

VINEESH NEDUMPALLY

Assembling the phylogenetic tree
of northern European
macroheteroceran moths



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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Press

Department of Zoology, Institute of Ecology and Earth Sciences
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LIST OF PUBLICATIONS

This dissertation is the summary of the following articles, which are referred to in the text by Roman numerals. All published articles are reproduced with the permission of the publishers.

- I. **Nedumpally, V.**, Öunap, E., & Tammaru, T. (2024). An insight into the molecular phylogeny of Drepanidae (Lepidoptera) with an emphasis on the European fauna. *European Journal of Entomology*, 121, 385–391.
<https://www.eje.cz/pdfs/eje/2024/01/41.pdf>
- II. Öunap, E., **Nedumpally, V.**, Yapar, E., Lemmon, A. R., & Tammaru, T. (2025). Molecular phylogeny of north European Geometridae (Lepidoptera: Geometroidea). *Systematic Entomology*, 50, 32–67.
<https://doi.org/10.1111/syen.12638>
- III. **Nedumpally, V.**, Zilli, A., Yapar, E., Tammaru, T., Lemmon, A. R., & Öunap, E. (2025). Elaborating the phylogeny of Noctuidae by focusing on relationships between north European taxa. *Systematic Entomology*, published online. <https://doi.org/10.1111/syen.70010>
- IV. **Nedumpally, V.**, Öunap, E., & Tammaru, T. Questioning the early Miocene origin of grass-feeding noctuids: evidence from a phylogenomic dataset. (Manuscript).

The author’s contribution to each of the the articles (* denotes a moderate, ** a high contribution, *** a leading role).

| | I | II | III | IV |
|-----------------------------|-----|----|-----|-----|
| Study design | ** | * | ** | *** |
| Laboratory work | *** | ** | *** | *** |
| Analysis and interpretation | *** | ** | ** | *** |
| Manuscript writing | *** | ** | ** | *** |

1. INTRODUCTION

Insects are the most species-rich animal class on the Earth and comprise over half of all described species (May, 1986). They play a vital role in e. g. nutrient cycling, pollination, seed dispersal, population regulation of other organisms, and serve as a major food source for many taxa (Scudder, 2017). Comprehending their evolutionary relationships is thus key to understanding the evolution of life. In recent decades, our understanding of the history and diversification of insects has grown substantially (Kristensen, 1981; Misof et al., 2014; Hailay Gebremariam, 2024). Technological improvements in DNA sequencing and computational analysis have increasingly clarified phylogenetic relationships between insect clades (Trautwein et al., 2012; Misof et al., 2014), notably resolving the relationships within Holometabola, clarifying the placement of Strepsiptera relative to Coleoptera, and refining divergence estimates for Hymenoptera, among other breakthroughs (Trautwein et al., 2012; Zhang et al., 2025).

Among insects, Lepidoptera represent one of the most successful lineages, occurring on all continents except Antarctica and occupying a wide variety of habitats (Grimaldi & Engel, 2005; Perveen & Khan, 2018). With nearly 160,000 described species worldwide (Kristensen, 2007; van Nieuwerkerken et al., 2011; Zhang, 2013), Lepidoptera represent one of the most species-rich insect orders and have been the subject of particularly extensive phylogenetic investigation. Because Lepidoptera include several model organisms (e.g. *Bombyx mori* (Linnaeus, 1758), *Manduca sexta* (Linnaeus, 1763), and *Plutella xylostella* (Linnaeus, 1758)), serious agricultural pests, and many species most familiar to the wider audience, studies of their phylogeny and evolution are of both scientific and public importance (Timmermans et al., 2014). Over the years, numerous landmark contributions have progressively shaped our understanding of lepidopteran systematics. For instance, Packard, (1895) divided Lepidoptera into suborders Laciniata and Glossata based on the morphology of their mouthparts, Börner (1925, 1939) established a division of Lepidoptera into Monotrysia and Ditrysia according to the structure of the female genitalia, and Minet (1986) introduced the concept of Obtectomera for a large subsection of ditrysians based on pupal characters. The most recent comprehensive treatment of the order in the Handbook of Zoology (Kristensen, ed. 1998, 2003) recognized 124 lepidopteran families, 52 of which were further subdivided into subfamilies. Significant advances on the higher classification of Lepidoptera have continued in the 21st century, with van Nieuwerkerken (2011) reporting 134 families, and several discoveries resulting in descriptions of new families have been done after that (e.g. Kristensen et al., 2015; Rajaei et al., 2015; Kaila et al., 2020). The “LepTree project” and the “Ditrysia project” provided considerable new resolution to the higher phylogeny of Ditrysia (Timmermans et al., 2014 and references therein). Today, the monophyly of Lepidoptera is firmly established, and the position of the order within the insect phylogenetic hierarchy as sister to Trichoptera is strongly supported by comprehensive molecular datasets (e.g. Kristensen et al., 2007; Misof et al., 2014).

In recent years, the elucidation of Lepidoptera phylogeny has made remarkable progress, driven by advances in phylogenetic methods, sequencing technologies, and bioinformatic tools. The following sections offer a brief insight into these developments.

1.1. Historical roots: Linnaean classification

The foundations of modern biosystematics were laid down by works of Carl Linnaeus, with the 10th edition of the *Systema Naturae* (Linnaeus, 1758) being universally recognized as the starting point of current zoological nomenclature. For over two centuries, systematists primarily relied on morphological characters in delimiting species and higher groups. Remarkably, the vast majority of currently recognized genera and higher taxonomic units were introduced during this morphology-based era. Along with a systematic treatment of all organisms known at his time, Linnaeus (1758) also provided the first family level classification of Lepidoptera, followed by a major contribution from Denis & Schiffermüller (1775), who published a faunistic list of the Lepidoptera of Vienna based on Linnaeus' classification. Subsequently, Hübner (1796–1838) described and illustrated numerous species of European moths and butterflies, introducing many generic names that remain still in use today. Later Herrich-Schäffer (1843–1856) provided numerous original descriptions of European Lepidoptera and carried out extensive studies on venation and other morphological features. Further landmark publications include Pierce's detailed studies on the genital structures of Noctuidae (1909) and Geometridae (1914) of British Islands, Janse's (1932, 1933–1935) richly illustrated overview on South African Geometridae, and Beck's (2000) insight to the systematics of Noctuidae based on larval characters. Morphology-based studies have been carried on in the 21st century as well, providing well-justified hypotheses on the classification of particular groups of Lepidopterans (e.g. Sihvonen & Kaila 2004, Fibiger & Lafontaine 2005).

1.2. From taxonomy to phylogenetics

A major breakthrough in biological thinking came with the work of Charles Darwin and his followers (Darwin, 1859; Haeckel, 1866; Weismann, 1893; Haldane, 1990; Hennig, 1950, 1966, 1982; Dobzhansky, 1951). Darwin (1859) introduced a unifying evolutionary framework for understanding biological diversity, demonstrating that all organisms share common ancestry and evolve through natural selection. As a consequence, in many taxonomic publications of late 19th and early 20th century, great emphasis was put on classifying known species into "natural" groups, which adequately reflect their relatedness (e.g. Prout 1912–1916). Hennig (1950, 1966, 1982), laid the foundation for modern approaches to classifying life based on their evolutionary history. He is widely regarded as the father of phylogenetic systematics (or cladistics) and brought a major shift to the

field by developing a method for grouping species and lineages that is both scientifically testable and reproducible. Hennig (1950, 1953) introduced the key idea of distinguishing between ancestral (plesiomorphic) and shared derived (synapomorphic) traits. He showed that synapomorphies could be used to identify sister groups and introduced the idea that only groups including a common ancestor and all its descendants (monophyletic groups) should be recognized as taxa and named as such (Schmitt, 2013), and developed methods for phylogenetic reconstruction.

1.3. Morphology based phylogenetics

The morphological structures of living organisms are highly diverse, and inferring phylogenetic relationships based solely on visual examination is often challenging. Consequently, numerous analytical approaches have been developed over time to resolve these relationships between organisms, including Lepidopterans. An early example of such practice can be seen in a work by Sterneck (1941), whose preliminary application of character coding grouped Sterrhinae (Lepidoptera: Geometridae) into smaller units that are almost fully compatible of modern concept of tribes in that subfamily. During the 1970s and 1980s, lepidopteran phylogenetics emerged through detailed anatomical studies combined with the early adoption of Hennigian phylogenetics (Kristensen, 1976; Kristensen, 1984;). For instance, Kristensen (1976) re-evaluated butterfly family-level relationships using the principles of phylogenetic (cladistic) systematics, providing important insights into their higher-level evolutionary relationships. Kristensen (1984) focused on understanding the evolutionary relationships and characteristics of the early-diverging moth and butterfly lineages, later updated by Kristensen & Skalski (1998), and they identified several traits unique to Lepidoptera. Although morphological phylogenetics offers advantages – such as its usefulness in studying museum specimens and fossil taxa, it also has drawbacks, including a limited number of informative characters, the prevalence of homoplasy, subjectivity in character definition and coding, and many more (see Sanderson & Donoghue, 1989; Wiens, 2001; Scotland et al., 2003). For over two centuries, morphology nevertheless served as the primary data source for reconstructing relationships across all taxonomic levels, with undeniable success.

1.4. Molecular phylogenetics

Since the 1960s, scientists have increasingly relied on various forms of molecular data—such as allozymes, DNA–DNA hybridization, and amino acid or nucleotide sequences for phylogenetic inference (Lee & Palci, 2015). These data allow researchers to compare homologous molecules across organisms, enabling them to measure genetic similarity and infer evolutionary relationships, which can be visualized as a phylogenetic tree. Molecular phylogenetics came into the spotlight

and gained prominence with the landmark study by Woese and Fox (1977), who used ribosomal RNA sequences to propose that the overall phylogenetic structure of the living world comprises three domains. Ever since then, molecular data have become central to evolutionary biology. Molecular phylogenetic studies on Lepidoptera started in the early 1990s and used the highly abundant sequences of the mitochondrial genome and nuclear ribosomal DNA (Sperling, 1993; Brower, 1994; Sperling & Hickey 1994). However, widespread incongruence often arises between phylogenies inferred from different single-gene datasets, and it is now widely accepted that building a phylogeny using only one gene and a single reconstruction method is generally unreliable (Rokas et al., 2003; Wahlberg & Wheat 2008). Therefore, increasing the length of gene fragments and number of genes (often termed as markers or loci) included in phylogenetic analyses is essential for producing more robust and stable evolutionary hypotheses.

