On the origin of geometrid moths: the phylogenetic relationships and taxonomy

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Abstract

The geometrid moths represent one of the largest radiations of Lepidoptera. Phylogenetic analyses based on morphological and molecular data supports the monophyly of this group of moths. However, the subfamilial and tribal compositions of major groups of geometrids are still unresolved, leading to unstable classifications. In this thesis, I investigate the phylogenetic relationships of higher geometrid taxa with the aim of resolving the tribal composition of the major lineages and provide a phylogenetic reference framework as a basis for elucidating their evolutionary relationships.

I built and analyzed the most comprehensive molecular dataset for geometrid moths to date. The molecular data were obtained by Sanger and Whole-Genome shotgun sequencing techniques, and analysed phylogenetically using maximum-likelihood and Bayesian methods.

My refined phylogenetic hypothesis revealed rampant polyphyly among several subfamilies, as well as among a large number of tribes. Based on the molecular data, I described a new subfamily of Geometridae called Epidesmiinae. To further evaluate the robustness of the molecular-based phylogenetic hypotheses, I also incorporated studies of morphological traits across the subfamily Epidesmiinae. I further proposed 15 new tribes across several subfamilies. Two new tribes belong to the subfamily Sterrhinae, eight to the subfamily Larentiinae, four to the Ennominae and one to the Geometrinae. Finally, I synonymized several groups (genera and tribes), proposed new tribal combinations, new subfamily status and discussed the most efficient way to deal with the polyphyly of higher taxa to arrive at a classification that reflects the evolutionary relationships in Geometridae.

The phylogenetic hypotheses generated in this study were also used for interpreting the evolutionary trends of the most-species tribe of Geometridae, Boarmiini. Boarmiines were suspected to constitute a rapid radiation of geometrids. In this study we provide a time-calibrated tree, biogeographical and diversification analyses to try to understand the evolutionary patterns of this group of moths.

Finally, I provide a species list and barcodes for geometrid moths of Colombia. The data obtained in this study is the first inventory of species numbers in one of the most biodiversity-rich countries of South America, Colombia. The results of my research highlight the compelling need to analyze more taxa from the entire global range of the family to create a robust evolutionary hypothesis that can be used in classification and in other studies in Geometridae.

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Para mi familia, con amor.

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DISCLAIMER

This publication, and names and nomenclatural acts in it are not available for purposes of zoological nomenclature in accordance with the International Code of Zoological Nomenclature (2012, 4th edition), Articles 8.2, 8.3.

Author contributions

I. **LM-R**, **GB**, **PS**, and **NW** conceived and designed the study. **AH**, **SH**, **HS**, **EF**, **TT**, **EÕ**, and **AT** contributed to specimen collection. **HRG, EÕ, SH,** and **AT** contributed to the lab work. **LM-R** performed all the analyses and took the lead in manuscript preparation. All co-authors contributed to writing the manuscript.

II. **PS** conceived the study and took the lead in manuscript preparation. **PS** and **LM-R** designed the study. **HS** contributed to specimen collection. **LM-R** performed all the analyses. All co-authors contributed to writing the manuscript.

III. **GB** conceived the study and took the lead in manuscript preparation. **PS**, **AH**, **BCS**, **EÕ**, **AM**, **RM**, **DB**, **FB**, **AL**, and **LEP** contributed to specimen collection. **LM-R** performed all the analyses. All co-authors contributed to writing the manuscript.

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V. **LM-R** conceived the study, designed it and performed all the analyses and took the lead in manuscript preparation. **VT** contributed to the lab work and bioinformatics pipelines. All co-authors contributed to writing the manuscript.

VI. **LM-R**, **TT**, and **NW** conceived and designed the study. **LM-R** performed all the analyses with advice from **NC** and took the lead in manuscript preparation. All co-authors contributed to writing the manuscript.

VII. **LM-R** conceived the study, designed it and performed all the analyses and took the lead in manuscript preparation. **ICR-M** contributed to specimen collection. All co-authors contributed to writing the manuscript.

Abstract

Geometrid moths represent one of the largest radiations of Lepidoptera. Phylogenetic analyses based on morphological and molecular data supports the monophyly of this group of moths. However, the subfamilial and tribal compositions of major groups are still unresolved, leading to unstable classifications. In this thesis, I investigate the phylogenetic relationships of higher geometrid taxa with the aim of resolving the tribal composition of the major lineages and provide a phylogenetic reference framework as a basis for elucidating their evolutionary relationships.

I built and analyzed the most comprehensive molecular dataset for geometrid moths to date. The molecular data were obtained by Sanger and Whole-Genome shotgun sequencing techniques, and analysed phylogenetically using maximum-likelihood and Bayesian methods.

My refined phylogenetic hypothesis revealed rampant polyphyly among several subfamilies, as well as among a large number of tribes. Based on the molecular data, I described a new subfamily of Geometridae called Epidesmiinae. To further evaluate the robustness of the molecular-based phylogenetic hypotheses, I also incorporated studies of morphological traits across the subfamily Epidesmiinae. I further proposed 15 new tribes across several subfamilies. Two new tribes belong to the subfamily Sterrhinae, eight to the subfamily Larentiinae, four to the Ennominae and one to the Geometrinae. Finally, I synonymized several groups (genera and tribes), proposed new tribal combinations, new subfamily status and discussed the most efficient way to deal with the polyphyly of higher taxa to arrive at a classification that reflects the evolutionary relationships in Geometridae.

The phylogenetic hypotheses generated in this study were also used for interpreting the evolutionary trends of the most-species tribe of Geometridae, Boarmiini. Boarmiines were suspected to constitute a rapid radiation of geometrids. In this study we provide a time-calibrated tree, biogeographical and diversification analyses to try to understand the evolutionary patterns of this group of moths.

Finally, I provide a species list and barcodes for geometrid moths of Colombia. The data obtained in this study is the first inventory of species numbers in one of the most biodiversity-rich countries of South America, Colombia.

The results of my research highlight the compelling need to analyze more taxa from the entire global range of the family to create a robust evolutionary hypothesis that can be used in classification and in other studies in Geometridae.

Popular Science Summary

Phylogenetic trees are diagrams that represent hypotheses of relationships among organisms. These hypotheses shed light on the history and evolutionary patterns of the tree of life. Phylogenetic trees can be inferred from many data sources, but mainly from morphological or DNA data.

A classical way of inferring trees was through the creation of morphological data matrices. Generally speaking species with similar morphological traits are potentially related. However, one of the most common problems of the morphological phylogenies were the potential errors in homology, which become more of a challenge in high level phylogenies. Later, DNA information began to be incorporated into phylogenetic studies and this has become a reliable source for inferring phylogenies.

In my PhD thesis, I took advantage of the use of DNA sequencing techniques to generate information, analyse phylogenetic patterns and reconstruct the phylogenetic relationships of one of the most species-rich groups of Lepidoptera, the geometrids. The family Geometridae is a group of moths that in my point of view, is a challenging taxon within the tree of life. First, because geometrids are highly diverse, there are more than 24 000 species distributed world-wide, and the reasons behind their evolutionary success are not well studied.

Secondly, the taxonomy of this family is highly neglected for some groups, mainly because of the lack of expert taxonomists, and because some areas are well explored, while from others (mainly tropical areas) we know practically nothing. Finally, because many of the evolutionary patterns of geometrid are poorly known, this prevents our ability to study why or how they have become so diverse.

Geometrids, as well as other insect groups, have a key role in different ecological processes such as pollination, herbivory and they are the source of food for a certain group of vertebrates. Some studies have suggested Geometridae as a biological indicator of well-preserved forests due to their close relationships with woody plants.

During my research, I used Sanger and whole-genome sequencing techniques to obtain DNA data. The sequences were used to infer phylogenetic trees and propose an overview of the phylogenetic relationships of higher taxa. Based on these results, I propose new classifications. The phylogenetic trees were used to interpret the evolutionary history of a species-rich tribe of geometrids in terms of their biogeographical and diversification patterns.

With the results of this research, I provide a more stable classification for the family, which will be a solid foundation for taxonomic and applied research to better understanding, and potential ideas of some of the macroevolutionary processes that have occurred in Geometridae.

The information generated in this study is relevant not only for evolutionary studies, it can also be used for conservation purposes. For instance, global diversity is being lost as a result of human activities, it is clear that geometrids play an important role in the food chains, but if we do not know the taxonomy/biology of species, we will hardly know what are we losing and what should be protected.

Resumen Popular

Los árboles filogenéticos son diagramas que representan hipótesis de relaciones evolutivas entre organismos. Estas hipótesis revelan datos interesantes sobre la historia y los patrones evolutivos del árbol de la vida. Los árboles filogenéticos se pueden inferir a partir de muchas fuentes de datos, pero principalmente de examinaciones morfológicas y de información genética.

Una de las formas clásicas de inferir árboles filogenéticos es a través de la elaboración matrices de datos morfológicos, y a manera general, se especula que grupos con rasgos morfológicos parecidos pueden estar estrechamente relacionados. En filogenética, estos rasgos son considerados como homologías (significa que tiene un origen común). Sin embargo, uno de los problemas más comunes en los estudios morfológicos comenzó a partir de los errores en homología (cuando se asume que algunos caracteres compartidos entre especies se originaron de un ancestro común, pero cuyo origen es diferente). Encontrar caracteres homólogos en taxones superiores y altamente diversos puede ser desafiante. Expertos taxónomos requieren de años de experiencia para poder entender las homologías de taxones de interés.

Más tarde, la información de ADN comenzó a incorporarse a los estudios filogenéticos y esta se ha convertido en una fuente más confiable para inferir filogenias. En mi tesis doctoral, aproveché las ventajas de técnicas de secuenciación de ADN para generar información, analizar patrones filogenéticos y reconstruir la historia evolutiva de un grupo de lepidópteros muy rico en especies, los geométridos.

La familia Geometridae es un grupo de polillas que, desde mi punto de vista, es un taxón desafiante dentro del árbol de la vida. En primer lugar, debido a que los geométridos son muy diversos, hay más de 24 000 especies distribuidas en todo el mundo, y las razones de su éxito evolutivo no se comprenden bien.

En segundo lugar, la taxonomía de esta familia está muy descuidada, principalmente por la falta de taxónomos expertos, y porque algunas áreas están bien exploradas, mientras que, de otras, principalmente en zonas neotropicales, no sabemos nada de la riqueza de especies.

Finalmente, porque muchos de los patrones evolutivos de los geométridos son desconocidos, lo que impide nuestra capacidad de analizar por qué o cómo se han vuelto tan diversos. Los geométridos al igual que otros grupos de insectos, juegan un papel clave en diferentes procesos ecológicos como polinización, herbívora y son la fuente de alimento de un determinado grupo de vertebrados.

Algunos estudios han sugerido a Geometridae como un indicador biológico de bosques bien conservados debido a su estrecha relación con las plantas maderables. Durante mi investigación, utilicé técnicas de secuenciación de Sanger y de genoma completo para obtener datos de ADN.

Las secuencias se utilizaron para construir árboles filogenéticos y proponer una visión general de las relaciones filogenéticas de taxones superiores de geométridos (a nivel de subfamilia) y además proponemos nuevas clasificaciones. Los árboles filogenéticos se utilizaron para interpretar la historia evolutiva de algunos geométridos en términos de sus patrones biogeográficos y de diversificación.

Con los resultados de esta investigación, brindamos una clasificación más estable para la familia, lo que será una base sólida para la investigación taxonómica, aplicada para un mejor entendimiento de algunos de los procesos macroevolutivos que han ocurrido en Geometridae.

La información generada en este estudio es relevante no solo para estudios evolutivos, también puede usarse con fines de conservación. Por ejemplo, la diversidad global se está perdiendo como resultado de las actividades humanas, está claro que los geométridos juegan un papel importante en las cadenas tróficas, pero si no tenemos conocimiento de la taxonomía / biología de las especies, difícilmente sabremos qué estamos perdiendo y lo que deberíamos proteger.

Introduction

Inferring the history of life on earth is a fundamental scientific challenge. Ever since Darwin's (1859) famous illustration of species diverging like branches on a tree, biologists have strived to estimate phylogenetic trees representing hypotheses about the evolutionary history of the species. Traditionally, phylogenetic hypotheses were derived from morphological characters, and many taxonomical studies, as well as classifications, relied largely on morphology. Nevertheless, phylogenetic hypotheses can also be based on other kinds of data, notably DNA sequences.

Morphological trees were the foundation of evolutionary studies, however, one of the main problems related to morphological hypotheses results from errors in homology and the time required by taxonomists to understand such homologies. Understanding how morphological traits have evolved on related/unrelated taxa can indeed be quite challenging, especially when investigating highly diverse groups. Due to their greater resolution, DNA sequence data have gradually replaced morphological characters as input data for phylogenetic analyses (Lemey and Vandamme, 2009). The development of DNA sequencing has since substantially increased our ability to estimate and interpret the evolutionary relationships of species, including insects. Many insect orders are extremely species-rich, thereby often making morphological homology and potential synapomorphic characters (derived characters that are unique to a particular group) difficult to interpret in deeper taxonomic levels.

