Daniel Maximo Corrêa de Alcantara

**Filogenia da subfamília Streblinae (Diptera:
Streblidae) e associação histórica
parasito-hospedeiro**

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(Diptera: Streblidae) and historical
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Orientador: Prof. Dr. Silvio Shigueo Nihei
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Prof. Dr. Silvio Shigueo Nihei
Orientador

*Aos pequenos e mal-amados;
Aos desleixados e maltrapilhos;
A todos os filhos bastardos da mesma nação, que
são crianças, porém não são filhos!*

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Nunca entendi muito bem como palavras escritas e/ou faladas seriam mais importantes do que as atitudes do dia a dia. É como se tudo que tivéssemos vivido fosse esquecido, e de alguma forma o texto gravado no papel fosse a única fonte válida capaz de demonstrar o que passou, o que se sentiu, o que se viveu. Talvez minha dificuldade se dê porque descobri cedo que quem muito dizia que me amava, no geral, pouco ou nada fazia por mim... ao contrário, era justamente quem pouco dizia, quem mais fazia... provavelmente porque estivesse muito ocupada fazendo. Ainda tenho dificuldade em entender... só que ao mesmo tempo, percebi que o “mundo” na minha cabeça não é o mesmo fora dela. Mais complicado ainda, aprendi que o “mundo” fora não se trata de um “mundo”, mas de um universo composto por diferentes “mundos”; mundos esses compostos por diferentes idéias, diferentes concepções, diferentes formas de sentir e de entender o que está ao redor. Pode ser que eu tenha demorado para tomar consciência disso, mas a verdade é que mesmo consciente, não me sinto capaz de demonstrar qualquer coisa aqui em palavras... de aqui agradecer. E como esse não é um trabalho pontual, mas fruto de um longo caminho, é muito difícil fazer um agradecimento, por correr o risco de deixar de fora pessoas que aqui deveriam estar. As pessoas com quem cruzamos até podem ir, mas elas sempre deixam algo capaz de abrir nosso próprio mundo e nos transformar. É incrível como algumas vezes, pessoas que cruzam nossas vidas, mesmo que seja por um curto intervalo de tempo, são capazes de mudar tanto o que está ao nosso redor...

Enfim, seguindo agora a linha tradicional e tão requisitada,

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*“De dia à procura de comida / A noite um lugar pra dormir / Carrega no corpo feridas e
ainda consegue sorrir / Dizem que o nosso país não vai mal / Porque o povo ainda faz
carnaval / Mas os pequenos e mal amados não compartilham da mesma visão / Há
tristeza no seu coração / Vivem a margem do nosso país / Assaltando e ferindo quem
passa / Tentam gritar do seu jeito infeliz / Que o país os deixou na desgraça / São alvos
de uma justiça que só sabe falar / Será que a solução é exterminar / Herodes não morreu
e hoje os dias estão piores / Esterilização em massa e chacina de menores / Mas eu
queria somente lembrar / Que milhões de crianças sem lar / São frutos do mal que floriu
/ Num país que jamais repartiu / Pátria amada, Brasil / FUTURO DO PAÍS / Esse é o
futuro do país / FUTURO DO PAÍS”*
(Futuro Do País, Planet Hemp)

*“Ninguém pode estar no mundo, com o mundo e com os outros de forma neutra. Não
posso estar no mundo de luvas nas mãos constatando apenas. A acomodação em mim é
apenas caminho para a inserção, que implica decisão, escolha, intervenção na realidade.*

*Há perguntas a serem feitas insistentemente por todos nós e que nos fazem ver a
impossibilidade de estudar por estudar. De estudar descomprometidamente como se
misteriosamente, de repente, nada tivéssemos que ver com o mundo, um lá fora e
distante mundo, alheado de nós e nós dele.”*

(Paulo Freire, Pedagogia da Autonomia)