1.4.1. Multigene phylogenies using Sanger sequencing

Although Friedlander et al. (1992) identified 14 single-copy nuclear protein-coding genes potentially useful for phylogeny inference in early 1990s, multigene phylogenetic analysis gained significant momentum several years later, in the early 2000s. This progress was driven by the increasing availability of nuclear protein-coding genes that greatly enhanced the resolution of phylogenetic relationships, for example, in arthropods (e.g. Giribet et al., 2001; Kopp & True, 2002; Peña et al., 2006). Later, Savard et al. (2006) conducted a phylogenomic analysis of four holometabolous insect orders, utilizing 185 nuclear genes made available through emerging genome sequencing projects. In the context of Lepidoptera, Wahlberg and Wheat (2008) proposed a set of eleven genetic markers for phylogenetic research, including six newly designed ones. These so-called “legacy genes” have since become a widely adopted and reliable tools for lepidopteran phylogenetics. Over the following years, the number of markers used in Lepidoptera studies expanded to 19–26 in more recent research (Cho et al., 2011; Zwick et al., 2011; Regier et al., 2013), and this increase in the amount of sequence data has contributed to improve resolution and support for higher-level relationships (Cho et al., 2011). Despite these advances, multigene phylogenetic analyses revealed that while relationships among non-ditrysian superfamilies and early-diverging lineages within Ditrysia were well supported and aligned with morphology-based hypotheses, deeper relationships within Apoditrysia, a large and highly diverse clade, remained weakly supported, underscoring the challenges of resolving rapid radiations in this group (Regier et al., 2013). Moreover, generating multilocus datasets through traditional PCR-based approaches remained labor-intensive, requiring extensive amplification and sequencing efforts.

1.4.2. Phylogenomics using next-generation sequencing

The emergence of next-generation sequencing (NGS) platforms has revolutionized phylogenetic studies by enabling the rapid and cost-effective generation of large-scale molecular data, facilitating the analysis of hundreds to thousands of loci across diverse taxa. Recent studies show that resolving species relationships despite gene tree variation often requires sequencing of hundreds of loci per sample, often exceeding million base pairs to infer both deep and shallow phylogenetic nodes (Lemmon et al., 2012; Espeland et al., 2018; Lee et al., 2018; Kawahara et al., 2019). Various sequencing methods, such as whole-genome sequencing, target enrichment, and transcriptome sequencing, have been introduced and have subsequently helped to meet this demand, thereby significantly advancing phylogenomics (Mamanova et al., 2010; Ekblom & Wolf, 2014; Kawahara & Breinholt 2014; Breinholt et al., 2018; Zhang et al., 2018; Kawahara et al., 2019). Anchored Hybrid Enrichment (AHE; Lemmon et al., 2012) is a target enrichment sequencing method that has become widely used in phylogenetic studies. It has proven effective for non-model taxa, ethanol-preserved tissues, stored DNA extractions, and, in some cases, also older museum specimens (Lemmon et al., 2012; Guschanski et al., 2013; Blaimer et al., 2016). AHE has been successfully applied across various insect orders (see Dietrich et al., 2017; Breinholt et al., 2018; Espeland et al., 2018; Kawahara et al., 2019; Buenaventura et al., 2020; Homziak et al., 2023; Cruaud et al., 2024; St Laurent et al., 2024, 2025)

Misof et al. (2014) conducted a landmark phylogenomic analysis of insects, using 1,478 single-copy nuclear protein-coding genes across 144 taxa (all extant hexapod orders along with few other arthropods used as outgroup) to resolve long-standing controversies in higher-level insect evolutionary relationships and providing a robust evolutionary framework for future comparative studies. Kawahara and Breinholt (2014) presented the first robust transcriptome-based phylogeny of Lepidoptera, which strongly challenged the traditional placement of butterflies and established a new evolutionary framework for genomic, developmental, and ecological studies of this diverse insect order. Later, Kawahara et al. (2019) provided most comprehensive phylogenomic insight to date, and traced the origin of major lepidopteran traits – from the evolution of the proboscis to the rise of day-flying butterflies and sonar-detecting moths, redefining our understanding of their diversification. Although lepidopteran phylogenomics has made significant advanced in recent years (e.g. Mitter et al., 2017 and reference therein: Zahiri et al., 2019; Kawahara et al., 2023), majority of families, including Drepanidae, Geometridae, and Noctuidae have received relatively little attention, particularly with respect to relationships at the subfamily and tribal levels.

1.5. Advancements in phylogeny reconstruction

1.5.1. Evolution of phylogenetic inference methods

In addition to increasing availability of genome-scale datasets which has facilitated the growth of phylogenetic research, further advances have become possible by the refinement of methods for tree construction. In phylogenetic inference, optimization principles are applied to identify the most likely tree topology. Over time, numerous approaches have been developed for reconstructing phylogenetic trees; however, the most widely used ones include Maximum Parsimony, Neighbor-Joining, Maximum Likelihood, and Bayesian inference.

Maximum parsimony (MP) seeks the phylogenetic tree that explains the observed data with the minimum number of character-state changes. However, MP may yield misleading results when evolutionary processes deviate from the principle of parsimony. Specifically, MP relies on the assumption that substitution rates are uniform across sites, nucleotide or amino acid types, and evolutionary lineages – assumptions that are often violated in real datasets (Yang, 1996). Another problem of using MP is that the analysis often results in numerous different, but equally good trees. In the Neighbor-Joining (NJ) method, phylogenetic trees are reconstructed from evolutionary distance data (Saitou & Nei, 1987), and this algorithm is widely appreciated for its ability to reconstruct phylogenetic trees with reasonable accuracy while relying on relatively few assumptions. It also offers rapid computation by employing a stepwise clustering approach instead of attempting an exhaustive search for the optimal topology. However, with larger datasets, the exponential growth of possible topologies reduces the probability of identifying the most accurate tree (Zou et al., 2024).

Maximum Likelihood (ML) inference is a widely used and statistically robust approach in phylogenetic analysis that identifies the tree topology and branch lengths most likely to explain the observed sequence data under a given model of molecular evolution (Patané et al., 2024). The topology with the highest likelihood value is selected as the optimal evolutionary tree. ML methods are statistically consistent and less prone to systematic errors, such as long-branch attraction, compared to approaches discussed above. The main limitations of ML are its high computational demands and dependence on the chosen evolutionary model (Zou et al., 2024).

Bayesian inference (BI) is a probabilistic approach to phylogenetic analysis that applies Bayes' theorem to estimate the posterior probability distribution of trees, integrating both the observed sequence data and prior assumptions about evolutionary processes (Huelsenbeck & Ronquist, 2001). Bayesian inference (BI) can incorporate complex models of sequence evolution, naturally handle parameter uncertainty, and simultaneously estimate topology, branch lengths, and model parameters. However, it is highly computationally demanding, its results may be sensitive to the choice of priors, and assessing the convergence of Markov chain Monte Carlo (MCMC) sampling is often challenging, with poor convergence potentially leading to misleading inferences (Barido-Sottani et al., 2024; Tay et al., 2024).

1.5.2. Open-source databases and their use for phylogenetic works

With the rapid development of sequencing technologies, vast numbers of gene sequences and complete genomes are being deposited into GenBank at an accelerating pace. This provides researchers unique opportunity to expand their datasets without the need for extensive sequencing. A cost-effective approach to acquire sequence data is to download, combine, filter, and analyze these datasets to construct a robust phylogenetic tree (Kjer et al., 2016). This approach has become widely used in multilocus phylogenetics, where individual genes are retrieved from public repositories and integrated into original datasets (e.g., Keegan et al., 2019, 2021). For whole-genome data, target loci can be extracted through sequence similarity searches using specialized bioinformatic tools (e.g., Zhang et al., 2019; He et al., 2024). The retrieved sequences can then be combined with newly generated data from one's own sequencing efforts and processed to construct a phylogenomic tree (Fonseca & Lohmann, 2018; He et al., 2024). However, the resulting phylogenies may still be limited by the quality and correct annotation of sequences in GenBank data (Kjer et al., 2016).

1.5.3. Backbone phylogenies

Modern phylogenetic software such as RAxML (Stamatakis et al., 2014) and IQ-TREE (Nguyen et al., 2015) support backbone constraint specifications, allowing to incorporate a well-established phylogeny from robust prior studies as a fixed “backbone” for further analyses. Such constraint trees are particularly useful for placing taxa of interest for which only short DNA sequences are available (Percy et al., 2018). In this approach, the constraint tree serves as a fixed higher-level topology during tree reconstruction from multilocus or genomic datasets. The software then restricts the search to topologies that preserve these predefined relationships, while still freely estimating the branching patterns within each constrained group. Using a backbone tree can significantly speed up phylogenetic analyses, as constrained topologies reduce the search space by limiting the number of alternative arrangements the software must evaluate. A backbone tree, derived from robust phylogenomic studies, can serve as a fixed higher-level framework for divergence time estimation (Espeland et al., 2018; Kawahara et al., 2019). This approach allows for more accurate and reliable estimates of evolutionary timelines, as the backbone phylogeny provides a well-supported framework onto which fossil data can be mapped, improving the precision of divergence time analyses (see Kawahara et al., 2019, Molleman et al., 2025).

1.6. Aim of the Thesis

The primary aim of this study was to infer the phylogenetic relationships among selected macroheteroceran moth families from northern Europe. While large-scale molecular analyses have significantly improved our understanding of lepidopteran classification at broader taxonomic levels (Misof et al., 2014; Kawahara et al., 2019), finer-scale phylogenetic relationships remain largely unresolved. Europe, and particularly Northern Europe, is exceptionally well suited for phylogenetic and comparative research due to its extensive and long-standing natural history data on moth ecology and life history. However, the lack of comprehensive molecular phylogenies continues to constrain such research. Among macroheteroceran families, for example, Drepanidae remained largely unexamined, whereas Geometridae were relatively well represented, with most Northern European genera (127 out of 153) included in recent molecular studies. In contrast, Noctuidae exhibited more limited phylogenetic coverage, with substantial gaps persisting within the subfamily Noctuinae (Davis et al., 2022). This gap provided the key motivation for the present work, in which we aimed to address it by constructing a robust phylogenetic tree for three families, Drepanidae, Geometridae and Noctuidae based on north European fauna. To illustrate the usability of recovered phylogenies, we used the one inferred for Noctuidae in a follow-up analysis focusing on timing of the major diversification events in the tribe Apameini.

To achieve the goals listed below (**I, II, III & IV**), we employed multiple strategies to acquire sequence data. These included Sanger sequencing, where individual genes were amplified and sequenced separately (**I, II**), next-generation sequencing using the Anchored Hybrid Enrichment (AHE) method (**II, III, IV**), which has proven effective for resolving phylogenetic relationships in diverse insect groups, and data mining from public resources (National Center for Biotechnology Information (NCBI), Barcode of Life Data System (BOLD)) to further enhance species and sequence coverage (**I, II, III, IV**). In addition to original material, we obtained DNA samples for critical species from Canadian Centre for DNA Barcoding (CCDB) and sequenced the “legacy” genes from these isolates (**I, II**).