Lepidoptera (from Greek *lepis* meaning scale and *pteron* meaning wing) is one of the largest radiations of plant-feeding insects. They are thought to have diverged rapidly, thus generating patterns of molecular and morphological evolution that for many groups are difficult to examine.

Within Lepidoptera, Geometridae is the second most species-rich family and they are globally distributed with over 24 000 described species (Nieukerken et al., 2011; Mitter et al., 2017). The study of Geometridae systematics has developed progressively, but the studies have often been geographically limited and have not been aimed at resolving phylogenetic relationships on a global scale. This lack of a global view has resulted in unstable classifications of the 7–10 subfamilies, tens of tribes, and about 2 500 genera. In recent years, the earlier morphology-based hypotheses have been reassessed and partially supported by DNA-based studies (Young, 2006; Ounap et al., 2008; Strutzenberger et al., 2010; Wahlberg et al., 2010; Sihvonen et al., 2011; 2015; Ounap et al., 2016). However, an important shortcoming is that our understanding of geometrid systematics is biased towards the well-studied European fauna, whereas the highest diversity of this family occurs in the tropics, which remain largely unexplored (Brehm et al., 2016).

The primary purpose of my thesis is to provide a substantial advance on the knowledge of the evolutionary history and classification of geometrid moths. To this purpose I produced a large data set of gene sequences obtained by Sanger and next-generation sequencing technologies, as well as the use of traditional morphological examinations.

In chapters **I, II, and III,** I explored how the major lineages of Geometridae are related. To do so, I analyzed a comprehensive dataset of Geometroidea consisting of up to 11 genetic markers for 1 200 species from all biogeographical regions. The ingroup in our phylogenetic analyses included all but one subfamily of Geometridae. Our hypothesis from this work led us to the discovery of a new subfamily of geometrids, Epidesmiinae. The genera included in this new subfamily were part of the Oenochrominae - Desmobathrinae complex, which was for a long time considered as the 'trash-bin' of the Geometridae group, and our results redefine a well-supported clade, based on molecular data.

Unsurprisingly, many taxa within Geometridae needed taxonomical rearrangements, and we tried in the most objective way to provide the taxonomic assignments to many geometrid lineages. Thus, in **chapter II** we defined two new tribes within the subfamily Sterrhinae and in **chapter III** we proposed 11 new tribes for the new world taxa, eight within the subfamily Larentiinae and three in Ennominae respectively.

Molecular data alone can however not tell us what the species look like and how to recognize them. Thus in **chapter IV** we provided an overview of the morphological traits of the new subfamily Epidesmiinae. We tried to find morphological synapomorphies that support a common origin of the included genera. We also provide a summary of the diagnostic characters of all subfamilies of Geometridae.

Another important outcome of **chapter I** was the unexpected phylogenetic position of the subfamily Sterrhinae, as it came out as a sister family to all Geometridae. This result conflicts with the previous Larentiinae + Sterrhinae phylogenetic relationship proposed by Holloway (1997), which was based on the analysis of morphological characters, and with the subsequent molecular analyses by Yamamoto and Sota (2007), Wahlberg et al. (2010), and Sihvonen et al. (2011).

Also, based on Sanger sequencing data of chapter I, we could not provide a taxonomical assignment for the tribe Eumeleini and the subfamily Orthostixinae. Eumeleini is a rogue taxon within Geometridae. Orthostixinae is a subfamily which validity is questioned by both morphological and molecular studies, as it shares morphological traits with Ennominae and Desmobathrinae.

Thus, in **chapter V** I used a phylogenomic approach in an attempt to further elucidate the phylogenetic positions of Larentiinae, Sterrhinae, Eumeleini and Orthostixinae. We sequenced the whole genome of representatives of the deepest lineages in Geometridae, to elucidate whether adding more genetic data can yield stronger support for the phylogenetic hypothesis proposed in **chapter I**. For this study, we successfully sequenced the genome of species of *Orthostixis*, the type genus of Orthostixinae, and *Eumelea* a single genus included in Eumeleini.

One big radiation within Geometridae is the tribe Boarmiini, which is by far the most species-rich tribe of geometrids, comprising ca. 3 000 known species. In **chapter VI** we inferred the evolutionary relationships of Boarmiini based on a dataset of 346 taxa and we studied the diversification patterns and historical biogeography of the radiation. Unsurprisingly, the evolutionary relationships among boarmiines were difficult to resolve, complicated by both numerous conflicting regional classifications and the paucity of molecular information.

Finally, our broad-level molecular phylogenetic hypotheses revealed that many Neotropical lineages urgently need taxonomical attention. However, geometrids are rarely collected and poorly known in the Neotropics. We took advantage of the efficiency of DNA barcodes in **chapter VII** to identify and provide a preliminary inventory of species numbers in one of the most biodiversity-rich countries of South America, Colombia.

With the data generated during this research, I would like to provide stakeholders with a better understanding of the macroevolutionary processes that have occurred in lineages of Geometridae, and to suggest a more stable classification for the family, which will form a solid basis for taxonomic and applied research.

Evolutionary trends in the history of Lepidoptera

The development of molecular systematics has changed many fields within the biological sciences, including taxonomy and classification, by transforming our approach to questions in need for an evolutionary view. The combination of DNA sequences and statistical phylogenetic inference has demonstrated greater explanatory power compared to morphology-based hypotheses, which in turn leads to more stable natural classifications (Prance, 2011).

Most of the progress in understanding evolutionary patterns in Lepidoptera has come about from multigene approaches which have led to major rearrangements of the group (Mitter et al., 2017). In particular, molecular data have yielded phylogenetic hypotheses that have helped to resolve deep divergences and some of the most enigmatic phylogenetic relationships at all levels of Lepidoptera clades

(Regier et al., 2009; Mutanen et al., 2010; Bazinet et al., 2013; Regier et al., 2013; Bazinet et al., 2017).

Putting this in context, Lepidoptera represents a large radiation of insects, which has been probably driven by the diversification of angiosperm (Ehrlich and Raven, 1964; Whitfield and Kjer, 2008). One of the major ideas behind this hypothesis comes from the classical work of Ehrlich and Raven (1964) who examined patterns of interactions between butterflies and their host plants. With information retrieved from molecular phylogenetic hypotheses, Wahlberg et al. (2013) published the first hypothesis of the timing of the origin of major groups within Lepidoptera. Their results shed light on the relationships and coevolutionary patterns between lepidopterans and their angiosperm hosts, suggesting that Lepidoptera appear to be as old as the angiosperms and started to diversify in the Late Triassic.

More recently, in a phylogenomic study, including more genetic information (thousand genes) generated by new sequencing technologies, Kawahara et al. (2019) also tested the hypothesis of Ehrlich and Raven (1964). Although their work resulted in different age estimates, many lepidopteran lineages seem to have proliferated with the rise of angiosperms, further confirming Ehrlich’s and Raven’s assertion of a tight association between the radiation of Lepidoptera and that of angiosperms.

Several lineages of Lepidoptera have been intensively studied morphologically (Kristensen, 1998; Kristensen, 2003; Kristensen et al., 2007), and the main patterns of their evolutionary history have been confirmed or rejected by molecular evidence. For instance, morphological examinations, supported by subsequent DNA studies divide Lepidoptera into non-ditryisian, families which include a paraphyletic set of early-diverging lineages, and their largest radiation Ditrysia, named for the presence of two separate openings for mating and oviposition in female genitalia. Ditrysia represents 98% of all Lepidoptera and 80% of the families (Regier et al., 2009; Mitter et al., 2017).

Non-ditryisians are a paraphyletic group of species-poor lepidopteran and it has been a challenge to recover a common origin of the superfamilies. Molecular studies have confirmed the morphological studies for non-ditrysians, their phylogenetic relationships have been fine-tuned with DNA data (Regier et al., 2015; Bazinet et al., 2017). Even though several important problems remain.

On the contrary, molecular data have been contradictory for some Ditrysia, but on broad-scale, the monophyly of Ditrysia is supported with some problems remaining in the superfamilies close to the root. For instance, the evolutionary history of Tineoidea has been a challenge to infer, and the phylogenetic and taxonomic placement of some clades remains enigmatic (Bazinet et al., 2013; Kawahara and Breinholt, 2014; 2017).

Within Ditrysia, some of the most species-rich clades include Geometroidea (ca. 25 000 species) and Noctuoidea (ca. 50 000 species), whose relationships were poorly known until recent studies based on extensive molecular data (Zahiri et al., 2011; Bazinet et al., 2013; 2013; Kawahara and Breinholt, 2014; Regier et al., 2017).

The higher systematics of Noctuoidea was discussed in terms of the morphology of wing venation until molecular evidence strongly supported the six subfamilies proposed by Zahiri et al. (2011). Molecular data have also resolved the evolutionary relationships of one of the richest families of Noctuoidea, Erebidae (Zahiri et al., 2012). The monophyly of Erebidae was supported by eight genetic markers. These results were confirmed using an expanded gene sample with up 19 genes by Regier et al. (2017) and in a phylogenomic study in Ghanavi (2020).

Geometroidea is a clade supported by molecular characters (Rajaei et al., 2015) whose members have typically been known by the presence of hearing organs (Minet and Scoble, 1999). However, these structures are differently developed or absent in the families Sematuridae (42 sp), Pseudobistonidae (2 sp), Epicopeiidae (25 sp), Uraniidae (700 sp), and Geometridae (24 000 sp) (Scoble, 1992; Hausmann, 2001; Rajaei et al., 2015).

Given their complexity and morphological variation, tympanal organs are of considerable taxonomic importance at high taxa levels. Kawahara et al. (2019) suggested that the tympanic organs have appeared in the Late Cretaceous in response to novel selective pressures. Yet, early morphological examinations suggested that tympanal organs were used to detect echolocation signal of bats or in courtship (Cook and Scoble, 1992).

The sister clade to the Geometroidea is still unclear, however, phylogenomic studies have gradually clarified the evolutionary history of this superfamily. Regier (2009) and Kawahara and Breinholt (2014) suggested Noctuoidea as sister taxa, which is also consistent with the result obtained in the phylogenomic study of Call (2020).

On the opposite, Mutanen et al. (2010) placed Geometroidea as sister to Bombycoidea, and Bazinet et al. (2013) suggested a sister relationship with the clade (Bombycoidea + Lasiocampoidea) + Noctuoidea. Morphological studies by Rajaei et al (2015) favour the Bazinet et al. (2013) hypothesis arguing that Noctuoidea, Lasiocampoidea, Bombycoidea and Geometroidea share the presence of a pair of struts in the metafurca and have lost of median tooth on the ventral edge of pretarsal claw.

The monophyly of Geometroidea is also supported by morphological traits and indirectly confirmed by molecular information (Rajaei et al., 2015; Murillo-Ramos et al., 2019; Call et al., 2020). The superfamily started to diversifying ca 83 mya ago (Wahlberg et al., 2013) and Geometridae, its most diverse family diverged ca 76 mya ago (Ghanavi et al., In prep). Molecular evidence favours the relationships of (Uraniidae + Geometridae), (Sematuridae + (Epicopeiidae + Pseudobistonidae) (Murillo-Ramos et al., 2019; Call et al., 2020), which is concordant with a previous morphological hypothesis (Rajaei et al. 2015).

The brief review above is only one example of how the taxonomy and systematics of many lineages in Lepidoptera have changed following the inclusion and analysis of different sources of data (mainly molecular data). We are aware that many important questions remain, and those questions could only be answered with the inclusion and analysis of all kind of evidence (phenotype, fossils, DNA, biology, etc.).

But certainly, what we currently know about Lepidoptera, especially in Geometroidea, have a strong foundation on DNA data. It is undeniable that molecular phylogenetic studies are helping to elucidate evolutionary patterns that were previously unknown, thus changing our view on classifications and also helping to reconstruct the history of lepidopteran evolution.

Geometridae: an "embarrassment of riches"

The family Geometridae is the most species-rich clade within Geometroidea, defined by the structure of the tympanal organ, which is positioned ventrally at the base of the abdomen, the presence of the tympanic handle or ansa (Holloway, 1997; Hausmann, 2001), and the reduction in the number of larval prolegs, which causes characteristic looping movements (Hausmann, 2001) (Fig. 1).

