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Análise cladística e distribuição de Thynninae (Hymenoptera: Tiphidae)

São José do Rio Preto
2017

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Tese apresentada como parte dos requisitos para obtenção do título de Doutora, junto ao Programa de Pós-Graduação em Biologia Animal, área de concentração Sistemática e Evolução, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Júlio de Mesquita Filho, São José do Rio Preto, em 17/04/2017.

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To all my professors.

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Dou respeito às coisas desimportantes
e aos seres desimportantes.
Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.

Manoel de Barros, O apanhador de Desperdícios

I care about unimportant stuff

and about unimportant beings.

I appreciate insects more than airplanes.

I appreciate the speed of the turtles more than that of the missile.

Manoel de Barros, The waste catcher. *Free translation*

PREFÁCIO

A tese intitulada “Análise cladística e distribuição de Thynninae (Hymenoptera: Tiphiiidae)” é submetida atendendo às normas do Programa de Pós-Graduação em Biologia Animal para obtenção do Título de Doutora em Biologia Animal na Universidade Estadual Paulista, Instituto de Biociências, Letras e Ciências Exatas, São José do Rio Preto, São Paulo, Brasil. A pesquisa foi conduzida sob orientação do Professor Doutor Fernando Barbosa Noll, no Departamento de Zoologia e Botânica, UNESP/IBILCE e um período de estágio sanduíche no Museu de História Natural *Carnegie Museum of Natural History, Pittsburgh, PA*, Estados Unidos sob orientação do Professor Doutor John Wenzel. A tese é composta por três seções: Seção I: Introdução geral a respeito do grupo de estudo; Seção II: “Análise cladística de Thynninae e novos registros para gêneros Neotropicais” apresentada em formato de manuscrito científico visando a publicação em revista científica internacional e, Seção III: Memorial.

PREFACE

The dissertation entitled: “Cladistics Analysis and distribution of Thynninae (Hymenoptera: Tiphiiidae)” is submitted attending the *Programa de Pós Graduação em Biologia Animal* norms to obtain the degree of Doctor of Philosophy in Animal Biology at the University of the São Paulo State, *Instituto de Biociências, Letras e Ciências Exatas*, São José do Rio Preto, São Paulo, Brazil. The research was conducted under supervision of Professor Dr. Fernando Barbosa Noll in the Department of Zoology and Botany, UNESP/ IBILCE and a period of internship at *Carnegie Museum of Natural History, Pittsburgh, PA*, United States of America under supervision of Professor Dr. John Wenzel. The dissertation is composed by three sections: Section I: General introduction about group of study; Section II: “Cladistic analysis of Thynninae and new records for Neotropical genera” presented following a scientific manuscript model, aiming to be published in an international journal, and Section III: Memorandum.

MSc Cíntia Eleonora Lopes Justino

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Section I

GENERAL INTRODUCTION

Vespoidea has been considered in most recent phylogenetic studies of Hymenoptera paraphyletic in relation to the other lineages of aculeate hymenopterans. Tiphidae is one of the families traditionally included in Vespoidea (Brothers 1999) and this is a diverse and cosmopolitan Coleoptera's parasitoid wasps that comprehends a great variety of forms (Pate 1947). The family encompasses more than 2,000 species classified in about 120 genera (Kimsey 1991b, 2004a). Tiphidae classification has change over time (Brothers 1999). Pate (1947) was the first to divide Tiphidae in eight subfamilies: Methochinae, Myrmosinae, Brachycistidinae, Bradynobaeninae, Anthoboscinae, Thynninae, Tiphinae and Myzininae. Later, Kimsey (1991b) moved Bradynobaeninae to Bradynobaenidae and Myrmosinae to Mutillidae. Brothers (1975) recognized six subfamilies: Anthoboscinae, Thynninae, Tiphinae, Brachycistidinae, Myzininae and Methochinae. The most recent classification includes seven subfamilies in Tiphidae, with inclusion of Diamminae, that was previously a tribe of Thynninae. Anthoboscinae is considered the most basal group, and Thynninae sister group of (Tiphinae + Brachycistidinae) + (Methochinae + Myzininae) (Kimsey 1991b). Nowadays with molecular data (Debevec *et al.* 2012; Pilgrim *et al.* 2008) the monophyly of Tiphidae has been refuted and according to these results subfamilies should be treated as families.

Aspects of Tiphidae biology is poorly explored in the literature and it is known that most of the subfamilies representatives parasite Scarabaeidae larvae in the soil, wood cavities or, less commonly, in decomposition material (Krombein 1982). Diamminae is an exclusively Australian subfamily that use Grillotalpidae (Orthoptera) as hosts (Kimsey 1991b). Some species are recognized by their importance as biological control, as *Tiphia*

pigidialis Allen and *Tiphia vernalis* Rohwer, which is used to control larvae population of *Popillia japonica* Newman (Rogers & Potter 2004). Given (1954) and Janvier (1933) gave great contributions to the behavior and biology of Thynninae, but this field remains unexplored in many levels. Known as cosmopolitan subfamily some groups remains with its distribution confined to the types description. This definitely is a consequence of the taxonomic impediment for tiphid research, which has to do with scarcity of specialists and difficulties related to the identification of specimens deposited in museums.

Tiphiidae turned out to be an open field to explore, with many more questions to be answered. In this dissertation, we add some contributions to the Tiphiidae understanding presenting the first cladistic analysis of Thynninae and some aspects of its distribution.

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Section II

A cladistic analysis of Thynninae (Hymenoptera: Tiphidae) and new records for Neotropical genera

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Abstract

We present the first cladistic analysis for Thynninae to evaluate its monophyly as well as of the taxa currently classified tribes. We also present a map with the distribution of the studied species and new records for Neotropical genera. Thynninae is a diverse subfamily of Tiphidae and, in spite of its unique characteristics, has been neglected in several different areas: taxonomy, systematics, distribution, and biology. The subfamily presents sexual dimorphism, with females wingless with ant-like morphology and winged males. Morphological study was conducted using 104 terminal taxa, of which 99 were from Thynninae and six were outgroups. Cladistic analysis was completed under implied weighting, and support was assessed by symmetric resampling. All currently accepted tribes were sampled, and in total, we studied 46 out of 65 Thynninae genera. We recovered the monophyly of Thynninae based on two wing characters. Rhagigasterini was recovered as a tribe; however, Scotanini, Thynnini, and Elaphropterini were not. The genera previously grouped in Elaphropterini were more related among them, than with other genera. According to our results, Rhagigasterini should be maintained as a tribe and Thynnini, Elaphropterini, and Scotanini should be included in one tribe: Thynnini. Our results regarding the distribution of Thynninae show the Gondwanan pattern of the species that are present in the Neotropical and Australasian regions. New records are important to expand the distribution of the species and add knowledge about the subfamily.

Keywords: parasitoid wasps, Gondwana, Thynninae tribes.

Introduction

Tiphiidae Pate 1947 is a Hymenoptera family of parasitoid wasps that comprises an aggregation of several forms of wasps that are currently organized into seven subfamilies: Anthoboscinae, Diamminae, Tiphiinae, Brachicistidinae, Methochinae, Myzininae, and Thynninae (Kimsey 1991b). It is a cosmopolitan family and includes more than 2,000 species (Kimsey 1991, 2004) that can have a considerable economic impact on the control of pests (Pate 1947). Thynnidae was defined by Erichson in 1842 (Turner 1910) and it was treated as a subfamily by Pate (1947), who included all related groups in the family Tiphiidae. Some works that came after Pate's (1947) kept the Thynnidae classification, even though most of them adopted Thynninae as a subfamily; we use Pate's classification based on the most recent papers.

Thynninae is the most diverse subfamily of Tiphiidae that contains the greatest number of genera and species (Brown 1995; Kimsey 1991, 2004). There are 75 genera and more than 600 species, although Brown (2009) estimated that more than 1,000 new species may be available for description in the collections. The subfamily occurs in Australasia and the Neotropics, with records from Costa Rica (Kimsey 1991c) to Patagonia, Australia, and adjacent islands (Kimsey 1991b). Species from Australasia are commonly named as flower wasps because of their importance as pollinators of deceptive orchids, as shown by many authors: Alcock (2000), Bower (2015), Brown (1989, 1996a; b 1998), Brown & Phillips (2014), Mant et al. (2002), Menz et al. (2013), Peakall et al. (2010), Peakall & Beattie (1996), Weston & Brown (2005), Phillips et al. (2011), Schiestl (2004), Schiestl et al. (2003), and Stoutamire (1983). Species from the Neotropics did not receive common names and were generally treated as fossorial wasps (Turner 1912; Pate 1947; Rohwer 1915) due to the female habits. The number of described genera shows a dominance in Thynninae fauna in

Australasia with 52 of the 75 total genera present. Even though fauna from the Neotropics has been neglected in terms of biology (Brown 2009), behavior, and taxonomy (Genise 1991), there are likely many Neotropical species and genera yet to be described and reviewed. Much of the presently accumulated knowledge concerns the Australasian species, and an exemplary indication of this scenario is that in the last 50 years, 17 new Australasian genera have been described (Brown 1983, 1992, 1995, 1996a; b, 2000, 2008, 2010, 2015, Kimsey 2001, 2002, 2003, 2005) and eight were reviewed (Brown 1987, 1989, 1995, 1998, 2001; 2007, Baptiste and Kimsey 2000; Kimsey 2000), whereas eleven new Neotropical genera were described (Genise 1991; Kimsey 1991a), but only four were reviewed (Genise & Kimsey 1993; Kimsey 1991c, 2005; Kimsey 1996).

In Thynninae, all females are wingless (ant-like morphology) and males are winged (Brown 2009). Female bodies are obviously specialized for burrowing with short, stout, and powerful legs (Stubblefield 1994), and they spend most of their time underground searching for Coleoptera larvae (Osten 1999; Ridsdill - Smith 1970). Males fly around in search of sugary food¹ and females (Stubblefield 1994; Ridsdill - Smith 1970). In this subfamily, the male carries the female in a nuptial flight (Brown 2009; Pate 1947), and sex encounters are probably mediated by odors (Ridsdill - Smith 1970). Given (1953) described a variety of morphological adaptations related to sexual dimorphism and a variety of behaviors during the mating time. These behaviors are associated with the position of the female in relation to the male's body position, feeding of the female by the male, self-feeding by the female, and the duration of the mate. After mating, females are dropped in the soil where they start to burrow in search of larvae that will be parasitized (Pate 1947). Like other Aculeata, Thynnine

¹ Sugary food: starch and sucrose are the typical carbohydrates that insects digest from plant food (Capinera 2008).

females use their sting to paralyze prey and for defense against large predators (Brown 2009).

Despite all of these unique characteristics of Thynninae, the subfamily has been neglected in the academic realm. Throughout history, the study of the Thynninae genera has been hampered by different aspects, potentially beginning with the fact that the name of the subfamily is derived from the genus type *Thynnus* Fabricius 1775, which has a curious etymology. The name *Thynnus* was previously used (Fabricius 1775) to describe a genus of fish, however, the name *Thynnus* was given to the wasps, and *Euthynnus* was adopted for the fish (Jordan 1963). According to Wood (1883), the maintenance of the name is very interesting, as *Thynnus* means “tunny fish.” Thynninae is described as a difficult group to work with, and the clearest reason for that is the difficulty of associating the sexes (Kimsey 2004a). In 1845, Westwood discussed this aspect and highlighted that, in many cases, males and females were described as different species because the identification of both sexes is nearly impossible if they are not collected while mating (Westwood 1845). To make things more challenging, there are records of miscoupling, which means that males and females from different species were collected in copula (Brown 1993; Rohwer 1915). According to Kimsey (2004a) miscoupling occurs in about 10% of the pairs of species in Thynninae. Distribution of the subfamily can be another issue. Most of the works in the last 50 years have been done in isolation. During the last 35 years, there were only two principal specialists working on the taxonomy of this group, and because of that, when the cladistic analysis was done, it was limited by the geographic distribution; for example, “Phylogenetic relations among the South American thynnine tiphiid wasps (Hymenoptera)” by Kimsey (1992). The most recent study that assembled information from both Australasian and Neotropical Thynninae is the taxonomic key presented by Kimsey (2004a). However, according to Brown (2005), the most comprehensive study of Thynninae is still from Turner (1910). Finally, in

many cases, the taxonomic changes that have been done require a phylogenetic evaluation. Here, we present the first cladistics analysis for Thynninae to test the monophyly of the subfamily, understand the relationship of the currently accepted tribes, and thus better understand the relationships among the subfamily genera. We also present a map with Thynninae species, with new records, and discuss aspects of its distribution.

Material and methods

Morphological study

The morphological study was performed with direct observation of the male wasps from the following museums' collections and was made possible by its respective curators: American Museum of Natural History, New York (AMNH) – Dr. James Carpenter; Carnegie Museum of Natural History, Pittsburgh (CMNH) – Dr. John Rawlings; Coleção Entomológica “Prof. J.M.F Camargo (RPSP), Departamento de Biologia, FFCLRP/USP, Ribeirão Preto – Dr. Eduardo A. B. Almeida; Coleção de Hymenoptera do Departamento de Zoologia e Botânica, São José do Rio Preto (HYMDZB) – Dr. Fernando Barbosa Noll; Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP) – Dr. Carlos Brandão; National Museum of Natural History, Washington (NMNH) – Dr. Brian Harris; Natural History Museum, London (NHM) – Dr. Gavin Broad; Natural History Museum of Denmark, Copenhagen (NHMD) – Dr. Lars Vilhelmsen; Senckenberg German Entomological Institute Müncheberg, Berlin (SDEI) – Dr. Andreas Taeger; Utah State University Hymenoptera Collection, Logan (UTAH) – Dr. James Pitts.

Only male morphology was employed for this study because the number of available females in the collections is low and females are unknown for some species. Information about *Scotaena* Klug 1810 species: *S. rosenbergi* Turner 1910, *S. clypearis* (Durán – Moya

1941), and *S. horni* (Turner 1927), was obtained from the morphological study and cladistics analysis of *Scotaena* made by Fernando Henrique Carnimeo (unpublished data).

The morphological study was performed using 104 terminal taxa, of which 99 were from Thynninae and six were from outgroups. All currently accepted tribes were sampled, and in the total we studied 46 out of 65 genera of Thynninae: nine out of 14 genera of Elaphropterini, four out of eight genera of Rhagigasterini, all the seven genera of Scotaenini, and 26 out of 52 genera of Thynnini. For the outgroups, we sampled three subfamilies: Tiphinae, Methochinae, and Myzininae and one species of Rhopalosomatidae which was used to root the tree. The list of examined material and the respective institutions where the material is deposited is provided in table 1 (Appendix 1). Some of the species could not be identified, so these are denoted by the name of the genus plus “sp.”. In some cases, we could observe well-marked morphological variation between specimens from the same species; in those cases, we use name of the species plus “sp. 1” and “sp. 2.”

A morphological data matrix (Table 1 – Appendix 2) with 112 characters was built using Winclada Asado version 1.89 software (Nixon 2002). When it was not possible to observe certain structures accurately, the state was coded as “?” and inapplicable states were coded as “-”. The list of characters and their coding is presented in Appendix 3. Characters from genitalia are difficult to access, and for most of the species, it was not possible to obtain them. This is because material from the museums is frequently old and needs to be prepared for dissection. In some cases, the museums did not allow dissection in order to avoid damage to the specimens. When a character was obtained from literature, the author was identified in the list of characters. We used contingent coding for characters as a solution to multistate characters. This type of coding allowed us to not lose the observed morphological variation.

Morphological terminology was based on previously published works regarding

species or genus descriptions, reviews, and taxonomic keys. In this regard, the most useful studies were those by Brothers (1975); Brown (1998, 2005, 2011); Genise & Kimsey (1993); Kimsey (1991a; c 1996b, 2004a); and Turner (1910).

Cladistic analysis

Cladistic analysis of the matrix was performed using TNT 1.1 software (Goloboff et al. 2000) under implied weighting of the characters (Goloboff 1993; Goloboff et al. 2008) with space for 10,000 trees in the memory. The concavity constant value (K), which determines how strongly homoplasious characters are (Goloboff et al. 2008), was set equal to 18.37, as determined by the script setk (Salvador Arías unpublished methodology) available for TNT (Goloboff et al. 2000). The search for the most parsimonious trees were accessed using TNT (Goloboff et al. 2000) with New Technology Search and a combination of four algorithms: Ratchet Parsimony (eight up/down-weighting percent and 200 iterations) (Nixon 1999), Tree-Drifting (default parameters) (Goloboff 1999), Tree-fusing (10 rounds) (Goloboff 1999), and Sectorial Searches (default parameter) (Goloboff 1999). Node support was obtained by implied weighting was accessed by symmetric resampling (Goloboff et al. 2003) run with 10,000 repetitions in TNT with Traditional Search. Winclada software (Nixon 2002) was used to study the trees and character optimization. Preparation of the images was done using Adobe illustrator CS5.1.

Distribution

A distribution map of the studied species was built using QGis 2.18 software. This map was built only for the studied species and aims to compare results found from cladistics analyses and species distribution. Localities were obtained from labels of the studied species and from the literature (Table 1 – Appendix 4). Google Earth was used to find the geographic coordinates. When geographical coordinates could not be found, the data was removed.

Records that had only general information, such as “Chile,” “Australia,” “Brazil,” etc. were not used as well. We kept a record that the locality was not available (it is present as “?” in Table 1 – Appendix 4), only the geographic coordinates. Geographic coordinates are presented as decimal fractions.

Results

From the cladistic analysis, we obtained two most parsimonious trees and the consensus strict tree that is shown in Figure 1. The adjusted homoplasy was equal to 12.34 for the two most parsimonious trees and 12.38 for the consensus tree. Figure 2 shows the consensus tree topology with support values for the nodes, which were calculated by symmetrical resampling.

Monophyly of Thynninae was recovered based on two wing characters: the presence of the 2r-m cell in the forewing (Character 56 – Appendix 3) (Figure 3, A) and the presence of jugal lobe in the hindwing marked by a strong incision (Character 61 – Appendix 3) (Figure 3, B). Thynninae was recovered as a sister group of Myzininae due to sharing the presence of supra-antennal projection (Character 1 – Appendix 3), antennae inserted under a plate (Character 6 – Appendix 3), the presence of fovea on the mesopleura (Character 51 – Appendix 3), and the forewing having three submarginal cells (Character 54 – Appendix 3). Tiphinae + Methochinae was sister group of Myzininae + Thynninae (Node one; Figure 1).

Thynninae was divided in two clades: one which includes the Rhagigasterini genera (Node six – Figure 1) and the second which contains Thynnini, Elaphropterini, and Scotanini genera (Node seven - Figure 1).

Rhagigasterini was recovered as a tribe: ((*Aelurus albofascies* Kimsey 1991 + (*A. ater* Duran, Moya 1941 + (*A. gayi* (Spinola 1851) + *A. plaumani* Kimsey ?))) + (*Eirone mutabilis*

Westwood 1844 + ((*Rhagigaster* sp. 1 + *Rhagigaster* sp. 2) + (*Dimorphothynnus apicalis* (Smith 1859) + (*D. dimidiatus* (Smith 1859) + *D. trunciscutus* Turner 1916)))) (Figure 4). Its monophyly was based on the presence of a visible metapostnotum (Character 81 – Appendix 3), a conspicuous tuft of hair turned inwards on the top of parameres (Character 111 – Appendix 3) and the presence of a reduced aedeagus inside the genital capsule (Figure 5) (Character 112 – Appendix 3). Australasian genera of Rhagigasterini were more related to each other than to *Aelurus* Klug 1840, the only Neotropical genus of the tribe. *Eirone* was a sister group of *Rhagigaster* Guérin 1839 + *Dimorphothynnus* Turner 1910 by sharing a well-marked flattened proximal carina in the pronotum (Character 47 – Appendix 3). *Dimorphothynnus* and *Rhagigaster* present the hypopygium plate expanded in the base with an apical hook (Character 93 – Appendix 3), and all species of *Dimorphothynnus* present an inverted V-shape carina on the clypeus (Character 44 – Appendix 3). *Aelurus* is a well-defined genus with supra-antennal projection reduced forming lobes over the antennal socket (Character 2 – Appendix 3) and apical margin of the hypopygium with spines (Character 99 – Appendix 3).