1.6.1. Revealing the phylogenetic relationships of European Drepanidae (I)

The family Drepanidae comprises approximately 650 species worldwide (Minet & Scoble, 1999; van Nieuwerkerken et al., 2011) and is divided into four subfamilies: Cyclidiinae, Drepaninae, Oretinae and Thyatirinae (Wu et al., 2010; Song et al., 2012; Jiang et al., 2016). However, beyond that, very little was known about the phylogeny of Drepanidae (Davis et al., 2022), even for the well-known and uncontroversial European drepanid fauna. To address this, we analyzed 21 of the 22 European species across all 14 genera using Sanger sequencing of 11 protein-coding genes. In addition to originally collected material, DNA samples obtained

from the CCDB, complemented with molecular data mined from public repositories were used to provide the results in a broader evolutionary context. The phylogenetic tree generated enhances our understanding of Drepanidae diversification and provides a foundation for future taxonomic and evolutionary studies.

1.6.2. Inferring the evolutionary relationships of northern European Geometridae (II)

The family Geometridae is the second largest family of Lepidoptera, comprising nearly 24,000 described species (Rajaei et al., 2022). The systematics of the family Geometridae has advanced significantly in recent decades, particularly due to making use of the progress in DNA sequencing technologies (Ban et al., 2018; Brehm et al., 2019; Murillo-Ramos et al., 2019 & Õunap et al., 2016, 2020). However, phylogenetic relationships at lower systematic levels of geometrids are still rather poorly known, as many genera have not been included in molecular phylogenetic studies, and their placement is considered uncertain. Additionally, numerous previous phylogenetic studies on geometrid moths have relied on the same set of sequences available from the NCBI GenBank, supplemented by varying amounts of newly generated data in each study. Until recently, no phylogenomic studies with large datasets had been conducted on Geometridae, except for the pioneering work of Murillo-Ramos et al. (2023). The present study first aimed to construct a phylogenomic tree for more than hundred species of Geometridae based on the AHE sequencing method, which subsequently served as a backbone tree for a follow-up larger-scale analysis relying on Sanger sequencing. Thereafter, molecular data for the “legacy genes” were generated for more than 130 species of Geometridae using Sanger sequencing, to ensure that there was enough data to place all the 376 north European geometrids into a comprehensive phylogenetic framework. Additionally, publicly available sequences of “legacy genes” were retrieved from GenBank, either downloaded directly as individual genes or extracted from whole genomes using bioinformatic tools. As a result, this study provided a high-quality phylogenetic tree including all species of Geometridae of the north European fauna.

1.6.3. Elaborating the phylogeny of north European Noctuidae (III)

Noctuidae are one of the most diverse families of Lepidoptera with more than 12,000 described species (Keegan et al., 2021). Although there are phylogenetic studies using a limited number of molecular markers which have helped in resolving evolutionary relationships within Noctuidae, there are many groups that have still received very little attention. The primary aim of the study was to infer the phylogenetic relationships within the family Noctuidae occurring in northern Europe, as these moths had got little attention in earlier phylogenetic studies (Davis et al., 2022). The AHE sequencing method was employed to sequence multiple nuclear protein coding loci for each species examined. Additionally,

whole genome assemblies of noctuids not present in our original material were downloaded from NCBI GenBank, and AHE loci were retrieved from these datasets using bioinformatic tools developed in article **II**. This comprehensive molecular dataset allowed to provide higher resolution of evolutionary relationships within several groups of Noctuidae, and helped to evaluate the taxonomic composition of the family in the phylogenetic context, as more than 130 genera were represented by their type species.

1.6.4. Time-calibrated phylogeny of Apameini with evolutionary implications (IV)

A major foundation to this study was laid by article **III**, where an unprecedentedly detailed phylogeny of north European noctuids was recovered. The tree inferred in this article allowed us to address conflicting estimations regarding the timing of the diversification events within the tribe Apameini. Recent studies have indicated that Miocene grassland expansion played a significant role in the radiation of grass-feeding herbivore lineages. The family Noctuidae, which includes numerous grass-feeding clades, provides an ideal target taxon for testing these hypotheses. The tribe Apameini, encompassing more than 850 species, almost exclusively comprises grass feeders with only few exceptions. A pioneering study using limited number of genetic markers suggested that the tribe Apameini emerged at least 29 million years ago, potentially coinciding with the expansion of grasslands during the late Oligocene or early Miocene (Toussaint et al. 2012). However, the time of emergence and diversification pattern of Apameini reported in a subsequent study appeared to be contradictory, around 22 million years ago in Kergoat et al. (2018), prompting our study to clarify the discrepancy. This study aimed to assess the age of Apameini and potential changes in diversification rate within this tribe utilizing the recently inferred phylogenetic tree of Noctuidae (**III**).

2. MATERIALS AND METHODS

2.1. Sample collection, species identification and DNA extraction

The study is based on moth specimens collected mainly from Estonia, but in cases where material from this country was not available, collection specimens originating from other regions were occasionally used. The moths were identified based on their external morphology (relying on expertise of some of the authors of respective papers); when necessary, genitalia dissection and DNA barcoding were performed for a reliable identification. Moths were stored as dry specimens at room temperature or as frozen samples at $-20\text{ }^{\circ}\text{C}$ until DNA extraction. Six drepanids, 375 geometrids, 243 noctuids and 27 species belonging to other (outgroup) families of Lepidoptera were included, with the age of the specimens varying between 2 months to 31 years. The genomic DNA was isolated (from the legs or abdomen of the moths) using the DNEasy Blood and Tissue kit (Qiagen N.V., Venlo, Netherlands) following the guidelines provided by the manufacturer. DNA concentration was determined by using the Qubit™ 1X dsDNA HS Assay Kit on Qubit™ 4 fluorometer (ThermoFisher Scientific).

2.2. Sequencing by the Sanger method

The eleven “legacy” genes were amplified using the Sanger sequencing method. These markers have frequently been used in phylogenetic and evolutionary studies of different families of Lepidoptera (Chazot et al., 2021; Murillo-Ramos et al., 2019; Öunap et al., 2016). Eleven “legacy” markers were sequenced from freshly extracted DNA (**I**, **II**) or DNA extracts obtained from CCDB (**I**, **II**). These markers include cytochrome oxidase subunit I [COI], elongation factor 1 alpha [EF-1 α], wingless [WGL], glyceraldehyde3-phosphate dehydrogenase [GAPDH], ribosomal protein S5 [RPS5], isocitrate dehydrogenase [IDH], carbamoyl phosphate synthetase [CAD], malate dehydrogenase [MDH], arginine kinase [ArgK], sarco/endoplasmic reticulum calcium ATPase [Ca-ATPase] and nexin-9-likeprotein [Nex9]. Primer details, as well as PCR and cycle sequencing conditions are described in Articles **I** and **II**.

2.3. Sequencing by the AHE method

Target loci suitable for reliable enrichment across Geometridae (**II**) and Noctuidae (**III**, **IV**) were identified using the AHE sequencing method developed by Lemmon et al. (2012), and later extended to Lepidoptera by Breinholt et al. (2018). This probe set targeted 794 loci, including the 10 legacy genes. The Translational Laboratory at Florida State University, USA, performed library sequencing

at a coverage of 10–30× (equivalent to 20–60 gigabases) using an Illumina HiSeq 2500 sequencer employing the paired-end 150-base pair protocol. The sequence data generated using the AHE method were processed as described in Articles **II** and **III** to construct a phylogenetic tree.

2.4. Data mining from public repositories

To broaden taxon sampling and increase the coverage of legacy genes, publicly available single gene fragments were downloaded from the NCBI GenBank (<https://www.ncbi.nlm.nih.gov/>) and incorporated into the data set (**I**, **II**). Additionally, genome assemblies were downloaded from the NCBI GenBank. Genes of interest (i.e., the 11 legacy markers) were retrieved from the downloaded whole genomes using an in-house pipeline using MetaEuk (vb94867b, Levy Karin et al., 2020), HMMER v3.3.2 (<http://hmmer.org/>) and a custom python script (developed by Etká Yapar, one of the co-authors) for extraction written for this purpose and added to the dataset (**I**, **II**). Furthermore, AHE loci were mined from genome assemblies (**III**, **IV**), and to facilitate the gene mining process, the original AHE datasets were modified (see Article **III**). The AHE loci retrieved from the genome assemblies were incorporated into the original dataset.

2.5. Phylogenetic tree construction

Two different strategies were employed to construct phylogenetic trees using IQ-TREE v2.1.2 (Nguyen et al., 2015): (1) partitioning by loci (**I**, **II**), and (2) using the GHOST model (**III**, **IV**). In the partitioning-by-loci approach, each locus was initially treated as a separate partition, and substitution rates were calculated for each site to determine the most optimal partitioning scheme using ModelFinder (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE v2.1.2. The parameters used for model selection and phylogenetic tree inference in IQ-TREE are described in Articles **I**, **II**, and **III**.

However, partitioning by loci assumes that the substitution rate for each site is constant across all lineages, or that heterotachy occurs exclusively between partitions rather than within them (Crotty et al., 2020). In reality, evolutionary processes are often both time and lineage-dependent (Crotty et al., 2020). To test the robustness of the tree search, in Article **III** we employed both the partitioning-by-loci method and the recently introduced GHOST model implemented in IQ-TREE (Crotty et al., 2020). The parameters used for the GHOST model are described in Article **III**. Phylogenetic trees inferred were visualized and edited in FigTree v1.4.3 software (Rambaut, 2018).

2.6. Dated phylogeny (IV)

For time calibration, the phylogenetic tree was constructed in IQ-TREE using 333 species (296 noctuids and 37 outgroup taxa) based on 548 protein-coding genes, totaling 249,138 nucleotides (see article III). This tree was used as a fixed topology for the time-calibration analyses, and was turned ultrametric using the R package *ape* (Paradis & Schliep, 2019). Due to software limitations, a reduced dataset was employed, comprising the 24 longest loci with at least 90% taxon coverage, totaling approximately 54,000 bp. Because node age estimation could not be performed on the full tree of 333 species, the tree was split into two subsets using the R package *ape*). In subset 1, majority of species from Xylenini and Apameini were excluded, while in subset 2, majority of species from Noctuini and Hadenini *s.l.* were excluded. In both subsets, 37 outgroup species from eight Macroheterocera families were retained along with ~90 Noctuidae species, resulting in 246 species in subset 1 and 227 in subset 2 (see Molleman et al., 2025). Optimal partitioning scheme based on predefined loci was calculated for both subsets using MODELFINDER (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE 2.3.2 (Nguyen et al., 2015) in the CIPRES portal (Miller et al., 2010). The results suggested by MODELFINDER were taken into account, and the data were divided into 13 partitions for node age calculations for subset 1 and into 15 partitions for node age calculations for subset 2, respectively (Molleman et al., 2025).

