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Phylogeny and divergence times of calyptrate flies (Diptera: Schizophora: Calyptratae), and classification of the tribe Tachinini (Oestroidea: Tachinidae).

Filogenia e tempos de divergência das moscas caliptradas (Diptera: Schizophora: Calyptratae) e classificação da tribo Tachinini (Oestroidea: Tachinidae).

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ABSTRACT

GUDIN, Filipe Macedo. **Phylogeny and divergence times of calyptrate flies (Diptera: Schizophora: Calyptratae) and classification of the tribe Tachinini (Oestroidea: Tachinidae).** 2020. 228 f. Tese (Doutorado) – Instituto de Biociências, Universidade de São Paulo, São Paulo, 2020.

In this thesis, divided in two chapters, we estimate the divergence times of Calyptratae and all its families, and we focus on the classification of the family Tachinidae proposing a phylogenetic hypothesis for the tribe Tachinini. Calyptratae is one of the most species-rich group of true flies and includes 18 families. The origin of Calyptratae was estimated between the mid-Paleocene to the Cretaceous-Paleogene boundary, but based on few taxa of some families. Using 458 species of Calyptratae, we estimate the divergence times for all families of Calyptratae, reflecting the relative diversity of species of each family. Using bayesian inference and models that include parameters of speciation, extinction and fossil sampling rates, we estimate that the origin of Calyptratae is older than previous estimates, having occurred in the mid-Late Cretaceous around 84.6 million years ago. Moreover, the diversification of all families happened throughout the Tertiary, mainly in the Eocene and Oligocene, confirming previous hypothesis of diversification of the group. In the second chapter, we focused on the classification of the family Tachinidae and worked with the tribe Tachinini, one of the largest tribes of the family. The tribe Tachinini exhibits severe problems of classification, especially in the Neotropical Region. Sampling 111 genera and 193 species of Tachinini, we propose a phylogenetic hypothesis inferred from morphological characters. Using parsimony as optimality criterion, the monophyly of Tachinini was confirmed and several genus groups were proposed and diagnosed with phylogenetic characters.

Keywords: Taxonomy. Phylogenetic systematics. Neotropical Region. Entomology.

RESUMO

GUDIN, Filipe Macedo. **Filogenia e tempos de divergência das moscas caliptradas (Diptera: Schizophora: Calyptratae) e classificação da tribo Tachinini (Oestroidea: Tachinidae).** 2020. 228 f. Tese (Doutorado) – Instituto de Biociências, Universidade de São Paulo, São Paulo, 2020.

Nesta tese, dividida em dois capítulos, nós estimamos os tempos de divergência de Calyptratae e todas as suas famílias, e focamos na classificação da família Tachinidae, propondo uma hipótese filogenética para a tribo Tachinini. Calyptratae é um dos grupos com maior diversidade de espécies em Brachycera, sendo classificado em 18 famílias. A origem de Calyptratae foi estimada entre a metade do Paleoceno e a transição Cretáceo-Paleoceno, mas baseada somente em poucos táxons de algumas famílias. Utilizando 458 espécies de Calyptratae, nós estimamos os tempos de divergência para todas as famílias de Calyptratae, refletindo a diversidade relativa de espécies de cada família. Utilizando inferência bayesiana como critério de otimização e modelos que incluem parâmetros de taxas de especiação, extinção e amostragem de fósseis, nós estimamos que a origem de Calyptratae é mais antiga que o estimado anteriormente, tendo ocorrido no Cretáceo Superior por volta de 84,6 milhões de anos atrás. Além disso, a diversificação de todas as famílias ocorreu ao longo do Terciário, principalmente no Eoceno e Oligoceno, confirmando hipóteses prévias sobre a diversificação do grupo. No segundo capítulo, nós focamos na classificação da família Tachinidae e trabalhos com a tribo Tachinini, uma das maiores tribos da família. A tribo Tachinini apresenta graves problemas de classificação, especialmente na Região Neotropical. Amostrando 111 gêneros e 193 espécies de Tachinini, nós propomos uma hipótese filogenética inferida com caracteres morfológicos. Utilizando parsimônia como critério de otimização, a monofilia de Tachinini foi confirmada e diversos grupos de gêneros foram propostos e diagnosticados com caracteres filogenéticos.

Palavras-chave: Taxonomia. Sistemática filogenética. Região Neotropical. Entomologia.

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GENERAL INTRODUCTION

When preparing the thesis project, Silvio and I were focused on answering questions about the phylogenetic relationships, the time of origin and the biogeographic events that impacted the history of the tribe Tachinini, one of the largest tribes of the family Tachinidae. Tachinidae is one of the most species-rich groups in Diptera and certainly the largest family of parasitic flies, having 8592 valid species around the world (O'HARA; HENDERSON; WOOD, 2020). Tachinids have endoparasitic first instar larvae that use arthropods, mainly insects, as hosts (STIREMAN; O'HARA; WOOD, 2006). This behavior associated with the diversity of species of hosts make many species of Tachinidae potential agents of biological control of pests (GRENIER, 1988) (DINDO; GRENIER, 2014) (CONTI et al., 2020).

