:gbif.org	0	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:gbif.org	1	en.wikipedia.org	http://en.wikipedia.org/wiki/global_biodiversity_information_facility	Global Biodiversity Information Facility - Wikipedia, the free
related:gbif.org	2	herpnet.org	http://www.herpnet.org	HerpNET
related:gbif.org	3	tools.gbif.org	http://tools.gbif.org	GBIF Tools
related:gbif.org	4	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:gbif.org	5	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:gbif.org	6	ubio.org	http://www.ubio.org	uBio Home
related:gbif.org	7	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:gbif.org	8	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:gbif.org	9	faunaeur.org	http://www.faunaeur.org	Fauna Europaea : Name Search
related:gbif.org	10	diversitas-international.org	http://www.diversitas-international.org	Welcome — DIVERSITAS
related:gbif.org	11	nlbif.nl	http://www.nlbif.nl	NLBIF.nl | Netherlands Biodiversity Information Facility
related:gbif.org	12	ecoinformatics.org	http://www.ecoinformatics.org	ecoinformatics.org :: home page
related:gbif.org	13	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:gbif.org	14	botanicus.org	http://www.botanicus.org	Botanicus.org - a freely accessible, Web-based encyclopedia of

Search Term	Rank	Host	Url	Title
related:gbif.org	15	epbrs.org	http://www.epbrs.org	EPBRS ›› home
related:gbif.org	16	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:idigbio.org	0	idigbio.org	https://www.idigbio.org	iDigBio Home | iDigBio
related:idigbio.org	1	amnh.org	http://www.amnh.org	American Museum of Natural History
related:idigbio.org	2	nhm.org	http://www.nhm.org	Natural History Museum of Los Angeles
related:idigbio.org	3	nhm.ac.uk	http://www.nhm.ac.uk	Natural History Museum
related:idigbio.org	4	sdnhm.org	http://www.sdnhm.org	theNAT :: San Diego Natural History Museum :: Your Nature
related:idigbio.org	5	vmnh.net	http://www.vmnh.net	Virginia Museum of Natural History: Home
related:idigbio.org	6	carnegiemnh.org	http://www.carnegiemnh.org	Carnegie Museum of Natural History
related:idigbio.org	7	spnhc.org	http://www.spnhc.org	The Society for the Preservation of Natural History Collections | Home
related:idigbio.org	8	delmnh.org	http://www.delmnh.org	Delaware Museum of Natural History
related:idigbio.org	9	brazosvalleymuseum.org	http://www.brazosvalleymuseum.org	Brazos Valley Museum of Natural History
related:idigbio.org	10	pgmuseum.org	http://www.pgmuseum.org	Pacific Grove Museum of Natural History
related:idigbio.org	11	tallahasseemuseum.org	http://tallahasseemuseum.org	Welcome to the Tallahassee Museum : Tallahassee Museum
related:idigbio.org	12	nasmus.co.za	http://www.nasmus.co.za	National Museum, Bloemfontein
related:idigbio.org	13	nmnh.nic.in	http://www.nmnh.nic.in	Homepage of National Museum of Natural History, Government of
related:idigbio.org	14	nmnhs.com	http://www.nmnhs.com	National Museum of Natural History, Sofia (NMNHS)
related:idigbio.org	15	nmnh.nic.in	http://www.nmnh.nic.in/home.html	Homepage of National Museum of Natural History, Government of
related:idigbio.org	16	si.edu	http://www.si.edu	Smithsonian
related:itis.gov	0	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:itis.gov	1	en.wikipedia.org	http://en.wikipedia.org/wiki/integrated_taxonomic_information_system	Integrated Taxonomic Information System - Wikipedia, the free
related:itis.gov	2	marinespecies.org	http://www.marinespecies.org	World Register of Marine Species: WoRMS
related:itis.gov	3	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:itis.gov	4	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:itis.gov	5	ubio.org	http://www.ubio.org	uBio Home
related:itis.gov	6	uniprot.org	http://www.uniprot.org/taxonomy	* in Taxonomy - UniProt
related:itis.gov	7	ars-grin.gov	http://www.ars-grin.gov	GRIN National Genetic Resources Program
related:itis.gov	8	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:itis.gov	9	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:itis.gov	10	iucnredlist.org	http://www.iucnredlist.org	The IUCN Red List of Threatened Species
related:itis.gov	11	arkive.org	http://www.arkive.org	ARKive - Discover the world's most endangered species
related:itis.gov	12	discoverlife.org	http://www.discoverlife.org	Discover Life
related:itis.gov	13	zipcodezoo.com	http://zipcodezoo.com	Welcome to ZipcodeZoo
related:itis.gov	14	marbef.org	http://www.marbef.org	MarBEF
related:itis.gov	15	organismnames.com	http://www.organismnames.com	Index to Organism Names: ION
related:itis.gov	16	ncbi.nlm.nih.gov	http://www.ncbi.nlm.nih.gov/taxonomy/taxonomyhome.html/index.cgi%3fchapter%3dresources	NCBI Taxonomy resources - National Center for Biotechnology
related:tdwg.org	0	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:tdwg.org	1	opengeospatial.org	http://www.opengeospatial.org	Open Geospatial Consortium | OGC
related:tdwg.org	2	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:tdwg.org	3	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:tdwg.org	4	ubio.org	http://www.ubio.org	uBio Home
related:tdwg.org	5	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:tdwg.org	6	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:tdwg.org	7	digir.net	http://www.digir.net	The Role of Air Purifiers in Your Home | DIGIR
related:tdwg.org	8	discoverlife.org	http://www.discoverlife.org	Discover Life
related:tdwg.org	9	nscalliance.org	http://www.nscalliance.org	Natural Science Collections Alliance
related:tdwg.org	10	pacificbio.org	http://www.pacificbio.org	Home of Pacific Biodiversity Institute
related:tdwg.org	11	e-taxonomy.eu	http://www.e-taxonomy.eu	EDIT | - European Distributed Institute of Taxonomy -
related:tdwg.org	12	biogeomancer.org	http://www.biogeomancer.org	BioGeomancer
related:ubio.org	0	ubio.org	http://www.ubio.org	uBio Home
related:ubio.org	1	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:ubio.org	2	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:ubio.org	3	marinespecies.org	http://www.marinespecies.org	World Register of Marine Species: WoRMS
related:ubio.org	4	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:ubio.org	5	iucnredlist.org	http://www.iucnredlist.org	The IUCN Red List of Threatened Species
related:ubio.org	6	tdwg.org	http://www.tdwg.org	TDWG: Homepage
related:ubio.org	7	delta-intkey.com	http://delta-intkey.com	DELTA - DEscription Language for TAxonomy