The sister group of Rhagigasterini (Node seven; Figure 1) included Elaphropterini, Thynnini, and Scotanini (Figure 6) and was defined by the presence of a transversal groove on the mesopleura (Character 52 – Appendix 3). The currently accepted tribes Elaphropterini, Scotanini, and Thynnini were not recovered. Scotanini was not monophyletic and it was divided in two main groups: nodes 12 and 15 (Figure 1).

The Node 12 (Figure 1) included three genera previously classified as Scotanini: which were *Scotaena* Klug, 1810, *Pseudelaphroptera* Ashmead 1903, *Ornepetes* Guérin - Meneville 1839, and *Rostrynnus* Genise 1991 and had the following relationship: (*Scotaena horni* + *S. vetusta* (Turner 1909) + (*Rostrynnus* sp. + *Rostrynnus tarsatus* (Klug 1842)) +

((*Ornepetes nigriceps* (Guérin 1839) + (*S. polistoides* (Turner 1910) + *S. pubescens* (Klug 1842)) + (*Scotaena flavovariegata* sp. 1 + *Scotaena flavovariegata* sp. 2)) + (*Ornepetes semisinctus* Turner 1910 + (*S. decora* Smith 1859 + *S. duckei* (Smith 1859) + *S. fastuosa* (Smith 1879)) + (*Pseudelaphroptera transandina* Turner 1929 + (*O. albonotata* Andre 1904 + *P. chilensis* Saussure 1867))). This clade is supported by the presence of a rounded lamellae in the apical margin of the hypopygium (Character 100 – Appendix 3), which is a homoplastic synapomorphy

The node 15 (Figure 1) included four genera previously classified as Scotanini: *Scotaena*, *Anodontyra* Westwood 1835, *Glottynnus* Genise 1991, and *Parelaphroptera* Turner 1910. The relationship is as follows: ((*Anodontyra haarupi* (Turner 1909) + *A. tricolor* Westwood 1835) + (*Scotaena clypearis* + (*A. strenua* (Smith 1879) + (*Glottynnus lara* (Brethes 1910) + (*Parelaphroptera flavomaculata* (André 1904) + *P. santacruciana* (Brethes 1910)))))). This relationship is supported by the presence of the carina on the proximal margin of the pronotum absent (Character 46 – Appendix 3) – homoplastic. Scotanini genera grouped in Node 15 was more related to Thynnini than to other Neotropical genera. From Scotanini, *Rostrynnus* was recovered as monophyletic, and the genus can be identified by the presence of an elongated and constricted clypeus (Character 29 – Appendix 3). *Rostrynnus* sp. is possibly a new species since the genus was erected only by the species *R. tarsatus*. *Rostrynnus tarsatus* has the apex of the clypeus bilobate and *Rostrynnus* sp. notched. The genera *Ornepetes*, *Pseudelaphroptera*, and *Anodontyra* were not recovered as monophyletic. *Parelaphroptera* Turner 1910 was recovered as monophyletic by two homoplastic synapomorphies: the presence of the 2m – cu reaching the 2rs - m vein in the forewing (Character 59 – Appendix 3) and the apex of the hind femur was symmetrical (Character 75 – Appendix 3). Even though the presence of the vein 2m-cu reaching the vein

2rs-m was used as an autapomorphy for *Parelaphroptera* in Kimsey (1992), the same condition was observed in *Rhagigaster* sp. 1 and *Thynnus zonatus* (Guérin 1839), so this character appears as a homoplasy in our topology.

All of the genera included previously in Elaphropterini were the sister group of the Scotenini (Node 12; Figure 1). Those genera were more related among them than with other Thynninae genera (Figure 7), except by the addition of *S. rosenbergi* (Turner 1910). Nodes 12 and 13 had almost the same support value. *S. rosenbergi* was closely related with *Eucyrtothynnus* Turner 1910 and shares the deeply curved mandible in the apex (Character 19 – Appendix 3). *Elaphroptera* Guérin 1839 was recovered as monophyletic with high support value for the genus and well supported relationship for the species as well (Figure 2). Its species share the mandible apart from the clypeus in the apex (Character 20 – Appendix 3) and the raised clypeal plate (Character 27 – Appendix 3). *Brethynnus infernalis* (Turner 1910), *B. steinbachii* sp. 1, and *B. steinbachii* sp. 2 share the clypeus plate transversely depressed submedially (Character – 45 – Appendix 3) as it was described for the genus (Genise & Kimsey 1991). However, *Brethynnus stygius* (Turner 1910) does not share this condition, and instead, this species shows the presence of a nose-like modification on the clypeal plate (Character 39 – Appendix 3). *Dolichothynnus carbonarius* sp. 1 and sp. 2 share the presence of the internal lamellae of the femur (Character 74 – Appendix 3), which is two times longer than the external (Character 76 – Appendix 3). The relationship found for the genera included in the node 13 (Figure 1) were well supported with most of the internal nodes with values of resampling bigger than ten.

All Thynnini genera, except for *Phymatothynnus monilicornis* and Scotenini (Node 15) were grouped by the presence of supra-antennal projection reduced (Character 3 – Appendix 3) and hypopygium rounded (Character 96 – Appendix 3), even though these were

homoplastic synapomorphies in our topology. Thynnini was divided in two groups. First, is represented in Node 14: (*Zeleboria* sp. + ((*Aeolothynnus* sp. 1 + *Aeolothynnus* sp. 2) + (*Acanthothynnus* sp. 1 + (*Doratithynnus* sp. + (*Encopothynnus* sp. 1 + *Iswaroides sanguinolentus* (Turner 1908)))))). These genera share the mandible with strongly reduced subapical teeth (Character 24 – Appendix 3). In this group, *Acanthothynnus* Turner 1910, *Doratithynnus* Turner 1910, *Encopothynnus* sp. Turner 1915, and *Iswaroides sanguinolentus* are closely related by the presence of a crescent callosity from sternite two to five, turning in a spine in sternite five (Character 92 – Appendix 3). *Encopothynnus* sp. and *Iswaroides sanguinolentus* are sister groups with callosity from sternum three to sternum five (Character 92 – Appendix 3).

Thynnini clade – Node 16 (Figure 8): ((*Tmesothynnus ingrediens* Turner 1916 + *T. zelebori* Saussure 1867) + (*Tachynoides flavopicta* (Ritsema 1876) + *Thynnoides fulvipes* Guérin – Meneville 1839) + (*Lophocheilus anilitatis* (Smith 1859) + *L. froggatti* (Turner 1908) + (*Lophocheilus villosus* Guérin -Meneville 1842 + (*Epactiothynnus pavidus* (Smith 1879) + *Neozeleboria proxima* Turner 1908))) + ((*Beithynnus* sp. + (*Elidothynnus* sp. (*Elidothynnus melleus* (Westwood 1844) + *Lestricothynnus illidgei* Turner 1910b))) + (*Catocheilus apterus* (Olivier 1811) + (*C. inconstans* (Smith 1859) + (*Ariphron tryphonoides* Smith 1859 + (*Belothynnus* sp. + (*Guerinius* sp.1 + *Guerinius flavilabris* (Guérin 1842)))))) + (*Leiothynnus spinigerus* Turner 1912 + (((*Thynnus* sp. + *Thynnus zonatus*) + (*Leptothynnus* sp. + (*Zaspilothynnus carbonarius* (Smith 189) + *Z. interruptus* (Westwood 1844)))) + ((*Tachynomyia* sp. + *Tachynomyia adusta* (Smith 1859)) + (*Agriomyia* sp. 2 (*Agriomyia* sp.1 + *A. luctuosa* (Smith 1859))))). This relationship has as synapomorphy the presence of epipygium with a well-marked transparent lamella (Character 100 – Appendix 3). Seven of the 26 studied genera, except those for which only one species was studied, were

monophyletic: *Aeolothynnus* Ashmead 1903, *Tmesothynnus* Turner 1910, *Guerinius* Ashmead 1903, *Thynnus*, *Zaspilothynnus* Ashmead 1903, *Tachynomyia* Guérin 1842, and *Agriomyia* Guérin 1839. The clades included in the node 16 had close values of support and higher than ten (Figure 2)

A map with the distribution of the Thynninae is presented in Figure 9. The studied genera hail from the Southern Hemisphere, distributed from the extreme south of South America to the northern portion of South America, Australia, Indonesia, and Tasmania. The distribution of the genera previously included in Elaphropterini and Scotanini almost completely overlaps and is more concentrated in the south portion of the Neotropics. This excludes three species of Scotanini: *Scotaena polistoides*, *Scotaena duckei*, and *Scotaena decora* that are in Colombia, Santarém, and Ceará in Brazil, respectively. Although we know from existing literature that other species of the genus *Merithynnus* Kimsey 1991 (Elaphropterini) are present in Venezuela. Australasian species are concentrated around the Australian coast; there are records of *Catocheilus apterus* and *Phymatothynnus monilicornis* in Tasmania and records of *Tachynoides flavopicta* in Indonesia (Table 1 – Appendix 4). From the studied specimens, we add new records for Neotropical genera and species that are shown in Figure 10 and listed below:

***Aelurus albofascies*:** this species was described as from Argentina (Kimsey 1991c) and our studied specimen is from Ubatuba Parque Estadual da Serra do Mar Núcleo Picinguaba. Alt. 203m, São Paulo state, Brazil. (23.319°S, -44.81°W).

***Aelurus gayi*:** the species was described as from Chile and our studied species is from Territorio Rio Negro, Argentina (40.4536°S, 66.5611°W).

Aelurus plaumani is from Mangaratiba, Rio de Janeiro, in the Southeast of Brazil (22.95° S, 44.04°W). *Aelurus*' distribution is already known for Southeast Brazil, however,

since the species is not described and its distribution is unknown, it is important to add this record here.

Dolichothynnus carbonarius: this species is recorded for the south of Brazil. Our studied species are from Rio de Janeiro, Brazil (22.9068°S, 43.1729°W) and Floresta da Tijuca, Rio de Janeiro, Brazil (22.9573°S, 43.2812°W). These localities are in the Southeast of Brazil.

Eucyrtothynnus rubescens: the species was described from Brazil and our studied species is from Quatro Ojos, Bolívia (16.8185°S, 63.5854°W).

Merithynnus: the genus was known from Venezuela and Colombia (Kimsey 1991a) and our studied species is from Catamarca Prov, Trampasacha 8 km W Chumbicha ME Irwen FD Parker, Argentina.650 m (28.83° S, 66.30°W).

Rostrynnus Genise 1991: the genus was known to be from Argentina, Misiones, and Southern Brazil, with no specification of locality. New records are from the São Paulo state, Brazil; Porto Cabral Rio Paraná, Brazil (21.73° S, 52.05° W) – Southeast of Brazil; and the Rio Grande do Sul state, Pelotas (31.76° S, 52. 33°W) – in the south of Brazil. The species *Rostrynnus* sp. is from Paraguay, however, it was not possible to find the geographic coordinates so we have not included this record in the map. As mentioned above, this is likely a new species. We need to search other specimens in more collections to confirm the diagnosis and confirm its distribution.

Telephoromyia rufipes: the species was described as from Argentina and our studied species is from No Montevideo Amer Paras lab, Uruguay (34.8175°S, 56. 1598°W).

New records for *Scotaena* were found as well but they are discussed by Fernando Henrique Carnimeo et al. (submitted).

Discussion

Our results evidenced Thynninae as a monophyletic group with a high support value (78) (Figure 2). The presence of the well-marked jugal lobe was previously discussed by Brothers (1975 1999), even though Kimsey (1991b) described a lack of the anal lobe in the hindwing as a Thynninae synapomorphy. From our morphological study and obtained topology, in fact, the well-marked jugal lobe in the hindwing is the synapomorphy for the subfamily. The presence of the cell 2r-m in the forewing is described in Turner (1910) as a Thynnidae synapomorphy, however, it is described as the first cubital cell usually more or less completely divided by a spur. We divided this character in three new characters: the presence of the 2-r-m cell, if the cell is closed or not, and if it is angulate or not (Character 58 – Appendix 3). The presence of the cell was observed in all studied specimens, therefore it is a synapomorphy for Thynninae (see Fig. 1).

In some Thynninae genera, supra-antennal projection can be modified: it could be reduced to forming lobes on the antennal sockets, evident only by the rounded margins, and in some cases it was completely flattened and did not form a real plate, but it was clear that the same region was delimited by the plate and secondarily reduced. Kimsey (1991b) uses the presence of well-developed frontal lobes as a distinguishing characteristic in Thynninae. The outgroups study showed that a species of Myzininae presents the well-developed supra-antennal projection as well, so it cannot be used as a Thynninae synapomorphy.

Aptery or brachyptery in one sex has arisen in numerous occasions independently in Aculeata (Brothers 1975, Stubblefield 1994). Aptery typifies sexual dimorphism and was considered a synapomorphy for Thynninae (Brothers 1975). However, according to the author, little weight should be given to aptery because of its sporadic occurrence. It is present in Myzininae and Diamminae, for example, even though Myzininae females can be wingless,

brachypteris, or full winged (Kimsey 1991b). In this way, we do not consider aptery as synapomorphy for Thynninae.

According to Brothers (1975), hypopygium and its modifications can provide very good evidence of relationships in thynnine. The author defends that the hypopygium modified in a hook could be a good character for Thynninae. In opposition to that, Kimsey (1991b – page 433), described the unciform (hook-like) hypopygium is present in “more primitive genus. The rest have the apical sternum elaborate lobate and sculptured.” Despite the use of a primitive concept that is not appropriate, our morphological study showed that hypopygium in fact presents many modifications that were coded in six characters in our analysis, and in many cases, each character was multistate. The hook-like hypopygium was only observed in *Rhagigaster* Ashmead 1903 and *Dimorphothynnus*. Hypopygium plate could not be used to define the subfamily monophyly or the relationship among tribes. By our analysis, hook-like modified hypopygium is a plesiomorphic condition in Tiphidae that is present in males of Myzininae and Tiphinae. In addition to that, a hypopygium plate with spines is an unquestionable synapomorphy to *Aelurus* (Figure 4)

Rhagigasterini was well established as a tribe with high support value (Figure 2) and defined by three synapomorphies (characters 82, 11 and 112). *Rhagigasterini* was treated as a subfamily by Turner (1910) including the four genera studied in this work. The tribe was reviewed by Kimsey (1996a), who attested its monophyly, however differently from first results, *Eirone* was more related to other Australasian genera instead of *Aelurus* in our work. *Aelurus albofascies* was recovered as a sister group of *A. ater* + (*A. gayi* + *A. plaumani*) as well as by the revision made by Kimsey (1991c). *Aelurus plaumani*, however, was not included in the *Aelurus* revision and there is no description for this species, despite the label in the collection citing Kimsey as the species' author. Our studied specimen is from the

National Museum of Natural History and there is another record from Natural History Museum of London (personal information, Graham Brown). Brown (2010) provided a key for Rhagigasterini genera including *Rhagigaster*, *Dimorphothynnus* and *Eirone*, *Curvothynnus* Brown 2010, *Rhythidothynnus* Brown 2008, *Umbothynnus* Brown 2008 (Brown 2008) and the most recent described genus *Rugosothynnus* Brown 2015 (Brown 2015). *Aelurus* was not included in his key.

Brothers (1975) cited the presence of a spine in the hind coxae in Thynninae. In our work, this structure was observed in Rhagigasterini (*Rhagigaster* and *Dimorphothynnus*) and in *Telephoromyia rufipes* Guérin 1839 (Elaphropterini), *Anodontyra tricolor*, *Glottynnus lara* (Scotaenini), *Ariphron tryphonoides*, *Belothynnus* sp., and *Guerinius flavilabris* (Thynnini). For this reason, as discussed by Brothers (1975), it has little importance in defining groups and is not synapomorphic for Thynninae.

In accordance with Brothers (1975), the clypeus shape is considered highly variable and difficult to interpret. Our morphological study showed the same: we could observe that many modifications accumulate in Thynninae clypeus regarding apical margins (Figure 11) and the presence of nose-like structures, concavity, carinas, and teeth. We described 19 different clypeus characters (Characters 27 – 45 - Appendix 3), and most of them have complex states as well. From our observations, genera that were included in Elaphropterini can be taxonomically recognized by different modifications on the clypeal plate: excavation on the clypeal plate, excavation apicomedial, nose-like structures, and depressions that are not present in other genera.

The clypeus concavity is another example in which bulging clypeus appears as a synapomorphy for *Ammodromus* Guérin - Meneville 1839 (Elaphropterini) in Kimsey (1992). However, this characteristic was extensively observed in the Thynnini genera as well

as the *Scotaenini* genera.

Turner (1910) cited the hypopygium and clypeus as features with considerable importance. These structures are perhaps more important in a taxonomic context than phylogenetic, since those from our analysis were very homoplastic. In other words, clypeus modifications and hypopygial plate shapes can be very useful to identify species, but it is not possible to use these structures to define more inclusive groups and establish phylogenetic relationships. The clypeus of *Dolichothynnus*, for example, is morphologically similar to the clypeus of *Scotaena sensu lato* with two acute apical teeth in the apical margin of the clypeus. Turner (1910) pointed out that *Dolichothynnus* could be closely related to *Scotaena*. Besides that, distribution of the studied species of *Dolichothynnus* is very close to the distribution of *S. flavovariegata*; both species are present in the Atlantic forest in Brazil but were not sister groups in our analysis.

S. rosenbergi was described as *Elaphroptera rosenbergi* by Turner (Turner 1910), and it was moved to *Scotaena* by Kimsey (Kimsey 2004b). However, it is clearly a species of *Eucyrtothynnus* and it is not related to other species of *Scotaena*. These results were confirmed taxonomically and phylogenetically by Fernando Henrique Carneiro (unpublished data).

Scotaena was not recovered as monophyletic, and from our tree topology, the species of the genus is present in the two clades that grouped formed *Scotaenini* genera; they form at least three group of species. *Scotaena* was considered as “dumping ground” by Kimsey (1992), with descriptions and synonymies without any revision, which resulted in problems as it was discussed for *S. rosenbergi*. Our results recover the results about *Scotaena* paraphyly found by Fernando Henrique Carneiro (unpublished data) that will erect three new genera regarding *Scotaena* species. In the introduction of his work, Turner (1910) considered that

the tendency for Thynninae would be the creation of more genera rather than sinking the existents. From our morphological observation and recent results, this might be the best option. Scotaenini genera and their paraphyly and taxonomic problems are extensively discussed in Justino et al. (submitted).

Regarding the *Ariphron* group, in addition to Brown (2001), we could also see that a sagittal carina is not apomorphic for the *Ariphron* group, occurring in *Ariphron*, *Phymatothynnus* Turner 1915, *Zeleboria*, *Tachyphron*, *Lophocheilus*, and *Agriomyia luctuosa*. The presence of an excavation (concave area) in the posterior region of the head (Brown 2001) (Character 9 – state 1) was described for *Tachyphron* and *Tachynomyia*, and we observed it in the same genera plus in *Tmesothynnus zelebori* and *Zaspilothynnus*. Genal modification (Character 14 – Appendix 3) was coded as present in *Tachynomyia* and *Tachyphron* (Brown, 2001), and from our morphological study, we observed the presence of the same structure in *Thynnus* sp. We did not recover the monophyly of the *Ariphron* group. This could be because we did not use many of the species that were used by Brown (2001) in our analysis, so we could not use same group of characters. However, we could see that some characters that were used for the *Ariphron* group were observed in other genera. This could be a result of the use of other groups of Thynninae that were not used as outgroups when the *Ariphron* monophyly was tested.