Resumo

O paradigma no qual grande parte do arcabouço teórico e empírico tem se baseado para o estudo de associações históricas não tem sido capaz de acomodar as evidências disponíveis. Essas inconsistências permitiram o surgimento do “Paradigma de Estocolmo”. Existem diferentes grupos com potencial para ser um sistema modelo para o estudo de associações históricas, como Streblidae. Esta família é caracterizada como um grupo altamente especializado de moscas ectoparasitas de morcegos, que se alimentam de sangue. Embora a associação entre Streblidae e seus hospedeiros possa ser um bom sistema modelo, reconstruir uma hipótese de relacionamento é crucial antes de iniciar um estudo de associação histórica. Para estudar as relações dentro de Streblidae e as associações parasita-hospedeiro, a tese foi dividida em duas partes principais. No capítulo 2, apresentamos a filogenia molecular mais abrangente para Streblidae do Novo Mundo até o momento, incluindo estimativas de tempos de divergência. Nossos resultados suportam a monofilia dos Streblidae do Novo Mundo, Nycterophiliinae e Streblinae, porém não suportam a monofilia de Trichobiinae. As estimativas sugerem que Streblidae do Novo Mundo surgiu no Mioceno Inferior. Novas colonizações foram recuperadas como o principal evento nas associações entre Streblidae e seus hospedeiros. Sugerimos a ecologia de abrigos como um mecanismo importante nas associações parasito-hospedeiro estudadas. No capítulo 3, é apresentada a filogenia da subfamília Streblinae com base em caracteres morfológicos. Foram amostradas todas as espécies válidas de Streblinae. Os resultados suportam a monofilia de Streblinae, com *Anastrebla*, *Metelasmus* e *Paraeuctenodes* também como monofiléticos. Por sua vez, *Strebla* foi recuperado como parafilético em relação a *Metelasmus*. Apresentamos uma visão histórica sobre a delimitação de Streblinae e discutimos a importância de uma nova interpretação dos caracteres para a classificação da subfamília.

Abstract

The paradigm upon which much of the theoretical and empirical framework was based for the study of historical associations has not been able to accommodate the available evidence. These inconsistencies enabled the emergence of the “Stockholm Paradigm”. There are different groups that have potential to be a model system for studying historical associations, such as Streblidae. The family is characterized as a highly specialized group of flies that are ectoparasitic on bats, feeding on the blood of their hosts. The association between species of Streblidae and their hosts may be a good model system to understand the host-parasite relationship under the Stockholm Paradigm. However, reconstructing a relationship hypothesis is crucial before starting a study of the historical association. To study the relationship within Streblidae and the host-parasite associations, the thesis was divided into two main parts. In chapter 2, we present the most comprehensive molecular phylogeny of New World Streblidae to date, including a fossil-calibrated estimates of divergence dates. Our analysis supports the monophyly of New World Streblidae, Nycterophiliinae and Streblinae, but a non-monophyletic Trichobiinae. Our estimates suggest that New World Streblidae arose at Lower Miocene. Host-switch is recovered as the main event in the associations between species of Streblidae and their hosts. We suggest roost ecology as an important mechanism in the association between species of Streblidae and their hosts. In chapter 3, the phylogeny of the subfamily Streblinae is presented based on morphological characters. We sampled all valid species of Streblinae. Results strongly support the monophyly of Streblinae, with *Anastrebla*, *Metelasmus* and *Paraeuctenodes* also as monophyletic. In turn, *Strebla* is recovered as paraphyletic in relation to *Metelasmus*. We present a historical overview on the delimitation of Streblinae, and discuss the importance of a new interpretation of the characters.

General Introduction

Coevolution is considered one of the main evolutionary forces capable of generating and structuring biological diversity (Brockhurst and Koskella, 2013). Possible coevolutionary interactions are present in many ways within biological communities and are generally placed into three categories: antagonism, mutualism, and commensalism. Within these, the most commonly studied examples of interactions are: host-parasite, predator-prey, and plant-pollinator (Fountain et al., 2017). The role of coevolution in interactions and species diversification is considered important in understanding how microevolutionary processes can result in broad patterns of lineage diversification (Althoff et al., 2014; Gilman et al., 2012; Poisot, 2015). Understanding the factors capable of generating, maintaining and limiting interactions between species may have ecological applications. Examples of applications include emerging disease dynamics, biological control, biological invasion, and biotic responses to climate change (Agosta, 2006; Brooks and Ferrao, 2005; Brooks and Hoberg, 2007; Hoberg and Brooks, 2015). Thus, many authors argue the need for data that integrates microevolutionary processes with macroevolutionary patterns to understand how coevolution affects speciation and extinction. Phylogenetic tools have been a widely used approach to understanding such a link, mainly through comparison of phylogenies, known as cophylogenies (Segraves, 2010; Thompson et al., 2017).

Most of the theoretical and methodological development for macroevolutionary approaches in coevolutionary studies was built on a “maximum cospeciation” paradigm. Within this paradigm, specificity is the cause of coevolution and it is predicted that the potential for new interactions will be minimal (Brooks et al., 2015; Hoberg and Brooks, 2008). However, this paradigm led to the misconception that examination of congruence between phylogenies would be a sufficient evidence of coevolution, even leading to the use