To calibrate the tree in BEAST v1.10.4, five secondary calibration points were adopted from Kawahara et al. (2019). The ages (in millions of years) were as follows: root of the tree (normal distribution, mean 93.7 ± 11.1 SD), Noctuoidea (normal distribution, mean 77.6 ± 11.0 SD), Erebidae + Noctuidae clade (normal distribution, mean 68.6 ± 10.2 SD), *Chloridea* Duncan & Westwood, 1841 + *Helicoverpa* Hardwick, 1965 clade (normal distribution, mean 9.3 ± 5.6 SD), and *Spodoptera* Guenée, 1852 (normal distribution, mean 10.6 ± 5.7 SD) (see Molleman et al., 2025). As test runs with more complex clock models failed to converge, strict molecular clock was used, clock and tree priors were linked across all partitions, and birth-death tree prior with incomplete sampling (Stadler, 2009) was implemented for the final runs. For both subsets one analysis with BEAST was performed, with Bayesian MCMC running for 30 million generations and sampling every 1000th generation. The results were inspected in TRACER v1.7.2 (supplementary software to BEAST), and 3 million generations were discarded from each run as “burn-in”. The final tree for both subsets were constructed using TREEANNOTATOR v1.10.4 (also a supplementary software to BEAST). The two trees were concatenated into a single 333-species tree using R package *phytools* (Revell 2012). For the follow-up analyses, only the tree of Apameini was used. To detect diversification rate heterogeneity across the tree, we employed the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) software, version 2.5.0.

3. RESULTS & DISCUSSION

3.1. Phylogeny of Drepanidae at the European scale (I)

A phylogenetic tree of 37 Drepanidae species, including 21 of the 22 European representatives, was reconstructed using eleven legacy markers, with two Cimeliidae species as the outgroup, providing new insights into the evolutionary relationships within this group of moths. Sequencing of freshly collected specimens from six species yielded 7–10 markers per species, while DNA extracts from four species obtained from the CCDB yielded 3–8 markers per species. Mining of “legacy” markers from the downloaded genome assemblies recovered 10–11 markers per species. Retrieval of stored “legacy” markers from GenBank was variable, resulting in 2–7 markers per species. For three species included in the phylogeny, only DNA barcodes were available. Outgroup species were represented by eight (*Axia margarita* (Hübner, 1813)) and six (*A. theresiae* (Korb, 1900)) markers.

While constructing the phylogenetic tree, all five runs in IQ-TREE produced identical topologies, and the tree with the best likelihood score (Fig. 1) was selected as the basis for further discussion. In this phylogenetic analysis, all four subfamilies of Drepanidae formed statistically very well supported (SH-Like ≥ 97.7 , UFBot 2 ≥ 98) monophyletic groups, confirming the earlier finding of Wu et al. (2010) (Fig. 1). This analysis divided Drepanidae into two clades: one comprising Drepaninae and Oretinae, and the other comprising Thyatirinae and Cyclidiinae (see Article I). This sister relationship of Cyclidiinae with Thyatirinae had already been reported by Regier et al. (2009) and Kawahara et al. (2019), the latter study using more than 2,000 protein-coding genes, and it challenged earlier findings by Mutanen et al. (2010), Wu et al. (2010), and Regier et al. (2013), which placed Cyclidiinae as sister to all other drepanids. Our study confirmed the subfamily-scale phylogenetic structure of Drepanidae suggested by Regier et al. (2019) and Kawahara et al. (2019).

The phylogenetic tree reconstructed in this study provided insights into the evolutionary history of Drepanids. For instance, Drepanidae are characterized by variable forewing shapes, ranging from rounded or sharp tips to small or prominent hooks, which has earned respective species different vernacular names (e.g. the English “hook-tips”, Estonian “sirptiiblased”). Our tree suggests that the hooked wingtips likely evolved once in the Oretinae + Drepaninae lineage and were subsequently lost multiple times in the course of the evolution of this clade, often in association with the evolution of white coloration, suggesting a shift in mimicry strategy from dry leaves to bird droppings. All Thyatirinae genera characterized by colorful (pink or orange blotches) forewing pattern were recovered as a distinct clade, indicating a potentially shared evolutionary origin of this trait.

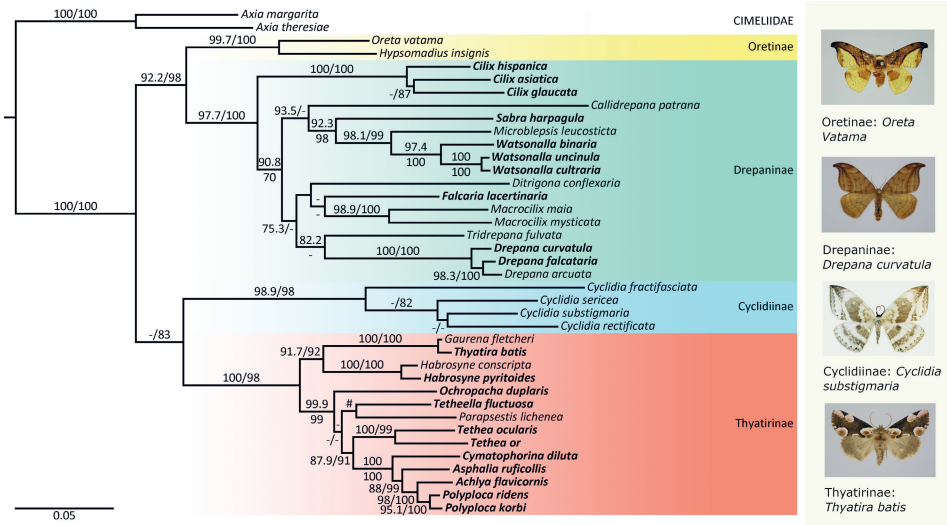


Fig 1. Maximum likelihood phylogeny of Drepanidae, modified from article I. Numbers above and below branches (separated by slashes) represent SH-like and UFboot2 support values, respectively. Support values below 70% are not shown. A very short branch with SH-like support of 84.4% and UFboot2 support of 94% is marked with the symbol #. European species are indicated in bold. Image credits: Cornelis Gielis (*Oreta vatama* Moore, 1866), Kenichiro Nakao (*Cyclidia substigmatica* (Hübner, 1831)), Egbert Friedrich (*Drepana curvatula* (Borkhausen, 1790), *Thyatira batis* (Linnaeus, 1758)).

Similarly, adult moths that are active very early or late in the year are known to exhibit correlated ecological traits, a phenomenon referred to as the “winter moth syndrome” (Hunter, 1995; Ude et al., 2025), and these species cluster closely together in the phylogenetic tree. Laszlo et al. (2007) divided Thyatiridae into two subfamilies, Thyatirinae and Polyplocinae; however, subsequent taxonomic revisions have downranked these groups to tribal level within a single subfamily. The phylogenetic results obtained in the present study are in conflict with the classification proposed by Laszlo et al. (2007). Specifically, the genera *Achlya* Billberg, 1820, *Asphalia* Hübner, 1821, *Cymatophorina* Spuler, 1908 and *Polyploca* Hübner, 1821 – previously assigned to Polyplocinae – form a distinct clade nested within Thyatirinae and were sister to *Tethea* Ochsenheimer, 1816. Furthermore, *Cymatophorina*, placed by Laszlo et al. (2007) in Demipsestini, was recovered as sister to the other three genera, indicating that Demipsestini sensu Laszlo et al. (2007) are paraphyletic. However, the present dataset almost exclusively includes European representatives, the taxon sampling is thus too limited to justify formal taxonomic revisions, and such changes were therefore not undertaken. In conclusion, this study offers further insights into the phylogeny of Drepanidae, enhancing our understanding of the evolutionary history of these moths while also contributing to knowledge about their ecological functions and adaptations. To elaborate on these outcomes, future research should broaden sampling efforts on a global scale and apply more sophisticated molecular approaches to further explore the evolutionary relationships within this fascinating family.

3.2. Molecular phylogeny of north European Geometridae (II)

A two-step analytical framework was employed to reconstruct an all-inclusive phylogeny of northern European Geometridae. In the first step, a backbone phylogeny was inferred from a dataset comprising 117 geometrid species and 35 outgroup taxa representing eight macroheteroceran families. The data matrix contained 209,499 base pairs from 648 protein-coding loci, generated using the anchored hybrid enrichment sequencing technique. This backbone was then used to construct a more comprehensive phylogeny of Geometridae, incorporating up to 11 traditional protein-coding genes for all 376 north European species, supplemented with data from 98 key taxa representing tribes occurring in other regions of the world. The combined maximum likelihood analysis, inferred using the phylogenomic backbone, produced a well-resolved tree, with majority of deeper nodes receiving maximum statistical support (SH-Like = 100%, UFBot2 = 100%). Taxonomic changes were made if necessary, with due consideration given to previously proposed actions, including synonymizations and changes in rank; where appropriate, new synonymies were established. In cases where already existing names or previously revoked combinations were not available, new names or new combinations were proposed.

All outgroup families (Drepanidae, Erebiidae, Lasiocampidae, Noctuidae, Notodontidae, Saturniidae, Sphingidae, Uraniidae) were recovered as monophyletic (Fig 2). Phylogenetic relationships among most subfamilies of Geometridae received maximum statistical support (SH-Like = 100%, UFBot2 = 100%), except for the Epidesmiinae + Oenochrominae + Geometrinae clade (Fig. 2).

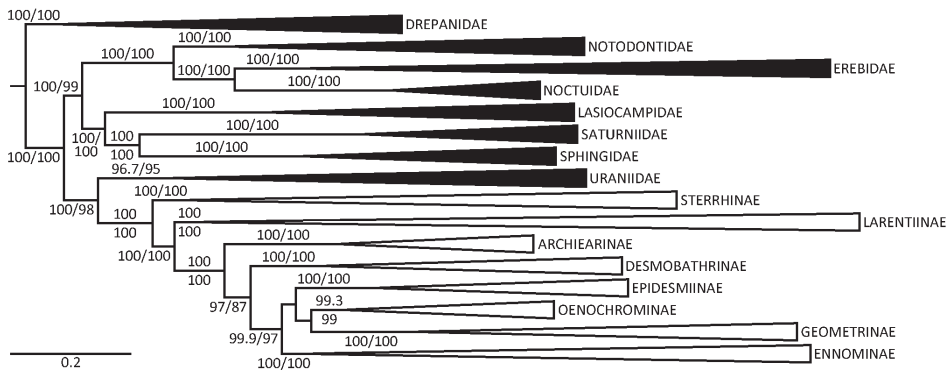


Fig 2. Maximum likelihood phylogeny of subfamilies of Geometridae (white triangles) and outgroup families (black triangles). Numbers above or below branches or slashes indicate SH-Like support and UFBot2 support, respectively. Support indice values inferior to 70% are not shown. Figure adopted from article II.

In the present study, Sterrhinae were recovered as the sister group to all other Geometridae, with Larentiinae diverging next; all relevant nodes received maximum statistical support. Within Sterrhinae, the two informal groups termed as “Timandriini lineage” and “Scopulini lineage” (Sihvonen & Kaila, 2004) were also supported in the present study. Phylogenetic relationships between the tribes of Sterrhinae were recovered as fully concordant with Murillo-Ramos et al. (2019) and Sihvonen et al. (2020).