Brown (1998) determined that *Neozeleboria* is closely related to *Aeolothynnus* Ashmead, *Agriomyia* Guérin, *Ariphron* Erichson, *Chilothynnus* Brown, *Leiothynnus* Turner, *Pentazeleboria* Brown, *Phymatothynnus*, *Psamothynnus* Turner, *Tachynomyia* Guérin – Meneville, and *Tachyphron* Brown. In our analysis, *Neozeleboria* was in the clade (Node 16; Figure 1) that includes *Ariphron*, *Leiothynnus*, *Tachynomyia*, and *Agriomyia*, however, only *Tachynomyia* and *Agriomyia* were sister - group (Figure 4), sharing the clypeus flattened

(Character 27 – state 0).

Kimsey (2000) reviewed *Leiothynnus* Turner 1910. However, according to the author, the relationship among *Leiothynnus* and other Australasian genera was not well established. The genus share many features with *Iswaroides* Ashmead 1899 and *Epactiothynnus* Turner 1910. From our study, we could not observe characteristics shared among *Leiothynnus*, *Iswaroides*, and *Leiothynnus*, positioning them as sister groups. *Leiothynnus* was more related to *Thynnus*, *Leptothynnus* Turner 1910, *Zaspilothynnus* Ashmead 1903, *Tachynomyia* Guérin 1842, and *Agryiomyia* (Guérin 1839).

Values obtained from symmetrical resampling show that some clades are strongly established. The relationship among Neotropical and Australasian genera outside of Rhagigasterini remains difficult to determine, with polytomies and weak support for some clades (Figure 2). From the morphological observation of many specimens, there was not a clear pattern that could differentiate Australasian from Neotropical species. Bulging clypeus, for example, is found in Neotropical and Australasian genera as discussed above. It is difficult to use the literature data because in many cases, the descriptions do not present the diagnosis for the genera, and when it is presented, we could observe those features in other genera as well; it is clearly represented by all homoplasies distributed on the topology. In addition, we have observed that, because we are dealing with a group with problematic taxonomy, it is not always that species which presents all of the characteristics described for the genus. Because of this, we cannot use characters described for the genus as exclusive as they may not be representative of all of the specimens observed.

Since we could not recover the monophyly of Scotanini and Thynnini, and Rhagigasterini, it is clearly sister group of (Thynnini + (Scotaenini + Elaphropterini) + (Thynnini + Scotanini + Thynnini)). Considering this phylogenetic scenario herein

presented and the confidence we can have on the different nodes the tribal classification better reflect the natural groups of Thynninae is the adoption of only two tribes: Rhagigasterini (in the sense currently accepted) and Thynnini (comprising all taxa currently classified as Scotaenini, Elaphropterini, Thynnini).

One of the diagnostic features of Tiphidae is the mesosternum with laminate expansions covering bases of contiguous mesocoxae (Goulet et al. 1993). Recent works (Debevec et al. 2012; Pilgrim et al. 2008) have shown that Tiphidae is not monophyletic and tends to turn Thynninae, a monophyletic group, into a family. We believe that more work must be done regarding Tiphidae *sensu stricto* to establish this relationship, since the available works were made to analyze Vespoidea (Hymenoptera: Aculeata). Additionally, considering the diversity of Thynninae, the analysis might be not representative. We used *Rhopalosoma* sp. (Hymenoptera: Rhopalosomatidae) to root the tree, and it was possible to observe the presence of the mesosternum expansions covering the bases of its mesocoxae as well. For this reason, the synapomorphy for Tiphidae is not so clear, and we recognize that if Tiphidae is not monophyletic, then Thynninae should be treated as Thynnidae. However, we reinforce that further studies need to be done to answer these questions.

Most of the genera included in Thynninae were studied only when the type was defined. Leaving, many questions unsolved. Most of the older Thynninae classification was done based on females, perhaps because they show unique features, which makes the identification and autapomorphies clearer. Ashmead (1899) made one of the first attempts of Thynninae classification and he used the hypopygium and clypeus forms in addition to female morphology. However, more recently, taxonomy and systematic works have been made based on male morphology. Sex association remains a difficult task in the study of Thynninae and should be improved.

Recognition of the similarities found in the Southern Hemisphere leads to the use of the Gondwanan distribution pattern. The Gondwanan land assembly includes the major modern Southern Hemisphere landmasses – South America, Africa, Madagascar, Australia, New Zealand, and Antarctica – with the recent addition of several small continental terranes from Asia, Southern Europe, and Florida (McLoughlin & McLoughlin 2001). The isolation of Africa from the other Gondwana land mass probably occurred in the mid-Cretaceous period, and after that, Antarctica played an important role as a corridor for the interchange of vascular plants (McLoughlin & McLoughlin 2001) and likely many animal species. This occurred between the Australian and South American regions, which explains the observed Thynninae distribution pattern. Gondwana is an area of great interest regarding the austral region (McLoughlin & McLoughlin 2001). Some groups have their distributions as more inclusive, with species present in Africa as well but some only in Neotropics, Australia, and adjacent islands (Grimaldi & Engel 2005). Together with Thynninae, many other Hymenoptera families have representatives in South America and Australia: Labeninae (Ichneumonidae), Ambositrinae (Diapriidae), and Epipompilinae (Pompilidae) (Nauman 1991). Nauman (1991) pointed out that there is a tendency that the Gondwanan species is more common in moist areas with temperate forests. Considering the biome classification presented in Brown & Lomolino (2006), the species of Thynninae are not only present in areas of forest but are present in areas of savanna, desert, and even in the Andes Mountains, showing that they can adapt to different environments. It is important to emphasize that this map is representative of the general Thynninae distribution, however, it represents the species studied in this work. From the literature, Neotropical Thynninae distribution is expanded from the extreme south of South America up to Central America – Costa Rica (Kimsey 1991c), and beyond Australia, there are more records of this in adjacent islands in

Australasia. From a more inclusive data survey (Justino et al. 2015), with 623 records of 171 Australasian and 75 Neotropical species, only 20 species had geographical coordinates on their labels, showing that the clear majority of the records are old and are not the result of recent collections. Of all the records, 113 did not have species identification, and 30 of them had very general locality identification which was not useful. An extensively used source for geographical data, Global Biodiversity Information Facility (GBIF), presents some records that are likely incorrect, like *Iswaroides* Ashmead 1899 and *Tachyphron* Brown 1995 in United States and *Aelurus* Klug 1840 in Australia. This scenario shows the fragility concerning data available for Thynninae. New records for genera, species, and exploration of the Thynninae distribution data can be a great resource to understand the natural history of these species.

The study of the species from Thynninae has confirmed the idea that Tiphiidae consists of an aggregation of diversified forms, as described by Pate in 1947, and we can affirm that much of this is assembled in Thynninae. The distribution of the subfamily remains a great field to be explored and this should be done in order to understand the evolution of this singular group of wasps.

Conclusions and remarks

From our analysis, we conclude that Thynninae is monophyletic and Rhagigasterini can be considered a tribe. Scotanini, Thynnini, and Elaphropterini should be grouped in a single tribe: Thynnini. Thynninae presents a Gondwanan distribution pattern, but information about it is still very scarce. New records as presented in this work and previously published works are very important to contribute to knowledge of the natural history of the species.

Turner (1910) started his work by justifying that he could not evaluate a quantity of

species and genera as it should be done. More than one hundred years later, we present the first cladistics analysis for the subfamily. Even though we could not include the females and a deep study of the genitalia, our analysis is the first attempt to understand the evolution of the group. New studies should be done to investigate all of the aspects of the family that are still not available in the existing literature.

Many questions remain unsolved. Morphological characters have shown their importance and, from now on, new data regarding new morphological characters, for example genitalia and even combinations with molecular data, will improve greatly the understanding of this diverse and unique group of wasps.

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Figures Captions

Figure 1: Tree showing the strict consensus topology of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$. On the left side, the numbers of characters are indicated above the circles. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies. On the right side, the consensus topology shows the tribes'

relationship. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies. Under each node is its unique identification number.

Figure 2: Consensus strict tree with resampling values listed above the nodes.

Figure 3: Thynninae wing. A: Thynninae forewing. B: Thynninae hindwing.

Figure 4: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$ showing the monophyly of the Rhagigasterini. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

Figure 5: Aelurus genitalia. A: *Aelurus nigrofasciatus* dorsal view showing the tuft of hair inwards on the top of the parameres. B: *A. nigrofasciatus* frontal view showing the aedeagus reduced inside the genital capsule. PR: paramere Ae: aedeagus.

Figure 6: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$ showing the clade that groups Thynnini, Elaphropterini, and Scotaenini. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

Figure 7: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$ showing the Elaphropterini genera. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

Figure 8: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 19.09$ showing the clade that group Thynnini genera by the presence of a transparent lamella in the margin of the epipygium. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

Figure 9: Distribution of the Thynninae tribes. Elaphropterini genera is represented by a blue triangle, Scotaenini by a red star, Rhagigasterini by a black circle, and Thynnini by a green

square.

Figure 10: South American profile with new records for the Thynninae genera. Red stars represent *Rostrynnus* species, the black circle represents *Aelurus plaumani*, *A. albofascies* is represented by gray circles, *A. gayi* is represented by light green circles, light blue triangle represents *Merithynnus* sp., *Dolichothynnus carbonarius* sp. 1 and *D. carbonarius* sp. 2 is represented by dark blue triangle, *Eucyrtothynnus rubescens* is represented by purple triangle, and *E. rufipes* is shown by pink triangle.

Figure 11: Thynninae clypeus plate diversity. A: *Acanthothynnus* sp. showing the round apical margin. B: *Thynnus* sp. showing the tridentate apical margin. C: *Brethynnus stygius* showing the bilobate apical margin. D: *Guerinius* sp. showing the straight apical margin. E: *Elaphroptera atra* showing the notched apical margin. F: *Upa nasuta* showing the trilobate apical margin. G: *Spilothynnus bituberculatus* showing the apical margin with teeth formed by invagination with polish excavation. H: *Dolichothynnus carbonarius* sp. 1 with two apical teeth formed by a central invagination.

Figure 12: Consensus strict tree of the cladistic analysis of Thynninae under equal weighting; L = 631; Ci = 0.318; Ri = 0.247. On the left side, the numbers of characters are indicated above the circles. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies. Bremer support values are presented in the square on each node of the tree. Nodes without a number did not have Bremer support.

Figure 13: Forewing details of Thynninae showing modifications. A: *Anodontyra* sp. right wing. B: *Ornepetes semisinctus* right wing. C: *Anodontyra* sp. left wing. D: *Dimorphothynnus apicalis* right wing. Black arrows indicate the modifications.

Appendix 1 – List of examined material

Table 1: List of studied species, institution acronym from where they were obtained and number of specimens of each studied species. Acronyms: AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; HYMDZB: Coleção de Hymenoptera do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University, USP - RPSP: Coleção Entomológica J.M.F Camargo (RPSP) do Departamento de Biologia da Universidade de São Paulo FFCLRP-USP, Ribeirão Preto.

Species	Institution	Number of studied species
<i>Acanthothynnus</i> sp.	UTAH	3
<i>Aeolothynnus</i> sp. 1	UTAH	2
<i>Aeolothynnus</i> sp. 2	UTAH	1
<i>Aelurus albofascies</i> Kimsey 1991	MZUSP	1
<i>Aelurus ater</i> Duran - Moya 1941	AMNH/ CMNH	7
<i>Aelurus gayi</i> (Spinola 1851)	AMNH/ CMNH/ NMNH	12
<i>Aelurus plaumani</i> Kimsey (?)	NMNH	1
<i>Agriomyia luctuosa</i> (Smith 1859)	NMNH	2
<i>Agriomyia</i> sp. 1	AMNH	4
<i>Agriomyia</i> sp. 2	AMNH	1
<i>Anodontyra haarupi</i> (Turner 1909)	AMNH/ NHM/ NMNH/ UTAH	11
<i>Anodontyra strenua</i> (Smith 1879) - type	NHM	1
<i>Anodontyra tricolor</i> Westwood 1835	AMNH/ CMNH/ NHM	14
<i>Ariphron tryphonoides</i> Smith 1859	NMNH	1
<i>Beithynnus</i> sp.	UTAH	1
<i>Belothynnus</i> sp.	NMH/ UTAH	2
<i>Brethynnus infernalis</i> (Turner 1910)	AMNH/ NMNH	7

Table 1 continuation: List of studied species, institution acronym from where they were obtained and number of specimens of each studied species. Acronyms: AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; HYMDZB: Coleção de Hymenoptera do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University, USP - RPSP: Coleção Entomológica J.M.F Camargo (RPSP) do Departamento de Biologia da Universidade de São Paulo FFCLRP-USP, Ribeirão Preto.

Species	Institution	Number of studied species
<i>Brethynnus steinbachii</i> sp. 1 (Turner 1910)	AMNH	14
<i>Brethynnus steinbachii</i> sp. 2 (Turner 1910)	AMNH	2
<i>Brethynnus stygius</i> (Turner 1910)	AMNH/ NMNH	17
<i>Catocheilus apterus</i> (Olivier 1811)	AMNH/ NMNH	3
<i>Catocheilus inconstans</i> (Smith 1859)	NMNH	3
<i>Dimorphothynnus apicalis</i> (Smith 1859)	NMNH	3
<i>Dimorphothynnus dimidiatus</i> (Smith 1859)	NMNH	3
<i>Dimorphothynnus trunciscutus</i> Turner 1907	NMNH	2
<i>Dolichothynnus carbonarius</i> sp. 1 (Smith 1859)	CMNH/ NMNH	9
<i>Dolichothynnus carbonarius</i> sp. 2 (Smith 1959)	CMNH	1
<i>Doratithynnus</i> sp.	UTAH	2
<i>Eirone mutabilis</i> Turner 1908	NMNH	1
<i>Elaphroptera arcuata</i> Turner 1908	AMNH/ CMNH/NMNH	21
<i>Elaphroptera atra</i> Guerin-Méneville 1839	AMNH/ CMNH/NHM	15
<i>Elaphroptera boliviana</i> Genise and Kimsey 1993	AMNH	2
<i>Elaphroptera dorada</i> Kimsey 1993	NHM	1
<i>Elaphroptera montifascies</i> Genise and Kimsey 1993	CMNH/ NHMD	3

Table 1 continuation: List of studied species, institution acronym from where they were obtained and number of specimens of each studied species. Acronyms: AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; HYMDZB: Coleção de Hymenoptera do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University, USP - RPSP: Coleção Entomológica J.M.F Camargo (RPSP) do Departamento de Biologia da Universidade de São Paulo FFCLRP-USP, Ribeirão Preto.

Species	Institution	Number of studied species
<i>Elaphroptera sanguinicauda</i> Duran-Moya, 1941	AMNH/ CMNH	9
<i>Elaphroptera scoliaeformis</i> (Haliday 1836)	AMNH/CMNH/ NHMD	41
<i>Elidothynnus melleus</i> (Westwood 1844)	NMNH/ UTAH	3
<i>Elidothynnus</i> sp.	AMNH	2
<i>Encopothynnus</i> sp.	UTAH	4
<i>Epactiothynnus pavidus</i> (Smith 1879)	UTAH	2
<i>Eucyrtothynnus bruchii</i> (Bréthes 1910)	NMNH	5
<i>Eucyrtothynnus cornutus</i> (Guérin - Meneville 1839)	NMNH	2
<i>Eucyrtothynnus rubescens</i> (Brethes 1910)	CMNH	2
<i>Glottynnus lara</i> (Brethes 1910)	AMNH	6
<i>Guerinius flavilabris</i> Guérin - Meneville 1842	AMNH/ NMNH	4
<i>Guerinius</i> sp.	AMNH	1
<i>Iswaroides sanguinolentus</i> (Turner 1908)	NMNH	4
<i>Leiothynnus spinigerus</i> Turner 1912	NMNH	4
<i>Leptothynnus</i> sp.	AMNH	1
<i>Lestricothynnus illidgei</i> Turner 1910b	NMNH	4

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Species	Institution	Number of studied species
<i>Pseudelaphroptera transandina</i> Turner 1929	NHM	1
<i>Rhagigaster</i> sp. 1	AMNH	2
<i>Rhagigaster</i> sp. 2	AMNH	1
<i>Rostrynnus</i> sp.	AMNH	1
<i>Rostrynnus tarsatus</i> (Klug 1842)	AMNH/ MZUSP/ NHM	3
<i>Scotaena clypearis</i> (Durán-Moya 1941)	SDEI	-
<i>Scotaena decora</i> Smith 1859	NHM	1
<i>Scotaena duckei</i> (Smith 1859) -paralectotype	NHM	1
<i>Scotaena fastuosa</i> (Smith 1879)	NHM	3
<i>Scotaena flavovariegata</i> sp. (Smith 1879)	NHM/ NMNH/ MZUSP	3
<i>Scotaena flavovariegata</i> sp. 2 (Smith 1879)	MZUSP	1
<i>Scotaena horni</i> (Turner 1927)	SDEI	-
<i>Scotaena rosenbergi</i> (Turner 1910)	NHM	-
<i>Scotaena polistoides</i> (Turner 1910)	NMNH/ NHM	7
<i>Scotaena pubescens</i> (Klug 1842)	NMNH/ NHM	7
<i>Scotaena vetusta</i> (Turner 1909)	NHM/AMNH	2

Table 1 continuation: List of studied species, institution acronym from where they were obtained and number of specimens of each studied species. Acronyms: AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; HYMDZB: Coleção de Hymenoptera do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University, USP - RPSP: Coleção Entomológica J.M.F Camargo (RPSP) do Departamento de Biologia da Universidade de São Paulo FFCLRP-USP, Ribeirão Preto.

Species	Institution	Number of studied species
<i>Spilothynnus bituberculatus</i> sp. 1 (Turner 1908)	NMNH	3
<i>Spilothynnus bituberculatus</i> sp. 2 (Turner 1908)	AMNH	2
<i>Spilothynnus laetus</i> (Klug)	AMNH/ NMNH	8
<i>Spilothynnus</i> sp.	AMNH	1
<i>Tachynoides flavopicta</i> (Ritsema 1876)	MNH	1
<i>Tachynomyia adusta</i> (Smith 1859)	NMNH/ UTAH	3
<i>Tachynomyia</i> sp.	UTAH	8
<i>Telephoromyia rhombica</i> (Bréthes 1910)	AMNH	6
<i>Telephoromyia rufipes</i> Guérin - Meneville 1839	AMNH/ NMNH	9
<i>Thynnoides fulvipes</i> Guérin - Meneville 1839	NMNH	3
<i>Thynnus</i> sp.	AMNH/ UTAH	8
<i>Thynnus zonatus</i> (Guérin - Meneville 1839)	NMNH	1

Table 1 continuation: List of studied species, institution acronym from where they were obtained and number of specimens of each studied species. Acronyms: AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; HYMDZB: Coleção de Hymenoptera do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University, USP - RPSP: Coleção Entomológica J.M.F Camargo (RPSP) do Departamento de Biologia da Universidade de São Paulo FFCLRP-USP, Ribeirão Preto.