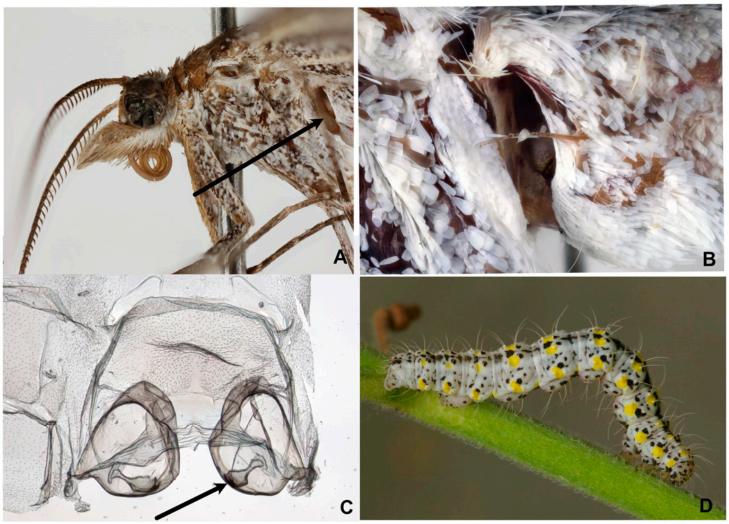

Figure 1. Geometrid tympanal organ and larva. A. Lateral view of *Phrataria transcissata* and tympanal organ, B. - C. Tympanal organ with scales and descaled of *P. replicataria* showing the shape of ansa., (Photo credits Pasi Sihvonen), D. Larva of *Orthostixis cribaria* (photo credit: Friedmar Graf, http://www.lepiforum.de/lepiwiki.pl?Orthostixis_Cribraria).

Before the present work, there were more than 24 000 described species worldwide and between 8-10 subfamilies (van Nieukerken et al., 2011; Mitter et al., 2017). Now, with the current taxonomic updates, Geometridae comprises nine subfamilies (Fig. 2) as follow: Sterrhinae (ca. 3 000 spp.), Larentiinae (ca. 6 300 spp), Archiearinae (18 sp), Epidesmiinae (new in the present study; 102 spp.), Desmobathrinae (ca. 200 spp.), Oenochrominae (ca. 300 spp.), Eumeleinae (new in the present study, 13 spp), Geometrinae (ca. 2 600 spp.), and Ennominae (ca 10 600 spp.) (Sihvonen et al., 2011; Brehm et al., 2019; Murillo-Ramos et al., 2019; Sihvonen et al., 2020).

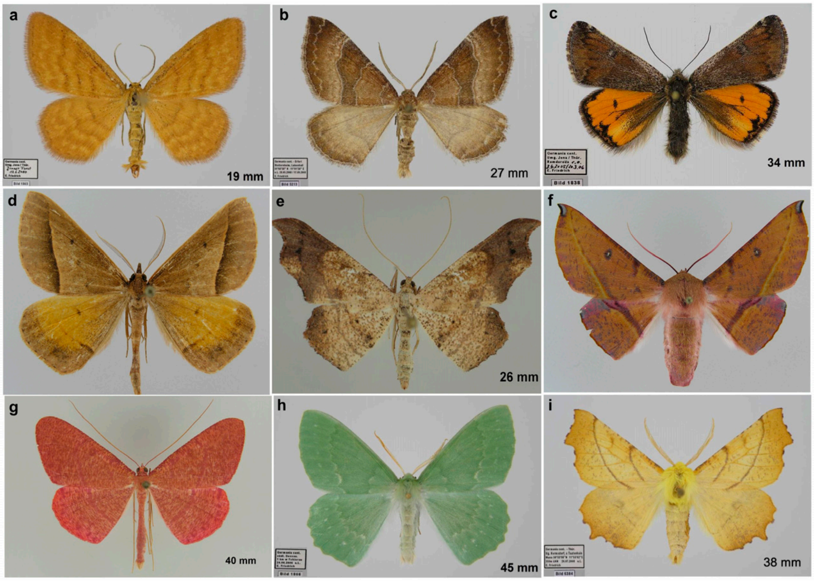

Figure 2. Subfamilies of Geometridae. a. Sterrhinae, b. Larentiinae, c. Archiearinae, d. Epidesmiinae, e. Desmobathrinae, f. Oenochrominae, g. Eumeleinae **stat. nov.**, h. Geometrinae, i. Ennominae. Photo credits: Egbert Friedrich.

The last 20 years have seen significant progresses in the elucidation of the phylogenetic relationships among higher geometrid taxa. Even though there are still unsolved relationships within Geometridae, some of the most influential taxonomic and phylogenetic studies include, for instance, in Sterrhinae (Holloway, 1997; Hausmann, 2004; Sihvonen and Kaila, 2004; Õunap et al., 2008), Larentiinae (Mironov, 2003; Viidalepp, 2011; Mironov, 2013; Õunap et al., 2016), Desmobathrinae (Holloway, 1996; Hausmann, 2001), Archiearinae (Hausmann, 2001; Young, 2006), Oenochrominae (Scoble and Edwards, 1989; Cook and Scoble, 1992; Holloway, 1996), Geometrinae (Cook et al., 1994; Pitkin, 1996; Beljaev, 2007; Ban et al., 2018), Orthostixinae (Holloway, 1997) and Ennominae (Holloway, 1994; Pitkin, 2002; Beljaev, 2008; Wahlberg et al., 2010; Õunap et al., 2011; Skou and Sihvonen, 2015; Müller et al., 2019).

However, there are still unsolved relationships within Geometridae. Early morphological studies have suggested Archiearinae as the sister group of all the other subfamilies (Hausmann, 2001), because the labial palps of this subfamily are exposed in the pupa (Nakamura, 1987), in contrast to the rest of the subfamilies (Scoble, 1992). In contrast, other studies placed Ennominae as sister to all other Geometridae (Müller, 1996), but in this case, no morphological details were provided. Studies support the placement of Sterrhinae + Larentiinae as sister to the rest of geometrid subfamilies (Yamamoto and Sota, 2007; Sihvonen et al., 2011). These two subfamilies share a hammer-headed ansa, the absence of a tympanic lacinia (Cook and Scoble, 1992), and the bursa copulatrix in female genitalia being spined or rugose (Holloway, 1997).

What we currently know about the systematics and evolutionary dynamics of Geometridae is largely attributable to the long-studied Palaearctic, Nearctic and Oriental faunas (Holloway, 1997; Wahlberg et al., 2010; Sihvonen et al., 2011). But significant contributions based on morphology have highlighted the high diversity of Geometridae of Neotropical species from groups such as Ennominae, Geometrinae (Pitkin, 1996, 2002), or the revision of Sterrhinae and Larentiinae (Viidalepp, 2011). Also, the book series on the geometrid moths of Europe (Hausmann, 2001; Mironov, 2003; 2004; Skou and Sihvonen, 2015) has greatly contributed to the taxonomic knowledge of the family.

One influential morphological study of the major groups within Geometridae was published by Jeremy Holloway (1997), whose taxonomic study has been the baseline work in the systematics of the family. In his morphological review of the Bornean fauna, which was placed in a wider taxonomic context, Holloway suggested the monophyly of Geometridae and included eight subfamilies. These relationships were established based on morphological characters, including structures on the male and female abdomen (Holloway, 1997).

The first geometrid molecular phylogenies were published in the early 2000s and aimed to overcome some of the taxonomic and phylogenetic uncertainties described above. The first molecular hypothesis was proposed by Abraham et al. (2001), with an analysis of three genes for 18 species. Despite the limited number of taxa included in that study, Geometridae was recovered as monophyletic, supporting the previously offered morphological hypotheses. However, Larentiinae was placed as sister to all other subfamilies and not Archiearinae as proposed by Holloway (1997). Subsequent molecular hypotheses, included more genetic markers and taxa, and also supported the monophyly of Geometridae and the sister relationship of Sterrhinae + Larentiinae. Sterrhinae + Larentiinae were recovered the sister to the rest of Geometridae (Yamamoto and Sota, 2007; Wahlberg et al., 2010; Sihvonen et al., 2011).

Sihvonen et al. (2011) analyzed a dataset of 164 taxa and up to eight genetic markers. The resulting phylogeny suggested that the most species-rich subfamilies within the Geometridae were monophyletic (Fig. 3). However, the systematic positions of small subfamilies like Oenochrominae and Desmobathrinae remained uncertain. Oenochrominae + Desmobathrinae were suspected to be polyphyletic. Moreover, many geometrid genera remained unassigned to tribes due to limited taxon sampling.

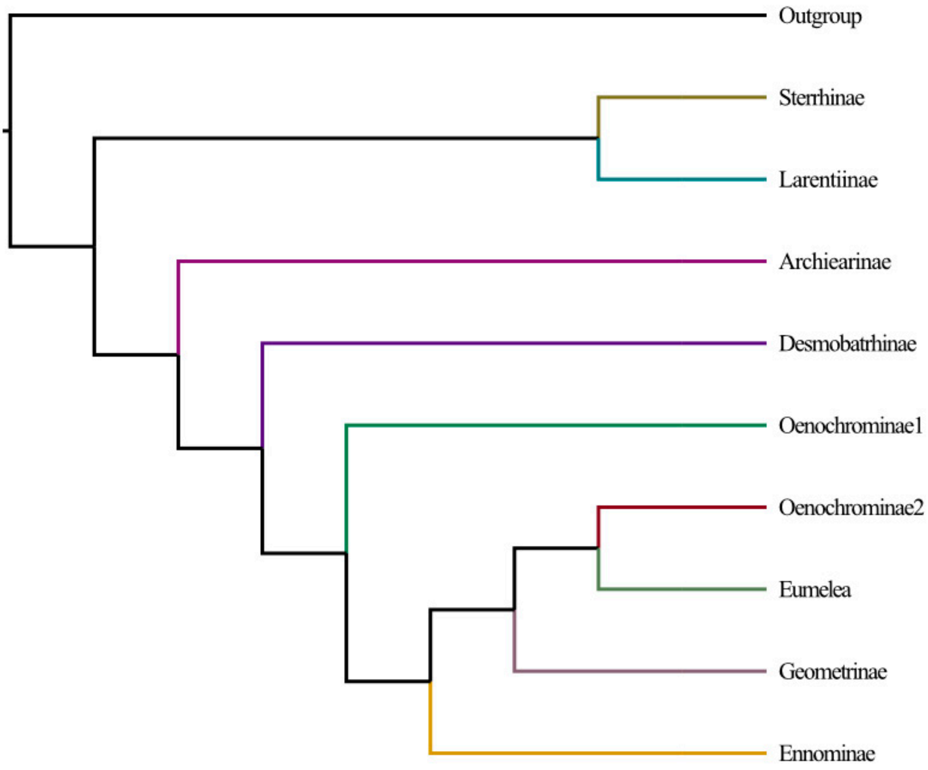

Figure 3. Simplified phylogenetic hypothesis of major lineages of Geometridae. (Sihvonen et al., 2011), 164 taxa, eight markers.

A brief review of phylogenetic inference methods

Phylogenetic inference methods were intensively developed during the last decades. Finding the ‘best’ tree in phylogenetic analyses always requires a considerable number of calculations, which increases as more data are added. This occurs because the number of bifurcating trees increases exponentially with the number of taxa (Felsenstein, 1978).

Distance-based clustering algorithms, as well as Parsimony-based analyses, were for a long time the dominant approaches to inferring phylogenetic trees (Zhou et al., 2018). However, since statistical methods like Maximum-Likelihood estimation (ML) and Bayesian Inference (BI) were applied to phylogenetics, studies have proven that model-based trees recover more reliable results (Whelan and Morrison, 2017).

Maximum Likelihood analysis for DNA sequences was developed for the first time by Felsenstein (1981). Theoretically, the likelihood is defined as the probability of observing the data, given the model with a set of parameters (Yang, 2014). Data in our case are the aligned homologous sequences, and the model mathematically describes the processes which generated the data such as base substitutions (i.e. a change from adenine (A) in one lineage to guanine (G) in another lineage).

For calculations of likelihood, we have to assume independent evolution among the sites, such that the probability of the data is the sum of probabilities of data at individual sites. Traditionally, the ML calculation is based on the pruning algorithm proposed by Felsenstein (1981).

The algorithm performs calculations to identify common factors among the sites. If two or more sites have the same pattern, the probabilities of observing each site are the same, therefore only a single calculation is needed for this site type. This in turn reduces the number of calculations required. The ML method has been implemented in computer programs such as RAxML (Stamatakis, 2006, 2014) RAxML-NG (Kozlov et al., 2019), IQTREE1x, 2x (Nguyen et al., 2015; Minh et al., 2020).

In contrast to ML methods, BI methods do not attempt to search only for the single best tree but target a probability distribution of trees. BI aims to estimate the probability that the model is correct given the observed data (Yang and Rannala, 2012). Thus, BI incorporates prior information into the calculations, which is then modified by the data to give the posterior.

Bayesian approaches are implemented in programs like MrBayes (Ronquist et al., 2012), RevBayes (Höhna et al., 2016), BEAST2 (Bouckaert et al., 2019). Computations use the Markov chain Monte Carlo (MCMC) algorithm to explore the parameter space and identify the regions maximizing the likelihood.