In Larentiinae, despite some notable discrepancies, this work was nevertheless largely concordant with earlier studies regarding its phylogenetic structure (Õunap et al., 2016, Murillo-Ramos et al., 2019). However, the new evidence suggests that some parts of this subfamily require taxonomic updates. Most importantly, two new tribes were described. First, the genera *Cosmorhoe* Hübner, 1825, *Lampropteryx* Stephens, 1831, and *Colostygia* Hübner, 1825 were recovered to form a well-supported monophyletic group sister to the rest of the “Xanthorhoini lineage” *sensu* Õunap et al. (2016). Consistent with earlier studies (Brehm et al., 2019; Murillo-Ramos et al., 2019), the phylogenomic analysis confirmed that this clade lies outside previously recognized tribes. As no close relationship with Cidariini or other recognized tribes was found, the group was formally described as tribe Lampropterygini (**Fig 3**). Second, the genus *Pelurga* Hübner, 1825 was recovered as an isolated lineage branching off after Cidariini as sister to the derived part of the “Xanthorhoini lineage” with maximum statistical support (Fig. 3). Previous studies have also placed it outside of recognized tribes (Õunap et al., 2016, 2020), despite earlier classifications assigning it to Larentiini or Hydriomenini (Choi, 2006; Hausmann & Viidalepp, 2012; Beljaev, 2016). Consistent results across multiple molecular datasets confirm its distinct position and the group was thus described as Pelurgini.

Other rearrangements include reviving *Ochyria* Hübner, 1825 from a synonym of *Xanthorhoe* Hübner, 1825 and moving *Costaconvexa* Agenjo, 1949 to *Epirrhoini*, as explained below. The study found that *Phalaena quadrifasiata* Clerck, 1759 was more closely related to *Camptogramma* Stephens, 1831 than to *Xanthorhoe*, contrary to previous classifications (Hausmann & Viidalepp, 2012; Aarvik et al., 2017). Due to significant morphological differences, it cannot however be merged with *Camptogramma* (Hausmann & Viidalepp, 2012). As a result, the genus *Ochyria* was revived, with *P. quadrifasiata* reclassified as *Ochyria quadrifasiata* (Clerck 1759), making *Ochyria* a monotypic genus. For the first time, *Costaconvexa* Agenjo, 1949 was analyzed using molecular phylogenetic tools. The results showed it was sister to *Epirrhoe* Hübner, 1825, with moderate support, leading to its transfer from the tribe Xanthorhoini to Epirrhoini.

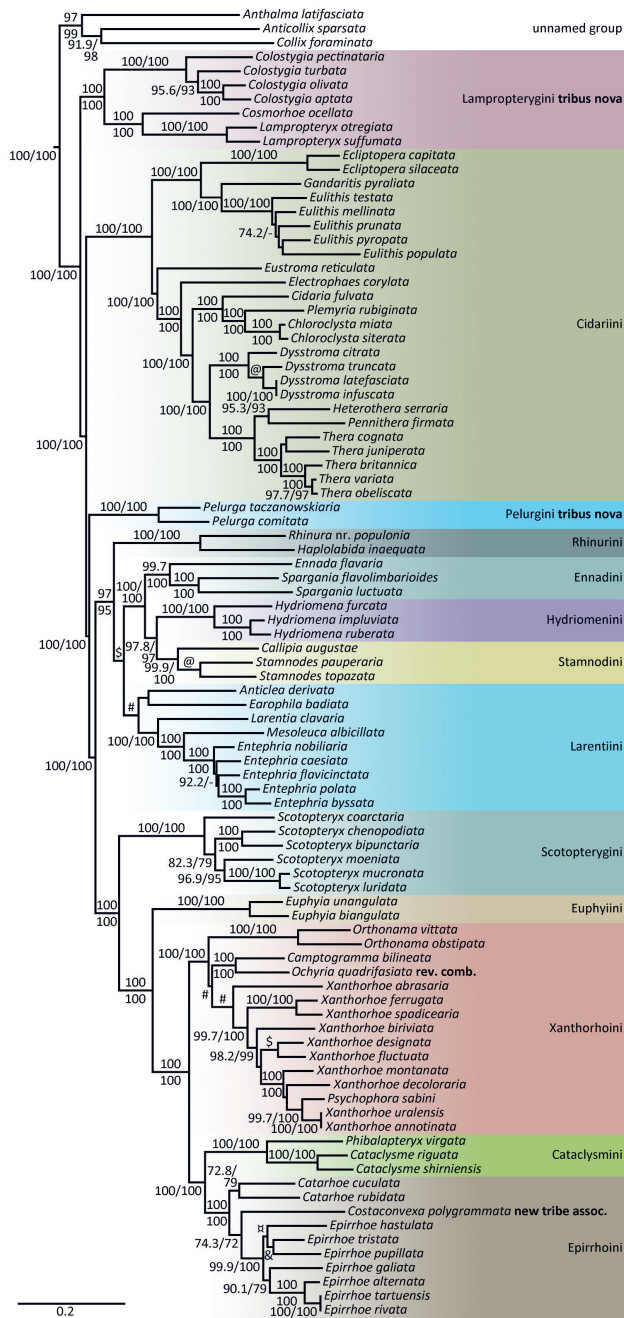


Fig 3. Maximum likelihood phylogeny of the “Xanthorhoini lineage” of the subfamily Larentiinae inferred from article II. Numbers above or below branches or slashes indicate SH-Like support and UFB00t2 support, respectively. Support index values inferior to 70 are not shown. Supports to very short branches are indicated as follows: #, both indices 100%; @, both indices $\geq 95\%$; \$, both indices $\geq 90\%$; &, both indices $\geq 80\%$; □, one index $\geq 70\%$, the other $< 70\%$.

Present analysis recovered *Bombyx sabini* (Kirby, 1824), the type species of *Psychophora* Kirby, 1824, nested deeply within *Xanthorhoe* as sister to the *X. annotinata* (Zetterstedt 1839) + *X. uralensis* Choi, 2003 clade, with maximal support for the monophyly of *Xanthorhoe*. These results confirmed that *Psychophora* does not represent a distinct genus, consistent with earlier morphological assessments (Hausmann & Viidalepp, 2012). Formal synonymization of *Psychophora* under *Xanthorhoe* would render *Xanthorhoe* a junior subjective synonym, generating significant nomenclatural instability given the cosmopolitan distribution of the genus and extensive use of *Xanthorhoe* in the literature, in contrast to the limited representation of *Psychophora*. To address this, a case will be submitted to the ICZN to suppress *Psychophora* as senior synonym and retain *Xanthorhoe* as the valid name. Pending the Commission's decision, both genera are provisionally maintained, resulting in the paraphyly of *Xanthorhoe*.

The analysis revealed several conflicts with previous phylogenetic studies (Ban et al., 2018; Brehm et al., 2019 & Murillo-Ramos et al., 2019) in the subfamily Geometrinae. While Hemitheini have consistently been recovered as monophyletic, its placement varied between the studies. Archaeobalbini appeared paraphyletic and closely allied with Pseudoterpnini, contradicting earlier findings (Ban et al., 2018; Brehm et al., 2019; Murillo-Ramos et al., 2019). Other relationships, such as Neohipparchini + Geometrini and Agathiini + Comibaenini + Nemoriini, also received mixed support. Overall, the phylogeny of Geometrinae remains largely unresolved and requires further study with broader taxon sampling.

Our molecular phylogenetic analysis supported the informal division of Ennominae into two major lineages: the “Ennomine” and “Boarmiine” clades (Forbes, 1948; Holloway, 1994). Few conflicts with the existing classification that necessitated taxonomic updates were recovered in both clades; these will briefly be discussed below. *Lycia* Hübner, 1825 was found sister to *Artiora* Meyrick, 1892 and most Boarmiini (excluding the *Ectropis* Hübner, 1825 + *Cleora* Curtis, 1825 + *Ascotis* Hübner, 1825 clade), contrasting with earlier phylogenies that placed *Lycia* deeper within Boarmiini (Murillo-Ramos et al., 2019, 2021). With strong molecular support from five markers, *Artiora* was newly reassigned from Ennomini of uncertain placement (Skou & Sihvonen, 2015) to Boarmiini.

Within the tribe Macariini, the genus *Epelis* Hulst, 1896 was revived from synonymy with *Macaria* Curtis, 1826, and *Phalaena carbonaria* Clerck, 1759 was transferred from *Macaria* to *Epelis* as *Epelis carbonaria* (Clerck, 1759). This revision was justified by the clear external morphological differences between *M. carbonaria* (Clerck, 1759) and *Narraga fasciolaria* (Hufnagel, 1767), which was recovered as its sister in our analysis. Moreover, *E. carbonaria* is externally highly similar to *Epelis truncataria* (Walker, 1862), the type species of *Epelis*, has similar diurnal lifestyle, and the small genetic distance between the two species' DNA barcodes was also small, only 0.059. This taxonomic change had been suggested previously, but was not formally implemented (Ferguson, 2008). The study also suggested reviving *Speranza* Curtis, 1828 from synonymy with *Macaria* to resolve paraphyly. As a result of this change following combinations appeared for the north European taxa: *Speranza fusca* (Thunberg, 1792), *Speranza artesiaria* (Denis & Schiffermüller, 1775), *Speranza brunneata* (Thunberg, 1784), *Speranza*

wauaria (Linnaeus, 1758) and *Speranza loricaria* (Eversmann, 1837). *Speranza* was justified as a separate genus based on its statistically well supported position away from *Macaria*, but also by morphological characters such as bipectinate male antennae and tendency towards female brachyptery in certain species, which are not known in *Macaria*.

The genus *Selenia* Hübner, 1823, traditionally placed in Ennomini (Viidalepp, 1996), had been moved to Epionini by Beljaev (2016). Sihvonen et al. (2015) classified *Selenia* as Ennomini of uncertain association, but also questioned its placement in that tribe. Based on phylogenomic evidence, *Selenia* was now reassigned to Epionini. The present analysis recovered *Selenia* as sister to *Apeira* Gistel, 1848 with maximum support, confirming this reassignment.

Opisthograptis Hübner, 1823 and *Epirranthis* Hübner, 1823 were recovered deep within Ennominae as sister genera with maximum support but without close relatives, as had been shown by Sihvonen et al. (2011, 2015). To avoid treating them as two separate tribes which both comprise only one genus, our study proposed uniting them under a single tribe and therefore transferred *Epirranthis* Hübner, 1823 from Epirranthini to Rumiini. Consequently, Epirranthini were synonymized with Rumiini.

