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PHYLOGENETIC AND BIOGEOGRAPHIC ANALYSIS OF ELAPHROPTERINI (HYMENOPTERA, TIPHIIDAE, THYNNINAE)

São José do Rio Preto
2021

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biodiversidade, junto ao Programa de Pós-Graduação em Biodiversidade, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Câmpus de São José do Rio Preto.

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Resumo

Thynninae, subfamília mais especiosa de Tiphiidae (Hymenoptera, Aculeata), é atualmente dividida em quatro tribos: Scotaenini, Elaphropterini (ambas exclusivamente Neotropicais), Thynnini (exclusivamente Australásica) e Rhagigasterini (que possui representantes em ambas regiões). Elaphropterini apresenta 14 gêneros e 94 espécies, porém, além de não ter sido formalmente descrita, é tradicionalmente definida através de caracteres diagnósticos ambíguos e pouco objetivos, o que coloca em dúvida a validade da tribo. Sendo assim, o presente trabalho teve como objetivo realizar uma análise filogenética de Elaphropterini, utilizando-se enfoque cladístico e pesagem implícita, a partir de 166 caracteres morfológicos, a fim de se testar a validade da mesma e elucidar seus relacionamentos intergenéricos e interespecíficos. Foram utilizadas 49 espécies de 12 gêneros de Elaphropterini no grupo interno e 14 representantes das demais tribos de Thynninae no grupo externo. A monofilia de Elaphropterini foi recuperada em uma única árvore mais parcimoniosa, suportada por sinapomorfias exclusivas. O mesmo pôde ser observado para a maioria dos gêneros, com excessão de *Telephoromyia*, mas apesar disso, algumas relações inter-genéricas apresentaram baixo suporte e grande quantidade de homoplasias. Espécimes não identificados utilizados neste trabalho foram descritos em quatro novas espécies: *Atopothynnus tumidus* **sp. nov.**, *Mesothynnus quadratus* **sp. nov.**, *Mesothynnus sulcatus* **sp. nov**. e *Mesothynnus unidentatus* **sp. nov.** A partir desses resultados, foram realizadas as análises biogeográficas BPA e S-DIVA para se entender a origem e distribuição da tribo na América do Sul. As análises biogrográficas realizadas basearam-se na distribuição de Elaphropterini e seus grupos externos em cinco bioregiões: Paraná, Patagônia, Páramo, Puna e Australasia. Os resultados de BPA indicaram uma relação mais antiga entre Australasia e as outras regiões Sul Americanas e uma relação mais recente entre Paraná e Patagônia. Já através de S-DIVA foi possível identificar Paraná como bioregião de origem para Elaphropterini, com eventos de vicariância e dispersão possivelmente associados ao soerguimento da Cordilheira dos Andes, transgressões marinhas, e surgimento de diagonais secas que moldaram a distribuição atual da tribo.

Palavras–chave: Filogenética. Cladistica. Taxonomia; Biogeografia. América do Sul. Paraná. Patagônia. Páramo. Puna. *Atopothynnus*. *Mesothynnus*.

Abstract

Thynninae, the most species-rich subfamily of Tiphiidae (Hymenoptera, Aculeata), is currently divided between four tribes: Scotaenini, Elaphropterini (both exclusively Neotropical), Thynnini (exclusively Australasian) and Rhagigasterini (present in both regions). Elaphropterini encompasses 14 genera and 94 species, however, the tribe was never formally described and is traditionally defined by ambiguous and unobjectives diagnostic characters, putting in doubt the tribe's validity. Therefore, the present study had as objective to perform a phylogenetic analysis of Elaphropterini, which was done under a cladistic approach, using implied weighting, from a 166 morphological characters matrix, in order to test the tribe's validity and elucidate its generic and specific relationships. A total of 49 species from 12 Elaphropterini genera were used as ingroups and 14 species represented the other Thynninae tribes as outgroups. Elaphropterini's monophyly was recovered from a single most parsimonious tree, supported by unequivocal synapomorphies. The same could be observed for most genera, except *Telephoromyia,* but despite that, some of the generic relationships presented low support value and several homoplastic synapomorphies. Unidentified specimens used in this study were described in four new species: *Atopothynnus tumidus* **sp. nov.**, *Mesothynnus quadratus* **sp. nov.**, *Mesothynnus sulcatus* **sp. nov**. and *Mesothynnus unidentatus* **sp. nov.** From these results, biogeographic analyses were performed (BPA and S-DIVA) in order to clarify the origin and distribution of the tribe in South America. These analyses were based on the distribution of Elaphropterini and its outgroups through five bioregions: Paraná, Patagônia, Páramo, Puna and Australasia. BPA results indicated older relationship between Australasia and the South American regions, and more recent relationship between Paraná and Patagônia. With S-DIVA it was possible to identify Paraná as the origin bioregion of Elaphropterini, where vicariance and dispersal events possibly associated with the Andes uprising, marine transgressions and formation of dry lowlands shaped the current distribution of the tribe.