In addition to the model-based inference of phylogenetic hypotheses, a Bayesian framework can be used to estimate divergence times. The framework applies prior probability distributions on branch rates and node ages, and BEAST2 has become one of the most popular programs used to estimate time using strict and relaxed molecular clocks (Bouckaert et al., 2019).

The estimation of the time of divergence of lineages has become a common question in molecular studies. These divergence times are normally shown on a time-tree (chronogram), which is a rooted phylogeny where branch lengths are proportional to absolute time (Bouckaert et al., 2014). The method uses molecular clocks, which converts the number of molecular changes between lineages into time. Molecular clocks estimate relative rates of mutation, but they can be calibrated using different sources of information that provide minimum and maximum ages for certain events.

Clade support

Phylogenetic trees represent estimates of the evolutionary history of the focal species, populations or genes. In the previous section of this chapter, I rapidly presented the main methods for estimating phylogenetic trees. However, to evaluate these hypotheses, it is always desirable to add a measure of confidence.

Measures of phylogenetic reliability not only point out which parts of the tree can be trusted but also guide us through future efforts for data collection (Huelsenbeck and Rannala, 2004). The standard bootstrap support (SBS) is one of the most common methods used for assessing the robustness of branches in phylogenetic hypotheses.

This measure of credibility was applied for the first time in systematics by Felsenstein (1985). The method works by resampling sites with replacement from the original dataset so that each bootstrap sample has the same number of sites as the original data (Yang, 2014). However, the standard bootstrap support (SBS) as proposed by Felsenstein is computationally demanding as datasets increase in size, with studies showing it can be biased and too conservative (Minh et al., 2013).

One method which resembles SBS is the rapid bootstrap support (RBS), as implemented in RAxML, RAxML-NG (Stamatakis et al., 2008; Stamatakis, 2014; Kozlov et al., 2019). This method performs faster than SBS on large datasets and is widely used. In short, the rapid bootstrap starts with the computation of a Maximum Parsimony (MP) starting tree on the original alignment. Then, the model parameters and branch lengths are optimized for the original alignment.

The RBS method conducts replicate SBS searches. At every 10th replicate, the program reloads the original alignment to compute a randomized stepwise addition MP starting tree. Once this starting tree has been computed, the program calculates and loads a bootstrapped alignment, which is then optimized under ML (Stamatakis et al., 2008). Values of SBS ≥ 85 indicate well-supported clades.

Recently another approach aiming to overcome the high computational cost of standard bootstrap was developed, the Ultrafast bootstrap UFBoot2 as implemented in IQ-TREE1x, 2x. UFBoot2 is less conservative than SBS and RBS (Minh et al., 2013; Hoang et al., 2018). This method keeps trees recovered during the ML-tree search from the original data set and uses them to evaluate tree likelihoods for the bootstrapped multiple sequence alignment (MSA) (Hoang et al., 2018).

To speed up computational time, IQ-TREE employs the resampling estimated log-likelihood (RELL) strategy (Kishino et al., 1990), which reuses the log-likelihood scores calculated for individual sites in the original alignment given the tree. For each bootstrap MSA, the tree with the highest RELL score (RELL-tree) represents the ML-bootstrap tree. Values of SH ≥ 80 and UFBoot2 ≥ 95 indicate well-supported clades (Minh et al., 2013; Hoang et al., 2018).

In contrast to ML searches, in BI approaches, the posterior probabilities at nodes, are the frequency at which one node in MCC is recovered across the posterior distribution of trees. Posterior distributions of tree topologies and branch lengths can be summarized in a MAP tree (the maximum a posteriori tree).

The MAP can be easily calculated when the data sets are very well resolved, or have a small number of taxa. The MAP represents the tree with the greatest posterior probability, averaged over all branch lengths and substitution parameter values (Bouckaert et al., 2019). However, for large data sets every sampled tree may have a unique topology, so, in programs like BEAST, the posterior distributions are commonly summarized in a maximum clade credibility tree, that is the tree in the posterior sample that has the maximum sum of posterior clade probabilities (Bouckaert et al., 2019).

Morphological studies in phylogenetics

The use of molecular data has undoubtedly provided substantial progress in the taxonomy of many lineages in which morphology is not enough for delineation. Molecular phylogenetic hypotheses have much better explanatory power over morphology and some of the earlier classifications have been completely revised after unexpected phylogenetic relationships were discovered.

However, we cannot ignore the valuable information that morphological studies provide to our understanding of the character distribution, homology and evolution in our taxa of interest (Mooi and Gill, 2010). The reasons for this are straightforward. Firstly, molecular data cannot tell us what the species look like physically, people want to have concrete descriptions of structures and illustrations of organisms and without this explicit evidence, molecular phylogenies may lack long-term impact.

Secondly, molecular phylogenies present relationships between terminal taxa but they often cannot inform us how the studied taxa should be classified on higher taxonomic levels. For a Linnean classification, it is quite arbitrary where we cut off the cladogram for defining a genus, subfamily, family, etc.

Often the molecular analyses include only a small fraction of the known diversity, thus the analyses cannot inform us if the sister-taxa should be classified in the same genus/tribe/subfamily or not. Even though detailed morphological studies are time-consuming, an integrated approach is needed: molecular information to construct stable phylogenetic hypotheses, and morphology and other biological data including life-histories such as food-plants to diagnose, to illustrate and to classify organisms into monophyletic groups.

One of the greatest advantages of morphology is that in the case where molecular techniques fail, analyses of morphological characters often reveal the path, especially for old and rare samples (Wipfler et al., 2016). For instance, the placement of extinct taxa cannot be done without morphological examinations and fossils are essential for dating molecular phylogenies (Wiens, 2004).

Although methods are available to estimate divergence times only with molecular data, those analyses still need external calibrations and those calibrations come mostly from fossil evidence. Perhaps most importantly, the species have changed through time and to understand why current species are the way they are today, the study of fossils and their morphology is required (Wiens, 2004; Lee and Palci, 2015). Fossils provide insights into phylogenetic history, and the interpretation of morphological variation in fossils requires the understanding of the morphology of living species (Hillis, 1987).

Another compelling reason to continue exploring morphological data is that molecular phylogenies are not error-free. Hence, it is very important to compare molecular inferences with morphology-based studies to help us to identify misleading hypotheses.

Such an approach creates a solid taxonomic/phylogenetic framework, into which further taxa can be integrated and classified. In the case of Lepidoptera, morphologically intuitive phylogenetic hypotheses have been the baseline for understanding the evolutionary patterns we see today in many diverse families (Kristensen and Skalski 1998).

The study of genital structures and wing venation have been the source in comparative studies aimed to understand relatedness among Lepidoptera lineages (Heikkilä et al., 2015). Among the most influential studies in comparative morphology of Lepidoptera are for instance the work by Kristensen (2003); Kristensen et al. (2007), Minet (1991) which have been the basis of a reconstruction of the phylogenetic trees of most species-rich lepidopteran families.

The role of DNA barcodes in taxonomy and systematics

The importance of having an integrative approach to classifications have led current taxonomical studies to use not only morphology but complement the species identifications with data such as DNA barcodes (Hebert et al., 2003a; Hebert et al., 2003b). The standard barcode for animals is a mitochondrial gene marker, the *Cytochrome c oxidase subunit I.*

The method works in a way that once the genetic region of interest is amplified, the sequence similarities are then analyzed using hierarchical clustering of genetic distances. Nowadays clustering algorithms like the Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012) and the General Mixed Yule Coalescent (GMYC) model (Pons et al., 2006) have been widely used for species delineation.

Species are assigned to operational taxonomic units (OTUs) by statistical evaluations where genetic distance thresholds are implemented (Ratnasingham and Hebert, 2013). Specifically, in the BOLD system platform, OTUs are delineated by the Refined Single Linkage (RESL) algorithm and subsequently assigned to a Barcode Index Number System (BIN).

The use of DNA barcodes has changed the traditional way of studying biodiversity, which over decades has relied on other characters for species identifications. One important advantage of DNA barcodes is the fact that many museum and holotype specimens can be easily barcoded, providing reference libraries (Prosser et al., 2016).

These barcode repositories are subsequently used to identify newly collected specimens strengthening species inventories and unifying species identifications. In species-rich groups such as Lepidoptera, barcodes have eased species descriptions, some classifications, but more importantly, have helped to speed up inventories of species diversity (Janzen and Hallwachs, 2016).

Molecular studies of diversification and biogeography

Phylogenies are paramount when understanding the evolution of organisms. They can be used for understanding for example the emergence and evolution of phenotypes, the evolution of the ecological niche, species interactions, geographic dispersal as well as speciation and extinction patterns.

How and why some groups have become more species-rich than others, and how past biogeographical processes may have shaped their current distribution are important long-standing questions in evolutionary biology. The estimation of diversification rates and biogeographical inference are among the most common approaches addressing these evolutionary questions. The latter approaches rely on dated molecular phylogenies as foundations and therefore make some assumptions about the processes driving the diversity of current taxa.

Methods employed to estimate diversification rates aim at explaining how biodiversity has varied over time, which implies a balance between the speed at which new lineages appear (speciation) and the speed at which lineages go extinction (extinction) on a scale of thousands to millions of years (Nee et al., 1992; Nee et al., 1994a; Nee et al., 1994b; Morlon, 2014).

By estimating how diversification rates changed through time and across lineages we can assess the role of species ecology, morphology or environmental changes in the emergence of diversity patterns (Meyer and Wiens, 2018). The fossil record has traditionally been the primary source to study these diversification dynamics, however, the lack of fossil information is a common pattern in groups where fossils do not form easily. This includes insects such as Lepidoptera.

Alternative approaches when fossil information is unavailable, attempt to estimate diversification rates from the distribution of branching times as inferred from molecular phylogenies of extant taxa (Morlon et al., 2011). The methods consist of using birth-death models to infer diversification patterns (Nee et al., 1992; Nee et al., 1994a; Nee et al., 1994b) and using phylogenetic hypotheses of extant species reconstructed from molecular data.

However, diversification analyses under the birth-death of cladogenesis model have been recently criticized. Louca and Pennell (2020) showed that given time-depend speciation and extinction functions, we can recover an infinite number of congruent models describing different diversification dynamics. The implication of those findings was nicely debated by Morlon et al. (2020).

Even though the birth-death model is the focus of debate, we aware that methods are not exempt from issues. Diversification analyses with the right data and priors can lead to well-founded hypotheses. Morlon (2014) provides an excellent overview of numerous approaches that can be used to estimate diversification rates.

What these methods have in common is that diversification analysis focuses on I) branching times and the topology, II) net diversification rates, which can be estimated from clade age and species richness data, and III) speciation and extinction rates that can both be estimated with a combination of branching times and species richness data (Morlon, 2014).

One of the widely used approaches to estimate diversification rates is the Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky et al., 2014). This program intends to detect shifts in diversification rates across phylogenies and models dynamics of speciation and extinction using a reversible jump Markov Chain Monte Carlo (Rabosky et al., 2013).

But global patterns of diversity can also be explaining in a geographic historical context. Differences in species richness and shifts in diversification rates can be highly correlated with the movement and exploration into a new geographic area. To identify these patterns and formulate hypotheses we not only require a well-supported phylogenetic hypothesis, but also the estimation of diversification rates and thus the biogeographical patterns for the group of interest.

The methods employed in biogeographical analyses use time-scaled trees and distribution data information to estimate past geographic ranges across the tree. In this case, phylogenetic hypotheses are essential in trying to understand how geographic ranges evolved through time and when and where did lineages disperse across geographic regions (Sanmartín, 2012; Matzke, 2013).

Biogeographical hypotheses can be inferred in a maximum likelihood or a Bayesian framework. BioGeoBEARS is one of the most popular programs used in historical biogeography (Matzke, 2014). The latter, implements models such as the DEC (Dispersal-Extinction Cladogenesis, Ree and Smith, 2008) , the modified version of the DIVA (parsimony-based Dispersal-Vicariance Analysis, Ronquist 1997) and BayArea (Historical Biogeography for Discrete Areas, Landis et al., 203) .

The assumptions of all these methods rely on a wide range of processes that may have produced the geographic ranges of observed taxa including within-area speciation, vicariance, range expansion, and extirpation (Dupin et al., 2017).

The DEC model is the most widely used in historical biogeography, and it is also implemented in a Bayesian framework (Landis et al., 2018) in the software RevBayes (Höhna et al., 2016). The DEC model assumes different possible events: dispersal (or range expansion) along branches, extirpation (or extinction within an area) also occurring along branches and different scenarios of range evolution at the speciation event (i.e. node) (Ree et al., 2005). The model also usually allows implementing changes in connectivity between areas through time in the model, which can be used to consider for example continental drift, montane uplift or the appearance of islands.