Overall, the expanded AHE dataset confirmed most previous subfamily- and tribe-level hypotheses while also supporting key taxonomic revisions, including the recognition of Lampropterygini and Pelurgini as new tribes and the placement of *Epirranthis* and *Opisthograptis* within Rumiini. The present study provides a robust phylogenetic framework for all northern European Geometridae species, offering a valuable resource for future comparative phylogenetic analyses like exploring patterns of diversification, trait evolution, and biogeography. For example, Ude et al. (2024) investigated the evolution of wing shape in Geometridae using a phylogenetic comparative approach encompassing 374 northern European species, employing the phylogenetic information generated in this study.

3.3. Molecular phylogeny of north European Noctuidae (III)

The phylogenetic tree of north European Noctuidae was inferred from a large dataset of 565 protein-coding genes, totaling 249,138 nucleotides, obtained through AHE technology and comprising 333 species (296 noctuids and 37 outgroup taxa). GHOST model implemented in IQ-TREE produced a well-resolved tree with maximum statistical support (SH-Like = 100%, UFBoot2 = 100%) for the vast majority of nodes (**Fig 4**). Many of the findings were concordant with previously published phylogenetic works (e.g. Zahiri et al., 2011, 2013; Rota et al., 2016; Keegan et al., 2019, 2021) and current classification of Noctuidae (Top et al., 2023), but this study also provided numerous new insights of relevance for the global phylogenetic context and taxonomy of the family. Taxonomic revisions were undertaken where necessary, with careful attention to previously published actions such as synonymizations and changes in rank. Where needed, new synonymies were established, and in cases lacking prior information, new names or combinations were proposed.

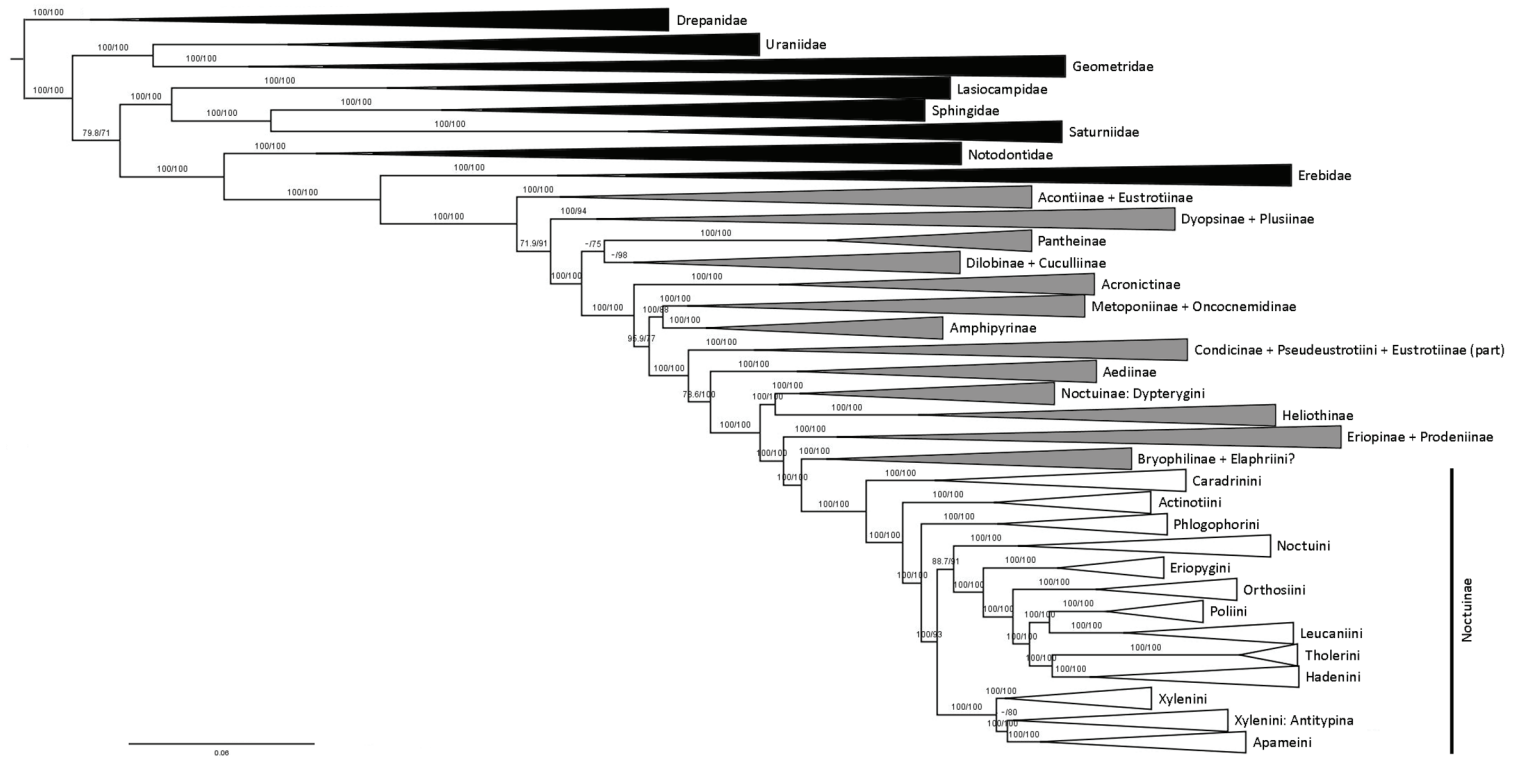


Fig 4. Maximum likelihood phylogeny of subfamilies of Noctuidae and outgroup families. Numbers with slashes indicate SH-Like support and UFBoot2 support, respectively. Support index values inferior to 70% are not shown. Black triangles: outgroup families; grey triangles: other subfamilies of Noctuidae; white triangles: tribes of subfamily Noctuidae.

In the present study, the Acontiinae + Eustrotiinae clade was recovered as sister to the rest of Noctuidae, identical to the results of Martinez (2022). The Plusiinae + Dyopsinae clade diverged next and was found to be sister to the remaining Noctuidae. One of the interesting findings of the analysis is the placement of *Cornutiplusia* Kostrowicki, 1961 within *Autographa* Hübner, 1821. Despite earlier distinctions based on genitalia, both morphology and phylogenetic results support its inclusion in *Autographa*. Hence, *Cornutiplusia* is hereby treated as a junior synonym of *Autographa*, and its only species, *Phalaena (Noctua) circumflexa* Linnaeus, 1761, was transferred to the latter genus as *Autographa circumflexa* (Linnaeus, 1761).

Our phylogenetic analyses recovered a strongly supported clade comprising Heliothinae and Dypterygiini (Noctuidae) as sister to the remaining part of Noctuidae. While the placement of Heliothinae was congruent with previous studies (Keegan et al., 2019, 2021; Li et al., 2024), the position of Dypterygiini differed from earlier hypotheses (Keegan et al., 2021). Both lineages were recovered as monophyletic with maximal statistical support. This represented the first evidence suggesting a sister-group relationship between Heliothinae and Dypterygiini. In the absence of corroborating morphological data, we refrain from proposing formal taxonomic changes but emphasize the need for further integrative analyses to validate this relationship.

The tribe Prodeniini, which includes several important agricultural pests, such as *Spodoptera exigua* (Hübner, 1808), *S. frugiperda* (Smith, 1797), and *S. littoralis* (Boisduval, 1833), has traditionally been treated within Noctuidae. However, species belonging to this tribe possess genitalia modified to such an extent that it is difficult to associate them with any other subgroup of Noctuidae (Fibiger, 1997). This study, together with those of Keegan et al. (2021), Kergoat et al. (2021), and Martinez (2022) indicates that Prodeniini should be removed from Noctuidae and treated as a separate subfamily. Therefore, Prodeniini were formally elevated to the subfamily rank: Prodeniinae.

Graphiphora subrosea Stephens, 1829, the type species of *Coenophila* Stephens, 1850, was placed within *Xestia* Hübner, 1818, as sister to *Xestia castanea* (Esper, 1798), with strong statistical support. Despite some distinctive genital traits, both external morphology and other genital features show affinities with other *Xestia* species. Therefore, *G. subrosea* was transferred to *Xestia* as *Xestia subrosea* (Stephens, 1829) and *Coenophila* was suggested to be treated as a subgenus: *Xestia (Coenophila)*. The genus *Epilecta* Hübner, 1821 (type species *Noctua linogrisea* Denis & Schiffermüller, 1775) was recovered within *Noctua* Linnaeus, 1758, with strong statistical support, branching off the evolutionary lineage after *N. pronuba* (Linnaeus, 1758). This placement conflicts with earlier hypotheses linking *Epilecta* to *Spaelotis* Boisduval, 1840 (Fibiger, 1997). Despite the absence of the clasper, the genitalia of *N. linogrisea* fit within the extreme variation of *Noctua*. To avoid unnecessary splitting of *Noctua*, we treat *Epilecta* as a junior subjective synonym of *Noctua* and restore the original combination *Noctua linogrisea*, while noting the need for further morphological study. *Cryptocala* Benjamin, 1921 was another genus recovered within *Noctua* with maximum

support in this study. *Cryptocala* spp. are notably smaller than *Noctua* spp., with some distinct differences in male genitalia, but the latter are known to be extremely heterogenous in *Noctua* anyway (Fibiger 1997). Hence, *Cryptocala* was treated as a junior subjective synonym of *Noctua*, resulting with a combination *Noctua chardinyi* (Boisduval, 1829) for its sole European species.

Pachetra Guenée, 1841 and *Polia* Ochsenheimer, 1816 were recovered in a clade sister to Leucaniini rather than within Hadenini. We thus suggested elevating Poliina from a subtribe of Hadenini (e. g. Beck, 1996; Varga et al., 2020) to full tribe Poliini and excluded these genera from Hadenini. Present analysis placed *Noctua munda* Denis & Schiffermüller, 1775 (type species of *Anorthoa* Berio, 1980), within *Orthosia* Ochsenheimer, 1816 as sister to *O. incerta* (Hufnagel, 1766) with strong support. This demonstrated that *Anorthoa* does not merit separate generic status; *N. munda* was therefore transferred to *Orthosia* as *O. munda* (Denis & Schiffermüller, 1775), and *Anorthoa* was downgraded to a subgenus of *Orthosia*.

Additionally, the analysis strongly supported merging *Senta* Stephens, 1834 with *Leucania* Ochsenheimer, 1816, as *Melia flammea* Curtis, 1828 (type species of *Senta*) was recovered as sister to the rest of *Leucania*. This resulted in a combination *Leucania flammea* (Curtis, 1828) for its type species, with the genus forming a well-supported clade closely related to *Mythimna* Ochsenheimer, 1816. The analysis placed *Pseudaletia* Franclemont, 1951 as sister to the rest of the *Mythimna–Leucania* complex with strong support, confirming similar findings by Martinez et al. (2024). In contrast to its earlier treatment as a subgenus of *Mythimna* (Hacker et al., 2002), our evidence supported reinstating *Pseudaletia* as a valid genus, with *Leucania separata* transferred to this genus as *Pseudaletia separata* (Walker, 1865). Our analysis demonstrated that the genus *Sideridis* Hübner, 1821 as currently defined is not monophyletic. *Sideridis reticulata* (Goeze, 1781) is more closely related to the type species *S. lampra* (Schawerda, 1913) (Hacker et al., 2002), representing the “true” *Sideridis*, whereas *Noctua rivularis* Fabricius, 1775 was recovered outside this group as sister to *Conisania* Hampson, 1905 + *Hadena* Schrank, 1802 clade with strong statistical support. This finding also contradicts earlier treatments that associated *N. rivularis* with *Hadena* (e.g. Nowacki & Fibiger, 1996; Skou, 1991). To resolve this paraphyly, the genus *Aneda* Sukhareva, 1973 was revived from synonymy and reinstated at full genus rank, resulting in the combination *Aneda rivularis* (Fabricius, 1775) for its type species.