Search Term	Rank	Host	Url	Title
related:ubio.org	8	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:ubio.org	9	virtualherbarium.org	http://www.virtualherbarium.org	The FTG Virtual Herbarium
related:ubio.org	10	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:ubio.org	11	plantsystematics.org	http://www.plantsystematics.org	PlantSystematics.org
related:ubio.org	12	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:www.eol.org	0	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:www.eol.org	1	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:www.eol.org	2	a-z-animals.com	http://a-z-animals.com	A-Z Animals - Animal Facts, Information, Pictures, Videos
related:www.eol.org	3	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:www.eol.org	4	eoearth.org	http://www.eoearth.org	Encyclopedia of Earth
related:www.eol.org	5	itis.gov	http://www.itis.gov	Integrated Taxonomic Information System
related:www.eol.org	6	ubio.org	http://www.ubio.org	uBio Home
related:www.eol.org	7	inaturalist.org	http://www.inaturalist.org	iNaturalist.org · A Community for Naturalists
related:www.eol.org	8	amazon.com	http://www.amazon.com/national-geographic-animal-encyclopedia-animals/dp/1426310226	National Geographic Animal Encyclopedia: 2, 500 Animals with
related:www.eol.org	9	discoverlife.org	http://www.discoverlife.org	Discover Life
related:www.eol.org	10	botanicus.org	http://www.botanicus.org	Botanicus.org - a freely accessible, Web-based encyclopedia of
related:www.eol.org	11	tolweb.org	http://tolweb.org	Tree of Life Web Project
related:www.eol.org	12	idigbio.org	https://www.idigbio.org	iDigBio Home | iDigBio
related:www.eol.org	13	en.wikipedia.org	http://en.wikipedia.org/wiki/encyclopedia_of_life	Encyclopedia of Life - Wikipedia
related:www.eol.org	14	marinespecies.org	http://www.marinespecies.org	World Register of Marine Species: WoRMS
related:www.eol.org	15	britannica.com	http://www.britannica.com	Encyclopedia Britannica
related:www.eol.org	16	coml.org	http://www.coml.org	A Decade of Discovery
related:zoobank.org	0	zoobank.org	http://zoobank.org	ZooBank
related:zoobank.org	1	en.wikipedia.org	http://en.wikipedia.org/wiki/zoobank	ZooBank - Wikipedia
related:zoobank.org	2	eol.org	http://eol.org	Encyclopedia of Life - Animals - Plants - Pictures & Information
related:zoobank.org	3	biodiversitylibrary.org	http://www.biodiversitylibrary.org	Biodiversity Heritage Library
related:zoobank.org	4	mycobank.org	http://www.mycobank.org	MycoBank in English
related:zoobank.org	5	treebase.org	http://www.treebase.org	TreeBASE Web
related:zoobank.org	6	ipni.org	http://www.ipni.org	The International Plant Names Index - home page
related:zoobank.org	7	catalogueoflife.org	http://www.catalogueoflife.org	Catalogue of Life: Home
related:zoobank.org	8	gbif.org	http://www.gbif.org	Free and Open Access to Biodiversity Data | GBIF.ORG
related:zoobank.org	9	indexfungorum.org	http://www.indexfungorum.org	Index Fungorum Home Page
related:zoobank.org	10	faunaeur.org	http://www.faunaeur.org	Fauna Europaea : Name Search

APPENDIX G

LABORATORY PROTOCOLS FROM CHAPTER III

DNA extraction

Chelex: method optimized by the Heraty lab (available upon request).

Qiagen protocol (DNA Blood and Tissue kit), modified in collaboration with K. Menard:

All material (especially tubes) used should be exposed to UV in hood before being used. Specimen can be used *whole*. Measurements of extractions with and without destruction of specimens did not show significant difference in the amount of DNA obtained.
-If insects are stored in freezer, let samples defreeze to room temperature.
-Transfer specimen to 90µL buffer ATL + 10µL new proteinase K = 100µL (1/2 regular protocol)
-Incubate at 56°C overnight (minimum of 8h)
-Carefully remove all fluid and transfer to a new tube. Remove the specimen and wash it in distilled water for 30 minutes before storing it back in alcohol or proceeding to card- or slide-mounting.
-Vortex the DNA samples, add 100µL buffer AL
-Vortex, 100µL ethanol 100%tu
-Transfer to mini spin column in collection tube, centrifuge at 8000rpm/1min, discard flow
-Place spin column in new collection tube, add 500µL buffer AW1, centrifuge at 8000rpm/1min, then discard flow
-Place spin column in new collection tube, add 500µL buffer AW2, centrifuge at 14,000rpm/3min (or maximum possible), discard flow
-Transfer spin to a microcentrifuge tube, add 100µL buffer AE, incubate at room temp, centrifuge (don't repeat as the Quiagen protocol suggests – makes DNA too diluted)

PCR reactions

Most reactions were performed using 3µL of DNA extract. The proportions of reagents are given in the table below, as optimized by Heraty lab. The Q-solution®, available from the Qiagen Taq kit, is used to improve amplification of "difficult" or GC-rich DNA; it was substituted by distilled water for AT-rich (mtDNA) DNA. Primers as indicated in text (Chapter III).

Reagent	5 reactions	8 reactions	12 reactions	24 reactions
D-water	46	73	111	222
Q-solution	20	32	48	96
buffer	10	16	24	48
dNTP's	2	3.2	4.8	9.6
Primer 1	2.5	4	6	12
Primer 2	2.5	4	6	12
Taq	1	2	3	5

PCR programs:

“COI 48”
(MJResearch/Genomyx cycleLR thermal cycler, used for most reactions for rDNA and COI)
1. 3 min @ 93°C
2. 0:15 @ 93°C
3. 0:45 @ 46°C
4. 0:45 @ 68°C
5. repeat 34 times the steps 2-4
6. 7 min @68°C
7. “ice bucket” mode (4°C ∝)

“COI 50” (used for some rDNA reactions)
1. 5 min @95°C
2. 0:30 @94°C
3. 1 min @50°C
4. 1:30min @72°C
5. repeat 34 times steps 2-4
6. 10 min @72°C
7. “ice bucket” mode (4°C ∝)

“Guelph4”
1. 1 min @ 94°C
2. 0:30 @ 94°C
3. 1:30 @ 45°C
4. 1 min @ 70°C
5. repeat 5 times steps 2-4
6. 0:30 @ 94°C
7. 1:30 @ 48°C
8. 1:30 @ 70°C
9. repeat 35 times steps 6-8
10. 7 min @ 68°C
11. “ice bucket” mode (4°C ∝)

ArgK (program #103 used at Johnston’s lab, also worked for 28S-D2)
1. 5 min @ 94°C
2. 0:30 @ 94°C
3. 0:30 @ 48°C
4. 0:45 @ 72°C
5. repeat 30 times steps 2-4
6. 7 min @ 72°C
7. “ice bucket” mode (4°C ∝)

EF1-alpha (Cruaud *et al.* 2011):

1. 3 min @ 94°C
2. 0:30 @ 94°C
3. 1 min @ 58°C
4. 1 min @ 72°C
5. repeat 35 times steps 2-4
6. 10 min @ 72°C
7. “ice bucket” mode (4°C ∝)

Gel Electrophoresis using SybrSafe (alternative to Ethidium Bromide)

The amount of loading dye and product may vary according to the size of the combs and how much product must be available. Generally used 2µL master mix + 4µL product.

Option A: Make a master mix:
-For N samples, add to a sterile eppendorf, 3*N µL loading dye (blue). Remember to include blank.
-Add SybrSafe = 10% of total dye (e.g. 10% of 3*N µL). For example, for 24 PCR reaction products, add 72µL of loading dye and 7.2µL of SybrSafe.
-Add each PCR reaction product to its respective drop.