Thesis aims

The objective of my project is to use phylogenetic methods to understand the phylogenetic history of geometrid moths (Lepidoptera). Particularly, I have the following aims:

- Provide a molecular phylogeny of higher geometrid taxa (chapters I, II and III).
- Revise the recently described geometrid moth subfamily Epidesmiinae (Lepidoptera: Geometridae) (chapter IV).
- Explore a set of protein-coding genes extracted from whole-genome shotgun sequencing data to infer the phylogenetic history of deep lineages of Geometridae (chapter V).
- Address how historical biogeography and diversification processes have shaped the evolution of the most species-rich geometrid tribe, Boarmiini (chapter VI).
- Inventory geometrid species in one of the most biodiversity-rich countries of South America, Colombia (chapter VII).

General methods

Material acquisition, taxon sampling and species identification

In addition to the 461 terminal taxa with publicly available sequences in GenBank, we provided the field of Lepidopteran phylogenetics with sequences from 745 new terminal taxa representative of all, but one, subfamilies recognized in Geometridae (**chapters I-III**). The Orthostixinae, remains the last small subfamily for which most molecular markers could not be amplified successfully with Sanger sequencing. A total of 93 tribes are represented in our study following recent phylogenetic hypotheses and classifications (Wahlberg et al., 2010; Sihvonen et al., 2011; Ounap et al., 2016; Ban et al., 2018). Also, 14 non-geometrid species belonging to other families of Geometroidea were included as outgroups based on the hypothesis proposed by Regier et al. (2013) (**chapters I-III**).

The morphological review of Epidesmiinae (**chapter IV**) included representatives and type species for all genera recognised by Murillo-Ramos et al. (2019), as well as representatives and type species of all geometrid subfamilies for morphological comparisons.

For the subsequent project, DNA extracts taken from 20 terminal taxa derived from the study in chapter I, were used for genome sequencing (**chapter V**). The taxa were chosen to represent the deepest divergences in the family, representatives of the recently discovered lineages, and taxa that could not be assigned with confidence in the phylogenetic hypothesis proposed by Murillo-Ramos et al. (2019).

For the historical biogeography and diversification analysis (**project VI)**, 349 terminal taxa were analyzed, which correspond to Boarmiini species and outgroups. Part of the data was retrieved from the Murillo-Ramos et al. (2019) dataset, while some data were generated specifically for this study.

Finally, in **chapter VII**, geometrids were collected from 26 localities in Colombia. The 384 specimens were barcoded. The samples that did not match with any BIN in the BOLD platform were amplified at two additional nuclear markers to provide additional information about their phylogenetic position and identifications.

Sampled individuals used in all chapters were provided (from field expeditions, donations) and identified by the authors using their expertise, appropriate literature, by comparing them with type material from different collections, museums and by using DNA barcode sequences. Specimens for chapter IV were loaned and examined from the Australian National Insect Collection, CSIRO, Division of Entomology, Canberra, Australia (ANIC); the Natural History Museum, London, UK (NHMUK); the Finnish Museum of Natural History, Helsinki, Finland (ZMH) and the private collections of Egbert Friedrich (Germany) and Pasi Sihvonen (Finland).

Molecular techniques

DNA was extracted from 1–3 legs of specimens either preserved in ethanol or dry. In a few cases, other sources of tissue were used, such as parts of larvae. The remaining parts of specimens have been preserved as vouchers and will eventually be deposited in public museum collections. Genomic DNA was extracted and purified using the NucleoSpin® Tissue Kit (MACHEREY-NAGEL), following the manufacturer's protocol.

For Sanger sequencing projects, DNA amplification and sequencing were carried out following protocols proposed by Wahlberg and Wheat (2008) and Wahlberg et al. (2016). PCR products were visualized on agarose gels, and subsequently cleaned enzymatically with Exo-FastAP and sent to Macrogen Europe (Amsterdam) for sequencing.

Depending on the research project one mitochondrial (*COI*) and up to 10 protein-coding nuclear gene regions *(Wingless, ArgK, MDH, RpS5, GAPDH, IDH, Ca-ATPase, Nex9, EF-1alpha* and *CAD*) were amplified. To check for potential misidentifications, DNA barcode sequences were compared to those on BOLD (Ratnasingham and Hebert, 2007) where references of more than 21 000 geometrid species are available, some 10 000 of them being reliably identified to Linnean species names (Ratnasingham and Hebert, 2007).

For genome sequencing (**chapter V**), we used the existing DNA extracts. As the DNA extractions are from relatively fresh samples, we fragmented the DNA into fragments approximately 200–300 bp in size with sonication. Libraries were prepared following a modified version of the protocol for Blunt-End Illumina Library construction in (Meyer and Kircher, 2010) and Twort et al. (2020). Each library was dual indexed and pooled together for sequencing on the Illumina NovaSeq 6000 system.

Alignment and cleaning sequences

Sanger sequences (**chapters I-III, VI, VII**) were cleaned to remove primers and low-quality regions in Geneious v 11.0.2 (https://www.geneious.com). Cleaned sequences were then aligned with MAFFT as implemented in Geneious for each gene based on a reference sequence of Geometridae downloaded from the Wahlberg group database on VoSeq (Peña and Malm, 2012).

The alignment of each gene was carefully checked by eye relative to the reference sequence, considering the respective genetic codes and reading frames. Heterozygous positions were coded with IUPAC codes. To check for possible errors in alignments, potentially contaminated or identical sequences and misidentifications, we constructed maximum-likelihood trees for each gene. These preliminary analyses were conducted using RAxML-HPC2 V.8.2.10 (Stamatakis, 2014) on the web-server CIPRES Science Gateway (Miller et al., 2010).

For whole-genome sequencing **(chapter V)**, the raw Illumina data were quality checked, followed by the removal of low-quality regions, adapters and reads with ambiguous bases. *De novo* genome assembly for each sample was carried out with SPAdes (Bankevich et al., 2012), using a multi-kmer approach. Gene regions of interest were identified and extracted using MESPA (Neethiraj et al., 2017). Gene alignment was carried out with MAFFT, followed by manual curation to ensure the preservation of open reading frames and the identification of pseudogenes and misidentifications/misalignments.

Phylogenetic analysis

Maximum likelihood analyses were run with a dataset partitioned by gene and codon position using IQ-TREE V1.6.10 (Nguyen et al., 2015) **(chapters I-III, VI),** and data partitioned by codon in RAxML-HPC2 V.8.2.10 (Stamatakis, 2014) **(chapters I-III)**. Best-fitting substitution models were selected by ModelFinder, which is a model-selection method that incorporates a model of flexible rate heterogeneity across sites (Kalyaanamoorthy et al., 2017). After the best partitioning strategy and model have been found, IQ-TREE starts the tree reconstruction under this scheme. The phylogenetic analyses were carried out with the *-spp* (edge proportional) option that allowed each partition to have its evolutionary rate. The RAxML analyses were carried out on CIPRES Science Gateway using the GTR+GAMMA option **(chapters I-III)**.

Genome data were analyzed in three datasets (**chapter V**): I) amino acids concatenated, II) nucleotides concatenated, and III) nucleotide gene sets. We ran maximum likelihood analyses using IQ-TREE2 V2.0.6 (Minh et al., 2020). Best-fitting substitution models were selected by ModelFinder as explained above.

Support for nodes **(chapters I-III, V, VI)** was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al., 2018) in IQ-TREE, and SH-like approximate likelihood ratio test (Guindon et al., 2010). To reduce the risk of overestimating branch supports in UFBoot2 test, we implemented the *-bnni* option, which optimizes each bootstrap tree using a hill-climbing nearest-neighbour interchange (NNI) search. Additionally, we implemented rapid bootstrap (RBS) in RAxML (Stamatakis et al., 2008) **(chapters I-III, VI)**. Trees were visualized and edited in FigTree v1.4.3.

Intra- and interspecific differences of the DNA barcodes were calculated under the Distance Summary and the Barcode Gap Analysis using the analytical tools of BOLD systems v4.0 (http://www.boldsystems.org) (**chapter VII**). Species identification with the sequences >500 bp was assessed by the Barcode Index Number (BIN) system as implemented on BOLD (Ratnasingham and Hebert, 2013).

The *COI* sequences that were without a BIN match on BOLD were submitted to follow-up analysis with two additional nuclear genes. We retrieved the dataset of Murillo-Ramos et al. (2019) stored in VoSeq. We ran maximum likelihood analyses with partitions by gene using RAxML-HPC2 V.8.2.12 (Stamatakis, 2014) on the web-server CIPRES Science Gateway. Support for nodes was evaluated with 1,000 rapid bootstraps in RAxML.

Dated tree inference

A time-calibrated tree was inferred to understand the evolutionary history of Boarmiini moths (**chapter VI**). We estimated divergence times under a relaxed molecular clock, which allows branch lengths to vary according to an uncorrelated Lognormal distribution. We fixed the topology with the tree inferred from IQ-TREE. To estimate times of divergences, we calibrated both the crown clade of Boarmiini as well as the root of the topology with a uniform distribution. We used a minimum age corresponding to the Lutetian according to the latest International Chronostratigraphic Chart (Cohen et al., 2013) and a maximum bound corresponding to the age of stem Geometroidea according to the results of (Wahlberg et al., 2013). The convergence of runs was checked in Tracer (Rambaut et al., 2018). See chapter VI for more details.

Morphological revision of Epidesmiinae

The molecular phylogeny provides the phylogenetic framework that I used as the basis to study the morphology of Epidesmiinae moths from museum collections in chapter IV. We created a data set of morphological characters including male and female genitalia, sclerites of the abdomen and thorax, wing pattern and wing venation. The comparative morphological analysis considered the taxonomic work and diagnostic characters proposed by earlier authors (Holloway, 1979). The study included at least one type species from each of the eight Epidesmiinae genera as defined by molecular phylogeny. Abdomens from the specimens were macerated in potassium hydroxide (10%), dissected, examined under stereomicroscope combined with *in-situ* photography. Homologies of structures were identified and described using the terminology of Klots (Klots, 1970; Wootton, 1979; Kristensen, 2003) and in cases where homologies of structures were difficult to identify, descriptive terms were used instead.

Results and discussion

As in previous lepidopteran studies, the phylogenetic hypotheses proposed in this research are a step forward in our comprehensive understanding of the evolutionary history of the major clades in geometrid moths. Our study is the first large-scale molecular phylogeny which includes representatives from all biogeographical regions. We discovered and named new lineages (**chapters I-III**) and proposed a framework for the classification system of higher geometrid taxa.

Maximum likelihood methods recovered well-supported topologies (RBS, UFBoot2: 100), which confirmed not only the monophyly of Geometridae moths (**chapter I**) (fig. 4) but also recovered the monophyly of most subfamilies, as traditionally accepted in pasts classifications (**chapters II, III**). This, except for the Desmobathrinae-Oenochrominae complex, for which the two subfamilies appear para- and polyphyletic respectively.

Many internal nodes remained questionable as not strongly supported, probably because some lineages were under-represented and the amount of molecular data available was low compared to the high number of sampled taxa. Nonetheless, the taxonomic decisions in our study rely on the molecular data, and well-supported clades suggested in our ML analyses (RBS, UFboot2=100). Additionally, we offered educated suggestions for several novel hypotheses, such as placing the Sterrhinae as sister to all geometrid subfamilies instead of the Sterrhinae + Larentiinae clade as in Sihvonen et al. (2011). We proposed a new subfamily Epidesmiinae, which is a previously unrecognized lineage of former slender-bodied Oenochrominae. Moreover, the tribe Archaeobalbini Viidalepp (Geometrinae) is raised from synonymy with Pseudoterpnini Warren to tribal rank and Chlorodontoperini (Geometrinae) and Drepanogynini (Ennominae) are described as new tribes. Other taxonomic changes are listed in **chapter I**.

In **chapter II** we further presented a revised classification of Sterrhinae. Based on the molecular phylogeny and extensive morphological examination, nine tribes are considered valid. Mecoceratini Guenée, 1858 (=Ametridini Prout, 1910) was transferred from Desmobathrinae to Sterrhinae, and it is considered valid at tribal level.

Haemaleini Sihvonen & Brehm is described as a new tribe and deemed sister to Scopulini + Lissoblemmini; Lissoblemmini Sihvonen & Staude is described as a new tribe and sister to Scopulini. Lythriini Herbulot, 1962 is now a junior synonym of Rhodometrini Agenjo, 1952; and Rhodostrophiini Prout, 1935 is now a junior synonym of Cyllopodini Kirby, 1892.

Also, 48 taxa were transferred from other geometrid subfamilies to Sterrhinae, or within Sterrhinae from one tribe to another, or they are classified into a tribe for the first time, or a new genus classification is proposed.