Keywords: Phylogenetics. Cladistics. Taxonomy. Biogeography. South America. Paraná. Patagônia. Páramo. Puna. *Atopothynnus*. *Mesothynnus*.

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LISTA DE ABREVIATURAS E SIGLAS

AHI: Alexander von Humboldt Biological Resources Research Institute

AMNH: American Museum of Natural History

BME: Bohart Museum of Entomology

BRI: Biosystematics Research Institute

CMNH: Carnegie Museum of Natural History, Pittsburgh, USA (J. Rawlins);

COP: Zoologisk Museum, Copenhagen, Denmark (L. Vilhelmsen);

CUIC: Cornell University Insect Collection, Ithaca, USA (C. Moreau);

DZSJRP-Hymenoptera: Coleção de Hymenoptera, Departamento de Zoologia e Botânica, São José do Rio Preto

FIGS: Figures

FSCA: Florida State Collection of Arthtopods

IBILCE: Instituto de Biociências, Letras e Ciências Exatas

INPA: Instituto de Pesquisas Amazônicas

IPE: Institute fur Pflanzenschutzforschung

MACN: Museo Argentino de Ciencias Naturales

MCZ: Museum of Comparative Zoology, Harvard University

MFN: Museum für Naturkunde Berlin

MHNG: Muséum d'histoire naturelle, Geneva

MZUSP: Museu de Zoologia da Universidade de São Paulo

NHM: The Natural History Museum

OUM: Hope Entomological Collections, Oxford University Museum

SDEI: Senckenberg Deutsches Entomologisches Institut

SMNH: Smithsonian Museum of Natural History

UFES: Universidade Federal do Espírito Santo

Summary

[1]Accompanies CD-ROM containing the appendix in a separate file.

1. INTRODUCTION

Insects (Hexapoda) constitute the most diverse group of organisms on the Earth, presenting more than one million species, which comprises 60% of the known fauna (Rafael, *et al,* 2012). The four most diverse insect orders are Hymenoptera, Coleoptera, Lepidoptera and Diptera all of which with more than 100.000 described species (Fernández & Sharkey, 2006). Hymenoptera, where are classified the ants, bees and wasps, surpasses 130,000 species, with 10,000 of them only in Brazil (Rafael, *et al,* 2012). This order contains several pollinator, predator and parasitoid species, being therefore considered largely beneficial to humans (Triplehorn & Johnson, 2011). Hymenoptera is traditionally divided into the suborders "Symphyta" and Apocrita. "Symphyta" consists in a paraphyletic group for the most basal groups of Hymenoptera. Apocrita is monophyletic and includes the majority of hymenopterans, which presents as its main characteristic the abdominal constriction (Fernández & Sharkey, 2006).

In the same way, Apocrita is divided into "Parasitica" (paraphyletic group of parasitoid wasps) and Aculeata, corresponding to the stinging hymenopterans (Hanson & Gauld, 2006). Aculeata encompasses three superfamilies: Chrysidoidea, Apoidea and Vespoidea. The last presents about 7,000 Neotropical species, with great morphological and biological diversity, and is composed by 10 families: Bradynobaenidae, Formicidae, Mutillidae, Pompilidae, Rhopalosomatidae, Sapygidae, Scoliidae, Sierolomorphidae, Tiphiidae and Vespidae (Fernández, 2001).

Tiphiidae (Hymenoptera) is a little studied family of stinging wasps, despite that more than 2,000 species and 120 genera are known (Hanson & Gauld, 2006). The family biology is largely unknown, but these wasps are traditionally referred as ectoparasitoids of scarab beetle larvae (Coleptera, Scarabaeoide), although there are records of Cerambycidae, Cicindelidae (Coleoptera), and Gryllotalpidae (Orthoptera) being parasitized by tiphiids (Brothers & Finnamore, 1995; Kimsey & Brothers, 2006;

Kimsey, 2006). Tiphiidae presents cosmopolitan distribution and is divided into seven subfamilies (Anthoboscinae, Brachycistidinae, Diamminae, Methochinae, Myzininae, Thynninae and Tiphiinae), of which Thynninae is the most species-rich (Fernández & Sharkey, 2006). The taxonomy of the South American Thynninae (Tiphiidae), similar to several Neotropical insect groups, is scarce and needs revisions. Several genera, especially *Elaphroptera* Guérin-Meneville, 1838 and *Scotaena* Klug, 1810 were considered dumping grounds for species for a long time (Genise & Kimsey, 1991; Carnimeo & Noll, 2018).