Species	Institution	Number of studied species
<i>Tmesothynnus ingrediens</i> Turner 1916	UTAH	7
<i>Tmesothynnus zelebori</i> (Saussure 1867)	NMNH	3
<i>Upa impreceps</i> (Turner 1910)	NMNH	2
<i>Upa longispina</i> Kimsey 1996	MZUSP	1
<i>Upa nasuta</i> Kimsey 1996	MZUSP	1
<i>Zaspilothynnus carbonarius</i> (Smith 1879)	NMNH	3
<i>Zaspilothynnus interruptus</i> (Westwood 1844)	NMNH	2
<i>Zeleboria</i> sp.	AMNH	1
OUTGROUPS		
<i>Elis quinquecincta</i> Fabricius (?) - Myzininae	CMNH	2
<i>Epimodipteron julli</i> Romand 1836- Tiphinae	CMNH	2
<i>Tiphia</i> sp. – Tiphinae	CEDZB	3
<i>Methoca</i> sp. – Methochinae	CEDZB	2
<i>Myzinum</i> sp. – Myzininae	CEDZB/ USP - RPSP	8
<i>Rhopalosoma</i> sp. – Rhopalosomatidae	CEDZB	2

Appendix 3 – List of the described characters and their coding

1. Supra antennal projection on the head: Absent (0); Present (1).
2. If present supra-antennal projection: forms a plate (0); reduced forming lobes on the antennae insertion (1). Coded as a contingent character in relation to [1].
3. If present supra-antennal projection forms a plate with margin: rounded (0); triangular – V-shape carina (Turner 1908) (1); straight (2); rounded apically split (3); and plate reduced (4). Coded as a contingent character in relation to [2].
4. If supra-antennal projection does not form a plate, it is reduced: evident only by the margins (0); region of the plate marked but not salient (1). Coded as a contingent character in relation to [2].
5. Supra-antennal projection directly connected with clypeus: Absent (0); Present (1).
6. Position of antennae insertion: On the junction clypeus/frons (0); Under frontal plate (1); Upwards, apart from the clypeus (2).
7. Eleventh antennal flagellum with bevel apex: Absent (0); Present (1).
8. Modification on the antennal flagellum: Absent (0); Two different textures on the internal and external side of each flagellum (1); A pair of spines in the flagellum junction (2).
9. Posterior region of the head with an excavation: Absent (0); Present (1).
10. Cross carina on the frontal top of the head: Absent (0); Present (1).
11. Expanded ocelli: Absent (0), Present (1).
12. Inner margin of the composed eye incised – eye shape reniform: Absent (0); Present with deep incision (1); Present with slight incision (2).
13. Outer face of the composed eye with longitudinal carina: Absent (0); Present (1).
14. Apex of the gena apically projected: Absent (0); Rounded (1); Acute (2).
15. Malar space: Absent (0); Present (1).

16. Basal maxillary palps enlarged and covered with long setae (Brown 2001): Absent (0); Present (1).
17. Inner margin of the mandible with a basal denticle: Absent (0); Present (1).
18. Mandible medially deep curved: Absent (0); Present (1).
19. Mandible deep curved on the apex: Absent (0); Present (1).
20. Mandible apex separate from clypeus forming a space between clypeus apical margin and mandible apex: Absent (1); Present (1).
21. Apical mandible tooth: One tooth (0); One apical tooth and one subapical tooth (1); Three apical teeth (2).
22. Subapical tooth of the mandible is enlarged: Rounded lateral margin (0); Acute lateral margin (1). Coded as a contingent character in relation to [21].
23. Mandible with carinas on the outer face: Absent (0); Present (1).
24. If mandible has apical and subapical tooth: subapical tooth is short and rounded (0); subapical tooth is strongly reduced (1); subapical tooth is enlarged with bilobate margin (2); subapical tooth is enlarged with straight margin (3); subapical tooth is subtriangular (4). Coded as a contingent character in relation to [21].
25. Subapical tooth broadly apart from apical tooth: Absent (0); Present (1). Coded as a contingent character in relation to [21].
26. Mandible straight: Absent (0); Present (1).
27. Concavity of the clypeus (Adapted from Carneio, 2017): Clypeus flattened (0); Clypeus slightly convex – slightly bulging clypeus (1); Clypeus strongly convex – strongly bulging clypeus (2).
28. Clypeus apically elongated: Absent (0); Present (1).

29. If clypeus is elongated: elongation is not constricted (0); elongation is constricted (1).
Coded as a contingent character in relation to [28].
30. Clypeal apex with lateral sides notched: Absent (0); Present (1).
31. Clypeus apical margin: straight (0); rounded (1); tridentate (2); notched (3); with a central invagination (4); with a central evagination (5); bilobate (6); sinuous (7); trilobate (8); teeth formed by invagination with polish excavation (9).
32. If clypeus is notched: Deep notched (0); Slightly notched (1). Coded as a contingent character in relation to [30].
33. Teeth in the apical margin of the clypeus formed by central invagination (Adapted from Carnimeo, 2017): teeth acute and towards down (0); teeth soft and slightly to the sides (1). Coded as a contingent character in relation to [31].
34. Teeth acute (Turner 1927) formed by a central invagination: invagination reaches lateral side (0); invagination reaches the middle of the lateral sides (1). Coded as a contingent character in relation to [33].
35. Invagination forming an apicomedial excavation in the apical margin of the clypeus: Absent (0); Present (1).
36. Tree teeth clypeus: three acute teeth (0); two acute lateral teeth and one central rounded tooth (1). Coded as a contingent character in relation to [31].
37. Sagittal carina on the clypeus (Brown, 2001): Absent (0); Present from proximal margin until the middle of the clypeus (1); Present from proximal until the apical margin of the clypeus (2).
38. Multiple curved sagittal carina on the clypeus: Absent (0); Present (1).
39. Nose-like modification on the clypeus: Absent (0); Present (1).

40. If is present, nose-like shape: parrot beak-like projection (0); acute projection (1); acute curved (2); rounded (3). Coded as a contingent character in relation to [39].
41. Flattened polish triangle on the clypeus plate: Absent (0); Present (1).
42. Apical margin of the clypeus carinate: Absent (0); Present (1).
43. Triangular polish excavation on the clypeus plate: Absent (0); Present (1).
44. Clypeus with an inverted V-shaped carina (Brown, 2011): Absent (0); Present (1).
45. Clypeus transversely depressed submedially (Genise and Kimsey 1991): Absent (0); Present (1).
46. Proximal margin of the pronotum with carina: Present (0); Absent (1).
47. If proximal carina on pronotum is present: Slight carina (0); Well-marked flattened carina (1); Well-marked rounded carina (2). Coded as a contingent character in relation to [46].
48. Pronotum with cross grooves: Absent (0); Present (1).
49. Pronotum in dorsal view: Short (0); Long (1.5 or 2 times longer than short pronotum) (1).
50. Proximal margin of the pronotum angulate: Absent (0); Present (1).
51. Fovea on the mesopleura: Absent (0); Present upwards (1); Central fovea (2).
52. Transversal groove on the mesopleura: Absent (0); Present (1).
53. Tegula: not expanded over the basis of the forewing (0); expanded over the base of the forewing (1).
54. Forewing with three submarginal cells: Absent (0); Present (1).
55. Venation in the hindwing reaching the apex: Absent (0); Present (1).
56. The 2r-m cell in the forewing: Absent (0); Present (1).

57. If 2r-m cell in the forewing is present it is closed: Absent (0); Present (1). Coded as a contingent character in relation to [56].
58. The 2r-m cell angulate: Absent (0); Present (1). Coded as a contingent character in relation to [56].
59. The 2rs-m reaching 2mc-u: Absent (0); Present (1). Coded as a contingent character in relation to [56].
60. Pterostigma in the hind wing: Absent (0); Present (1).
61. Jugal lobe in the hindwing: Not well marked (0); Well marked by a deep incision (1).
62. Hindwing with more than four closed cells: Absent (0); Present (1).
63. Cavity well marked in the mesepisternum in ventral view: Absent (0); Present (1).
64. Coxa of the foreleg expanded laterally: Absent (0); Present – well pronounced (1); Slightly pronounced (2).
65. Coxa of the foreleg flattened ventrally: Absent (0); Present (1).
66. Base of the femur of the foreleg bilobate: Absent (0); Present (1).
67. Apex of the femur of the foreleg with a spine: Absent (0); Present (1).
68. Mid coxa and hind coxa apart: Absent (0); Present (0).
69. Apex of the coxa of the mid leg bilobate: Absent (0); Present (1).
70. Trochanter of the mid leg with acute apex: Absent (0); Present (1).
71. Coxa of the poster leg with carina forming a tooth: Absent (0); Present (1).
72. Serrate on the outer face of the posterior tibia: Absent (0); Present (1).
73. Coxae of the posterior leg apart from each other: Absent (0); Present (1).
74. Apex of the femur of the posterior leg elongated over the basis of the tibia: Absent (0); Present (1).

75. Apex of the femur of the posterior leg asymmetric: Absent (0); Present (1). Coded as a contingent character in relation to [74].
76. If apex of the femur of the posterior leg is asymmetrical, the inner lamella is two times longer than the outer lamella: Absent (0); Present (1). Coded as a contingent character in relation to [75].
77. Tarsal claw bidentate: Slightly asymmetrical (0); Strongly asymmetrical with inner claw enlarged.
78. Carinas on propodeum forming sculptures: Present (0); Absent (1).
79. Propodeum concavity of distal region: Not flattened (0); Posterior region deeply flattened (1); Posterior region deeply flattened and apart from proximal region by a transversal carina (2).
80. Triangular metanotum expanded over the propodeum: Absent (0); Present (1).
81. Metapostnotum visible: Absent (0); Present (1).
82. Tergum one petiolate nodosum: Present short (0); Present with tergum one very elongated (1).
83. Wisp of hairs on the first metasomal sternite (Adapted from Carnimeo, 2017): Absent (0); Present (1).
84. Longitudinal sulcus on tergum one: Absent (0); Present, extending from base of the tergum to the middle (1); Present, trans-passing middle of the tergum.
85. Tubercle (protrusion) spiracle aperture raised in tergum one (Adapted from Carnimeo, 2017): Absent (0); Present (1).
86. Longitudinal sulcus on sternum one: Absent (0); Present (1).
87. Ventral expansion in the metasomal sternum one: Absent (0); Callosity (1); Callosity with acute apex (2); Carinate callosity (3).

88. Longitudinal carina on the metasomal sternum one: Absent (0); Present with denticles (1); Present with carina forming a denticle (2).
89. Hook-like modification in the metasomal sternum one: Absent (0); Present (1).
90. Sternum one and sternum two apart from each other and sternum two ventrally expanded: Absent (0); Present (1).
91. Acute expansion in the lateral side of the sternite six: Absent (0); Present (1)
92. Lateral callosity in the metasomal sternites: Absent (0); Callosity from sternum three to sternum five (1); Callosity from sternum two to sternum six (2); Callosity being elongated until forming a spine from S2 to sternum five (3).
93. Hypopygial plate modified in a hook: Absent (0); Present with hypopygial plate expanded in the basis and apical hook (1).
94. Hypopygium with an apical tooth: Base rounded and a denticle on the apex (0); Subquadrate with a denticle on the apex (1); Long curved tooth (2); Rounded in the base and straight long apical tooth (3); Serrated lateral with a long tooth (4).
95. Hypopygium tridentate – two lateral invaginations: three acute teeth (0); almost straight lateral with a long central tooth (1); two lateral teeth to the sides and a central long apical tooth (2); three rounded teeth (3).
96. Hypopygial plate rounded: Simple rounded (0); Ligulated (1); Enlarged (2).
97. If hypopygium plate is enlarged: Rounded (0); Acute (1). Coded as a contingent character in relation to [96].
98. Hypopygial plate narrow: Absent (0); Present (1).
99. Apical margin of the hypopygium with spines: Absent (0); Present (1).

100. Apical margin of the epipygium: With transparent lamellae well marked following the apical margin (0); With rounded margin following the apical margin (1); Lamellae under the hypopygial plate (2).
101. Epipygium flattened on the genital aperture: Absent (0); Present (1).
102. If epipygium is flattened: Completely flattened (0); Rounded on the basis and flattened posteriorly (1). Coded as a contingent character in relation to [101].
103. If epipygium is not flattened is bulging: Absent (0); Present (1). Coded as a contingent character in relation to [101].
104. When epipygium is flattened without lamellae: Margin is straight (0); Margin is rounded (1).
105. Sagittal carina on the epipygium plate: Absent (0); Multiple longitudinal carinas (1); Multiple Curved carinas (2).
106. Longitudinal lateral carina: Absent (0); Present (1).
107. Transversal carina in the apical margin of the epipygium: Absent (0); Present (1).
108. Longitudinal carina in the apical margin of the epipygium: Absent (0); Present (1).
109. If longitudinal lateral carina is present in the epipygium, it is modified in lobes: Absent (0); Present (1). Coded as a contingent character in relation to [108].
110. Rounded plate overlapped to the epipygium plate: Absent (0); Present with groves only in the rounded plate overlapping the epipygium plate (1); Present with grooves on both epipygium plate and overlapping epipygium plate (2).
111. Tuft of hairs inwards on the top of the parameres: Absent (0); Present (1).
112. Aedeagus reduced inside the genital capsule: Absent (0); Present (1).

Appendix 4 – List of records for the studied species

Table 1: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Acanthohynnus</i> sp.	Australia, NT keep River NP	-15.1086	129.1086	UTAH
<i>Acanthohynnus</i> sp.	Australia, Western Australia Marble Bar 131km E, 300m	-21.29	121.225	UTAH
<i>Aeolothynnus</i> sp. 1	Australia, Vic. 37Km N Hwy 1 on Pinnaroo Rd	-37.919	145.0458	UTAH
<i>Aeolothynnus</i> sp. 2	Australia, W Aust., Moresby Range Oakajee dist.	-28.5963	114.6105	UTAH
<i>Aelurus albofascies</i>	Argentina, Cataratas do Iguazu, Misiones	-25.6999	-54.4402	Kimsey 1991
<i>Aelurus albofascies</i>	Brazil, Ubatuba Parque Estadual da Serra do Mar. Núcleo. Picinguaba. Alt. 203m, São Paulo state	-23.319	-44.818	MZUSP
<i>Aelurus ater</i>	Chile, Nuble: Las Trancas, SE Recinto in Chillan area 1100m	-36.7218	-71.7628	AMNH
<i>Aelurus ater</i>	Chile, Santiago	-33.4691	-70.642	CMNH
<i>Aelurus ater</i>	Chile, Vilches	-35.5654	-71.1733	CMNH
<i>Aelurus gayi</i>	Chile, Concepcion	-36.8189	-73.0503	Kimsey 1991
<i>Aelurus gayi</i>	Chile, Valparaiso	-33.0456	-71.6204	CMNH
<i>Aelurus gayi</i>	Chile, Coquimbo	-29.9537	-71.3437	Kimsey 1991
<i>Aelurus gayi</i>	Chile, Illapel	-31.6293	-71.1625	Kimsey 1991
<i>Aelurus gayi</i>	Argentina, Território Rio Negro	-40.6536	-66.5611	AMNH
<i>Aelurus gayi</i>	Chile, Las trancas, SE Recinto in Chillan area 1100m	-36.9134	-71.4984	AMNH
<i>Aelurus gayi</i>	Chile, Malleco: Victoria	-38.2327	-72.3515	AMNH

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Species	Locality	Latitude (°)	Longitude (°)	References
<i>Aelurus gayi</i>	Chile, Osorno Prov PN Puyehue 600m Ag. Calientes to 2km	-40.5762	-74.2508	NMNH
<i>Aelurus gayi</i>	Chile, Santiago	-33.4691	-70.642	CMNH
<i>Aelurus plaumani</i>	Brazil, Rio de Janeiro, Mangaratiba	-22.9599	-44.0414	NMNH
<i>Agriomyia</i> sp. 1	Australia, NS Wales Austral	-33.8253	151.2519	AMNH
<i>Agriomyia</i> sp. 2	Australia, S Wales Austral	-33.8253	151.2519	AMNH
<i>Agriomyia luctuosa</i>	Australia, Bombala NSW	-36.9123	149.2382	NMNH
<i>Agriomyia luctuosa</i>	Australia, Moreton Bay	-27.2061	153.2504	NMNH
<i>Agriomyia luctuosa</i>	Australia, New South Wales	-33.8253	151.2519	Turner 1910/ NMNH
<i>Anodontyra haarupi</i>	Argentina, Chubut prov. 3km N puerto Lobos, 20m	-42.0037	-65.0741	NMNH
<i>Anodontyra haarupi</i>	Argentina, Neuquen, 25 km E. Pto trown Rio Malleo	-38.9353	-69.2538	UTAH
<i>Anodontyra haarupi</i>	Argentina, Santa Rosa, Mendoza	-36.6182	-64.2597	Turner 1909
<i>Anodontyra haarupi</i>	Argentina, Mendoza	-32.8834	-68.8406	Turner 1910/NHM
<i>Anodontyra haarupi</i>	Argentina, Neuquen Prov Mariano Moreno 750m	-38.7326	-70.0107	NMNH
<i>Anodontyra haarupi</i>	Argentina, Neuquen: Rio Agrio, N-Zapala	-38.9529	-68.1767	AMNH
<i>Anodontyra haarupi</i>	Argentina, Rio Negro Choele- Choel	-39.2894	-65.6623	AMNH
<i>Anodontyra tricolor</i>	Chile, Concepcion	-36.8191	-73.05	NHM
<i>Anodontyra tricolor</i>	Chile, FDO El Radal Cord. Talca	-35.4355	-70.9393	CMNH

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Species	Locality	Latitude (°)	Longitude (°)	References
<i>Anodontyra tricolor</i>	Chile, Nuble: El Marchant, in Chilán area	-34.4663	-71.6775	AMNH
<i>Anodontyra tricolor</i>	Chile, Santiago	-33.4691	-70.642	CMNH
<i>Anodontyra tricolor</i>	Chile, Talca: Alto Vilches	-35.7064	-71.3027	AMNH
<i>Anodontyra tricolor</i>	Chile, Tongoy Coquimbo	-30.2519	-71.4998	CMNH
<i>Ariphron tryphonoides</i>	Australia, Wannon Vic	-37.6707	141.8385	NMNH
<i>Ariphron tryphonoides</i>	South - Australia, Adelaide - holotype	-13.2247	131.1111	Smith 1859
<i>Ariphron tryphonoides</i>	Austrália: S.A. Adelaide	-34.929	138.5974	Smith 1859
<i>Belothynnus</i> sp.	Australia, WA Drummond Cove, t mi N og Geraldton	-28.6714	114.6126	UTAH
<i>Belothynnus</i> sp.	Australia, Quensland	-20.912	142.7078	AMNH
<i>Brethynnus infernalis</i>	Argentina, Tucuman	-26.8607	-65.3143	Turner 1910
<i>Brethynnus infernalis</i>	Argentina, Catamarca Minas Capillatas 50km Andalgala	-27.3451	-66.3761	NMNH
<i>Brethynnus infernalis</i>	Argentina, Catamarca Prov 330m Cuesta Minas Capillita	-27.3451	-66.3761	NMNH
<i>Brethynnus infernalis</i>	Argentina, Salta Province: Yacochuya, near Cafayate	-25.2434	-64.7116	AMNH
<i>Brethynnus infernalis</i>	Argentina, Santa Maria Catamarca	-26.6988	-66.0486	AMNH
<i>Brethynnus infernalis</i>	Argentina, Tafi del Valle	-26.8458	-65.7001	AMNH
<i>Brethynnus steinbachii</i>	Argentina, Salta POcitos	-24.3333	-67.0167	AMNH
<i>Brethynnus steinbachii</i>	Argentina, Salta, Cuesta obispo, 250m	-25.1767	-65.8585	AMNH