Option B: Make each droplet with 3µL loading dye and 1µL SybrSafe, then add the PCR product.
Option C: dissolve 1:10000X in agarose. For example, if gel is made of 100mL agarose in buffer, add 10µL of SybrSafe

Run gel approximately 15 minutes at 104V.
Store the PCR product at -20°C.

DNA product purification (GeneClean kit)

Protocol from Heraty Lab, original by David Hawks and Roger Burks. Gene cleaning is ideally done after sufficient samples to submit a plate (48) have been accumulated. Times in bold were modified by Jason Mottern. Sterilize all tubes in UV prior to use.

- Allow frozen PCR products to thaw:"ice bucket" mode in thermal-cycler or keep in fridge at 4°C.

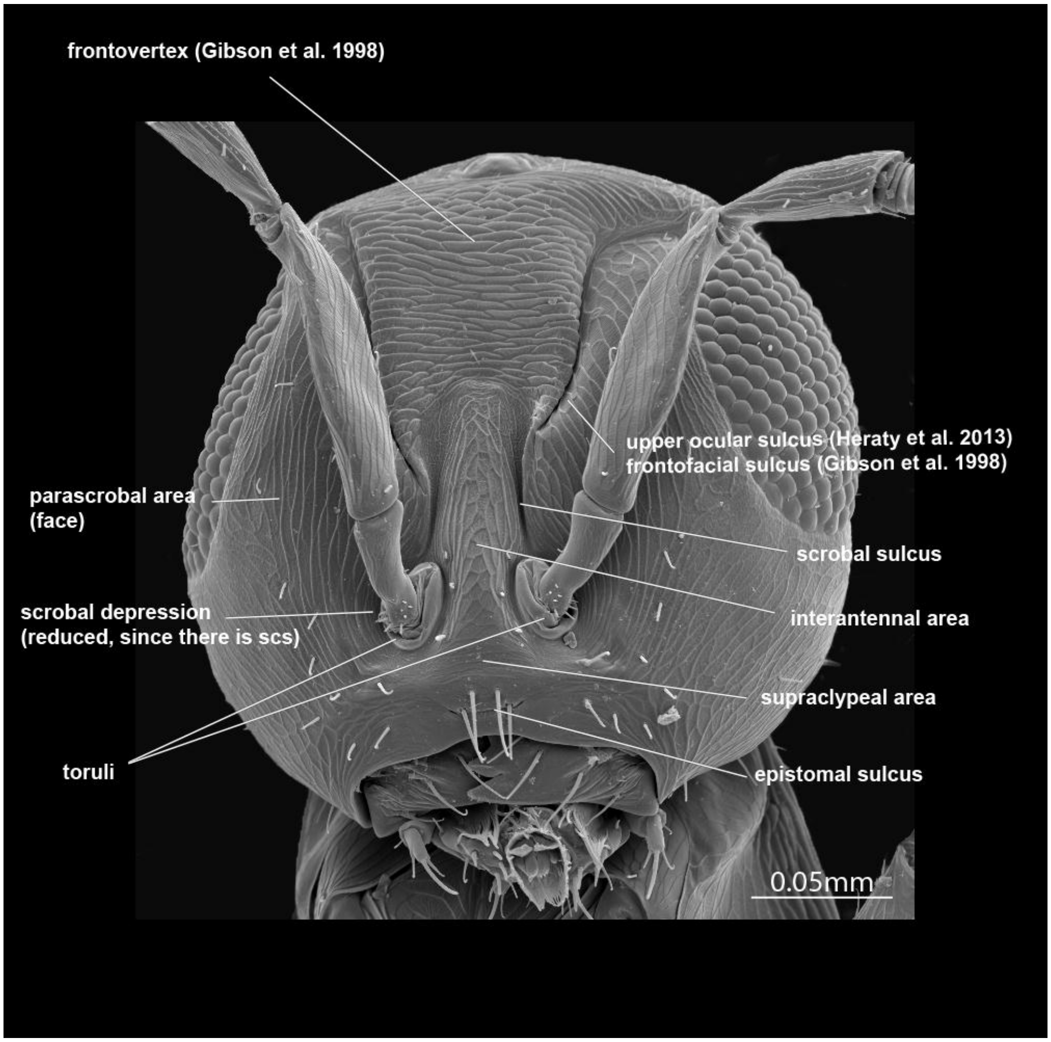
Add to each eppendorf tube:
- All PCR product: usually 16-18µL unless combined for enhancement of results, or reduced due to repeated gel runs. Discard PCR strips after transfer.
- NaI: 50µL
- Glassmilk®: 5µL. Shake and vortex vigorously the vial frequently to keep the glassmilk in suspension.
- Let Glassmilk® bind the DNA: Shake the set of vials (e.g. once per minute for 5 minutes.)
- Centrifuge vials for 30 seconds (**3 mins**) at top speed.
- Gently pour off supernatant (without dislodging pellet).
- Add 500µL "New Wash" to each epp vial. Close caps and vortex to resuspend the pellet. Alternately vortex and sharply shake vial twice to dissolve the pellet.
- Centrifuge for 1 minute (**3 minutes at top speed**)
- Discard supernatant, again without dislodging the pellet. Wick each vial upside down on a Kimwipe after pouring off supernatant to make sure all the liquid is removed. Re-centrifuge for about 30sec if it looks like the pellet dissolved.
- Centrifuge vials for 1 minute (**3 minutes**). Remove as much supernatant as possible.
- Leave vials open and allow the pellet to dry in protected, clean, covered area.
- The dry samples can be stored in freezer and should be resuspended when the plate is being prepared for sequencing.

Resuspending the clean DNA:
-Add 24µL distilled H2O to each cleaned and dried product.
-Vortex briefly to re-suspend Glassmilk®.
-Centrifuge for 1 minute at top speed. The silica pellet will accumulate at the bottom and DNA will be suspended in water.
-Move the solution into the plate lanes carefully so as to not resuspend Glassmilk® pellet.

APPENDIX H

TERMINOLOGY

Head of *Thysanus ater* under SEM, with labels indicating terminology used in this text (Chapter IV):



APPENDIX I

KEYS FOR THE IDENTIFICATION OF SPECIES OF *Clytina* AND *Thysanus*

Key to species of *Clytina*

1. Body uniformly dark, antennae short (antennal clava not longer than 1.5x the scape and about ½ of the head height), scrobal impression inconspicuous, eyes glabrous, small (less than ½ head height), surface sculpture in mesosoma faint, reticulate, setae in pronotum short, delicate, randomly distributed (Appendix D: Figure 6E), seta M1 present in forewing…………………………………………………………………………………………… *Clytina giraudi*

1'. Body light brown with head and antennal clava dark brown, antennae, antennal scrobes impressed and well defined in face, eyes pilose, about ½ head height, surface sculpture in mesosoma conspicuous, reticulate in pronotum and striate to reticulate in mesoscutum, setae in pronotum long, thick, more or less uniformly distributed (Appendix D: Figure 7E), seta M1 absent in forewing………………………………*Clytina* n.sp.1

Key to species of *Thysanus*[7]

1. Head conspicuously wider than tall (Appendix D: Figure 14B, 15B), antennae short, with clava with the same length as head height or little longer, clava and scape each not more than 6x as long as wide, antennal scrobes separate along their entire length or, if merging dorsally, there is no difference in sclerotization or sculpture compared to surrounding head plates, ovipositor projecting beyond metasoma.................................2