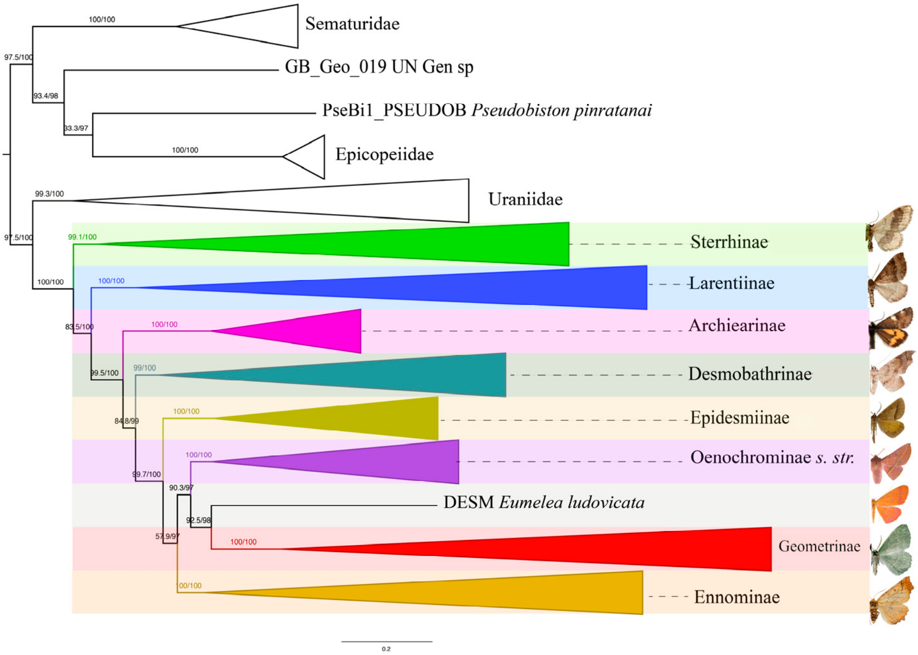

Figure 4. Phylogenetic hypothesis of major groups of the family Geometridae. Numbers above branches are SH-aLRT support (%)/ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH ≥ 80 and UFBoot2 ≥ 95 indicate well-supported clades. Epidesmiinae is proposed as a new subfamily in this study.

In the same way, we updated the new world geometrids in **chapter III**. Our analysis concentrates on the level of tribes and genera, many of which were shown to be para- or polyphyletic. We proposed 11 new tribe names (Larentiinae, authors Brehm, Murillo-Ramos & Õunap): Brabirodini, Chrismopterygini, Psaliodini, Pterocyphini, Rhinurini, Ennadini, Cophocerotini, Erebochlorini; (Ennominae, authors Brehm, Murillo-Ramos & Sihvonen): Euangeronini, Oenoptilini, Pyriniini.

We assigned 27 genera for the first time to a tribe, proposed 29 new tribe assignments and 26 new generic combinations, we synonymized one tribe and seven genera, revived one tribe, and proposed to exclude 119 species from non-monophyletic genera (*incertae sedis*). Our study provides the data and foundation for numerous future taxonomic revisions of New World geometrid moths.

We also examined the broad-scale biogeographic patterns of New World Geometridae: While Nearctic species are often nested within the predominantly Neotropical clades, the South American fauna forms distinct clades, hinting at long isolation from the remaining New World fauna.

In most of the cases, the taxonomic changes proposed in **chapters I-III** agreed with the current taxonomic literature and the knowledge of taxonomic experts. We attempted to address the needed taxonomic changes, to recognize monophyletic entities and to favour taxonomic stability of the subfamilies and many tribes, even if in an interim way.

We identified areas for further research, such as the uncertain phylogenetic position of *Eumelea*. It was not possible to assign this genus with confidence to any subfamily of Geometridae.

In **chapter IV,** Epidesmiinae were found to have an Australasian distribution, with one species occurring in the Indo-Malayan realm. This lineage was diagnosable by a combination of morphological characters such as male antennae; labial palps, the shape of the vom Raths organ; wing venation and male/female genitalia morphology (fig 5).

Figure 5. Right, diagnostic morphological structures of Epidesmiinae. **A.** Labial palps with scales, **B.** Labial palps descaled and pit-organ (vom Rath's organ) enlarged, **C.** Metathorax furca, dorsal view, **D.** Tympanal organ with scales intact, **E.** Tympanal organ, descaled, **F.** Hind leg with hair-pencil, **G.** Part of male reproductive organ. Left, **A.** Adult female, **B-E.** Male reproductive organ, aedeagus with everted vesica, ansa of tympanal organ, male 8th abdominal segment, **F.** Female head and labial palps, **G-I.** Female reproductive organ, elongated signum, stellate signum.

These diagnostic characters support the subfamily hypothesis of Murillo-Ramos et al. (2019) and further validate the classification of the lineage at subfamily-level. We also presented a summary of diagnostic characters of all geometrid subfamilies, which confirmed the lack of single unique morphological characters.

The limited information on the biology and ecology of Epidesmiinae species was also summarized, indicating that some species fly during the day, most adult records are from the Southern Hemisphere summer months, and larvae are found on species of the plant family Myrtaceae.

The phylogenomic dataset analysed in **chapter V** confirmed the monophyly of Geometridae but contrary to chapter I, Sterrhinae + Larentiinae were recovered as sister taxa, as in Sihvonen et al. (2011).

The validity of Orthostixinae as a subfamily was tested and the result suggested that this small lineage is part of Desmobathrinae. Our results support the morphological examinations proposed by Beljaev (2008) and Murillo-Ramos et al. (submitted) so that we formally synonymized Orthostixinae with Desmobathrinae. Also, 300 markers did not place *Eumelea* within Oenochrominae or Geometrinae, instead, *Eumelea* came out as a single lineage. So, we raised this taxon to a subfamily status.

The monophyly of Boarmiini is strongly supported in Chapter VI. However, the phylogenetic position of many taxa did not correspond to their current taxonomy, although the monophyly of most major genera within the tribe is supported after minor adjustments in classification.

Our results supported the idea of rapid initial diversification of Boarmiini, which also implies that no major taxonomic subdivisions of the group could currently be proposed. The time-calibrated tree and biogeographical analyses suggested that boarmiines probably appeared in the Holarctic region ca. 52 Mya, followed by dispersal events throughout the Australasian, African and Neotropical regions (Fig 6).

Most of the transcontinental dispersal events occurred in the Eocene, which was characterized by intense geological activity and rapid climate change. Diversification analyses showed a relatively constant diversification rate for all Boarmiini, except in one clade containing one species-rich geometrid genus, the genus *Cleora*.

Our results represent a substantial contribution towards understanding the evolutionary origin of Boarmiini. However, the results presented are inevitably biased by taxon sampling. Our study highlights the difficulties of working on species-rich groups that have not received much attention outside of Europe.

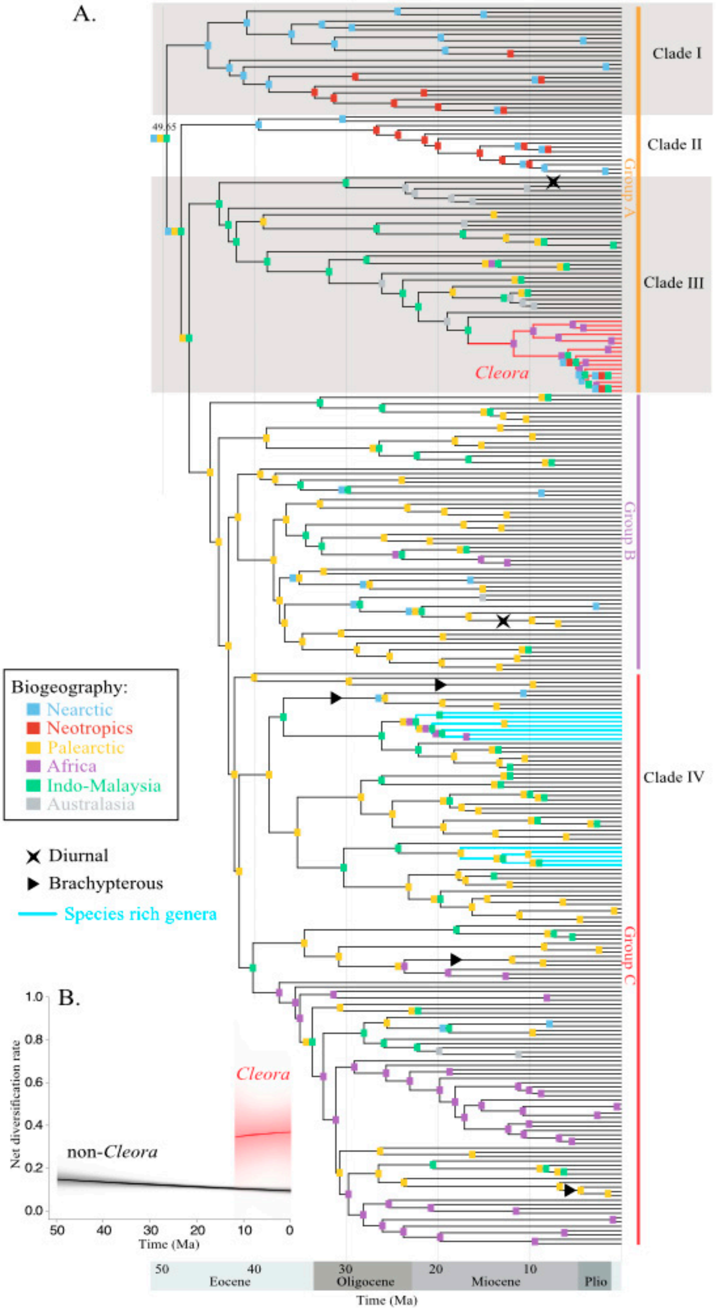

Figure 6. A. Time-calibrated phylogeny, biogeography. B. Estimated net diversification of Boarmiini moths. Coloured squares on nodes indicate the most likely biogeographical area from BioGeoBEARS estimations.

In **chapter VII**, we released a DNA barcode library of Geometridae from Colombia. We enriched the Colombian Geometridae database significantly and it now includes DNA barcodes, two nuclear markers, photographs of vouchers, and georeferenced occurrences of 284 specimens from different localities in Colombia.

These specimens are classified into 81 genera and analytical tools on BOLD clustered 86 of the mentioned sequences to species level BINs, identified earlier by experts. Another 142 were assigned to BINs (another 56 sequences were duplicates), but those were identified to genus or tribe level only.

Some of these unidentified samples did not match any existing BIN on BOLD, therefore being new additions to the database, and some of those probably represent undescribed species. Unsurprisingly, more than 50% of the barcodes which correspond to the subfamilies Sterrhinae and Larentiinae could not be assigned to species level identifications.

Most of the unassigned species correspond to the genera *Idaea* and *Eupithecia,* which are full of unidentified records, not only in this study but also in public databases such as BOLD. Although the data released as part of this study are a significant contribution to the knowledge of neotropical Geometridae, the current species list from Colombia, which includes 128 species (about 10% of the fauna), stresses the gap in the knowledge of geometrids, and compared to other well-monitored countries like Ecuador or Costa Rica, it very likely that our species list represents only a small part of the fauna.

Until recently, the classification of geometrids have relied on morphological characters, which have been very useful at species and sometimes genus level. However, using morphology to test the evolutionary relationships of higher taxa and diverse groups can be complicated, especially if we try to find homologous characters among the lineages.

In that sense, molecular systematics has led to strongly supported phylogenetic hypotheses for better understanding of the diversity of geometrids. For instance, tribal compositions of Geometrinae and Larentiinae remained largely unexplored until molecular data became available (Ounap et al., 2016; Ban et al., 2018). These subfamilies are widespread, with many species complexes and problematic taxonomy.

The advantage of a molecular-based taxonomic framework is that it provides a backbone for further understanding of the evolution of Lepidoptera. Divergence studies, life history and biogeographical patterns are better understood when robust phylogenetic classifications are proposed. Nevertheless, the importance of traditional taxonomy, based on morphological characters, should not be ignored. Traditional taxonomy work must continue so that organisms are described and named based on reliable synapomorphies. However, only by combining molecular, morphological and biological information can we hope to get a more complete understanding of not only the evolutionary history of this group but also gain insights into how various processes and events have shaped the diversity we see today.

Future perspectives

Revolving outstanding issues on the phylogenetic history, taxonomy and classification of geometrid moths will require a significant effort of sampling the unexplored areas (mainly the tropics), and gathering more genomic data from key taxa. From the subfamilial level phylogeny, the geometrids are well-understood taxon.

However, deeper studies are required from the genus and tribe level. And not less important, the future research should be redirected to the study of the biological patterns of the geometrid species. Gathering all this data is fundamental for understanding the patterns of diversity of this amazing insect radiation.

References

Abraham, D., Ryrholm, N., Wittzell, H., Holloway, J.D., Scoble, M.J., Lofstedt, C., 2001. Molecular phylogeny of the subfamilies in Geometridae (Geometroidea: Lepidoptera). Mol Phylogenet Evol 20, 65-77.