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Species	Locality	Latitude (°)	Longitude (°)	References
<i>Brethynnus steinbachii</i>	Argentina, Salta La Vira	-24.7832	-65.4104	AMNH
<i>Brethynnus steinbachii</i>	Argentina, Tucuman	-26.8083	-65.2176	Brethes 1910
<i>Brethynnus steinbachii</i>	Argentina, Salta El Maray 200m	-24.7827	-65.4122	AMNH
<i>Brethynnus steinbachii</i>	Argentina, Salta - El Maray	-25.1764	-65.7967	AMNH
<i>Brethynnus steinbachii</i> sp. 2	Argentina, Salta - El Maray	-25.1764	-65.7967	AMNH
<i>Brethynnus stygius</i>	Argentina, Catamarca Prov 3000m Cuesta Minas Capillita	-27.3451	-66.3761	AMNH/ NMNH
<i>Brethynnus stygius</i>	Argentina, Salta La Vira	-24.7832	-65.4104	AMNH
<i>Brethynnus stygius</i>	Argentina, Catamarca Capillitas, 2650 m	-27.3432	-66.3762	AMNH
<i>Brethynnus stygius</i>	Argentina, Salta Cuesta Obispo	-25.1195	-65.8589	AMNH
<i>Catocheilus apterus</i>	Australia, Victoria Austral South Eastern Australia - Tasmania	-37.4713	144.7852	AMNH
<i>Catocheilus apterus</i>	Australia, Rose Bay	-33.8705	151.2683	Turner 1910 NMNH
<i>Catocheilus inconstans</i>	Australia, Moreton Bay	-27.2061	153.2504	NMNH
<i>Dimorphothynnus</i> <i>apicalis</i>	Australia, Moreton Bay Brisbane	-27.2057	153.2532	NMNH
<i>Dimorphothynnus</i> <i>dimidiatus</i>	Australia, Botany Bay NS Wales	-33.9928	151.1755	NMNH
<i>Dimorphothynnus</i> <i>dimidiatus</i>	Australia, N.S.W., Sydney	-33.8675	151.2	Turner 1910/ NMNH
<i>Dimorphothynnus</i> <i>trunciscutus</i>	Australia, Moreton Bay	-27.2061	153.2504	NMNH
<i>Dolichothynnus</i> <i>carbonarius</i>	Brazil, Rio de Janeiro	-22.9068	-43.1729	NMNH/CMNH

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<i>Dolichothynnus carbonarius</i>	Brazil, Rio de Janeiro, Floresta da Tijuca	-22.9573	-43.2812	CMNH
<i>Doratithynnus</i> sp.	Australia, W. A. Moresby Range, Howatharra Rd.	-28.5369	114.6275	UTAH
<i>Eirone mutabilis</i>	Australia, Queensland Townesville	-19.2576	146.8179	NMNH
<i>Eirone mutabilis</i>	Australia, N. T. Adelaide	-13.2247	131.1111	Turner 1908
<i>Elaphroptera arcuata</i>	Argentina, Chubut PN Los Alerces	-42.8333	-71.8333	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Argentina, Rio Negro: San Carlos de Bariloche	-41.1333	-71.3107	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Chile, Concepcion: Salto de Laja	-37.2117	-72.3808	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Chile, Valdivia, Curico	-34.9856	-71.2416	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Argentina, Chubut	-43.6834	-69.2739	Turner 1908
<i>Elaphroptera arcuata</i>	Argentina, Patagonia	-40.7744	-72.2012	Turner 1910
<i>Elaphroptera arcuata</i>	Chile, Santiago Macul	-33.4868	-70.6038	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago San Ramon	-33.5381	-70.6417	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago: Macul, NE Santiago	-33.5	-70.5667	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Chile Santiago: Rio Yeso	-33.7295	-70.1588	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Chile Valparaiso El Salvador	-33.0494	-71.5737	Genise & Kimsey 1993
<i>Elaphroptera arcuata</i>	Chile, Aysen Coihaique	-45.5008	-72.1285	AMNH
<i>Elaphroptera arcuata</i>	Chile, Bio Bio Prov. Caledonia 700-900m	-37.7245	-72.2389	NMNH
<i>Elaphroptera arcuata</i>	Chile, Macul Santiago	-33.4868	-70.6038	Genise & Kimsey 1993

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<i>Elaphroptera arcuata</i>	Chile, Maule Prov. Rio Teno 800m ca. Aprox 40km E Curico	-34.9804	-71.217	NMNH
<i>Elaphroptera arcuata</i>	Chile, O'Higgins: Bajo de Los Maitenes W. of Rancagua, 1600m	-34.3925	-71.6205	AMNH
<i>Elaphroptera arcuata</i>	Chile, O'Higgins: Pilay NE Roncagua 800m	-33.9102	-70.5902	AMNH
<i>Elaphroptera arcuata</i>	Chile, O'Higgins: Pilay NE Roncagua 800m	-33.9167	-70.6	AMNH
<i>Elaphroptera arcuata</i>	Chile, Pucatrihue	-40.5353	-73.7088	CMNH
<i>Elaphroptera arcuata</i>	Chile, Pucon	-39.2723	-71.9776	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago	-33.4691	-70.642	CMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago Las Vacachas (vicachas)	-33.4911	-70.758	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago Macul	-33.4868	-70.6038	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago San Ramon	-33.5381	-70.6417	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago, Cjn Del Maipo	-33.8104	-70.7643	CMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago: Macul, NE Santiago	-33.5	-70.5667	AMNH
<i>Elaphroptera arcuata</i>	Chile, Santiago: Rio Yeso	-33.7295	-70.1588	AMNH
<i>Elaphroptera arcuata</i>	Chile, Valparaiso El Salvador	-33.0494	-71.5737	AMNH
<i>Elaphroptera arcuata</i>	Chile-Macul Santiago	-33.4868	-70.6038	AMNH
<i>Elaphroptera arcuata</i>	Chile-Santiago Las Vacachas (vicachas)	-33.4911	-70.758	AMNH
<i>Elaphroptera atra</i>	Argentina, Aconcagua: San Felipe	-32.7502	-70.7208	Genise & Kimsey 1993
<i>Elaphroptera atra</i>	Chile: Aysen: Aysen- Coyhaique	-45.5687	-72.0655	Genise & Kimsey 1993

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<i>Elaphroptera atra</i>	Chile: Cautín: Pucon	-39.2713	-71.9755	Genise & Kimsey 1993
<i>Elaphroptera atra</i>	Chile: Concepcion	-36.8155	-73.0495	Genise & Kimsey 1993
<i>Elaphroptera atra</i>	Chile: Coquimbo: Pichidanguí	-32.1331	-71.5333	Genise & Kimsey 1993
<i>Elaphroptera atra</i>	Chile, Concepción: Salto de Laja	-37.2117	-72.3808	Genise & Kimsey 1993
<i>Elaphroptera atra</i>	Chile, Santiago	-33.4691	-70.642	CMNH/NMNH
<i>Elaphroptera atra</i>	Chile, Angol	-37.7979	-72.7172	NMNH
<i>Elaphroptera atra</i>	Chile, Maipo	-33.8088	-70.7644	NMNH
<i>Elaphroptera atra</i>	Chile, Santiago El Canelo Maipo	-33.6796	-70.5085	AMNH
<i>Elaphroptera boliviana</i>	Bolívía, 50 mi N Potosi	-18.8451	-65.772	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Bolívía, Rio Mauri General Campero	-17.4587	-68.8872	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Bolívía, La Paz 4000m	-16.5	-68.15	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Bolívía, Cochabamba Prov: Siberia	-17.837	-64.7107	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Peru, Cuzco Prov: Machu Pichu 2400m	-13.1628	-72.545	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Bolívía, Pacajés Prov Near Caquiaviri 4000m	-17.4247	-68.7149	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Peru, Puno Prov: Puno	-15.2349	-70.0503	AMNH
<i>Elaphroptera boliviana</i>	Bolívía, Potosi Prov. E Ocuri 4000m	-18.8398	-65.7962	Genise & Kimsey 1993
<i>Elaphroptera boliviana</i>	Peru, Puno: 10milhas N Ayaviri	-14.8817	-70.5902	Genise & Kimsey 1993

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<i>Elaphroptera boliviana</i>	Bolívia, Cochabamba Prov Coari, 3500m	-17.4265	-65.5883	Genise & Kimsey 1993
<i>Elaphroptera dorada</i>	Argentina: Capillitas	-27.3532	-66.3739	Genise & Kimsey 1993
<i>Elaphroptera dorada</i>	Argentina: Catamarca	-27.0692	-66.9953	Genise & Kimsey 1993
<i>Elaphroptera dorada</i>	Bolívia, Chulumani, La Paz	-16.4296	-67.5268	NHM
<i>Elaphroptera montifascies</i>	Brazil, Rio de Janeiro, Teresópolis	-22.417	-42.9756	NHMD
<i>Elaphroptera montifascies</i>	Brazil, Rio Grande do Sul	-30.0044	-51.189	CMNH
<i>Elaphroptera montifascies</i>	Brazil, Santa Catarina Nova Teutonia	-27.159	-52.4143	Genise & Kimsey 1993
<i>Elaphroptera montifascies</i>	Brazil, Rio Grande do Sul, Pelotas	-31.7654	-52.3376	Genise & Kimsey 1993
<i>Elaphroptera montifascies</i>	Brazil, Teresópolis Brazilien	-22.417	-42.9756	Genise & Kimsey 1993
<i>Elaphroptera sanguinicaudade</i>	Chile, Metropolitana Reg. Chacabuco Prov. 9 km w. Tilttil, Cuesta La dormida	-33.0839	-70.9279	CMNH
<i>Elaphroptera sanguinicaudade</i>	Chile, Santiago Cerro Colorado near Renca	-33.39	-70.7401	AMNH
<i>Elaphroptera sanguinicaudade</i>	Chile, Santiago: Cuesta la Dormida NW of Tilttil 600- 800m	-33.0661	-71.0196	Genise & Kimsey 1993
<i>Elaphroptera sanguinicaudade</i>	Chile, Coquimbo	-29.9557	-71.3361	Genise & Kimsey 1993
<i>Elaphroptera sanguinicaudade</i>	Chile, RM:Chcabuco Caleu,nr Cerro del Roble	-33.0136	-70.9831	AMNH
<i>Elaphroptera sanguinicaudade</i>	Chile, Santiago Cerro Colorado near Renca	-33.39	-70.7401	AMNH

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<i>Elaphroptera sanguinicaudade</i>	Chile, Santiago: Cuesta la Dormida NW of Tilttil 1800-2000m	-33.0715	-70.9669	AMNH
<i>Elaphroptera sanguinicaudade</i>	Chile, Valparaíso: las Vizcachas	-32.8466	-70.6019	Genise & Kimsey 1993
<i>Elaphroptera sanguinicaudade</i>	Chile, Metropolitana Reg., Cachabuco Prov. 9km W Tilttil, Cuesta La dormida	-33.0839	-70.9279	CMNH
<i>Elaphroptera scoliaeformis</i>	Argentina, Rio Negro 7: S. C. de Bariloche Colonia Suiza	-41.128	-71.3271	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Rio Negro: 14km W Bariloche	-41.1333	-71.3107	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Cautín: La Selva W Temuco	-38.7352	-72.6183	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Aysen 26 km S Cochrane	-47.2466	-72.5774	Genise & Kimsey 1996
<i>Elaphroptera scoliaeformis</i>	Chile, Cord. Las Raices, Malleco	-38.1615	-72.5214	Genise & Kimsey 1997
<i>Elaphroptera scoliaeformis</i>	Chile, Curacautin, Malleco	-38.4405	-71.8874	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, FDO. El Radal Cord. Talca 700m	-35.4355	-70.9393	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, L. Chapo, Llanquihue	-41.4304	-72.5328	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, R. A. Neuquen Parque Nac. Lanin	-40.1663	-71.3468	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, Santiago	-33.4691	-70.642	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, Santiago, Huelquen	-33.8239	-70.6447	CMNH

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<i>Elaphroptera scoliaeformis</i>	Chile, Talca Alto de Vilches	-35.7064	-71.3027	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Valdivia	-39.8171	-73.2439	CMNH
<i>Elaphroptera scoliaeformis</i>	Chile, BioBio: El Abanico	-37.3428	-71.5336	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Cautín: Villarrica	-39.282	-72.2308	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Concepción: Salto de Laja	-37.2117	-72.3808	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Chubut: Parque Nacional Los Alerces	-42.8333	-71.8333	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Concepcion	-36.8155	-73.0495	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Chile, Curicó: Rio Colorado	-34.9791	-71.2175	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Neuquén: Parque Nacional Nahuel Huapi	-41	-71.5	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Neuquén Lago Lacar	-40.1646	-71.5097	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Rio Negro: Bariloche	-41.1333	-71.3107	Genise & Kimsey 1993
<i>Elaphroptera scoliaeformis</i>	Argentina, Rio Negro: Lago Mascaridi	-41.319	-71.5665	Genise & Kimsey 1993
<i>Elaphroptera scoliaeforms</i>	Chile, Talca Alto de Vilches	-35.7064	-71.3027	Genise & Kimsey 1993
<i>Elaphroptera scolieformis</i>	Argentina, Rio Negro 9: S. C. de Bariloche Colonia Suiza, 800m	-41.128	-71.3271	Genise & Kimsey 1993
<i>Elidothynnus melleus</i> - holotype	Australia, King George's Sound, Melbourne	-35.0333	117.9333	Smith 1859

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<i>Elidothynnus melleus</i>	Australia, Balhannah S.	-34.9902	138.827	NMNH
<i>Elidothynnus melleus</i>	Australia, Myponga S.	-35.392	138.463	NMNH
<i>Elidothynnus melleus</i>	Australia, Vic. Brisbane range	-27.471	153.0235	UTAH
<i>Elidothynnus</i> sp.	Australia, NS Wales Austral	-33.8253	151.2519	AMNH
<i>Encopothynnus</i> sp.	Australia, Western Australia; Mt Augustus Natl. Park 427m	-27.3617	116.8367	UTAH
<i>Epactiothynnus pavidus</i>	Australia, Moreby Range Red Peak Chapman Valley	-28.5013	114.7895	UTAH
<i>Epactiothynnus pavidus</i>	Australia, Woy Woy NSW	-33.4857	151.3248	UTAH
<i>Eucyrtothynnus bruchii</i>	Argentina, Tafi del Valle	-26.8459	-65.7	AMNH
<i>Eucyrtothynnus bruchii</i>	Argentina, Tucuman - Taffi	-26.8528	-65.7083	Brethes 1910
<i>Eucyrtothynnus cornutus</i>	Brazil, Rio Grande do Sul, Pelotas	-31.7654	-52.3376	NMNH
<i>Eucyrtothynnus rubescens</i>	Bolivia, Quatro Ojos	-16.8185	-63.5854	CMNH
<i>Eucyrtothynnus rubescens</i> - holotype	Brazil, San Leopoldo	-29.76	-51.1469	Brethes 1910
<i>Gerinius</i> sp.	Australia, Victoria	-37.4713	144.7852	AMNH
<i>Glottynnus lara</i>	Argentina, Catamarca	-28.4716	-65.7877	Brethes 1910
<i>Glottynnus lara</i>	Argentina, Tucuman Colalao Valle	-26.362	-65.957	AMNH
<i>Guerinius flavilabris</i>	Australia, NS Walles	-33.8253	151.2519	AMNH
<i>Guerinius flavilabris</i>	Australia, Woy Woy NSW	-33.4857	151.3248	NMNH
<i>Guerinius flavilabris</i>	Australia, National Park NSW	-33.4272	151.3418	NMNH
<i>Guerinius flavilabris</i>	Australia, Bombala NSW	-36.9123	149.2382	NMNH
<i>Iswairoides sanguinolentus</i>	Australia, Botany Bay NS Wales	-33.993	151.1755	NMNH

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Species	Locality	Latitude (°)	Longitude (°)	References
<i>Leiothynnus spinigerus</i>	Australia, Moreton Bay	-27.2061	153.2504	NMNH
<i>Leiothynnus spinigerus</i>	Australia: Qld, Stradbroke I	-27.5269	153.4647	Turner 1912
<i>Leptothynnus</i> sp.	Australia, NS Wales Austral	-33.8253	151.2519	AMNH
<i>Lestricothynnus illidgei</i> - holotype	Australia, Moreton Bay	-27.2061	153.2504	NMNH
<i>Lestricothynnus illidgei</i>	Australia: Qld, Mooraree [possibly present-day Brisbane suburb of Murarrie] near Brisbane	-27.457	153.0284	Turner 1910b
<i>Lophocheillus anilitatis</i>	Australia, Kaloruma Vic	-37.8182	145.3658	UTAH
<i>Lophocheilus froggatti</i>	Australia, Mosman, New South Wales	-33.8292	151.2441	Turner 1910/ NMNH
<i>Lophocheilus froggatti</i>	Australia: N.S.W. Woodford	-33.735	150.4791	NMNH
<i>Lophocheilus villosus</i>	Australia, Woy Woy NSW	-33.4857	151.3248	UTAH
<i>Merithynnus</i> sp.	Argentina, Catamarca Prov. Trampasacha 8 km W Chumbicha ME Irwen FD Parker 650 m	-28.8328	-66.3048	UTAH
<i>Mesothynnus gracillis</i>	Brazil, Nova Teutonia	-27.1619	-52.4171	NMNH
<i>Mesothynnus novatus</i>	Brazil, Rio de Janeiro, Mangaratiba	-22.9599	-44.0414	NMNH
<i>Neozeleboria proxima</i>	Australia: N.S.W., Leura	-33.7119	150.3309	NMNH
<i>Neozeleboria proxima</i>	Australia, NSW Bondi State, Forest	-37.1618	149.219	NMNH
<i>Ornepetes albonotata</i>	Chile, Concepcion	-36.8189	-73.0503	NMNH
<i>Ornepetes nigriceps</i>	Chile, Angol	-37.7979	-72.7172	NMNH

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Ornepetes nigriceps</i>	Chile, Santiago, Cjn. Del Maipo	-33.8104	-70.7643	CMNH
<i>Ornepetes semisinctus</i>	Chile, Las trancas Curico	-34.9796	-71.253	CMNH
<i>Ornepetes semisinctus</i>	Chile, Vilches Talca	-35.5654	-71.1733	CMNH
<i>Parelaphroptera flavomaculata</i>	Argentina, Campo San Ramon, Right bank of River Limay, about 25000m NE Bariloche.	-40.9236	-71.0902	NHMD
<i>Parelaphroptera flavomaculata</i>	Argentina, Punto Ricon Chico, Campo San Ramon Right bank of River Limay, about 25km NE Bariloche,	-40.9236	-71.0902	NHMD
<i>Parelaphroptera flavomaculata</i>	Chile, Concepcion	-36.8189	-73.0503	Turner 1910/ MZUSP
<i>Parelaphroptera flavomaculata</i>	Argentina, Punto Ricon Chico	-40.9236	-71.0902	NHM
<i>Parelaphroptera santacruciana</i> - holotype	Argentina, Santa Cruz, Patagonia	-48.62	-70.01	Brethes 1910
<i>Parelaphroptera santacruciana</i>	Uruguay, Montevideo Amer Paras Lab	-34.8175	-56.1598	NMNH
<i>Phymatothygnus monilicornis</i>	Tasmania, Laucestor	-414.332	147.1441	Rowland & Turner
<i>Phymatothygnus monilicornis</i>	Australia, Montrose Vic	-37.8104	145.3446	NMNH
<i>Pseudelaphroptera chilensis</i>	Chile, Santiago	-42.5121	-71.4476	NHM
<i>Pseudelaphroptera transandina</i>	Argentina, north-west Patagonia	-41.7276	-68.8958	Kimsey & Brown 1993
<i>Pseudelaphroptera transandina</i>	Argentina, Patagonia	-40.7744	-71.1235	NHM