1’ Head approximately round, antennae long, with clava at least 1.5x head height, clava more than 6x as long as wide, antennal scrobes merging dorsally, at least the upper part of the interantennal area less sclerotized and with different sculpture compared to surrounding head plates, ovipositor not conspicuously projecting beyond metasoma......3

2 Body light brown, clypeus and distal articles of antennae (pedicel, annelli, clava) darker, genae projecting ventrally beyond clypeus (Appendix D: Figure 15A), frontovertex white interrupted by a transverse v-shaped brown band (Appendix D: Figure 15A), sculpture in propodeum faint to smooth, first metasomal tergite (Mt1) conspicuously bilobed with a concave round “bridge” between lobes (Appendix D: figure 15E).........*Thysanus* n.sp.5

2’ Body uniformly brown except for small patches next to eyes and sulci in head, clypeus and ventral margins of genae aligned ventrally, frontovertex not as above, first metasomal tergite (Mt1) transverse or, if bilobed, the lobes broadly round and linked by a transverse “bridge” (Appendix D: Figure 14E)....................................*Thysanus* n.sp.3

3 First metasomal tergite (Mt1) transverse or, if bilobed, the lobes are broadly rounded and not well separated (e.g. Appendix D: Figure 12E)..4

3’ First metasomal tergite bilobed, the two lobes separated by a concave or transverse “bridge” (e.g. Appendix D: Figure 9E)...5

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[7] This key is available online at http://mx.speciesfile.org/projects/76/clave/show/1698 (Woolley lab/PEET members only: it’s not public)

4 Antennae elongated, all articles more or less with the same width, the pedicel more than 2x as long as wide, body predominantly dark brown, a conspicuous white band at the posterior margin of the pronotum, legs predominantly dark, 6 or more thick setae in posterior margin of scutellum, 1 or 2 lines of thick setae along outer plates of ovipositor…………………………………………………………………………*Thysanus melancholicus*

4' Antennae not as above, the pedicel conspicuously wider than basal annelli and less than 2x as long as wide, body brown, the mesoscutum, scutellum and metanotum lighter than the rest of the body, legs predominantly light tan to white, setae in posterior margin of scutellum delicate, usually 4, outer plates of ovipositor with few, delicate setae………………………………………………………………………………………………*Thysanus rusti*

5 Seta M1 of forewing present, legs all brown, or at most tarsi light brown to yellowish, posterior margin of the propodeal plate transverse or medially concave……………………….6

5' Seta M1 of forewing absent, legs often with areas surrounding articulations between femur-tibia and tibia-tarsi yellowish to white, posterior margin of the propodeal plate medially convex, projecting posteriorly along with the medial triangle ……………………….7

6 Anterior margin of mesoscutum transverse to very broadly curved, not medially projected forward, axillae conspicuously projected anteriorly relative to the scutellum (Appendix D: Figure 11E), when 2 sensilla placoidea are present, they are about equally distant from the lateral margins of scutellum than from each other, antennal scape and clava not conspicuously enlarged in males………………………………………*Thysanus nigrellus*

6' Anterior margin of mesoscutum medially projected forward, or, if not projected, conspicuously curved, axillae aligned with the anterior margin of the scutellum, sensilla placoidea much closer to each other than to the lateral margins of the scutellum, male with antennal scape and clava enlarged (Appendix D: Figure 13B)………*Thysanus* n.sp.2

7 Antennal scrobes very narrow, often reduced to sulci, frontovertex less sclerotized and with distinct sculpture than the rest of the head, longitudinally striate, 1 submarginal seta in forewing, pronotum uniformly brown, setae along outer plates , if conspicuous, fine and delicate...*Thysanus ater*

7' Antennal scrobes depressed, not significantly narrowed, only upper face above interantennal area less sclerotized and longitudinally striate, vertex reticulate, 2 submarginal setae in forewing, pronotum with white patches in lateral-posterior margin, setae along outer plates short and stout..*Thysanus* n.sp.6

APPENDIX J

LABEL AND LOCALITY INFORMATION

(see next page)

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Clytina giraudi	TAMU-ENTO X0424811	ZIS	46.98373	19.132363	Hungary || 50 km S. Budapest || Ex. galls of || Lipara lucens || On: Phragmites ++ communis || iii-iv.1972 || E.P.Narchuk || 1972/001
Clytina giraudi	TAMU-ENTO X0424812	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424813	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424814	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424815	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424816	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424817	TAMU	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0424818	TAMU	55.6	12.55	DENMARK: Nez || Amajer || Kalvebod Falled ++ 09.v.2004 || L.Krogmann || TAMU 2004/007
Clytina giraudi	TAMU-ENTO X0424819	TAMU	47	28.916667	Moldavia || Kishinev || 15.ii.71 Kiauka
Clytina giraudi	TAMU-ENTO X0852617	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852618	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852619	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852620	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852621	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852622	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852623	ZIS	41.278993	69.220619	Keles, Tashkent || Oblast || Soviet Central Asia || Ex. Pupa Haplegis nigritarsis Duda || on: Phagmites communis || Coll. I. Rozanov || 28.VIII.1950
Clytina giraudi	TAMU-ENTO X0852625	ZIS	46.98373	19.132363	Hungary, 50km || South Budapest || Ex. galls of || Lipara lucens || on Phragmites || communis collected || III, emerged IV, 1972 || E. P. Narchuk
Clytina giraudi	TAMU-ENTO X0852630	ZIS	46.98373	19.132363	Hungary, 50km || South Budapest || Ex. galls of || Lipara lucens || on Phragmites || communis collected || III, emerged IV, 1972 || E. P. Narchuk
Clytina giraudi	TAMU-ENTO X0852631	TAMU	47	28.916667	Moldavia || Kishinev || 15.ii.71 Kiauka || From Haplegis || tarsata
Clytina giraudi	TAMU-ENTO X0855073	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855074	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855075	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855076	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Clytina giraudi	TAMU-ENTO X0855077	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855078	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855079	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855080	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855081	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855082	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855083	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855084	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855085	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855086	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855087	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855088	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855089	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	TAMU-ENTO X0855090	ZIS	41.278993	69.220619	Uzbekistan || Tashkent Oblast || Ex. Phragmites ++ communis 1960/001 || 28.viii.1960 || coll. I.Rozanov
Clytina giraudi	USNM 763271	USNM	44.1383	4.8097	Orange, Fr[ance] || May 8, 1852 || Sapr. Diptera || Coll. H.L. Parker ++ 52-8556 || #5350-3-Chloropidae
Clytina giraudi	USNM ZIL_42	USNM	46.98373	19.132363	Hungary, 50km || South Budapest || Ex. galls of || Lipara lucens || on Phragmites || communis collected || III, emerged IV, 1972 || E. P. Narchuk
Clytina n. sp. 1	BMNH(E) #990995	BMNH	10.847198	-85.619431	[Costa Rica] Est. Pitilla (ACG), 4-9.2.2001, C. Moraga & P. N. Thomas
Clytina n. sp. 1	CNCHYMEN 122495	CNC	-0.5	-76.5	[Ecuador] Rio Napo, Sacha Lodge, MT, 22.2-4.3.1994, P. Hibbs
Clytina n. sp. 1	CNCHYMEN 122496	CNC	15.670809	-88.633919	[Guatemala] Las Escobas, 8km SW Puerto Barrios, sifted bark and bracket fungi on log, 12-14.11.1986, M. Sharkey
Clytina n. sp. 1	CNCHYMEN 122497	CNC	15.670809	-88.633919	[Guatemala] Las Escobas, 8km SW Puerto Barrios, sifted bark and bracket fungi on log, 12-14.11.1986, M. Sharkey
Clytina n. sp. 1	CNCHYMEN 122498	CNC	15.670809	-88.633919	[Guatemala] Las Escobas, 8km SW Puerto Barrios, sifted bark and bracket fungi on log, 12-14.11.1986, M. Sharkey
Clytina n. sp. 1	CNCHYMEN 122499	CNC	3.816667	-70.616667	[Colombia] Siete Agosto Environs, YPT, 3-4.3.2009, P. Jansta
Clytina n. sp. 1	CNCHYMEN 122500	CNC	10.509612	-61.269191	[Trinidad & Tobago] Quesnell Farm, 13km S Talparo, rainforest FIT, 22.4-8.7.1993, S. & J. Peck
Clytina n. sp. 1	CNCHYMEN 122501	CNC	10.3494	-67.6856	VENEZUELA: Aragua, Parque Nac. H. Pittier: Rancho Grande, env. 10-14.iv.1994, L. Masner, S.S. & P.T., 10.3494 N, 67.6856 W, 1100 m, V94 1994/085
Clytina n. sp. 1	CNCHYMEN 122544	CNC	10.453698	-84.003526	[Costa Rica] La Selva Biological Station, nr. Puerto Viejo, screen-sweeping, 2.1980, W. R. Mason