Ban, X.S., Jiang, N., Cheng, R., Xue, D.Y., Han, H.X., 2018. Tribal classification and phylogeny of Geometrinae (Lepidoptera: Geometridae) inferred from seven gene regions. Zool J Linn Soc-Lond 184, 653-672.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., Pyshkin, A.V., Sirotkin, A.V., Vyahhi, N., Tesler, G., Alekseyev, M.A., Pevzner, P.A., 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. J Comput Biol 19, 455-477.

Bazinet, A.L., Cummings, M.P., Mitter, K.T., Mitter, C.W., 2013. Can RNA-Seq resolve the rapid radiation of advanced moths and butterflies (Hexapoda: Lepidoptera: Apoditrysia)? An exploratory study. Plos One 8, e82615.

Bazinet, A.L., Mitter, K.T., Davis, D.R., Van Nieukerken, E.J., Cummings, M.P., Mitter, C., 2017. Phylotranscriptomics resolves ancient divergences in the Lepidoptera. Syst Entomol 42, 305-316.

Beljaev, E.A., 2007. Taxonomic changes in the emerald moths (Lepidoptera : Geometridae, Geometrinae) of East Asia, with notes on the systematics and phylogeny of Hemitheini. Zootaxa, 55-68.

Beljaev, E.A., 2008. Phylogenetic relationships of the family Geometridae and its subfamilies (Lepidoptera), St. Petersburg.

Bouckaert, R., Heled, J., Kuhnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput Biol 10, e1003537.

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchene, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kuhnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Muller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.H., Xie, D., Zhang, C., Stadler, T., Drummond, A.J., 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Comput Biol 15, e1006650.

Brehm, G., Hebert, P.D., Colwell, R.K., Adams, M.O., Bodner, F., Friedemann, K., Mockel, L., Fiedler, K., 2016. Turning Up the Heat on a Hotspot: DNA Barcodes Reveal 80% More Species of Geometrid Moths along an Andean Elevational Gradient. Plos One 11, e0150327.

Brehm, G., Murillo-Ramos, L., Sihvonen, P., Hausmann, A., Schmidt, B.C., Õunap, E., Moser, A., Mötter, R., Boldt, D., Bodner, F., Lindt, A., Parra, L.E., Wahlberg, N., 2019. New World geometrid moths (Lepidoptera: Geometridae): Molecular phylogeny, biogeography, taxonomic updates and description of 11 new tribes. ARTHROPOD SYSTEMATICS & PHYLOGENY 77, 457-486.

Call, E., 2020. The age of museomics: how to get genomic information from museum specimens of Lepidoptera. Biology. Lund University, Lund, p. 79.

Call, E., Mayer, C., Dietz, L., Twort, V., Wahlberg, N., Espeland, M., 2020. Museomics: phylogenomics of the moth family Epicopeiidae (Lepidoptera) using target enrichment. . Insect Systematics & Diversity in press.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. The ICS International Chronostratigraphic Chart. Episodes 36, 199-204.

Cook, M.A., Harwood, L.M., Scoble, M.J., Mcgavin, G.C., 1994. The Chemistry and Systematic Importance of the Green Wing Pigment in Emerald Moths (Lepidoptera, Geometridae, Geometrinae). Biochem Syst Ecol 22, 43-51.

Cook, M.A., Scoble, M.J., 1992. Tympanal Organs of Geometrid Moths - a Review of Their Morphology, Function, and Systematic Importance. Syst Entomol 17, 219-232.

Darwin, C., 1859. On the Origin of Species by Means of Natural selection, or, the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Dupin, J., Matzke, N.J., Särkinen, T., Knapp, S., Olmstead, R.G., Bohs, L., Smith, S.D., 2017. Bayesian estimation of the global biogeographical history of the Solanaceae. J Biogeogr 44, 887-899.

Ehrlich, P.R., Raven, P.H., 1964. Butterflies and plants: a study in coevolution. Evolution 18, 586-608.

Felsenstein, J., 1978. Cases in which parsimony and compatibility methods will be positively misleading. Systematic Zoology 27, 401-410.

Felsenstein, J., 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17, 368-376.

Felsenstein, J., 1985. Confidence Limits on Phylogenies: An Approach Using the Bootstrap. Evolution 39, 783-791.

Ghanavi, H., 2020. Using big data to understand evolutionary patterns in Geometridae and Erebidae, the two most diverse families of Lepidoptera., Faculty of Science, biology. Lund University, Lund.

Ghanavi, H., Chazot, N., Sanmartín, I., Murillo-Ramos, L., Duchêne, S., Sihvonen, P., Brehm, G., Wahlberg, N., In prep. Biogeography and Diversification Dynamics of the Moth Family Geometridae (Lepidoptera). 28.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst Biol 59, 307-321.

Hausmann, A., 2001. The Geometrid Moths of Europe. Apollo Books, Stenstrup.

Hausmann, A., 2004. Sterrhinae. In: Hausmann, A. (Ed.), The Geometrid moths of Europe. Apollo Books, Srebstrup, Denmark, pp. 1-600.

Hebert, P.D.N., Cywinska, A., Shelley, L.B., deWaard, J.R., 2003a. Biological identifications through DNA barcodes. Proceedings of the Royal Society B 270, 313-321.

Hebert, P.D.N., Ratnasingham, S., deWaard, J.R., 2003b. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. . Proceedings of the Royal Society B.

Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P., Kaila, L., 2015. Elusive ditrysian phylogeny: an account of combining systematized morphology with molecular data (Lepidoptera). Bmc Evol Biol 15, 1-27.

Hillis, D.M., 1987. Molecular versus morphological approaches to systematics. Annu. Rev. Ecol. Syst. 18, 23-42.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q., Vinh, L.S., 2018. UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular Biology and Evolution 35, 518-522.

Höhna, S., Landis, M.J., Heath, T.A., Boussau, B., Lartillot, N., Moore, B.R., Huelsenbeck, J.P., Ronquist, F., 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. Systematic Biol 65, 726-736.

Holloway, J.D., 1979. A Survey of the Lepidoptera, Biogeography and Ecology of New Caledonia. Cornell University.

Holloway, J.D., 1994. The moths of Borneo, part 11: Familia Geometridae, Subfamilia Ennominae. Malayan Nature Journal 47, 309.

Holloway, J.D., 1996. The moths of Borneo: Family Geometridae (incl. Orthoxtixini), subfamilies Oenochrominae, Desmobathrinae and Geometrinae. Malayan Nature Journal 49, 179.

Holloway, J.D., 1997. The moths of Borneo: Family Geometridae, subfamilies Sterrhinae and Larentiinae. Malayan Nature Journal 51, 242.

Huelsenbeck, J.P., Rannala, B., 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biol 53, 904-913.

Janzen, D.H., Hallwachs, W., 2016. DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservacion Guanacaste, northwestern Costa Rica. Genome 59, 641-660.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A., Jermiin, L.S., 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat Methods 14, 587-589.

Kawahara, A.Y., Breinholt, J.W., 2014. Phylogenomics provides strong evidence for relationships of butterflies and moths. P Roy Soc B-Biol Sci 281.

Kawahara, A.Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E.F.A., Donath, A., Gimnich, F., Frandsen, P.B., Zwick, A., Dos Reis, M., Barber, J.R., Peters, R.S., Liu, S., Zhou, X., Mayer, C., Podsiadlowski, L., Storer, C., Yack, J.E., Misof, B., Breinholt, J.W., 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Proc Natl Acad Sci U S A 116, 22657-22663.

Kishino, H., Miyata, T., Hasegawa, M., 1990. Maximum-Likelihood Inference of Protein Phylogeny and the Origin of Chloroplasts. Journal of Molecular Evolution 31, 151-160.

Klots, A.B., 1970. Lepidoptera. In: Tuxen, S.L. (Ed.), Taxonomists' glossary of genitalia in insects, Munksgaard, Copenhagen., pp. 115-130.

Kozlov, A.M., Darriba, D., Flouri, T., Morel, B., Stamatakis, A., 2019. RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35, 4453-4455.

Kristensen, N.P., 1998. Lepidoptera, Moths and Butterflies. 1. Evolution, Systematics and Biogeography. Handbook of Zoology 4 (35), Lepidoptera. de Gruyter, Berlin.

Kristensen, N.P., 2003. Skeleton and muscles: adults. In: Kristensen, N.P. (Ed.), Lepidoptera, Moths and Butterflies, Walter de Gruyter, Berlin., pp. 39–122.

Kristensen, N.P., Scoble, M.J., Karsholt, O., 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa, 699-747.

Landis, M.J., Freyman, W.A., Baldwin, B.G., 2018. Retracing the Hawaiian silversword radiation despite phylogenetic, biogeographic, and paleogeographic uncertainty. Evolution 72, 2343–2359.

Landis, M.J., Matzke, N.J., Moore, B.R., Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. Syst Biol 62, 789-804.

Lee, M.S.Y., Palci, A., 2015. Morphological Phylogenetics in the Genomic Age. Current Biology 25, R922-R929.

Lemey, P.S.M., Vandamme, A., 2009. The Phylogenetic Handbook: A Practical Approach to Phylogenetic Analysis and Hypothesis Testing. Cambridge: Cambridge University Press. 430 p. Cambridge University Press.

Louca, S., Pennell, M.W., 2020. Extant timetrees are consistent with a myriad of diversification histories. Nature 580, 502-505.

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder- event speciation, imperfect detection, and fossils allow im- proved accuracy and model-testing. Frontiers in biogeography 5, 242-248.

Matzke, N.J., 2014. BioGeoBEARS: BioGeography with Bayesian (andLikelihood) Evolutionary Analysis in R Scripts.

Meyer, A.L.S., Wiens, J.J., 2018. Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts. Evolution 72, 39-53.

Meyer, M., Kircher, M., 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harb Protoc 2010, pdb prot5448.

Miller, M.A., Pfeiffer, W., Schwartz, T.W., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE),, 1-8.

Minet, J., 1991. Tentative reconstruction the ditrysian phylogeny (Lepidoptera: Glossata). Entomol Scand 22, 69-95.

Minet, J., Scoble, M.J., 1999. The Drepanoid/Geometroid Assemblage. In: Kristensen, N.P. (Ed.), Lepidoptera: Evolution, Systematics and Biogeography, Walter de Gruyter, Berlin, pp. 301–320.

Minh, B.Q., Nguyen, M.A.T., von Haeseler, A., 2013. Ultrafast Approximation for Phylogenetic Bootstrap. Molecular Biology and Evolution 30, 1188-1195.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A., Lanfear, R., 2020. IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Mol Biol Evol 37, 1530-1534.

Mironov, V., 2003. Larentiinae II. In: Hausmann, A. (Ed.), The Geometrid moths of Europe. Apollo Books, Strenstrup, Denmark, pp. 1-463.

Mironov, V., 2013. New species and checklist of Turkish Eupithecia Curtis (Geometridae: Larentiinae). Zootaxa 3717, 39-52.

Mitter, C., Davis, D.R., Cummings, M.P., 2017. Phylogeny and Evolution of Lepidoptera. Annu Rev Entomol 62, 265-283.

Mooi, R., Gill, A.C., 2010. Phylogenies without Synapomorphies—A Crisis in Fish Systematics: Time to Show Some Character. Zootaxa 2450, 26-40.

Morlon, H., 2014. Phylogenetic approaches for studying diverfication. Ecol Lett 17, 508-525.

Morlon, H., Hartig, F., Robin, S., 2020. Prior hypotheses or regularization allow inference of diversification histories from extant timetrees. bioRxiv.

Morlon, H., Parsons, T.L., Plotkin, J.B., 2011. Reconciling molecular phylogenies with the fossil record. Proc Natl Acad Sci U S A 108, 16327-16332.

Müller, B., 1996. Geomtetridae. In: Karsholt, O., Razowski, J. (Eds.), The Lepidoptera of Europe, a Distributional Checklist. Apollo Books, Stenstrup, p. 380.

Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen, P., Skou, P., 2019. Geometrid Moths of Europe. Brill, Leiden.

Murillo-Ramos, L., Brehm, G., Sihvonen, P., Hausmann, A., Holm, S., Ghanavi, H.R., Ounap, E., Truuverk, A., Staude, H., Friedrich, E., Tammaru, T., Wahlberg, N., 2019. A comprehensive molecular phylogeny of Geometridae (Lepidoptera) with a focus on enigmatic small subfamilies. Peerj 7, e7386.

Murillo-Ramos, L., Friedrich, E., Williams, S., Wahlberg, N., Brehm, G., Sihvonen, P., submitted. A morphological appraisal of the new subfamily Epidesmiinae (Lepidoptera: Geometridae) with an overview of all geometrid subfamilies. Zoological Journal of Linnean Society, 42.

Mutanen, M., Wahlberg, N., Kaila, L., 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. Proc Biol Sci 277, 2839-2848.