The remaining part of the phylogeny included Xylenini and Apameini with strong statistical support. However, contrary to current classifications, Xylenini was not recovered as monophyletic, since Antitypina formed a well-supported clade as sister to Apameini. The remaining lineages of Xylenini, comprising Xylenina and *Cosmiina sensu* Top et al. (2023), are therefore recognized here as Xylenini *sensu stricto*. Present analysis revealed that *Cosmiina* was placed near the root of Xylenina with strong support, rendering the latter paraphyletic. Since *Cosmiina* is most closely related to the *Fissipunctia* Beck, 1991 + *Parastichtis* Hübner, 1821 clade, and similar results were also reported by Martinez et al.

(2024), we proposed abandoning *Cosmiina* and treating it as a synonym of *Xylenina* to maintain monophyly.

The present study fills a major gap resulting from the poor representation of North European noctuids in earlier molecular research. This work sampled 140 genus-types, providing a robust phylogenetic and taxonomic framework for comparative evolutionary and ecological research (see **IV**, Molleman et al., 2025), particularly given the exceptionally well-documented life histories of northern European species.

3.4. Time-calibrated tree of Noctuidae and diversification of Apameini (IV)

Phylogeny of Noctuidae inferred in article **III** was well resolved in most nodes, with Apameini recovered as one of the well-supported clades. This tree was then used as a fixed topology for the time-calibrated analysis. The time-calibrated phylogeny inferred in this study indicates that the diversification of Apameini began approximately 8.66 (95% HPD 7.37–10.04) million years ago, i.e. substantially more recently than suggested in previous studies (**Fig 5**). Earlier studies in Apameini provided conflicting estimates: Toussaint et al. (2012) suggested that Apameini originated ~29 Ma, and linked this event with grassland expansion and rapid diversification in the Middle Miocene, whereas Kergoat et al. (2018) dated Apameini to ~22.3 Ma, with initially elevated speciation rates followed by a gradual slowdown.

The incongruences in node age estimates between the present and previous studies may be attributable to differences in dataset size and calibration approaches: Toussaint et al. (2012) used dataset with 1.9 kb and calibration points from Douglas & Stockey, (1996); Wolfe & Wehr, (1987) and Douglas, (1991). Kergoat et al. (2018) applied 4.7 kb with calibrations from Mutanen et al. (2010) and Wahlberg et al. (2013), whereas the present study employed 54 kb and more recent calibrations from Kawahara et al. (2019). Recent studies suggest that another major radiation of modern grasslands occurred between 3–9 Mya, driven by environmental changes (Edwards et al., 2010). Notably, present results place the diversification of Apameini precisely within this time window. BAMM analysis indicated a major radiation in Apameina, with diversification slowing after the tribe's formation but later accelerating independently in *Apamea* Ochsenheimer, 1816 (~4 Ma) and the crown group of predominantly endophagous Apameina (~5 Ma) (**Fig 6**).

It is widely hypothesized that the evolutionary shift from internal to external larval feeding in the Cretaceous was a key adaptation in Lepidoptera (Kawahara et al., 2019), as internal feeding imposes ecological and physiological constraints such as limited mobility, host specificity, and susceptibility to plant defenses (Kawahara et al., 2019; St Laurent et al., 2021). In Apameini, while *Apamea* larvae are mostly external feeders, the crown group of Apameina predominantly feeds internally (Zilli et al., 2005). Rather than limiting diversification, internal

feeding may have promoted it by providing ecological advantages such as niche expansion and predator protection, with host specialization further driving speciation. Future research should investigate whether the primary drivers of Apameini diversification are the ecological benefits associated with internal feeding itself, or rather the results of shifts and expansions in host plant use, particularly in relation to thriving grassland ecosystems.

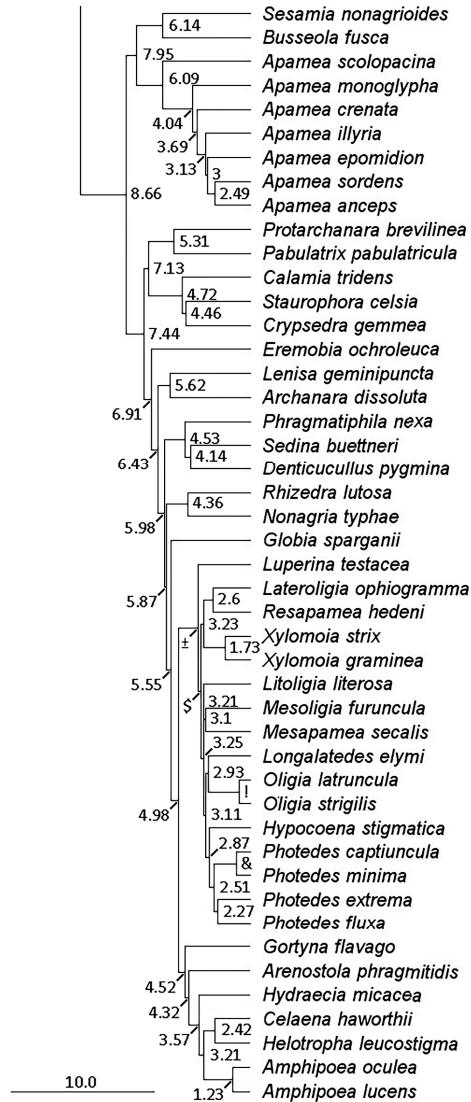


Fig 5. Time calibrated tree of the tribe Apameini constructed using Beast 1.10.4. Numbers indicate node ages in millions of years. Node ages of branches marked with symbols are as follows: \$ = 3.43 Mya; ± = 3.63 Mya; & = 0.92 Mya; ! = 0.74 Mya.

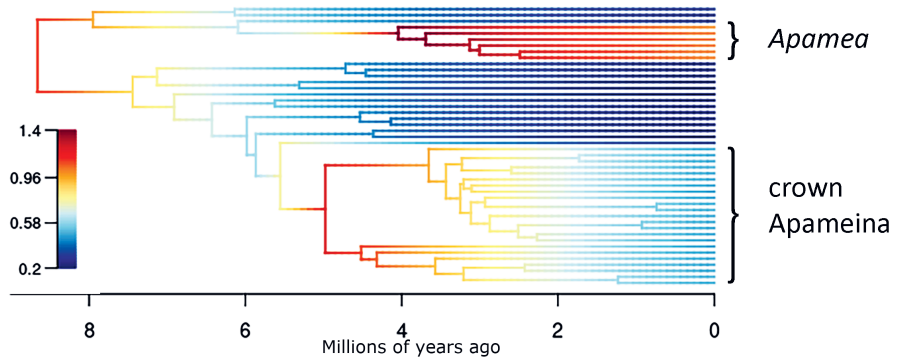


Fig 6. Mean phylo-rate plot from BAMM, indicating two instances of rapid radiation in Apameini, one in the genus *Apamea* and other in crown Apameina. Diversification rates are indicated using a gradual scale (cool colours = slow; warm colours = fast).

SUMMARY

The present study aimed to infer the phylogeny of Drepanidae, Geometridae and Noctuidae with special emphasis on the northern European fauna. It took advantage of recent advances in sequencing and phylogenetic methodologies which have the potential to greatly improve our understanding of phylogenetic relationships within Lepidoptera at all taxonomic levels. To infer the phylogenies of the target groups, this study combined data generated using Sanger sequencing and next-generation sequencing with publicly available sequences and genome assemblies.

The family Drepanidae includes around 650 species worldwide, yet it has received relatively little attention in phylogenetic research. In fact, no molecular phylogenies have been published even for the well-documented and uncontroversial European species. To address this gap, we investigated the phylogenetic relationships within Drepanidae using eleven molecular markers, totaling over 7,500 bp (I). Present analysis, based on 37 species – including 21 of the 22 European drepanid species – confirmed the monophyly of all four recognized subfamilies. The results further showed that Oretinae and Drepaninae form a sister-group within one major clade, whereas Cyclidiinae and Thyatirinae comprise the other. The analysis revealed that hooked wingtips, typical of the Drepaninae + Oretinae lineage, have been lost multiple times during evolution. Within Thyatirinae, the “winter moths” (species active very early in spring or late in the year) form a distinct and well-supported clade. In addition, the thyatirine genera characterized by pink or orange forewing blotches consistently formed a statistically well-supported clade.

A comprehensive phylogeny of northern European Geometridae was reconstructed using a two-step approach (II). In the first step, a backbone phylogeny was inferred using a dataset of 117 geometrid species and 35 outgroup species, comprising 648 protein-coding loci (209,499 bp) generated using the anchored hybrid enrichment (AHE) method. This backbone tree was then combined with a taxonomically wider dataset of 376 north European species, supplemented by 98 key taxa from other parts of the world, for which 11 traditional protein-coding genes were obtained using the Sanger sequencing method. The resulting maximum likelihood phylogeny was well-resolved, with most deeper nodes receiving maximal statistical support. Several taxonomic revisions were proposed: new tribes Lampropterygini and Pelurgini were described, *Ochyria* was revived as a monotypic genus, and genera such as *Costaconvexa*, *Artiora*, *Selenia* and *Epirranthis* were assigned to appropriate tribes based on phylogenomic and morphological evidence. Additional revisions included reviving genera from synonymy (e.g., *Ochyria*, *Epelis*, *Speranza*), transferring species to correct genera (e.g., *Xanthorhoe quadrifasiata* to *Ochyria quadrifasiata*, *Macaria carbonaria* to *Epelis carbonaria*) and redefining tribes to maintain monophyly (most importantly, moving *Epirranthis* to Rumiini). The study confirmed many previously proposed subfamily- and tribe-level relationships while resolving several conflicts,

particularly within Larentiinae and Ennominae. Overall, this study provides a robust phylogenetic framework for all northern European Geometridae and supports key taxonomic revisions that reflect both molecular and morphological evidence.