This first project, however, proved to be much more challenging than expected. First of all, the current state of the taxonomy of the tribe Tachinini is a great impediment to assess questions about the divergence times of the group and even the biogeographic events that impacted its diversity. Tachinini have many monotypic genera, especially in the Neotropical Region (EVENHUIS; PONT; WHITMORE, 2015) (O'HARA; HENDERSON; WOOD, 2020), which makes the correct identification of specimens more difficult and, consequently, the sampling of genetic material and geographical data. Moreover, the fossil record in Tachinidae is very scarce and none fossil specimen can be unambiguously classified in a certain group (O'HARA et al., 2013). To obtain accurate estimates of divergence times of Tachinini, we had to include fossils of other families of Calyptratae, therefore amplifying the scope of our project.

Considering these questions, we reformulated our project to address both a broader question and a more specific question. Combining the data generated for the molecular phylogeny of Calyptratae (a parallel project conducted by several Brazilian dipterists) and for our own project, we aimed to estimate accurate diverge times not only for Tachinidae, but for all calyptrate families using the few unambiguous fossils described for the group and a broad sampling of species to represent the relative diversity of each family of Calyptratae. This is the content of Chapter 1. In addition, we also focused on the main issue of the tribe Tachinini, i.e., its classification of genera. We aimed to improve the classification of genera of Tachinini by inferring a phylogenetic hypothesis based on morphological data, sampling the majority of monotypic genera. This is the content of Chapter 2.

We expect the results of these two questions will open new possibilities for investigations on the systematics, evolution and biogeography not only of tachinid flies, but for all families of Calyptratae.

GENERAL CONCLUSION

The results of Chapters 1 and 2, although preliminary, offer robust and evidence-based conclusions that will certainly be essential for investigations regarding the systematics, evolution and biogeography of calyptrate flies. The main conclusions of each chapter are described below.

The origin of Calyptratae is older than previously estimated, occurring in the mid-Late Cretaceous, although all its families originated only during the Tertiary. However, the diversification of families throughout the Tertiary did not happen at the same time interval. The oldest family is Hippoboscidae, occurring in the Paleocene, followed by the origin of the families Muscidae, Nycteribiidae, Streblidae, Tachinidae and Sarcophagidae in the Eocene. The majority of families originated during the Oligocene, and the oestroid families Oestridae, Polleniidae and Rhiniidae are the youngest in Calyptratae, having originated in the Miocene. The superfamily Hippoboscoidea appeared very early in the diversification of calyptrate flies, in the Late Cretaceous, whereas the origin of the superfamily Oestroidea occurred only in the Early Eocene. The divergences of the monotypic families Mystacinobiidae (from Oestridae) and Ulurumyiidae (from Mesembrinellidae) are old, having occurred in the Late Eocene. The node dating approach using CladeAges proved to be a suitable model to estimate divergence times in Calyptratae, which will serve as a reference for future studies of divergence times in Diptera and other lineages of species-rich groups. This is the first hypothesis of divergence times for all families of Calyptratae, including several of their respective subfamilies and tribes due to the increased sampling of calyptrate species. For instance, as originally intended in our first project, the tribe Tachinini originated at the transition of the Oligocene to Miocene, suggesting a recent and fast diversification of a group that has so many species distributed around the world.

Moreover, the diversity of genera and morphological features of species of the tribe Tachinini were summarized in the phylogenetic hypothesis of Chapter 2. This is the first comprehensive phylogenetic hypothesis for the group, representing 79% of genera of the tribe. Despite previous classifications that divided the fauna of Tachinini in different suprageneric groups, Tachinini is indeed a monophyletic group. Traditional diagnostic characters used to classify the fauna of Tachinini (e.g., relative size of the first flagellomere and pedicel, development of palpi and presence of parafacial setae) are actually homoplastic and no traditional suprageneric taxa previously proposed for Tachinini was recovered as

monophyletic. The most informative characters to delimit and diagnose genus groups of Tachinini are usually found in features of the male terminalia. Additional characters, however, such as the female terminalia, first instar larvae and molecular sequences, might shed more light and provide a higher support for the genus groups proposed herein.

After our efforts to understand the origin of calyptrate flies and to provide phylogenetic evidence to improve the classification of Tachinini, we consider that our results are going to positively impact and promote new taxonomic revisions, phylogenetic hypotheses, macroevolutionary studies and recovery of the biogeographical history of these flies.

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