1.1 Systematics and distribution of Thynninae

The first phylogenetic analysis conducted for Thynninae (Kimsey, 1992) included only South American genera and resulted in three clades: Rhagigasterini (represented only by *Aelurus* Klug, 1840), Scotaenini (a tribe described by the author to encompass seven genera related to *Scotaena*) and a clade of 14 genera apparently related to *Elaphroptera*: *Ammodromus* Guérin-Menéville, 1838; *Argenthynnus* Genise, 1991; *Atopothynnus* Kimsey, 1991; *Brethynnus* Genise, 1991; *Chrysothynnus* Turner, 1910; *Dolichothynnus* Turner, 1910; *Elaphroptera*; *Eucyrtothynnus* Ashmead, 1903; *Merithynnus* Kimsey, 1991; *Mesothynnus* Kimsey, 1991; *Spilothynnus* Ashmead, 1903; *Telephoromyia* Guérin-Méneville, 1838; *Upa* Kimsey, 1991; and *Zeena* Kimsey, 1991. Kimsey suggests that the last 14 genera should be related to the Australian genera of the tribe Thynnini, although it was not shown in the analysis. The author provided a list of Australian species used as outgroups, but decided not to include them in the analysis' matrix, using a hypothetical ancestor instead. Years later, Kimsey (2004b) started to use the tribal name Elaphropterini when referring to the 14 genera clade established in her last analysis (Kimsey, 1992), despite never formally describing it. Besides Kimsey's studies, very little was done in the last decades in order to advance

in the knowledge of phylogenetic relationships between the Thynninae genera, particularly the Neotropical ones. Research in the group is difficult to get started regarding, mainly, the scarcity of taxonomic information and identification keys, mostly on species level, and also the impediments on obtaining deposited identified species for reference from several museums' collections.

The subfamily presents Gondwanan distribution, the tribes Elaphropterini and Scotaenini are exclusive to the Neotropical region, Thynnini is Australasian and Rhagigasterini occur in both regions (Kimsey, 1992; 2004). As well as Elaphropterini, the tribe Thynnini apparently was never formally described, being a conglomerate of the Australasian species not classified in Rhagigasterini. Despite its biogeographycally interesting distribution, studies that explore that kind of information are also scarce, and the ones that do usually are limited to cite the tribe's Gondwanan distribution, and almost never using maps for it (Kimsey, 1992; 2004; Fernández & Sharkey, 2006; Kimsey, 2006). A few studies can be cited by presenting distribution maps, and most of them are generic revisions: *Aelurus* (Kimsey, 1991b), *Elaphroptera* (Genise & Kimsey, 1993), *Upa* (Kimsey, 1996a; Justino *et al*, 2013), Rhagigasterini (Kimsey, 1996b), *Oncorhinothynnus* Salter, 1954 (Kimsey, 2000), *Merithynnus* (Kimsey, 2005). Therefore, in our previous studies, efforts were made in order to try to elucidate and present distribution patterns for the South American genera studied: *Scotaena*; *Kaysara* Carnimeo, 2018; *Pampathynnus* Carnimeo, 2018; and *Pseudoscotaena* Carnimeo, 2018 (Carnimeo *et al*, 2017; Carnimeo & Noll, 2018).

Considering all the bibliography cited above, potential distribution patterns could be observed for Elaphropterini: several species are associated to the Andean region, many others are distributed through the Atlantic Rainforest and some can be found between these regions, in the Chaco. Similar distribution patterns could be observed in

lizards and birds, that were originated in the Andean region and dispersed later to the Atlantic Rainforest through corridors of Chaco and Cerrado, respectively (Prates *et al.*, 2017; Trujillo-Arias *et al*, 2017). However, in Thynninae, we also must consider the Australasian components in order to try to understand the origin and route of diversification of the group, which can only be uncovered by systematics and biogeographic studies.

1.2 Objectives

In view of the discussed above, the present study has the following objectives:

- To conduct a phylogenetic analysis in order to test the monophyly of Elaphropterini and elucidate the relationships between its genera;
- To perform biogeographic analyses that could recognize the origin and diversification events for the Elaphropterini genera, as well as the relationship between its occurrence areas.

5. FINAL CONSIDERATIONS

The monophyly of Elaphropterini was recovered, as well as most of its genera, with exception of *Telephoromyia*. The majority of the genera obtained high support values, especially *Elaphroptera* and *Eucyrtothynnus*, that besides being the most diverse genera, showed the highest support value. On the other hand, the more inclusive clades were not well supported, what shows difficulty in uncovering the relationships between genera. Therefore, more phylogenetic studies are still needed, once intra-generic, inter-generic and tribal relationships are yet to be better understood.

In order to make studies like this feasible, collecting more specimens and producing taxonomic bibliography that allows its proper identification is still much needed, mainly on species level. Only then the use of invasive characters, such as those from genitalia and molecular data, will be possible. With the increase of sampling and phylogenetic data, description of new species and clarification of taxonomic problems will be much more viable and reliable. Revisions and phylogenetic analyses for the genera should be performed, more urgently for the most complicated ones, like *Ammodromus*, *Spilothynnus* and *Telephoromyia*.

The ancestral distribution of Elaphropterini must have been associated with tropical forests that extended through southeastern South America and north to south of the Andes, which allowed dispersal of populations, before being posteriorly isolated by increasing altitudes and formation of dry plains. This resulted in a disrupted distribution between forested highlands of four South American bioregions, although increasing number of records and altitudinal information is still needed in order to track a more accurate biogeographic history. Increasing samples for the obtainment of molecular data will also enhance biogeographic information by allowing phylogeographic studies.

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