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Clytina n. sp. 1	CNCHYMEN 122585	CNC	-0.628955	-79.420853	[Ecuador] 47km S Santo Domingo, Rio Palenque Station, 25.5.1975, S. & J. Peck
Clytina n. sp. 1	TAMU-ENTO X0616350	TAMU	10.3494	-67.6856	VENEZUELA: Aragua Parque Nac. H. Pittier Rancho Grande, env. 9-10.iv.1994, L. Masner 10.3494°N, 67.6856°W 1100 m, V94 TAMU 1994/082
Clytina n. sp. 1	UCRC_ENT 300241	UCR	9.890828	-83.652956	Costa Rica, Prov. Cartago, C.A.T.I.E. Turrialba, XI-10.1980, screen-sweeping rainforest, reventazon gorge, Woolley 1980/104
Thysanus ater	BMNH(E) #990656	BMNH	51.011595	-1.527643	England: Hants || Romsey, Awbridge || vii.1981 || Coll. C. Vardy
Thysanus ater	BMNH(E) #990657	BMNH	51.011595	-1.527643	England: Hants || Romsey, Awbridge || vii.1981 || Coll. C. Vardy
Thysanus ater	BMNH(E) #990658	BMNH	51.011595	-1.527643	England: Hants || Romsey, Awbridge || vii.1981 || Coll. C. Vardy
Thysanus ater	CNCHYMEN 122397	CNC	44.262745	-111.28189	[USA] Targhee || Nat. Forest || Idaho || Mass reared || Lodgepole Needle || Miner Recurvaria || milleri Busck ++ 18357-H || -51-619B || 55F || 15-vii-51
Thysanus ater	CNCHYMEN 122398	CNC	44.262745	-111.28189	[USA] Idaho || Mass Reared || Recurvaria | milleri Buck ++ 18357-H || -50-618 || 55F || 6-ix-50
Thysanus ater	CNCHYMEN 122399	CNC	44.262745	-111.28189	[USA] Targhee || Nat. Forest || Idaho || Mass reared || Lodgepole Needle || Miner Recurvaria || milleri Busck ++ 18357-H || -51-619B || 55F || 15-vii-51
Thysanus ater	CNCHYMEN 122400	CNC	45.485681	-76.072004	[Canada] Constance Bay, ONT. || 6-13.vii.1973 || Yellow pan trap || Coll. G. Gibson
Thysanus ater	CNCHYMEN 122401	CNC	44.262745	-111.28189	[USA] Idaho || Mass Reared || Recurvaria | milleri Buck ++ 18357-H || -50-618 55 || 23-viii-50
Thysanus ater	see above	MNHG	45.816667	15.983333	Yougoslavie [Croatia] || 1958 || Avec Aspidiotus || perniciosus || Coll. Tadic ++ No. Zagreb || 41
Thysanus ater	see above	MNHG	45.833333	17.383333	Yougoslavie [Croatia] || avirovitica || 19.iii.59 || Ex. ? Aspidiotus || perniciosus || Coll. Tadis
Thysanus ater	see above	MNHG	46.41215	16.063778	Yougoslavie [Slovenia] || S. Pristava || 5.x.59 || Ex. ? Aspitiotus || pernicicosus || Coll. Tadic
Thysanus ater	see above	IEUC	45.733333	8.833333	[Italy] Caronno Varesino || Tasso || 8.ix.61
Thysanus ater	see above	WSU	46.4646	-113.2342	[USA:Montana] Maxville, Mont || Spring, 1956 || Lab. Reared || Ex. /fol. Douglas-fir|| Coll. H.R. Dodge ++ Hopk. US || 15850 ++ Paratype Thysanus piza Dodge
Thysanus ater	TAMU-ENTO X0460209	TAMU	38.53823	-121.72648	[USA] California: Yolo Co. || Putah Cyn. || v-11-1988 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460210	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460211	TAMU	38.53823	-121.72648	[USA] California: Yolo Co. || Putah Cyn. || v-11-1988 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460212	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460213	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460214	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460215	TAMU	38.53823	-121.72648	[USA] California: Yolo Co. || Putah Cyn. || v-11-1988 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460216	TAMU	38.53823	-121.72648	[USA] California: Yolo Co. || Putah Cyn. || v-11-1988 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460217	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Thysanus ater	TAMU-ENTO X0460218	TAMU	38.53823	-121.72648	[USA] California: Yolo Co. || Putah Cyn. || v-11-1988 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460219	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TAMU-ENTO X0460220	TAMU	38.570938	-122.23526	[USA] CAL: Napo Co. || Lake Berrysa || vii.1.1987 || Coll. R.E. Rice
Thysanus ater	TBD (1 male, 15 females)	WSU	46.4646	-113.2342	[USA: Montana] Maxville, Mont || 1956 || Coll. H.R. Dodge ++ Hopk. US || 15850
Thysanus ater	TBD (11 females, 13 males)	MNHG	44.174444	5.278889	France || Mt. Ventoux || vii.62 || Ex. Leucaspis pini || Coll. Benassy
Thysanus ater	TBD (2 females)	IEUC	44.411111	8.932778	[Italy] Genova || 6/vi
Thysanus ater	TBD (3 females, 6 males)	MNHG	46.385833	16.433333	Yougoslavie [Croatia] || 1958 || Avec Aspidiotus || perniciosus || Coll. Tadic ++ No. Cakovec || 48
Thysanus ater	UCRC_ENT 299673	UCR	33.107648	-116.37978	[USA] Anza Borrego State Park || CA San Diego Co. || Coyote Canyon || 15-vi-1981 || Coll. J.T. Huber
Thysanus ater	UCRC_ENT 299674	UCR	35.940212	-117.18041	[USA] Panamint Valley || CA. Inyo Co. || 8 mi. S.W. Balarat || v-26-1980 || sweeping || On: Prob. Larreta || tribentata || Coll. JB Woolley ++ No 80/026
Thysanus ater	UCRC_ENT 299675	UCR	33.829772	-116.09855	[USA] 6.7 mi Fr. Dillon Rd. || CA. Riverside Co. || Berdoo Canyon || iv-26-1979 || Sweeping || larreta tridentata || Coll. J.B. Woolley ++ No. 79/034A
Thysanus ater	UCRC_ENT 299676	UCR	33.829772	-116.09855	[USA] 6.7 mi Fr. Dillon Rd. || CA. Riverside Co. || Berdoo Canyon || iv-26-1979 || Sweeping || larreta tridentata || Coll. J.B. Woolley ++ No. 79/034A
Thysanus ater	UCRC_ENT 299677	UCR	33.107648	-116.37978	[USA] Anza Borrego State Park || CA San Diego Co. || Coyote Canyon || 15-vi-1981 || sweeping || Coll. G. Gordh
Thysanus ater	UCRC_ENT 299678	UCR	35.666222	-118.04031	[USA] Calif. Kern Co. || Walker Pass || x-2-1980 || Evel. 5250' || Sweeping pinyon || Coll. J.B. Woolley ++ No 80/076
Thysanus ater	UCRC_ENT 299679	UCR	33.65	-117.21667	[USA] Calif. Riverside Co. || Menifee Valley, W. End || vi-1-15-1980 || Malaise trap || Pinto property || Coll. J.B. Woolley ++ No 80/042
Thysanus ater	UCRC_ENT 299680	UCR	31.92452	-109.13004	[USA] Ariz. Cochise || 1 Mi. NE Portalco || ix-14-1978 || Sweeping || grass clumps || Coll. J.B. Woolley ++ No 78/030
Thysanus ater	UCRC_ENT 299681	UCR	33.107648	-116.37978	[USA] Anza Borrego State Park || CA San Diego Co. || Coyote Canyon || 15-vi-1981 || Coll. J.T. Huber
Thysanus ater	UCRC_ENT 299682	UCR	36.059167	-117.24417	[USA] Calif. Inyo Co. || Panamint Valley || 2 mi. W Indian Ranch || v-26-1980 || Sweeping || Coll. G. Gordh
Thysanus ater	UCRC_ENT 299683	UCR	33.107648	-116.37978	[USA] Anza Borrego State Park || CA San Diego Co. || Coyote Canyon || 15-vi-1981 || Coll. J.T. Huber
Thysanus ater	UCRC_ENT 299684	UCR	33.107648	-116.37978	[USA] Anza Borrego State Park || CA San Diego Co. || Coyote Canyon || 15-vi-1981 || Coll. J.T. Huber
Thysanus ater	UCRC_ENT 299689	UCR	32.7153	-117.1573	[USA] Old San Diego, Calif. || Mar 12, 1952 || Parlatoria pittospori material || On: Pittosporum tobira || Coll. Cyril Gammon
Thysanus ater	UCRC_ENT 299690	UCR	34.293282	-116.78287	[USA] CA. San Bern Co. || 1.2 mi. NE Baldwin Lake || viii-31-1978 || sweeping || Pinyon Pine || Coll. J.B. Woolley
Thysanus ater	UCRC_ENT 299691	UCR	41.6	-72.7	[USA] Connecticut || 12-viii-1953 || Ex. Quadraspidiotus || perniciosus || Det Flanders || Coll. Flanders
Thysanus ater	UCRC_ENT 299691	UCR	41.6	-72.7	[USA] Connecticut || 12-viii-1953 || Ex. Quadraspidiotus || perniciosus || Det Flanders || Coll. Flanders
Thysanus ater	UCRC_ENT 299692	UCR	35.666222	-118.04031	[USA] Calif. Kern Co. || Walker Pass || x-2-1980 || Evel. 5250' || Sweeping pinyon || Coll. J.B. Woolley ++ No 80/076
Thysanus ater	UCRC_ENT 299693	UCR	34.293282	-116.78287	[USA] CA. San Bern Co. || 1.2 mi. NE Baldwin Lake || ix-22-1979 || Beating Pinyon || Coll. J.B. Woolley