Nakamura, M., 1987. Pupae of Japanese Geometridae I (Lepidoptera). Tinea, 213-219.

Nee, S., Holmes, E.C., May, R.M., Harvey, P.H., 1994a. Extinction rates can be estimated from molecular phylogenies. Philosophical Transactions of the Royal Society of London B Biological Sciences 344, 77-82.

Nee, S., May, R.M., Harvey, P.H., 1994b. The reconstructed evolutionary process. Philos Trans R Soc Lond B Biol Sci 344, 305-311.

Nee, S., Mooers, A.O., Harvey, P.H., 1992. Tempo and mode of evolution revealed from molecular phylogenies. P Natl Acad Sci USA 89, 8322-8326.

Neethiraj, R., Hornett, E.A., Hill, J.A., Wheat, C.W., 2017. Investigating the genomic basis of discrete phenotypes using a Pool-Seq-only approach: New insights into the genetics underlying colour variation in diverse taxa. Mol Ecol 26, 4990-5002.

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A., Minh, B.Q., 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32, 268-274.

Nieukerken, E.J.v., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.C., Minet, J., Mitter, C., Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S., Zahiri, R., Adamski, D., Baixeras, J., Bartsch, D., Bengtsson, B.Å., Brown, J.W., Bucheli, S.R., Davis, D.R., Prins, J.d.P.W.d., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A., Holloway, J.D., Kallies, A., Karsholt, O., Kawahara, A.Y., Koster, J., Kozlov, M., Lafontaine, J.D., Lamas, G., Landry, J., Lee, S., Nuss, M., Park, K., Penz, C., Rota, J., Schintlmeister, A., B.C., S., Sohn, J., Solis, M.A., Tarmann, G.M., Warren, A.D., Weller, S., Yakovlev, R.V., Zolotuhin, V.V., Zwick, A., 2011. Order Lepidoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa, pp. 212-221.

Õunap, E., Javois, J., Viidalepp, J., Tammaru, T., 2011. Phylogenetic relationships of selected European Ennominae (Lepidoptera: Geometridae). Eur J Entomol 108, 267-273.

Ounap, E., Vidalepp, J., Saarma, U., 2008. Systematic position of lythriini revised: transferred from Larentiinae to Sterrhinae (Lepidoptera, Geometridae). Zool Scr 37, 405-413.

Õunap, E., Vidalepp, J., Saarma, U., 2008. Systematic position of Lythriini revised: transferred from Larentiinae to Sterrhinae (Lepidoptera, Geometridae). Zool Scr 37, 405-413.

Ounap, E., Viidalepp, J., Truuverk, A., 2016. Phylogeny of the subfamily Larentiinae (Lepidoptera: Geometridae): integrating molecular data and traditional classifications. Syst Entomol 41, 824-843.

Õunap, E., Viidalepp, J., Truuverk, A., 2016. Phylogeny of the subfamily Larentiinae (Lepidoptera: Geometridae): integrating molecular data and traditional classifications. Syst Entomol 41, 824-843.

Peña, C., Malm, T., 2012. VoSeq: a voucher and DNA sequence web application. Plos One 7, e39071.

Pitkin, L.M., 1996. Neotropical Emerald moths: A review of the genera (Lepidoptera: Geometridae, Geometrinae). Zool J Linn Soc-Lond 118, 309-440.

Pitkin, L.M., 2002. Neotropical ennomine moths: a review of the genera (Lepidoptera : Geometridae). Zool J Linn Soc-Lond 135, 121-401.

Pons, J., Barraclough, T.G., Gomez-Zurita, J., Cardoso, A., Duran, D.P., Hazell, S., Kamoun, S., Sumlin, W.D., Vogler, A.P., 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Syst Biol 55, 595-609.

Prance, G.T., 2011. Systematics: Relevance to the Twenty-first Century. In: (eLS), E.o.L.S. (Ed.). John Wiley & Sons, Ltd: Chichester.

Prosser, S.W., deWaard, J.R., Miller, S.E., Hebert, P.D., 2016. DNA barcodes from century-old type specimens using next-generation sequencing. Mol Ecol Resour 16, 487-497.

Puillandre, N., Lambert, A., Brouillet, S., Achaz, G., 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Mol Ecol 21, 1864-1877.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W., Huang, H., Larson, J.G., 2014. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in Ecology and Evolution 5, 701-707.

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J., Alfaro, M.E., 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. Nature Communications 4:1958.

Rajaei, H., Greve, C., Letsch, H., Stuning, D., Wahlberg, N., Minet, J., Misof, B., 2015. Advances in Geometroidea phylogeny, with characterization of a new family based on Pseudobiston pinratanai (Lepidoptera, Glossata). Zool Scr 44, 418-436.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. Systematic Biol 67, 901-904.

Ratnasingham, S., Hebert, P.D., 2007. bold: The Barcode of Life Data System (http://www.barcodinglife.org). Mol Ecol Notes 7, 355-364.

Ratnasingham, S., Hebert, P.D., 2013. A DNA-based registry for all animal species: the barcode index number (BIN) system. Plos One 8, e66213.

Ree, R.H., Moore, B.R., Webb, C.O., Donoghue, M.J., 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 59, 2299-2311.

Ree, R.H., Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst Biol 57, 4-14.

Regier, J.C., Mitter, C., Kristensen, N.P., Davis, D.R., van Nieukerken, E.J., Rota, J., Simonsen, T.J., Mitter, K.T., Kawahara, A.Y., Yen, S.-H., Cummings, M.P., Zwick, A., 2015. A molecular phylogeny for the oldest (non-ditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life history evolution. Syst Entomol 40, 671-704.

Regier, J.C., Mitter, C., Mitter, K., Cummings, M.P., Bazinet, A.L., Hallwachs, W., Janzen, D.H., Zwick, A., 2017. Further progress on the phylogeny of Noctuoidea (Insecta: Lepidoptera) using an expanded gene sample. Syst Entomol 42, 82-93.

Regier, J.C., Mitter, C., Zwick, A., Bazinet, A.L., Cummings, M.P., Kawahara, A.Y., Sohn, J.C., Zwickl, D.J., Cho, S., Davis, D.R., Baixeras, J., Brown, J., Parr, C., Weller, S., Lees, D.C., Mitter, K.T., 2013. A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). Plos One 8, e58568.

Regier, J.C., Zwick, A., Cummings, M.P., Kawahara, A.Y., Cho, S., Weller, S., Roe, A., Baixeras, J., Brown, J.W., Parr, C., Davis, D.R., Epstein, M., Hallwachs, W., Hausmann, A., Janzen, D.H., Kitching, I.J., Solis, M.A., Yen, S.H., Bazinet, A.L., Mitter, C., 2009. Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. Bmc Evol Biol 9, 280.

Ronquist, F., 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. Systematic Biol 46, 195-203.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biol 61, 539-542.

Sanmartín, I., 2012. Historical Biogeography: Evolution in Time and Space. GEOGRAPHY AND EVOLUTION 5, 555-558.

Scoble, M.J., 1992. Lepidoptera:Form, Function and Diversity. Oxford University Press, The Natural History Musem.

Scoble, M.J., Edwards, E.D., 1989. Parepisparis Bethune-Baker and the composition of the Oenochrominae (Lepidoptera, Geometridae). Entomol Scand 20, 371-399.

Sihvonen, P., Kaila, L., 2004. Phylogeny and tribal classification of Sterrhinae with emphasis on delimiting Scopulini (Lepidoptera : Geometridae). Syst Entomol 29, 324-358.

Sihvonen, P., Murillo-Ramos, L., Brehm, G., Staude, H., Wahlberg, N., 2020. Molecular phylogeny of Sterrhinae moths (Lepidoptera: Geometridae): towards a global classification. Syst Entomol.

Sihvonen, P., Mutanen, M., Kaila, L., Brehm, G., Hausmann, A., Staude, H.S., 2011. Comprehensive molecular sampling yields a robust phylogeny for geometrid moths (Lepidoptera: Geometridae). Plos One 6, e20356.

Sihvonen, P., Staude, H.S., Mutanen, M., 2015. Systematic position of the enigmatic African cycad moths: an integrative approach to a nearly century old problem (Lepidoptera: Geometridae, Diptychini). Syst Entomol 40, 606-627.

Skou, P., Sihvonen, P., 2015. Ennominae I. In: Hausmann, A. (Ed.), The Geometrid moths of Europe. Brill, Brill, Leiden, pp. 1-657.

Stamatakis, A., 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688-2690.

Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312-1313.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML Web servers. Syst Biol 57, 758-771.

Strutzenberger, P., Brehm, G., Bodner, F., Fiedler, K., 2010. Molecular phylogeny of Eois (Lepidoptera, Geometridae): evolution of wing patterns and host plant use in a species-rich group of Neotropical moths. Zool Scr 39, 603-620.

Twort, V., Minet, J., Wheat, C., Wahlberg, N., 2020. Museomics of a rare taxon: placing Whalleyanidae in the Lepidoptera Tree of Life. bioRxiv.

van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.C., Minet, J., Mitter, C., Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D., Baixeras, J., Bartsch, D., Bengtsson, B.Å., Brown, J.W., Bucheli, S.R., Davis, D.R., De Prins, J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A., Holloway, J.D., Kallies, A., Karsholt, O., Kawahara, A., Koster, J.C., Kozlov, M., Lafontaine, J.D., Lamas, G., Landry, J.-F., Lee, S., Nuss, M., Park, K.-T., Penz, C., Rota, J., Schmidt, B.C., Schintlmeister, A., Sohn, J.C., Solis, M.A., Tarmann, G.M., Warren, A.D., Weller, S., Yakovlev, R.V., Zolotuhin, V.V., Zwick, A., 2011. Order Lepidoptera. In: Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa, pp. 212-221.

Viidalepp, J., 2011. A morphological review of tribes in Larentiinae (Lepidoptera: Geometridae). Zootaxa, 1-44.

Wahlberg, N., Pena, C., Ahola, M., Wheat, C.W., Rota, J., 2016. PCR primers for 30 novel gene regions in the nuclear genomes of Lepidoptera. Zookeys, 129-141.

Wahlberg, N., Snall, N., Viidalepp, J., Ruohomaki, K., Tammaru, T., 2010. The evolution of female flightlessness among Ennominae of the Holarctic forest zone (Lepidoptera, Geometridae). Molecular Phylogenetics and Evolution 55, 929-938.

Wahlberg, N., Wheat, C.W., 2008. Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of lepidoptera. Syst Biol 57, 231-242.

Wahlberg, N., Wheat, C.W., Pena, C., 2013. Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). Plos One 8, e80875.

Whelan, S., Morrison, D.A., 2017. Inferring Trees. Methods Mol Biol 1525, 349-377.

Whitfield, J.B., Kjer, K.M., 2008. Ancient rapid radiations of insects: Challenges for phylogenetic analysis. Annual Review of Entomology 53, 449-472.

Wiens, J., 2004. The role of morphological data in phylogeny reconstruction. Syst Biol 53, 653-661.

Wipfler, B., Pohl, H., Yavorskaya, M.I., Beutel, R.G., 2016. A review of methods for analysing insect structures - the role of morphology in the age of phylogenomics. Curr Opin Insect Sci 18, 60-68.

Wootton, R.J., 1979. Function, homology and terminology in insects wings. Syst Entomol 4, 81-93.

Yamamoto, S., Sota, T., 2007. Phylogeny of the Geometridae and the evolution of winter moths inferred from a simultaneous analysis of mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 44, 711-723.

Yang, Z., 2014. Molecular evolution: a statistical approach. Oxford University Press.

Yang, Z., Rannala, B., 2012. Molecular phylogenetics: principles and practice. Nat Rev Genet 13, 303-314.

Young, C.J., 2006. Molecular relationships of the Australian Ennominae (Lepidoptera : Geometridae) and implications for the phylogeny of the Geometridae from molecular and morphological data. Zootaxa, 1-147.

Zahiri, R., Holloway, J.D., Kitching, I.J., Lafontaine, J.D., Mutanen, M., Wahlberg, N., 2012. Molecular phylogenetics of Erebidae (Lepidoptera, Noctuoidea). Syst Entomol 37, 102-124.

Zahiri, R., Kitching, I.J., Lafontaine, J.D., Mutanen, M., Kaila, L., Holloway, J.D., Wahlberg, N., 2011. A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera). Zool Scr 40, 158-173.

Zahiri, R., Lafontaine, D., Schmidt, C., Holloway, J.D., Kitching, I.J., Mutanen, M., Wahlberg, N., 2013. Relationships among the basal lineages of Noctuidae (Lepidoptera, Noctuoidea) based on eight gene regions. Zool Scr 42, 488-507.

Zhou, X.F., Shen, X.X., Hittinger, C.T., Rokas, A., 2018. Evaluating Fast Maximum Likelihood-Based Phylogenetic Programs Using Empirical Phylogenomic Data Sets. Molecular Biology and Evolution 35, 486-503.

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