of cospeciation as a synonym for coevolution (Anderson, 2015; Page, 2003; Poisot, 2015; Thompson, 2005; Thompson et al., 2017; Vienne et al., 2013). While coevolution may lead to cospeciation, it is neither necessary nor sufficient to originate and maintain a pattern of parallel speciation (Poisot, 2015; Thompson et al., 2017). In this sense, theoretical and empirical studies are important in understanding how ecological and coevolutionary dynamics can affect interactions between organisms and, in turn, species diversification. Overall, these studies demonstrate that the effect of coevolution on diversification is extremely dependent on the type of ecological interaction present, as well as the phenotypic mechanisms behind these interactions. They suggest that many interactions considered as generators of diversification may not do so. In cases where selection acts on the convergence of phenotypes, coevolution may even reduce diversification. In turn, antagonistic interactions that impose a cost on phenotype matching can increase diversity, such as in host-parasite associations. Given sufficient time, the selection regime in this type of interaction is altered and tends to increase genetic and phenotypic variability. Increased variability promotes the emergence of generalists and the possibility of new ecological opportunities (Best et al., 2010; Gilman et al., 2012; Hall et al., 2011; Paterson et al., 2010; Scanlan et al., 2011; Simmons et al., 2011; Thompson, 2012; Yoder and Nuismer, 2010). However, this opens the opportunity for further colonization (host-switch) and a cophylogenetic structure would emerge through phylogenetic tracking rather than cospeciation (Brockhurst et al., 2005; Poisot, 2015; Vienne et al., 2013).

Currently, the theoretical and empirical framework on which maximum cospeciation was built is unable to accommodate the available evidence on macroevolutionary processes and patterns. Colonization events (host-switch) are the most obtained as an explanation for speciation. (Huysse et al., 2005; Jackson and Charleston, 2004; Vienne et al., 2007, 2013). The inconsistencies between what has been inferred and observed, with what is expected in the current paradigm, makes room for the emergence of new paradigms. One option widely discussed as a substitute is the “Stockholm Paradigm”. This proposal seeks to integrate ecological and evolutionary processes, providing a new theoretical and empirical framework for understanding the mechanisms that lead to diversification on a macroevolutionary scale (Agosta, 2006; Agosta and Klemens, 2008; Agosta et al., 2010; Brooks et al., 2014, 2015; Hoberg and Brooks, 2008). Although it has been elaborated within a context of host-parasite interaction, with a focus primarily on emerging infectious diseases, it allows us to

understand the evolution of interspecific ecological associations as a whole (Araujo et al., 2015; Brooks and Hoberg, 2007; Hoberg et al., 2015; Hoberg and Brooks, 2015).

One of the most commonly used system models for studying historical associations has been organisms of Phthiraptera, the order of insects popularly known as lice (*i.e.*, Johnson et al. 2011, 2009; Sweet et al. 2016; Sweet and Johnson 2016, 2018). Although Phthiraptera is a good model system, there are some other groups that have the same potential to be a model system, such as Streblidae (Graciolli and Carvalho, 2012). Streblidae is a family of obligate ectoparasite bat flies, hematophagous and considered highly specialized in relation to their hosts (Dick et al., 2016). The long and close association between Streblidae species and their hosts provides an interesting scenario from which is possible to study the ecological and coevolutionary dynamics between parasites and hosts, and enhance our knowledge of the coevolutionary process by testing hypothesis in a broad context (Dick and Patterson, 2006; Graciolli and Carvalho, 2012; Tello et al., 2008).

Assuming the Stockholm Paradigm as a theoretical framework for understanding the relationship between species of Streblidae and their hosts on a macroevolutionary scale, it would be expected to find a cophylogenetic pattern that pointed to a greater number of host-switch than cospeciation events, regardless of the specificity considered in the association. In the only cophylogenetic study done so far with Streblidae, Graciolli and Carvalho (2012) analyzed the historical association between *Trichobius phyllostomae* group and their hosts. They found host-switch as the main event in the association between lineages. Streblidae contains five subfamilies, 33 genera and 239 species, and it has a geographic distribution where species, genera and subfamilies that occur in the New World do not occur in the Old World (Dick and Graciolli, 2013). Given this characteristic geographical distribution, even cases of tree congruence need to be carefully analyzed before assuming any hypothesis of coevolution. In such cases, it would be important to look at the host biogeography to understand the patterns. Studies on the main host family of Streblidae in the New World (Phyllostomidae) suggest the importance of biogeographic events, as well as changing in the feeding behaviours, for the diversification of these bats (Pavan and Marroig, 2017; Rojas et al., 2011, 2016; Shi and Rabosky, 2015). However many questions are still open regarding relationships within Streblidae. Most phylogenetic studies with Streblidae have focused on the relationships between the families of Hippoboscoidea, and have been performed based only on some molecular markers (*i.e.*, Nirmala et al. 2001, with

16S and 18S; Dittmar et al. 2006, with 16S, 28S, COI and CAD; Petersen et al. 2007, with 16S, 18S, COII and CytB; Kutty et al. 2010, with 12S, 16S, 18S, 28S, COI, CytB, EF1 α and CAD). The relationship between Streblidae subfamilies is still uncertain and poorly defined, as are the internal relationships. Therefore, reconstructing a relationship hypothesis for the interest group in Streblidae is crucial before starting a study of the historical association between the species of Streblidae and their hosts.