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Thysanus ater	UCRC_ENT 299694	UCR	34.293282	-116.78287	[USA] CA. San Bern Co. || 1.2 mi. NE Baldwin Lake || ix-22-1979 || Beating Pinyon || Coll. J.B. Woolley
Thysanus ater	UCRC_ENT 299695	UCR	34.329359	-116.85207	[USA:California] 5 mi. NE || Baldwin Lake || vii-16-1970 || On: Pinyon Pine || Coll. Medved ++ B-27
Thysanus ater	UCRC_ENT 299696	UCR	34.310042	-116.83684	[USA] 3 mi. NE || Baldwin Lake || vii-16-1970 || On: Pinyon Pine || Coll. Medved ++ B-26
Thysanus ater	UCRC_ENT 299697	UCR	34.310042	-116.83684	[USA] 3 mi. NE || Baldwin Lake || vii-16-1970 || On: Pinyon Pine || Coll. Medved ++ B-31
Thysanus ater	UCRC_ENT 299698	UCR	39.053931	-76.81721	[USA: Maryland] Md, Prince George Co. || Patuxent || v-16-25-1979 || In pan trap || edge of meadow-hardwoods || Coll. Schauff, Grissell ++ PT1
Thysanus ater	USNM_ENT 763255	USNM	50.8167	-1.5667	[England] Pignal Pond || Brockenhurst || 7.vi.1927
Thysanus melancholicus	BMNH(E) #990350	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 15.x.1949 || Coll. F. Plaumann || B.M. 1957-341 ++ From BMNH P173
Thysanus melancholicus	BMNH(E) #990351	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 15.x.1949 || Coll. F. Plaumann || B.M. 1957-341 ++ From BMNH P173
Thysanus melancholicus	CNCHYMEN 122402	CNC	10.653934	-61.402128	Trinidad || W.I. Curepe || Sta. Margarita || Circular Rd. || 24.v-8.vi.74 || Coll. F.D. Bennett
Thysanus melancholicus	CNCHYMEN 122403	CNC	10.653934	-61.402128	Trinidad || W.I. Curepe || Sta. Margarita || Circular Rd. || 24.v-8.vi.74 || Coll. F.D. Bennett
Thysanus melancholicus	USNM_ENT 763259	USNM	-34.8581	-56.1708	Uruguay || Montevideo || So. Amer. Par. Lab || VII-VIII.1944 || coll. Berry || No. 1166-25
Thysanus melancholicus	USNM_ENT 763260	USNM	-34.8581	-56.1708	Uruguay || Montevideo || So. Amer. Par. Lab || VII-VIII.1944 || coll. Berry || No. 1166-26
Thysanus melancholicus	USNM_ENT 763261	USNM	25.944153	-97.465553	[USA] Texas: Cameron Co. || Southmost Ranch (7mi. || SE Brownsville) || 3-5 December 1978 || Coll. E. Grissell & A. Menke
Thysanus n.sp.2	BMNH(E) #990344	BMNH	-27.146228	-52.429556	Brazil: Sta. Cat. || Nova Teutonia || 26.i.1944 || F. Plaumann || B.M. 1957-341
Thysanus n.sp.2	BMNH(E) #990345	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 26.i.1944 || Coll. F. Plaumann || B.M. 1957-341
Thysanus n.sp.2	BMNH(E) #990346	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 26.i.1944 || Coll. F. Plaumann || B.M. 1957-341
Thysanus n.sp.2	BMNH(E) #990347	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 26.i.1944 || Coll. F. Plaumann || B.M. 1957-341
Thysanus n.sp.2	BMNH(E) #990348	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 26.i.1944 || Coll. F. Plaumann || B.M. 1957-341
Thysanus n.sp.2	BMNH(E) #990349	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || 26.i.1944 || Coll. F. Plaumann || B.M. 1957-341
Thysanus n.sp.3	CNCHYMEN 122405	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Mar 1948 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A-9 ++ 9
Thysanus n.sp.3	CNCHYMEN 122406	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Dec 1947 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A-3 ++ 3
Thysanus n.sp.3	CNCHYMEN 122407	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Mar 1948 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A-10 ++ 10
Thysanus n.sp.3	CNCHYMEN 122408	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Mar 19, 1948 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A-11 ++ 11
Thysanus n.sp.3	CNCHYMEN 122409	CNC	45.963889	-66.528103	[Canada] Noonan, N.B. || 4-viii-1946 || Ex. eggs of Agrilus || anxius || Coll. G.W. Barter ++ 20-iv-1947 Balsam O. Peck
Thysanus n.sp.3	CNCHYMEN 122410	CNC	45.963889	-66.528103	[Canada] Noonan, N.B. || 4-viii-1946 || Ex. eggs of Agrilus || anxius || Coll. G.W. Barter ++ 20-iv-1947 Balsam O. Peck