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Rhagigaster</i> sp. 1	Australia, Victoria austral	-37.4713	144.7852	AMNH
<i>Rhagigaster</i> sp. 2	Australia, N. S. Wales	-33.8253	151.2519	AMNH
<i>Rostrynnus</i> sp.	Paraguay, Pacara	?	?	AMNH
<i>Rostrynnus tarsatus</i>	Brazil, Rio Grande do Sul, Pelotas	-31.7654	-52.3376	NHM
<i>Rostrynnus tarsatus</i>	Brazil, Sao Paulo, Porto Cabral Rio Paraná	-21.7387	-52.0525	MZUSP
<i>Rostrynnus tarsatus</i>	Uruguay, Rio Negro: Arroyo Negro, 15km. S. Paysandu	-32.5264	-57.8114	AMNH
<i>Scotaena clypearis</i>	Chile: Bio Bio	-36.9777	-72.3311	SDEI
<i>Scotaena duckei</i>	Brazil, Ceará, Caridade	-4.2276	-39.1907	NHM
<i>Scotaena fastuosa</i>	Bolivia, Dept Beni Rio Mamore aprox. 10km E San Antonio	-13.9654	-65.1215	AMNH
<i>Scotaena fastuosa</i>	Colombia, Meta Villavicencio	4.15	-73.6331	NHM
<i>Scotaena fastuosa</i>	Bolivia, Dept Beni Rio Mamore aprox. 10km E San Antonio	-13.9654	-65.1215	AMNH
<i>Scotaena flavovariiegata</i>	Brazil, Santa Catarina, Nova Teutonia	-27.1619	-52.4171	NHM
<i>Scotaena flavovariiegata</i>	Brazil, Rio de Janeiro Mangaratiba	-22.9599	-44.0414	NMNH
<i>Scotaena flavovariiegata</i> sp. 2	Brazil, Sao Paulo, Ubatuba, Parque Estadual da Serra do Mar. Núcleo de Picinguaba, Alt. 396m	-23.3060	-44.8100	MZUSP
<i>Scotaena horni</i>	Paraguay, Villarica	-25.7759	-46.549	SDEI
<i>Scotaena polistoides</i>	Argentina, PT Bemberg Misiones	-25.9158	-54.6151	NMNH

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Scotaena polistoides</i>	Paraguay, Asuncion, San Bernardino	-25.3106	-57.2961	NMNH
<i>Scotaena polistoides</i>	Colombia, Meta Villavicencio	4.15	-73.6333	NHM
<i>Scotaena pubescens</i>	Uruguai, Canasco (Carrasco*)	-34.8806	-56.069	NHM
<i>Scotaena pubescens</i>	Uruguay, Montevideo Amer Paras Lab	-34.8175	-56.1598	NMNH
<i>Scotaena rosenbergi</i>	Bolivia: Parotani	-17.5997	-66.3405	SDEI
<i>Scotaena vetusta</i>	Brazil, Nova Teutonia, Santa Catarina State	-27.1619	-52.4171	AMNH
<i>Scotaena vetusta</i>	Brazil, Santa Catarina, Nova Teutonia	-27.1619	-52.4171	NHM
<i>Scotaena vetusta</i>	Argentina, Victoria Misiones	-34.4691	-58.5302	AMNH
<i>Scotaena vetusta</i>	Brazil: Minas Gerais, Barbacena	-21.2219	-43.7708	Turner 1909
<i>Spilothynnus bituberculatus</i>	Argentina, Prov. Mendoza, Altura 400ft	-32.8882	-68.8345	NMNH
<i>Spilothynnus bituberculatus</i>	Argentina, Uspallata, Mendoza	-32.5921	-69.3467	AMNH
<i>Spilothynnus bituberculatus</i>	Argentina, Prov. Mendoza	-32.8895	-68.8458	Turner 1908
<i>Tachynoides flavopicta</i>	Australia, Queensland Townesville	-19.2576	146.8179	NMNH
<i>Tachynoides flavopicta</i>	Indonesia, Aru Is	1.8875	125.0987	Turner 1910
<i>Tachynomyia adusta</i>	Australia, Argalong Buccleugh NSW	-35.2589	148.4857	NMNH
<i>Tachynomyia</i> sp.	Australia, Qld Brisbane Forest Park	-27.4181	152.8369	UTAH
<i>Telephoromyia rhombica</i>	Argentina, Salta El Maray	-24.7827	-65.4122	AMNH
<i>Telephoromyia rhombica</i>	Argentina, Catamarca	-28.4716	-65.7877	Brethes 1910

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Telephoromyia rhombica</i>	Argentina, Salta Alto de Tastil, 3100m	-24.7379	-65.3986	AMNH
<i>Telephoromyia rufipes</i>	Argentina, Rio Negro, Lamarque	-39.4256	-65.702	AMNH
<i>Telephoromyia rufipes</i>	Uruguay, No Montevideo Amer Paras lab	-34.8175	-56.1598	NMNH
<i>Telephoromyia rufipes</i>	Argentina, Córdoba	-31.4541	-64.1897	Brethes 1910
<i>Telephoromyia rufipes</i>	Argentina, Rio Negro, Darwin	-39.2047	-65.74	AMNH
<i>Thynnoides fulvipes</i>	Australia, Port Jackson	-33.8583	151.2333	Guerin 1830
<i>Thynnoides fulvipes</i>	Australia, Epping NSW	-37.6459	145.0403	NMNH
<i>Thynnoides fulvipes</i>	Australia, N. South Wales	-33.8253	151.2519	NMNH/ Turner 1910
<i>Thynnus</i> sp.	Australia, Brown's Creek Pascoa River, N Q 200ft?	-33.862	151.21	AMNH
<i>Thynnus</i> sp.	Australia NSW 6km Narromine	-32.1833	148.1833	AMNH
<i>Thynnus</i> sp.	Australia, Brown's Creek Pascoa River, N Q Australia 200ft?	-33.4951	149.1732	UTAH
<i>Thynnus</i> sp.	Australia, Keep River. Nat. Park, Bail-Me-Up CK, 23.7km SSW Jammam Cmpgrd	-15.9653	129.0311	UTAH
<i>Thynnus</i> sp.	Australia, Northern Territory Gregory N. P., 8.3 km N Humbert lunction m	-15.6339	131.2668	UTAH
<i>Thynnus</i> sp.	Australia, W. Ivanhoe Crossing 8mi N. Kununurra	-32.5439	116.9901	UTAH
<i>Thynnus zonatus</i>	Australia, NT Katherine Gorge National Park	-14.0873	132.4971	NMNH

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Tmesothynnus ingrediens</i>	Austrália: Qld, Brisbane	-27.457	153.0284	Turner 1916
<i>Tmesothynnus ingrediens</i>	Australia, Vic: 37km N Hwy 1 on Pinnarco Eucalyptus	-37.919	145.0458	UTAH NMNH/ Turner 1910
<i>Tmesothynnus zelebori</i>	Australia, NS Wales	-33.8253	151.2519	Turner 1910
<i>Upa impreceps</i> - holotype	Paraguay, San Bernardino	-25.3106	-57.2961	Turner 1910
<i>Upa impreceps</i>	Argentina, PT Bemberg Misiones	-25.9158	-54.6151	NHM
<i>Upa longispina</i> - holotype	Brazil, São Paulo, H. Florestal J. Land -holotype	-23.4592	-46.6339	Kimsey 1996b
<i>Upa longispina</i> - paratype	Brazil, São Paulo, Cantareira	-23.458	-46.6309	Kimsey 1996b
<i>Upa longispina</i>	Brazil, Núcleo Picinguaba - Parque Estadual Serra do Mar, SP	-23.3361	-44.8375	(Justino et al. 2013)
<i>Upa longispina</i>	Brazil, Sao Paulo, Salesópolis Est. Biológica Boraceia Trilha dos Pilões	-23.6505	-45.8933	MZUSP
<i>Upa nasuta</i> - holotype	Brazil, São José do Barreiro, SP	-22.6437	-44.5795	Kimsey 1996b
<i>Upa nasuta</i>	Brazil: SP Ubatuba PESM N Picinguaba Alt 8111m	-23.297	-44.792	MZUSP/ Justino et al. 2013
<i>Zaspilothynnus carbonarius</i>	Australia, Adelaide - holotype	-34.929	138.601	Smith 1859
<i>Zaspilothynnus carbonarius</i>	Australia, Moreton	-27.2061	153.2504	NMNH

Table 1 continuation: Locality of the studied species, geographic coordinates, and reference. We used “?” when information was not available. AMNH: American Museum of Natural History, New York; CMNH: Carnegie Museum of Natural History, Pittsburgh; MZUSP: Museu de Zoologia da USP, São Paulo; NHM: Natural History Museum, London; NHMD: Natural History Museum of Denmark, Copenhagen, NMNH: National Museum of Natural History, Washington, SDEI: Senckenberg German Entomological Institute Müncheberg, Berlin, UTAH: Entomological Collection of the UTAH state University.

Species	Locality	Latitude (°)	Longitude (°)	References
<i>Zaspilothynnus interruptus</i> - holotype	Australia, New South Wales	-33.8253	151.2519	Turner 1910
<i>Zaspilothynnus interruptus</i>	?	-37.1618	149.219	NMNH
<i>Zaspilothynnus interruptus</i>	Australia, Woy Woy NSW	-33.4857	151.3248	NMNH
<i>Zeleboria</i> sp. <i>Saussure</i>	Australia, No Sidnei	-33.8675	151.207	AMNH

Supplementary Material to the Cladistic Analysis of Thynninae

The cladistic analysis presented in the manuscript was conducted under implied weighting since this kind of analysis generated a consensus topology with better resolution than the analysis conducted under equal weighting of the characters. Farris (1982, 1983) explained that the most parsimonious tree is the one that has better explained your data. During the process to obtain the results presented in the manuscript we ran the analysis under equal weighting with New Technology Search with the same parameters that were applied under implied weighting. We obtained 13 most parsimonious trees plus the consensus topology (Figure 12). The length of the trees was $L = 487$ and for the consensus $L = 575$; consistency index of the trees was $Ci = 0.324$ and $Ci = 0.275$ for the consensus; retention index for the trees was $Ri = 0.635$ and consensus $Ri = 0.537$. The consensus topology obtained under equal weighting recovered the monophyly of the subfamily, and Thynninae was divided into two clades, as it was under implied weighting. Rhagigasterini was monophyletic and Thynnini + Elaphropterini + Scotaenini was included in a polytomy. In the polytomy some of the clades that were recovered under implied weighting were recovered under equal weighting as well, however it was not possible to define their relationship with other genera. Thus, the consensus tree recovered the most inclusive groups but it was not able to define internal relationships. We calculated the support of the tree under equal weighting using Bremer analysis with default parameters and searching 100 times, the values are present in the figure 12.

As it was determined by Goloboff (2008) estimated consensus under implied weighting provided much more resolution than under equal weighting. As we could observe in Figure 1 homoplasies were important to support some clades. So, given different weights

for the characters was important to have a phylogenetic hypothesis for Thynninae. The support for the clades was calculated by different analysis based in Goloboff *et al.* (2003) that affirms that when characters have higher weights Jackknife and Bremer can lead to wrong conclusions regarding support. Symmetric Resampling “denotes the frequency of group *G* when probability of up or downweighting equals *p*.” (Goloboff *et al.* 2003, page, 328). Symmetric Resampling measures the difference of frequencies between a group and a contradictory group, while Bremer support measures the increase in length required to lose a branch (Bremer 1988). By doing the implied weighting length of the three is not comparable with the length of the three under equal weighting, so does not make sense to uses the same analysis to calculate the support.

The final topology presented in our study has homoplasies defining groups in many cases. This was observed during the morphological study, with the presence of structures in groups that are distantly related. During the morphological study, it was possible to observe an interesting and recurrent characteristic of the structures in Thynninae. In many cases, the characters are continuous with gradual and slightly differences among the states, and in many cases, it was not possible to use these characters because it was not possible to define when it was a state and when it was another state. Another important observation that was not included in our analysis are the cases when there is a variation among specimens that should be from the same species. For example: sp. 1 with clypeus “X” and hypopygium “Y”, sp. 2 with clypeus “X” and hypopygium “Z”, sp. 3 with clypeus “W” and hypopygium “Y” etc. This situation happened for *Glottynnus lara*, and for this set of species the genitalia dissection was done and surprisingly all genitalia were the same. According to Eberhard (1985) because of the rapid divergence in male genitalia it has highly specific information. Sadly, we had not

enough material to do a good comparison and see if it occurs frequently, but for sure is an interesting observation that needs to be explored.

During all the morphological study the idea of miscoupling and possibility of hybridization it was present. It is known that the fact of the males and females of different species being collected attached does not mean that it will occur fertilization. Fertilization can be prevented by many isolational barriers, as the death of sperm, or by death of the zygote due to genetic imbalances (Rao & DeBach 1969). However, thinking in terms of energy why does the males expend so much energy carrying the female and feeding her if he will not be able to transmit his genes? There is a quite extensive literature discussing hybridization in Hymenoptera parasitoids used as biological control and description of new species as a results of hybridization (de León *et al.* 2006). These questions were especially important when we found specimens from different species and genera with wing modifications that are shown in Figure 13. Could the presence of new cells, the asymmetry among left and right wing, and veins modifications be a strong evidence for mutations that could be related with hybrid forms? Unfortunately, all these observations could not be deeply studied yet, we need much more information and available specimens to have an idea about frequency of this kind of observed modifications.

All the discussion made for the obtained topology is made based on the distribution of the characters in the tree and in the relationship found in previously works made for less inclusive groups. Unluckily we do not have additional information about biology or habitat adaptation that could contribute for a discussion of the found relationship. Of course, it is one of our futures goals to contribute with this kind of information. This work, besides the cladistic analysis and new data about Thynninae distribution, represents an effort to assembly the available information about Thynninae, since one of the biggest challenges during the

work it was to gather the old literature with the new information that is available. Most basic information like species author, records for the species are not easily found, even with the amazing quantity of resources for search that we have available. In this way, we believe that this work can be a great source of information about Thynninae.

Section III: Memorandum – MSc. Cíntia Eleonora Lopes Justino

This section of my dissertation will present the steps of my academic education, with comments regarding the projects and challenges that I have gone through during my young academic career.

Research areas

Taxonomy of Tiphidae (Hymenoptera, Vespoidea). Exocrine glands of wasps and Neotropical bees.

Undergrad

2010-2012: Bachelor's Degree in Biological Sciences. Universidade Estadual Paulista Júlio de Mesquita Filho. UNESP/IBILCE, São Paulo State, Brazil.

2007- 2010: Teaching Degree in Biological Sciences. Universidade Estadual Paulista Júlio de Mesquita Filho. UNESP/IBILCE, São Paulo State, Brazil.

In some Universities of Brazil, we have opportunity to get both degrees, bachelor and teaching. I could have both done, in spite of follow the scientist carrier teaching always fascinates me.

I joint to the “Laboratório de Vespas Sociais” under supervision of Professor Fernando Noll in 2007 and started work in a project called Biota/ FAPESP. The large amount of material collected over different areas during two years made me learn how to organize my time to produce reports, sheets, and tables, and mainly, sort an amazing diversity of insects from Atlantic Forest.

Because of this work, I start to be interested in parasitoid wasps, although that was not the specialty of the laboratory, I decided to work with Tiphidae and did my undergrad

research and final work about the diversity of Tiphidae in the Atlantic Forest. As result of that, we have published two papers:

Justino, C.E., Santos E. F., Noll, F.B (2013) Geographic note on species of the genus *Upa* Kimsey, 1991 (Hymenoptera: Tiphidae, Thynninae) in the Atlantic Forest Brazil; Check List 9(5): 1057–1061.

Justino, C.E., Santos E. F., Noll, F.B (2016) Diversity of Tiphidae (Insecta: Hymenoptera) in the fragmented Brazilian semi-deciduous Atlantic Forest. J Insect Conserv (2016) 20:417–431.

Master degree

2011-2013: Master Degree in Animal Biology. Universidade Estadual Paulista Júlio de Mesquita Filho. UNESP/IBILCE, São Paulo State, Brazil. “*Análise filogenética de Scotaenini (Hymenoptera, Tiphidae, Thynninae)*.”

As result of the work that I started as undergrad, we could see how problematic it was the taxonomy of Tiphidae and how poorly known it was the group. Maybe because of the challenge I decided to keep studying Tiphidae. Having my master done was like open the Pandora’s box and discover that there was a lot of work to do, many questions to be answered and that we had a new open field to work on. The results of my thesis are under review to be published.

PhD degree

2013 – 2017: PhD candidate in Animal Biology. Universidade Estadual Paulista Júlio de Mesquita Filho. UNESP/IBILCE, São Paulo State, Brazil. “*Análise cladística e distribuição de Thynninae*”.

The Project of my PhD was a continuation of the findings of my master. We conclude that only with a global view of the subfamily we would be able to better understand the relationship among the genera.

In the beginning of my PhD, Fernando Carnimeo joined the group and has gotten interested in Tiphidae. Based on my previously results, Fernando decided to study more deeply the genus *Scotaena* and I was co-adviser of his undergrad research and final work. That was the first time that I had a colleague to discuss about “our wasps” and share how difficult and, sometimes, confused was to get information about them. This was another super important activity that I had developed during my academic formation. Being involved in a project that was not mine, helping to solve some problems (or not) and discussing about the results expanded my views about how to develop a research. Currently, Fernando Carnimeo is finishing his Master, producing a revision of the *Scotaena*.

2015- 2016 – Science without boards – Internship at the Carnegie Museum of Natural History

Brazil has an important financial project that allows graduate students to do part of their PhDs abroad. I have decided to apply for a Science Without Borders scholarship to Carnegie Museum of Natural History under supervision of Professor John Wenzel, who annually visits Brazil to teach classes in a systematics workshop, organized by our researcher group since 2008.

This experience was very important as well, gave me the opportunity to work with Professor John Wenzel and visit many other important collections of Tiphidae in the United States to do my morphological study. Study species from Australasia, that I did not have the

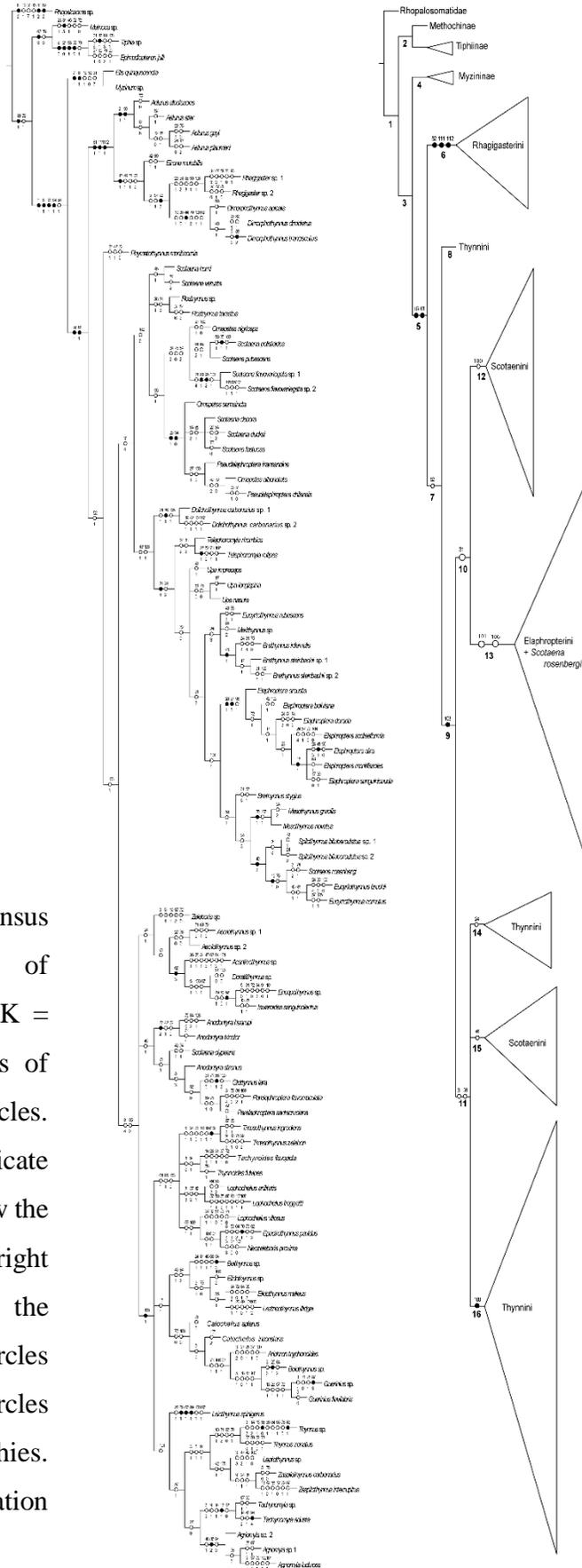
chance of include in my master was important to solve some issues and create other ones, as it is usual during a scientific work.