A phylogenetic analysis of 333 species (296 noctuid + 37 outgroup species) based on 565 protein-coding genes (249,138 bp, AHE data) produced a strongly supported tree for Noctuidae that both confirms earlier studies and introduces important taxonomic revisions (III). Acontiinae + Eustrotiinae were recovered as sister to all other Noctuidae, with Plusiinae + Dyopsinae diverging next. Several taxonomic rearrangements were made, including synonymizing *Cornutiplusia* with *Autographa*, *Senta* with *Leucania*, and *Epilecta* and *Cryptocala* with *Noctua*. *Coenophila* was ranked down as a subgenus of *Xestia*, and *Anorthoa* as a subgenus of *Orthosia*. Prodeniini were elevated to subfamily rank (Prodeniinae), Poliina to tribe (Poliini), Additional changes include reinstating *Pseudaletia* as a valid genus, reviving *Aneda* for *Sideridis rivularis*, and synonymizing *Cosmiina* with *Xylenina* to maintain monophyly of the latter. Together, these revisions refine noctuid systematics and provide a robust phylogenetic framework for future evolutionary and ecological research.

The phylogenetic tree obtained in article III was thereafter used for evolutionary analyses. First, it was time-calibrated in order to infer divergence times and evolutionary patterns. This time-calibrated phylogeny shows that Apameini diversified around 8.7 Mya (IV), much more recently than previous estimates (20–29 Mya). These differences likely reflect variation in dataset size and calibration approaches among studies. Current results place Apameini diversification within the major grassland radiation (3–9 Mya), with BAMM analyses indicating subsequent independent accelerations of diversification in *Apamea* and the endophagous Apameina. While *Apamea* larvae are mostly external feeders, the crown group Apameina feeds internally; rather than constraining diversification, internal feeding may have facilitated it through niche expansion, predator protection, and host specialization. Future work should clarify whether diversification was primarily driven by internal feeding itself or by shifts in host plant use linked to grassland expansion.

SUMMARY IN ESTONIAN

Põhja-Euroopa suurliblikate fülogeneesipuu koostamine

Käesoleva uurimuse eesmärk oli koostada kolme liblikasugukonna – sirptiiblaste, vaksiklaste ja öölaste – fülogeneesipuud, pöörates põhitähelepanu Põhja-Euroopa faunale. Uuringus tugineti viimase aja arengutele DNA sekveneerimise ja fülogeneetilise analüüsi meetodite vallas, millel on suur potentsiaal parandada meie arusaamist liblikaliste (*Lepidoptera*) sugulussuhetest kõigil taksonoomilistel tasemetel. Sihtrühmade fülogeneesipuude koostamiseks kombineeriti selles uuringus Sangeri sekveneerimise ning järgmise põlvkonna sekveneerimise abil saadud originaalandmeid avalikult kättesaadavate järjestuste ja genoomiandmetega.

Sugukonda sirptiiblasted (*Drepanidae*) kuulub ligikaudu 650 liiki üle maailma, kuid senistes fülogeneetilistes uurimustes on sellele rühmale pööratud suhteliselt vähe tähelepanu. Isegi hästi tuntud ja ühemõtteliselt piiritletud Euroopa liikide kohta polnud avaldatud ainsatki molekulaarset fülogeneesipuud. Selle puuduse kõrvaldamiseks uuriti käesolevas töös sirptiiblaste sugulussuhteid, kasutades ühtteist molekulaarset markerit kogupikkusega üle 7 500 aluspaari (I). Analüüs, mis põhines 37 liigil – sealhulgas hõlmates 22-st Euroopa sirptiiblastest 21 – kinnitas kõigi nelja tunnustatud alamsugukonna monofüleetilisust. Lisaks näitasid tulemused, et alamsugukonnad *Oretinae* ja *Drepaninae* moodustavad sõsarühmade paarina ühe põhiklaadi, samas kui alamsugukonnad *Cyclidiinae* ja *Thyatirinae* moodustavad teise. Analüüs näitas, et *Drepaninae* + *Oretinae* rühmale iseloomulikud sirpja kujuga tiivatipud on korra tekkinuna evolutsiooni käigus korduvalt kadunud. Alamsugukonna *Thyatirinae* sees moodustavad „talveliblikad“ (liigid, mis on aktiivsed varakevadel või hilissügisel) selgelt eristuva ja tugevalt toetatud klaadi. Lisaks moodustasid statistiliselt hästi toetatud klaadi need *Thyatirinae* perekonnad, mille liikide eestiabadel leidub roosasid või oranžse laike.

Põhja-Euroopa vaksiklaste (*Geometridae*) täielik fülogeneesipuu (II) rekonstrueeriti kaheetapilise lähenemise abil. Esmalt koostati aluspuu 117 vaksikuliigi ja 35 välisrühma liigi andmestiku põhjal, mis tugines hübriidse rikastamise (AHE) meetodil sekveneeritud 648 valke kodeerivale lookusele (209 499 bp). Saadud aluspuu ühendati seejärel taksonoomiliselt laiema andmestikuga, mis hõlmas 376 Põhja-Euroopa liiki ning täiendavalt 98 võtmetaksonit mujalt maailmast, mille jaoks sekveneeriti Sangeri meetodi abil 11 traditsioonilist valku kodeerivat geeni. Suurima tõepära meetodil saadud fülogeneesipuu oli hästi lahenenud, enamik sügavaid harusid sai maksimaalse statistilise toetuse. Tehti mitu taksonoomilist muudatust: kirjeldati uued triibused *Lampropterygini* ja *Pelurgini*, taastati *Ochyria* kui eraldiseisev monotüüpne perekond, mõned teised perekonnad (näiteks *Costaconvexa*, *Artiora*, *Selenia* ja *Epirranthis*) paigutati fülogenoomilistele ja morfoloogilistele tõenditele tuginedes teistesse triibustesse. Täiendavad muudatused hõlmasid seni sünonüümidena käsitletud perekondade „taaselustamist“ (nt *Ochyria*, *Epelis*, *Speranza*), liikide üleviimist „õigesse“ perekonda (nt *Xanthorhoe*

quadrifasiata on nüüd *Ochyria quadrifasiata*, *Macaria carbonaria* on nüüd *Epelis carbonaria*) ning triibuste ümberkujundamist monofüleetilise säilitamiseks (kõige olulisema sellise muutusena viidi *Epirranthis* triibusesse *Rumiini*). Uuring kinnitas paljusid varem oletatud fülogeneetilisi suhteid alamsugukondade ja triibuste vahel ning lahendas mitmeid vastuolusid, eriti alamsugukondades kirivaksiklased (*Larentiinae*) ja metsavaksiklased (*Ennominae*). Kokkuvõttes asetab see töö kõik Põhja-Euroopa vaksiklased usaldusväärsete andmetega toetatud fülogeneetilise raamistikku ning toetab võtmetähtsusega taksonoomilisi muudatusi, mis tuginevad nii molekulaarsetele kui morfoloogilistele tõenditele.

Järgmises töös (III) viidi fülogeneetiline analüüs läbi 296 öölaste (*Noctuidae*) sugukonna liigiga, kaasates lisaks 37 välisrühma liiki. Analüüs, mis põhines 565 valku kodeerival geenil (249 138 bp, AHE andmed), andis tugevalt toetatud sugupuu, mis kinnitab paljusid varasemaid arusaamu, kuid toob kaasa ka olulisi taksonoomilisi muudatusi. Alamsugukondi *Acontiinae* ja *Eustrotiinae* hõlmav klaad osutus kõigi teiste öölaste sõsarrühmaks, millele järgnes *Plusiinae* + *Dyopsinae* haru lahknemine ülejäänud öölastest. Tehti mitu taksonoomilist ümberkorraldust, sealhulgas *Cornutiplusia* sünonümiseerimine *Autographa*-ga, *Senta* sünonümiseerimine *Leucania*-ga ning *Epilecta* ja *Cryptocala* ühendamine perekonnaga *Noctua*. Perekond *Coenophila* viidi *Xestia* alamperekonnaks ning *Anorthoa* omakorda *Orthosia* alamperekonnaks. Varasem triibus *Prodeniini* tõsteti alamsugukonna tasemele kui *Prodeniinae*, alamtriibus *Poliina* aga triibuse tasemele kui *Poliini*. Täiendavate muudatuste hulka kuulus *Pseudaletia* taastamine kehtiva perekonnana, *Aneda* taaselustamine liigi *Sideridis rivularis* jaoks ning alamtriibuse *Cosmiina* sünonüümimine alamtriibusega *Xylenina*. Need muudatused täpsustavad öölaste süstemaatikat ja loovad tugeva fülogeneetilise raamistiku edasiseks evolutsiooni- ja ökoloogiaalasteks uuringuks.

Artiklis III konstrueeritud fülogeneesipuud kasutati seejärel evolutsiooniliste analüüside jaoks. Kõigepealt kalibreeriti puu ajas, et hinnata eri harude lahkneamise aega ja evolutsioonilisi mustreid. Saadud ajaliselt kalibreeritud fülogeneesipuud näitab, et triibus *Apameini* kujunes välja umbes 8,7 miljonit aastat tagasi ehk oluliselt hiljem kui varem arvatud (20–29 miljonit aastat tagasi) (IV). Need erinevused peegeldavad tõenäoliselt erinevusi andmestike suuruses ja kalibreerimismeetodites. Käesoleva töö tulemused asetavad *Apameini* mitmekesisustumise rohumaaade suure laienemise perioodi (3–9 miljonit aastat tagasi), kusjuures BAMM-analüüsid näitavad sõltumatuid liigitekke kiirenemisi perekonnas *Apamea* ja alamtriibuses *Apameina*. Kui juureöölaste (*Apamea*) röövikud toituvad valdavalt väliselt, siis *Apameina* röövikud kaevandavad toidutaimede sees; niisugune toitumisviis ei pruukinud mitte piirata, vaid hoopis soodustada mitmekesisuse kasvu, võimaldades laiendada nišse ja toidutaimedele spetsialiseerumist ning pakkudes kaitset röövloomade eest. Edasised uuringud peaksid täpsustama, kas mitmekesisuse suurenemise ajendas eeskätt taimede sees toitumine ise või sellega kaasnenud toidutaimede vahetus, mis oli seotud rohumaaade laienemisega.

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PUBLICATIONS

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2025 Congress of the European Society for Evolutionary Biology (ESEB 2025), Barcelona, Spain. Poster: Questioning the early Miocene origin of grass-feeding noctuids: evidence from a phylogenomic dataset.
2023 XXIII European Congress of Lepidopterology, Orléans, France. Oral: Phylogenomics of North European Noctuidae based on Anchored Hybrid Enrichment technology.
2022 XXII European Congress of Lepidopterology, Laulasmaa, Estonia. Poster: Phylogenomics of North European Noctuinae based on anchored hybrid enrichment technology.

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Scientific publications:

- Nedumpally, V.**, Zilli, A., Yapar, E., Tammaru, T., Lemmon, A. R. & Öunap, E. (2025). Elaborating the phylogeny of Noctuidae by focusing on relationships between north European taxa. *Systematic Entomology*. <https://doi.org/10.1111/syen.70010>
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