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Thysanus n.sp.3	CNCHYMEN 122411	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Nov 1947 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A5 ++ 5
Thysanus n.sp.3	CNCHYMEN 122412	CNC	45.95	-66.6333	[Canada] Fredericton, N.B. || Nov 1947 || Ex. A anxius || Coll. G. W. Barter ++ 18835-A5 ++ 5
Thysanus n.sp.3	CNCHYMEN 122504	CNC	46.519379	-84.328666	Canada:ON, || Sault Ste. Marie || 46°30.259'N || 84°18.283''W, ||17.vii.2007 || D. B. Lyons, ex. || Agrilus anxius || egg #0112.
Thysanus n.sp.3	UCRC_ENT 299708	UCR	41.2464	-79.8976	[USA] Pennslyvania || Bullion, || Venango Co. || 8-vii-1982 || Ex. eggs of || Agrilus anxius || Coll. C.R. Loerch
Thysanus n.sp.3	UCRC_ENT 299709	UCR	41.2464	-79.8976	[USA] Pennslyvania || Bullion, || Venango Co. || 8-vii-1982 || Ex. eggs of || Agrilus anxius || Coll. C.R. Loerch
Thysanus n.sp.3	UCRC_ENT 299710	UCR	41.2464	-79.8976	[USA] Pennslyvania || Bullion, || Venango Co. || 8-vii-1982 || Ex. eggs of || Agrilus anxius || Coll. C.R. Loerch
Thysanus n.sp.3	UCRC_ENT 299711	UCR	41.2464	-79.8976	[USA] Pennslyvania || Bullion, || Venango Co. || 8-vii-1982 || Ex. eggs of || Agrilus anxius || Coll. C.R. Loerch
Thysanus n.sp.3	UCRC_ENT 299712	UCR	35.704147	-83.532257	[USA] Cacle's Cove || Tenn. || Gt. Smoky Mtns. Nat. Pk. || 1-6-vi-1979 || Borrowed from || M. Schauff || Coll. N. Johnson & M. Sharkey
Thysanus n.sp.3	UCRC_ENT 299713	UCR	45.95	-66.6333	Canada, N.B. || Fredericton || 1956 || Ex. eggs of || Agrilus anxius || On: birch || Coll. G.W. Barter ++ Hoyers Rmnt.
Thysanus n.sp.3	UCRC_ENT 299716	UCR	45.95	-66.6333	Canada, N.B. || Fredericton || 1956 || Ex. eggs of || Agrilus anxius || On: birch || Coll. G.W. Barter ++ Hoyers Rmnt.
Thysanus n.sp.3	UCRC_ENT 299717	UCR	45.95	-66.6333	Canada, N.B. || Fredericton || 1956 || Ex. eggs of || Agrilus anxius || On: birch || Coll. G.W. Barter ++ Hoyers Rmnt.
Thysanus n.sp.3	UCRC_ENT 299718	UCR	45.95	-66.6333	Canada, N.B. || Fredericton || 1956 || Ex. eggs of || Agrilus anxius || On: birch || Coll. G.W. Barter ++ Hoyers Rmnt.
Thysanus n.sp.5	BMNH(E) #990935	BMNH	14.0667	-86.3667	Honduras : El || Zamorano || 27.vi.88 || Ex. diaspidid || On: acalypha || Coll. F.D. Bennett ++ AP prep/det iv.90 ++ 88-202
Thysanus n.sp.5	BPBM_TCN 0344	BPBM	21.443482	-157.99999	[USA] Honolulu, OAHU || 20.iii.1998 ++ ex hibiscus inf. With || Pinnaspis strachani and || Conchaspis angraecum || M.E.Chun/98-90 ++ W.S.R. Euparal vii.99 || 1 other point mt. ++ Bernice P. Bishop Museum
Thysanus n.sp.5	CNCHYMEN 122413	CNC	10.653934	-61.402128	Trinidad || W.I. Curepe || Sta. Margarita || Circular Rd. || 24.v-8.vi.74 || Coll. F.D. Bennett ++ 77.06.08.03
Thysanus n.sp.5	TAMU-ENTO X0616310	FSCA	10.0739	-69.3228	Venezuela || Barquisimeto || 3 V 1991 || Ex. Saccharum || officinarum || flying adult || Coll. FD Bennett 1010 ++ hoyers
Thysanus n.sp.5	TAMU-ENTO X0616333	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0616334	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0616335	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0616336	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0616337	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0616338	FSCA	28.1761	-80.5901	Signiphoridae|| Thysanus ++ [USA] Fl: Broward Co || Satellite Beach || 27 II 1987 || A. Hamon || Conchaspis angraeci || Pittosporum tobira
Thysanus n.sp.5	TAMU-ENTO X0626307	FSCA	30.5452	-83.8702	[USA] Florida, Jefferson || Monticello Co. [sic] || 29-xi-1973 || Ex. Rhododendron || twigs infested || with conchaspis || angraeci || Cockerell || Coll. Q.C. Anglin & W.H. Pierce
Thysanus n.sp.5	TAMU-ENTO X0626308	FSCA	30.5452	-83.8702	[USA] Florida, Jefferson || Monticello Co. [sic] || 29-xi-1973 || Ex. Rhododendron || twigs infested || with conchaspis || angraeci || Cockerell || Coll. Q.C. Anglin & W.H. Pierce