Of course, more than scientific skills to live in another country, learn another language and participate of another culture was an amazing and enriching experience.

In parallel with the work on Thynninae we have a partnership with professor Johan Billen, from Leuven, Belgium who is specialized in glands of insects. This partnership leads us start a collaboration to study Myzininae glands. This project has been revealed to be another area to explore, since the literature about Tiphidae glands is scarce. As a result, we will be able to publish the first description of *Myzinum* female glands, contributing with the first record of its internal morphology and the overall knowledge of the group.

Working on Tiphidae wasps has been challenging. Since the first time that I googled it and only got a single result, I realized how difficult it would be. I believe that after all this years that I have spent with Tiphidae and specially with Thynninae, I could greatly improve the knowledge about these wasps. At the same time, develop this work in a laboratory and with an advisor that gave autonomy and support for my decisions was fundamental for my growth as researcher. Therefore, this dissertation is an attempt to put together most of the information that I have been assembled studying the species and visiting important collections, combined with information that has been published, but it is hard to access.

Figure 1: Tree showing the strict consensus topology of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$. On the left side, the numbers of characters are indicated above the circles. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies. On the right side, the consensus topology shows the tribes' relationship. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies. Under each node is its unique identification number.



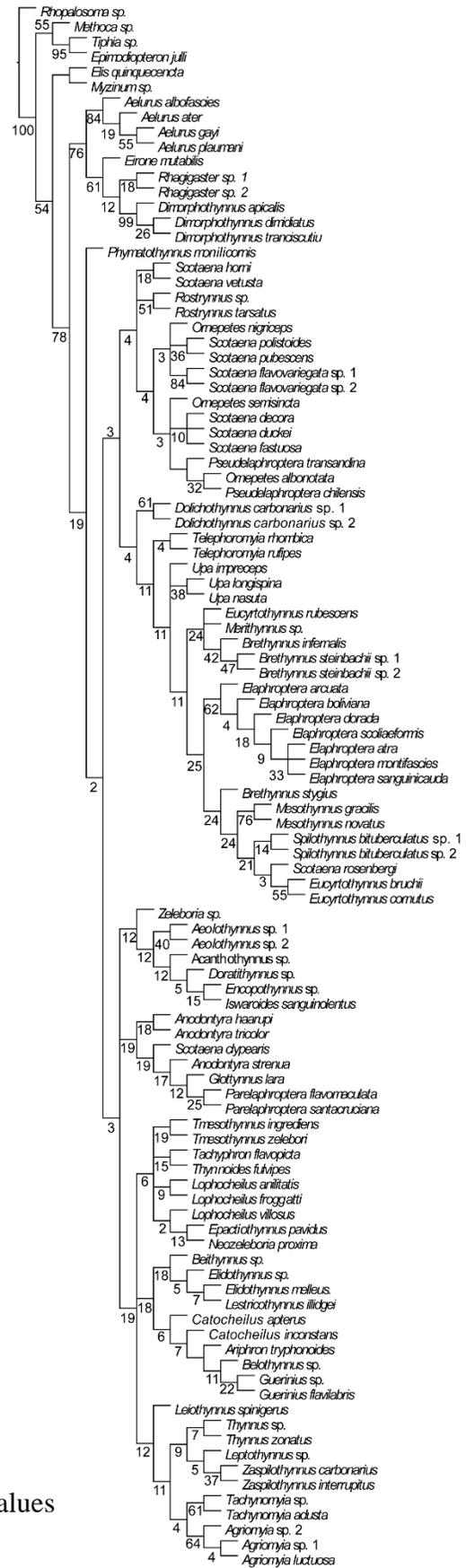


Figure 2: Consensus strict tree with resampling values listed above the nodes.

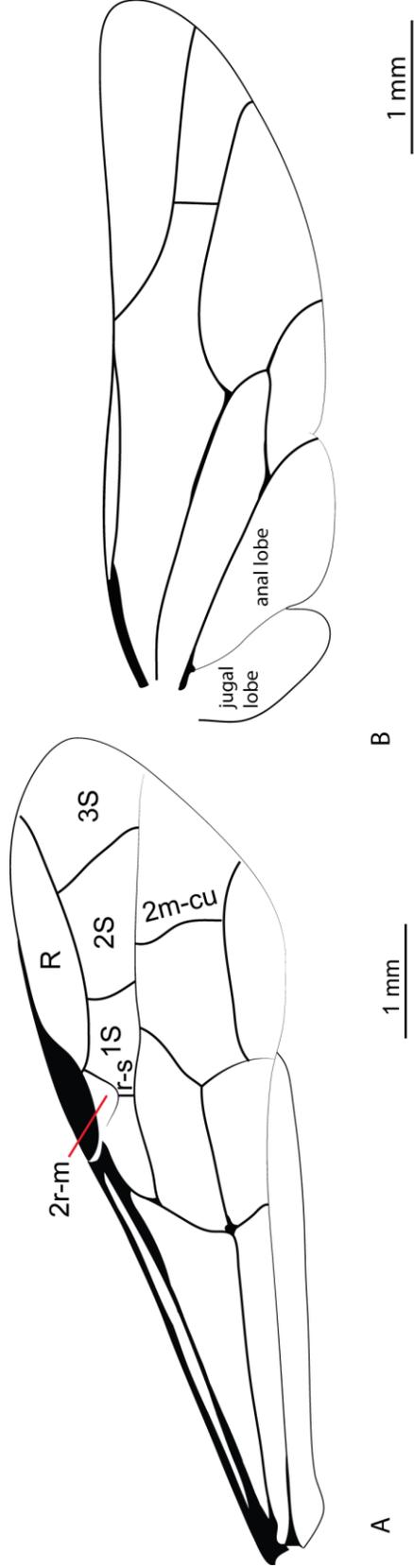


Figure 3: Thynninae wing. A: Thynninae forewing. B: Thynninae hindwing.

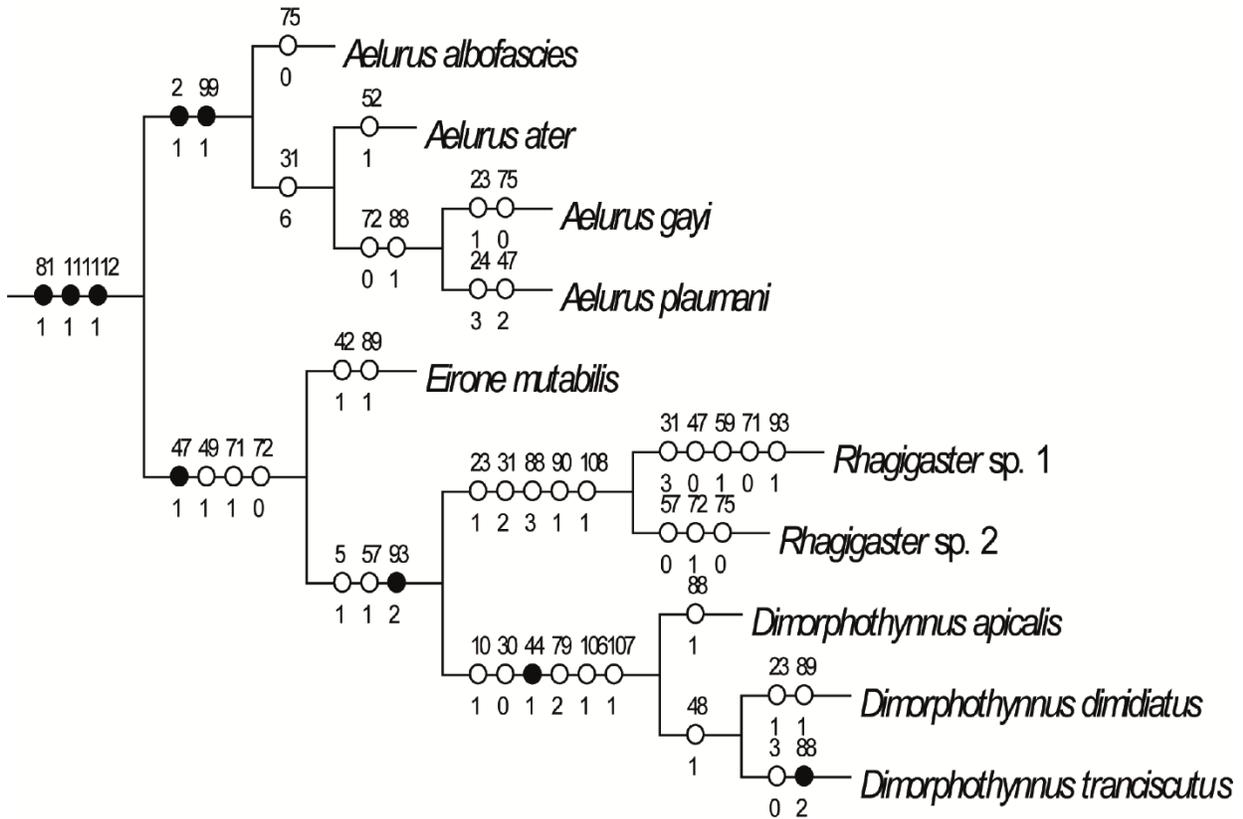


Figure 4: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; K = 18.37 showing the monophyly of the Rhagigasterini. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

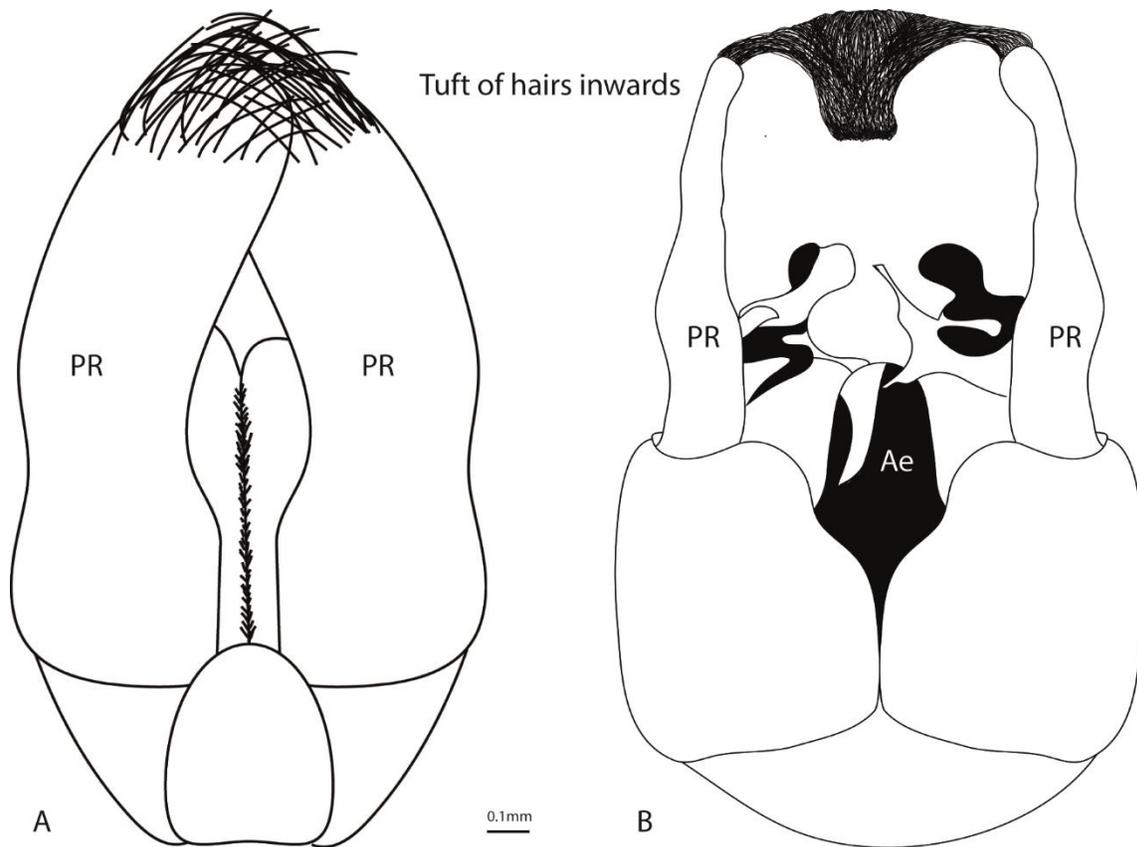


Figure 5: Aelurus genitalia. A: Aelurus nigrofasciatus dorsal view showing the tuft of hair inwards on the top of the parameres. B: A. nigrofasciatus frontal view showing the aedeagus reduced inside the genital capsule. PR: paramere Ae: aedeagus.

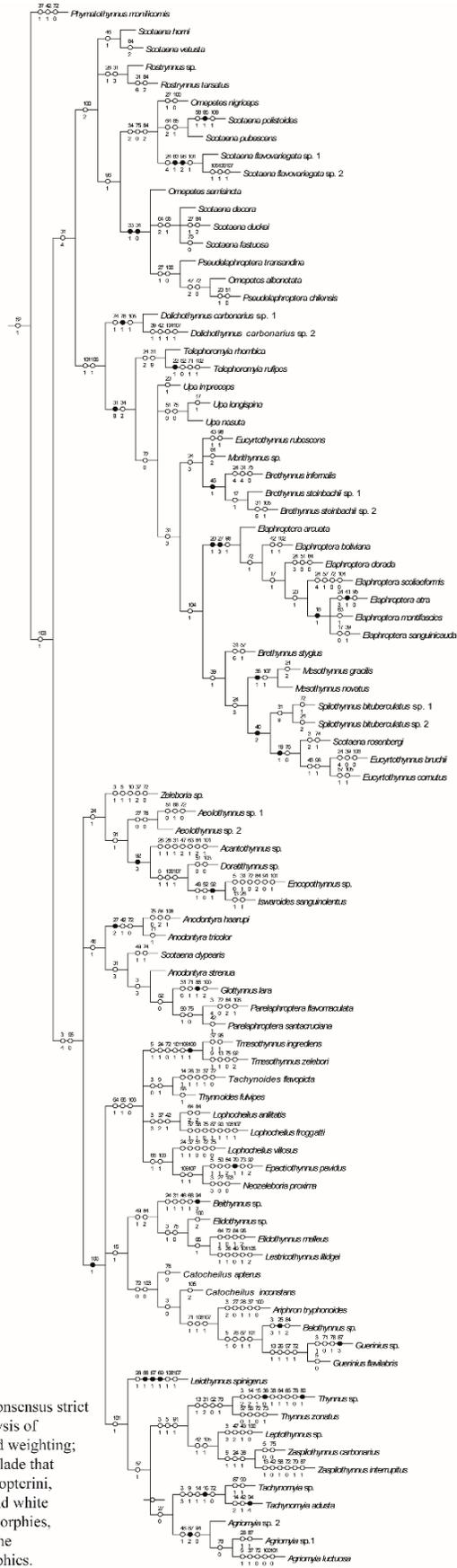


Figure 6: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 18.37$ showing the clade that groups Thynnini, Elaphropterini, and Scotaenini. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

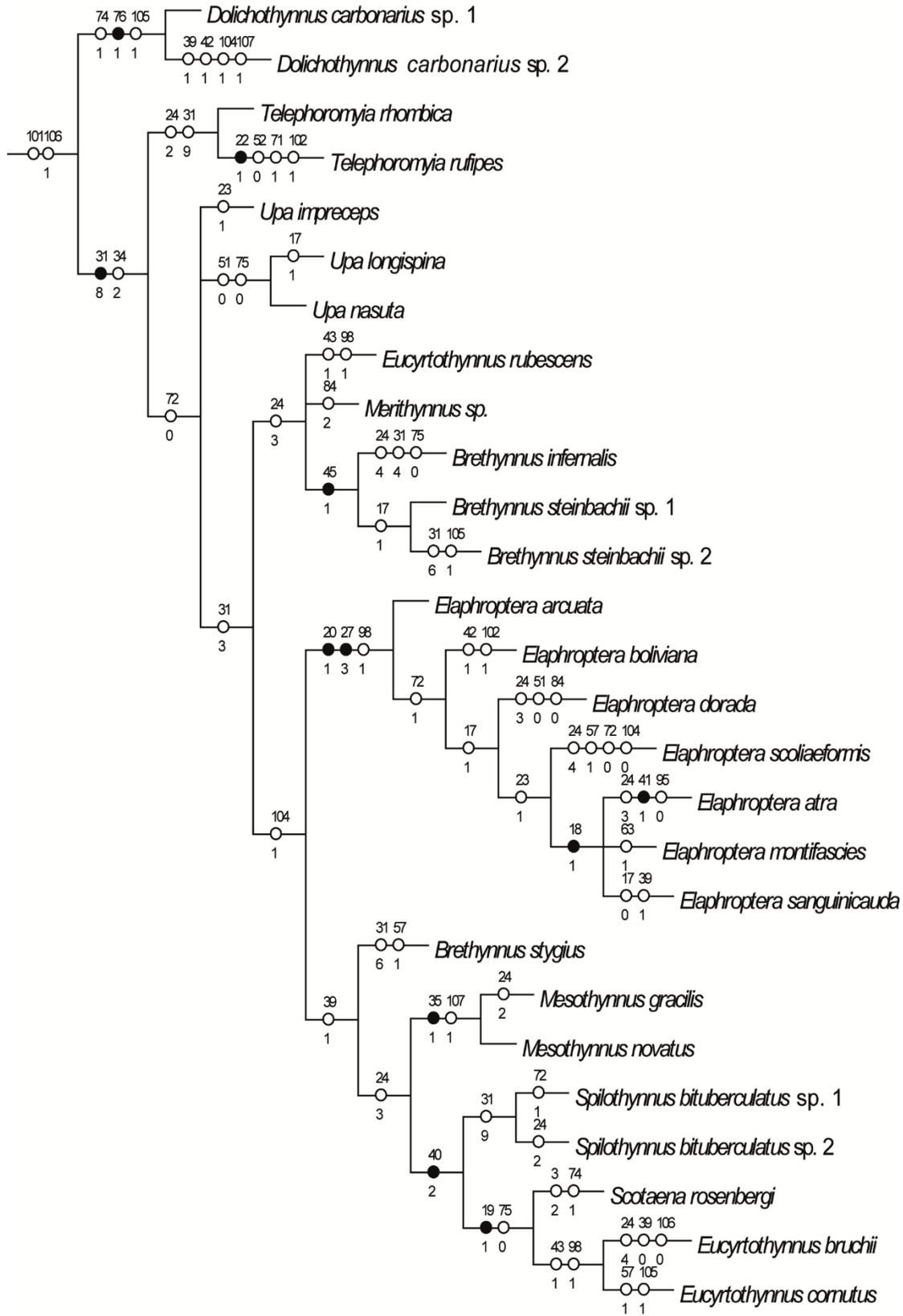


Figure 7: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; K = 18.37 showing the Elaphropterini genera. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

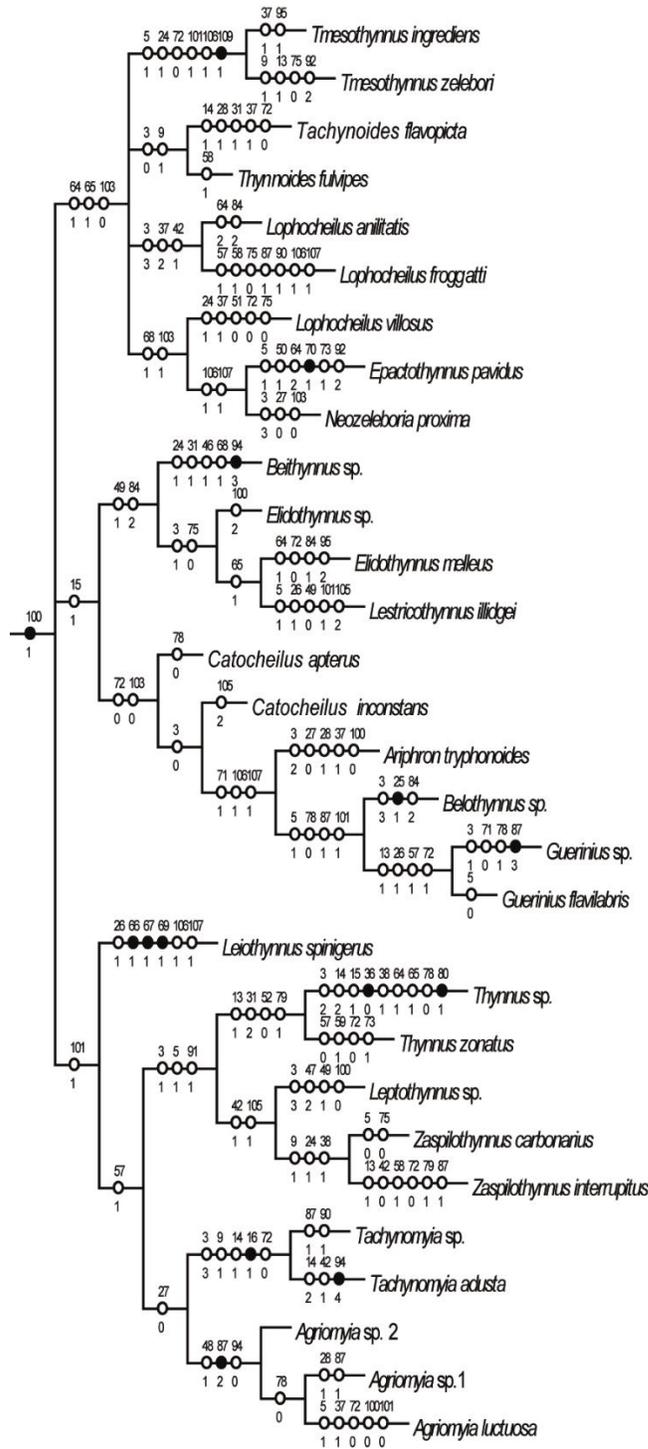


Figure 8: Detail of the consensus strict tree of the cladistic analysis of Thynninae under implied weighting; $K = 19.09$ showing the clade that group Thynnini genera by the presence of a transparent lamella in the margin of the epipygium. Black and white circles indicate synapomorphies, and white circles show the homoplastic synapomorphies.