Although the initial project proposal was focused on the subfamily Streblinae (Diptera: Streblidae), we decided to expand the scope of the study in the chapter 2 to allow us to make better use of the data at our disposal. Still, in chapter 3 we kept the study focused only on the subfamily Streblinae. Thus, in chapter 2 we present a molecular phylogeny of the New World Streblidae inferred from mitochondrial genes, which includes calibrated divergence time estimate. We sequenced 32 mitochondrial genomes to complement the existing data, representing 34 species of New World Streblidae. The phylogeny is composed by 67 species and 20 genera of the three subfamilies of the New World Streblidae. Based on a much broader taxon sample for the subfamily Streblinae, we combined cophylogenetic analysis with ancestral host reconstruction to address three objectives: (*i*) propose a phylogenetic hypothesis among the three subfamilies of Streblidae of the New World, including an estimate of divergence times, (*ii*) assess the monophyly and relationships among genera of Streblinae, and (*iii*) understand the evolutionary history of associations between Streblidae species and their hosts using the species of Streblinae as a model system. In chapter 3, we perform the phylogenetic analysis of the subfamily Streblinae based on morphological evidence to verify its monophyly, propose a relationship hypothesis between the genera of the subfamily, as well to evaluate the characters used so far to delimit and characterize the subfamily and the genera included in it. Taxonomic sampling for subfamily includes all currently valid genera and species, except the species *Strebla mexicana* Rondani whose the only known type specimen is lost.

General conclusion

The present study contributes with unprecedented results to understand the evolutionary history of Streblidae, as well as the association with their hosts. In chapter 2, we presented the first molecular phylogeny with the largest sample of species and genera of New World Streblidae to date, especially for the subfamily Streblinae. We recovered the monophyly of the New World Streblidae, and of the subfamilies Nycterophiliinae and Streblinae. Furthermore, we corroborate the well-known non-monophyly of the subfamily Trichobiinae and the genus *Trichobius*. The proposed classification of Wenzel et al. (1966) for Streblinae is corroborated, but for the first time the monophyly of *Strebla* is contested, indicating it is a paraphyletic taxon in relation to *Metelasmus*. We also provide the first estimates of divergence times of the New World Streblidae, with the estimated age of origin to the Lower Miocene (15.3, 22.7–12.7 Ma 95% HPD). Our results further provide an insight into the historical association between the species of Streblidae and their bat hosts. The origin of the New World Streblidae, in particular of the subfamily Streblinae, is consistent with the period of diversification of the main host clades. Our study supports host-switch as the main process operating in the associations, even though the group is considered highly specialized and host-specific. This is in congruence with the results previously found by Graciolli and Carvalho (2012), and with the expectations of the Stockholm Paradigm (Brooks et al., 2015). Regarding associations, we hypothesized that host roosts may act as a key mechanism, weakening the filters argued by Dick and Patterson (2007) to keep host-parasite specificity, and favoring host-switch over cospeciation.

The morphological phylogeny of chapter 3 is the first to rely on all valid species of the subfamily Streblinae. The monophyly of Streblinae is well supported by numerous synapomorphies. Despite the low branch support, we have recovered *Anastrebla*, *Metelasmus* and

Paraeuctenodes as monophyletic. We corroborate the result of chapter 2, demonstrating that *Strebla* is not monophyletic. The species of *Strebla* have been splitted into species with a complete frontoclypeus and the anterior pigmented prescutal suture absent, and species with frontoclypeus with anterior detached plates and the anterior pigmented prescutal suture present. In addition, species with a complete frontoclypeus were recovered more closely related to *Metelasmus*. Based on our results, we propose a new interpretation of the head characters for the species of *Strebla* with the complete frontoclypeus. However, an improvement in the morphological analysis is important to increase the number of characters from thorax, abdomen and genitalia.

Finally, we believe that the data presented in this thesis provide a valuable contribution to the growing knowledge of both the group in question (Streblidae) and the understanding of the dynamics of host-parasite associations. Our study along with Graciolli and Carvalho (2012) establishes Streblidae as a good model to answer questions in a broad context, such as: the role of ecological timescale interactions over evolutionary timescale associations; how host-switches impact the eco-evolutionary dynamics of highly specialized parasites; what is the role of host ecology on parasite diversification, and so on. In addition, our study demonstrates that numerous aspects of Streblidae systematics remain to be explored, including the classification of Trichobiinae, *Trichobius* and *Strebla*, besides the need of morphological studies that improve the interpretation of the characters.

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