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Thysanus n.sp.5	TAMU-ENTO X0855959	HDOA	10.653934	-61.402128	Trinidad || Curepe || ix-22-1981 || Ex. Angraecum || scale || Coll. R. Burkhart ++ Hawaii Dept. Agric. || RB-12-81(6)
Thysanus n.sp.5	TAMU-ENTO X0855960	HDOA	10.653934	-61.402128	Trinidad || Curepe || ix-22-1981 || Ex. Angraecum || scale || Coll. R. Burkhart ++ Hawaii Dept. Agric. || RB-12-81(6)
Thysanus n.sp.5	TAMU-ENTO X0855961	HDOA	10.653934	-61.402128	Trinidad || Curepe || ix-22-1981 || Ex. Angraecum || scale || Coll. R. Burkhart ++ Hawaii Dept. Agric. || RB-12-81(6)
Thysanus n.sp.5	TAMU-ENTO X0855962	HDOA	10.653934	-61.402128	Trinidad || Curepe || ix-22-1981 || Ex. Angraecum || scale || Coll. R. Burkhart ++ Hawaii Dept. Agric. || RB-12-81(6)
Thysanus n.sp.5	TAMU-ENTO X0855963	HDOA	10.653934	-61.402128	Trinidad || Curepe || ix-22-1981 || Ex. Angraecum || scale || Coll. R. Burkhart ++ Hawaii Dept. Agric. || RB-12-81(6)
Thysanus n.sp.6	CNCHYMEN 122414	CNC	-22.532778	-52.167778	Brazil,|| S. Paulo,|| Teodoro Sampaio|| Coll:|| F. M. Oliveira|| xi.1973
Thysanus n.sp.6	CNCHYMEN 122415	CNC	-22.532778	-52.167778	Brazil,|| S. Paulo,|| Teodoro Sampaio|| Coll:|| F. M. Oliveira|| xi.1973
Thysanus nigrellus	UCRC-ENTO 299700	UCR	19.17241	-102.09703	Mexico: Michoacan || 10 mi N. Nueva Italia || vii-12-1981 || sweeping || Coll. J. LaSalle ++ 81-7-12-2
Thysanus nigrellus	UCRC-ENTO 299701	UCR	19.17241	-102.09703	Mexico: Michoacan || 10 mi N. Nueva Italia || vii-12-1981 || sweeping || Coll. J. LaSalle ++ 81-7-12-2
Thysanus nigrellus	UCRC-ENTO 299702	UCR	18.796793	-102.06854	Mex[ico]: Michoacan || 3 km. N. Capirio || 12-vii-1981 || sweeping || Prob on mesquite || Coll. J. LaSalle ++ 81-vii-12-1
Thysanus nigrellus	UCRC-ENTO 299703	UCR	18.796793	-102.06854	Mex[ico]: Michoacan || 3 km. N. Capirio || 12-vii-1981 || sweeping || Prob on mesquite || Coll. J. LaSalle ++ 81-vii-12-2
Thysanus nigrellus	UCRC-ENTO 299704	UCR	18.796793	-102.06854	Mex[ico]: Michoacan || 3 km. N. Capirio || 12-vii-1981 || sweeping || Prob on mesquite || Coll. J. LaSalle ++ 81-vii-12-3
Thysanus nigrellus	UCRC-ENTO 299705	UCR	18.796793	-102.06854	Mex[ico]: Michoacan || 3 km. N. Capirio || 12-vii-1981 || sweeping || Prob on mesquite || Coll. J. LaSalle ++ 81-vii-12-4
Thysanus nigrellus	UCRC-ENTO 299706	UCR	16.600662	-93.60157	Mexico: Chiapas || 30 km SW Ocozocoaulta || 30-vi-1981 || sweeping || Coll. J. LaSalle ++ 81-vi-30-3
Thysanus nigrellus	UCRC-ENTO 299707	UCR	30.054831	-110.95802	Mexico: Sonora || 40km N Carbo || vi-22 1981 || sweeping ++ Thysanus || J. LaSalle
Thysanus nigrellus	USNM_ENT 763262	USNM	30.6944	-88.0431	[USA] Mobile, Ala. || Feb 17-1926 || Ex. Chrysomphalus tenebricosus || comst. || On: silver maple || Coll. H.L. Dozier
Thysanus nigrellus	USNM_ENT 763263	USNM	30.6944	-88.0431	[USA] Mobile, Ala. || Feb 27-1926 || Ex. Chrysomphalus tenebricosus || comst. || On: maple || Coll. H.L. Dozier
Thysanus nigrellus	USNM_ENT 763264	USNM	30.6944	-88.0431	[USA] Mobile, Ala. || Feb 16-1926 || Ex. Chrysomphalus tenebricosus || comst. || On: silver maple twigs || Coll. H.L. Dozier
Thysanus rusti	CNCHYMEN 122404	CNC	10.653934	-61.402128	Trinidad || W.I. Curepe || Sta. Margarita || Circular Rd. || 24.v-8.vi.74 || Coll. F.D. Bennett ++ 77.06.14.05
Thysanus rusti	TAMU-ENTO X0616339	FSCA	24.919601	-80.633912	Thysanus sp. || det. J. Woolley 91 ++ [USA] Fl: Munroe Co. || Upper Matacoumbe Key || 25 VII 1990 || FD Bennett 789 || diaspine || Cereus pentagona || hoyers
Thysanus rusti	TAMU-ENTO X0616342	FSCA	29.7516	-82.4248	Thysanus sp. ++ [USA] Florida: Gainesville, Alachua Co. || 17 III 1989 || W.A.A. Klerks || ex. coll. Pseudaulacaspis pentagona || Hoyers
Thysanus rusti	TAMU-ENTO X0616343	FSCA	29.7516	-82.4248	Thysanus sp. ++ [USA] Florida: Gainesville, Alachua Co. || 17 III 1989 || W.A.A. Klerks || ex. coll. Pseudaulacaspis pentagona || Hoyers
Thysanus rusti	TBD (15 females)	BMNH	-27.146228	-52.429556	Brazil: Sta. Catarina || Nova Teutonia || Coll. F. Plaumann (several dates between 1941 and 1966)
Thysanus rusti	USNM_ENT 763265	USNM	-5.3	-80.7667	Chaquira, Peru || 12 Aug 1910 || Ex. Hemichionaspis minor || Coll. C.H.T. Townsend letter ++ 1,3d ++ 1,3 (s) Chaquira || 1,32 (i) Aug 12, 1910 (all in pencil)
Thysanus rusti	USNM_ENT 763266	USNM	-5.3	-80.7667	Chaquira (near Catacaos) || Peru || letter 12 Aug 1910 || Ex. Hemichionaspis minor || Coll. C.H. T. Townsend ++ 1,3d

Taxon	Identifier	Repository	Latitude	Longitude	Verbatim Label
Thysanus rusti	USNM_ENT 763267	USNM	18.829444	-71.936389	Lascahobas || Haiti || Dec 26-1930 || Ex. Vinsonia stellifera material || association with A. lounsburyi || Coll. H.L. Dozier
Thysanus rusti	USNM_ENT 763268	USNM	18.537574	-72.610652	Mariani, Haiti || Apr 16, 1930 || Ex. Green scale, Coccus || vividis || On: shrub || Coll. H.L.Dozier