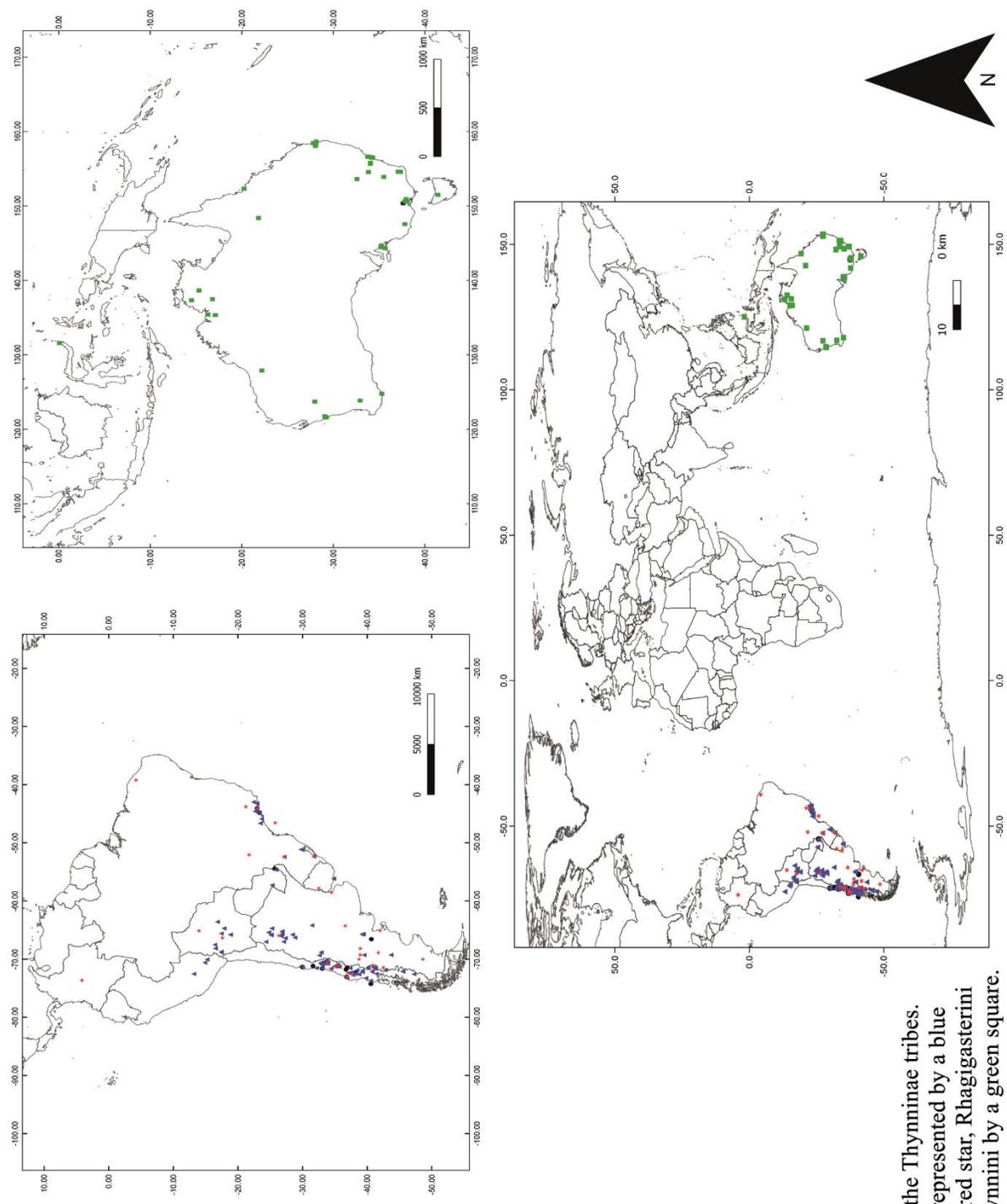


Figure 9: Distribution of the Thynninae tribes. Elaphropterini genera is represented by a blue triangle, Scotænini by a red star, Rhagasterini by a black circle, and Thynnini by a green square.

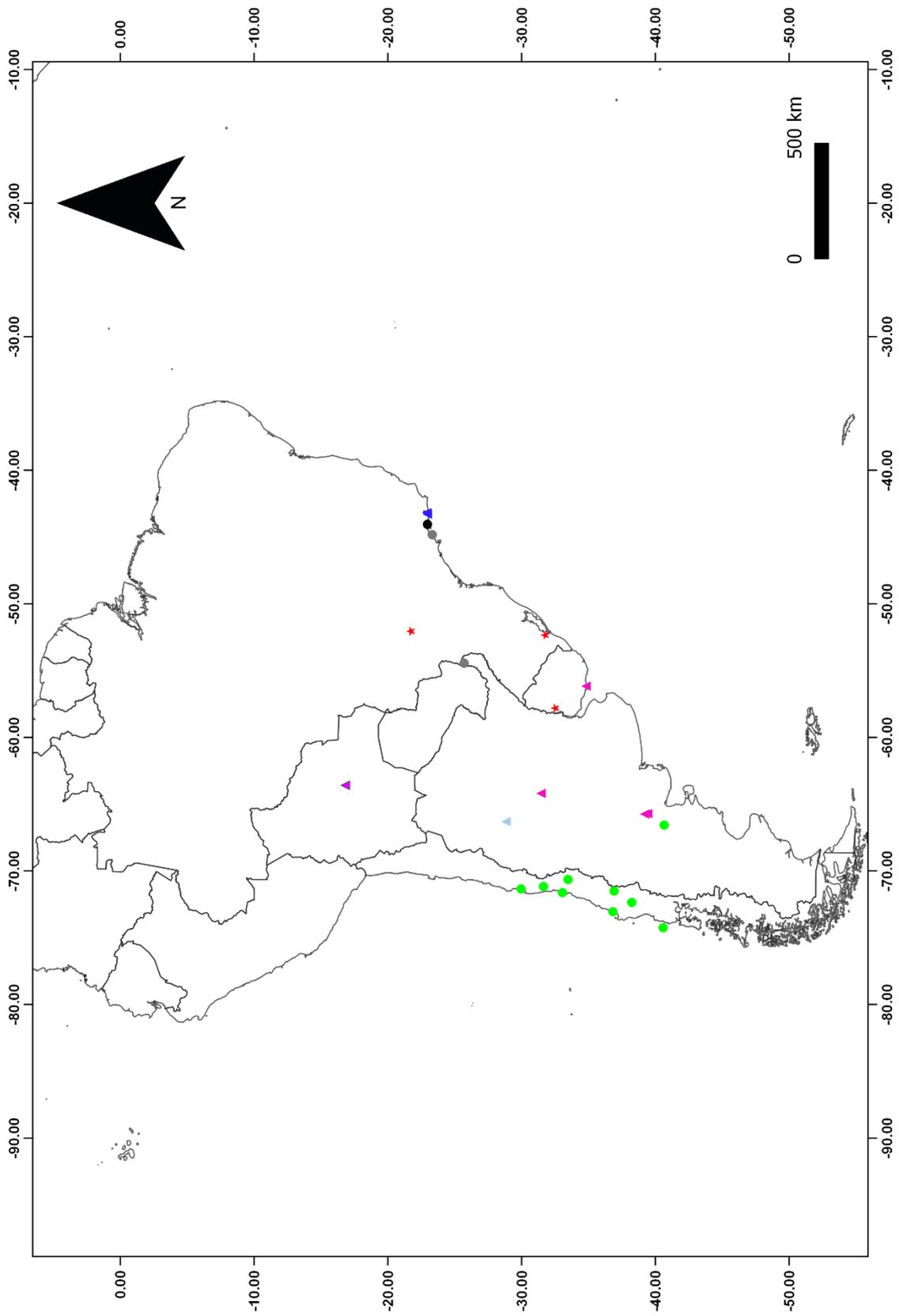


Figure 10: South American profile with new records for the Thynninae genera. Red stars represent Rostrynnus species, the black circle represents Aelurus plaumani, A. albofascies is represented by gray circles, A. gayi is represented by light green circles, light blue triangle represents Merithynnus sp., Dolichothynnus carbonarius sp.1 and D. carbonarius sp. 2 is represented by dark blue triangle, Eucyrtothynnus rubescens is represented by purple triangle, and E. rufipes is shown by pink triangle.

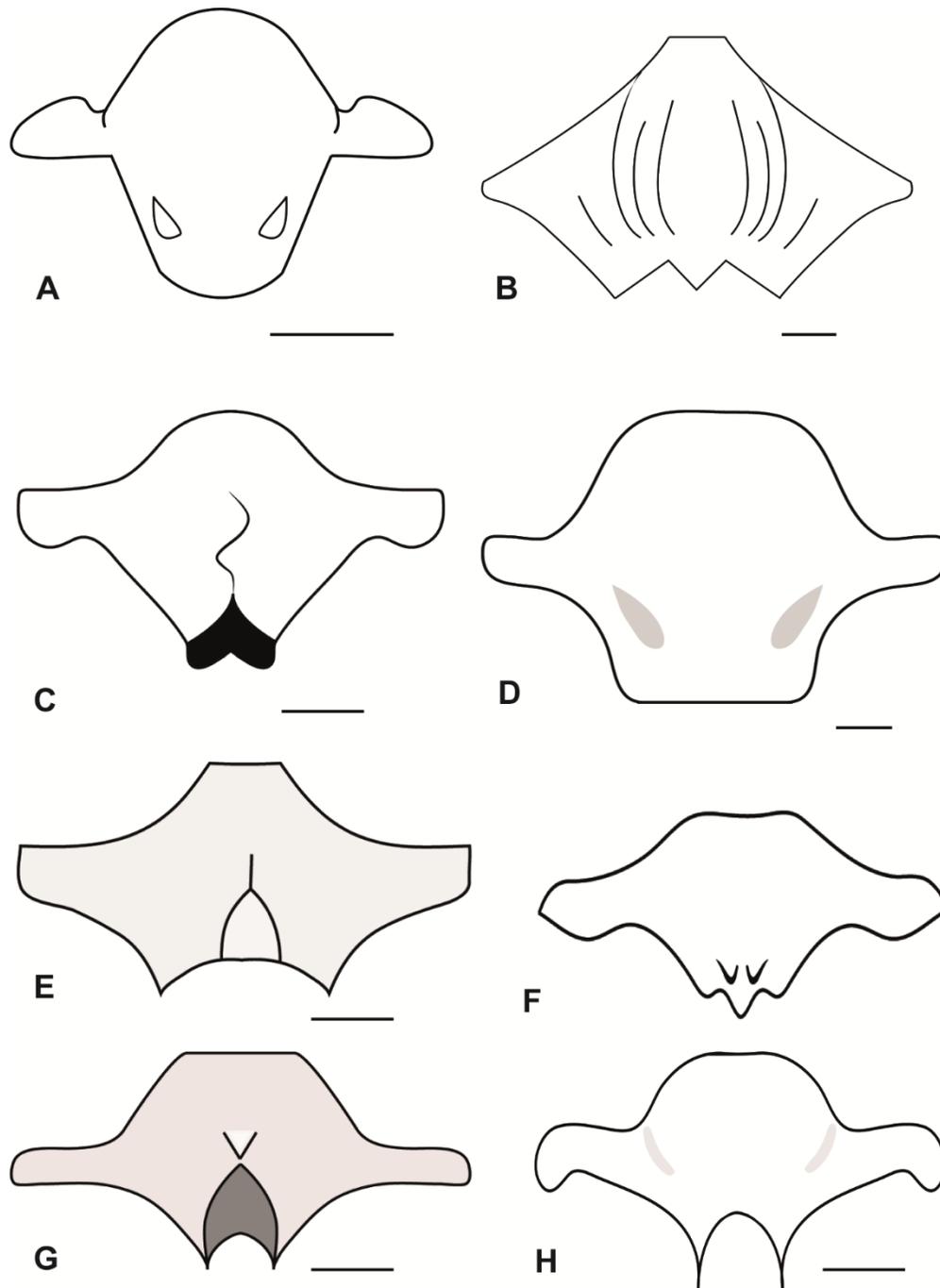


Figure 11: Thynninae clypeus plate diversity. A: Acanthothynnus sp. showing the round apical margin. B: Thynnus sp. showing the tridentate apical margin. C: Brethynnus stygius showing the bilobate apical margin. D: Guerinius sp. showing the straight apical margin. E: Elaphroptera atra showing the notched apical margin. F: Upa nasuta showing the trilobate apical margin. G: Spilothynnus bituberculatus showing the apical margin with teeth formed by invagination with polish excavation. H: Dolichothynnus carbonarius sp. 1 with two apical teeth formed by a central invagination.

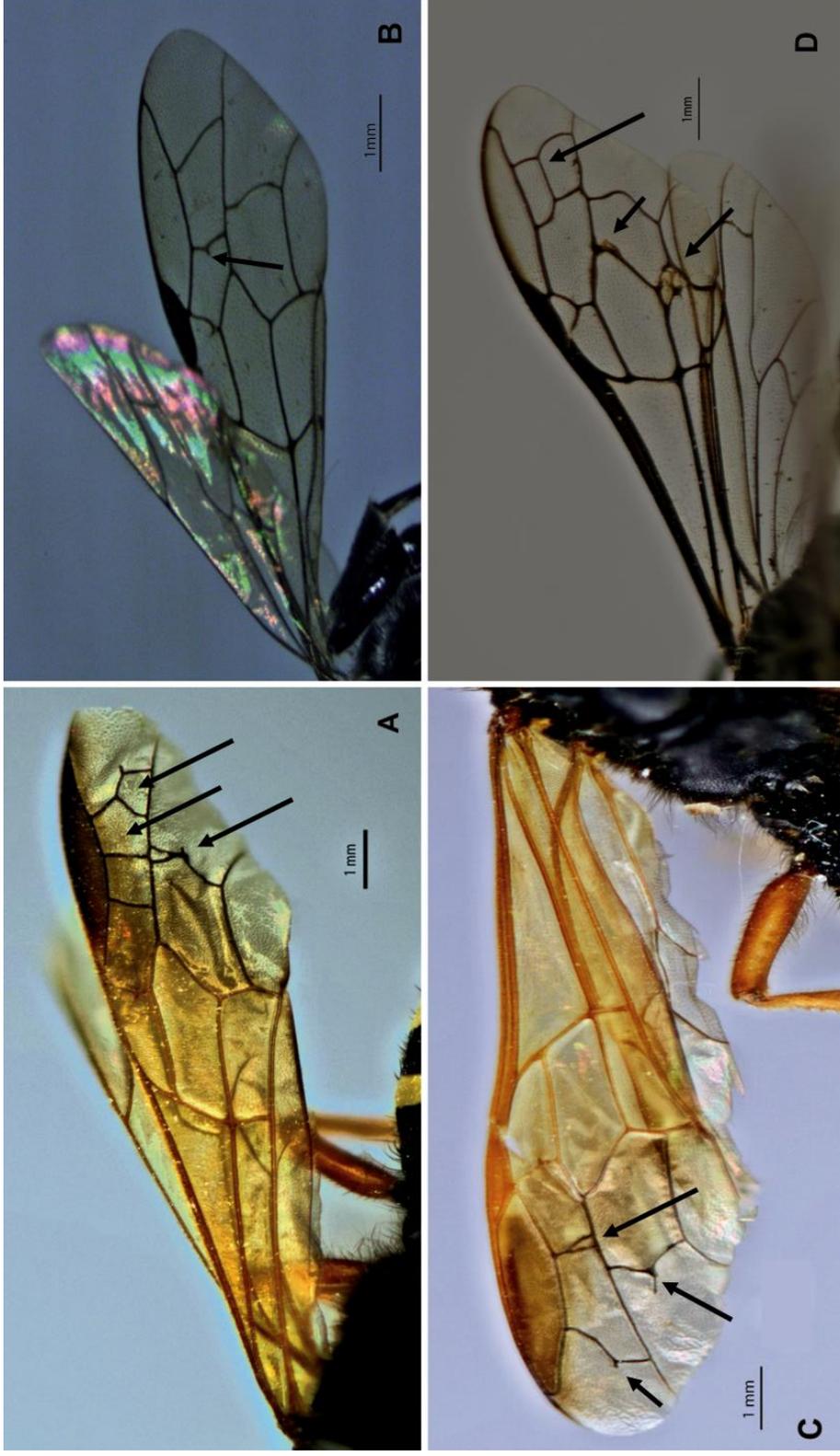


Figure 13: Forewing details of Thynninae showing modifications.

A: *Anodontyra* sp. right wing. B: *Ornepetes semisinctus* right wing.

C: *Anodontyra* sp. left wing. D: *Dimorphothynnus apicalis* right wing. Black arrows indicate the modifications.

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Autorizo a reprodução xerográfica do presente Trabalho de Conclusão, na íntegra ou em partes, para fins de pesquisa.

São José do Rio Preto, 11/05/2017



Assinatura do autor